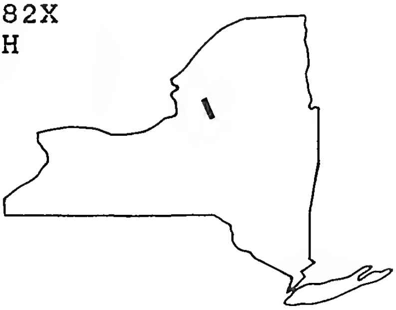

Stratigraphy and Environmental Sedimentology of Middle Ordovician Black River Group in the Type Area—New York State

by Kenneth R. Walker
Temporary Geologist
Geological Survey

BULLETIN NUMBER 419

New York State Museum and Science Service

The University of the State of New York
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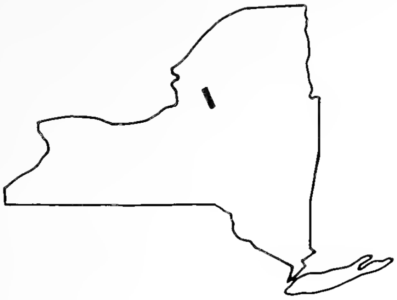

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Stratigraphy and Environmental Sedimentology of Middle Ordovician Black River Group in the Type Area—New York State[1]

by Kenneth R. Walker [2]

ABSTRACT

Eight stratigraphic sections of the Middle Ordovician Black River Group were studied between Boonville, Oneida County, and Lowville, Lewis County. In this type area, the group varies from 60 to 150 feet thick (18.3 to 45.8 meters), and includes three formations: Pamelia, Lowville, and Chaumont. The group consists of a complex interbedding of 11 lithologies, seven of which are volumetrically important. About 450 large samples were analyzed in the laboratory.

Each stratigraphic unit is characterized by one or more dominant lithologies. The basal Pamelia Formation is composed of dolostone and terrigenous sandstone. The Lowville Formation contains four informal rock units (A, B, C, D) and an upper newly defined member (House Creek). Unit A is characterized by mudcracked, thin-bedded limestone, thick beds of internally laminated limestone, and thin to thick beds of bioclastic limestone. Units B and C, which are temporally equivalent, are made up of *Tetradium* (coral) bioclastic limestone. Unit D is composed of mudcracked, thin-bedded limestone. The House Creek Member *(new)* of the Lowville Formation is characterized by dome-shaped colonies of *Tetradium* in life position surrounded by *Tetradium* and other bioclastic debris. The uppermost Chaumont Formation is composed of very thick-bedded, mottled, fine-grained limestone.

The eight stratigraphic sections can be correlated by using a bentonite, several other key horizons, and certain transgressive-regressive cycles. Most lithologic contacts are roughly time-parallel along the outcrop. This is a consequence of an approximate parallelism between the present outcrop and the Ordovician shoreline. A three-dimensional reconstruction suggests facies boundaries that are roughly time-parallel in a north-south direction and asynchronous in an east-west direction. It is believed that previous conflicting interpretations of Black River time relationships can be thus reconciled.

The Black River carbonates are close analogs of sediments in certain modern carbonate environments. Seven major facies represent major paleo-environments, which in their simplest possible onshore-offshore array are: supratidal dolomite forming mud flats; intertidal pelletal-mud flats; shallow subtidal quiet water pond muds and bioclastic channel sands; subtidal *Tetradium*-constructed wave-baffle boundstone; subtidal wave-baffle margin bioclastic sands; and subtidal, level-bottom bioclastic muds. The contemporaneity of these facies can be inferred from lateral gradations, contact features, shared grain-types, and other evidence.

Each stratigraphic unit is dominated by one to three facies and appears to have been formed in specific environments as follows:

Chaumont Formation	Subtidal, level-bottom muds
Lowville Formation	
House Creek Member	Subtidal, *Tetradium*-constructed wave-baffle
Unit D	Intertidal pelletal-mud flats
Units B and C	Subtidal, wave-baffle margin, bioclastic sands
Unit A	Intertidal pelletal-mud flats, shallow subtidal quiet water pond muds, and bioclastic tidal-channel sands
Pamelia Formation	Supratidal dolomite forming mud flats, and supratidal terrigenous sand flats

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[1] Submitted for publication May 8, 1972.

[2] Temporary Geologist, Geological Survey.

Introduction

The Black River Group is a sequence of Middle Ordovician dolostones and limestones whose type area is in the Black River Valley (fig. 1). Since the work of Conrad (1837, 1839), these carbonates have been a part of the standard of comparison for work done elsewhere in North America on the Middle Ordovician. Prior to the present contribution, little paleoenvironmental analysis has been done (see, however, Textoris, 1968, for a preliminary environmental interpretation based on limited sampling).

PURPOSE AND PROCEDURE

Carbonates of the Black River Group were sampled, studied in the laboratory, and compared with Recent sediments in carbonate environments. Several major facies were delineated within the group and paleoenvironments were inferred for each. Ideally, such an environmental study should be carried out within a previously well-known detailed stratigraphic classification and nomenclatural framework. But previous analyses have been regional and the existing classification and nomenclature proved unsatisfactory for present purposes. Thus a partial revision of the stratigraphy of the group in its type area was undertaken.

This discussion is divided into four parts: 1) stratigraphy, 2) environments of deposition, 3) contemporaneity of facies, and 4) summary of environments.

GEOGRAPHIC SCOPE

Black River Group formations have their type localities in the Black River Valley of northwestern New York State (fig. 1). The group crops out from Ingham Mills, Herkimer County, northwestward to the shores of Lake Ontario beyond Watertown, Jefferson County, and thence westward into Ontario.

Fieldwork was conducted in the summers of 1965 through 1968. Eight sections were chosen for detailed study occurring between Boonville, Oneida County, on the south and Lowville, Lewis County, on the north, a distance of 22 miles (35.5 kilometers). These are well exposed, fairly evenly spaced, and constitute the closest spaced series of major exposures in the Black River Valley. Exposures north and south of the chosen series are either of poor quality or are too widely spaced for detailed study. Southeast of the Delia Boonville Quarry section there are no complete exposures of the group. North of Lowville Quarry the nearest complete exposure is along Deer River, 11 miles (17.5 kilometers) to the northwest.

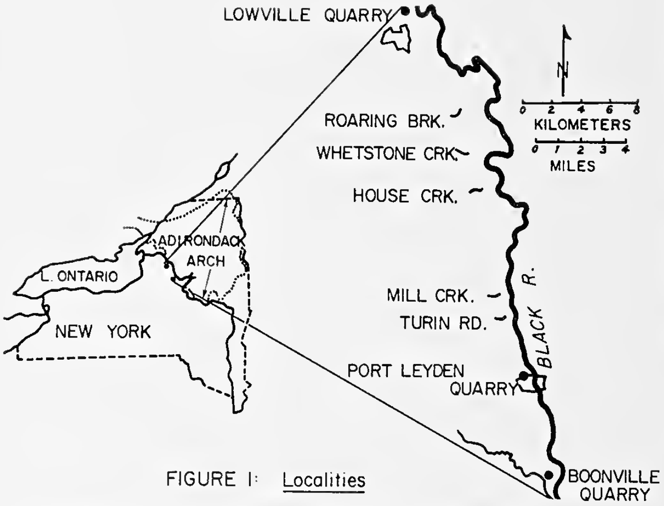


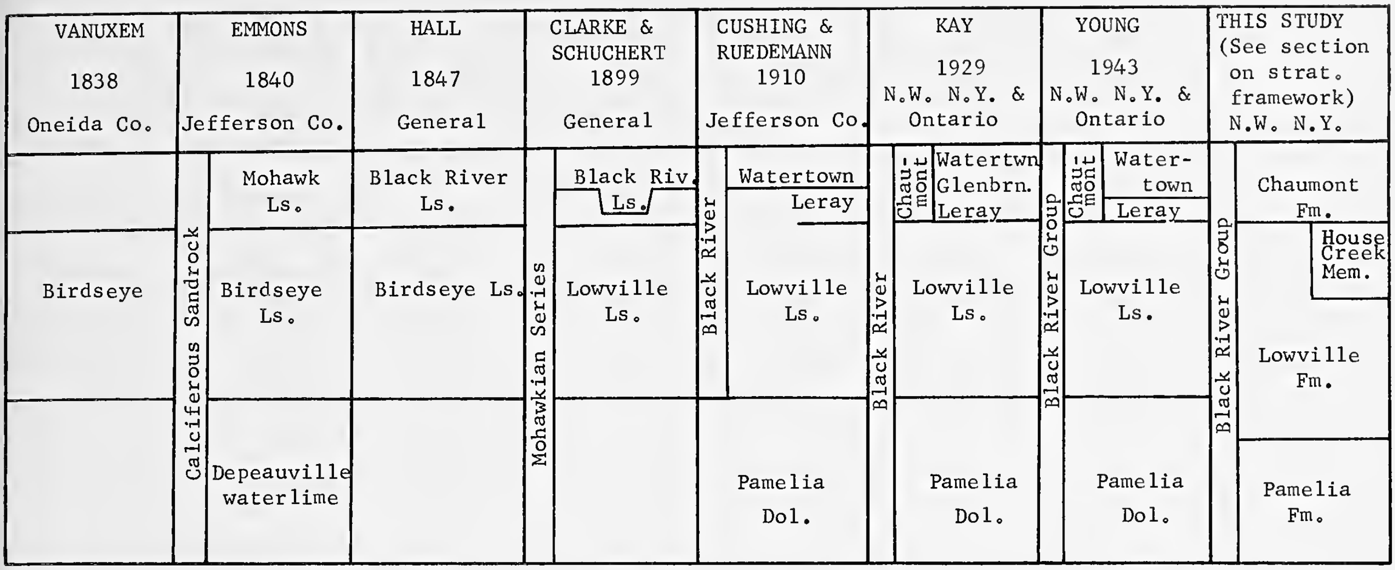
FIGURE 1: Localities

Reconnaissance around Watertown suggests that the stratigraphic and environmental conclusions of this study apply there as well. Some biotic changes do occur and these are noted in the discussion of the Black River environments. The reader also is referred to Johnsen, 1971, and data of that author on open file at the New York State Museum and Science Service, Geological Survey office in Albany, particularly for information pertinent to the Black River Group north of the study area.

HISTORICAL BACKGROUND

A history of Black River Group rock-stratigraphic classification prior to 1940 was given by Young (1943) (fig. 2). A complete review of the entire Middle Ordovician of New York was given by Kay (1937); an especially useful bibliographic review is embodied in his " Glossary of Terms Applied to Mohawkian Divisions " (1937, p. 296–297).

Young's study (1943) is the most recent published stratigraphic analysis of the Black River Group in the study area. However, the reader is also referred to J. H. Johnsen's open file maps at the New York State



VANUXEM 1838 Oneida Co.	EMMONS 1840 Jefferson Co.		HALL 1847 General	CLARKE & SCHUCHERT 1899 General		CUSHING & RUEDEMANN 1910 Jefferson Co.		KAY 1929 N.W. N.Y. & Ontario			YOUNG 1943 N.W. N.Y. & Ontario			THIS STUDY (See section on strat. framework) N.W. N.Y.		
		Mohawk Ls.	Black River Ls.	Mohawkian Series	Black Riv. Ls.	Black River	Watertown Leray	Black River	Chau-mont	Watertwn Glenbrn. Leray	Black River Group	Chau-mont	Water-town Leray	Black River Group	Chaumont Fm.	
Birdseye	Calciferous Sandrock	Birdseye Ls.	Birdseye Ls.		Lowville Ls.		Lowville Ls.			Lowville Ls.			Lowville Ls.		Lowville Fm.	House Creek Mem.
		Depeauville waterlime					Pamelia Dol.			Pamelia Dol.			Pamelia Dol.		Pamelia Fm.	

Figure 2: Tabular history of the rock-stratigraphic classification of the Black River Group in northwestern New York State, modified from Young, 1943, figure 1.

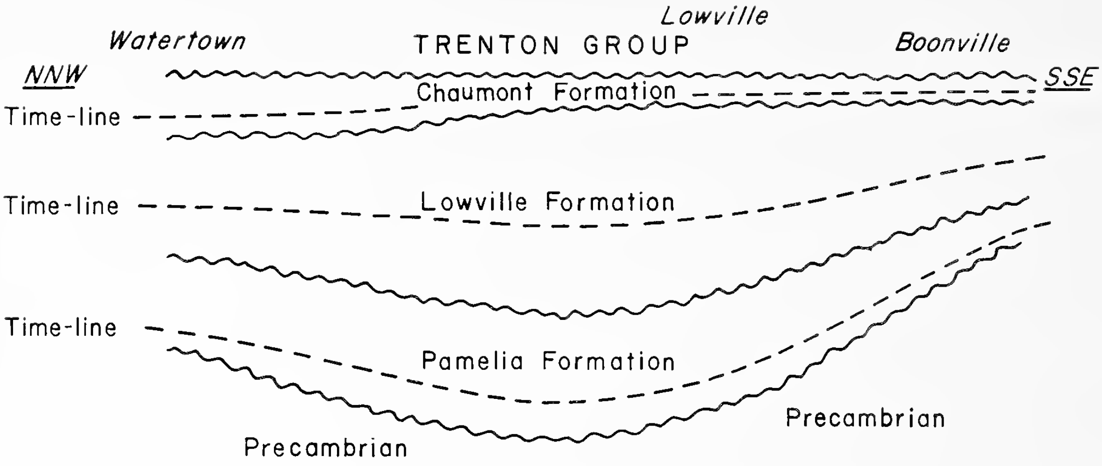
Museum and Science Service, Geological Survey office in Albany. Young adopted older stratigraphic names proposed by Cushing (1908), Clarke and Schuchert (1899), and Kay (1929), and redefined them to fit his understanding of the stratigraphy. He believed that many unconformities existed within the group and he chose these as his formation boundaries. However, these " unconformities " do not coincide with lithologic breaks and, in addition, there is overwhelming evidence that Young's " unconformities " do not exist. It is the writer's opinion that Young's formations are unnatural groupings of several lithologies and do not conform to the recommendations of the American Code of Stratigraphic Nomenclature (1960).

There is good reason to retain as many older stratigraphic names as possible because they are entrenched in the literature and frequently their definitions can easily be brought into line with modern usage. These older names originally were applied to lithologic units, but subsequently have been used for both rock- and time-stratigraphic units. They are used herein only as lithologic units (formations or members), with redefined boundaries. One change proposed here is the formal recognition of the upper Lowville Formation as a distinct and separate division, the House Creek Member. Informal lithologic units have been designated elsewhere within the group to clarify facies relationships.

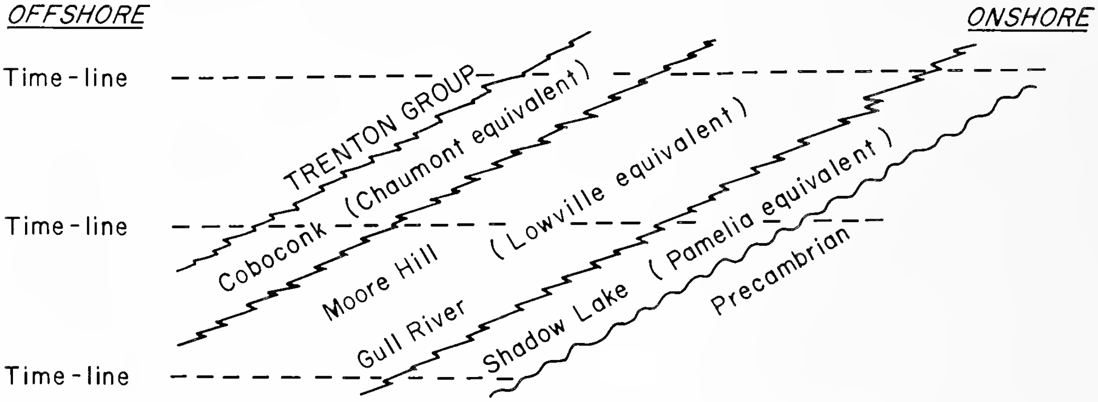
Time-stratigraphic classification and terminology of the group has had a complicated history. There are three extant interpretations of the relationships involved. These are partly reviewed by Fisher (1962). All three are based on regional stratigraphic analyses and various theoretical considerations, as shown in figure 3.

Kay (1929, 1937, and 1960) and Young (1943) considered the various lithologically and faunally defined formations to be time parallel throughout their distribution. This was based on the contained faunas which are quite similar wherever the formations are found. Thus, their understanding of the time relationships was predicated on the usability of these fossil assemblages for correlation. However, the distribution of the biotas involved is strongly controlled by the environments of deposition in which they lived. The latter are reflected in the lithologies on which the formations are based. It is not surprising, therefore, to find the same facies fossils in two geographically separated, nonsynchronous exposures of the same formation. In addition, Young (1943, p. 158, p. 211, p. 218) thought there was a disconformity between each of the formations of the group. No such disconformable relationships could be found. Kay has suggested use of the term " Blackriverian " (1960) as a stage name indicating his belief that the group is time parallel. These interpretations are embodied in the Geological Society of America Ordovician correlation chart (Twenhofel, *et al,* 1954).

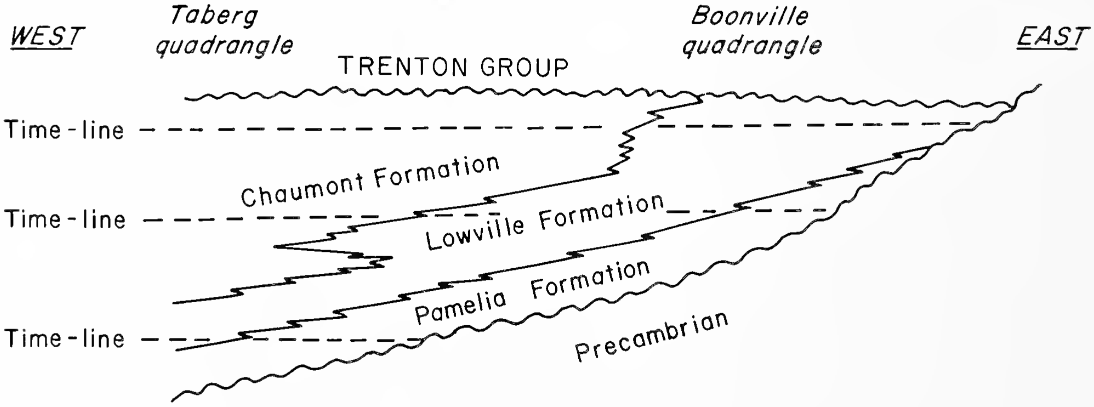
Winder (1960), in Ontario suggested a different set of time relationships. He postulated that all of the Black River and Trenton Groups were deposited as a facies pattern with any one of the contained forma-



A: Kay (1937, Pl. 2) and Young (1943, fig. 2).



B: Winder (1960, fig 3) simplified and reversed to correspond to figure 2C below.



C: Fisher (1962, and pers. comm.)

Figure 3: Three extant hypotheses concerning the time relationships of the Black River Group in the type area.

tions being temporally equivalent to all others in the two groups at some point in their distribution. Winder (pers. comm.) no longer believes in so simple a facies pattern. He does, however, still feel that such a relationship exists between a part of the Trenton Group and all of the Black River Group.

Fisher (1962) has summarized the problems involved in interpreting time relationships within the Ordovician of New York State. He adopted the stages suggested by G. A. Cooper (1956) and views the Black River Group as a part of a facies pattern. He now believes (pers. comm.) that the Black River and Trenton Groups are separated by an unconformity which truncates the Black River Group east-southeastward. These workers have accepted the placement of the Black River Group within the Mohawkian Series; it is the time relationships within this series (i.e., the stages and substages) that are in question.

Most of the confusion involved in correlation of the Black River Group results from lack of consideration of the three-dimensional geometry and lack of environmental studies of these carbonates. Once the depositional environments are understood, and the geometric relation of the present outcrop belt to the Ordovician shoreline is considered, the various interpretations can be reconciled.

ACKNOWLEDGMENTS

This study is a revised portion of research done in partial fulfillment of the Ph.D. requirements at Yale University. The investigation was supported by funds from the Geological Survey, New York State Museum and Science Service, and Yale University. Some of the publication preparation expenses were paid by the Department of Geology, University of Tennessee.

Leo F. Laporte of Brown University first suggested the possibility of studying the Black River Group, and through discussion aided in developing many of the concepts in the present paper. Donald C. Rhoads and Karl M. Waage of Yale University read and criticized the original draft of the manuscript. John Rodgers of Yale spent several days with the writer in the field, and his ideas concerning stratigraphy of the Black River Group and Ordovician rocks in general helped to develop many of the concepts expressed herein.

Finally, Donald W. Fisher of the New York State Geological Survey discussed Black River stratigraphy with the author several times during the investigation. His knowledge of rocks of the same age elsewhere in the State was of particular help. He, Lawrence V. Rickard, and William B. Rogers of the Survey also read and edited the final manuscript.

Stratigraphy

The term stratigraphy as used here implies an understanding of the temporal and spatial geometry of the lithologies in the Black River sequence, and a tenable classification and nomenclature. The stratigraphic framework previously proposed is unsatisfactory because it was based on incomplete data. The basic assumptions made in interpreting that data were problematical. The time-stratigraphic and rock-stratigraphic classification and nomenclature of the Black River Group in the type area are here revised, based on detailed measurement and description of eight stratigraphic sections (fig. 1). The descriptions of these sections, revised by reference to 445 lithologic samples, are on open file at the State Geological Survey, New York State Museum and Science Service, Albany.

TEMPORAL AND SPATIAL GEOMETRY

The regional correlation of the Black River Group is not in question here. Most previous workers have agreed that the group is part of the Middle Ordovician Mohawkian Series, based on the general evolutionary level of the Black River faunas. However, the local correlations are in dispute (fig. 3), but analysis of the measured sections can resolve this dispute.

The eight measured sections studied reveal that the Black River Group is composed of a complex interbedding of 11 lithologies, seven of which are volumetrically important. All lithologies are described in figure 4.

Figure 4: Lithologies of the Black River Group in the outcrop belt between Boonville and Lowville, New York. Volumetrically important lithologies marked *. See appendix 1 for bed thickenss, grain size, mudcrack scale and other descriptive conventions.

Lithology	Description
1 *	Thin to medium bedded, dolomitic, medium to coarse grained sandstone. Color and mineralogy similar to underlying Precambrian gneiss. Sparse ripple marks.
2 *	Buff to very pale gray, fine to medium grained, externally thin to medium bedded, internally wavy, very thin to thin laminated, very small scale mudcracked dolomite. Algal ridges on some bed surfaces. Rare to common ostracodes.
3 *	Pale to medium gray, fine to coarse grained, externally thin bedded, internally wavy thin to thick laminated, vertically burrowed, medium to large scale mudcracked limestone (pelmicrite, pelsparite, rare intrasparite after Folk's, 1959, classification). Sparse ripple marks. Rare to common ostracodes and trilobites.
4 *	Consists of two lithologies interbedded on all scales: a) Dark gray, fine to very fine grained, externally medium to thick bedded, internally very thin to thin laminated, stylolited limestone (pelmicrite). Laminae usually nonwavy. Sparse algally coated grains. b) Medium to dark gray, medium to coarse grained, externally medium to thick bedded, internally thin bedded, intraclastic stylolited limestone (intrapelsparite). Abundant algally coated grains. Fossils abundant, broken, diverse taxonomically.
5	Medium gray, medium to thick bedded, intraclastic, rarely low angle cross-bedded oolite. Cross beds, when present, dip bidirectionally. Rare to common *Cyrtodonta.*
6 *	Consists of two lithologies interbedded on all scales: a) Medium to dark gray, coarse grained (with fine grained matrix), thin to medium lumpy bedded, bioclastic limestone (biomicrite to biosparite) with more than 50% of rock made up of fallen *Tetradium* colonies. Abundant *Cyrtodonta,* common *Stictopora,* rare to common *Loxoplocus,* rare *Actinoceras* and *Michelinoceras.*

Figure 4, con.

	b)	Similar to 6a, but with 10 to 75% of beds composed of dome-shaped supercolonies of *Tetradium* in living position. *Tetradium* usually much replaced by sparry calcite.
7	*	Similar to 6a, but with abundant *Loxoplocus* and much less than 50% of rock composed of fallen *Tetradium* colonies.
8		Dark brownish gray, thin to medium even bedded, brachiopod bioclastic limestone with a fine grained matrix (biomicrite). Common to abundant *Strophomena,* rare *Lambeophyllum,* rare *Batostoma.*
9	*	Dark gray, medium to coarse grained, thick to very thick lumpy discontinuously bedded, thoroughly horizontal burrow mottled limestone (biomicrite to micrite). Biota sparse, but taxonomically diverse. Rare to common *Stromatocerium, Foerstephyllum,* and *Lambeophyllum,* all usually in life position. Rare to common *Actinoceras* and *Endoceras.* Common codeacean algal debris. Rare crinoid debris and brachiopod valves. Common, irregular, black chert nodules, usually in zones parallel to bedding.
10		Similar to 9, but with scattered clumps of *Dalmanella.*
11		Dark browish gray, coarse grained, thin to medium bedded, bioclastic limestone composed of whole and disarticulated brachiopod shells, ramose trepostome bryozoa, trilobite debris, and crinoid debris.

Before the measured sections could be used to reconstruct Black River stratigraphy, it was necessary to infer time relationships. The fauna could not be used because it is composed entirely of taxa which are nearly always facies controlled. In addition, all the common taxa are found through nearly the entire thickness of the group. No physical or biological evidence of a major stratigraphic hiatus was found. Diastems occur, but the group represents essentially continuous deposition.

The four central stratigraphic sections (fig. 1) can be related in time by reference to a bentonite which is best exposed along Turin Road near Lyons Falls (fig. 5). This bentonite is exposed 0.7 miles (1.1 kilometer) north of Turin Road along Mill Creek, and a very prominent reentrant occurs in the same part of the House Creek and Whetstone Creek sections (fig. 5). It is believed that these reentrants correspond to the Turin Road bentonite because: 1) they are the only such prominent reentrants in these sections, 2) they have the same relative stratigraphic position as the bentonite, and 3) the reentrants have the same relationship as the bentonite to other prominent lithic boundaries in the group. Thus the Turin Road, Mill Creek, House Creek, and Whetstone Creek sections can be correlated by using the bentonite as a time marker.

In the central four sections several prominent lithologic contacts occur which have a nearly constant geometric relation to the bentonite; these contacts, summarized in figure 6, also occur in exposures without the bentonite. All contacts nearly parallel the bentonite. The base of lithology 9 (fig. 4), which corresponds to the base of the Chaumont Formation, was chosen as a datum in all the sections. This contact is easily recognized and there are no similar ones elsewhere in the sequence with which it might be confused. Figure 5 shows the eight sections plotted in terms of the 11 lithologies of figure 4 using this contact as a horizontal datum. Because the contacts of figure 6 and the bentonite are nearly horizontal in figure 5, it is suggested that any horizontal line in figure 5 approximates a time-line.

ROCK-STRATIGRAPHIC CLASSIFICATION AND NOMENCLATURE

Consideration of figure 5 and the lithologic descriptions of figure 4 suggests a revision of the rock-stratigraphic nomenclature of the Black River Group. Figure 5 shows the formal formations and members and the informal rock units of the group proposed herein. Their properties are summarized in figure 7.

Pamelia Formation

The basal unit is composed mainly of two lithologies; a basal dolomitic sandstone overlain by a variable thickness of pale gray to buff dolostones. In the study area these lithologies uncomformably overlie the Precambrian basement complex. Cushing (1908, p. 158) called this sequence of pale dolostones the Pamelia Formation for exposures in Pamelia Township, Jefferson County. Cushing and later Young (1943, p. 145) included several lithologies in their Pamelia and did not place the top of the formation at the top of the dolostones. Thus they did not use the term "forma-

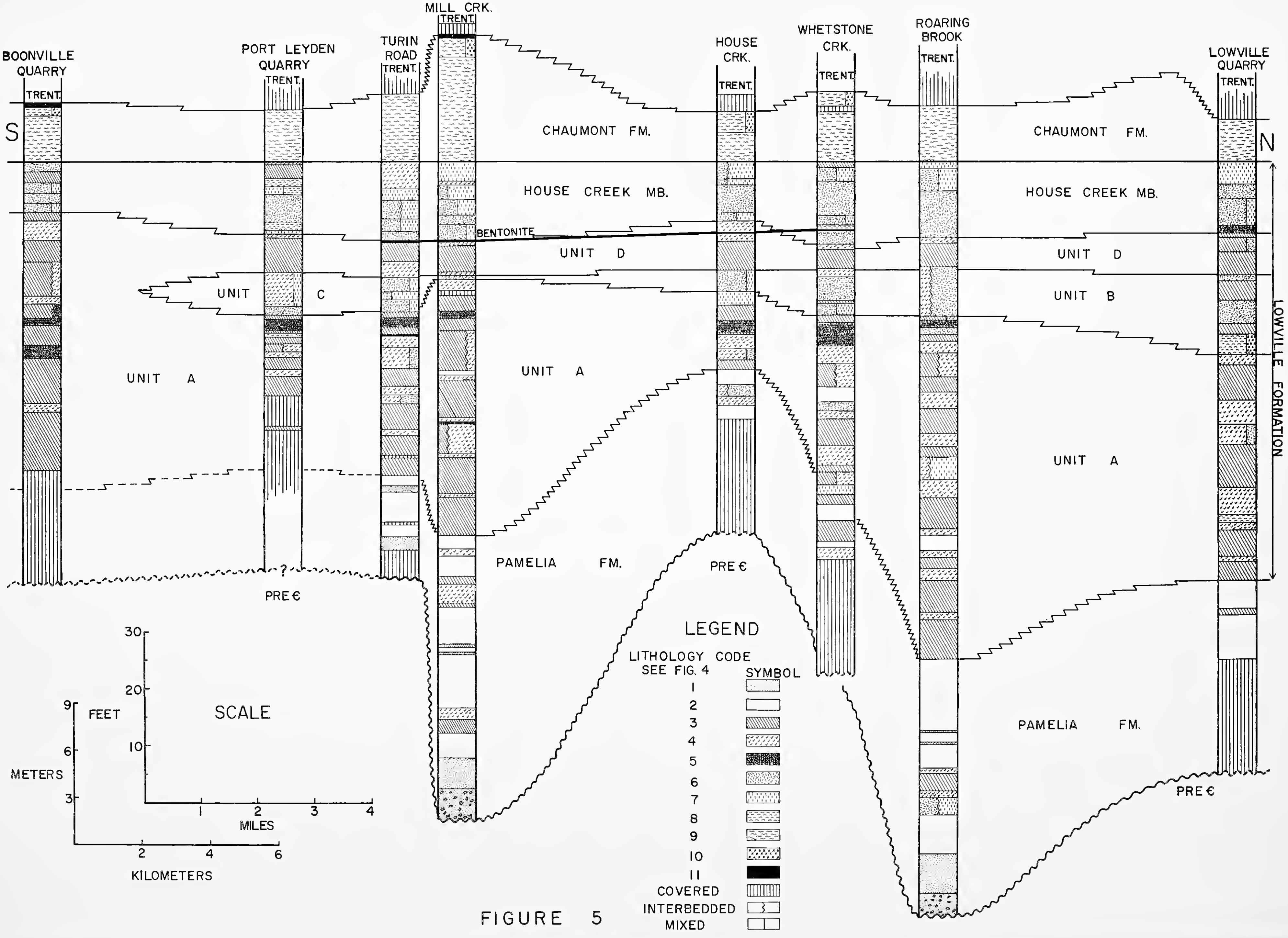

BOONVILLE QUARRY
PORT LEYDEN QUARRY
TURIN ROAD
MILL CRK.
HOUSE CRK.
WHETSTONE CRK.
ROARING BROOK
LOWVILLE QUARRY
TRENT.
S
N
CHAUMONT FM.
HOUSE CREEK MB.
BENTONITE
UNIT D
UNIT C
UNIT B
UNIT A
LOWVILLE FORMATION
PAMELIA FM.
PRE €
?
SCALE
FEET
30
20
10
METERS
9
6
3
MILES
1
2
3
4
KILOMETERS
2
4
6
LEGEND
LITHOLOGY CODE SEE FIG. 4
SYMBOL
1
2
3
4
5
6
7
8
9
10
11
COVERED
INTERBEDDED
MIXED

FIGURE 5

Figure 6: Lithologic contacts with a nearly constant geometric relationship to the bentonite at Turin Road, Mill Creek, House Creek, and Whetstone Creek.

CONTACT	Distance of Contact above (+) or below (—) Bentonite			
	Turin Road	**Mill Creek**	**House Creek**	**Whetstone Creek**
Base of Chaumont Fm. (base of lithology 9, see fig. 4)	14 ft.+	13 ft. 5 in.+	11 ft. 10 in.+	11 ft. 1 in. +
Base of House Creek Member, Lowville Fm. (base of thickest lithology 6, see fig. 4)	0 ft.	0 ft.	2 ft.—	2 ft. 1 in.+
Top of zone B and zone C, see fig. 5 (top of lowest persistent lithology 6, see fig. 4)	6 ft. 2 in.—	5 ft. 7 in.—	7 ft. 2 in.—	7 ft. 9 in.—
Top of highest oolite bed (lithology 5, see figs. 4 and 5)	13 ft. 2 in.—	11 ft. 8 in.—	16 ft. 1 in.—	15 ft. 9 in.—

tion" in the customary lithologic sense. It is here proposed to redefine the Pamelia Formation as the thin dolomitic sandstone and superjacent buff dolostones overlying the Precambrian complex in the Black River Valley. This is in general agreement with the work of Johnsen, 1971, in Jefferson County.

Cushing did not designate a type section for the Pamelia but did note that it is well exposed throughout Pamelia Township, Jefferson County. The exposures at Roaring Brook, the best continuous outcrop of the formation, are suggested as a primary reference section.

The contact with the overlying Lowville Formation is not abrupt but is arbitrarily defined as the top of the highest dolostone within the highest 10-foot interval containing greater than 50 percent dolostones. Using the upper and lower boundaries as defined here, the Pamelia ranges from 18 ft. (5.6 meters) at Turin Road to 51 ft. (15.5 meters) at Mill Creek.

Lowville Formation

The Lowville Formation in the study area comprises a complex interbedded sequence of mudcracked, laminated dolostone; mudcracked, thin-bedded, medium grained, bioclastic limestone; oolite; *Tetradium* bioclastic limestone; and *Loxoplocus* bioclastic limestone (lithologies 2, 3, 4a, 4b, 5, 6a, and 7 of fig. 4). Clarke and Schuchert (1899, p. 877) called this sequence the Lowville Formation for exposures in and around the town of Lowville, Lewis County (fig. 1). They did not describe the formation or designate a type section, but replaced the former " Birdseye Limestone " with the term " Lowville." Cushing, *et al.* (1910, p. 83) designated the section along Mill Creek in Lowville as the type section. That section is not well exposed now, and Roaring Brook is suggested as a primary reference section for the revised Lowville Formation.

Young (1943, p. 157) noted the difference between the lower, dove-gray part of the Lowville and the upper part, which is characterized by abundant colonies of the coral *Tetradium*. This upper part is separated here as the House Creek Member (discussed below).

The lower contact of the revised Lowville Formation is conformable with the revised Pamelia Formation. The upper contact is defined as the base of the uppermost, thickest, and best developed lithology 9 (fig. 4, massive horizontal-burrow mottled limestone). The formation varies in thickness from 35½ ft. (10.8 meters) at House Creek to 87 ft. (26.5 meters) at Roaring Brook.

The Lowville is the most lithologically complex unit in the Black River Group. The formation may be divided into four informal units and one formal member. These divisions are (in ascending order): informal units A, B, C, and D, and the House Creek Member. Their properties are summarized in figure 7.

Unit A

This basal unit is composed of mudcracked, thin-bedded lime-mudstone; evenly-laminated, stylolitic lime-mudstone; and medium-bedded, medium grained, bioclastic limestone (lithologies 3, 4a, and 4b of fig. 4), with minor interbeds of oolite; *Tetradium* bioclastic limestone; and *Loxoplocus* bioclastic limestone (lithologies 5, 6a, and 7 of fig. 4). Most of the thickness variation of the group occurs within unit A because its deposition involved infilling of topographic irregularities of the underlying Precambrian surface.

Unit A is overlain by two higher Lowville units everywhere except in the Boonville Quarry where unit A comprises the lower part of the formation and is directly overlain by the House Creek Member (fig. 5).

Figure 7: Properties of rock-stratigraphic units of Black River Group in study area.

Unit name	Lithology (see definition of numbers in figure 4).	Original definition of name.	Revision here.	Type section or locality	Primary reference section.	Definition of lower contact.	Definition of upper contact.	Geometry and relation to time in the plane of the outcrop (see figure 5).
Chaumont Formation	9, rarely 10 or 11 near top.	Kay (1929, p. 664).	Not revised.	Area around Chaumont Bay, Jefferson Co., N.Y.	None.	Base of uppermost, well developed, and thickest lithology 9.	Top of uppermost lithology 9, 10, or 11.	Tabular with base nearly synchronous and top asynchronous from place to place.
Lowville Formation	2, 3, 4a, 4b, 5, 6a, 6b, and 7.	Clarke and Schuchert (1899, p. 877).	Redefined.	Along Mill Creek in Lowville, Lewis Co., N.Y. Cushing, *et al.* (1910, p. 83).	Along Roaring Brook	Top of highest dolomite within highest 10 foot interval containing more than 50% dolomite.	Base of thickest lithology 6a, which contains lithology 6b.	Lower Roaring Brook Member varies in thickness, upper members tend to be tabular and synchronous.
House Creek Member	6a with central zone of 6b.	Newly defined here.	Newly defined	Along House Creek (measured section in text)	Along Whetstone Creek	Base of the uppermost thickest lithology 6a which contains lithology 6b.	Base of uppermost, well developed, and thickest lithology 9.	Tabular with upper and lower contact nearly synchronous.
Unit D	3, 4a, and 4b.	Newly defined here.	Newly defined	Port Leyden Quarry	Along Roaring Brook and Whetstone Creek	Upward change from lithology 6a of Glendale Road Member or Turin Road Lense to lithology 3, 4a, or 4b.	Base of thickest lithology 6a which contains lithology 6b.	Tabular and nearly synchronous.
Units C and B	6a.	Newly defined here.	Newly defined	Glendale Road: along Whetstone Creek Turin Road: along Turin Road	None.	Upward change from predominant lithologies 3, 4a, and 4b to the lowest thick unit of lithology 6a.	Upward return to lithologies 3, 4a, or 4b.	Glendale Road is tongue-like, and Turin Road is lense-shaped. Axis of both is nearly synchronous. Both members absent at Boonville.
Unit A	3, 4a, and 4b, with rare 2, 5, 6a, and 7.	Newly defined here.	Newly defined	Along Roaring Brook	None.	Top of highest dolomite within the highest 10 foot interval containing more than 50% dolomite.	Upward change from predominant lithologies 3, 4a, and 4b to the lowest thick unit of lithology 6a.	Varies widely in thickness. Upper part at Boonville correlative to Turin Road Lense, Glendale Road Member, and Port Leyden Tongue to north.
Pamelia Formation	1 and 2 with occasional interbeds of 3, 4a, 4b, and 6a.	Cushing (1908, p. 158).	Redefined.	Pamelia Township, Jefferson Co., N.Y.	Along Roaring Brook	Unconformably overlies the Precambrian basement in the study area.	Top of highest dolomite within the highest 10 foot interval containing more than 50% dolomite.	Varies somewhat in thickness. Markedly asynchronous from place to place. Conforms to underlying Precambrian topography.

The relation of the Boonville section to other sections is clarified by study of the oolite unit which occurs in each section. The oolite (figs. 4 and 5, lithology 5) is roughly time parallel and near the center of unit A at Boonville, but lies near the unit's top in the other sections. Thus the upper half of unit A at Boonville is temporally equivalent to units B-C and unit D further north. The lower half of unit A at Boonville is approximately correlative with all of that unit in the other sections.

The best exposure of unit A of the Lowville is along Roaring Brook. The unit varies in thickness from 56½ ft. (17.3 meters) at Roaring Brook to 11 ft. (3.4 meters) at House Creek.

Unit B and Unit C

Units B and C are composed of biomicrite in which the bioclasts are fallen colonies of *Tetradium* (lithology 6a of fig. 4). *Tetradium* colonies in living position are absent from most exposures. These two units are approximately correlative (fig. 5), and are horizontally separated by a section at Mill Creek in which the lithology is nearly absent. In the Turin Road section, unit C contains very rare *in situ* colonies. Units B and C differ from the House Creek Member by the absence or rarity of *Tetradium* in life position, and are separated from that member by unit D (fig. 5). Units B and C are absent at Boonville where equivalent rocks are part of unit A.

The best exposure of unit B is along Whetstone Creek near the town of Glendale. Thickness varies from 12 ft. (3.6 meters) along Roaring Brook to 7 in. (0.2 meters) at Mill Creek. Unit C is 7.5 ft. (2.3 meters) thick at Port Leyden and 6 ft. (1.8 meters) thick along Turin Road just west of Lyons Falls.

Units B and C, and the House Creek Member are characterized by *Tetradium* bioclastic limestone; based on environmental evidence these units may be connected in the subsurface.

Unit D

This unit typically is composed of three lithologies: 1) a basal massive, internally laminated micrite (lithology 4a or b of fig. 4), 2) a medial thin bedded, mudcracked pelmicrite (lithology 3 of fig. 4), and 3) an upper massive, laminated micrite. These lithologies also characterize Lowville unit A. Unit D is separated from unit A by units B or C except at Boonville, where the latter two units are absent. At Boonville equivalents to unit D cannot be distinguished within unit A, which makes up most of the Lowville Formation there.

Unit D represents a thin regressive cycle within more normal marine lithologies, and one might expect this unit to be roughly parallel to a time plane; it is parallel to the bentonite (fig. 5).

The best exposures of unit D are along Roaring Brook and in the Port Leyden quarry, in the town of Port Leyden. The zone ranges from 5 ft. to 6 ft. (1.5 to 2.3 meters) in all its exposures except at Lowville Quarry where it attains a maximum thickness of 13 ft. (4 meters).

House Creek Member (New)

This member comprises the upper 9 to 14 ft. (2.7 to 4.3 meters) of the Lowville Formation of previous workers. It is composed of *Tetradium* bioclastic limestone (lithology 6a, fig. 4) with a central zone of colonies of *Tetradium* in life position (lithology 6b, fig. 4). This unit is given member status because: 1) lithologically the House Creek is quite unlike the bulk of the Lowville, 2) the member is continuous and mappable in the study area, and 3) the unit represents an ecologically important restricting influence within the Black River facies mosaic.

In the study area the lower and upper contacts of the member (fig. 7 for definitions) tend to be approximately synchronous. The lower one is often gradational through 4–6 cm; the upper contact tends to be abrupt, but is occasionally gradational. A thin interval of mudcracked pelmicrite occurs in the upper part of the member at Boonville and Port Leyden, and an interval of massive, laminated micrite occurs in the same stratigraphic position at Turin Road and Mill Creek. These intervals represent a short period of progradation of nearshore sediments northward into the more seaward sediments that form the House Creek Member. The axis of this regressive pulse is nearly horizontal (fig. 5) and should approximate a timeline, supporting the time relationships previously postulated.

The following is the type section along House Creek, Lewis County, on the Port Leyden Quadrangle (1: 62,500). Black River Group section begins about 75 yards west of bridge on Searls Road; the member is exposed about 50 yards west of section base, 31′8″ stratigraphically above the base.

		Unit Thickness	Group Cumulative Thickness
10.	Similar to unit 8, but in one medium bed with rare, carbonaceous seams subparallel to bedding.	0′11″	45′0″

		Unit Thickness	Group Cumulative Thickness
9.	Similar to unit 8, but in lumpy, thin beds to medium laminae; fallen *T. cellulosum* more abundant.	0′9″	44′1″
8.	Medium gray, fine to medium grained, fossil fragmentary, pyritic limestone in one thick bed. Fossils 40–50% of rock: ostracode valves, 30% of fauna; trilobite fragments 20%; fine trilobite and ostracode debris 20%; *Loxoplocus* 5%; strophomenid valves 10%; rare crinoid columnals and fallen *Tetradium*. Rare pyrite as granules around fossils and scattered cubes. Abundant ovoid areas of spar. Rare internal laminae. Coarse grain size mottles common.	1′4″	43′4″
7.	Same as unit 4.	0′6″	42′0″
6.	Same as unit 4, but in single lumpy bed.	0′7″	41′6″
5.	Medium to dark gray, medium to very coarse grained, very lumpy thin to medium bedded, *Tetradium* limestone. Fauna 50–75% of rock: *T. cellulosum* 75% of fauna with common domate colonies in life position; high spired gastropods 5%; *Loxoplocus* 10%; unidentified fossil debris 5–10%. Common concentrations of fallen *Tetradium* on bedding planes without preferred orientation. Much spar replacing *Tetradium*.	4′11″	40′11″
4.	Dark gray, medium to coarse grained, *Loxoplocus-Tetradium* limestone in one thick bed. Fauna 40–50% of rock: *Loxoplocus* 50% of fauna; fallen *T. cellulosum* 25%; fine trilobite and ostracode debris 10–15%; unidentified fragments 10–15%; rare *Strophomena* valves. Much spar as fossil replacement. Rare internal, lumpy, thin beds.	1′6″	36′0″
3.	Dark gray, medium to fine grained, lumpy bedded limestone in two beds. Upper surface makes wide shelf at top of falls. Abundant carbonaceous seams as in unit 1. Abundant dark brown anastomosing mottles where weathered. Abundant trilobite and ostracode debris.	1′3″	34′6″
2.	Prominent reentrant. Original lithology highly weathered, to sticky clay. Faint laminae. Probably corresponds to bentonite beds at Turin Road and Mill Creek.	0′2″	33′3″
1.	Medium gray, fine grained, stylolitic, fossiliferous limestone in one bed. Stylolites medium scale, continuous, very abundant. Fossils 5% of rock: *Loxoplocus*, cryptostome bryozoa, ostracode valves, fine ostracode and trilobite debris. Replaced *Tetradium* common in lower part. Rare random discontinuous carbonaceous seams. Rare internal medium beds. Fetid.	1′5″	33′1″

The immediately underlying 5 feet of beds are characterized by thinner beddings, mudcracks, and vertical burrows. Total thickness of House Creek Member in type section = 11 ft. 11 in. This member is also well exposed along Whetstone Creek. The member ranges from 14 ft. (4.3 meters) at Turin Road to 9 ft. (2.7 meters) at Boonville.

Chaumont Formation

The uppermost unit of the Black River Group is composed of massive, horizontal-burrow mottled biomicrite (lithology 9, fig. 4), with a rare upper zone of brachiopod biomicrite or biosparite (lithologies 10 and 11, fig. 4). The Chaumont Formation was defined by Kay (1929, p. 664) to include " beds younger than the Lowville and older than the Rockland " in the area around Chaumont Bay, Jefferson County. He defined the unit to include the Watertown Formation and the Leray Member of the Lowville Formation as originally defined by Cushing, *et al.* (1900, p. 84–86). Both the Watertown and Leray were originally described as lithologic units. Thus, Kay's Chaumont is a lithologic unit. Most subsequent workers have used the term Chaumont Formation for a lithologically defined rock-stratigraphic unit (cf. Young, 1943, p. 209–211, or Swartz, 1948, p. 1571; Johnsen, 1971). Kay has recently stated (pers. comm. 1968) that he " firmly believes that the terms Lowville and Chaumont were applied as time-stratigraphic terms." It would appear that the problem of rock-stratigraphic vs. time-stratigraphic terminology of the Chaumont is mainly one of semantics (Barnes, 1967; Kay, 1968; Barnes, 1968; Johnsen, 1971).

I prefer to use Chaumont as a lithologic unit at the formational level. The formation approximates a time-stratigraphic unit in the line of outcrop, but a separate set of terms, if needed, should be devised for time-stratigraphic units represented by rocks of the Black River Group. Such a dual terminology may seem irrelevant to some, but the present confused state of Black River terminology is an outgrowth of the failure of some workers to clearly separate rock-stratigraphic and time-stratigraphic names.

The type area of the Chaumont Formation is the region around Chaumont Bay, Jefferson County, at the northern end of the Black River Valley. The formation is well exposed in the study area along Whetstone Creek and Mill Creek. Properties of the unit are given in figure 7. The base of the formation is approximately time parallel; evidence for this conclusion has been summarized above. The upper contact is seldom well exposed, probably because the basal beds of the overlying Trenton Group (composed of alternating thin beds of fissile, dark gray, calcareous shales and dark gray, highly fossiliferous biomicrite) are more easily weathered. This upper contact of the Chaumont apparently is asynchronous, judging by the thicknesses of the formation at Port Leyden, Turin Road, and Mill Creek (fig. 5).

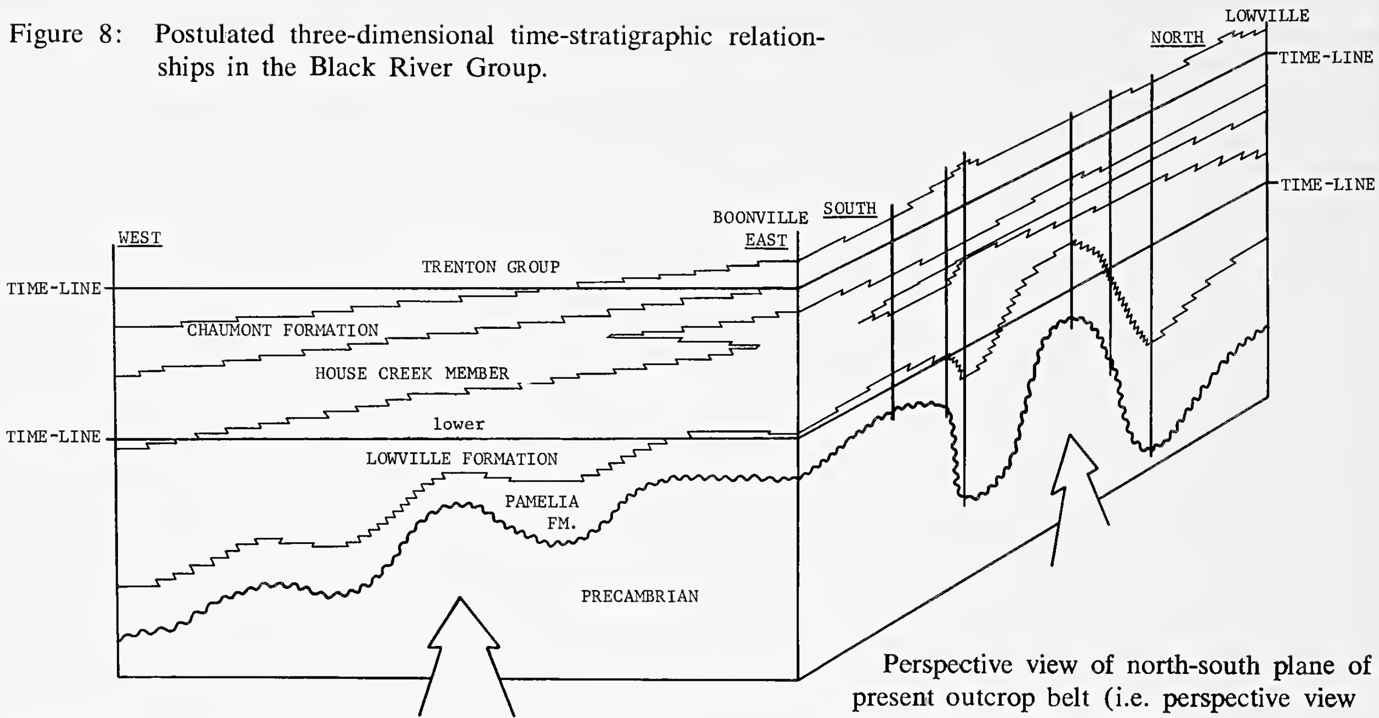
REEVALUATION OF TIME-STRATIGRAPHIC RELATIONSHIPS

The stratigraphic framework developed for the outcrop sections permits a reevaluation of the hypotheses of time-stratigraphic relationships within the Black River Group, and between that group and the Trenton Group. The hypotheses of Kay, Young, Winder, and Fisher are shown in figure 3; notice that the frame of reference for each is different. Kay and Young have emphasized time relationships along the outcrop, which trends roughly north-south. Winder portrayed the facies along a theoretical cross section normal to shore, and Fisher's cross section trends east-west, nearly at right angles to the outcrop belt. To reconcile these hypotheses, one must consider: 1) the array of facies to be expected along a shoreline, and 2) the location and orientation of the shoreline during deposition of the Black River and Trenton Groups.

Facies patterns along a shoreline generally show elongation parallel to the strand. This is dictated by the control of currents by bottom topography, which generally slopes downward away from shore. Thus an aerial view of a near-shore facies pattern will show a series of environmental bands or ellipses which are elongate parallel to shore. Shorelines migrate through time depending on the transgressive or regressive nature of the regional sedimentation pattern, and facies patterns migrate with the shoreline. This coupling of shoreline and facies pattern yields a three-dimensional facies mosaic in which lithofacies units tend to cross time planes when traced perpendicular to shore, but tend to parallel time planes when followed parallel to shore. Thus the geometric relationship of lithofacies units to time lines in a two-dimensional stratigraphic cross time planes when traced perpendicular to shore, with the ancient shoreline. The more nearly parallel to shore the cross section, the more nearly parallel will be the time line and lithofacies units.

Relationship of the present Black River Group outcrop belt to the "Black River" shoreline can be inferred from sedimentologic studies. Pamelia and Lowville sediments were largely deposited in a tidal flat complex as suggested by presence of mudcracks, supratidal dolomite, and fossils of euryhaline organisms. These features are related to the strand zone, and are present at the base of the group above the unconformity on the Precambrian basement. Ripple marks are abundant in the group. Potter and Pettijohn (1963, p. 89–99) concluded that the strike of ripples in marine sands "tends to parallel depositional strike." McKee (1957, fig. 28) and Evans (1965, p. 213) have shown that when tidal flat ripples have a strong preferred orientation, their strike is subparallel to shore. The ripple marks of the Black River Group (50 sets measured) have a strong preferred orientation between northwest-southeast and north-south. Potter and Pettijohn (p. 83–86) note that

Figure 8: Postulated three-dimensional time-stratigraphic relationships in the Black River Group.



Perspective view of north-south plane of present outcrop belt (i.e. perspective view of fig. 4). Compare with fig. 2A.

Postulated relationships in east-west plane at right angle to present outcrop belt. Compare with figs. 2B & 2C.

marine cross-bed dip directions tend to be normal to the strand line. Cross-stratification in the Black River oolite units dips east or west, thus the evidence suggests that the "Black River" shore in the Black River Valley trended north-south; the present outcrop belt subparallels that trend. Therefore, in the outcrop belt the lithofacies units roughly parallel time lines, as in the cross section by Kay and Young (fig. 3).

The Black River Group is a transgressive sequence, with more seaward marine rocks becoming more common upward in each stratigraphic section. Because the Adirondack Arch was intermittently positive since the later Precambrian (cf. Clarke and Stearn, 1968), it is reasonable to assume that the Black River sea transgressed eastward onto this element. Therefore, in an east-west (onshore-offshore) direction one should expect lithofacies units to cross time lines, as in the cross sections by Winder and Fisher (fig. 3).

Figure 8 is a block diagram showing the three-dimensional relations postulated here. No outcrops occur along a line normal to the main outcrop belt, so this interpretation cannot be field tested. Figure 8 indicates that the use of lithologic unit names in a time-stratigraphic sense is confusing for most of the group. The entire Pamelia Formation at Roaring Brook is older than the oldest Pamelia at House Creek. The base of the Lowville Formation is also markedly asynchronous. The Pamelian and Lowvillian substages of Kay (1960, p. 32) should not be used because of possible confusion with the lithologically defined, asynchronous Pamelia and Lowville formations. Kay's Chaumontian Stage (1960, p. 32) is less confusing because the Chaumont Formation is roughly synchronous in the outcrop belt. Kay has made it clear (1968, p. 168) that he recognizes facies changes within the stage, and that only near Watertown, N.Y. does he consider the Chaumontian Stage to correspond to the Chaumont Formation. Using a rock-stratigraphic unit name for a stage at its type locality is supported by precedent (American Code of Stratigraphic Nomenclature, 1961, p. 659). To avoid confusion, however, it is advisable to use the term Chaumont only for a lithologically defined formation.

Cooper (1956, p. 7) has proposed several stages based on North American Ordovician brachiopod faunas. Although some problems have since developed with the application of these stages as noted by Kay (1960, p. 30–31), there is little doubt that the Black River Group and the lowermost Trenton Group of New York are within the Wilderness Stage of Cooper. That name should be applied in the Black River Valley. However, local time relationships can be considered without the encumbrance of formal terminology.

Environments of Deposition

Each of the 11 described lithologies records a distinct environment inferred from features of the rocks. Seven of these are volumetrically important — lithologies 1–4, 6, 7, and 9. In addition, oolite represented by lithology 5 of figure 4, is an important lithology. The remaining lithologies represent variations of the major environments.

The inferences made here are based on field descriptions and analyses of 445 large samples. From these, 300 cellulose acetate peels with an average cross-sectional area of 75–100 square cm and 261 5 x 7.5 cm (2 x 3 in.) thin-sections were prepared and analyzed; 135 thin-sections were analyzed in greater detail. The carbonate terminology used is that of Folk (1959, 1962). Because Black River biotas are discussed in detail in another publication (Walker, 1972), they are treated here only as aids in making environmental interpretations.

Although the seven main lithologies occur most often in pure form, they are best considered as ideal end members. Intermixtures occur between some of them and vertical gradations are common. Lateral gradations also can be seen, although exposures large enough to include a complete gradation are not abundant. Figure 5 shows the vertical and lateral complexity of the lithologies.

The seven major lithologies of figure 4 are the lithologic aspect of seven facies representing deposition in the environments listed below. Each facies is defined and its environment is inferred on the basis of texture, constituent particle types, physical and biogenic sedimentary structures, lateral and vertical lithologic associations, and, to some degree, paleontologic considerations. Listed by corresponding lithology numbers from figure 4, the environments are:

1) supratidal regolith
2) supratidal mudflat dolomites
3) intertidal mudflat intraclastic pelmicrites
4) a. very shallow subtidal, quiet water pelmicrites or micrites
   b. very shallow subtidal, channel intrasparite or intraclastic pelsparite
6) a. *Tetradium* biopelsparite or biopelmicrite, marginal to
   b. shallow subtidal, bioconstructed, *Tetradium* wave-baffle
7) gastropod-bearing facies marginal to the *Tetradium* wave-baffle
9) normal marine, coralgal biopelsparite.

The detailed environmental conclusions derived in the present study are in rough agreement with the generalized interpretation made by Textoris (1968) based on a suite of samples from the Roaring Brook locality.

The terms "supratidal, intertidal, and subtidal" are used as follows:

Supratidal: that strand zone only rarely flooded by marine water, but with a distinct marine influence

Intertidal: that strand zone which is regularly and periodically flooded by marine water at unspecified intervals and for unspecified duration

Subtidal: that zone which is nearly always covered by marine water.

SUPRATIDAL REGOLITH (LITHOLOGY 1 OF FIGURE 4)

The basal sandstones at Roaring Brook, Mill Creek, and Turin Road, and probably present but unexposed elsewhere, represent a paleo-soil which was reworked during the earliest phase of the Black River marine transgression. Mineralogically, the terrigenous fraction of the sandstone and associated sandy dolostone mirrors closely the composition of the underlying Precambrian rocks. Figure 9 is a comparison of the Precambrian and overlying sandstone at Roaring Brook and Mill Creek. The variety of perthite in the sandstone is the same as that in the Precambrian, the grain sizes are similar, and rock fragments in the sandstone are from the Precambrian. The sandstone is poorly sorted, and the terrigenous clasts are mostly angular. Figures 10a and 10b show thin section photographs of the Precambrian and the lowermost sandstone at Roar-

Figure 9: Comparison of the mineralogical compositions of Precambrian basement rocks and overlying Black River Group basal sandstones at Roaring Brook and Mill Creek.

	Sample RB 1 Precambrian	Sample RB 2 Sandstone *	Sample MC 1 Precambrian	Sample MC 2 Sandstone *	Sample MC 5 Sandstone *
Quartz	33.2	58.8	26.4	58.5	74.9
Orthoclase-perthite	36.2	22.3	Trace	Trace	Trace
Microcline-perthite	Trace	Trace	38.7	14.5	19.9
Orthoclase	6.4	1.5	6.5	4.1	Trace
Microcline	1.2	0.3	14.2	1.7	0.3
Other feldspars	12.4	2.5	4.2	Trace	0.7
Biotite	4.4	Trace	5.1	Trace	Trace
Heavy accessories	6.2	1.9	4.9	4.7	0.7
Rock fragments (quartz & perthite)		12.7		16.5	3.5
TOTALS	100.0	100.0	100.0	100.0	100.0
Approx. modal grain size in mm; two values indicate bimodal size distribution.	0.3	0.13	0.34 & 0.47	0.17 & 1.0	0.3 & 0.4

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* Only terrigenous detrital fraction of the sandstones is considered here. Dolomite cement, clay matrix, and carbonate allochems are eliminated.

ing Brook. The high percentage of feldspar and rock fragments, angularity of clasts, and poor sorting all suggest that these sands have not moved far from their provenance. Some movement has occurred, because the sandstone is bedded and sometimes ripple marked.

These sands are vertically and laterally mixed with supratidal dolomite (fig. 10c). In addition, most samples have dolomite cement, and some are very sandy dolostones with terrigenous clasts "floating" in dolomicrite. Every variation occurs between sandstone with dolomite cement and dolostone (fig. 13d).

Oscillation ripple marks and flat, even bedding, and the close association of these sandstones with supratidal dolostones indicate that the sands also were deposited on supratidal flats. They represent the highest, most landward part of the Black River supratidal environment. Extremely rare ostracode and trilobite fragments confirm the marine association of the sands.

SUPRATIDAL DOLOSTONES (LITHOLOGY 2 OF FIGURE 4)

These dolostones are analogs of Recent carbonates which were deposited and modified above mean high tide. Modern supratidal environments are characterized by sediment features unique to that zone. These features are summarized in the left column of figure 11, and are mainly the result of the intermittent nature of sediment deposition, presence of blue-green algal mats, long term dessication of the sediment between wettings, or the high Mg^{++}/Ca^{++} ionic ratio of interstitial water. The reader is referred to figure 11 for environmental inferences made from these features, and to the references in figure 11 for a more complete discussion. .

The features reviewed in figure 11 as characteristic of modern supratidal carbonates occur commonly in dolostones of the Black River Group. Many of these features are illustrated in figures 12 and 13. Most exposures contain wavy laminae 0.02 to 1 or 2 mm thick, which are usually visible on outcrop. Rarely, dolomitization has destroyed all internal structure. In a few beds the lamination can only be seen in thin-section or peel (fig. 12a). Horizontal, lensoid "birdseye" structures are abundant (fig. 10d). These laminae are inferred to be of algal origin because of the "spongy" rock texture, the waviness of the laminae, abundant "birdseyes", occasional 2–5 micron diameter vertical spar filled tubes, and common very thin organic laminae (remains of buried algal mat?) between sediment laminae.

Small scale mudcracks with polygons 1 to 8 cm in diameter are common. Figure 12c shows a peel from a bed which illustrates most of the supratidal features in these dolostones. The top of this bed is mudcracked (fig. 12b).

Black River dolostones are only sparsely fossiliferous, containing rare to occasionally abundant disarticulated

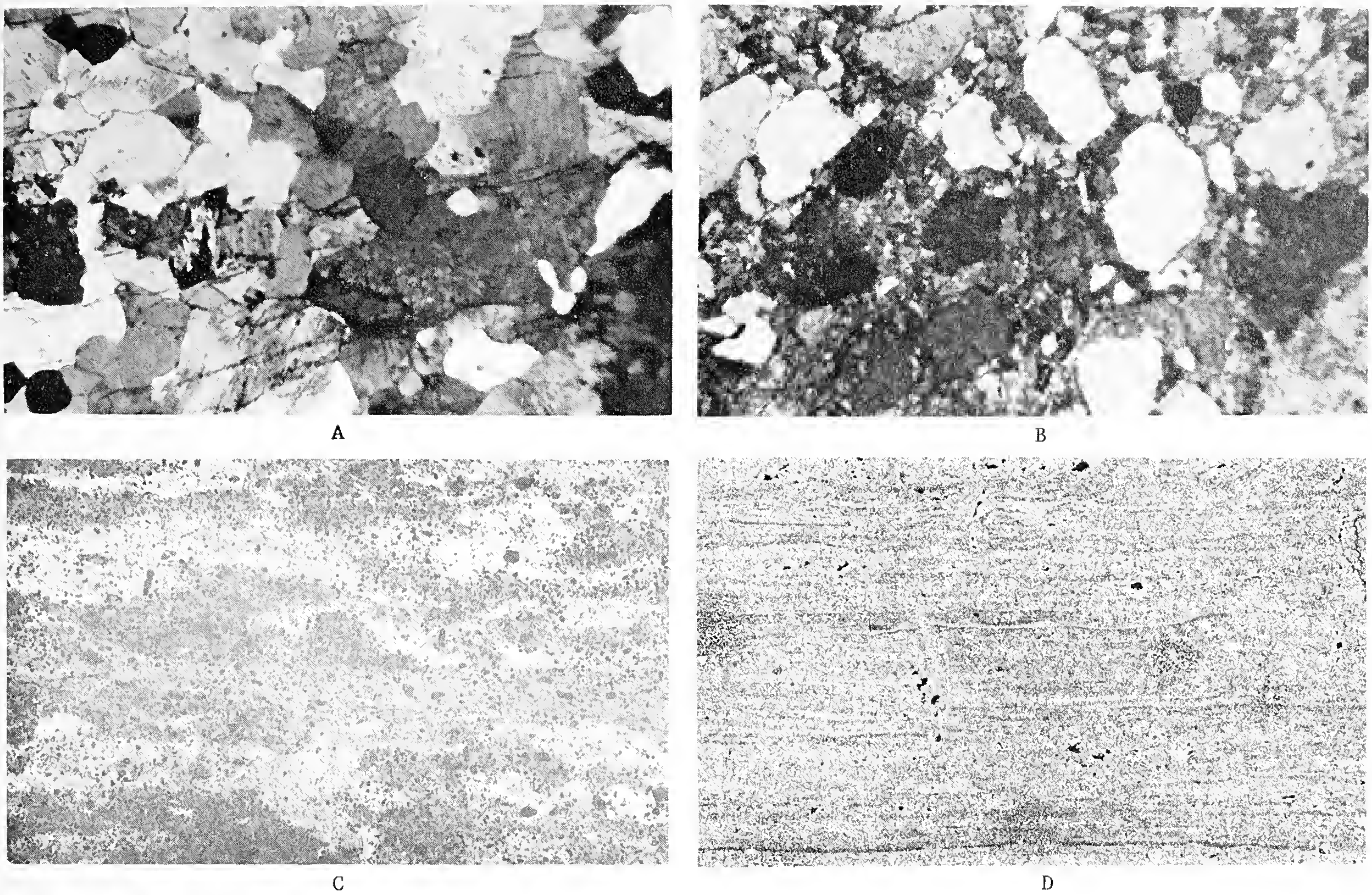


Figure 10

Figure 10a: Negative print of thin-section from Precambrian basement at Roaring Brook. Grains are about 1 to 2 mm in diameter. Compare with fig. 10b.

Figure 10b: Negative print of thin section of Black River Group basal sandstone at Roaring Brook about 1 foot above basement rock shown in figure 10a above. Median grain diameter about 1 mm.

Figure 10c: Negative print of basal sandstone thin section from Mill Creek showing interlamination of sandstone (dark, grainy laminae and dolomite (lighter laminae). Height of specimen about 3 cm.

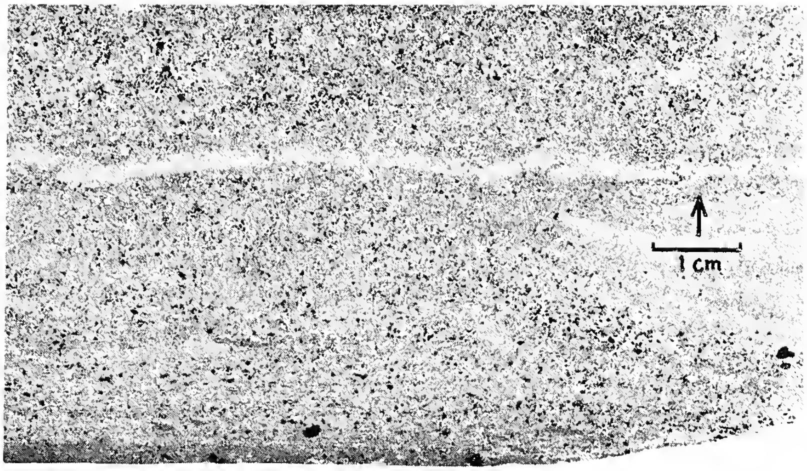
Figure 10d: Negative print of cellulose acetate peel of supratidal dolomite from Mill Creek showing abundant, thin, algal laminae with sparry calcite birdseyes (black on negative print) beneath laminae. Specimen is about 3 cm high.

valves and rare articulated shells of the ostracode *Leperditia* sp., and rare trilobite fragments. These shelly remains were probably transported onto the supratidal flats from adjacent environments. Rare vertical burrows were probably formed during a short period after each incursion of marine water.

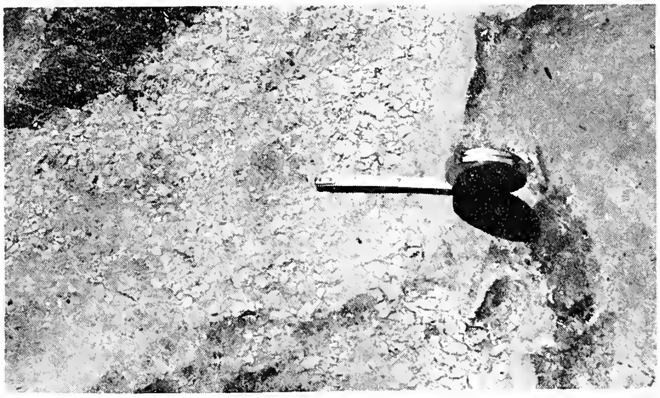
Blue-green algae, as mat-like colonies of filaments, were probably the only continuous inhabitants of these flats. These mats produced laminae by binding sediment, but also modified the sediment surface in another way. Figure 13a shows a bed surface which is covered by sinuous, elongate ridges and ovoid depressions. The upper surface of the bed is mudcracked, so the ridges and depressions are primary structures and not weathering phenomena. Illing, *et al.* (1965, figs. 3b and 4h), have figured similar structures from supratidal flats of the Persian Gulf. There, the ridges are algally formed and parallel to shore. The Black River examples trend north-south and thus suggest the orientation of the Ordovician shoreline. They are intimately associated with algal lamination and were probably algally formed.

Characteristic feature	Relative abundance in lithology 2	Environmental inference	Reference for Recent occurrence
Wavy, ultrathin lamination.	Very abundant.	Laminae formed by sediment binding algae. Characteristic of supra- or intertidal.	Ginsberg, *et al.*, 1954. Logan, 1961.
Vertical, spar filled, 2–5 micron diameter, 0.1–0.3 mm. long tubes.	Rare.	Tubes formed by algal filaments in the binding mat.	Johnson, 1946. Shinn, *et al.*, 1969.
2–10 micron thick, wavy, organic laminae.	Common.	Remains of buried algal mats.	Shinn, *et al.*, 1969.
Sinuous ridges and ovoid depressions on surfaces of algally laminated beds.	Rare.	Formed by algal mats on tidal flats. Retains water between times of highest tides.	Illing, *et al.*, 1965.
Horizontal lensoid birdseyes between laminae.	Very abundant.	Voids caused by desiccation, subsequently filled by sparry carbonate. Most characteristic of supratidal.	Shinn, 1968.
Interlamination of dolomite and dolomitic limestone.	Common to abundant.	Discontinuous dolomitization in a thin, planar zone of optimum chemical conditions. Modern dolomite only in supratidal.	Shinn, *et al.*, 1965.
Crystal molds.	Rare.	Precipitation of Ca^{++} evaporites increases Mg^{++}/Ca^{++} ratio leading to dolomitization.	Illing, *et al.*, 1965.
Slump breccia.	Very rare.	Precipitation of beds of evaporate which subsequently dissolve causing slump of overlying carbonate.	Illing, *et al.*, 1965.
Mudcracks. Polygons ½ to 3 inches wide.	Common to abundant.	Periodic, rather complete drying of environment. Most common in high inter- and supratidal.	Ginsburg, 1957.
Intraclastic zones and laminae.	Common.	Desiccation of mudcrack polygon edges.	Ginsburg, 1957.
Low shelly faunal content, mostly transported.	....	Transported onto flats from adjacent environments.	Pers. observ. on Crane Key, Florida Bay, 1965.

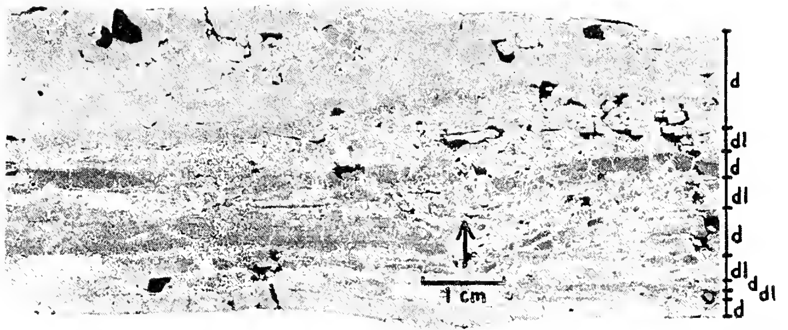
Figure 11: Supratidal characteristics of lithology 2, the dolomites of the Black River Group.



A



B



C

Figure 12

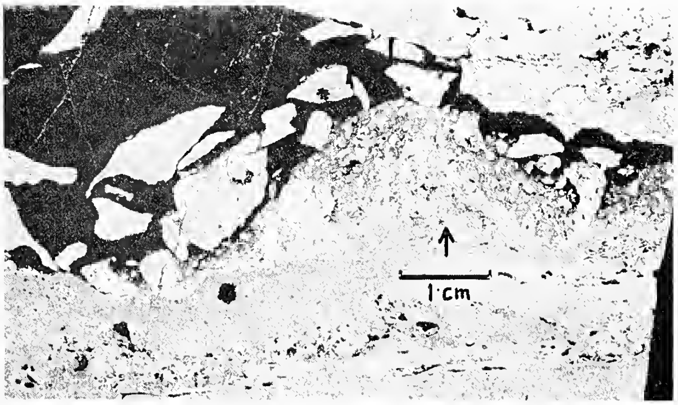
Figure 12a: Negative print of peel from supratidal dolostone sample from Roaring Brook showing nearly complete dolomitization; only cryptic lamination remains. Arrow indicates stratigraphic up-direction.

Figure 12b: Outcrop photograph showing very small scale mudcracks on bed surface in supratidal dolostones at Roaring Brook. Inch divisions on tape measure give scale.

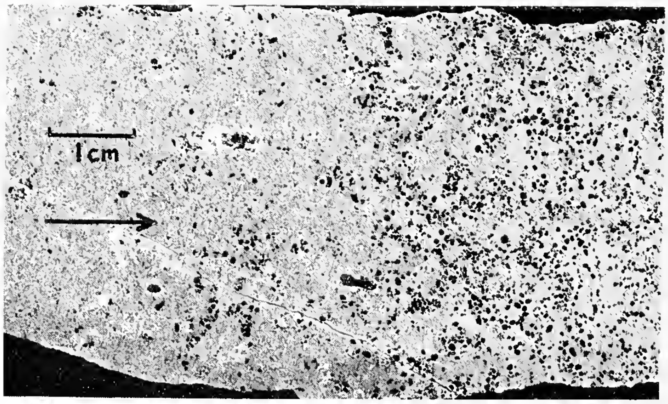
Figure 12c: Negative print of peel from supratidal dolostone sample from Roaring Brook showing most of the characteristics of supratidal deposition: 1) letters on right of peel illustrate intimate interlamination of dolostone (d) and slightly dolomitic limestone (dl), 2) laminae are ultrathin and minutely wavy suggesting algal origin, 3) sparry calcite birdseyes show black on negative print, 4) note intraclastic zone just above scale, 5) top of bed sampled is shown in figure 12b.

A

B



C



D

Figure 13a: Oblique outcrop photograph showing sinuate algal ridges on a dolostone bed surface at Roaring Brook. Tape measure is about 5 cm (2 in.) in diameter.

Figure 13b: Outcrop photograph of conformable breccia lens within a sequence of supratidal dolostones at Roaring Brook. Note tabular, very angular, but slightly bent clast 2.5 cm (1 in.) from end of tape measure. Tape scale in inches.

Figure 13c: Negative print of peel from dolostone sample from Roaring Brook showing algal lamination, horizontal lensoid birdseyes, and large area of drusy-growth spar at upper left (black on negative print).

Figure 13d: Negative print of peel from supratidal dolostone sample from Mill Creek showing vertical gradation from dolostone at base (left) to dolomitic sandstone at top (right).

If the Black River dolostones are supratidal and penecontemporaneous, one might expect associated evaporite minerals as in Recent examples. Scattered elongate, wedge-shaped areas of sparry calcite are common in Black River dolostones, and these may be crystal molds of gypsum. Young (1943, p. 153) noted these crystal molds in Ontario outcrops. In addition, at Roaring Brook a conformable 30 cm thick lens of breccia occurs within the dolostone sequence. The dolostone clasts are angular but sometimes bent (figs. 13b and c); thus they were only semilithified when formed and could not have moved far. This appears to be a slump breccia, perhaps formed by solution of an underlying evaporite bed. In other dolostone beds, large areas of drusy-growth sparry calcite (see Bathurst, 1958), may be filling voids left after solution of evaporites.

Black River dolostones are gradational with other lithologies. Vertical and lateral gradations occur with dolomitic sandstone (lithology 1, fig. 4) and with pelletal, intertidal limestone (lithology 3, fig. 4).

INTERTIDAL LIMESTONE (LITHOLOGY 3, FIGURE 4)

The intertidal facies shows evidence of alternating periods of high and low water turbulence, periods of desiccation, algal lamination, and a more diverse fauna than that which occurs in the supratidal dolostones. Dolomite is rare. These properties indicate an environment subject to periodic subaerial exposure and variable water turbulence similar to that suggested for Black River dolostones, but the rarity of dolomite suggests shorter periods of desiccation. Abraded fossils, typical of more seaward facies, are common in the limestones suggesting a closer association with normal marine waters than postulated for the supratidal.

Intertidal samples are alternating units of wavy laminated pelmicrite or micrite, and pelsparite or intraclastic pelsparite (fig. 14a). Constituent particle composition of selected samples is shown in figure 15. Most of the spar occurs as interlaminar "birdseyes" or as partial fillings of vertical burrows. Ovoid pellets range from 0.015 to 0.050 mm in diameter. Because of limited size distribution in any one lamina, small size, and discontinuity between pellet and intraclast sizes, it is believed the pellets are of fecal origin. Some were transported from more seaward environments, but some originated in the intertidal zone by burrowing suspension feeders. Concentrations of pellets about the openings of vertical burrows such as that shown in figure 14a

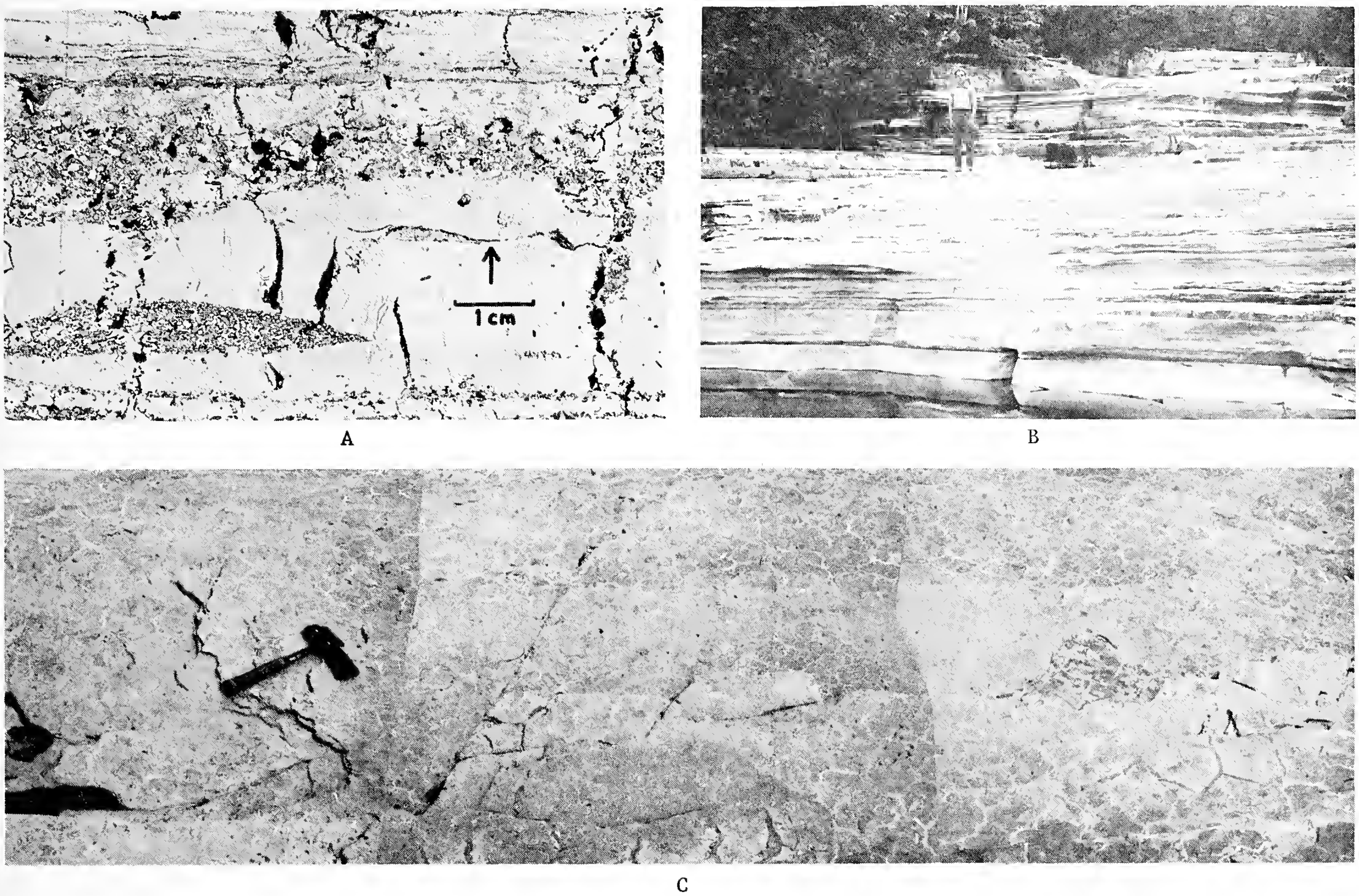
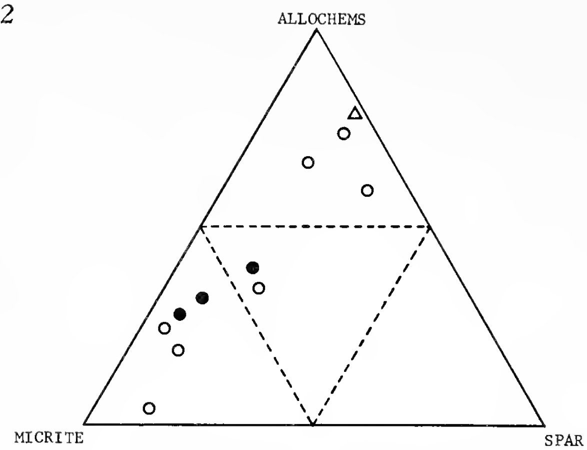


Figure 14

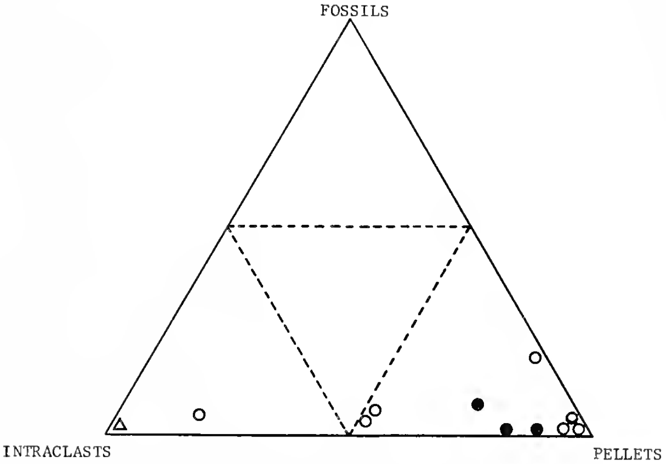
Figure 14a: Negative print of peel from intertidal limestone sample from Roaring Brook showing interlamination of laminated pelmicrite and intrapelsparite. Note pellet filled vertical burrows, and mound of intrapelsparite associated with burrow at lower left.

Figure 14b: View of intertidal limestone outcrop along Roaring Brook showing the typical thin bedding in this facies. Man is about 5 feet tall.

Figure 14c: Panoramic view of mudcrack exposure in intertidal facies at Roaring Brook showing typical mudcrack polygon size.



A: TOTAL CONSTITUENT PARTICLE COMPOSITION



B: ALLOCHEM COMPOSITION; MINUS MICRITE AND SPAR

Figure 15: Constituent particle composition of selected samples from lithology 3, the Black River intertidal facies. Symbols stand for samples from the following stratigraphic sections: Roaring Brook open circles, Whetstone Creek up-pointing triangle, House Creek down-pointing triangle, and Mill Creek closed circles.

indicate the association of the vertical burrows and pelleting activity.

The thin bedded nature of intertidal limestone is shown in figure 14b. Deposition of each successive coarser-grained unit was preceded by scouring of the surface of the underlying fine-grained unit. Coarser units were probably storm deposited; fine-grained beds, which are algally laminated, represent quieter periods.

Mudcracked surfaces are abundant in the intertidal facies and always show larger polygons (7 to 15 cm in width) than similar surfaces in the supratidal facies (fig. 14c). This size difference is probably due to the greater thickness of sediment deposited in the intertidal zone between periods of drying. Anderson, *et al.* (1965,

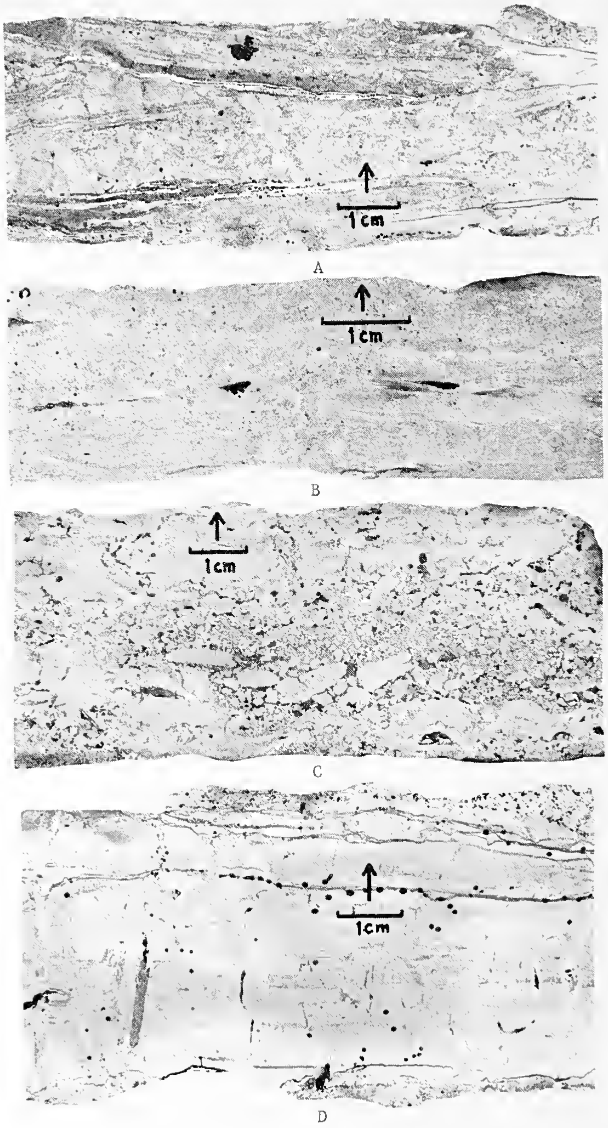


Figure 16

Figure 16a: Negative print of peel from intertidal lithology from Whetstone Creek showing jumbled, internally algal laminated mudcrack polygons.

Figure 16b: Negative print of peel of sample from Mill Creek showing ultrathin, wavy, algal lamination in intertidal lithology.

Figure 16c: Negative print of peel from intertidal sample at Whetstone Creek showing intraclastic pelmicrite storm layer.

Figure 16d: Negative print of peel from Roaring Brook intertidal sample showing typical U-shaped burrows (right of print) and vertical burrows of that facies.

p. 5) have shown experimentally that polygon size is controlled by the thickness of the layer desiccated. In the exposure shown in figure 14c, the mudcracks cut through several thin beds of pelmicrite and are filled by coarser pelsparite.

Intraclastic beds of jumbled mudcrack polygons are common (fig. 16a), and some mudcracked surfaces are oscillation ripple marked. These features indicate alternate periods of drying which produced mudcracks and periods of water movement which formed the ripples and disturbed the polygons.

Algal lamination is abundant in the finer-grained parts of the intertidal facies (figs. 14a, 16b and d). Algally coated grains are conspicuously absent except for rare, thin, obviously abraded coatings on intraclasts. Logan (1960, p. 518) has noted in Shark Bay, Australia " continuous flat, algal laminated sediments . . . occur in the protected intertidal mudflat environment, where mechanical energy of waves and currents is normally negligible." Where current and wave activity is higher, growth of a continuous mat is inhibited and discrete algal heads form. Absence of heads from the Black River intertidal facies, despite the abundance of algal bound sediment, suggests a quiet environment.

The shelly fauna of this facies is not diverse, but more so than that of the supratidal. Articulated shells and disarticulated valves of the ostracode *Leperditia* sp., and carapace segments of the trilobite *Bathyurus extans* are common. U-shaped vertical burrows and straight, tube-like, vertical burrows are very abundant and suggest the dominance of burrowing, soft-bodied fauna in this facies. Various features indicate that these are burrows of sessile suspension feeders: 1) constant geometric orientation of the burrows; 2) absence of sediment manipulation at their borders, and 3) association of burrow-mouths with bed surfaces. Such burrows are common in modern shallow water areas and on tidal flats, where variable environmental conditions make the protection afforded by a burrow desirable (pers. comm. D.C. Rhoads). Figures 14a and 16d show typical examples of Black River intertidal burrows. Irregular, randomly oriented, deposit feeder burrows are present but not characteristic of this facies.

INTERTIDAL OOLITE (LITHOLOGY 5, FIGURE 4)

Modern oolite formation is restricted to narrow, often irregular zones of shoal water (Ball, 1967). As such zones migrate they should lead to deposition of a time transgressive stratigraphic unit. The Black River oolite beds appear to be parts of a single, contemporaneous unit (excepting the Lowville Quarry exposure), suggesting that these deposits are not analogous to Recent examples.

The oolite bed is overlain, underlain, and sometimes interbedded with intertidal facies. Figure 17a shows a locality at which the oolite contains algally laminated intertidal limestone which grades laterally into intraclastic oolite. Because of the intimate association of the oolite with intertidal lithologies, it is thought that the environment of oolite deposition was intertidal.

In contrast to Recent ooids which have up to 90 coatings, those in this facies have only 1 to 6. Also, all Black River oolite contains some micrite, and most outcrops have interlaminae of oolitic pelmicrite. These features and occasional aggregates composed of several ooids cemented together suggest periods of quiet water during deposition. The coated grains are pellets, well rounded intraclasts, and fossils.

Except for abraded fragments, the oolite contains only rare fossils. Algal mats were common in the oolite environment as evidenced by algally laminated interlaminae. *Cyrtodonta* sp., a byssally attached, semi-infaunal bivalve (pelecypod), is occasionally found in life position. Presence of this form suggests a more stable sediment surface than is common in Recent oolite environments.

PROTECTED SUBTIDAL LIMESTONES (LITHOLOGIES 4A AND 4B, FIGURE 4)

These lithologies are interbedded on all scales and are discussed together. Their biotas are nondiverse when compared with those deposited more seaward. The lithologies show no evidence of desiccation, and their environments of deposition are therefore considered to have been subtidal.

QUIET WATER POND (LITHOLOGY 4A, FIGURE 4)

This facies consists of thick beds of ultrathin, nonwavy to slightly wavy laminae of dark gray micrite or pelmicrite; figure 17b shows a typical exposure. No evidence of desiccation is present. The laminae are algal in origin, because they frequently preserve 2 to 5 micron diameter, vertical spar-filled tubes which are probably fillings of voids left after decay of algal filaments (see Johnson, 1946). One to two micron thick organic rich interlaminae are abundant and may be buried algal mats (see Laporte, 1967, p. 78). Acetate peels from samples of this lithology are shown in figures 17c and 18a.

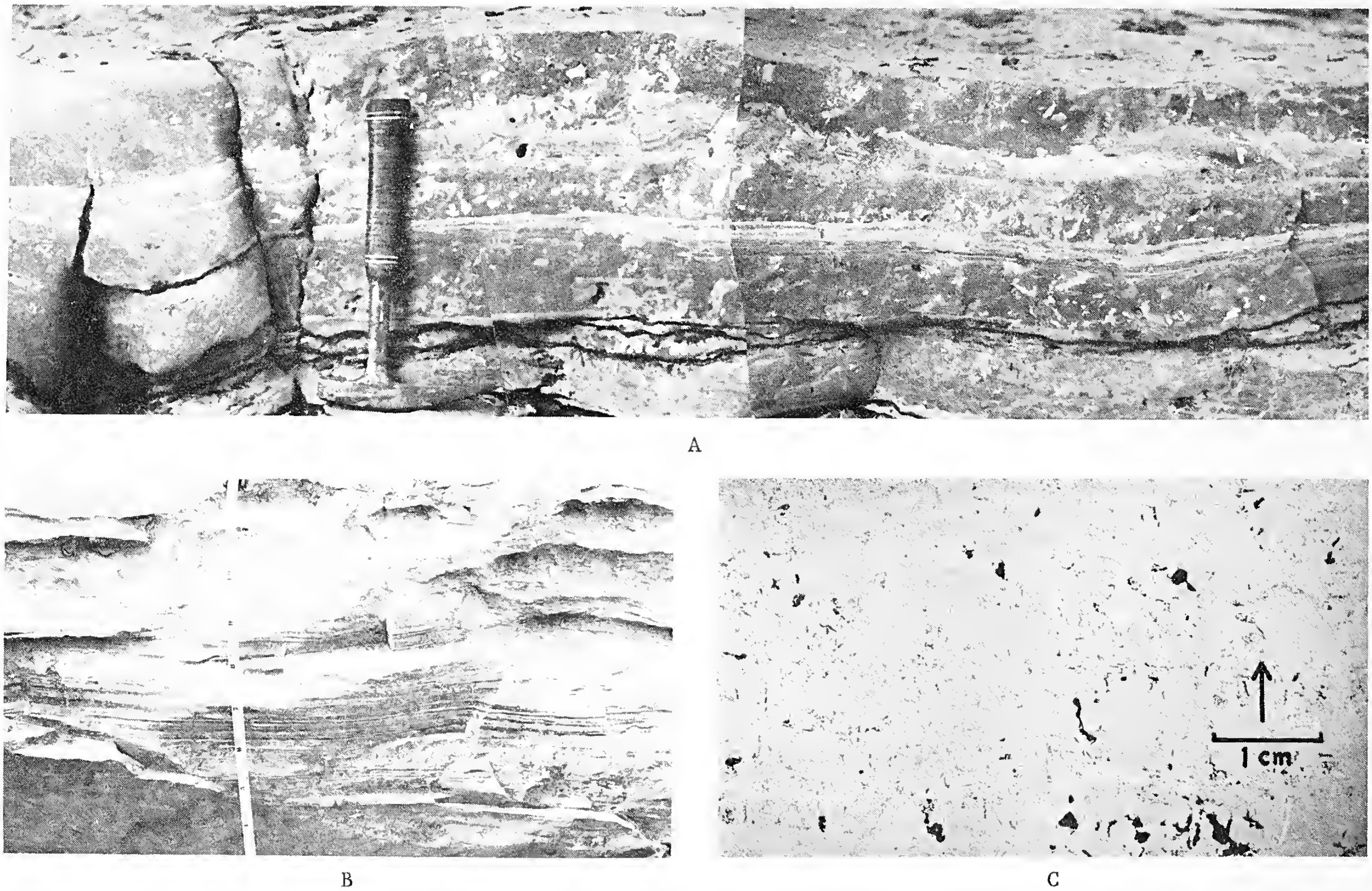


Figure 17

Figure 17a: Panoramic view of oolite lithology at Roaring Brook showing algally laminated pelmicrite interlaminae and intraclasts.

Figure 17b: Outcrop photograph of quiet water subtidal lithology at Roaring Brook showing thin, nonwavy algal laminae typical of facies. Tape measure subdivisions are in inches.

Figure 17c: Negative print of thin section of quiet water subtidal lithology from House Creek showing thin laminae, and vertical, spar-filled algal tubes (vertical dark gray to black structures 0.01 mm wide by 0.5–1.0 mm long).

Until recently, flat algal laminae were thought diagnostic of environments above mean low tide, but modern occurrences of subtidal algal lamination have now been discovered (see Monty, 1965, and Gebelein, 1967). Modern subtidal algal mats are restricted to areas with very low current velocities (Gebelein, 1967, p. 75). Because of absence of desiccation in the environment the mats are rarely crinkled and should produce flat laminae. Lamination is often cryptic in the sediment of Recent mat areas because of biogenic reworking. In the Black River quiet-subtidal lithology, flat laminae are preserved because of the absence of biogenic reworking. Burrowers may have been excluded from the environment by the soft, fine grained substrate and by reducing conditions induced by a very high organic content (now evidenced by the dark color of quiet subtidal limestones and by scattered iron sulfide crystals). These conditions would also explain the near absence of shelly invertebrate fossils (for a similar modern situation, see Bader, 1954). Articulated shells and disarticulated valves of *Leperditia* sp. (ostracode) and trilobite fragments (probably *Bathyurus extans*) are rare. Very rare articulated specimens of *Strophomena* sp. may be in life position.

Unabraded algally-coated grains (oncolites), which form today only in permanently submerged shoal-water areas, are sometimes present. Their occurrence confirms a subtidal environment for this facies.

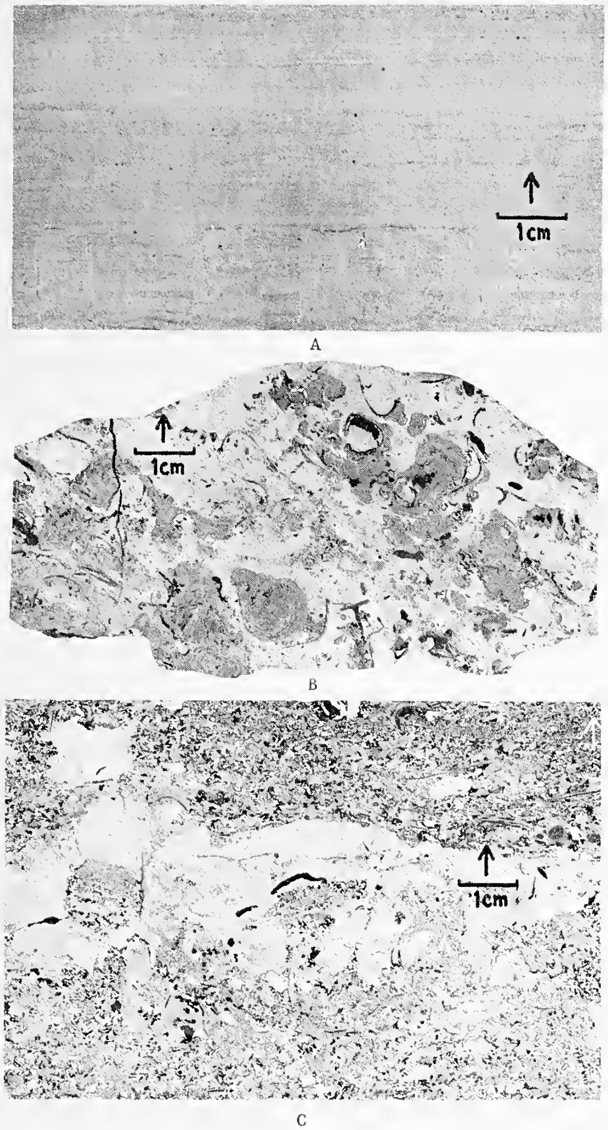


Figure 18

Figure 18a: Negative print of peel from quiet subtidal lithology at Roaring Brook showing ultrathin, flat algal lamination. The laminae of this sample contain vertical, spar-filled algal tubes (not visible at this magnification). Note stylolite near base of print.

Figure 18b: Negative print of peel of subtidal channel lithology from Roaring Brook showing abundant oncolites (algally coated grains). These coatings often contain algal tubes oriented normal to the coated surface.

Figure 18c: Negative print of peel from Roaring Brook showing typical texture of subtidal channel lithology. Note algal coated brachiopod fragment at upper left center.

Stylolites are characteristic. Most modern theories of stylolite formation have emphasized a solution-pressure mechanism during diagenesis (Park, *et al.,* 1968, p. 187). One problem is determining the kind of surface which localizes solution. Evidence bearing on the timing of stylolitization and the surface problem is present in rocks of this facies. A bed of channel lithology in Port Leyden Quarry contains stylolited intraclasts derived from an underlying bed of quiet water lithology. The stylolites parallel laminae in the intraclasts, but are at high angle to bedding of the surrounding matrix. Stylolites do not occur in the matrix. Thus the stylolites were probably formed before the intraclasts were produced, suggesting a very early diagenetic origin.

Stylolites in the quiet subtidal lithology are parallel to lamination, and the stylolite plane is frequently overlain by an unusually thick lamina of organically rich, very dark gray micrite containing vertical algal tubes. These features may record the burial of an algal mat by sediment so thick that the filaments of the mat could not escape to become reestablished at the new sediment surface. Such a buried mat would soon decay, creating a planar zone of lowered pH which would promote solution of carbonate in that zone. Such an hypothesis would explain the parallelism of stylolites and laminae, planar localization of stylolite formation, and the association of stylolites and subtidal algal laminae. Black River intertidal and supratidal algal laminated sediments are not stylolited, perhaps because oxidizing conditions and tidal flushing precluded development of solution conditions in these sediments.

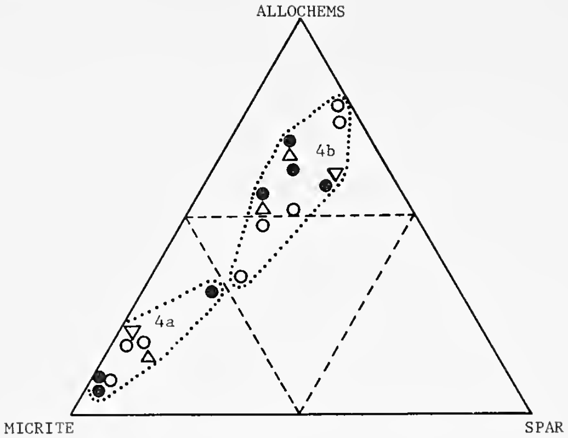
Constituent particle composition of selected quiet water subtidal samples is shown in figure 19 (lithology 4a samples). The uniformly micritic texture suggests quiet water deposition.

The environment of deposition for lithology 4a may have been analogous to the subtidal ponds of the Andros Island tidal flats which are discussed by Shinn, *et al.,* 1969. Although these modern ponds do not contain algal laminae, they are intimately associated with channel lithologies as are the Black River rocks of this facies.

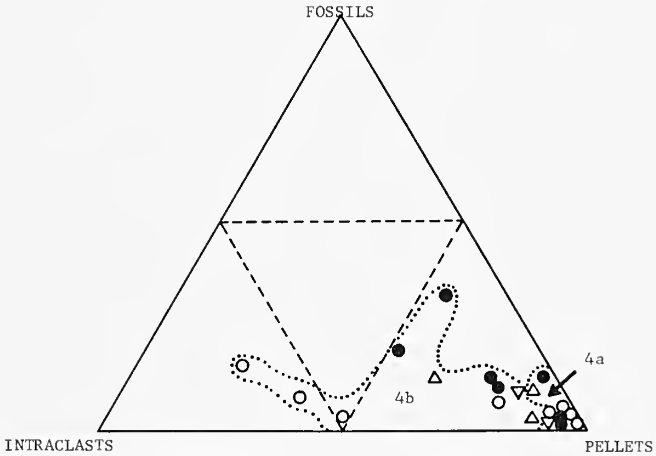
CHANNEL (LITHOLOGY 4B, FIGURE 4)

Quiet water subtidal limestones are interbedded on all scales with a coarser grained facies. The coarse facies is also interbedded with thick intertidal limestones. Several lines of evidence indicate the coarse facies is the record of broad, shallow tidal channels.

The constituent particle composition of channel limestone is shown in figure 19 (samples marked 4b). The



A: TOTAL CONSTITUENT PARTICLE COMPOSITION



B: ALLOCHEM COMPOSITION; MINUS MICRITE AND SPAR

Figure 19: Constituent particle composition of selected samples from lithologies 4a and 4b, the protected subtidal facies. Symbols stand for samples from the following stratigraphic sections: Roaring Brook open circle, Whetstone Creek up-pointing triangle, House Creek down-pointing triangle, Mill Creek closed circles.

spar in the samples is interstitial. Much of the micrite has a clumpy texture, with clumps about the same size as accompanying pellets; the micrite probably originated as coarse silt size pellets which lost their distinct outline during early compaction. Most allochems are pellets in the size range 0.03 to 0.4 mm median diameter, so the sediment was a coarse silt to medium sand. Coarser fossil debris and intraclasts are common.

Algally coated grains, or oncolites, are very abundant. Logan, *et al.,* 1960, have discussed these in detail; they found that oncolites are most characteristic of subtidal environments. Figure 18b shows a sample in which concentric oncolites are well developed, and figure 18c shows a more typical sample in which oncolites are abundant, but less well developed.

When the basal contact of channel limestone is well exposed, minor scouring of the underlying unit is visible. No large channel structures occur, however, and thin sets of high angle cross-laminae are rare. Absence of channel sedimentary structures does not preclude a channel origin. Very gently sloping mudflats often have very broad, very shallow, meandering tidal channels which would produce even beds of coarse grained, mud free sediment.

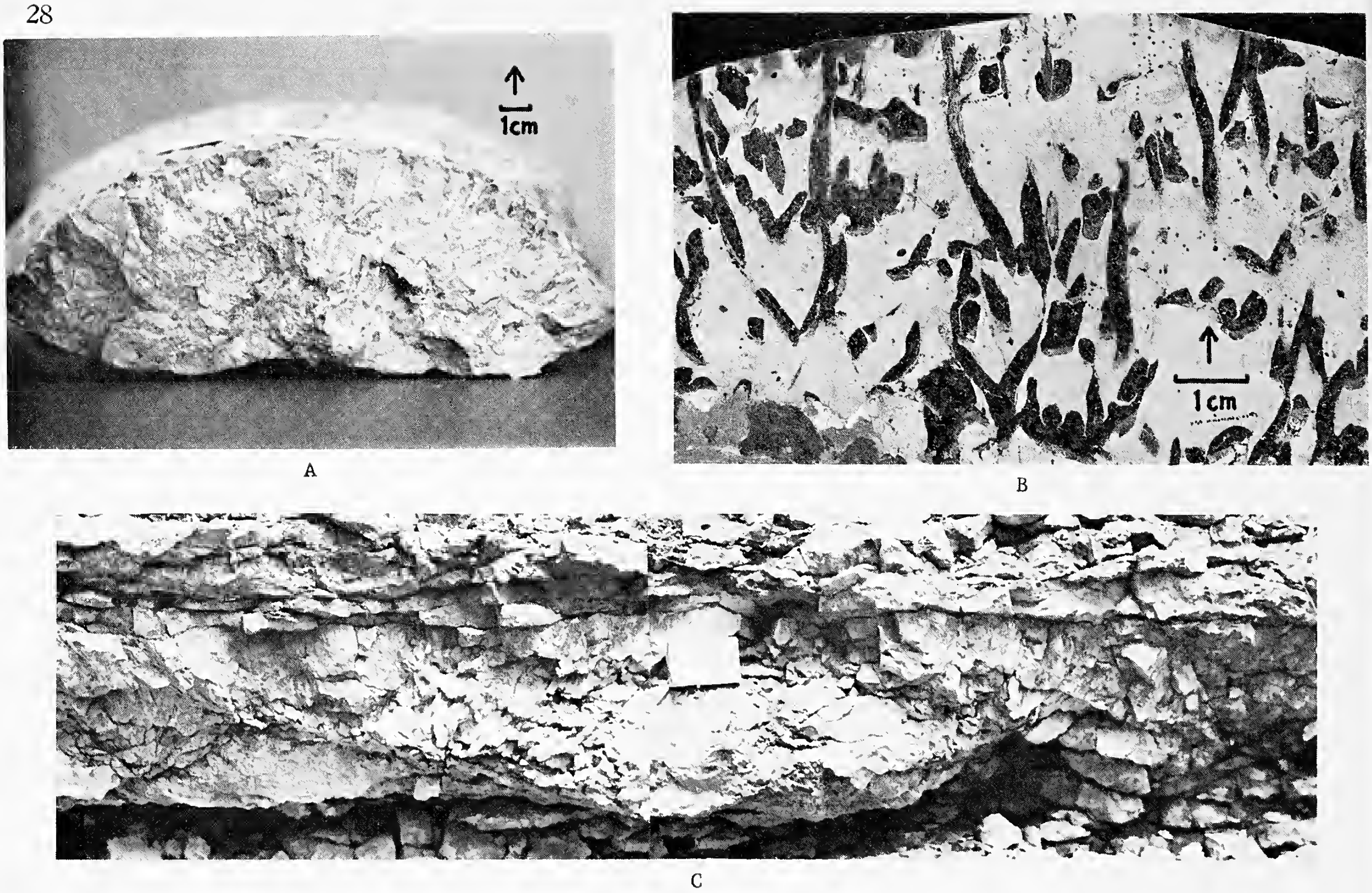
The channel biota is very diverse, and contains scattered specimens of nearly all Black River forms. Most forms are more abundant in other facies, and their fragmented and worn condition in the channel lithology suggests that most were transported from their life sites. Figure 20 summarizes the channel biota. Abundance of fossils characteristic of other facies requires an environment contiguous to those facies and in which abrasion of clasts was more efficient. A tidal channel environment fits these requirements. Only a few forms probably inhabited the channels. The small brachiopod *Zygospira,* and the cryptostome ectoproct (bryozoan) *Stictopora* are usually unabraded and the former is often articulated. These may have lived in the channels. Oncolitic blue-green algal mats must have been abundant. The oncolites preserve two types of algal filament tubes: 1) 5–15 micron diameter tubes oriented normal to the coated surface, and 2) 10–30 micron diameter tangled tubes of the algal form-genus *Girvanella.* Two types of deposit feeder burrows are abundant: 1) 5–10 mm diameter horizontal pellet filled burrows, and 2) 2–4 mm diameter randomly oriented ones which are also pellet-filled. Both types often show geopetal fillings. They are deposit feeder burrows because they are always within beds and never associated with bed surfaces, sediment at their borders has been manipulated, and the burrows wander as though produced during directed locomotion. The evidence suggests a low-gradient, meandering, tidal channel environment for the facies represented by lithology 4b.

TETRADIUM WAVE-BAFFLE AND WAVE-BAFFLE MARGIN (LITHOLOGIES 6A AND 6B, FIGURE 4)

These lithologies are characterized by the coral *Tetradium cellulosum* which is in life position in the wave-baffle lithology and transported in the baffle margin lithology. The lithologies are intimately interbedded, and intergrade laterally over short distances.

Figure 20: Abundance and surface condition of biotal elements in lithology 4b; subtidal channel environment.

Fossil form	Abund. in lith. 4b	Typical of following lithology	Surface condition in 4b	
			Abraded	Non-abraded
Trilobite debris *(Bathyurus?)*	Rare to common	3	X	
Leperditia sp.	Rare to common	3	X	X
Microscopic ostracode	Rare	6a & 4b		X
Loxoplocus sp.	Rare to common	6a & 7	X	
Bivalve fragments *(Cyrtodonta?)*	Rare	6a	X	
Zygospira recurvirostris	Rare to common	4b	X	X
Strophomena sp.	Very rare	8	X	
Stictopora labyrinthica	Rare to common	6a & 6b	X	X
Batostoma sp.	Very rare to rare	9, 10, & 11	X	
Tetradium cellulosum	Rare	6a & 6b	X	
Echinoderm fragments	Rare	9, 10, & 11 & basal Trenton	X	
Hedstroemia sp.	Rare	9	X	
Girvanella sp.	Rare to common	6a & 4b	X	X
Oncolites (tubes normal to coated surface)	Common to abundant	4b		X
Unidentified " chain of cells" microfossil	Very rare	4a & 4b		X
Large horizontal burrow	Common to abundant	4b	—	—
Small random burrows	Common	4a & 4b	—	—



A

B

C

Figure 21

Figure 21a: Closeup of weathered-out, dome-shaped *Tetradium cellulosum* supercolony from outcrop at Whetstone Creek.

Figure 21b: Negative print of peel from *T. cellulosum* supercolony from Roaring Brook, showing replacement of spindle shaped colonies by sparry calcite (black on negative print). Occasional colonies show wall stucture when filled by fine sediment (gray on print).

Figure 21c: Panoramic view of bed composed of coalesced *T. cellulosum* supercolonies which formed a mat in life. Lighter is 2 inches long. (From outcrop along Whetstone Creek).

The wave-baffle represents the restricting influence which led to variable salinities nearer shore. Such variable salinity is evidenced by presence of dolomite and evaporites, and the nondiverse and predominantly euryhaline biotas in the Black River supratidal, intertidal, and protected subtidal lithologies.

WAVE-BAFFLE (LITHOLOGY 6B, FIGURE 4)

This lithology contains *Tetradium cellulosum* in life position. Because this coral makes up a large proportion of these rocks, a brief discussion of its life habit is pertinent here. Each colony consisted of one to 10 corallites at one end of a spindle-shaped 3–10 mm by 1–5 cm corallum. Some coralla branch irregularly upward (fig. 21b) with several corallites at the upper end of each branch. A number of these upward-branching coralla are associated in dome-shaped aggregates (fig. 21a), but not all the coralla in a dome are derived from a single ancestral corallite. No satisfactory term is available for such groupings of a number of individual colonies into a higher level of organization. Although not ideal, the term supercolony will be used here.

The wave-baffle lithology contains isolated or laterally coalesced dome-shaped supercolonies of *T. cellulosum.* Sediment between coralla or branches of coralla is pelmicrite or micrite, which was trapped by baffling action of the vertical coralla. Scoffin, 1970, has discussed

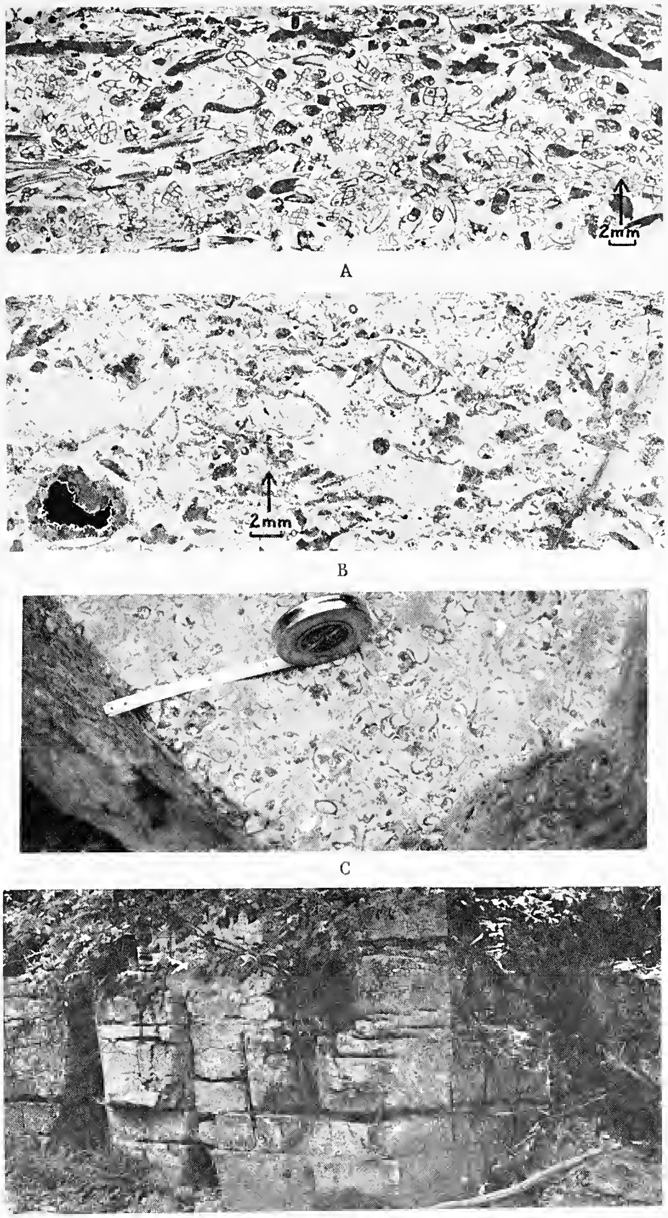


Figure 22

Figure 22a: Negative print of peel from wave-baffle margin lithology at Roaring Brook showing abundance and typical transverse cross section of unreplaced *T. cellulosum* colonies.

Figure 22b: Negative print of peel showing wide size range in wave-baffle margin lithology. Sediment includes bioclasts, pellets, and micrite.

Figure 22c: Outcrop photograph showing abundance of the pleurotomarid gastropod *Loxoplocus* in a variant of the wave-baffle margin lithology at Roaring Brook. Tape scale in inches.

Figure 22d: Outcrop photograph of level bottom subtidal facies at Roaring Brook showing typical discontinuous to absent bedding of this facies. Hammer at lower center shows scale.

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modern current and sediment baffles such as those formed by *Thalassia testudinum,* the marine grass of the Caribbean. The interstitial sediment in *Tetradium* supercolonies has a clumpy texture, and was probably deposited as silt size pellets. This size suggests baffled currents with velocities of about 10 cm/sec. (derived from Hjulstrom, 1939, fig. 1).

In the supercolonies, individual coralla were not cemented or rooted to the bottom, but were held vertical by friction between the lower part of the corallum and surrounding sediment. This weak anchoring mechanism must have been disturbed by each storm, which would uproot and transport many coralla. Abundant fallen *Tetradium* colonies in the baffle-margin lithology is evidence of this process.

Figure 21c shows a panoramic view of many coalesced supercolonies. Such continuous mats of *Tetradium* in place are not common, but separate dome-shaped supercolonies make up 10–30 percent of an outcrop of the baffle facies.

Individual vertical coralla in the supercolonies are often replaced by drusy-growth spar (fig. 21b). Partly replaced colonies show wall structure and septae of *Tetradium cellulosum.* Replacement of colonies in life position contrasts with partial replacement in fallen colonies in which walls and septae are replaced but gross structure preserved by mud or pellet fillings in the corallites (fig. 22a). Completely replaced *Tetradium* form one of several structures termed " birdseyes " by previous workers. Spar filled burrows and desiccation voids form most of the other " birdseyes " in the Black River Group.

The known biota of the baffle consists of three taxa. *T. cellulosum* was most abundant. The cryptostome ectoproct *Stictopora labyrinthica* is sometimes found attached to coralla in *Tetradium* supercolonies. *Loxoplocus (Lophospira) perangulata,* a low-spired pleurotomarid gastropod, is common.

WAVE-BAFFLE MARGIN (LITHOLOGY 6A, FIGURE 4)

This lithology is a biopelsparite containing fallen *T. cellulosum* coralla and coarse silt to fine sand size pellets with sparry calcite cement. Other fossils are also common. Grain size distribution of the sediment is bimodal; the rock is a bioclastic conglomerate with some interstitial fine sand size pellets and sparry calcite cement. Bedding is thin to medium and very uneven. This lithology is composed of debris derived from the wave-baffle.

A large part of the framework grains are abraded and were not indigenous to the baffle-margin environment. The allochems are about evenly divided between pellets and fossils (see fig. 23). The pellets, with a modal size of about 0.05 mm may be indigenous; they have a high organic content, uniformly elliptical outline, and very narrow size range (0.03 to 0.08 mm), and are probably of fecal origin. Transported skeletal debris composes 15–50 percent (average 30–40 percent) of the rock. *Tetradium* coralla are not in life position, are often broken and abraded, and are frequently filled with micrite or small pellets unlike the surrounding matrix. Some other fossils are usually abraded, in particular echinoderm fragments and pieces of *Hedstroemia*, a codiacean alga.

Certain other components of the lithology probably represent faunal elements indigenous to the environment of deposition. The most abundant are *Cyrtodonta* sp., a byssate semi-infaunal bivalve (pelecypod), and ramose colonies of *Stictopora labyrinthica*, a cryptostome ectoproct. Both occur commonly in life position. These were probably suspension feeders; their abundance suggests a stable substrate with sufficient water movement to supply abundant suspended food. *Loxoplocus perangulata* is more abundant in this facies than in any other (except as concentrations in related lithology 7), and the depositional environment of this facies probably was its habitat. *?Plectonotus* sp. (small belerophontid gastropod), *Bathyurus extans* and *Bumastus* sp. (trilobites), *Leperditia* sp. (ostracode), *Strophomena* sp., and a microscopic unidentified ostracode are all rare but seldom broken or abraded. These probably lived in the baffle-margin environment. Juvenile specimens of *Actinoceras ruedemanni* and *Michelinoceras* sp. (cephalopods) are rare to common.

Algal oncolites are rare to common and are distinct from those of more shoreward facies. Coatings in the baffle-margin facies preserve the tangled tubes of the algal form-genus *Girvanella* with tubes parallel to the coated surface. Other oncolites in the group have tubes normal to the coated surface. Unbraded coatings in this facies indicate a subtidal environment of deposition.

The volume of fossils in the baffle-margin lithology ranges from 10 to 47 percent but is nearly always greater than 25 percent. Burrows are rare. The overlapping fallen *Tetradium* coralla produced a felted texture which probably excluded burrowing infauna.

Two other Black River Group facies are minor variants of the baffle-margin facies. Lithologies 7 and 8 (see fig. 4) are similar to the baffle-margin lithology, but differ by having higher relative abundances of certain fossils. Lithology 7 has very abundant *Loxoplocus* and much less abundant fallen *Tetradium*, but *Cyrtodonta* is as abundant as in the normal baffle-margin facies and often is in growth position. This lithology also contains many fossils which are characteristic of the subtidal level bottom facies (lithology 9, discussed below), a more seaward environment. Lithology 7 was probably deposited on the seaward margin of the wave-

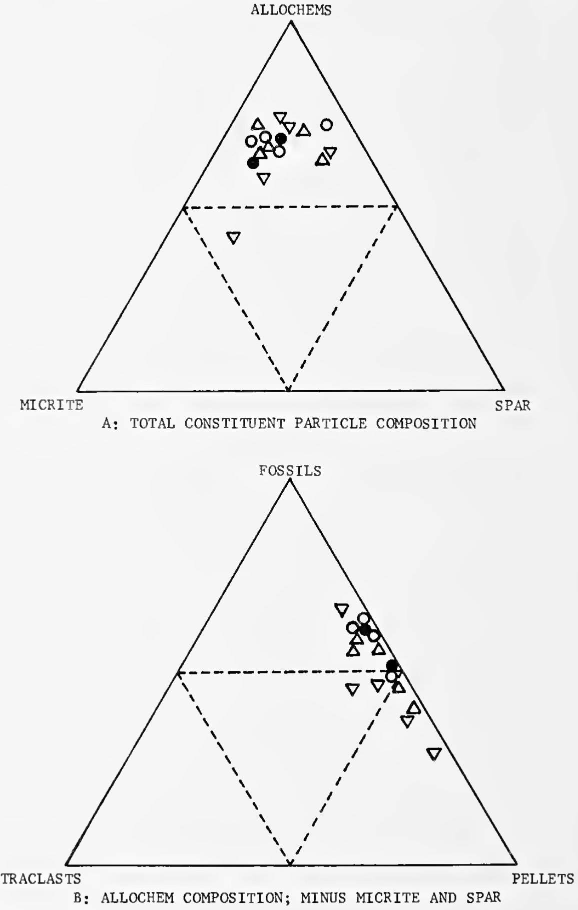


Figure 23: Constituent particle composition of selected samples from lithology 6a, the wave-baffle margin facies. Symbols stand for samples from the following stratigraphic sections: Roaring Brook open circles, Whetstone Creek up-pointing triangle, House Creek down-pointing triangle, Mill Creek closed circle.

baffle in local depressions where *Loxoplocus* shells were concentrated.

The second minor variant of the baffle-margin facies is lithology 8, characterized by abundant *Strophomena* and rare fallen *Tetradium.* Abraded echinoderm fragments make up about 10 percent of this facies and other abraded fossils characteristic of the level bottom subtidal environment are rare. Presence of *Tetradium* suggests proximity to the wave-baffle, and this lithology probably also represents the seaward margin of that environment. The seaward position also is suggested by rare abraded fragments of *Prasopora,* a genus usually restricted to the overlying marine Trenton group.

SUBTIDAL, LEVEL BOTTOM (LITHOLOGY 9, FIGURE 4)

This normal marine facies corresponds to the Chaumont Formation. It is distinct from other facies of the group, but was related to them as part of a contemporaneous facies pattern. This relationship is suggested by: 1) sharing of transported fossils, 2) vertical gradations between facies, 3) mixtures with other facies, and 4) consideration of logical, predicted facies changes.

This facies is thoroughly mottled and stratification is virtually absent. Bedding characteristics are shown in figure 22d. The mottles are 2–4 mm diameter horizontal burrows which are surrounded by an irregular opaque-rich halo 3–10 mm thick. Figure 24a shows the churned nature of the sediment and abundant burrows. Deposit feeding organisms probably made the burrows as evidenced by: 1) very irregular borders, indicating manipulation of sediment, 2) randomly wandering horizontal paths of the burrows, and 3) confinement of burrows to the body of the sediment and lack of association with former sediment-water surfaces. These features result in a sediment in which the relative amount of biogenic reworking as opposed to physical reworking is much greater than in any other Black River facies. Such thorough biogenic reworking characterizes modern level bottom subtidal environments (see Moore and Scruton, 1957, and especially the carbonate " adjacent marine " environment discussed by Shinn, *et al.,* 1969).

The abundance and diversity of fossils in this facies exceeds that of other Black River facies. Some fossils are transported from other facies of the group and indicate contiguous environmental relationships. Others are often found in life position, or for other reasons are thought to be indigenous to the level bottom environment. Figure 25 summarizes the biota and indicates those elements which were indigenous. The major groups of fossils are related to Recent taxa which usually require constant, normal marine salinities: echinoderms, codiacian algae, ectoprocts, corals, cephalopods, and brachiopods. Volume abundance of fossils ranges from 4 to 53 percent, but is usually between 10 and 30 percent.

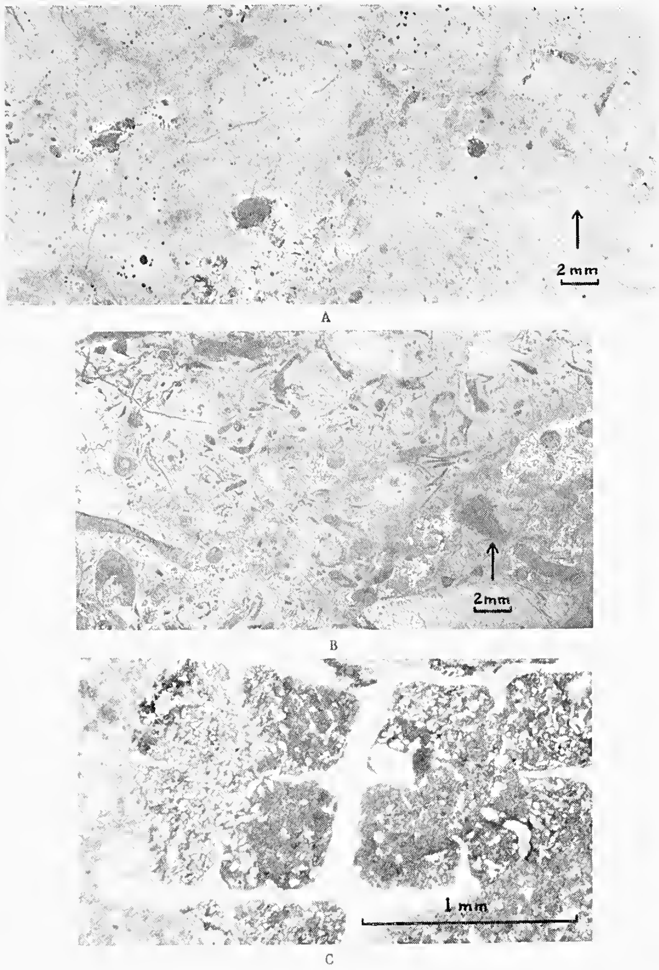


Figure 24

Figure 24a: Negative print of a peel from level bottom subtidal lithology at Whetstone Creek showing churned nature of sediment and abundant horizontal burrows in that facies.

Figure 24b: Negative print of thin section of level bottom subtidal facies showing concentration of *Hedstroemia* (codiacean alga) debris.

Figure 24c: Negative print of an enlarged area of a level bottom subtidal facies thin section showing *Girvanella* tubes in an algal coating on an abraded *Tetradium* fragment.

Biotic group by decreasing order of abundance	Biotic element by decreasing abundance in biotic group	In life position in lith. 9	Surface condition in lith. 9	Typical of following lithology	Not in life position but indigenous to lith. 9
Echinoderm fragments	Unidentified irreg. fragments		Abraded	Basal Trenton	
	Pelmatozoan columnals		Abraded	Basal Trenton	
Calcareous algae	*Hedstroemia* (codiacean) plates & stem segments		Unabraded	9	X
	Vermiporella (dasyclad)		Unabraded	9	X
	Girvanella (blue-green?)		?	9, 4b, 6a	?
	Solenopora (red)		?	9	?
Ectoproct fragments	*Eridotrypa* sp. Ramose Trepostomata		Abraded?	Basal Trenton?	?
	Pachydictya Ramose Cryptostomata		Abraded	Basal Trenton	
* Stromatoporoid colonies	*Stromatocerium rugosum*	X	Unabraded	9	
* Rugose corals	*Lambeophyllum profundum*	X	Unabraded	9	
* Tabulate corals	*Foerstephyllum halli*	X	Unabraded	9	
Actinoceratoid nautiloids	*Actinoceras ruedemanni*		Abraded & unabraded	9	X
	A. tenuifilum		Abraded & unabraded	9	
Endoceratoid	*Endoceras* sp.		Abraded & unabraded		X
ALL GROUPS BELOW THIS LINE OCCUR ONLY RARELY					
Orthoceratoid nautiloids	*Michelinoceras* sp.		Abraded	6a, 7, 9	
Strophomenid brachiopods	*Strophomena* sp.	X?	Unabraded	8, 9	
	Rafinesquina sp.	?	Unabraded	9	
Orthid brachiopods	*Dalmanella rogata*	X?	Unabraded	9 (near boundary with basal Trenton)	
Rhynchonellid brachiopods	*Rhynchotrema* sp.	?	Abraded	Basal Trenton	
Tetradidae (coral)	*Tetradium*		Abraded	6a, 6b	
Ostracoda	Unidentified microscopic form		Unabraded but disarticulated	6a, 7, 9	
Various extremely rare elements	*Prasopora* (Trepostome)		Abraded	Basal Trenton	
	Leperditia sp. (ostracode)		Abraded & disarticulated	3, 4b, 6a, 7, 8	
	Molluscan debris		Abraded	?	
	Maclurites sp.		?	9	

Figure 25: Summary of known biotic elements of lithology 9, the normal marine, level bottom facies of the Black River Group. Taxa marked * are coequal in abundance.

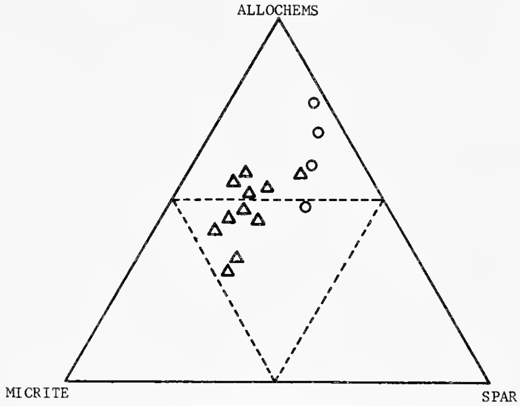
Constituent particle composition of selected samples of this lithology is shown in figure 26. The unusual volume of sparry calcite in these fine-grained rocks occurs mainly as burrow fillings and partial replacements of halos around burrows. Rare lenses of pelsparite and biosparite do, however, occur. The micrite has a clumpy texture, and may have been deposited as pellets. Distinct pellets and micrite clumps range from 0.02–0.09 mm in median diameter, with a strong mode at 0.03–0.04 mm. The size range in any one field of view is narrow, usually ±0.007 mm, and a distinct break occurs between pellet and intraclast size distributions. From this evidence, pellets and " micrite " originally deposited as pellets are inferred to be of fecal origin. The deposited material may have been pellets, or alternatively might have been micrite which was later pelleted by burrowing deposit feeders.

Bioclasts " float " in the basic mixture of pellets (25 ± vol. percent) and clumpy micrite (35 ± vol. percent), and range in size from fine to coarse sand. The larger size may be due to an abundance of porous echinoderm fragments, possibly hydrodynamically equivalent to silt size pellets. Pebble-size *Hedstroemia* plates and stem segments occur as concentrations, probably where they fell after death of the plant. Algal coatings on bioclasts, though not abundant, are ubiquitous in this facies, and usually contain tangled filament tubes of *Girvanella* (fig. 24c).

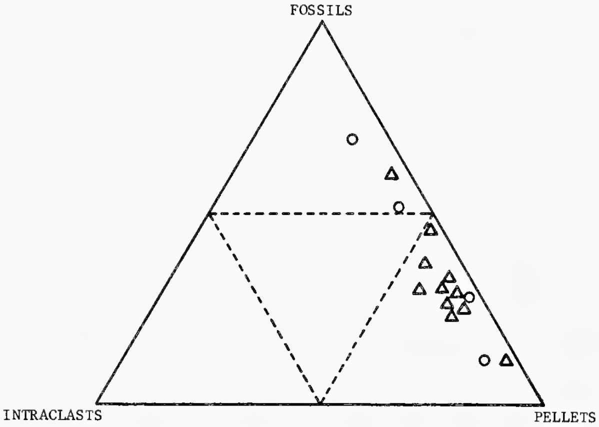
The fine texture, presence of oncolites, normal marine character of the biota, and thorough biogenic reworking suggest a relatively quiet subtidal, normal marine environment. Compensation depth is the deepest point at which photosynthesis can balance respiration, and is the deepest a plant can permanently live in the sea. In clear, tropical waters this depth may be 80 meters, but in more turbid near shore areas it is as little as 10 meters (Clarke, 1933). The fine grain size of Black River level bottom sediment suggests a relatively turbid environment with a shallow compensation depth. The abundance of algae indicates deposition above that depth in relatively shallow water.

Lithology 10 (fig. 4) is similar to the level bottom lithology, but contains clumps of *Dalmanella rogata* (brachiopod) which may be in life position. Lithology 11 (fig. 4) is like basal Trenton Group bioclastic limestones except for more abundant *D. rogata.*

As one approaches the top of level bottom lithology in all the sections (top of Chaumont Formation), samples contain more transported skeletal debris which characterize the overlying basal Trenton Group. These fossils are: 1) echinoderm debris, especially pelmatozoan columnals, 2) trepostome ectoproct debris, especially *Prasopora* fragments and an unidentified encrusting trepostome, and 3) certain brachiopods, especially *Doleroides gibbosus,* and *Rhynchotrema* sp.



A: TOTAL CONSTITUENT PARTICLE COMPOSITION



B: ALLOCHEM COMPOSITION; MINUS MICRITE AND SPAR

Figure 26: Constituent particle composition of selected samples of lithology 9, the normal marine, level bottom facies. Symbols stand for samples from the following stratigraphic sections: Roaring Brook open circle, Whetstone Creek up-pointing triangle, House Creek down-pointing triangle, Mill Creek closed circle.

Contemporaneity of Facies

The contemporaneity of Black River facies is suggested by the following field observations:

1) lateral gradations or interfingerings
2) vertical gradations
3) intermixtures of facies
4) abraded particles from one facies in another (especially fossils).

Further, an application of Walther's " Law " also suggests contemporaneity. Walther's " Law " has frequently been misstated, and a direct quote from the original is, therefore, included here.

> " The contemporaneous areas of deposition continuously change location on the earth's surface, so that they either overlie former areas of erosion or former areas where another sediment type was laid down. . . . The horizontal migration of facies is responsible for differences in the rocks superimposed vertically in a given section."

Walther, 1894, p. 620–621, translation by present author.

Thus those facies which represent laterally contiguous environments will be in vertical contact most frequently. Figure 27 is a plot of frequency of contact between facies of the Black River Group. For many facies, the total number of contacts is so small that no conclusions are suggested (e.g., lithologies 7, 10, 11). For other facies, the contiguous relationships are indicated quite strongly by the data. Basal sandstone (lithology 1) is always in contact with the Precambrian or supratidal dolostone (lithology 2). The dolostones are always in contact with intertidal limestone (lithology 3) or protected subtidal limestone (lithology 4). Intertidal limestone is nearly always in contact with protected subtidal limestone (lithology 4). Other contact relationships and additional lines of evidence bearing on contemporaneous facies relationships in the Black River Group are summarized in figure 28.

Thus the Black River Group contains a facies mosaic closely related to the strand line and represents an onshore to offshore sequence of environments as follows:

	Lithology Code (see figure 4)											
Lithology Code (see figure 4)	1	2	3	4	5	6a	6b	7	8	9	10	11
1												
3	5											
3		14										
4		12	73									
5			16	5								
6a		3	25	22	2							
6b		1		1		16						
7			3	3		1						
8			4	1		5	1					
9			1	1		5	1					
10										4		
11											2	
Trenton Group											1	2

Figure 27: Contact frequency between Black River lithologies.

EVIDENCE-BEARING ON LATERAL RELATIONSHIPS

Lithology and environment of deposition	Most frequent contact with lithology (see figure 4)	Lateral gradations with lithology—(and locations)	Abraded fossils from lithology—	Mixtures common with lithology—	Verticle gradations common with lithology—
Precambrian basement	1	....	....	....	....
1) supratidal sands	Precamb. or 2	2 Mill Creek, Unit 6	2 & 3	2 Roaring Brk., & Mill Crk.	2
2) supratidal dolostones	1, 3, or 4	....	3	1 & 3	1 & 3
3) intertidal limestones	4, rarely 5 or 6a	4 Port Leyden Q., Units 8 & 9, and Whetstone Crk., Unit 14 5 Whetstone Crk., Unit 29–31	4 & 6a	2, 4, & 5	2, 4, & 5
4) shallow subtidal quiet water & channel	3 or 6a	3 Port Leyden Q., Units 8 & 9, and Whetstone Crk., Unit 14	3, 6a, 6b, & 7	3, rarely 6a	3 & 6a
5) intertidal oolite	3	3 Whetstone Crk., Units 29–3	3, 4, & 6a	3	3
6a) fallen *Tetradium* wave-baffle margin	3 or 4	6b Turin Rd., Unit 40, Roaring Brk., Unit 53, Whetstone Crk., Unit 46	6b, rarely 9	6b, rarely 4	6b & 4
6b) *Tetradium* wave-baffle	6a	6a (see above)	....	6b	6b
7) *Loxoplocus* subtidal limestones	4?	....	6b, 9, rarely Trenton Grp.	6a, rarely 9	6a, rarely 9
8) *Strophomena* subtidal limestones	6a or 3	....	6a or 6b & 9	6a	6a, rarely 4
9) coralgal level-bottom marine limestones	6a	10 Mill Crk., Unit 66, House Crk., Unit 37	Trenton Grp., rarely 6a & 7	10	Rarely 6a
10) lith. 9 with *Dalmanella*	9	9 (see above)	9 & Trenton Grp.	9	9
11) brachiopod, bryozoan, crinoid limestone	10	....	9 & Trenton Grp.	Trenton Grp. limestones	9
Basal Trenton Grp. limestones	10	....	?	11	....

Figure 28: Summary of evidence bearing upon lateral contemporaneous facies relationships within the Black River Group. Unit numbers refer to measured sections on open file at N.Y. State Geological Survey offices in Albany, N.Y.

supratidal sand flats, supratidal dolomite mudflats, intertidal limestone mudflats, protected subtidal channels and ponds, inshore wave-baffle margin, *Tetradium* wave-baffle, offshore wave-baffle margin, and an outer subtidal, level bottom environment. Such a listing places these environments in their simplest possible array. The actual relative geographic locations of the environments at any time probably was controlled by an irregular bathymetry as in Recent carbonate environments.

Summary of Depositional Environments

Figure 29 shows the relation of the environments of deposition to mean sea level and some of the properties of the sediment types. Such a diagram is only representative of the actual pattern that probably was much more complex geographically. Figure 30 shows a simplified stratigraphy of environmental units in the outcrop belt.

Several general conclusions may be drawn from this study. First, environmental analysis confirms the interpretation of stratigraphic units in the group as facies of one another rather than independent rock bodies. Second, the entire pattern is related to the position of the tidal zone during deposition. Third, the facies array represents a transgressive depositional pattern with many internal, transgressive-regressive cycles. Fourth, the stratigraphic nomenclature and geometric interpretation proposed earlier in this study are supported by facies analysis. Fifth, although many strand line deposits are rarely preserved, the Black River Group represents very near shore deposition which has left a well preserved record. Finally, these near shore carbonates have analogs throughout the geologic record, for example, Recent (Purdy, 1963; Illing, *et al.*, 1965; and Shinn, *et al.*, 1969), Devonian (Laporte, 1967). The Black River and Devonian examples are compared by Walker and Laporte, 1970.

One of the purposes of this detailed treatment of environments was to allow inference of ecologically important environmental parameters. The reader is referred to Walker, 1972, for a study of the Black River communities. For that study it is important to know the relative values of these parameters. They are summarized with the data from which they are derived in figure 31.

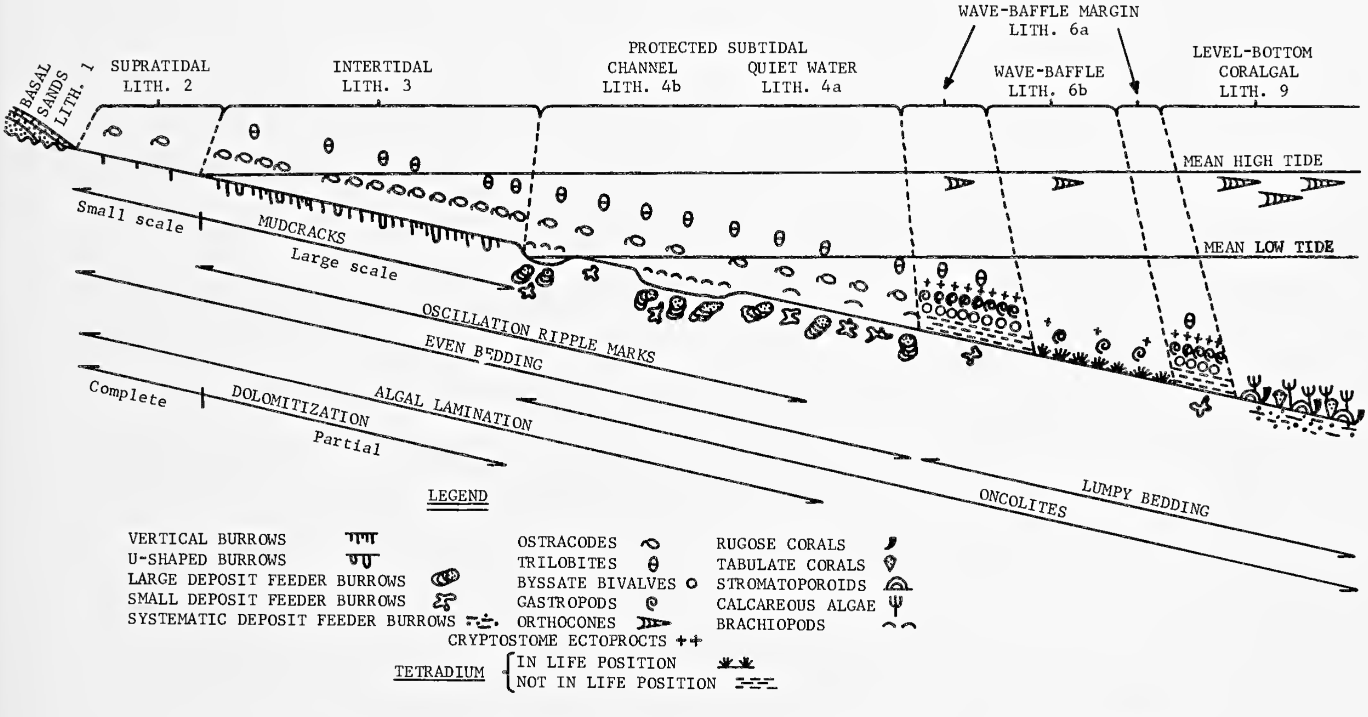


Figure 29: Summary of the major depositional environments of the Middle Ordovician Black River Group of New York State.

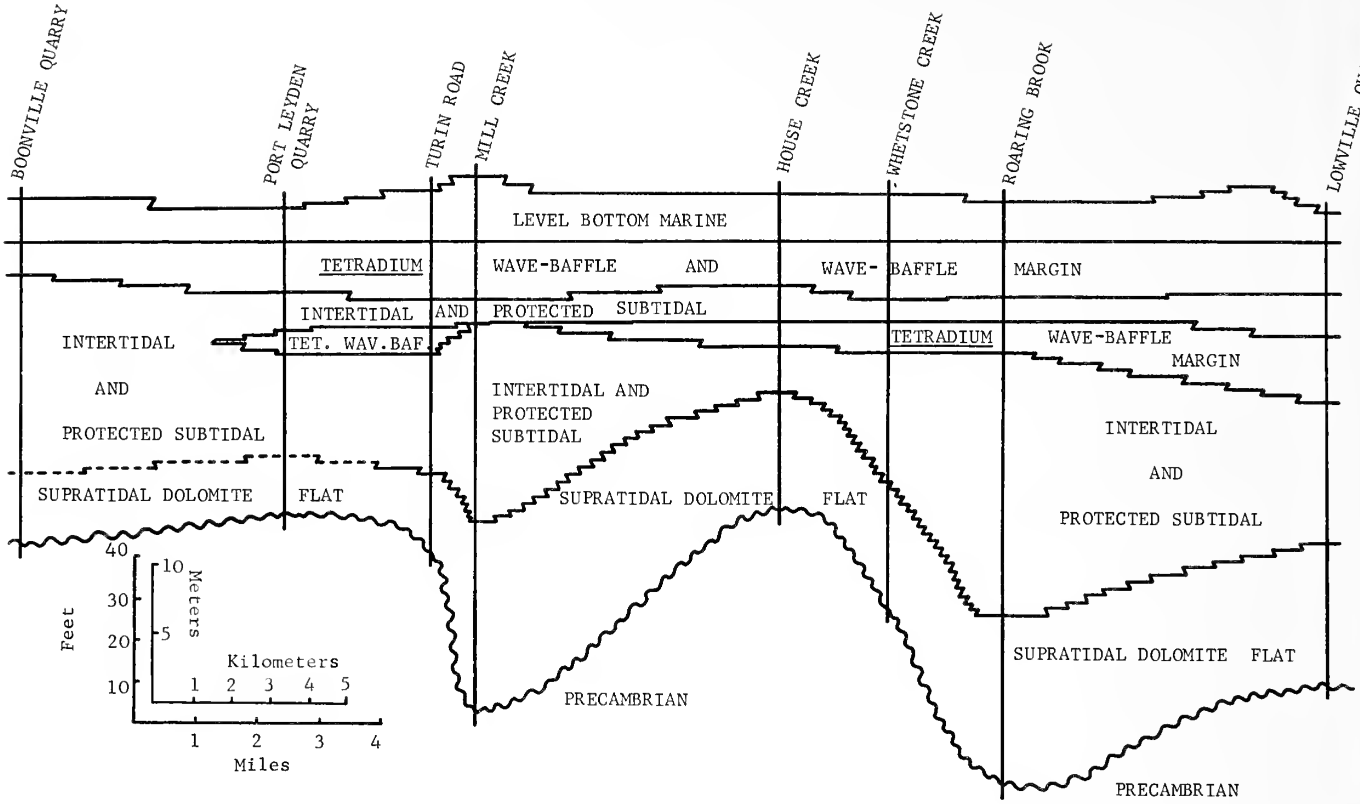


Figure 30. Simplified stratigraphy of environmental units of the Black River Group in the line of outcrop.

	ECOLOGICALLY IMPORTANT PARAMETERS										
Lithology code (see figure 29)	Substrate grain size (Wentworth mode in mm)	Mud (less than 4 microns) content of sediment	Substrate mobility	Original porosity (larger than few microns)	Organic content of sediment	Probable water turbidity	Current velocities and/or turbulence	Frequency and length of subaerial exposure	Rate of water exchange	Salinity range	Temperature range
1	0.2–1.0	Nil to 50%	Low	Mod. to high	Nil	——	——	Nearly continuous	——	——	——
2	0.015–0.05	Mod. to very high	Very low	Low	Low	High	Low	Frequent & very long	Low to mod.	Very high	Very high
3	0.015–0.05	Mod. to very high	Very low	Low	Mod. to low	Low	Mod. to low	Frequent & long	High	Mod. to high	Mod. to high
4a	0.002	Very high	Low	Very low	Very high	Moderate	Low	Infrequent & short	Low	Moderate	Low
4b	0.04–0.4	Low	Mod. to high	High	Mod. to low	Low	High	Infrequent & short	High	Mod. to high	Low
5	0.20	Very low to low	High	High	Low	Low	Mod. to high	Frequent & short	Mod. to high	Mod. to high	Mod. to high
6a	Bimodal 0.05 & 1.5	Low to mod.	Moderate	Moderate	High	Moderate	Moderate	Very rarely if ever	High	Low	Low
6b	0.05	Mod. to high	Low	Low	Moderate	Moderate	Mod. to high	Very rarely if ever	Very high	Low	Low
7	Bimodal 0.5 & 1 cm.	Low	Low to mod.	High	Moderate	Low	Moderate?	Never	High	Low	Low
9	Bimodal 0.04 & 0.25	Low to mod.	Low to mod.	Low	High	Moderate	Mod. to high	Never	Very high	Very low	Very low

FIGURE 31: Inferred ecologically important parameters of the depositional environments of the Black River Group.

References

American Commission on Stratigraphic Nomenclature
1960. American code of stratigraphic nomenclature. Amer. Assoc. Petrol. Geol. Bull. 45:645–655.

Anderson, J. J., and Everett, J. R.
1965. Mudcrack formation studied by time lapse photography (abst.). *In* Abstracts for 1964. Geol. Soc. Amer. Spec. Pap. 82:4–5.

Bader, R. G.
1954. The role of organic matter in determining the distribution of pelecypods in marine sediments. J. Mar. Res. 13:32–47.

Ball, M. M.
1967. Carbonate sand bodies of Florida and the Bahamas. J. Sed. Petrol. 37:556–591.

Barnes, C. R.
1967. Stratigraphy and sedimentary environments of some Wilderness (Ordovician) limestones, Ottawa Valley, Ontario. Can. J. Earth Sci. 4:209–244.

————
1968. Reply to discussion G. M. Kay of: Stratigraphy and sedimentary environments of some Wilderness limestones, Ottawa Valley, Ontario, by C. R. Barnes. Can. J. Earth Sci. 5:169–172.

Bathurst, R. G. C.
1958. Diagenetic fabrics in some British Dinantian limestones. Liverpool Manchester Geol. Soc. J. 2:11–36.

Clarke, G. L.
1933. Diurnal migration of plankton and its correlation with changes in submarine irradiation. Biol. Bull. 65:402–436.

Clarke, J. M., and Schuchert, C.
1899. Nomenclature of the New York Series of geologic formations. Sci., n.s. 10:874–878.

Clarke, T. H., and Stearn, C. W.
1968. Geological evolution of North America. 2d ed. The Ronald Press, N.Y., 570 p.

Conrad, T.A.
1837. First annual report on the geological survey of the third district of the State of New York. N.Y. State Mus., 1st Ann. Rept.:155–186.

————
1839. Second annual report on the paleontological department of the survey. N.Y. State Mus., 3d Ann. Rept.:57–66.

Cooper, G. A.
1956. Chazyan and related brachiopods. Smithsonian Misc. Coll. 127, 1024 p.

Cushing, H. P.
1908. Lower portion of the Paleozoic section in northwestern New York. Geol. Soc. Amer. Bull. 19:155–176.

————**, Ruedemann, R., Fairchild, H. L., and Smyth, C. H.**
1910. Geology of the Thousand Islands region. N.Y. State Mus. Bull. 145; 194 p.

Deffeyes, K. S., Lucia, F. J., and Weyl, P. K.
1965. Dolomitization of Recent and Plio-Pleistocene sediments by marine evaporite waters on Bonaire, Netherlands Antilles. *In* Dolomitization and Limestone Diagenesis. Soc. Econ. Paleontol. and Min., Spec. Pub. 13:71–88.

Evans, Graham
1965. Intertidal flat sediments and their environments of deposition in the wash. Geol. Soc. London, Quart. J. 121:209–245.

Fisher, D. W.
1962. Correlation of the Ordovician rocks of New York State. N.Y. State Mus. Sci. Serv., Map and Chart Ser. 3.

Folk, R. L.
1959. Practical petrographic classification of limestones. Amer. Assoc. Petrol. Geol. Bull. 43:1–38.

———

1962. Spectral subdivision of limestone types. *In* Classification of Carbonate Rocks. ed. Ham, W. Amer. Assoc. Petrol. Geol. Mem. 1:62–84.

Gebelein, C. D.

1967. Origin and growth rate of subtidal algal stromatolites, Bermuda (abst.). Geol. Soc. Amer. Ann. Meeting, New Orleans: 75–76.

Ginsburg, R. N.

1957. Early diagenesis and lithification of shallow-water carbonate sediments in South Florida. *In* Regional Aspects Carbonate Deposition. Soc. Econ. Paleontol. and Min., Spec. Pub. 5:80–100.

———, Isham, L. B., Bein, S. J., and Kuperburg, J.

1954. Laminated algal sediments of South Florida and their recognition in the fossil record. Univ. Miami Mar. Lab. unpub. Rept. 54–21:1–33.

Hjulstrom, F.

1939. Transportation of detritus by moving water. *In* Recent Marine Sediments. ed. Trask, P. D. Soc. Econ. Paleontol. and Min., Spec. Pub. 4:5–31.

Illing, L. V.

1954. Bahaman calcareous sands. Amer. Assoc. Petrol. Geol. Bull. 38:1–95.

———, Wells, A. J., and Taylor, J. C. M.

1965. Penecontemporary dolomite in the Persian Gulf. *In* Dolomitization and Limestone Diagenesis. Soc. Econ. Paleontol. and Min., Spec. Pub. 13: 89–111.

Johnsen, J. H.

1971. The limestones of Jefferson County, New York. N.Y. State Mus. and Sci. Serv., Map and Chart Ser. 13.

Johnson, J. H.

1946. Lime-secreting algae from the Pennsylvanian and Permian of Kansas. Geol. Soc. Amer. Bull. 57:1087–1120.

Kay, Marshall

1929. Stratigraphy of the Decorah Formation. J. Geol. 37:639–671.

———

1937. Stratigraphy of the Trenton Group. Geol. Soc. Amer. Bull. 48:233–302.

———

1960. Classification of the Ordovician System of North America: Ordovician and Silurian stratigraphy and correlations. 21st Inter. Geol. Cong., Copenhagen, Denmark: 28–32.

———

1968. Discussion: Stratigraphy and sedimentary environments of some Wilderness (Ordovician) limestones, Ottawa Valley, Ontario. by C. R. Barnes. Can. J. Earth Sci. 5:166–169.

Laporte, L. F.

1967. Carbonate deposition near mean sea level and resultant facies mosaic; Manlius Formation (Lower Devonian) of New York State. Amer. Assoc. Petrol. Geol. Bull. 51:73–101.

Logan, B. W.

1961. *Cryptozoon* and associated stromatolites from the Recent, Shark Bay, Western Australia. J. Geol. 69:517–533.

———, Rezak, R., and Ginsburg, R. N.

1964. Classification and environmental significance of algal stromatolites. J. Geol. 72:68–83.

McKee, E. D.

1957. Primary structures in some Recent sediments. Amer. Assoc. Petrol. Geol. Bull. 41:1704–1747.

Monty, C.

1965. Recent algal stromatolites in the windward lagoon, Andros Island, Bahamas. Ann. Soc. Geologique Belgique. 88:Bull.6:269–276.

Moore, D. G., and Scruton, P. C.

1957. Minor internal structures of some Recent unconsolidated sediments (Gulf of Mexico). Amer. Assoc. Petrol. Geol. Bull. 41:2723–2751.

Park, W. C., and Schot, E. H.

1968. Stylolites: their nature and origin. J. Sed. Petrol. 38:175–191.

Potter, P. E., and Pettijohn, F. J.

1963. Paleocurrents and basin analysis: Springer-Verlag, Berlin, 296 p.

Powers, M. C.

1953. A new roundness scale for sedimentary particles. J. Sed. Petrol. 23:117–119.

Purdy, E. G.

1963. Recent calcium carbonate facies of the Great Bahama Bank. 1. petrography and reaction groups, and 2. sedimentary facies. J. Geol. 71: 334–335, 472–497.

Scoffin, T. P.
1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. J. Sed. Petrol. 40:249–273.

Shinn, E. A.
1964. Recent dolomite, Sugarloaf Key. *In* South Florida Carbonate Sediments. Geol. Soc. Amer. Field Guide 1, Miami Ann. Meeting:62–67.

———
1968. Practical significance of birdseye structures in carbonate rocks. J. Sed. Petrol. 38:215–223.

———, Ginsburg, R. N., and Lloyd, R. M.
1965. Recent supratidal dolomite from Andros Island. *In* Dolomitization and Limestone Diagenesis. Soc. Econ. Paleontol. and Min. Spec. Pub. 13:112–123.

———, Lloyd, R. M., and Ginsburg, R. N.
1969. Anatomy of a modern carbonate tidal-flat, Andros Island, Bahamas. J. Sed. Petrol. 39:1202–1228.

Swartz, F. M.
1948. Trenton and sub-Trenton of outcrop areas in New York, Pennsylvania, and Maryland. Amer. Assoc. Petrol. Geol. Bull. 32:1493–1595.

Textoris, D. A.
1968. Petrology of supratidal, intertidal, and shallow subtidal carbonates, Black River Group, Middle Ordovician, New York, U.S.A. 23d Inter. Geol. Cong. 8:227–248.

Twenhofel, W. H., & others
1954. Correlation of the Ordovician formations of North America. Geol. Soc. Amer. Bull. 65:247–298.

Walker, K. R.
1972. Community ecology of the Middle Ordovician Black River Group of New York State. Geol. Soc. Amer. Bull. 83.

———, and Laporte, L. F.
1970. Congruent fossil communities from Ordovician and Devonian carbonates of New York. J. Paleontol. 44:928–944.

Walther, Johannes
1894. Einleitung in die Geologie als historische Wissenschaft. Part 3. Lithogenesis der Gegenwart. Fischer Verlag, Jena, 800 p.

Winder, C. G.
1960. Paleoecological interpretation of Middle Ordovician stratigraphy in southern Ontario, Canada. Ordovician and Silurian stratigraphy and correlations. Inter. Geol. Cong., Copenhagen, Denmark 21:18–27.

Young, F. P.
1943. Black River stratigraphy and faunas. Parts I, II. Amer. J. Sci. 241:141–166, 209–240.

Appendix I

This is a listing of various measurement conventions used throughout the preceding discussion. Most of these conventions are pragmatic in nature in that they seem to separate natural groupings of the measurements taken.

Bed thickness conventions	*Thickness*
Very thick bedded	more than 1 meter
Thick bedded	30 cm to 1 m
Medium bedded	8 cm to 30 cm
Thin bedded	2.5 cm to 8 cm
Thick laminated	1.25 cm to 2.5 cm
Medium laminated	0.75 cm to 1.25 cm
Thin laminated	3 mm to 7.5 mm
Very thin laminated	less than 3 mm

Sediment grain size conventions	*Description*
Coarse grained	Grains readily identifiable with unaided eye (generally more than 1 mm).
Medium grained	Individual grains visible but not identifiable with unaided eye (generally about ¼ to 1 mm).
Fine grained	Grains not visible with unaided eye, but visible with hand lens (about 1/10 to ¼ mm).
Very fine grained	Grains not clearly visible, even with hand lens (less than about 1/10 mm).

Stylolite scale and continuity	*Description*
Large scale	More than 12 mm peak to peak
Medium scale	3 mm to 12 mm peak to peak
Small scale	Less than 3 mm peak to peak
Continuous	Traceable more than 30 cm along outcrop
Moderately continuous	Traceable for 15 to 30 cm along outcrop
Discontinuous	Traceable less than 15 cm along outcrop

Mudcrack scale conventions	*Width of Polygons*
Large scale	More than 20 cm
Medium scale	5 cm to 20 cm
Small scale	Less than 5 cm

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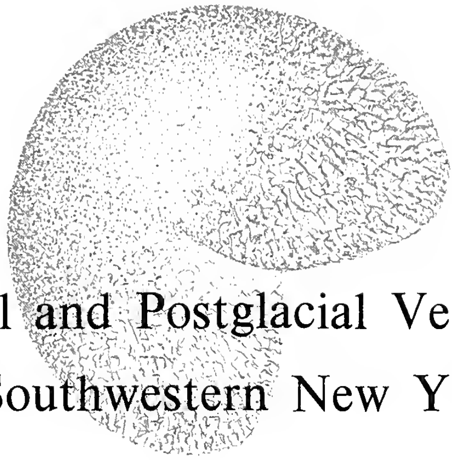

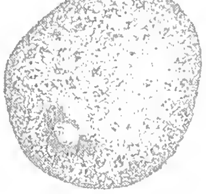

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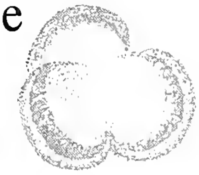

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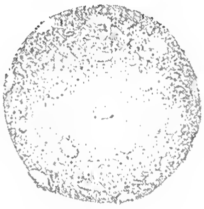

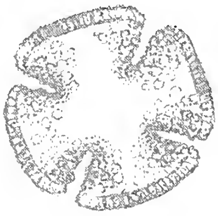

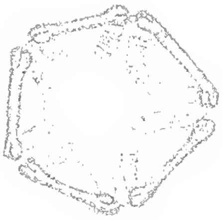

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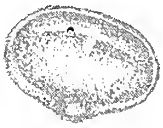

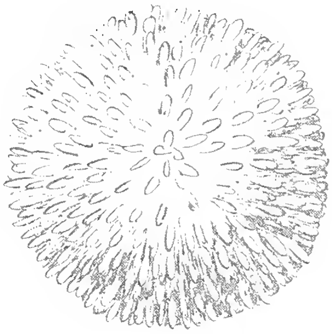

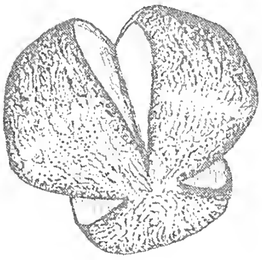

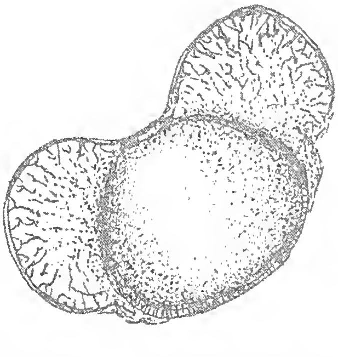

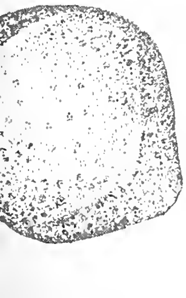

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Late-glacial and Postglacial Vegetation Change in Southwestern New York State

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Temporary Botanist, Biological Survey

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Late-glacial and Postglacial Vegetation Change in Southwestern New York State[1, 2]

Norton G. Miller[3]

ABSTRACT

Pollen stratigraphy in sediments from four small lake basins was determined and used as evidence for vegetation change on the Allegheny Plateau of southwestern New York State. The sites studied are within 35 mi of the unglaciated Salamanca reentrant and are on an important migration route for species spreading northward following Late Wisconsin glaciations.

Forests of the hemlock-northern hardwoods type occur in southwestern New York at the present time. Point-quarter sampling of upland stands shows *Acer saccharum, Fagus grandifolia,* and *Tsuga canadensis* to be the leading species in order of decreasing importance values. An analysis of bearing-trees recorded in the original lot survey notes for the areas around three of the sites studied palynologically revealed the precolonial forests to be dominated by the same leading species, except *Fagus* was first in importance and *Acer* second. R values were calculated using the precolonial data and a recent survey of existing timber resources in the region.

The basins studied include the Genesee Valley Peat Works in central Allegany County — on Olean drift (pre-Cary), Allenberg Bog in east-central Cattaraugus County — near the Kent terminal moraine (pre-Cary), and Houghton and Protection bogs in southeastern Erie County — on Valley Heads drift (= Port Huron?). The profiles obtained were divided into A, B, and C zones following the Deevey classification. In addition, a T zone characterized by high nonarboreal pollen (NAP) percentages occurs at Allenberg Bog. The T zone pollen assemblages compare well with the modern pollen rain at Fort Churchill, Manitoba.

The A zones differ according to the age of the drift on which the basins are situated. Most unique was the Genesee Valley site where spruce (ca. 25 percent) occurs with abundant NAP (40 to 45 percent). Spruce values decrease upward. The significance of the assemblages is obscure, but taken at face value, the presence of an open vegetation type, perhaps similar to park-tundra, is indicated. At Allenberg Bog, fluctuations in *Fraxinus nigra* and *Quercus* percentages suggest correlation with climatic modifications associated with glacier advance and retreat. However, absolute pollen frequency data from this site indicate that the fluctuations occurred as a response to increasing deposition rates for pine and spruce pollen. Wood near the bottom of zone A at Houghton Bog has been dated at 11,880 ± 730 B.P. (I-3290). Upper A zone spectra, except for the presence of pollen from temperate deciduous trees, are similar to surface spectra occurring today in the boreal woodland of central Quebec.

The spruce woodland disappeared around the Valley Heads sites about 10,500 years ago and was replaced by B zone forests dominated by *Pinus Strobus.* At several sites, lower pine-birch and upper pine-oak subzones can be distinguished. At Protection Bog, where the pine peak has been dated at 9030 ± 150 B.P. (I-3551), a *P. Strobus* cone was recovered from sediments deposited about 10,500 years ago.

Zone C-1 records the development of hemlock-northern hardwoods forests. With the exception of gradually increasing *Fagus* values, the profiles demonstrate stability in the regional vegetation during the interval between about 8000 and 4400 B.P. An abrupt decline in hemlock percentages marks the end of pollen zone C-1, which is dated at 4390 ± 110 B.P. (I-3550) at Protection Bog.

---

[1] Submitted for publication May 19, 1969. Accepted for publication May 5, 1972.

[2] This study, in somewhat different form, comprised most of a thesis submitted to Michigan State University in partial fulfillment of the requirement for the Ph.D. degree. An abstract has previously appeared (Miller, 1969).

[3] Department of Botany and Plant Pathology, Michigan State University, East Lansing, Mich. Present address: Department of Botany, The University of North Carolina, Chapel Hill, N.C. 27514.

Increased relative numbers of *Acer saccharum, Betula, Carya, Fagus,* and *Quercus* pollen types occur in zone C-2. *Tsuga* percentages remain low. Absolute pollen frequency determinations affirm the C-1/C-2 hemlock decline but show only slight increases in the numbers of broadleaf tree pollen types being deposited. This fact and the tendency for hemlock to exhibit high drought mortality may indicate a series of severe droughts occurring over a relatively short time span.

Zone C-3 which began 1270 ± 95 years ago (I-3549) at Protection Bog was divided into the following subzones: C-3a across which *Tsuga* pollen regains its position of prominence in the profiles and C-3b in which abruptly increasing percentages of NAP, including *Ambrosia, Plantago,* and *Rumex,* record European settlement and attendant forest clearance.

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Introduction

This report treats a problem that is historical in nature — vegetation change through time following deglaciation. The region involved is in western New York State where surfaces, according to available data, have been ice-free for at least 12,500 years, or longer southward toward the Pennsylvania border. Temperate broadleaf-deciduous or deciduous-coniferous forests now characterize the region. The history of their development as well as information on vegetation types that no longer exist in the area are major objectives in this investigation.

The principal technique used is pollen analysis whereby the vertical succession of pollen and spores is determined in sediments that have been accumulating in small lake basins for thousands of years. Changes in relative and absolute frequency of various pollen types through time serve as the basis for inferences concerning the history of past vegetation. When possible, supplemental data from other kinds of plant fossils are also included. Present forests of western New York must serve as reference points to which comparisons of past vegetation can be directed. Therefore, the existing forest vegetation of the region will be treated in some detail. In addition, certain historical records are used to develop a record, however incomplete, of the character of forests prior to the arrival of European man. Pollen analysis also provides a way to determine former climates because major vegetation classes presumably develop in response to regional climates.

The unglaciated Allegheny Plateau and Appalachian Mountains doubtless served as a refuge for many species of plants during Pleistocene glaciations, so southern New York State is a particularly critical area in which to conduct research of this kind. It is along an important migration route for species that participated in the revegetation of glaciated eastern North America.

The Region

For purposes of this report, southwestern New York State includes Cattaraugus, Chautauqua, Allegany, and southern portions of Erie and Wyoming Counties. However, because the whole of western New York forms a coherent unit historically, vegetationally, and otherwise, this area, which includes Genesee, Niagara, and Orleans Counties in addition to those already named, will be emphasized in the introductory material that follows.

The eight-county region (see figure 1) includes nearly 6550 square miles. It lies between 42° 00′ and 43° 25′ N. lat. and 77° 45′ and 79° 45′ W. long., or in more general terms, extends southward from Lake Ontario nearly 100 mi to the Pennsylvania border and eastward from Lake Erie and the Niagara River 65 to 100 mi depending on the latitude, to the Genesee River. The counties along the Pennsylvania border are by far the largest in area, though least in population. At present the greatest concentration of population occurs at Buffalo and extends northward into the southwestern corner of Niagara County.

As political units, the counties date from the early part of the 19th century. Prior to this time, the region was visited by few Europeans, although in 1679, slightly more than 50 years after the formation of the Plymouth Colony in Massachusetts, an expedition under Robert Cavelier de La Salle established a short-lived outpost at the mouth of the Niagara River (Williams, 1947). It wasn't until 1720, however, that the region had its first permanent resident and not until the late 18th century and early 19th century that more than a handful of settlers were present. In 1810, for example, there were only about 16,000 inhabitants in the eight-county region, but a decade later the population totaled about 75,000 and hardly any district lacked the beginnings of settlement (Meinig, 1966).

Before arrival of settlers of European descent, western New York was occupied by a succession of Indian tribes. The Iroquois controlled much of the state prior to the Revolutionary War, and the Senecas, one of five original Iroquois tribes, originally occupied the region between Cayuga Lake and the Genesee River, but later extended their influence to Lake Erie and the Niagara River by conquering the Erie and Neutral tribes which previously controlled these areas. The Iroquois generally lived in stockaded villages containing about 250 people. Their homes were often surrounded by small, partially cleared fields where corn, beans, and squash were cultivated. It has been estimated that about 20,000 Iroquois lived throughout New York State during the 18th century (Rayback, 1966). While a complete summary of the archeology of Iroquoian and pre-Iroquoian Indians in New York has been provided by Ritchie (1969), the effect of aboriginal hunting and agricultural practices on the vegetation of western New York is little known.

Today, outside the growing urban centers of the region, farming constitutes the largest percentage of land use. The most heavily cultivated areas occur in Niagara, Orleans, Genesee, and northeastern Erie Counties and in a narrow strip in Chautauqua and southern Erie Counties immediately adjacent to Lake Erie (Thompson, 1966). Vegetables and fruits are the principal crops throughout this region. Niagara and Orleans Counties contain the highest percentages of nonforest land — 83 percent and 80 percent, respectively (see table 2, p. 14). Southward, but north of the Allegheny River and southeastern Allegany County, dairy farming and the supportive growing of feed crops for cattle accounts for most of the land use. Here, and in the largely nonagricultural lands of southern Cattaraugus and Allegany Counties, secondary forest covers about 60 percent of the area.

PHYSIOGRAPHY

Extending southward from Lake Ontario to southern Genesee and east-central Erie Counties, thence southwestward along the south shore of Lake Erie, in a strip about 15 mi wide in central Erie County and about 2 mi wide at the Pennsylvania border (figure 1), is the Erie-Ontario Lowland, one of two principal physiographic regions of western New York State. The lowland is mostly underlain by easily-eroded shales, although two prominent east-west trending limestone escarpments occur in the area adjacent to Lake Ontario. These features subdivide this part of the low-

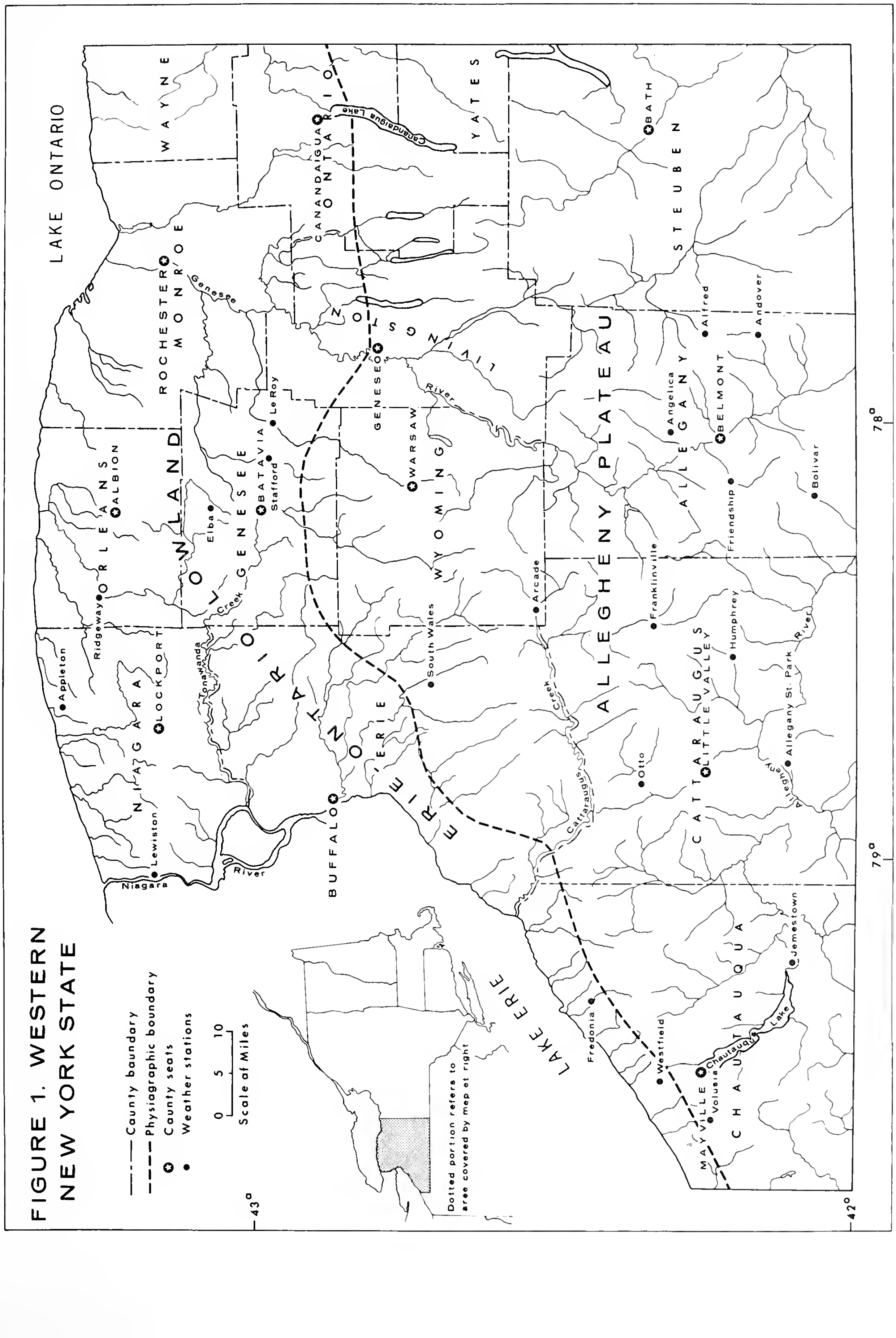

FIGURE 1. WESTERN NEW YORK STATE

land into three more or less flat plains which are in part covered by lacustrine sediments deposited during ancestral stages of Lakes Erie and Ontario.

The Allegheny Plateau or Appalachian Upland, the other main physiographic region of western New York, is bounded on the north by the Portage escarpment. Elevation and relief increase southward, and the highest point in western New York, 2,548 ft, is found near Bolivar in southern Allegany County. The plateau is usually divided into glaciated and unglaciated sections. Southeastern Chautauqua, southern Cattaraugus, and southwestern Allegany Counties, an area approximately bounded by the Allegheny River, were apparently never completely invaded by ice. Muller (1963) points out that the unglaciated region is characterized by less smoothly eroded ridges, more continuous crest lines, and deeply incised V-shaped valleys. He further notes that as far as 15 mi north of the limit of glaciation, summit reduction by glacial scour was as little as 50 to 100 ft although, farther to the north, greater lowering occurred. Throughout most of southern New York less than 200 ft of bedrock was removed from the plateau tops (Muller, 1964a).

The drainage of western New York is generally northward into the St. Lawrence River (figure 1). Streams in only the southern portions of Chautauqua and Cattaraugus Counties and the southwestern corner of Allegany County empty into the Allegheny River which is connected to the Mississippi by way of the Ohio River. The drainage divide separating the St. Lawrence and Mississippi watersheds extends northeastward in Chautauqua County approximately following the crest of the Lake Escarpment moraine, several miles inland from Lake Erie. From there, it may be followed eastward across northern Cattaraugus County with a dip southward toward Little Valley and, finally, southeasterly across eastern Cattaraugus and western Allegany Counties. Part of eastern Allegany County is drained eastward into Susquehanna River.

The only large inland lake in the region is Lake Chautauqua, which occupies the axis of a through valley in south-central Chautauqua County. A number of smaller lakes exist and many of these developed in kettles by melting of partly buried ice blocks. Several artificial lakes occur in lowland areas and along the beds of major rivers and streams.

BEDROCK GEOLOGY

Western New York State is entirely underlain by Paleozoic sedimentary rocks (Fisher *et al.,* 1961) which are exposed at the surface in only limited areas. The beds dip gently to the south so that rocks of greater age are encountered successively northward. More or less east-west trending belts of shale, siltstone, and sandstone are present throughout the region, but the most important exposures of limestone and dolomite are found in the lowland north of the Allegheny Plateau. Complete summaries of the bedrock geology of Erie and Chautauqua Counties have been published by Buehler and Tesmer (1963) and Tesmer (1963), respectively.

Red shales and siltstones of Late Ordovician age outcrop in the area adjacent to Lake Ontario and are the oldest rocks exposed in the region. To the south, the predominantly calcareous deposits comprising the Niagara escarpment accumulated during Middle Silurian time, while farther southward still, the Onondaga escarpment is composed of limestone deposited during the early part of Middle Devonian time. The 10 miles separating the two zones of calcareous rock are mostly occupied by weak shales, Late Silurian in age. Later in Middle Devonian time, shales replace limestones. Upper Devonian rocks, mostly siltstones and shales, subordinate sandstones, and rarely conglomerates and thin limestones are found southward from central Erie and southern Genesee Counties. Near the Pennsylvania border, largely within the unglaciated portion of western New York, occur Lower Mississippian and Lower Pennsylvanian shales, sandstones, and conglomerates. These deposits have been greatly dissected by erosion and may be considered outliers of more continuous strata of the same age to the south. Muller (1963) suggests that the resistant conglomerates in this area may have terminated southward glacial movement.

GLACIAL GEOLOGY

In contrast to the age relationships of the bedrock units, surficial deposits resulting from Pleistocene glaciations are oldest in the south and youngest in the north. Only drift from Illinoian and Wisconsin glaciations has been identified in western New York, although study of the development of the present Allegheny River indicates pre-Illinoian glacial activity (Muller, 1963, 1965).

The earliest recognized deposit of Wisconsin age is the Olean drift which in western New York is found at the surface on the north and east sides of the unglaciated portion of the Allegheny Plateau (figure 2). This roughly triangular area, often referred to as the

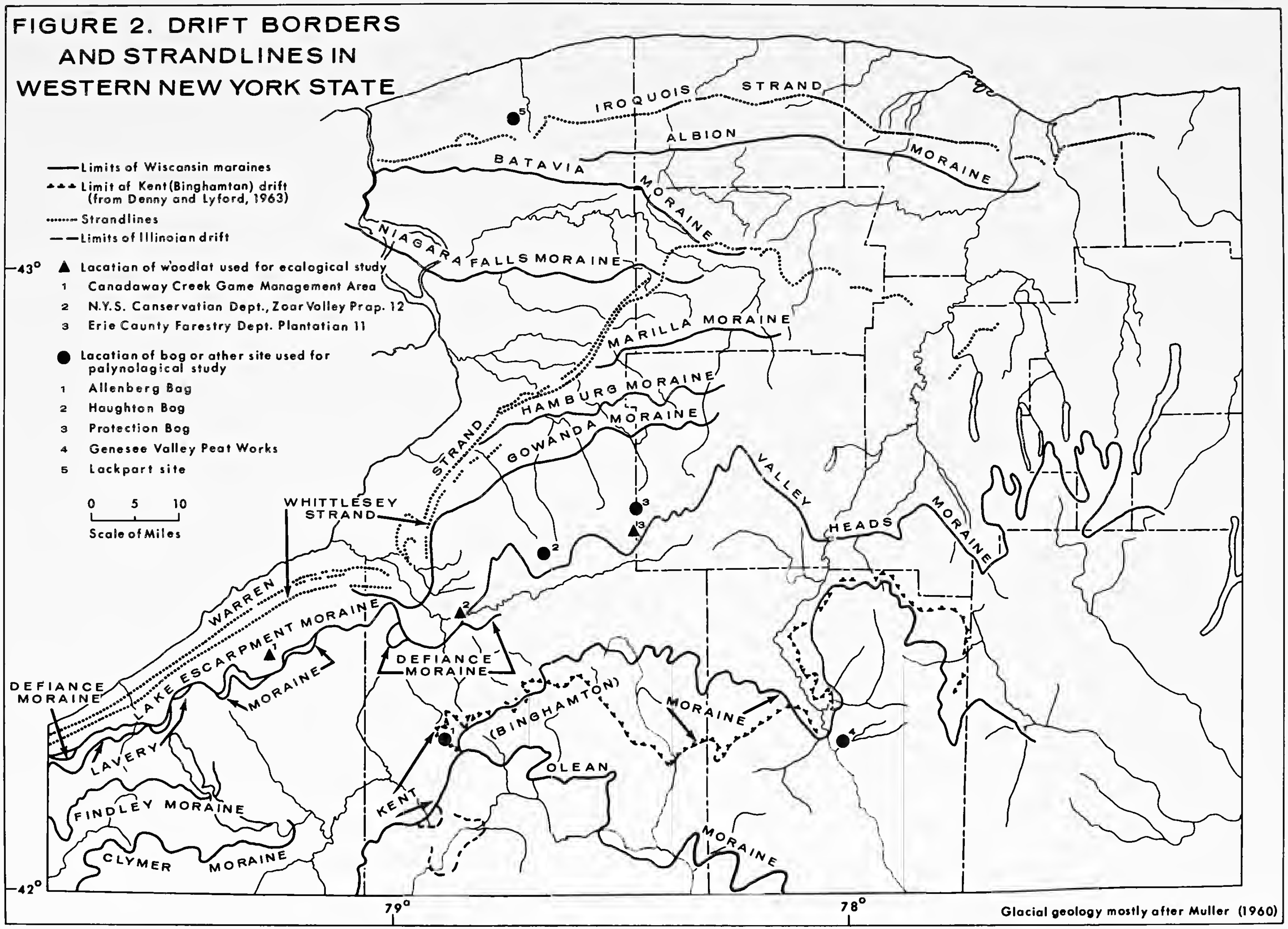
FIGURE 2. DRIFT BORDERS AND STRANDLINES IN WESTERN NEW YORK STATE

Salamanca reentrant, is located at the junction of deposits produced by ice moving southeastward out of the Lake Erie basin and similarly derived deposits from the north and east from the Lake Ontario basin. Olean drift as mapped by MacClintock and Apfel (1944; however, cf. Denny & Lyford, 1963) forms the terminal moraine on the north and east sides of the reentrant and follows a greatly convoluted course extending slightly south of east from about 3 mi northeast of Napoli to near Humphrey where its position extends abruptly southward toward the village of Allegany. From this point, it angles southeastward toward the corner of Cattaraugus County. It is a very subdued terminal moraine but the limit of glaciation can be determined by the presence of erratic cobbles (Muller, 1965). The exact age of the Olean moraine is not known. MacClintock and Apfel (1944) consider it Iowan or Tazewell in age; other authors concur with this disposition. However, Denny and Lyford (1963) point out that it may be a pre-Farmdale-post-Sangamon substage. There is, at any rate, general agreement that it is pre-Woodfordian in age.

A section exposed near the village of Otto in northwestern Cattaraugus County displays evidence of a long history of successive glaciations now considered to have occurred entirely within the Wisconsin Stage (Muller, 1964b). Near the base of the section and in association with Olean drift (Denny & Lyford, 1963) are peats, initially determined to be more than 35,000 years old (W-87; Suess, 1954) but later to have a finite age of 63,900 ± 1700 B.P.[4] (GRN-3213; see Muller, 1964b), which have been correlated (Muller, 1965) with deposits of the early Wisconsin St. Pierre Interstade in the St. Lawrence lowland (see Terasmae, 1958). The several distinct peaty layers which make up the Otto organic deposit have been examined for pollen by four workers whose results are available in Muller (1964b). The pollen assemblages obtained indicate that the vegetation surrounding the site was similar to that found today in the boreal forest of Canada, roughly 50 mi north of North Bay, Ontario. Upward in the section, rhythmites alternate with layers of till. The former represent separate developments of glacial Lake Zoar, and the latter, repeated invasions of ice sheets correlative with the " classical " Wisconsin glacial advances.

On the west side of the Salamanca reentrant, the terminal moraine is formed of Kent drift. The basic distinctions between it and the Olean drift to the east have been described by MacClintock and Apfel (1944) who note that the former is characterized by unmodified constructional topography and a relatively high content of carbonates which are only shallowly leached. The Olean drift is less calcareous, the carbonates are more deeply leached, and there is a greater modification of its constructional topography. The Kent terminal moraine, as mapped by MacClintock and Apfel (1944; cf. Denny & Lyford, 1963), separates from the Salamanca reentrant at a point 3 mi northeast of Napoli where the westernmost deposits of Olean drift are encountered (figure 2). From there, it may be traced over a generally eastward course to near Belmont in central Allegany County from where the margin extends northward to a point near the Wyoming County line. It can be further traced southeastward across northeastern Allegany County but is lost in eastern Steuben County near Almond.

The name " Binghamton " was originally given to Kent drift because of its apparent equivalence to kame deposits near the city of Binghamton in south-central New York State, although this relationship has been questioned by Denny and Lyford (1963) and others. The Binghamton drift border in far southwestern New York State has been correlated with the Kent moraine of northwestern Pennsylvania and northeastern Ohio by continuous tracing (Muller, 1963). White *et al.* (1969) have recently stressed that the Kent moraine in northwestern Pennsylvania is cored with Early Wisconsin drift and that the Kent till is only a thin layer on top of this, extending at places beyond the mapped boundary of the moraine. This relationship may apply also to parts of western New York. A possible equivalent of the Kent moraine in the western Finger Lakes region, the Almond moraine, has been traced eastward from the Genesee River toward Bath by Connally (1964).

The minimum age of the Kent drift is provided by a radiocarbon date of 14,000 ± 350 B.P. for marl collected at the bottom of a kettle hole in Kent drift near Corry, Pennsylvania, 9 mi inside the Wisconsin drift border (W-365; Droste *et al.,* 1959). Although this age determination indicates the Kent glaciation may be early Cary in age, more recent study has shown it to be considerably older. From sections exposed near Cleveland, Ohio, White (1968) has obtained radiocarbon dates for two wood samples embedded in lacustrine sediments interpreted as having been deposited from a proglacial lake ponded in front of the advancing Kent ice. These age determinations, 24,000 ± 800 B.P. and 23,313 ± 391 B.P., imply that the Kent ice overrode this area about 23,250 years ago.

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[4] Radiocarbon Years Before Present. In this report ages based on radiocarbon dating whether noted or not are in radiocarbon years which generally differ somewhat from calendar years.

A number of other moraines occur on the west side of the reentrant (Muller, 1963). These have been interpreted as recessional features developed during retreat of the ice sheet that produced the Kent (Binghamton) terminal moraine (Findley and Clymer moraines), or to mark a readvance of the ice margin following the northwestward retreat of the Kent ice (the Lavery moraine).

The well-marked Valley Heads moraine occurs to the north across midcentral and midwestern New York State. It is represented by a group of parallel morainic deposits at the edge of the Allegheny Plateau in western Chautauqua and southern Erie Counties where the complex is called the Lake Escarpment moraine. According to Muller (1965), mapping has established the equivalence of the Lake Escarpment and Valley Heads moraines. Woody detritus, 14,900 ± 450 years old (I-4216; Calkin, 1970), from a depression in the Chaffee outwash plain, which is located near the southeast corner of Erie County, provides a minimum date for withdrawal of ice from the distal edge of the moraine. Although the Valley Heads-Lake Escarpment moraine is often cited as equivalent to the Port Huron moraine in the Midwest, this relationship is now in question because radiocarbon dates on material associated with the Port Huron maximum are considerably less than 14,900 years old.

A series of moraines, most of which were first traced by Leverett (1902), occur north of the Valley Heads-Lake Escarpment complex. Many of these are not prominent topographically because deposition occurred in proglacial lakes where erosion was rapid. Northward they are the Gowanda, Hamburg, Marilla, Alden, Buffalo, Niagara Falls, Barre, Batavia, and Albion moraines. Most are illustrated in figure 2. A recently obtained radiocarbon date, 12,730 ± 220 B.P. (I-3665; Calkin & McAndrews, 1969), which provides a minimum date for recession from the Gowanda moraine, has lead Calkin (1970) to suggest that deposition of either the Gowanda or Hamburg moraine may correlate with the Port Huron maximum. Studies of sediments in Lake Erie support the contention that the Port Huron equivalent in western New York represents a major readvance of glacier ice. A fluvially eroded drift sheet identified beneath the waters of modern Lake Erie by seismic reflection and believed to be of Cary (Lake Border) age indicates that drainage was eastward probably over the Niagara escarpment during the Cary-Port Huron Interstade (Wall, 1968). This could only have taken place if the glacier margin was north of this point.

Final withdrawal of glacier ice from western New York must have been rapid, for a series of radiocarbon dates associated with sediments of Lake Iroquois, which developed in the Lake Ontario basin north of the Albion moraine, average 12,000 B.P. (Goldthwait *et al.*, 1965; Karrow *et al.*, 1961). By this time the ice margin had melted to an unknown distance north of the Niagara escarpment and may have freed much of the Lake Ontario basin, although the St. Lawrence lowland was still blocked. New York State was apparently not invaded by Valders ice (MacClintock & Terasmae, 1960; Terasmae, 1959).

Beaches and strand lines marking the shorelines of the ancestral stages of Lakes Erie and Ontario are found in northwestern Chautauqua County and from central Erie and Genesee Counties northward. This subject is treated in detail by Hough (1958, 1963). Calkin (1970) has recently summarized the chronology of the glacial Great Lakes in reference to his own work in northwestern New York State.

SOILS

The soils of western New York, with the possible exception of those found in the Salamanca reentrant, are relatively young because they have been formed from surface material in a region that was ice-covered during the Wisconsin glaciation. These soils are distributionally related to and mostly derived from the east-west trending bedrock units of the area. However, due to the direction of ice movement and the intensity of glacial scour, there has been a general distribution of parent material southward. As a result, the limestone and dolomites of the Erie-Ontario Lowland are found not only in the drift that mantles the lowland plains but also along the northern edge of the Allegheny Plateau. The amount of calcareous material transported away from the lowland gradually decreases toward the Pennsylvania border permitting a distinction to be made between the predominantly limy soils of northern western New York and the acid ones of the southern upland.

New York State is in a transition zone between cool, humid climates which generally produce podzols and climates characterized by warmer temperatures which favor the formation of gray-brown podzolic soils (Cline, 1955). Although soils of the latter type predominate at the west end of the state, podzols occur in southwestern Allegany, southern Cattaraugus, and southwestern Chautauqua Counties. The region directly south of Lake Ontario encompassing Niagara, Orleans, and the northern part of Genesee Counties is broadly categorized as an area of intrazonal soils. Gray-brown podzolic soils are located in the intervening region (Soil Survey Division, 1938). Further details, including descriptions of the soil associations recognized in New York State, are found in Cline (1955).

Little work has been done in western New York relating soils and vegetation. It has been pointed out that there is an approximate equivalence between the Hemlock-white pine-northern hardwood forest region and the area characterized by podzols, and that a similar relationship holds for the Eastern deciduous forest and the region of gray-brown podzolic soils (Braun, 1950; Gordon, 1940). However, the boundary separating the two major vegetation units in western New York (Braun, 1950) is the Portage escarpment — deciduous forests occupy the lowland adjacent to Lakes Erie and Ontario while coniferous-deciduous forests are situated on the upland. The podzol/gray-brown podzolic boundary, in contrast, occurs far south of the escarpment.

The forest communities occurring on certain soils in Cattaraugus County have been described in less general terms by Gordon (1940) to which the reader is referred for information other than that presented here. On the higher parts of the plateau grow forests of hemlock, white pine, red maple, chestnut (now absent), sweet birch, and cucumber tree, while certain other podzols support forests dominated by hemlock and beech. Mixed mesophytic forests of red oak, beech, chestnut (now absent), red maple, sweet birch, white ash, black cherry, and often other species characterize thinner, drier podzols. Oak associations, originally containing chestnut, are found on the driest upland soils. Similar data from elsewhere in western New York have not been published.

CLIMATE

Warm to hot summers, cold winters, and adequate precipitation, typical of humid continental climates in general, characterize New York State. In the eight-county region, the terrain and nearby Lakes Erie and Ontario have a marked influence on the overall climate. During fall the lakes liberate heat, thereby lengthening the frost-free period, while at the end of winter they keep the surrounding area cool and delay plant growth until the danger of frost is past. Nearly all lowland areas have from 140 to 180 frost-free days. At higher elevations, however, the tempering effect of the lakes is less apparent, and southward, the length of the growing season decreases until 100 days or less is reached in southeastern Cattaraugus and southwestern Allegany Counties.

Specific differences in climate between upland and lowland sections of western New York are documented by data in table 1. Mean annual temperatures at stations in the Erie-Ontario Lowland are nearly uniformly 2–3° F higher than those in the upland. Plateau stations have recorded the lowest winter temperatures but both regions experience nearly the same summer maxima, although summers are generally cooler in the upland. High elevation and the comparatively dry atmosphere over the plateau combine to give high day and low night temperatures which result in an almost typical continental type of climate in this region (Mordoff, 1949).

The basic difference between energy reception in the upland and in the lowland is well illustrated by figures for potential evapotranspiration and growing degree months, which are higher in the lowland than in the upland (Carter, 1966). Plant distribution in western New York correlates well with these indices. Southern species are found principally in the lowland where the more favorable climate presumably ensures their survival, although other factors perhaps also exert some control.

Moisture is brought to New York State from the Gulf of Mexico and the Atlantic Ocean through the activity of cyclonic storms and, locally, Lakes Erie and Ontario are important sources of moisture also. Annual precipitation in the upland generally exceeds that in the lowland, often by 10 in or more. In western New York, per annum precipitation increases irregularly southward until a maximum of 48 in is reached in northwestern Cattaraugus County (Johnson, 1960) where, significantly, one of the largest areas of upland sphagnum bog occurs. The northern half of Niagara County and nearly all of Wyoming County, in contrast, are among the driest parts of the state.

Precipitation is fairly evenly distributed throughout the year, but summer months characteristically receive more than others. During the growing season, somewhat less rain falls in lowland areas than on the upland. Although summer is the season of greatest rainfall, it is also the time of greatest moisture need, so small moisture deficits occasionally occur. Few major droughts, however, have affected the region. A serious one occurred in 1899 when total precipitation for the three summer months was less than 3 in at localities

TABLE 1

Selected Climatic Data from Weather Stations in Western New York State by Physiographic Region *

Location	Mean Annual Temp.	Mean January Temp.	Mean July Temp.	Mean Growing Season † Temp.	Highest Temp.	Lowest Temp.	Ave. Date of Last Spring Frost	Ave. Date of First Fall Frost	Mean Annual Precip.	Mean Growing Season † Precip.
Erie-Ontario Lowland										
Appleton (300′) ‡	47.1	25.7	70.1	63.8	106	—13	May 4	Oct. 16	27.33	12.01
Buffalo (693′)	47.0	25.2	70.0	64.0	97	—20	Apr. 26	Oct. 22	35.16	14.57
Elba (750′)	45.7	23.4	69.7	63.4	100	—21	May 8	Oct. 6	36.72	15.21
Fredonia (750′)	48.6	27.6	71.3	65.4	98	—26	May 1	Oct. 21	36.72	16.89
Le Roy (900′)	46.1	23.2	68.9	64.0	99	—14	May 8	Oct. 6	36.45	15.86
Lockport (520′)	47.1	24.9	70.3	64.3	103	—24	May 5	Sept. 19	30.91	14.39
Ridgeway (420′)	47.4	24.8	71.3	64.9	96	—9	May 4	Oct. 3	32.98	16.79
Stafford (925′)	47.6	25.4	71.7	65.8	103	—33	May 12	Oct. 4	31.63	14.39
Intermediate										
South Wales (1073′)	46.0	24.5	69.5	63.7	103	—31	May 13	Oct. 1	38.99	16.25
Westfield (1050′)	47.7	25.1	70.2	64.6	98	—19	May 2	Oct. 21	38.53	18.91
Allegheny Plateau										
Alfred (1760′)	44.8	22.9	67.2	61.8	101	—35	May 18	Sept. 28	35.83	17.84
Allegany State Park (1500′)	45.6	25.2	66.6	61.7	101	—35	May 28	Sept. 18	42.82	19.95
Andover (1670′)	45.4	24.1	67.4	62.3	100	—34	May 21	Sept. 25	33.64	17.25
Angelica (1420′)	45.3	23.7	67.8	62.3	104	—40	May 25	Sept. 24	35.26	17.61
Arcade (1707′)	44.0	20.6	67.4	61.6	95	—38	May 22	Sept. 28	41.96	21.08
Bolivar (1800′)	45.1	22.9	66.7	61.5	101	—37	June 1	Sept. 17	39.83	19.87
Franklinville (1590′)	45.0	23.0	67.3	61.9	99	—45	May 21	Sept. 22	38.76	18.09
Humphrey (1951′)	45.4	22.7	68.3	62.8	93	—17	May 14	Sept. 25	44.45	22.30
Jamestown (1390′)	47.6	25.3	70.0	64.7	100	—31	May 12	Oct. 5	43.83	19.26
Otto (1260′)	46.8	23.3	69.7	64.3	99	—24	May 13	Oct. 16	33.09	16.79
Volusia (1560′)	45.6	23.4	68.4	62.9	98	—18	May 10	Sept. 22	38.53	17.26

* Data from Mordoff (1949); temperatures in degrees Fahrenheit, precipitation in inches.

† May 1 to September 30.

‡ Elevation in feet above sea level.

bordering Lake Ontario (Mordoff, 1949). There has been at least one noteworthy period of drought every 20 years.

FLORA

Floristic research in western New York State began in earnest during the mid-1800's. Before this time, however, Niagara Falls had attracted naturalists and plant collectors to the region, many of whom published botanical observations made at the Falls (see Dow, 1921) or while travelling across the Erie-Ontario Lowland. Unfortunately, most of this information seems to have been gathered casually or, in some cases, by untrained people, making its value questionable for purposes of defining the plant cover of the region. Three of the more notable visitors were Peter Kalm, who viewed the cataract in 1750 (Kalm, 1751), François André Michaux, who travelled throughout the eastern Great Lakes area in 1806 or 1807, and Thomas Nuttall, who undertook a pedestrian trip from Philadelphia to Canandaigua and west to Niagara Falls in 1809 (Graustein, 1967). Zenkert (1934), in addition to reporting a total of 1,587 species of vascular plants (1,187 native, 400 introduced) from within a 50-mile radius of Buffalo, has also traced the history of botanical exploration in western New York from early times through the 1930's.

Floristically, three more or less distinct regions are present in western New York. The Wisconsin terminal moraine (see figure 2), which approximately separates glaciated and nonglaciated districts, marks the southern limit of a group of boreal species, thereby defining the first region, the unglaciated upland. The species involved are mostly bog plants which presumably are not found south of the drift limit because kettle holes and other suitable habitats generally associated with glaciated terrain are absent.

The second and third floristic regions are delimited by physiography and correspond to the Erie-Ontario Lowland and the Allegheny Plateau. Typical upland species can occur on both sides of the glacial limit. The boundary between the two regions is usually depicted as part of the well-known tension zone that crosses Minnesota, Wisconsin, Michigan, southern Ontario, and extends across western and central New York to the eastern end of Lake Ontario. In New York State, it is mostly coincident with the Portage escarpment. The tension zone has not been studied extensively in central and western New York, and plant distribution maps similar to those which support its existence elsewhere are not available. However, in western New York, it is clear that the upland is characterized by species which are absent or are of greatly restricted occurrence in the lowland. Conversely, *Asimina triloba,*[5] *Celtis occidentalis, Nyssa sylvatica,* and others grow in the lowland or rarely on the flank of the Allegheny Plateau and are absent from higher portions of the upland. Zenkert (1934), who recognizes the distinction between the lowland and upland flora, lists 96 species which represent an austral element best developed in the region adjacent to Lakes Erie and Ontario. This distribution pattern is also the basis for Bray's recognition (1915) of two zones in western New York separated approximately by the Portage escarpment and characterized by different tree species. His Zone B, in which chestnut (now absent), oaks, hickories, and tulip-poplar are common, occurs across the lowland, while Zone C, characterized by sugar maple, yellow birch, hemlock, and white pine, corresponds in area to the Allegheny Plateau.

It is noteworthy that northern species are best represented on the plateau, while plants characteristic of southern regions are most common in the lowland, a situation directly opposite that found in Michigan and Wisconsin. In western New York, climate may be the major factor controlling this pattern, although soil and other edaphic factors probably have a role also. The more rigorous climate of the upland would tend to eliminate species adapted to higher mean winter temperatures and a longer growing season.

To further describe the nature and geographical relationships of western New York's flora, it can be divided into phytogeographic elements, each of which is made up of species that share a similar type of distribution pattern today. These species are typical of a certain natural area; that is, the entire geographical range of a taxonomic unit attained through natural dispersal mechanisms, whether it now grows within that area or not (Cain, 1944). Such species have the same center of dispersal, but may or may not share a common center of origin. The identification of elements in a regional flora is based upon their being characteristic of certain well-defined phytogeographical areas elsewhere. Elements may be categorized as either extraneous or intraneous. The former contains species at or near the limits of their ranges which may, therefore, exhibit disjunctions of various types, while the latter includes plants of widespread distribution whose occurrence in a particular region is well within the total range of the species (Braun, 1937; Cain, 1944). Intraneous species, which may comprise as much as 60 percent of a flora (Parker, 1936; Thompson, 1939), tell little about the affinities of that flora, but extraneous ones are considerably more helpful in this regard.

The Alleghenian element (see Curtis, 1959) contains a group of species of Arcto-Tertiary origin which center in the southern Appalachians and extend northward into southern Canada. Such well-known and important forest trees as *Acer saccharum, Betula alleghaniensis, Fraxinus americana, Pinus Strobus, Quercus alba, Tilia americana,* and *Tsuga canadensis* are members of this element. Also of Tertiary origin is the Ozarkian element which contains more drought tolerant species developed in isolation from the southern Appalachians on the Ozark upland of Missouri and Arkansas. *Acer saccharum* var. *nigrum, Carya* spp., *Quercus macrocarpa, Q. Muhlenbergii,* and *Q. velutina* are components of this element. For certain other species now found in western New York (e.g., *Magnolia acuminata*), both the Appalachians and the Ozarks presumably acted together as a single center of origin and dispersal (see Steyermark, 1939).

Members of the Boreal element are not rare in western New York, but, in most cases, they occupy restricted positions in bog communities developed in undrained depressions. *Abies balsamea, Larix laricina,* and *Picea mariana* are members of this element. These trees are characteristic of the boreal forest which ranges across central Canada from eastern Alaska to the Atlantic seaboard and south to the upper Great Lakes. Another group of species characteristic of northern regions but often found southward in the mountains belongs to the Arctic-alpine element. As expected, it is very poorly represented in western New York but has better expression in the Adirondack and Catskill Moun-

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[5] Plant nomenclature throughout this report follows Fernald (1950) with the exception of binomials used for yellow birch and leatherleaf which are *Betula alleghaniensis* Britton and *Cassandra calyculata* (L.) D. Don, respectively.

tains to the east. *Pinguicula vulgaris* and *Saxifraga aizoides,* which grow together near a falls of the Genesee River in southeastern Wyoming County (their only station at the west end of the State; Zenkert, 1934), are members of this element.

Species typical of western North America but also found eastward are members of what can be broadly called a Western element. Actually, this category includes several distinct distribution patterns, two of which in particular pertain to western New York. The Prairie element is made up of species whose ranges center on the existing prairies. Certain members of this element such as *Andropogon Gerardi, A. scoparius,* and *Sorghastrum nutans* now have a wide distribution across the Erie-Ontario Lowland where they are generally found in abandoned fields, in hedgerows, and in thin, second growth oak stands often associated with prairie forbs. Prior to settlement, these species apparently grew in prairie-like oak openings characteristic of the lowland. Shanks (1966) felt that the oak openings in this area were essentially edaphic prairies, remnants of more extensive grasslands which occurred in this region at some time in the past. The shallow dry soils and the occasional water deficits characteristic of the Erie-Ontario Lowland favor persistence of prairie species and exclude more mesophytic competitors. A Cordilleran or Western Mountain element was early recognized in eastern North America by Fernald (1925), and more recently Iltis (1965, 1966) has redirected attention to it, pointing out that " . . . the ranges of many of our commonest as well as rarest species in the northeastern United States . . . fall into the standard pattern of eastern North America — western North America vicarious species pairs with the post-glacially produced modern ranges overlapping in glaciated northeastern North America " (1965, p. 149). As examples, Iltis (*ibid.*) cites a substantial list of paired species of which *Actaea rubra* (western) and *A. pachypoda* (eastern), among others, both occur in western New York.

Having a limited distribution along the beaches of Lakes Erie and Ontario and westward around the upper Great Lakes are species which belong to the Atlantic Coastal Plain element (Peattie, 1922). These species apparently attained their current ranges sometime during late or postglacial time, perhaps by migrating along the St. Lawrence or Mohawk River valleys and thence along the shores of the ancestral Great Lakes. *Cakile edentula, Euphorbia polygonifolia, Lathyrus maritimus,* and *Xyris caroliniana* are a few Coastal Plain species found in our area.

Also present in western New York is an exotic element, containing non-native species which have entered the region through the activities of man. Of particular interest to the pollen analyst are certain species of *Plantago* introduced from Europe, especially *P. lanceolata* and *P. major.* The appearance of *Plantago* pollen in postglacial sediments, which mostly can be attributed to these species, clearly marks the arrival and spread of Europeans in America. About 25 percent of the flora within 50 miles of Buffalo is comprised of introduced species.

VEGETATION

General Statement

Authors of the earliest histories published about western New York are uniform in stating that the region was completely wooded at the time of settlement except for discontinuous openings in the oak forests of the Erie-Ontario Lowland and other small partially cleared areas associated with Indian villages.

The observations of an accomplished botanist, Rev. E. J. Hill, while made four to six decades after clearing began, provide an accurate description of the forest cover of western New York. Rev. Hill was born at Le Roy in Genesee County in 1833 and spent much of the early part of his life in this region at a time when undisturbed tracts of forest were still fairly abundant. Hill (1895) reports that:

> The most abundant trees of the upland woods are the Beech and Hard Maple. On light soils, and where there is a considerable mixture of sand or gravel with the clay loam, the Oaks predominate, interspersed with Hickory, and sometimes with the Chestnut. In colder and higher tracts or along the banks of streams, the Hemlock is frequent or even abundant. The Basswood is common in the richer uplands, among Beeches and Maples. Here also the White Ash is most often seen. . . .
>
> Where the Beech and Maple abound the White Oak is occasionally mixed with them, but is mostly confined to the low land, where it is much more common than the Swamp White Oak. The Red Oak is much more commonly seen with the Beech and Maple. In flinty and gravelly soils the most common Oaks are the White, Red and Black Oaks. Here also occurs the Chestnut Oak; it is usually less abundant than the other kinds and may also be found in the wet lands (p. 382).

Turning briefly to historical records which pertain to either of the two physiographic regions, an account of the original timber covering of Orleans County indicates in a general way the nature of the forests throughout the Erie-Ontario Lowland during the period of European settlement (Thomas, 1871).

> In its natural state Orleans County was thickly covered with trees. On the dry, hard land, the prevailing varieties of timber were beech, maple, white, red and black oak, white wood or tulip tree, basswood, elm, hickory, and hemlock. Swamps and low wet lands were covered with black ash, tamarack, white and yellow cedar, and soft maple; large sycamore or cotton ball trees were common on low lands and some pine grew along Oak Orchard Creek, and in the swamps in Barre; and a few chestnut trees grew along the Ridge [Lake Iroquois strandline] in Ridgeway, and in other places north of the Ridge (p. 29).

In comparison, C. G. Locke's description of the forests of Cattaraugus County, which pertains to much of the western Allegheny Plateau in New York State, emphasizes the prevalence of hemlock and pine in this region at the time of settlement (*in* Adams, 1893).

> This table-land was originally covered with a heavy growth of deciduous trees intermixed with hemlock and some pine, and this same description of the original forest would apply to the entire northern portion of the county, excepting that pine was generally found along the low-lands. The southern part of the county was covered with forest of the choicest pine and hemlock, with a mixture of deciduous trees. Here we find the home of the white and red oak and chestnut, which apparently did not cross the dividing ridge, as very little of this timber is found in the northern part of the county (p. 50).

These passages clearly indicate that, in general, forests of the lowland and upland were of a different type with beech, maple, oaks, and other deciduous species predominating in the former, while a mixed forest of conifer and deciduous trees occurred in the latter. Most botanists who studied the vegetation of this region in more recent years have also made this distinction. For example, Küchler (1964) recognizes three main types of forest in western New York (see figure 3, map A): (1) Beech-maple forest dominated by *Acer saccharum* and *Fagus grandifolia;* (2) Northern hardwoods forest dominated by *Acer saccharum, Betula alleghaniensis, Fagus grandifolia,* and *Tsuga canadensis;* and (3) Appalachian oak forest in which *Quercus alba* and *Q. rubra* are dominant, but generally occur with many other subdominant species. The boundary between (1) and (2) roughly corresponds to the Portage escarpment with the Northern hardwoods forest area in the upland and the Beech-maple forest area in the lowland, although inclusions of one type are mapped in the other and vice versa. The Appalachian oak forest is restricted to the Allegheny River Valley and to several small areas in the upland north of the Salamanca reentrant and adjacent to the Genesee River. It occurs more widely in the region of the Susquehanna River drainage immediately to the east of the area treated in this study.

Küchler has drawn heavily on the map of major forest types in Armstrong and Bjorkbom's study (1956) of the timber resources of New York State. Although the boundaries of the units being mapped are essentially the same in both publications, the units themselves differ somewhat. This is a result of two different approaches used in the preparation of the maps. In one case, the potential natural vegetation, or " the

TABLE 2

TOTAL AREA, NONFOREST LAND AREA, AND FOREST LAND AREA OF WESTERN NEW YORK STATE BY COUNTIES*

Counties	Total Land Area †	Nonforest Land Area Acres‡	 Percent	Forest Land Area Noncommercial § Acres ‡	 Percent	 Commercial Acres ‡	 Percent
Chautauqua	691.2	343.0	49.6	1.8	0.3	346.4	50.1
Cattaraugus	854.4	326.1	38.2	61.3	7.2	467.0	54.7
Allegany	670.7	259.4	38.7	2.5	0.4	408.8	60.9
Erie	674.7	468.4	69.4	2.5	0.4	203.7	30.2
Wyoming	382.7	259.8	67.9	6.6	1.7	116.3	30.4
Niagara	341.1	283.0	83.0	0.1	0.0	58.0	17.0
Genesee	320.6	227.1	70.8	1.3	0.4	92.2	28.8
Orleans	253.4	202.5	79.9	1.2	0.5	49.7	19.6

* Data from, " Preliminary forest survey statistics by counties and units, New York — 1967," Northeastern Forest Experiment Station, U.S. Forest Service, Upper Darby, Pennsylvania.

† In thousands of acres.

‡ Times 1000.

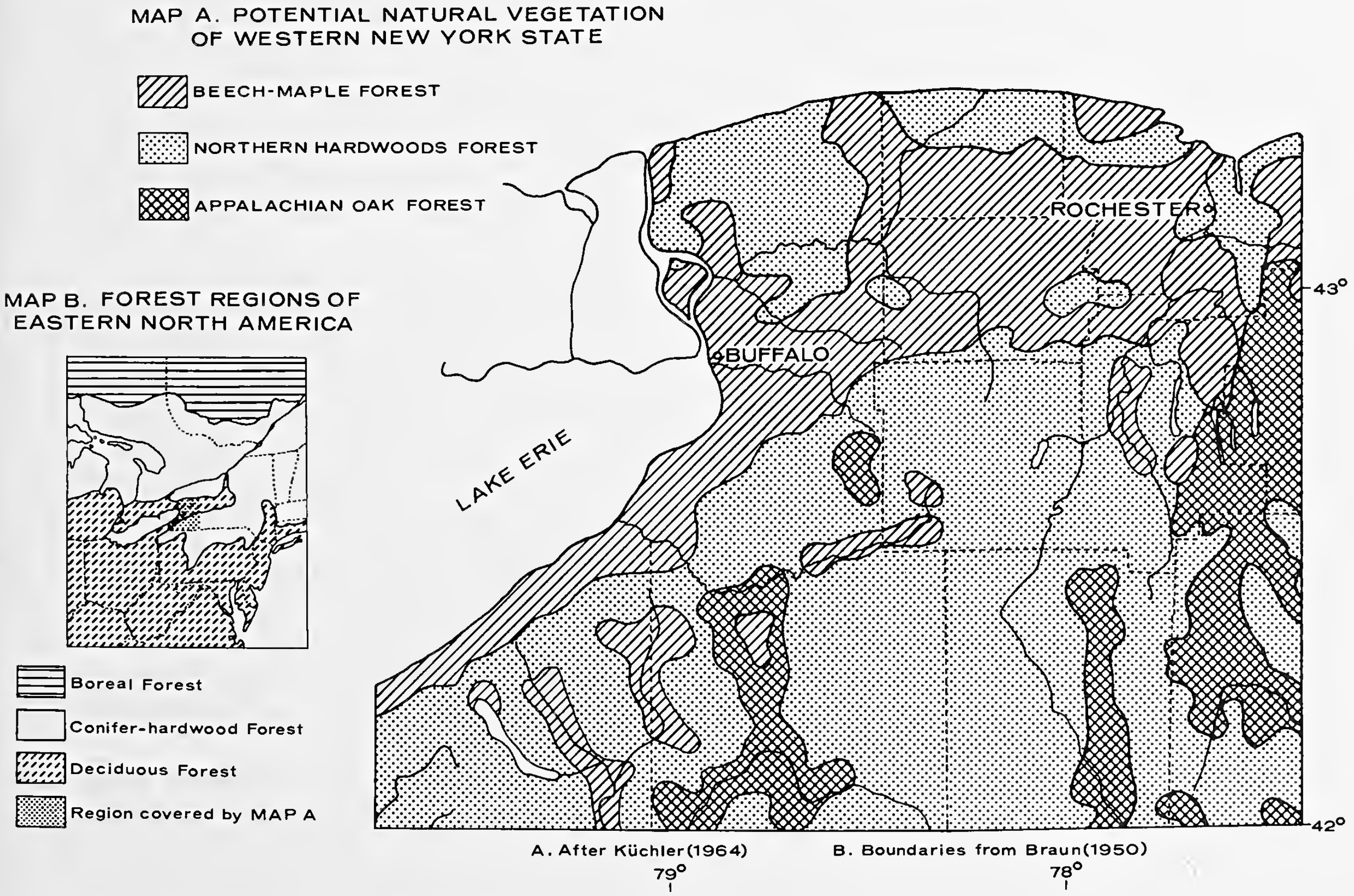
§ Includes nonproductive and productive but reserved forest land.

vegetation that would exist today if man were removed from the scene and if the resulting succession were telescoped into a single moment" (Küchler, 1964, p. 2), is mapped, while in the other, the actual or "real" vegetation determined by a survey of existing forests (during the period 1949–1952) is represented. Armstrong and Bjorkbom's work tells us what the general pattern and composition of existing forest vegetation is and, for this reason, a brief discussion of their units and those of Küchler follows. The area of currently existing forests in western New York is given in table 2.

The Northern hardwoods forest is distributionally equivalent to the Maple-beech-birch forest type of Armstrong and Bjorkbom. Maple-beech-birch forest is mapped as occurring widely across the upland but having a more restricted distribution in the lowland. It is made up of stands in which 50 percent or more of the trees are *Acer saccharum, Betula alleghaniensis,* and *Fagus grandifolia,* either singly or in combination. In addition, *Pinus Strobus, Tilia americana, Tsuga canadensis,* and *Ulmus* sp. often occur in such stands. Similarly, the Beech-maple forest region of Küchler is nearly the same as Armstrong and Bjorkbom's region of Elm-ash-maple forest, which is composed of stands in which 50 percent or more of the trees are *Acer rubrum, Fraxinus* sp., and *Ulmus* sp., by themselves or together. The widespread occurrence of this forest type north of the Portage escarpment today indicates the prevalence of swamp forests in the lowland. The Appalachian oak forest of Küchler is areally equivalent to the Oak-hickory forest of Armstrong and Bjorkbom. In the latter type of forest, 50 percent or more of a stand is in oak species.

Limited areas of other types of forest not noted by Küchler are also recognized by Armstrong and Bjorkbom. Small tracts of the White-red pine type are mapped southwest of Lake Chautauqua and along Cattaraugus Creek in southern Erie and northern Cattaraugus Counties. White pine is the dominant species in stands of this type and common associates include *Tsuga canadensis, Populus* spp., *Betula* spp., and *Acer* spp. Native red pines are very rare in western New

FIGURE 3. VEGETATION MAPS



MAP A. POTENTIAL NATURAL VEGETATION OF WESTERN NEW YORK STATE

MAP B. FOREST REGIONS OF EASTERN NORTH AMERICA

A. After Küchler (1964)

B. Boundaries from Braun (1950)

York. Small areas typed as Aspen-birch forest occur in the Cattaraugus Creek Valley just west of the white-red pine area, in south-central Erie County, and in north-central Allegany County. These forests contain mainly aspen because, of the two birch codominants listed, only *Betula papyrifera* is native to western New York and is a rare species that does not occur in either area of Aspen-birch forest (see Zenkert, 1934). The other birch, *Betula populifolia,* is found eastward from central New York State to New England.

The distinction between the deciduous forest of the lowland and the coniferous-deciduous forest of the upland is discussed more fully by E. Lucy Braun (1950) in her monograph on the forests of eastern North America. As depicted by Miss Braun, the boundary separating these two forest types also coincides with the Portage escarpment (see figure 3, map B). The Beech-maple forest region (which is mapped as extending from central Indiana, southern Michigan and western Ohio; around Lake Erie, and across southern Ontario and northeastern Ohio to northwestern New York State) is located north of the escarpment, and a portion of the Hemlock-white pine-northern hardwoods forest region occurs south of it. This forest region extends westward from maritime Canada and northern New England, across southern Ontario and Quebec, to western Minnesota, and includes seven subdivisions characterized by forests of somewhat different composition, each of which occurs in distinct parts of the total region.

The Mixed mesophytic and the Oak-chestnut forest regions, as these are mapped by Miss Braun, closely approach western New York. The former extends from the Allegheny and Cumberland plateaus northward along the Allegheny River to the New York State border, while Oak-chestnut forest occurs across the east flank of the Appalachians to central Pennsylvania and northward to southern New England, with an extension up the Hudson River Valley.

Forests of the Erie-Ontario Lowland

The forests of the Beech-maple region in northwestern New York are imperfectly known. Although, as its name implies, *Fagus grandifolia* and *Acer saccharum* are the dominant trees throughout the entire forest region, many other species are present, and in the Erie-Ontario Lowland, oaks and hickories are particularly abundant. This suggests that the beech-maple area in western New York may not be solely an eastward extension of the deciduous forest of the Midwest, but that it may have affinity to the Oak-chestnut region of the eastern United States. This relationship has been emphasized by Bray (1915). It is also clearly depicted by Shantz and Zon (1924) who, in treating the vegetation of the United States, map what they call Chestnut-chestnut oak-yellow poplar forest throughout the lowland areas adjacent to Lakes Erie and Ontario in a wide band on either side of the Hudson River up to about Glens Falls and in most of the larger river valleys in the southern part of New York State. They represent these areas as northern extensions of oak forests of the same type which occur in broad areas on both sides of the Appalachians.

The only available detailed study of the vegetation of the deciduous forests of western New York (Shanks, 1966) deals specifically with Monroe County (see figure 1). However, its findings apply in general to other parts of the Erie-Ontario Lowland. Analysis of notes made by the first land surveyors and study of existing woodlots and original forest remnants permitted Shanks to prepare a map of the original vegetation of the county. Planimetric measurements of areas occupied by the vegetation types recognized shows the Beech-sugar maple type to account for 61 percent of the original vegetation cover. In order of decreasing areas, the remaining types were Hemlock-northern hardwoods (12 percent), Upland oak and Oak-hickory (11 percent), swamp forest (6 percent), Oak-chestnut-pine (4 percent), Mixed mesophytic (2 percent), and bog forest (2 percent). Today, in contrast, only 16 percent of the county is forested (Northeastern Forest Experiment Station, 1967).

Occurring on a wide variety of soil types, Beech-sugar maple forest covered more than half of Monroe County at the time of settlement. Both beech and sugar maple tend to maintain themselves at the better sites, and data are available which indicate that they succeed less mesophytic species. Typical beech-sugar maple stands exhibit abundant regeneration of the dominants. Sugar maple seedlings often form a continuous undergrowth, and beech root sprouts are generally abundant. Often codominant in forests of this type is *Tilia americana.* Other common associates include *Ulmus americana, Fraxinus americana, Ostrya virginiana, Acer rubrum, A. nigrum, Quercus rubra, Carya ovata, Prunus serotina,* and *Liriodendron tulipifera.*

Areas of Hemlock-northern hardwoods forest were originally found at the northeastern and northwestern corners of the county, mostly on the Lake Iroquois plain and in sheltered ravines near the Genesee River.

This forest type is dominated by *Tsuga canadensis, Fagus grandifolia,* and *Acer saccharum* which at places occur with *Betula alleghaniensis, Tilia americana, Acer rubrum, Fraxinus americana, Quercus rubra, Ostrya virginiana, Prunus serotina,* and *Ulmus americana.* Hemlock-northern hardwoods forests have a dense canopy, and light intensity on the forest floor typically is very low. Characteristic shrubs and herbs include *Acer pensylvanicum, Aster acuminatus, Dryopteris spinulosa* var. *intermedia, Lonicera canadensis, Lycopodium lucidulum, Maianthemum canadense, Sambucus pubens,* and *Taxus canadensis.*

The Oak-chestnut-pine type occurs on the driest sites which, in Monroe County, are underlain mostly by sandy deltas deposited in glacial lakes. An exact equivalent is probably not present westward across Genesee, Orleans and Niagara Counties for (although the three dominant oaks, *Quercus alba, Q. rubra,* and *Q. velutina* occur in these areas as does one of the dominant pines, *Pinus Strobus*) *P. rigida* is at present native no farther west than the vicinity of Rochester. There are no records of its occurrence westward in the State. Originally a member of this kind of forest, *Castanea dentata* has been eliminated as a canopy dominant by the chestnut blight.

Several other types of oak forest grow at slightly more mesophytic sites. The Upland oak type, in which *Quercus alba, Q. rubra,* and *Q. velutina* are the usual dominants, occurs on the tops and sides of drumlins and kames and on dry, flat-lying, gravelly soils of high porosity. *Carya ovata* is a frequent codominant and, at certain locations, additional species of *Carya* may attain dominance resulting in the Oak-hickory type. Transitional Oak-sugar maple associations occur at favorable locations between lowland Beech-sugar maple and Upland oak forests. Other transitional communities called Mixed mesophytic forests occupy positions between Oak-chestnut-pine and Hemlock-northern hardwoods types and, in some cases, in conjunction with Upland oak forests. Such transitional types, which generally are characterized by a large number of tree species occurring in about equal abundance, are of limited distribution in the county.

Large swamp forests were widely distributed in Monroe County and probably occupied about 6 percent of the total area. Deficient soil aeration is an important factor preventing invasion of the swamp habitats by more mesophytic species. In order of decreasing abundance, the following species occur in various combinations as dominants in different phases of the swamp forest: *Ulmus americana, Acer rubrum, A. saccharinum, Tilia americana, Fraxinus americana, Quercus bicolor, Fraxinus pennsylvanica,* and *F. nigra.*

Across the Erie-Ontario Lowland in forests of all types, Dutch elm disease has made serious inroads on *Ulmus* populations. The role of *U. americana* as a dominant or subdominant has ceased to exist over wide areas.

Forests of the Allegheny Plateau

The forest vegetation of the upland south of the Portage escarpment, as already noted, is mapped by Braun (1950) as part of the Hemlock-white pine-northern hardwoods forest region. More specifically, nearly all of southern New York and northern Pennsylvania is placed in the Allegheny Section of the Northern Appalachian Division which includes forests covering much of the northeastern United States and Canada south of the Gulf of St. Lawrence. It differs from the other major unit of the forest region, the Great Lakes-St. Lawrence Division, in the presence of *Picea rubens* which occurs at higher elevations throughout the mountains of the Northeast; in the absence of *Pinus Banksiana* and the rarity of *P. resinosa;* in the admixture of *Liriodendron tulipifera, Magnolia acuminata,* and other species characteristic of the central deciduous forest; and in the presence of certain herbs and shrubs including *Aster acuminatus, Tiarella cordifolia,* and *Viburnum alnifolium.*

The Hemlock-white pine-northern hardwoods region includes the Birch-beech-maple-hemlock (northeastern hardwoods) forest of Shantz and Zon (1924); the Beech-birch-maple forest type as it is recognized in Pennsylvania (Illick & Frontz, 1928); the Lake forest of Weaver and Clements (1938) the Maple-beech-birch forest type as it is applied by Armstrong and Bjorkbom (1956) to New York State; the Great Lakes-St. Lawrence forest region of Canada (Rowe, 1959); the Northern hardwoods region as identified in south-central New York State and north-central Pennsylvania (Goodlett & Lyford, 1963); the Northern hardwoods, the Northern hardwoods-fir, the Great Lakes pine, the Great Lakes and Northeastern spruce-fir, and the Conifer bog forests of Küchler (1964); and the Beech-birch-maple and White pine-hemlock-hardwood forest regions as applied throughout the northeastern United States by Lull (1968). Further equivalents and a review of the literature pertaining to the recognition of the Hemlock-white pine-northern hardwoods forest region are given by Nichols (1935).

The original forest cover of upland southwestern New York has been greatly modified by lumbering and by clearing for agricultural purposes. However, because of low agricultural potential, upland counties have at present the largest areas of commercial and noncommercial forest land of any at the west end of the State (see table 2). Here, as elsewhere in western New York, an important stimulus for forest clearance during the early period of settlement was the demand for ashes which remained after burning cut trees. Crude field ashes were worth four to nine cents a bushel and, if the settler wished to refine these somewhat, 600 bushels could be leached and boiled down into a ton of pot or pearl ash (also called black salts) worth $125 to $150 (Munro, 1804; Young, 1875). Lye manufactured in this manner was used to make soap.

The nature and composition of the original forest is indicated by several virgin tracts preserved in northwestern Pennsylvania. These include the East Tionesta Creek Tract (Hough, 1936a) and Hearts Content (Lutz, 1930b) (both of which are in the Allegheny National Forest) and nearby Cook Forest (Morey, 1936). Hough and Forbes (1943) have summarized the numerous studies of forest remnants in this region.

Judging from early land survey records for a 175,000 acre tract in northwestern Pennsylvania (Lutz, 1930a), the forest existing today along the East Tionesta Creek is fairly typical of that which originally covered dissected areas of the Allegheny Plateau, particularly N-facing slopes. In both abundance and frequency values, *Tsuga canadensis* and *Fagus grandifolia* are the dominant canopy trees on plateau tops and on middle and lower slopes (Hough, 1936a). Third in order on middle and lower slopes is *Betula alleghaniensis,* but *Acer saccharum* holds this rank on plateau tops. In order of decreasing totals of abundance and frequency values, associated species are *Acer rubrum, Prunus serotina, Fraxinus americana, Liriodendron tulipifera, Magnolia acuminata,* and *Tilia americana. Viburnum alnifolium* is the most abundant shrub in forests of this kind and common herbaceous plants include *Dryopteris spinulosa, Lycopodium lucidulum, Maianthemum canadense, Mitchella repens, Oxalis montana,* and *Tiarella cordifolia.*

Within this type of forest, there is a tendency toward segregation of hemlock-beech, beech-hemlock-sugar maple, and beech-sugar maple communities, which differ from one another in the relative abundance of dominants. Hough (1936a) and Morey (1936) suggest that there is an alternation in the occupation of a given spot by hardwoods and hemlock-hardwoods. Uprooting or death of the hemlocks permits understory hardwoods to become established as canopy trees, while removal of canopy hardwoods, either catastrophically or by aging, allows hemlock seedlings to grow and dominate the canopy once again. In Cattaraugus County, forest of the Beech-sugar maple type originally occupied the better drained soils near ridge tops and was apparently more extensive in the glaciated portion of the plateau (Gordon, 1940). However, in this region today, most is of secondary origin, having developed after the removal of hemlock and white pine for lumber. *Fagus grandifolia* and *Acer saccharum* comprise 97 percent of the canopy in an undisturbed beech-sugar maple stand on a northeast slope in the Big Basin at Allegany State Park (Braun, 1950, Table 82).

White pine has an interesting position in the virgin forests of northwestern Pennsylvania. It is absent from the East Tionesta tract, but at Hearts Content, 30 mi to the west, it is abundant both in the hemlock and in the hemlock-beech communities. An age analysis shows the pine to have started as an even-aged stand at about 1680 (Lutz, 1930b). Similar data gathered at other localities on the Allegheny Plateau indicate that the presence of white pine can nearly always be correlated with fire, windfall, or some other event that opens a portion of the forest for seeding (Hough & Forbes, 1943). If no openings are made, the white pine apparently matures, dies, and is replaced by hemlocks or hardwoods, but not by other white pines.

Forest communities essentially the same as those in the Allegheny National Forest have been preserved at a few places in southwestern New York State, both outside and inside the glacial boundary. Gordon's map (1940) of the vegetation of Cattaraugus County at the time of settlement, which was prepared by analyzing the original lot survey data in conjunction with an examination of stands existing in the 1930's shows that the prevailing forest type in this area belonged to the Hemlock-white pine-northern hardwoods forest. Hemlock-northern hardwoods communities with little or no white pine comprised the typical stand. Quantitative data are unfortunately not available but a virgin tract of forest in Stoddard Hollow in the Big Basin at Allegany State Park has " a composition almost exactly similar to the Hemlock-Beech association at Heart's Content " (Gordon, 1937, p. 39). The principal trees on lower slopes in the Big Basin in order of decreasing abundance are *Fagus grandifolia, Tsuga canadensis, Acer saccharum,* and *A. rubrum* (Braun, 1950, Table 82). Together they total 87 percent of the canopy. The leading dominants in the Hemlock-beech association at Hearts Content are *Tsuga canadensis, Fagus grandifolia, Acer rubrum, Pinus Strobus,* and *Castanea dentata* in order of decreasing totals of relative frequency and density for each species, recalculated in part from data provided by Lutz (1930b).

A number of other forest types are also recognized in Cattaraugus County (Gordon, 1940). As in Monroe County, drier sites which, in the upland, occur on ridges and exposed south and southwest slopes, were occupied by forest of the Oak-chestnut type. *Quercus alba, Q. rubra, Q. prinus,* and *Q. velutina* are now typically the dominant trees at these sites, but prior to about 1934, before being eliminated by the chestnut blight, *Castanea dentata* was codominant. Associated species, which sometimes reach dominant status, include *Pinus Strobus, Acer rubrum, Carya glabra, Betula alleghaniensis, Populus tremuloides,* and occasionally others. Similar communities also occur on dry S-facing slopes throughout northwestern Pennsylvania (Hough, 1936a). In Cattaraugus County, secondary forests rich in oak species commonly result after fires and excessive logging. Goodlett and Lyford (1963) have mapped the current extent of oak forest, using *Quercus alba* as an indicator species, to the east just beyond Allegany County. Species with frequencies greater than 50 percent in oak forests studied by these workers include *Quercus rubra, Q. alba, Acer rubrum, Pinus Strobus, Quercus velutina,* and *Q. Prinus.* Such forests occupy a greater area in this region than they do in western New York and Pennsylvania.

Communities transitional between the Oak-chestnut type of dry slopes and ridges and the Beech-sugar maple and Hemlock-beech types of the lower, more mesophytic sites are considered to be somewhat attenuated examples of Mixed mesophytic forests which occur across much of the southern part of the unglaciated Allegheny Plateau. Similar communities have been recognized at places in the Erie-Ontario Lowland associated with Upland oak forest (Shanks, 1966). Mixed mesophytic forests in Cattaraugus County occupy moist, well-drained, and well-aerated sites favorable to the growth of a wide variety of tree species. Such forests are dominated by *Quercus rubra, Fagus grandifolia, Acer rubrum, Betula alleghaniensis, Fraxinus americana, Prunus serotina* and, formerly, *Castanea dentata. Magnolia acuminata, Quercus alba, Liriodendron tulipifera, Pinus Strobus, Tilia americana, Carya cordiformis, Acer saccharum, Ostrya virginiana,* and *Acer pensylvanicum* can also occur.

Similar communities occur today in other areas of the upland. For example, in a stand near Lily Dale in Chautauqua County (Braun, 1950, table 85), the following trees comprised the canopy (in percent): *Tsuga canadensis* (20.9), *Fagus grandifolia* (16.9), *Prunus serotina* (12.4), *Acer rubrum* (11.3), *A. saccharum* (8.5), *Pinus Strobus* (8.5), *Magnolia acuminata* (5.7), *Quercus rubra* (5.6), *Fraxinus americana* (4.5), *Betula alleghaniensis* (2.8), *Tilia americana* (1.7), and *Carya ovata* (1.1). *Acer saccharum* accounted for 37 percent of trees in the second layer indicating potential for greater dominance by this species in the future.

Two additional forest types restricted to bottomlands have been recognized in Cattaraugus County (Gordon, 1940). The White pine-American elm forest occupied flood plains of the major rivers and streams in the county, especially those filled with impervious lacustrine sediments. The great value of *Pinus Strobus* as a timber tree led to the early destruction of these forests, but their former distribution has been well documented (*ibid.*). The largest area of this forest, occu-

TABLE 3

FOREST STAND DATA: GENERAL INFORMATION

Stand Name	Date Sampled	Soil Type	Drainage Class	Topography
Canadaway Creek	Sept. 1966	Volusia silt loam or Bath (Wooster) silt loam (Morrison *et al.,* 1919)*	well, or somewhat poorly	gently rolling, nearly flat-lying; lacustrine sediments (Muller, 1963)
Erie County Plantation #11	June 1966	Bath (Wooster) gravelly loam (Taylor *et al.,* 1929)	well	rolling, weak morainic topography
NYS Zoar Valley Property #12	Aug. 1966	Bath (Wooster) silt loam (Taylor *et al.,* 1929)	well	gentle NW-facing slope

* The topographic base on which this soil map was printed is apparently misdrawn in the vicinity of the stand as more recent maps show somewhat different relief and stream arrangement in the area. For this reason, it is impossible to determine which of the two soil types lay beneath the stand. A more recent soil association map for Chautauqua County shows the area covered by soils of the Langford-Erie Association, which contains soils very similar to those belonging to the Bath-Mardin-Volusia Association (Feuer *et al.,* 1955).

pying many hundreds of acres, occurred along the axis of the preglacial Allegheny River whose course ran toward Lake Erie from the northwest side of the Salamanca reentrant along what is today Conewango Creek (see Muller, 1963 for further details). These forests also contain *Fraxinus nigra, Quercus bicolor, Acer rubrum, Betula alleghaniensis, Tsuga canadensis,* and, occasionally, *Abies balsamea* and *Larix laricina.*

Of less widespread occurrence are the Bottomland hardwood forests which are found on recently deposited alluvium, especially along the Allegheny River and Cattaraugus Creek and their tributaries. These forests are variable in composition, but they are by no means as rich in numbers of species as the bottomland forests of Ohio and southern Michigan. *Populus deltoides, Salix nigra, Acer Negundo,* and *A. rubrum* are frequent along disturbed stream courses, while *Platanus occidentalis* and *Juglans cinerea* are found on the more stabilized flood plains.

Stands Sampled by the Point Quarter Method

During the summers of 1965 and 1966, the composition of some existing forest remnants in the upland around sites where cores for pollen analysis were collected was determined by studying 35 woodlots. The samples were scattered across southwestern New York State from western Chautauqua County to central Steuben County. Notes were taken on nearly all of the stands and three were sampled by the point quarter method (Cottam & Curtis, 1956) using an eight by six point grid in which the points were 20 m apart along the line of march. The presence of seedlings[6] over and under 30 cm tall and the presence of herbs was tallied by species within a meter-square quadrat centered over each of the 48 points. The area around each point was then divided into four quarters using the transect line as a bisect and a second line passed through the point at right angles to the bisect. Bamboo wands temporarily marked these lines. For each of the quarters, the distance between the point and the nearest tree, its species and diameter at breast height were recorded. The four trees were generally well beyond the original meter-square quadrat. Within an area one meter on each side, of a line between the points, the number of saplings of various species was tabulated.

The three stands were chosen because they met the following criteria: (1) size greater than 15 acres to reduce the influence of surrounding fields and secondary forests, (2) absence of disturbance in the form of fire, grazing, or excessive cutting (none or very little during the past 40 years), and (3) occurrence on upland soil types. The data for each stand were divided into four equal parts and a Chi-square test of homogeneity was applied to determine if the number of major tree species within any segment deviated significantly from the number expected on the basis of uniform distribution (Curtis & McIntosh, 1951). In no case did Chi-square values exceed the expected values at the 5 percent level, indicating that the stands were homogeneous according to this test.

The location of the stands in relation to the sites selected for palynological study is shown in figure 2. Other pertinent data concerning the stands are summarized in table 3. Relative frequency (percent frequency), density (percent occurrence), dominance (percent basal area), and the sum of these three figures (the importance value), in addition to the absolute density (number of trees/acre) and dominance (basal area/acre), were calculated for each species in the tree and sapling classes (Curtis, 1956). The relative frequency of seedling and herb species was also computed. These data are given in appendixes A through F.

Although too few in number to permit complete assessment of variability in existing forests of southwestern New York, the sampled stands nevertheless provide quantitative data on the composition of several upland communities. *Acer saccharum, Fagus grandifolia,* and *Tsuga canadensis,* in order of decreasing importance values, are the dominants in all three stands. High importance values for sugar maple, beech, and hemlock saplings indicate continued dominance by these species, although hemlock seedlings are less frequent than seedlings of the other two species. While quantitative data for comparison are not available, the three stands belong to the Hemlock-white pine-northern hardwood forest of Nichols (1935). This unit is recognized by Gordon (1937, 1940) to be the climatic climax of the entire upland in southwestern New York State where it is expressed by associations in which *Tsuga canadensis* occurs by itself or mixed with *Fagus grandifolia, Acer saccharum,* and *Betula alleghaniensis.* Although present in all three of the stands sampled, *Betula alleghaniensis* has uniformly low importance values. Since this species reproduces best at moist sites (Hough & Forbes, 1943), the three stands may not be edaphically suited to greater domination by yellow birch.

In Erie County Forestry Department Plantation #11 (appendix C), *Prunus serotina* has a relatively high im-

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[6] Size classes follow Curtis (1959). *Trees* are greater than 4 in (ca. 10 cm) in diameter at breast height (d.b.h.); *saplings* are between 1 in (2 cm) and 4 in d.b.h., and *seedlings* are less than 1 in d.b.h.

portance value as a tree, but the sample includes no saplings. However, seedlings, mostly plants with cotyledons still attached, ranked second in frequency in the meter-square quadrats. These data accord well with the behavior of black cherry as it is known in the forests of northwestern Pennsylvania *(ibid.)*. Although black cherry seedling mortality is high in this region, a few always survive, growing slowly in moderate shade, and if logging, fires, or windthrow expose them to full sunlight, they are able to outgrow all important competitors. Several well-rotted stumps in Plantation ♯11 are evidence that selective cutting, perhaps as long ago as the turn of the century, may have been the factor which opened the stand enough to allow the establishment of *Prunus serotina* in the canopy.

The fourth and fifth most important tree in two of the stands is *Tilia americana,* but this species was not encountered while sampling the third. Judging by early land survey notes (Lutz, 1930a) and data published by Braun (1950), Gordon (1940), and Hough (1936a), basswood is a fairly consistent member of forests in various successional stages across the northern Allegheny Plateau. It is also a member of the mature forests in the East Tionesta Tract. White ash, *Fraxinus americana* occurs in all three sampled stands, but its importance values (in the tree class) are slightly lower than those for *Tilia*. Seedlings and saplings of *Fraxinus americana* are fairly abundant in the virgin forests of northwestern Pennsylvania, and while this species maintains itself there as well as *Betula alleghaniensis* does, *Fraxinus americana* is more successful in terms of persistence than *Prunus serotina* (Hough & Forbes, 1943).

Of the 16 herbs listed by Nichols (1935) as characteristic of the Hemlock-white pine-northern hardwood forest region, only the following appeared in quadrats in all three sampled stands: *Dryopteris spinulosa* var. *intermedia, Viola canadensis, V. incognita,* and *V. rotundifolia.* Others such as *Actaea pachypoda, Lycopodium lucidulum, Maianthemum canadense, Mitchella repens, Oxalis montana, Trillium erectum,* and *T. grandiflorum* were present in one or two of the stands, but eight additional species mentioned by Nichols were not encountered in any quadrats. A total of 49 species of herbs was recorded, although many other species were noted outside the quadrats. It is interesting that in all three stands at the time of sampling, *Arisaema triphyllum* and *Viola incognita* had the highest relative frequency values of herbaceous plants identified to species.

R Values

One assumption basic to using pollen analysis to investigate vegetation change is that a relationship exists between the number of pollen grains in a sediment sample and the abundance of the one or more species that produced this pollen in the vegetation surrounding the site of deposition. However, studies which have related pollen rain to contemporary vegetation demonstrate that the relationship is often not proportionate (Curtis, 1959; Davis & Goodlett, 1960; Janssen, 1967; McAndrews, 1966). Although some pollen types in surface samples apparently are represented accurately in relation to the abundance of the parent plants, others are either overrepresented or underrepresented. The causes of disproportionate representation are many, but most important are the great variability in pollen production by different species, the type of pollination and ease with which pollen dispersal takes place in wind pollinated species, and differential susceptibility of pollen to degradation by chemical and biological agents once deposition has taken place.

When interpreting fossil pollen assemblages, one way to compensate for disproportionate representation is to apply numerical correction factors based on the relationship between the percentage of one type of pollen in a sample and a quantitative abundance measure of the one or more species producing that type in the vegetation (Davis, 1963). Pollen percentages are available throughout a sediment column, but there is no known method of determining corresponding forest composition in other than two levels: (1) the surface pollen spectrum, where the vegetation can be directly sampled or its composition derived from published studies, and (2) the pollen spectrum immediately below the presettlement to postsettlement boundary where original survey records, which include quantitative data amenable to ecological analysis, can be used to estimate composition. It is the ratio between the pollen percentage of a given species and its vegetational percentage that provides a correction factor, or R value (*ibid.*, 1963), which, when divided into the number of pollen grains of that species as they are tallied by spectra along the sediment column, adjusts pollen counts to conform more closely to presumed abundance of species in the vegetation. Pollen types with R values <1 are underrepresented in sediments, those with values >1 are overrepresented, and those with values about 1 are proportionately represented.

At present, pollen of different species of *Betula, Carya, Quercus,* and *Ulmus* cannot be identified except, in the case of *Betula,* by time consuming size-frequency measurements. Therefore, only generic level R values can be obtained for these taxa. Because other pollen types can be identified to species, however, R values for these apply to units which are of greater usefulness in ecological interpretation.

R Values From U.S. Forest Service Survey Statistics

The Northeastern Forest Experiment Station (1967) has published the most recent quantitative data on the present vegetation of southwestern New York State. This information was collected during a resurvey of the forest resources of the state undertaken to update an initial survey completed in 1952 (Armstrong & Bjorkbom, 1956) and to obtain an estimate of the total timber volume, total periodic tree growth, and other statistics of use principally to foresters and economic planners. The sampling design used in both surveys is fully described by Bickford *et al.* (1963).

Perhaps the most meaningful figures in the resurvey data for calculating R values are those of total volume by species on commercial forest land. To facilitate this computation, raw data listing commercial timber species 5 in and greater in diameter in millions of cubic feet have been recalculated as percentages. The percent total volume figures for species recognized in the survey are listed by county in table 4. The figure which pertains to a given species within the county where the bog is located was used in R value calculation.

Surface samples analyzed for pollen were collected at sites where sediment sampling was done. In each case, the sample taken was from a fairly dense but actively growing sphagnum polster and comprised the upper 1 to 2 cm from an area of about 10 cm^2. Two subsamples from each were macerated in the laboratory and their residues were ultimately combined and counted together. Inasmuch as about 50 percent of the total pollen in surface spectra is contributed by herbaceous plants, reflecting the large area of nonforest land in southwestern New York State (see table 2), counts were recalculated using the sum of arboreal pollen as the percentage base. This is necessary because the forest composition percentages are based on total forest land, not on land of all classes. R values calculated from these two sets of data are listed in table 7.

R Values From Original Lot Survey Data

The original land survey of western New York was privately sponsored, but was similar in organization to the rectangular pattern used in the General Land Office Survey of public lands west of the Appalachian Mountains. This system of surveying was authorized by Congress in 1785. Prior to this time metes and bounds, the establishment of property boundaries according to

TABLE 4

PERCENT TOTAL VOLUME OF TREES * ON COMMERCIAL FOREST LAND IN EIGHT WESTERN COUNTIES IN NEW YORK STATE †

County Tree Species	Chautauqua	Cattaraugus	Allegany	Erie	Wyoming	Niagara	Genesee	Orleans
Acer saccharum	23.7	21.8	24.9	18.6	19.3	18.6	17.6	18.1
Fagus grandifolia	8.6	9.0	8.5	4.6	4.7	4.4	4.3	4.5
Tsuga canadensis	8.6	8.4	8.9	5.1	4.7	5.0	5.1	4.9
Betula alleghaniensis	1.0	1.2	1.0	1.8	1.7	1.7	1.8	1.4
B. lenta	1.1	1.3	1.0	0.5	0.4	0.6	0.4	0.3
Fraxinus americana	6.5	6.0	5.7	8.9	9.0	9.2	9.4	9.4
Tilia americana	3.8	4.0	3.6	8.0	8.3	8.6	7.8	7.6
Prunus serotina	3.4	3.6	3.3	3.9	3.8	3.9	3.9	4.2
Ulmus sp. or spp.	2.7	3.0	2.8	9.4	8.5	8.6	10.8	9.0
Acer rubrum	13.2	12.9	13.5	14.7	14.3	14.2	14.9	13.9
Quercus spp.	15.0	15.0	14.6	5.9	5.6	6.4	5.5	6.6
Carya spp.	2.1	2.4	2.0	5.6	5.7	5.6	5.3	5.9
Pinus Strobus	2.0	2.1	1.9	4.0	4.4	4.2	3.5	4.9
P. resinosa	3.7	3.6	3.5	2.1	3.2	2.5	1.8	2.8
Populus sp. or spp.	3.1	3.9	3.3	2.7	2.3	2.8	3.3	3.1
Misc.‡	1.6	1.8	1.5	4.4	4.0	3.9	4.7	3.5

* Commercial tree species 5 in in diameter or greater.

† Data from Table 11 in " Preliminary forest survey statistics by counties and units, New York — 1967," Northeastern Forest Experiment Station, U.S. Forest Service, Upper Darby, Pennsylvania.

‡ Includes other hardwoods and softwoods.

natural features, was practiced (Bourdo, 1956). In the rectangular survey of western New York a grid of north-south range and east-west township lines bounding townships generally 6 miles square was laid out west of a line extending north from central Allegany County through eastern Wyoming, Genesee, and Orleans Counties, the area encompassed by the Holland Purchase (Evans, 1924; Turner, 1850). The number of townships per range varied from 16 in the eastern ranges to three in far western Chautauqua County. These townships have only partly retained their identity as political units in contrast to those in the region surveyed by the rectangular method to the west.

The surveying of township and range lines began under the direction of Joseph Ellicott in the spring of 1798, shortly after the Holland Land Company acquired clear title to western New York, and continued until 1800. The internal survey of townships into lots was largely completed by 1810 but a few of the townships in southern Cattaraugus County were not divided until 1819. It was the custom in the Ellicott survey to mark each lot corner with a post. Records were kept of the direction, diameter, and species of from one to four bearing-trees located in different quarters surrounding the post. Since land sale was of paramount concern, Ellicott directed his surveyors to take careful notes on the topography, soils, timber, windfalls, springs, and other natural features along the survey lines. When running a lot line the surveyors made a list of the predominant timber encountered and, if the forest composition varied along a lot line, several lists were recorded. It is perhaps reasonable to assume that species listed were arranged in order of decreasing abundance, as they were in the General Land Office surveys, but no evidence exists that this was the case.[7]

Lot survey data[8] for the region around the sites where the presettlement to postsettlement boundary is preserved in the pollen record have been compiled. Estimates vary as to the area which contributes to the pollen rain accumulating at a given point. Faegri and Iversen (1964) consider that in forested regions pollen is not transported in significant quantities for more than 50 km (ca. 30 mi), while Tauber (1967) mentions much shorter distances. Data for an area, seven lots by seven lots (ca. 30 mi^2), was used around Allenberg and Houghton bogs. The area of study around Protection Bog had to be restricted to a tract of 16 mi^2, however, because the notes for western Wyoming County could not be located. Examination of additional data beyond the included lots suggests that the basic data would not be altered greatly by enlarging the areas investigated except that more species of infrequent mention would appear.

The data collected were analyzed in two ways. Since the bearing-trees recorded by the surveyors represent a low density sample of the forest within each of the three areas, the relative frequency, relative density, and relative dominance of each species noted can be calculated following the methods used in treating the forest stands discussed earlier. The sum of these three measures, or the Importance Value, for all the species within one area totals 300, but for purposes of R value computation, the percent total for each of the species, or an importance percentage (McAndrews, 1966), was calculated. Trees mentioned along lot lines were treated in a different manner. For each area the total number of times a given species was mentioned was tallied and this sum was rendered as a percentage of the total trees of all kinds mentioned throughout the area. Percentages from both kinds of data were used as denominators for R value calculation. Pollen percentages used as numerators in the ratios were provided by the first spectrum immediately below the presettlement to postsettlement boundary which is clearly marked by a sharp increase in the pollen of *Ambrosia, Plantago,* and other genera associated with forest clearance. The percentage

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[7] The richness of data included in the Ellicott survey is illustrated by notes pertaining to Lot 60, T. 9 R. 5 (southeastern Erie County) extracted from field books kept at the Erie County Clerk's Office, Buffalo, New York.

The boundary line of this lot begins at a beech post marking the northeast corner and passes westward across an upland of the first quality timbered with beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), bass (*Tilia americana*), and elm (*Ulmus* sp.) to an upland of the second quality, then across a deep gully and abruptly back again to an upland of the first quality with hemlock, beech, and sugar maple (*Acer saccharum*) timber, and finally to a beech post at the northwest lot corner. Southward from this point the line passes through land considered excellent for meadow and timbered with sugar maple, cherry (*Prunus serotina*), bass, and elm, to a sugar maple post at the southwest corner of the lot. A short distance to the east of the post, the line descends into an intervale of the first quality timbered with buttonwood (*Platanus occidentalis*), elm, white ash (*Fraxinus americana*), and bass, crosses a stream, and rises onto an upland of the first quality. It then crosses two adjacent streams separated by land with hemlock and beech timber, from where it passes through a sugar maple stand on upland of second quality with yellow loam soil to a beech post at the southeast corner of the lot. Northward, returning to the point of origin, the line extends through land broken by deep gullies and covered with hemlock, beech, and sugar maple timber. The surveyor listed seven bearing-trees, two at each of three posts, and one at the fourth. One of these was a hemlock 8 in in diameter; the remaining six were beeches, 6, 7, 8, 12, 24, and 30 in in diameter.

[8] Notes for Houghton and Protection Bog areas are kept by the Erie County Clerk. Both areas were surveyed by Cotton Fletcher in 1807 and 1808. Notes pertaining to the Allenberg Bog area are on file with the Cattaraugus County Clerk, County Building, Little Valley, New York. Also available for this county are plat maps on which bearing-trees are noted at lot corners. I have been unable to determine who made the survey.

base used in this calculation includes both arboreal and nonarboreal pollen types because the latter were only sparsely represented and did not greatly reduce percentages of tree pollen types.

In all three areas, *Fagus grandifolia* accounts for 50 to 75 percent of the sum of bearing-tree importance values (see table 5). *Acer saccharum* is consistently second in importance. *Tsuga canadensis* and *Betula alleghaniensis* rank third and fourth in the Houghton and Protection Bog areas and sixth and fifth around Allenberg Bog. About the same arrangement of species occurs in the frequency of mention values which are listed in decreasing order in table 6. *Fagus grandifolia* is the most frequently mentioned tree, followed by *Acer saccharum*. *Tsuga canadensis* shares the third position with *Tilia americana* around Allenberg Bog; it ranks fourth around Houghton Bog, being preceded by *Tilia americana,* and third around Protection Bog where *T. americana* directly follows it in importance. In most cases the three species with the highest bearing-tree importance and frequency of mention values in the survey data are also the three leading species in the data from the stands studied by the point quarter method.

Both estimates of presettlement forest composition may be biased. *Fagus grandifolia* was by far the commonest bearing-tree, but whether beech was indeed the dominant tree in the forest around the bogs might be questioned. Presumably, surveyors selected trees closest to the lot corner irrespective of species, but because beech has a light colored, easily marked bark and is of lesser value as a timber tree, they may have chosen it as a bearing-tree over other species. Noting the preponderance of beech bearing-trees throughout Cattaraugus County, Gordon (1940) has concluded, however, that in spite of possible bias, beech was probably the most common tree in the original forest, a conclusion substantiated by the high percentage of beech pollen in presettlement spectra. *Tilia americana* was not used at all as a bearing-tree, although it had a fairly high rank in the frequency of mention data. This discrepancy perhaps can be explained because *Tilia* is not a long-lived, rot-resistant tree and is therefore not entirely suitable as a bearing tree. Its high position in the frequency of mention data may be in part a reflection of its value as an easily worked wood often employed in pioneer carpentry.

Discussion of R Values

The three sets of R values from the different bog areas are compared in table 7. Although ratios for certain pollen taxa are fairly consistent, others vary widely. The best example of the latter group is *Pinus* spp. whose values range from about 1 to 5 using the modern data and from 7 to 57 using the presettlement data. These figures, and particularly the ones derived from the presettlement data, emphasize pine pollen's typical overrepresentation. However, one difficulty in using surface sample pollen percentages to obtain R values representative of pine as it occurs in natural forests is that both native and exotic species now grow and contribute to the pollen rain in western New York. Thus pollen dispersal capacity of pines of both types influences surface counts. Since only native species are represented in presettlement spectra, the R values obtained from surface spectra cannot be applied indiscriminately throughout postglacial time. Another problem is that locally growing reforested pine stands may contribute more pollen to surface spectra than is typical of the region from which the vegetation composition data were derived. An R value of 5.0 at Protection Bog probably reflects the influence of several nearby mature, planted *Pinus resinosa* and *P. Strobus* stands. That local overrepresentation is indeed operative at this site is substantiated by the sharp decrease in *Pinus* subg. Pinus (*diploxylon* type) and *P.* subg. *Strobus* (*haploxylon* type) pollen percentages in the upper 5 cm of sediments. Pollen below this depth accumulated before the plantations existed.

R values for *Ulmus* spp. are also variable but to a lesser degree. They range from 0.5 to about 5.0, but most values are over 1.0, implying overrepresentation. Similarly, overrepresentation is indicated for *Quercus* spp. The R values for this pollen type calculated from the modern data suggest that the oaks are somewhat less than twice overrepresented, while the only presettlement value implies that they are nearly 13 times overrepresented. Little emphasis should be given to this one presettlement value, however, because of the rather small area used to obtain the percentage of oaks in the vegetation. Since *Quercus* pollen seems to be transported for fairly long distances, a much larger area should perhaps be sampled to gain an accurate estimation of the abundance of oak trees contributing to the pollen rain. In northern Vermont where *Quercus rubra* is the principal pollen-producing oak, Davis and Goodlett (1960) have found oak pollen to be the most overrepresented of all pollen types in their spectra. R values for *Tsuga*, with one exception, are fairly constant and imply that *Tsuga* pollen is also somewhat overrepresented. My figures compare fairly well with those calculated for hemlock in northern Vermont (*ibid.*), but differ from the correction factor for the species used

TABLE 5

Presettlement Survey Data: Relative Frequency, Relative Density, Relative Dominance, Importance Values, and Importance Percentages of Bearing-Trees used in the Original Lot Survey of the Areas Around Allenberg, Houghton, and Protection Bogs

Tree Species and Bog Area	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Importance Percentage
Fagus grandifolia					
Allenberg Bog area	70.1%	86.5%	84.1%	240.7	80.2
Houghton Bog area	65.2%	74.7%	71.4%	211.3	70.4
Protection Bog area	53.8%	62.3%	47.9%	164.0	54.7
Acer saccharum					
Allenberg Bog area	17.2%	8.7%	8.1%	34.0	11.3
Houghton Bog area	16.7%	12.1%	11.8%	40.6	13.5
Protection Bog area	26.2%	21.7%	22.2%	70.1	23.4
Tsuga canadensis					
Allenberg Bog area	1.2%	0.4%	1.4%	3.0	1.0
Houghton Bog area	7.6%	5.1%	9.8%	22.5	7.5
Protection Bog area	7.7%	6.6%	14.9%	29.2	9.7
Betula alleghaniensis					
Allenberg Bog area	2.3%	0.9%	2.3%	5.5	1.8
Houghton Bog area	3.0%	2.0%	2.1%	7.1	2.4
Protection Bog area	4.6%	2.8%	5.2%	12.6	4.2
Prunus serotina					
Allenberg Bog area	2.3%	0.9%	3.2%	6.4	2.1
Houghton Bog area	3.0%	3.0%	1.1%	7.1	2.4
Protection Bog area	——	——	——	——	——
Acer rubrum					
Allenberg Bog area	——	——	——	——	——
Houghton Bog area	——	——	——	——	——
Protection Bog area	3.1%	2.8%	5.8%	11.7	3.9
Ulmus sp.					
Allenberg Bog area	——	——	——	——	——
Houghton Bog area	3.0%	2.0%	2.1%	7.1	2.4
Protection Bog area	1.5%	0.9%	1.0%	3.4	1.1
Carpinus/Ostrya					
Allenberg Bog area	4.6%	1.7%	0.4%	6.7	2.2
Houghton Bog area	——	——	——	——	——
Protection Bog area	1.5%	0.9%	0.2%	2.6	0.9
Fraxinus americana					
Allenberg Bog area	1.2%	0.4%	0.4%	2.0	0.7
Houghton Bog area	——	——	——	——	——
Protection Bog area	1.5%	1.9%	2.9%	6.3	2.1
Pinus Strobus					
Allenberg Bog area	——	——	——	——	——
Houghton Bog area	1.5%	1.0%	1.7%	4.2	1.4
Protection Bog area	——	——	——	——	——
Juglans cinerea					
Allenberg Bog area	1.2%	0.4%	0.1%	1.7	0.3
Houghton Bog area	——	——	——	——	——
Protection Bog area	——	——	——	——	——

TABLE 6

Presettlement Survey Data: Frequency of Mention of Tree Species Along Lot Survey Lines for Areas Around Allenberg,* Houghton,* and Protection† Bogs

Tree Species	Allenberg Bog Area	Houghton Bog Area	Protection Bog Area
Fagus grandifolia	30.6%	30.0%	28.2%
Acer saccharum	22.1%	24.3%	17.3%
Tsuga canadensis	14.6%	11.1%	19.7%
Tilia americana	14.6%	13.0%	14.6%
Ulmus sp.	5.1%	6.2%	3.2%
Betula sp.	1.6%	3.2%	5.1%
Fraxinus americana	1.4%	5.4%	2.9%
F. nigra	1.0%	2.5%	3.9%
Acer rubrum	0.4%	0.5%	3.2%
Magnolia acuminata	1.8%	0.2%	0.7%
Prunus serotina	0.2%	2.1%	0.2%
Alnus sp.	1.4%	0.8%	0.2%
Castanea dentata	2.4%	——	——
Quercus rubra and/or *velutina*	1.0%	——	——
Juglans cinerea	——	0.3%	0.5%
Pinus Strobus	0.2%	0.3%	0.2%
Picea mariana	0.4%	0.2%	——
Abies balsamea	0.4%	——	——
Larix laricina	0.4%	——	——
Quercus alba	0.2%	——	——

* Area equal to 17,640 acres.

† Area equal to 10,080 acres.

in Wisconsin by Curtis (1959) who has multiplied numbers of hemlock pollen in fossil spectra by three to obtain proportional representation. Since R values differ from one major geographic region to another (see Comanor, 1968), the use of one correction factor over a wide area is inappropriate.

The R values for *Betula* spp., using both modern and presettlement data, indicate that it is greatly overrepresented, a finding that substantiates the studies in Vermont and Wisconsin cited above. Although I cannot be certain which species of birch produced a given pollen grain, it is likely that only two species, *Betula lenta* and *B. alleghaniensis*, contributed most of the birch pollen to the spectra because the other species reported from western New York, *B. papyrifera* and *B. pumila*, are rare in this region and occur mainly in the Erie-Ontario Lowland (Zenkert, 1934).

According to my data, only *Fagus grandifolia* and *Juglans cinerea* are proportionately represented. To these may be added *Carpinus-Ostrya* if the average of the two R values in the table is taken to be meaningful. The pollen of *Carpinus caroliniana* and *Ostrya virginiana* is morphologically very similar, so no attempt was made to tally these species separately. Since their autecology differs and the abundance of *Carpinus* in the vegetation is unknown, significance cannot be given to R values for this pollen type. Davis and Goodlett

TABLE 7

R VALUES CALCULATED USING VARIOUS ESTIMATES OF VEGETATION COMPOSITION

	Allenberg Bog			Houghton Bog			Protection Bog		
R values		Presettlement			Presettlement			Presettlement	
Pollen taxa	Modern	Importance % age	Freq. of mention	Modern	Importance % age	Freq. of mention	Modern	Importance % age	Freq. of mention
Pinus spp.	1.04	——	56.50	1.61	7.14	33.33	5.00	——*	38.00
Tsuga canadensis	1.40	23.60	1.62	2.08	2.81	1.90	1.33	2.53	1.24
Betula spp.	9.92†	8.61	9.69	10.26†	5.67	4.25	7.43†	2.43	2.00
Fagus grandifolia	0.70	0.22	0.58	1.37	0.36	0.85	1.48	0.42	0.82
Quercus spp.	0.97	——*	12.83	1.83	——*	——*	1.90	——*	——*
Acer saccharum	0.55	0.46	0.24	0.67	0.52	0.28	0.42	0.34	0.49
A. rubrum	0.22	——*	1.00	0.13	——‡	——‡	0.06	——‡	0.25
Carya spp.	0.79	——*	——*	0.25	——*	——*	0.23	——*	——*
Ulmus spp.	2.56	——*	0.57	1.23	1.38	0.53	0.53	4.73	1.63
Tilia americana	0.03	——*	0.03	0.03	——*	0.02	0.01	——*	0.07
Fraxinus									
4-colpate	0.22	0.57	0.29	0.11	——*	0.15§	0.17	1.00§	0.48
3-colpate	——	——*	0.70	——‖	——*	——*	——‖	——*	0.18
Populus spp.	0.38	——*	——*	0.74	——*	——*	0.81	——*	——*
Carpinus/Ostrya	——‖	0.23	——*	——*	——*	——*	——‖	2.11	——*
Juglans cinerea	——‖	0.67	——*	——*	——*	1.00	——‖	——*	——*
Castanea dentata	——‖	——*	0.29	——*	——*	——*	——‖	——*	——*

* Not present in presettlement vegetation data; † Forest survey percentages of *Betula lenta* lumped with *B. alleghaniensis;* ‡ Lumped with *Acer saccharum;* § Includes *Fraxinus* 3-colpate; ‖ No forest survey statistics available.

(1960) found the basal area percentage of *Ostrya virginiana* in a forest in northern Vermont to be nearly equal to the percentage of its pollen in surficial pond sediments. These authors have also found *Fagus grandifolia* to be ± proportionately represented, although the percentage of beech pollen in their surface sediment was slightly greater than the percentage of beech in the surrounding forest.

Acer rubrum, A. saccharum, Carya spp., *Castanea dentata, Fraxinus* 4-colpate (incl. *F. americana* and *F. pennsylvanica*), *F.* 3-colpate (*F. nigra*), *Populus* spp., and *Tilia americana* are underrepresented. Also in this category, although not listed in table 7, is *Prunus serotina*, a species which apparently is entirely insect-pollinated because its pollen was not found in any of the spectra analyzed even though black cherry did occur in the surrounding forest. The low values for *Tilia* and *Acer* species may likewise reflect the influence of insect pollen vectors.

Sangster and Dale (1964) have emphasized an additional reason for underrepresentation. They demonstrate that pollen of different species vary in their resistance to degradation, implying that species of low resistance will be underrepresented regardless of the amount of pollen they produce or the effectiveness of its dispersal. Working mostly with species native to eastern North America, these authors have experimentally shown *Acer saccharinum* and *A. saccharum* pollen to be less well preserved in peat than the pollen of species of *Betula, Fraxinus, Pinus, Quercus,* and *Ulmus,* and that *Populus tremuloides* pollen is the most severely degraded of all types investigated.

Similar results pertaining to *Populus* are implied in data from New York State. At the four stations in the southwestern corner of the state where airborne pollen data have been collected (Ogden & Lewis, 1960), *Populus* pollen is well represented, exceeding *Pinus* in numbers of grains per cm^2 of slide surface, and occasionally equalling such other heavy producers as *Quercus* and *Ulmus*. Similar counts do not occur in samples analyzed from bog surfaces. This may reflect both the ease and the speed with which *Populus* pollen is decomposed. Sangster and Dale in an earlier study (1961) show that 80 percent of fresh poplar pollen samples placed at the surface of a peat bog was degraded within 32 days.

Perhaps the most significant set of R values from the standpoint of the accuracy of the method used to estimate vegetation composition is that calculated from the Forest Service survey statistics. Since the three sites where the current pollen rain was determined are relatively close together and have more or less similar surface pollen spectra, one way to summarize R values of pollen taxa included in table 7 is to compute an average value for each. Arranged in decreasing magnitude and placed in the three classes of representation, these are: (1) overrepresentation—*Betula* spp., *Pinus* spp., *Tsuga canadensis, Quercus* spp., and *Ulmus* spp.; (2) proportional representation — *Fagus grandifolia*; and (3) underrepresentation — *Populus* spp., *Acer saccharum, Carya* spp., *Fraxinus americana* and/or *pennsylvanica, Acer rubrum,* and *Tilia americana.*

The Pollen Diagrams

(see page 102)

METHODS

Field Techniques

The four basins selected for palynological study (see figure 2) appear to be ice-block depressions. Protection and Houghton bogs are associated with the Valley Heads moraine and were chosen because their proximity permits regionally-significant trends to be determined in the pollen profiles. Parallel trends duplicated at many sites throughout a region are more important in reconstructing the pattern of vegetation change than smaller, short-term changes present at only one site. The two other deposits are located south of the Valley Heads moraine on drift deposited at an earlier time. Allenberg Bog is near the terminal position of the Kent moraine, and the Genesee Valley Peat Works is on a still older surface, apparently of Olean age.

At each site along a series of compass-oriented transects, sediment lithology and depths were determined with a Davis sampler (Eberbach, Ann Arbor, Michigan). As three of the four sites lack a central bog lake, traverses were easily made across the semi-firm bog surface. At the fourth site, a series of soundings around the mat at the edge of a small lake 50 m in diameter was made. The goal in all cases was to find the deepest spot in the basin at which samples for pollen analysis could be collected. At two of the sites, the upper sediments were too watery to be sampled with the equipment used so a supplementary sample series was taken in the firmer sediments to one side of the main sampling point.

Three standard samplers were available and these were employed depending on the nature of the sediments encountered. At most sites a Hiller sampler (Borros, Solna, Sweden) with a 50 cm chamber was used. This instrument worked best in coarse, fibrous peat of variable compactness, in finer peat deposited from water, and in the stiffer lake muds or gyttjas. Lake sediment was also collected with a Livingstone piston corer of the style described by Cushing and Wright (1965). An adapter, which allowed the sturdy Livingstone rods to be coupled to the head of the Davis sampler, was found to be particularly effective in penetrating heavier clayey sediments.

At Protection Bog, two samples for radiocarbon analysis were obtained with the Livingstone piston corer, equipped with a 2-inch barrel, from a location 50 cm to one side of the point where samples were taken for pollen analysis. Subsamples 10 cm in length were removed from the cores and submitted to Isotopes, Inc. for age determination. To check the location of the dated sediments in reference to the pollen diagram at this site, the pollen content of sediments immediately above and below the 10 cm segments was determined. These spectra match well those expected on the basis of depth alone (cf. diagram 1 and appendix G). The uppermost date at Protection Bog was based on peat collected with a specially made sampler, 4 in in diameter, built after the principle of the Livingstone piston corer. The bottom 10 cm of wet peat from the core was submitted for age determination.

The Houghton Bog date was obtained from wood which lodged in the Davis sampler during an exploratory probe of the area adjacent to the site where samples for pollen analysis were taken. An insufficient amount of wood was collected to permit both C-14 analysis and microscopic study, so identification was not attempted.

Extreme care was taken not to contaminate the samples collected for pollen analysis. When using the Hiller sampler, successively deeper samples 50 cm long were collected alternately from two holes 50 cm apart. The outer several millimeters of sediment uncovered by turning the outer sleeve to open the sediment chamber were cut away and discarded. The sediments thus exposed were removed with a micro-spatula from points midway between lines 5 cm apart stamped on the sampler head.

Individual samples were placed in pint polyethylene bags labeled with appropriate data. Cores collected with the Livingstone sampler were extruded in the field, wrapped in aluminum foil, labeled, and placed in plywood core boxes. Cores taken with the Davis sampler were also wrapped in foil and labeled in the field. Subdivision of the cores was done in the laboratory. All samplers were washed with clean water after each use. The sediment samples were refrigerated until macerated in the laboratory.

Laboratory Techniques

The standard methods for separating and concentrating pollen from sediments by removing inorganic and unwanted organic material were used in the preparation of the samples. A 1 cc subsample, measured with a glass graduated cylinder cut down to hold 1 ± 0.05 ml of water, was macerated in each case. The schedule employed during the maceration procedure depended on the type of sediment being analyzed.

Two main types of organic sediment were encountered. Pollen in peat was concentrated by following successively the steps detailed below:

(1) Place sample in 40 ml tapered centrifuge tube, cover with 10 percent KOH, and heat for 5 min in boiling water bath;

(2) Wash sample through ♯60 mesh sieve (250 μ) with enough distilled water to stop the KOH reaction (use sieve residue for identifying plants making up the peat);

(3) Centrifuge and decant; and

(4) Glacial HAc wash, acetolysis solution (Erdtman, 1960) in boiling water bath for 3 minutes, and glacial HAc wash.

Since gyttja, the other main kind of organic sediment found generally does not deflocculate in KOH, a partial breakdown of this sediment was accomplished using cold 10 percent HCl. The sediment was gently teased apart with a glass rod. After centrifuging and decanting the HCl, the sample was acetolyzed. If deflocculation had not completely taken place, the sample was heated for 5 minutes in 10 percent KOH in a boiling water bath. KOH was removed from the residue by centrifugation and distilled water washes.

Inorganic sediments containing calcium carbonate were treated first with 10 percent HCl, then acetolyzed, and, if necessary, finally treated with 10 percent KOH. Silty and clayey samples were exposed to cold, 72 percent HF for 24 hours culminated by an additional 30 minutes in a boiling water bath. After removal of HF by centrifuging and decanting, 10 percent HCl was added to the residue and the mixture heated in a boiling water bath for 3 minutes to dissolve colloidal silicon dioxide and silicon-fluorides. Residual acids were thoroughly washed from the organic residue with distilled water. Acetolysis, and in some cases exposure to 10 percent KOH, completed the maceration. If heavy minerals such as pyrite were present, heavy liquid separation (with zinc chloride, sp. gr. 1.93) immediately followed HF treatment.

After maceration, all residues were washed successively in distilled water, 96 and 100 percent ethyl alcohol, stained with 2–4 drops of safranin-0 in 100 percent ethyl alcohol, given a final 100 percent ethyl alcohol wash, and pipetted into labeled 3 dr vials. The staining was best if the residues soaked for 24 hours in distilled water prior to alcohol dehydration. Residues were stored in vials at room temperature until mounted for counting.

The technique used in mounting residues for microscopic study was devised to enable the calculation of the number of pollen grains per unit volume of sediment and is an adaptation of the method described by Davis (1965a, 1966). The residue was washed into a 12 ml graduated centrifuge tube with tertiary butyl alcohol (TBA) and brought to a known volume. After thoroughly mixing residue and TBA by vigorous pumping with a large bulb pipette, a certain volume of the mixture was removed from the tube with the pipette and from 3 to 15 drops were released onto a small amount of silicone oil (2000 cs) placed at the center of a slide on a slide warming table (ca. 75° C). Heat from the warming table rapidly evaporated the TBA leaving a mixture of silicone oil and residue.

To produce an even distribution of pollen grains under the cover slip, a dissecting needle was used to blend the pollen and the silicone oil. The needle was wiped clean on the underside of the cover slip, which was placed promptly downward over the preparation. After making three slides from each residue, TBA was removed from what remained of the residue with a 100 percent ethyl alcohol wash and the residue-ethyl alcohol mixture was pipetted back into the appropriate vials. It is necessary to carry out these procedures in a fume hood because of the noxious character of vaporized TBA. The volume of TBA-residue mixture in the graduated centrifuge tube and the number of drops of this used to make each slide were recorded.

Since the same pipette was used to mount every residue, the volume of one drop delivered by this pipette was more or less constant for all preparations. It was found, after 20 trials, that the pipette delivered 48.95 drops per ml. When counting, the number of traverses completed across a cover slip was recorded. Since in most cases the basic sum was reached before the entire area was examined, the following equation was used to determine the total number of pollen and spores under a cover slip: number of traverses / total number of possible traverses = sum of terrestrial pollen and spores / x, where x is the number of grains per slide or per y drops of residue-TBA mixture. Multiplying x by a factor, z ml of residue-TBA mixture in the centrifuge tube · 48.95 / y drops delivered to the slide, gives the number of grains per ml of wet sediment.

Although many potential sources of error are present in this technique, it is considered to give reasonably reliable results for the amount of time expended. To test the accuracy of the mounting technique, the number of arboreal pollen grains for an equal number of traverses in each of two or three slides prepared from the same residue was determined. These data, listed in table 8, show that the method delivers similar numbers of pollen grains to individual slides in a series.

TABLE 8

DATA FOR CHECK ON MOUNTING TECHNIQUE USED IN THE DETERMINATION OF ABSOLUTE POLLEN FREQUENCY

Sample Number	Number AP	Number of Traverses *
Pb 7020–1	262	22
Pb 7020–2	236	22
Pb 7156–1	116	44
Pb 7156–2	117	44
Pb 7156–3	122	44
Pb 7157–1	264	44
Pb 7157–2	261	44
Pb 7180–1	266	22
Pb 7180–2	272	22
Pb 7906–1	159	44
Pb 7906–2	156	44
Pb 7906–3	160	44
Pb 7907–1	188	44
Pb 7907–2	185	44
Pb 7907–3	207	44

* Using a magnification of 250 diameters, 44 traverses are generally possible with little or no overlap across a 22 mm^2 cover slip.

One serious cause of error develops when the residue becomes concentrated under some sector of the cover slip. If, for example, pollen counts were made only in a zone of high concentration, fewer traverses would be necessary to reach a given sum than if the residue were evenly dispersed under the whole cover slip area. In this case, the calculated estimate of the number of grains per unit volume would be greater than was actually true. Visual inspection and adjustment in the location of the traverses was used to overcome this potential source of error. In most cases parts of several slides were also counted to obtain a representative sample of the residue.

Counts were uniformly made using equispaced traverses controlled by a calibrated mechanical stage. Distance between the traverses was initially chosen with reference to the density of the pollen under the cover slip. At low density, traverses were made closer together. Counting was done routinely at a magnification of 250 diameters using a Leitz Ortholux microscope. Grains difficult to identify were examined using a 95 X apochromatic oil immersion lens. As an aid to identification of pollen encountered in the preparations, a large collection of reference slides was assembled and the standard pollen identification manuals were frequently used (Erdtman, 1943, 1957, 1965, 1966; Faegri & Iversen, 1964; Wodehouse, 1935).

At least 500 pollen grains of trees were counted in nearly all samples. The percentage base used to calculate the relative pollen frequencies at a given level is the sum of arboreal pollen (AP) and nonarboreal pollen (NAP) at that level (spores and pollen of aquatics and bog plants were excluded), as this figure best represents the regional upland pollen rain (Wright & Patten, 1963). The percentage base varied from spectrum to spectrum with the greatest differences occurring in the uppermost postsettlement and in the basal inorganic sediments where NAP is abundant. Relative frequencies of other pollen taxa, mostly bog plants, aquatics, and pteridophytes, were calculated using as a new percentage base the sum of the first percentage base and the total number of pollen and spores of the miscellaneous taxa at a given level.

Pollen grains and spores which were well preserved but which could not be identified due to inadequacies in the pollen reference collection were classified as unfamiliar. Grains in the unknown category were in part corroded or broken, in part obscured by debris, and in other ways rendered indeterminable.

SITES ASSOCIATED WITH THE VALLEY HEADS MORAINE

Protection Bog

This basin is a large, fairly shallow, ice-block kettle now nearly completely filled with sediment. Peat comprises the upper 3 to 4 m, and the bog plant communities which currently occupy the surface continue to add to the deposit. The kettle occurs at an elevation of 1410 ft in an area of morainic topography of Valley Heads age somewhat north of the head of the Chaffee outwash plain. To the east, north, and west, the surrounding hills rise 300 to 400 ft. The bog is located in the Town of Holland near the southeast corner of Erie County, 0.2 mi west of the Erie-Wyoming County line, 1.8 mi northeast of Protection at 42° 37′ 20″ N. lat. and 78° 28′ W. long. It is shown as a wooded marsh in the northwest sector of the Arcade 7½′ quadrangle. The bog and much of the surrounding land is currently

Figure 4

owned by the County of Erie whose Bureau of Forestry administers the area as Plantation #5.

The bog surface is covered with vegetation (figure 4), and there is no standing water except for a temporary lagg along the north edge of the mat. As measured by planimetry on an aerial photograph, the original lake occupied an area of about 22 acres. Of this, 15 acres are now nonforested and covered mainly by ericaceous shrubs with occasional clumps of tamaracks. The basin has an irregular outline with the long axis trending east-west. There is a prominent bay extending northward, and smaller bays, which are now covered with deciduous swamp forest, occur at the east and west ends of the basin. The steepest slopes above the basin are found on the north and south sides. An intermittent shallow stream occurs at the east end, but the basin has no permanent outlet or inlet. The stream which discharges into a tributary of Buffalo Creek apparently functions only at the peak of spring runoff as it is nearly dry during the summer.

In spite of the advanced stage of basin infilling, most of the major vegetation zones characteristic of bog succession are still evident. On the north, east, and west sides occurs a prominent, almost impenetrable, high shrub zone composed of *Vaccinium corymbosum, Pyrus melanocarpa,* and *Nemopanthus mucronata. Rhododendron nudiflorum* is also present but is less frequent. The western one-third of the open mat is occupied by a low shrub heath in which *Cassandra calyculata* is dominant. *Andromeda glaucophylla, Kalmia polifolia,* and *Vaccinium myrtilloides* are other shrubs occurring in this zone. *Eriophorum virginicum* and *Sarracenia purpurea* are typical herbs. *Sphagnum capillaceum, S. magellanicum,* and *S. recurvum* form a continuous carpet beneath the shrubs, and at places *Polytrichum juniperinum* var. *gracilius* and *Sphagnum fuscum* have built up hummocks. *Larix laricina* and *Pinus Strobus* seedlings are present throughout the low shrub zone. An island of *Larix laricina* trees 4 to 6 in in diameter occurs near the middle of the mat and extends eastward and southward. Large *Pinus Strobus* trees are present on humified peat along the west and northwest sides near the edge of the basin. *Picea mariana* does not occur at this bog.

Much of the upland around the basin was formerly under cultivation, although conifer stands planted during reforestation projects and secondary forests developing on abandoned fields currently occupy much of the area. The woodlot to the east and southeast of the bog is the least modified of any nearby forest remnant. On muck in the lower areas, *Acer rubrum, Betula alleghaniensis, Carpinus caroliniana, Prunus serotina,* and *Tsuga canadensis* are the principal trees. Typical herbs in this area include *Clintonia borealis, Coptis groenlandica, Oxalis montana, Medeola virginiana,* and *Trillium undulatum.* Upslope on better drained soil, *Acer saccharum* and *Fagus grandifolia* are abundant, and they occur with *Fraxinus americana, Tilia americana,* and *Tsuga canadensis.* Plantations of *Pinus resinosa, P. Strobus,* and *Larix decidua,* interspersed with untilled fields, occur south, east, and north of the bog. To the west and northwest, contiguous with the bog, is a narrow zone of open swamp forest in which *Acer rubrum* and *Ulmus americana* are the dominant trees. *Populus grandidentata* and *Crataegus* sp. are common at disturbed sites and abandoned fields around the bog.

Sediment Stratigraphy

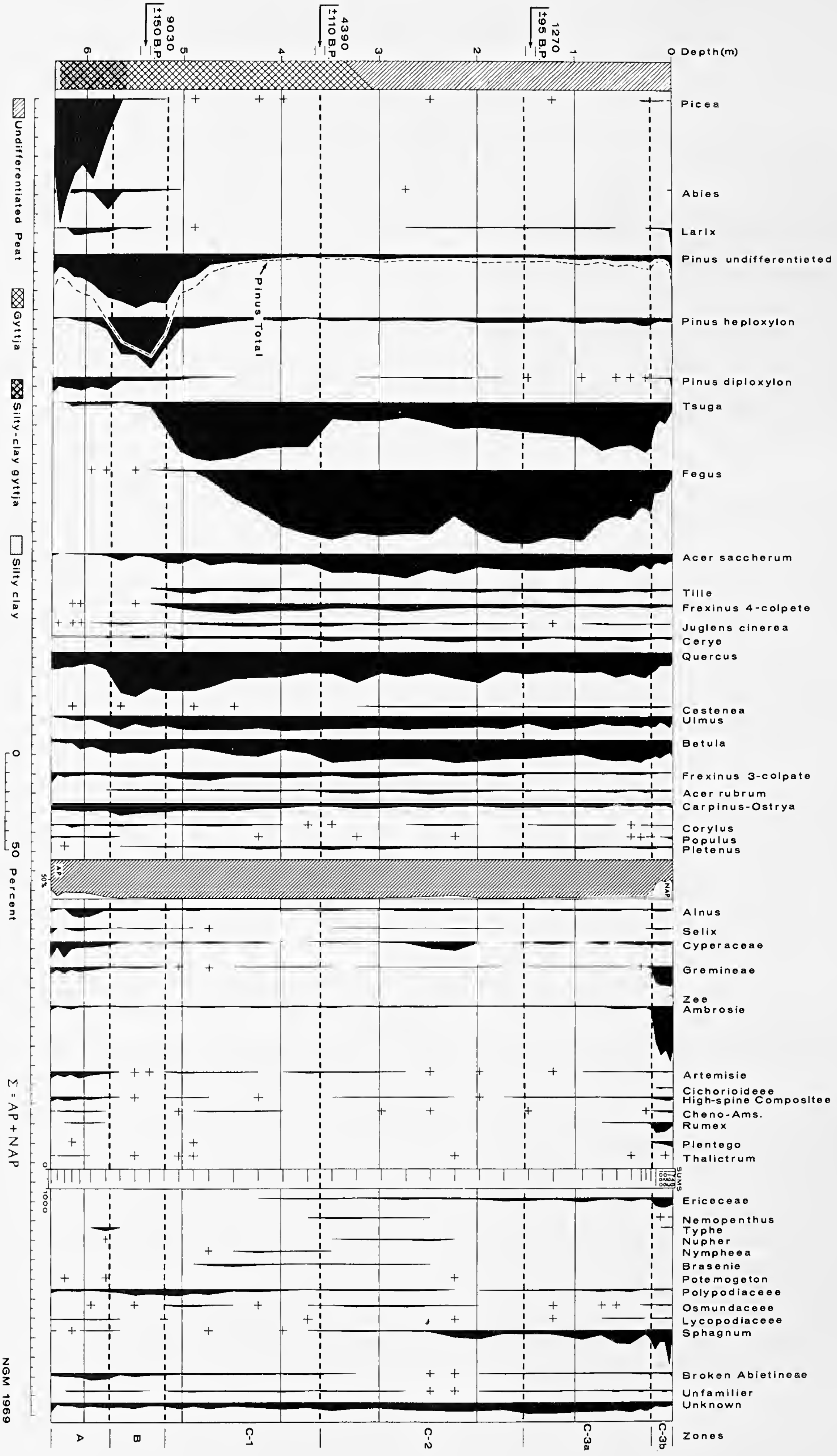
The bog was sampled on August 24, 1967, near the center of the basin. The Hiller sampler was used from the surface downward to 6 m, but, because of the compactness of the sediments, it was necessary to substitute the Davis head attached to the Livingstone extension rods to sample beyond this depth. The stratigraphy at the sampling point is:

Diagram 1

Protection Bog: Relative Pollen Frequency

0.00–0.10 m : peat, with sphagnum leaves, humified, dark brown;
0.10–0.90 m : peat, undifferentiated but with sphagnum leaves, reddish brown;
0.90–3.25 m : peat, undifferentiated but with sedge leaf fragments and other plant debris, coarse near the top but

PROTECTION BOG: RELATIVE POLLEN FREQUENCY



gradually becoming finer downward, reddish;

3.25–6.30 m : gyttja, soft, somewhat gelatinous, brown at top, gradually becoming stiffer and rubbery downward, with *Najas* seeds from 4.75 to 5.40 m, silt and clay admixture beginning at 5.60 m, mostly brown or reddish brown;

6.30–6.33 m : silty-clay, with some medium sand at bottom; bluish-gray. The sediments could not be penetrated farther with equipment used.

Houghton Bog

Located 12 mi southwest of Protection Bog, Houghton Bog occupies an ice-block depression in a pitted outwash plain which extends southward from the Valley Heads moraine past the village of Springville to Cattaraugus Creek. Houghton Bog is one of the larger of the many basins which dot this plain. Most of the depressions have filled with sediment, but several open lakes are also present. Of these, Dead Mans Lake is most prominent. The outwash fan forms a minor divide, separating drainage in a general northward direction to Eighteen Mile Creek and the West Branch of Cazenovia Creek from drainage southward to Cattaraugus Creek.

Houghton Bog is situated in the Town of Concord, 2.3 mi north of Springville between US 219 and Sharp Street at 42° 32′ 30″ N. lat. and 78° 40′ 13″ W. long. and is shown as an area of wooded marsh on the Springville 7½′ quadrangle. The basin occurs in a forest remnant about 45 acres in area, which is completely surrounded by tilled and fallow fields. Little of the original forest remains within a 3 mi radius of the bog. The basin, as measured on an aerial photograph, covers about 18 acres. The shoreline occurs between the 1400 and 1410 ft contour lines. Except for about 5 acres occupied by an open mat (figure 5), the depression is now entirely forested. The bog is owned by the Nature Sanctuary Society of Western New York, Inc., which attempts to maintain it in an unmodified condition.

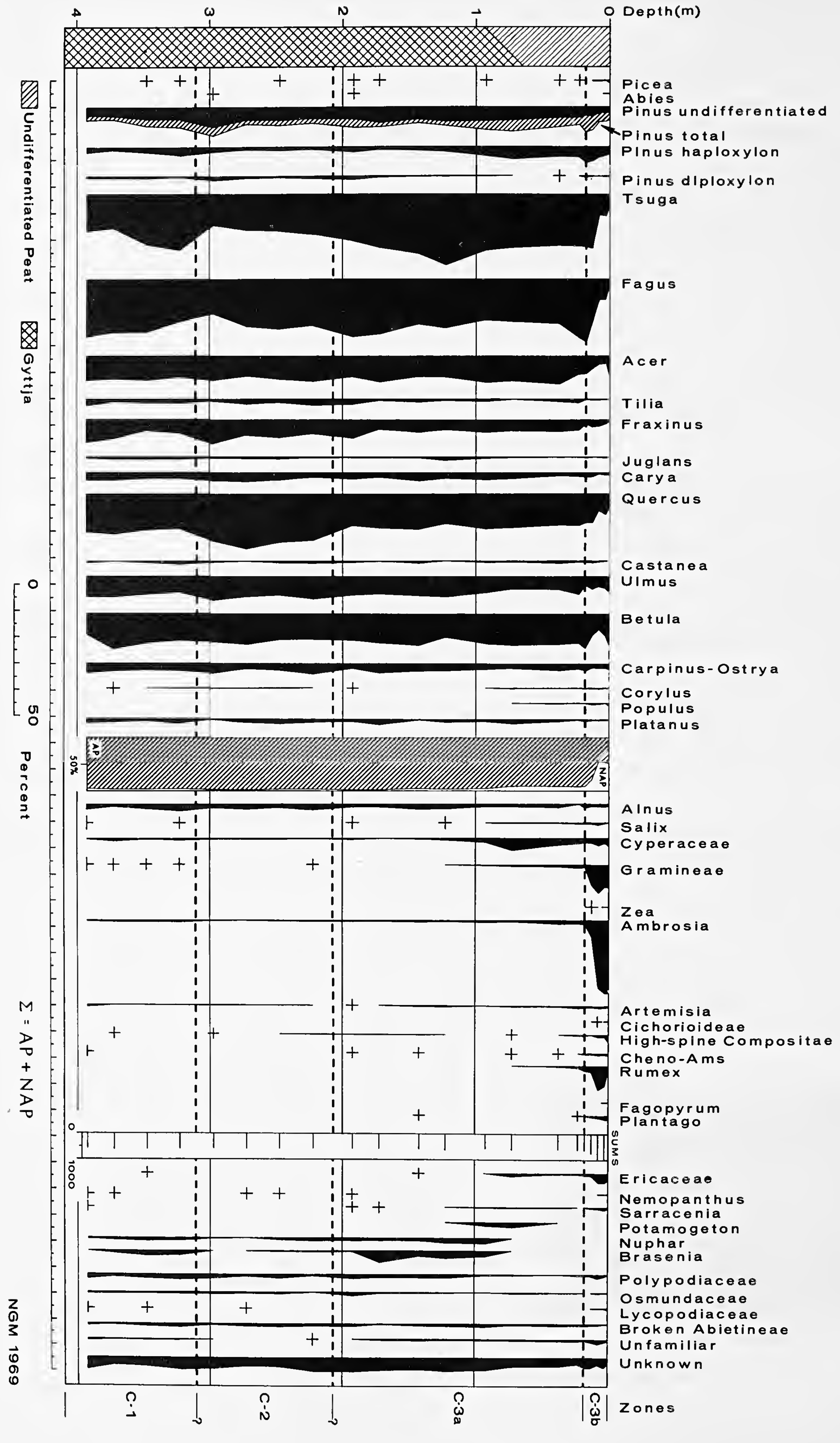

Figure 5

The long axis of the basin has a north-south orientation. Beyond the main depression, two shallow bays extend to the north and south (Brosius, 1953). These must have rapidly filled with sediment for the upper layer is strongly humified and now supports a swamp forest. The 5 acre bog mat extends entirely across the surface in a northwest-southeast direction. The mat is thinnest near the southeast end where the weight of a man is sufficient to cause water to seep upward. No permanent outlet or inlet is present, although a low area which apparently is the route for excess spring runoff extends southward to join a tributary of Spring Brook. The slopes immediately above the basin are gentle. The surface of the outwash plain is rolling and uneven and in general no more than 20–30 ft above the mat surface. Nearby hills rise about 300 ft above the surface of the plain.

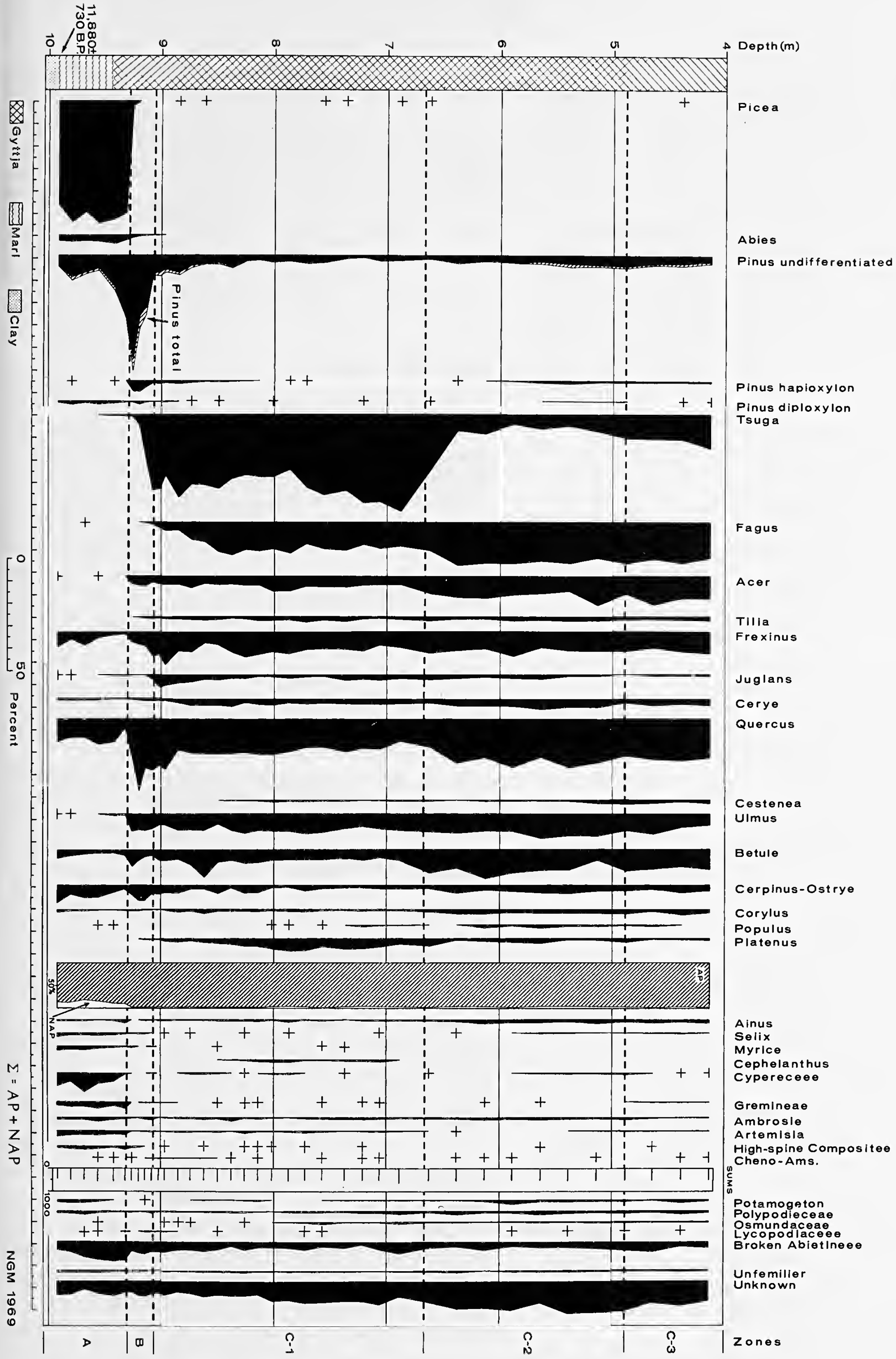
The bog is surrounded by a strip of forest of variable width. On the slope above the mat, the main tree species are *Acer saccharum, Betula alleghaniensis, Fagus grandifolia, Prunus serotina, Tsuga canadensis,* and *Ulmus americana.* Adjacent to the north and northeast bog margin occurs a somewhat larger woodlot. This stand was heavily logged in the past and is now occupied by trees of small diameter, mostly *Acer saccharum* and *Fagus grandifolia.* A few *Prunus serotina* trees are also present, and *Tsuga canadensis* seedlings were noted. On the wetter, organic-rich soil between the edge of the basin and the open mat, a swamp forest of *Acer rubrum, A. saccharinum, Betula alleghaniensis, Pinus Strobus, Prunus serotina, Tsuga canadensis,* and *Ulmus americana* occurs. At places in the swamp forest, *Taxus canadensis* forms a dense cover. *Pinus Strobus* is particularly abundant along the south and west margins of the bog mat.

A narrow high shrub zone of *Nemopanthus mucronata, Pyrus melanocarpa,* and *Viburnum cassinoides* occurs between the swamp forest and the open mat. *Cassandra calyculata* is the dominant shrub throughout most of the open mat, but *Kalmia polifolia, Vaccinium myrtilloides,* and *V. Oxycoccos* are also present. *Carex canescens, C. pauciflora, C. trisperma, Rhynchospora alba, Sarracenia purpurea,* and various bog orchids are restricted to certain parts of the mat. The main *Sphagnum* species include *S. capillaceum* var. *tenellum, S. fuscum, S. magellanicum,* and *S. teres; S. cuspidatum*

HOUGHTON BOG-SECTION A: RELATIVE POLLEN FREQUENCY



HOUGHTON BOG - SECTION B: RELATIVE POLLEN FREQUENCY



occurs in the wetter areas near the southeast end. *Pinus Strobus* seedlings are abundant on the grounded mat; *Larix laricina* is restricted to the southeast and northeast corners of the mat. *Picea mariana* does not occur at Houghton Bog.

Sediment Stratigraphy

Because of a water pocket beneath the mat, two series of samples were collected at Houghton Bog. Section A was taken on October 17, 1966, with the Hiller sampler near a small stand of tamarack located one-half the distance toward the center of the basin, 56 m S. 10° E. of the sampling point for section B. The stratigraphy of section A is:

Diagram 2

Houghton Bog — Section A: Relative Pollen Frequency

0.00–0.10 m : peat, humified, dark brown;
0.10–0.60 m : peat, undifferentiated but with sphagnum leaves, light reddish brown;
0.60–0.85 m : peat, undifferentiated but with sedge leaf fragments, somewhat coarse grading downward into finer texture, gray to dark gray;
0.85–4.00 m : gyttja, soft, with some sedge leaf debris near top, becoming stiffer downward, gray.

Section B was collected on September 1, 1966, somewhat east of the center of the open mat using a Hiller sampler between 4.00 and 8.00 m and a Livingstone piston corer with a 2 in tube beyond 8.00 m. The stratigraphy at this point is:

Diagram 3

Houghton Bog — Section B: Relative Pollen Frequency

Diagram 4

Houghton Bog—Section B: Absolute Pollen Frequency

0.00–0.75 m : peat, watery, fibrous, with sphagnum leaves, no samples taken;
0.75–4.00 m : finely comminuted plant debris in water, few seeds present near bottom, no samples taken;
4.00–9.43 m : gyttja, soft and gelatinous at top with small amount of plant debris, gradually becoming stiffer and more rubbery downward, brownish throughout;
9.43–9.95 m : marl, with dark brown and reddish laminae; Mollusca and charophyte oogonia abundant, strongly calcareous, whitish gray;
9.95–10.04 m : clayey silt, dense with gravel near bottom, carbonized wood fragments present sporadically, mostly dark gray but somewhat brownish, sharp contact with marl above. Further penetration impossible.

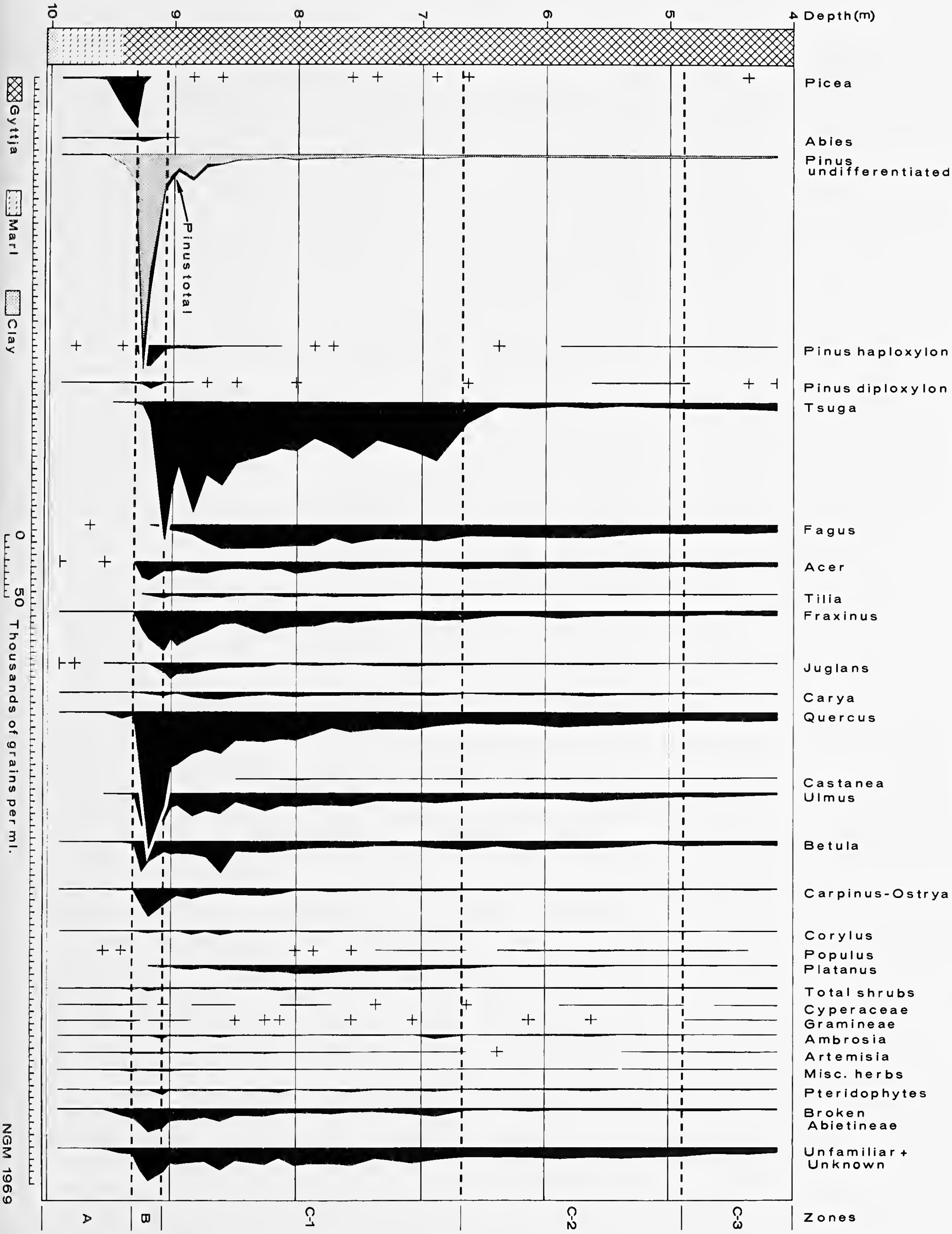
Pollen Stratigraphy

In the following discussion, pollen diagrams have been divided into zones using the letter designations that Deevey (1939) first applied to his New England pollen profiles. These have found wide usage in the Northeast. Zone C, the uppermost, is characterized by pollen of hardwoods and hemlock and can generally be subdivided into three main parts. Below this in order are zone B which is dominated by pine pollen and zone A in which abundant spruce pollen is found. Zone T (Leopold, 1956b) is an interval beneath the A zone in which NAP percentages are high.

I am aware of the recent trend toward describing pollen assemblage zones from bog and lake sediments in accord with the Code of Stratigraphic Nomenclature (see Cushing, 1967) rather than extending the use of letter zone designations developed in one region to distant geographical areas. But I feel, as does Livingstone (1968), that zones are " to be regarded as temporary divisions of convenience, to be used as reference points in discussions of the underlying trends in the pollen curves . . . [and that they] . . . should not be enshrined under the protection of a code involving strict rules of description and priority " (p. 95). There are chronological reasons, and perhaps climatic ones as well, for extending Deevey's zones to western New York. It should be understood, however, that floristically and vegetationally, the zones are not the same in New England and western New York nor, for that matter, in most other places where they are used. This is clearly brought out by Deevey (1957) in a summary table in which he compares pollen sequences from northern Maine, southern Connecticut, and Michigan by subdividing them into A, B, and C zones.

Because of the close similarity between the pollen diagrams for Protection (diagram 1) and Houghton bogs (diagrams 2, 3, and 4), they will be discussed together. Minor pollen types not included in the diagrams are listed in appendixes H, I, and J.

HOUGHTON BOG-SECTION B: ABSOLUTE POLLEN FREQUENCY



Zone A. In the lowermost spectra at both bogs, 40 to 50 percent of the sum is comprised of *Picea* pollen. It is about five times more abundant than pollen of any other type. Although both records may be truncated at the bottom, there is no clear indication of a T zone beneath zone A at either site. At Protection Bog, however, the abrupt decline in the spruce curve which, below the maximum at 6.265 m, is caused by a 25 percent NAP high may, in part, record the transition from herb- to spruce-dominated vegetation. The number of terrestrial pollen grains and spores rises rapidly from about 18,000 to 140,000 grains/ml of wet sediment between 6.325 and 6.195 m. Assuming a constant rate of sedimentation across this interval, the change parallels that reported for Rogers Lake, Connecticut during the T to A zone transition (Davis, 1967b).

At Houghton Bog a similar change occurs, but it is not as readily interpreted (diagram 4). The deepest sediment sampled at this location was a dark gray, silty clay, apparently barren of pollen. Upward, passing abruptly into marl, the number of grains per unit volume is at first very low, 2000 to 3000 grains/ml (figure 6), but rises to 60,000 grains/ml in the first gyttja sample immediately above. Because of the change in sediment stratigraphy, it is unlikely that the rate of sedimentation was constant from the clay upward through the marl to the base of the gyttja. It seems probable that the marl was deposited rapidly, resulting in a lower number of pollen and spores per unit volume. Unfortunately, close interval radiocarbon dating is the only method at present which can be used to determine accurately the sedimentation rate, and age determinations are not available for Houghton Bog. However, at Rogers Lake (Davis & Deevey, 1964; Davis, 1967b), Seth's Pond, Massachusetts, and Silver Lake, Ohio (Ogden, 1967a), fairly uniform rates have been demonstrated. These involve about a twofold to threefold increase from the late-glacial time through nearly all of the postglacial except the most recent.

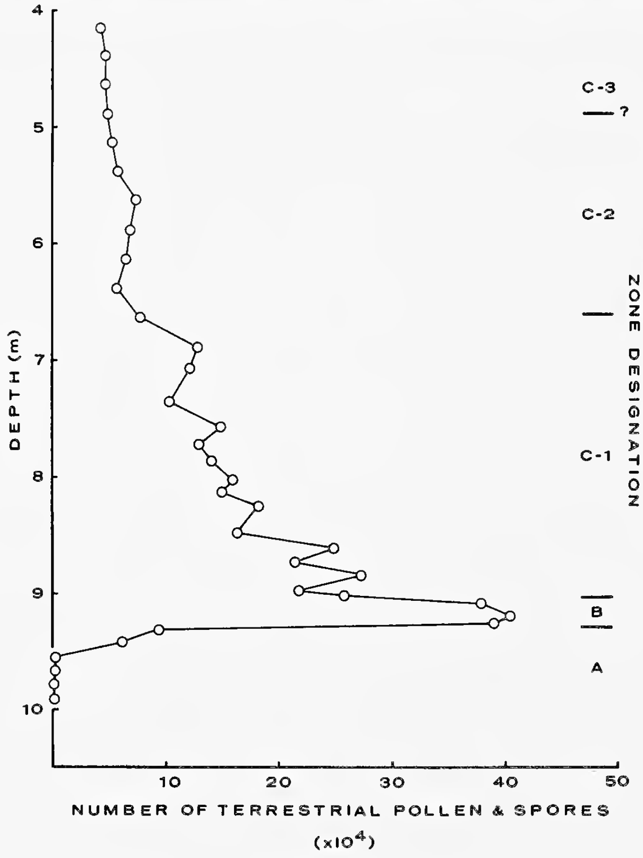


Figure 6

At Protection Bog, possible subdivision of the A zone into a *Picea-Abies* subzone is suggested by the prominent peak in the *Abies* curve near the top of the zone. The greatest percentage of *Abies* pollen at Houghton Bog also occurs in the upper part of the A zone. *Larix,* although not encountered in zone A sediments at Houghton Bog, accounts for about 5 percent of the sum in the middle portion of the A zone at Protection Bog, decreases upward, and finally drops out of the counts in zone B. *Pinus* pollen regularly comprises 10 to 15 percent of the total in the lower levels of both bogs, but, upward, its percentage gradually increases until the maximum is reached in zone B.

Three different categories of pine pollen were counted. The basic separation was between grains which could be identified as belonging to the softwood pines, *Pinus* subg. Strobus, which in northeastern North America includes only *Pinus Strobus* (see Little & Critchfield, 1969) and the hardwood pines, *P.* subg. Pinus, which in this region includes *P. Banksiana, P. resinosa,* and *P. rigida.* The germinal furrow (Ueno, 1958), located between the bladders on the distal face of the pollen grain, is verrucose in subg. Strobus (called *Pinus* haploxylon in the pollen diagrams), whereas the furrow is smooth in subg. Pinus (*Pinus* diploxylon in the diagrams). The third category, *Pinus* undifferentiated, contains grains that could not be oriented to permit observation of the furrow, those grains in which the exine between the bladders was missing, and reassembled grains (the number of which was determined by keeping track of the larger fragments and then dividing the sum of these by an appropriate figure to reduce the sum to the number of whole grains). Diagram 1 shows that pollen of subg. Pinus was most abundant in zone A. This also is illustrated in diagram 3, but less prominently. The sum of the three categories is graphed as *Pinus* total.

Ulmus pollen is found in low percentages near the bottom of zone A but gradually increases to about 7 percent near the top of the zone at Protection Bog. From 1 to 2 percent *Ulmus* occurs at an equivalent stratigraphic position at Houghton Bog. About 5 percent of *Carpinus* and/or *Ostrya* pollen is present in all A zone spectra, and, at both bogs, there is a small but definite *Carpinus-Ostrya* peak near the A to B zone transition. Low precentages of *Corylus* pollen occur in all A zone spectra at both bogs. *Betula* pollen is regularly present in A zone sediments, although in fairly low percentages. At Protection Bog, *Betula* representation gradually increases upward, and, near the beginning of the B zone, a maximum is reached which persists throughout the lower part of this zone. A similar but sharper peak is present at Houghton Bog. *Populus* pollen accounts for 2 to 3 percent of zone A totals at Protection Bog.

Low percentages of tricolpate *Fraxinus* pollen occur throughout the A zone at Protection Bog. Pollen of this type, which at most sites was tabulated separately from *Fraxinus* pollen with four and five colpi, is produced mainly by *F. nigra,* judging from pollen reference slide examinations. Tetracolpate pollen is typically produced by *F. americana* and *F. pennsylvanica,* although a few 3- and 5-colpate grains are occasionally found in reference slide preparations of these species, as are some 4-colpate grains in reference slides of *F. nigra* pollen. At Houghton Bog, *Fraxinus* pollen was not differentiated in this way, but it is reasonable to assume that 4-colpate grains are as poorly represented in zone A at this site as they are at Protection Bog.

Pollen of several taxa characteristic of the Hemlock-white pine-northern hardwoods and Beech-sugar maple forest regions appear in zone A. At Protection Bog, 2 to 3 percent of *Tsuga* pollen occurs in the upper part of this zone and 1 percent or less is found in the same stratigraphic position at Houghton Bog. At one or both sites, sporadic grains of *Castanea, Fagus, Fraxinus* 4-colpate, *Juglans cinerea, Liquidambar,* and *Platanus* were also encountered. At Protection Bog, about 1 percent of *Acer saccharum* pollen is present and trace percentages of undifferentiated *Acer* grains also occur at Houghton Bog. At both sites *Carya* (ca. 1 percent) and *Quercus* pollen (ca. 10 percent) are present throughout zone A.

With the exception of the top 20 cm of the sediment column, zone A contains the highest percentages of nonarboreal pollen anywhere in the diagrams. At both bogs, pollen produced by unknown members of the Cyperaceae and Gramineae amounts to 5 to 8 percent of the total. Associated pollen types include *Ambrosia, Artemisia, Rumex, Thalictrum,* periporate grains belonging to species in the Chenopodiaceae, Amaranthaceae, or both (Cheno-Am. pollen), and other herbaceous taxa listed in appendixes H and J. Significant percentages of pollen belonging to unknown members of the Asteroideae (Compositae) are regularly present in zone A. In all diagrams, these are graphed under the heading, high-spine Compositae. From 1 to 5 percent of *Alnus* and *Salix* pollen occurs in zone A at both bogs. Low percentages of *Myrica* pollen are found throughout the A zone at Houghton Bog.

An age determination of 11,880 ± 730 B.P. (I-3290) on wood near the bottom of the marl at Houghton Bog affords a minimum date for the beginning of zone A at this site. This correlates well with a comparable date, 12,000 ± 300 B.P. (W-507; Rubin & Alexander, 1960), on wood from a marly silt in a depression on the Chaffee outwash plain near the Cheery Tavern Crossroads 10 mi to the east, although it is considerably younger than the date, 14,900 ± 450 B.P. (I-4216), recently reported by Calkin (1970) from the same site. Mollusks found in the marl at the Cheery Tavern locality indicate the sediment accumulated near the margin of a heavily vegetated pond. Pollen analysis and the fossil snails suggest a climate somewhat cooler than the present prevailed at the time of deposition (Daily, 1961). Remains of a mastodon were also uncovered at this site.

The Mollusca which occurred in the marl at Houghton Bog were not identified, but charophyte oospores, removed from the residue after HCl treatment, and part of the original core were sent to Fay Kenoyer Daily for study. The collection contained only *Chara sejuncta* A. Br. (Daily, 1968, and letter, April 11, 1968), a species that often grows in ponds with mud bottoms at the present time (Daily, 1961). Wood (1965) reports that *C. sejuncta* ranges from Massachusetts to the Great Lakes southward to the West Indies, Brazil, and Uruguay, and its distribution in New York State is given by Wood and Muenscher (1956).

Zone B. Pine pollen dominates zone B at both bogs, although substantial percentages of *Quercus* pollen are also present. The boundary separating zones A and B was drawn where *Quercus* pollen begins to increase. This also is at about the middle of the *Picea* decline which marks the demise of spruce in the area. Pine pollen accounts for about 50 percent of the total in zone B; oak pollen for an additional 20 percent. High percentages of *Pinus* subg. Strobus pollen indicate that *P. Strobus* was the dominant pine surrounding the sites when B zone sediments accumulated. At Protection Bog, a *P. Strobus* cone was found at 5.75 m in stiff gyttja collected with a 2-in diameter Livingstone corer that was being used to obtain material for radiocarbon assay. The presence of white pine immediately adjacent to the basin during early zone B time is clearly established.

Small but significant percentages of *Ulmus* and *Carpinus-Ostrya* pollen occur in zone B and a slight increase in the amount of birch pollen across the A to B zone transition is present. Only 2 percent of the total pollen in the B zone is contributed by nonarboreal species. In both diagrams this amount continues to occur upward to the presettlement to postsettlement boundary.

Diagram 4, in which the number of grains per ml of wet sediment is plotted, shows that the greatest numbers of pollen grains in the B zone were contributed by *Pinus* and *Quercus*. *Pinus* reaches a maximum of 176,000 grains/ml at 9.25 m. At Protection Bog, the B zone *Pinus* peak has been dated at 9030 ± 150 B.P. (I-3551).

Zone C-1. The boundary between zones B and C-1 is drawn at the middle of the *Tsuga* increase. Pine pollen at this point still accounts for about 30 percent of the total, but it subsequently decreases to 7 percent in the lower third of zone C-1 and to about 3 percent at the end. *Abies* pollen disappears in the beginning of zone C-1. The percentage of *Quercus* remains high and amounts to nearly 20 percent of the total at Protection Bog. Its decline is gradual at this site and, with a slight lag, parallels that of *Pinus,* although at the end of the C-1 zone, *Quercus* still accounts for 10 percent of the total. A similar pattern in the curve for this species occurs at Houghton Bog. The lower third of C-1 is dominated by pollen of *Tsuga, Quercus,* and *Pinus*. Upward, percentages of *Quercus* and *Pinus* pollen decrease and are replaced in part by *Fagus* pollen, which at the end of zone C-1 accounts for 35 percent of the total at Protection Bog and about 10 at Houghton Bog.

At the beginning of zone C-1 at Houghton Bog are maxima in the curves for *Fraxinus* and *Juglans. Fraxinus* is strongly represented through much of the zone, and, at Protection Bog, the highest C zone percentages of *Fraxinus* 4-colpate occur in the C-1. At both bogs *Betula* increases somewhat over lower levels and it reaches a peak in the lower half of the zone. Represented in all C-1 spectra in amounts ranging from 5 to 10 percent are *Acer, Ulmus, Carpinus-Ostrya,* and *Carya*. Both *Acer rubrum* and *A. saccharum* are present at Protection Bog in this zone. Smaller percentages of *Tilia* and *Corylus* occur throughout. At Protection Bog there is a *Tilia* maximum of modest size at the beginning of zone C-1.

Castanea first appears in the lower half of zone C-1 at Houghton Bog, and, although sporadic grains occur in the same zone and at lower levels at Protection Bog, *Castanea* was not regularly encountered in the counts until just above zone C-1 at this site. The highest percentages of *Platanus* pollen found occur near the middle of this zone at Houghton Bog and a similar but smaller peak occurs at about the same stratigraphic position at Protection Bog. At both bogs fairly high percentages persist into the lower part of zone C-2.

As shown in diagram 4, *Tsuga* contributed the greatest number of pollen grains of any one type per ml of sediment in zone C-1 at Houghton Bog. Upward, from zone B to zone C-1, *Tsuga* replaces *Pinus* and *Quercus* as the major component of the pollen rain.

Zone C-2. The middle of the prominent *Tsuga* decline was chosen to mark the C-1/C-2 boundary, and, at Protection Bog, this point has been dated at 4390 ± 110 B.P. (I-3550). Associated with the decreasing *Tsuga* percentages at both bogs are increases in the *Acer, Betula, Carya, Fagus,* and *Quercus* curves. At Protection Bog, where species of *Acer* were identified, percentages of *A. saccharum* pollen are greater and increase more than those of *A. rubrum*. The number of *Tsuga* grains per ml decreases from 30,000 to 5,000 across the C-1/C-2 transition. Small increases in the number of grains per unit volume for *Fagus, Acer, Quercus,* and *Betula* are evident.

At Protection Bog, there is a small decrease in the percentage of *Fagus* pollen at about the middle of zone C-2. This probably does not reflect a decrease of *Fagus* in the surrounding forest as the decrease is mainly compensated for by an increase in Cyperaceae pollen, which is most likely of local origin. Other than the two spectra at Protection Bog in which Cyperaceae pollen accounts for about 7 percent of the total, NAP percentages average less than 3 percent of sums in zone C-2.

Zone C-3. It is difficult to place the C-2/C-3 boundary, but at both sites it was drawn after the decline of *Quercus* which was taken to mark the end of zone C-2. *Tsuga* percentages increase across this interval. At Protection Bog, these changes are dated at 1270 ± 95 B.P. (I-3549).

It cannot be conclusively determined whether sediments of zone C-3 are represented in diagram 3 for Houghton Bog because of the obvious absence of the upper spectra. Diagram 2 was prepared to overcome this deficiency. The exact relationship between diagrams 2 and 3 can perhaps be determined only by radiocarbon dating, but examination of the pollen curves in relation to the complete diagram for Protection Bog indicates that zones C-3, C-2, and probably part of C-1 are present in diagram 2. In the absence of dates, however, the boundaries have been drawn to indicate their questionable positions. The best markers in diagram 2 are the low in the *Tsuga* curve and the corresponding highs in the *Carya, Fagus,* and *Quercus* curves. The percentages are about the same magnitude at the edge and at the center of the basin.

Zone C-3 has been divided into two subzones. In subzone C-3a, the lowest, *Tsuga* increases to 25 percent and *Fagus* correspondingly decreases at both sites. At Protection Bog, *Quercus, Betula, Carya,* and *Acer saccharum,* which decrease slightly at the C-2/C-3 transition, increase somewhat toward the end of the C-3a. These changes are not evident at Houghton Bog.

The C-3a/C-3b boundary records the influx of settlers to the area and associated forest clearance. The change is quite abrupt and (above the boundary) about 50 percent of the total pollen is contributed by nonarboreal species, mainly those associated with agriculture. Since the percentage base includes both AP and NAP, decreases in tree taxa percentages are directly related to the large numbers of NAP.

At both sites *Ambrosia* accounts for about 25 percent of the total. Other important herbaceous taxa include Gramineae (incl. Cerealia), *Rumex,* and *Plantago.* The latter is perhaps the best zone marker since it appears abruptly at the presettlement to postsettlement boundary, although occasional grains are found in zone C below this level. Cheno-Am. pollen also occurs in the C-3b and the small increases in *Artemisia* and high-spine Compositae may be attributed to introduced, weedy species. *Zea* occurs in this zone at both bogs, and *Fagopyrum* was found in the surface spectrum at Houghton Bog. Clay- and silt-sized mineral particles, presumably blown into the basin, were abundant in subzone C-3b at both bogs.

Populus and *Picea* pollen reappear in upper C-3 spectra. Increases in percentages of *Acer, Betula, Larix,* and *Pinus* occur at one or both sites between 2.5 and 7.5 cm levels and the surface. In spite of the absence of mature trees in nearby forests, a few *Castanea* grains were found in the surface samples at both bogs.

SITES ASSOCIATED WITH PRE-VALLEY HEADS MORAINES

Allenberg Bog

Situated in Cattaraugus County in the Town of Napoli a few miles north of the Wisconsin drift limit, this bog occupies a deep, northeast-southwest trending basin about 10 acres in extent at the outer edge of an area mapped as Kent (Binghamton) moraine by MacClintock and Apfel (1944). It is approximately 30 mi southwest of Houghton and Protection bogs and is shown on the southeastern quarter of the New Albion 7½′ quadrangle at 42° 15′ 4″ N. lat. and 78° 52′ 57″ W. long. as a small lake with a marsh on the southwest side, 2.7 mi south of New Albion and 1.2 mi north of the Pigeon Valley Cemetery. A lake which occurs near the northeast end of the basin is about 40 m in diameter.

Less than one-half mile north of Allenberg Bog is Waterman Swamp, a roughly triangular tract of swamp and bog forest about 300 acres in extent. The swamp probably began as a lake ponded between drift deposits to the south and north. The basin occupied by Allenberg Bog does not seem to have been connected originally to the lake and at present is separated from the swamp by a hill and other intervening high ground. Since both occur at 1620 ft A.T., however, a possible connection may have been present around the south and east edge of the upland. A small bog lake, Black Pond, is located at the west end of the swamp.

The bog occurs in a valley above which hills to the east and west rise 250 to 300 ft. The valley floor in the vicinity of Allenberg Bog is slightly higher in elevation than the area to the south permitting drainage in this direction through Cold Spring Creek. Waterman Swamp is the headwaters of Little Valley Creek which, as an outlet, functions mostly in the spring carrying waters charged with humic acids to the northeast away from the swamp. The two streams eventually empty into the Allegheny River. The swamp, Allenberg Bog, and some of the surrounding land are owned by the Buffalo Audubon Society, which maintains the area as a wildlife sanctuary.

The vegetation of the region has been described by Gordon (1940) and Schick and Eaton (1963). Most of Waterman Swamp is characterized by the latter as an elm-ash-rhododendron swamp. On the several knolls which rise above the level of the swamp *Pinus Strobus* is particularly abundant, and *Betula alleghaniensis* and *Tsuga canadensis* are common associates. *Rhododendron maximum* and *Viburnum alnifolium* are typical understory shrubs in this area. Below the 1720 ft con-

Figure 7

tour, *Abies balsamea, Fraxinus nigra, Larix laricina, Picea mariana, Pyrus americana,* and *Ulmus americana* are frequent. At certain places, dense thickets of *Nemopanthus mucronata* and *Vaccinium* sp. occur. Large *Abies, Larix,* and *Picea* trees, 18, 21, and 16 in d.b.h. respectively, have been found at the southeast corner of the swamp. Black Pond is surrounded on all sides by an invading *Cassandra calyculata* heath, but an extensive sedge mat is absent. Small *Picea, Larix,* and *Pinus Strobus* trees are scattered across the heath.

At Allenberg Bog, the zonation of plant communities around the lake is fairly distinct (figure 7). Photographs in Gordon (1940) taken in the mid 1930's show a narrow low shrub zone separating the lake from the bog forest. Beavers, sometime after these pictures were taken, dammed the outlet and raised the water level high enough to kill most of the trees and many other plants then inhabiting the mat. They cut a shallow channel through the peat to the lake and constructed houses near the northeast and southeast ends of the basin. The beavers were last seen in 1951 and the disappearance of the dam has since allowed the water level to return to normal. Pollen stratigraphy seems not to have been disturbed by their activity.

Nuphar microphyllum and *Nymphaea odorata* have been reported from the edge of the open water, although currently only the former is present. A narrow quaking mat of *Carex limosa* and *Sphagnum* spp. is located along the south and southwest margin of the lake, but northward the mat becomes grounded. Here *Cassandra calyculata* and *Decodon verticillatus* are invading the open water directly. A discontinuous low shrub zone interspersed with dead trees occurs across the southwest two-thirds of the bog. *Andromeda glaucophylla, Carex* spp., *Cassandra, Decodon, Eriophorum virginicum, Ledum groenlandicum, Rubus hispidus,* and *Vaccinium macrocarpon* are the main species present. *Xyris caroliniana,* an apparent Coastal Plain disjunct, has been found near the south end of the bog mat.

Around the periphery of the basin, particularly along the north edge, *Larix laricina* and *Picea mariana* occur. Nearer the upland, they are found with *Acer rubrum, Betula alleghaniensis, Fraxinus nigra, Pinus Strobus,* and *Tsuga canadensis.* The understory shrubs in this area are *Viburnum cassinoides* and *Pyrus melanocarpa. Rhododendron maximum* is present along the west edge.

The upland vegetation has been described as a *Tsuga canadensis-Fagus grandifolia* forest with an admixture of *Acer saccharum* (Gordon, 1940). Other upland trees include *Juglans cinerea, Ulmus rubra, Fraxinus americana, Prunus serotina, Acer pensylvanicum, A. rubrum,* and *Betula alleghaniensis.* The typical forest herbs are *Dryopteris spinulosa* var. *intermedia, Lycopodium lucidulum, Mitchella repens, Medeola virginiana, Oxalis montana, Trillium undulatum, Viola incognita,* and *V. rotundifolia.* Oak forest does not occur in the nearby upland.

Cultivated fields surround the entire area and approach within 0.25 mi on the west and northeast sides of Allenberg Bog. However, about one-half of the area within a 3 mi radius of the bog is forested. A narrow strip of cutover forest occurs on the east and west sides, and a similar but more extensive forested area occurs immediately to the south. Much of Waterman Swamp has been heavily logged. Secondary forests on abandoned farmland are abundant in the area, but mature conifer plantations are rare. Southeast of Allenberg Bog, the New York State Conservation Department has flooded about 30 acres for use as a waterfowl breeding preserve.

Sediment Stratigraphy

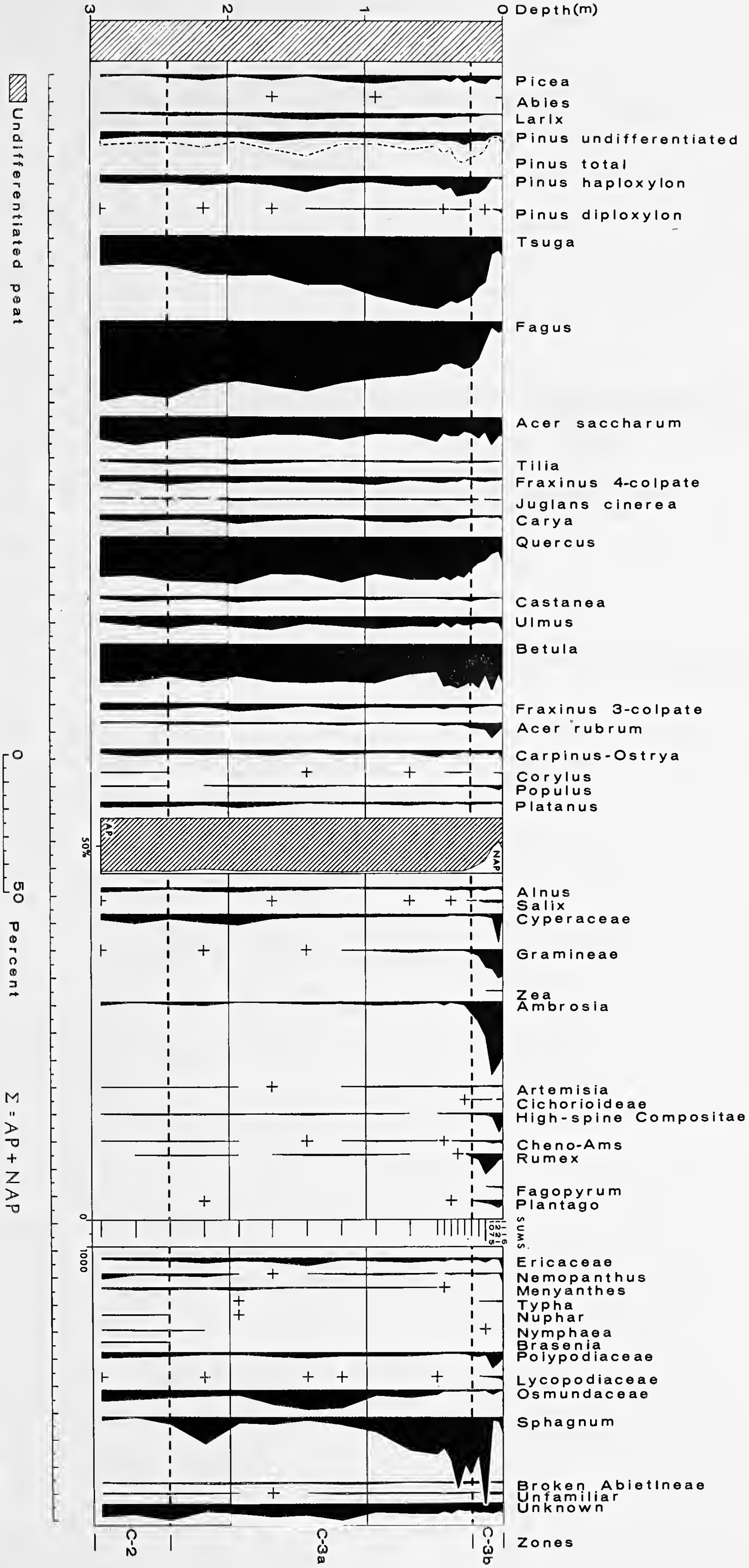
Sediments from Allenberg Bog were collected in three series. Section A was taken on October 17, 1966, with a Hiller sampler southwest of the bog lake from solid peat peripheral to the sedge mat. The stratigraphy of section A is:

Diagram 5

Allenberg Bog — Section A — Relative Pollen Frequency

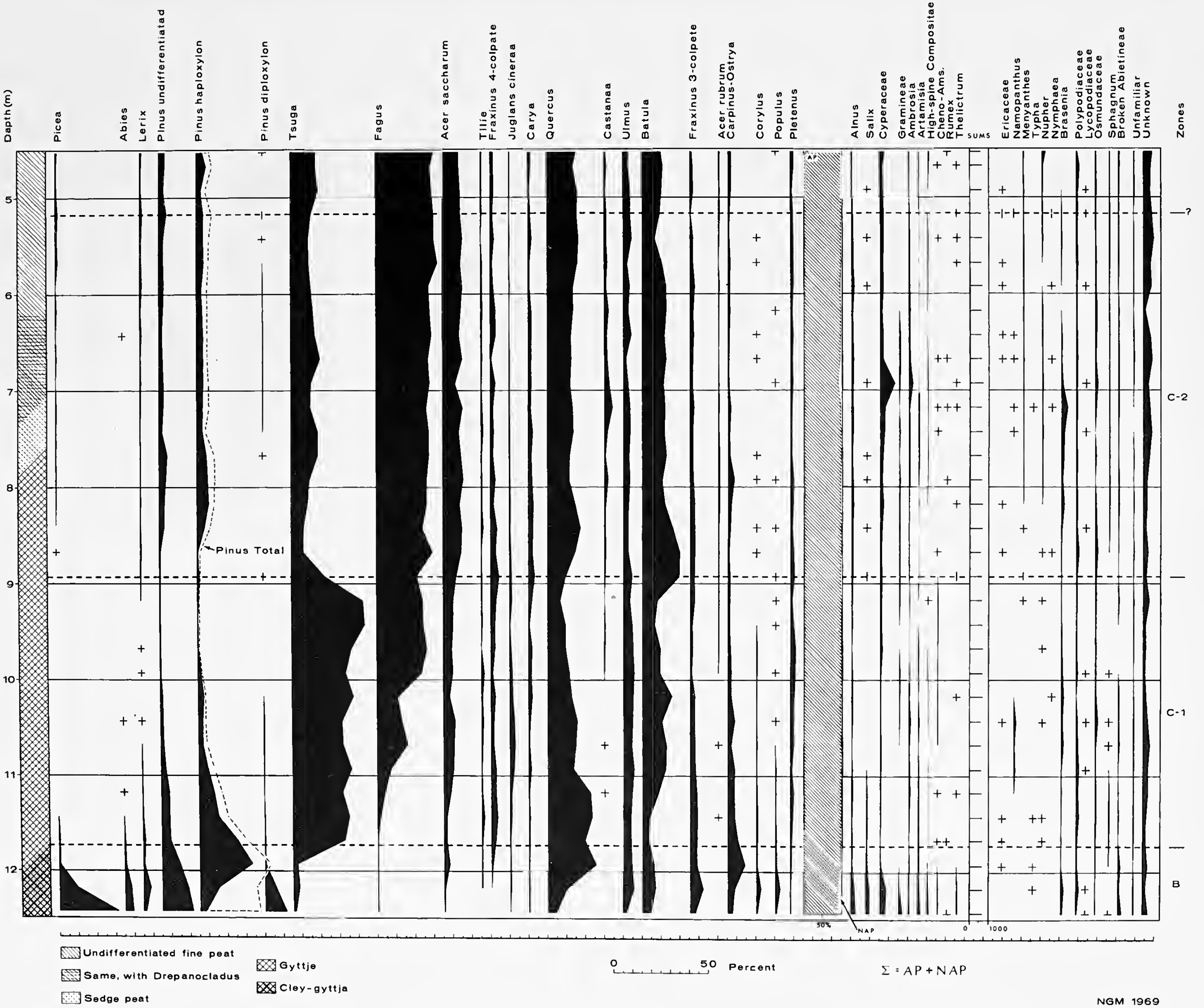
0.00–0.15 m : peat, sphagnum leaves abundant, humified, dark brown;

0.15–3.00 m : peat, undifferentiated, fibrous at top grading into medium to fine dissected peat downward, sphagnum leaves abundant above 1.5 m, *Drepanocladus fluitans* from 1.7 to 3.0 m, reddish brown throughout.



ALLENBERG BOG-SECTION A: RELATIVE POLLEN FREQUENCY

ALLENBERG BOG-SECTION B: RELATIVE POLLEN FREQUENCY



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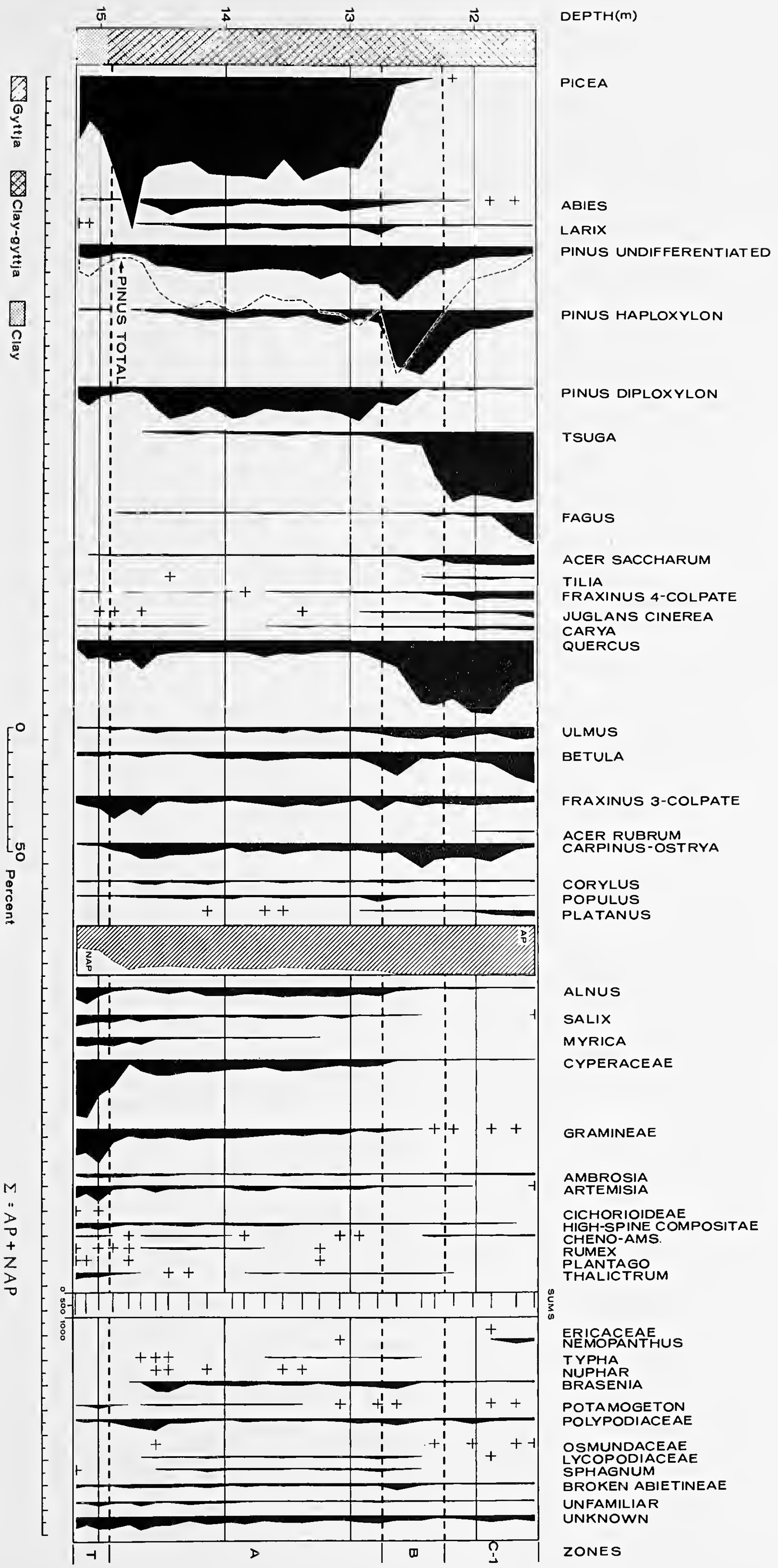


ALLENBERG BOG-SECTION C: RELATIVE POLLEN FREQUENCY

Section B was collected on October 15, 1966, again with the Hiller sampler, at a point 60 m N. 39° E. of section A. Sampling was discontinued at 12.5 m because insufficient extension rods were available to reach beyond this depth. The stratigraphy of section B is:

Diagram 6

Allenberg Bog — Section B: Relative Pollen Frequency

0.00–0.70 m : peat, fibrous, not compacted, watery, no samples taken;
0.70–4.50 m : water, some fine plant debris, no samples taken;
4.50–6.25 m : peat, undifferentiated, finely dissected, brown;
6.25–7.20 m : peat, undifferentiated, finely dissected but with *Drepanocladus fluitans,* brown;
7.20–7.93 m : peat, with abundant sedge leaf fragments, gyttja percentage increasing downward, brown;
7.93–11.90 m : gyttja, soft gelatinous at top, becoming stiffer downward, dark brown;
11.90–12.50 m : gyttja with silt and clay, dark brown.

Section C was taken through a *Cassandra* heath on April 12, 1968, 1.5 m west of the point where section B was collected. At this time more extension rods were available and the Hiller sampler was used to a depth of 14.5 m. The Davis head coupled to the Livingstone rods enabled further sampling to 15.17 m. The stratigraphy of section C is:

Diagram 7

Allenberg Bog — Section C: Relative Pollen Frequency

Diagram 8

Allenberg Bog — Section C: Absolute Pollen Frequency

11.50–12.30 m : gyttja, soft, dark brown;
12.30–14.90 m : gyttja, with increasing amounts of clays and fine sand, some plant debris present, dark brown above, becoming light brown to gray to light gray at bottom;
14.90–15.17 m : clay, stiff and dense, with dark brown stains, small specks of vivianite present, bluish gray. Not sampled further because of the difficulty of withdrawing the sampler from the sediments.

Pollen Stratigraphy

Zone T. The lowest sediments sampled at Allenberg Bog, including the basal clay and a portion of the clay-gyttja above, contain a pollen assemblage rich in NAP (see diagram 7 and appendix M). At 14.87 m, just above the base of the T/A zone boundary, as it was placed in the diagram, 28 percent of the sum was contributed by nonarboreal species. In the next lower spectrum, NAP increases to over 51 percent, and at 15.165 m it reaches a maximum of 55 percent.

The largest NAP contributor to the zone is the Cyperaceae, which accounts for over 20 percent of the total. Also present is about 10 percent Gramineae pollen. From 5 to 7 percent *Artemisia* pollen occurs, and *Ambrosia, Thalictrum,* and high-spine Compositae pollen are found regularly but in lower percentages in all T zone spectra. Of the less common types, pollen of the Caryophyllaceae, Chenopodiaceae-Amaranthaceae, Cichorioideae, and Labiatae; and *Plantago, Ranunculus,* and *Rumex* appear most regularly. Microspores of *Selaginella selaginoides* were found at 14.985 and 15.085 m. Pollen from the shrubs *Alnus, Myrica,* and *Salix* aggregate 15 percent of the total.

The most frequent AP type in zone T, *Picea,* accounts for nearly 20 percent of the total. About 10 percent *Pinus* pollen is present, and in general half of this is of the diploxylon type. Very low percentages of *Pinus* subg. Strobus pollen also occur. *Quercus* pollen is uniformly present in amounts which range from 5 to 8 percent. A high in the *Quercus* curve occurs near the top of the T zone and carries over to the lower A zone spectra where the A zone maximum is found. Increasing percentages of *Fraxinus* 3-colpate pollen are found from the lowest spectrum upward across the T/A zone transition where a high of 9 percent occurs. *Abies, Betula, Carpinus-Ostrya,* and *Ulmus* are weakly represented and a few grains of *Acer saccharum, Carya, Corylus, Fraxinus* 4-colpate, *Juglans cinerea, Larix,* and *Populus* occur in some or all of the spectra.

Diagram 8, which shows the number of grains per ml of wet sediment, was prepared for the same spectra graphed in diagram 7. The number of grains in the three lowest samples is relatively small and ranges from 26,000 to 40,000 per ml (figure 8). In the

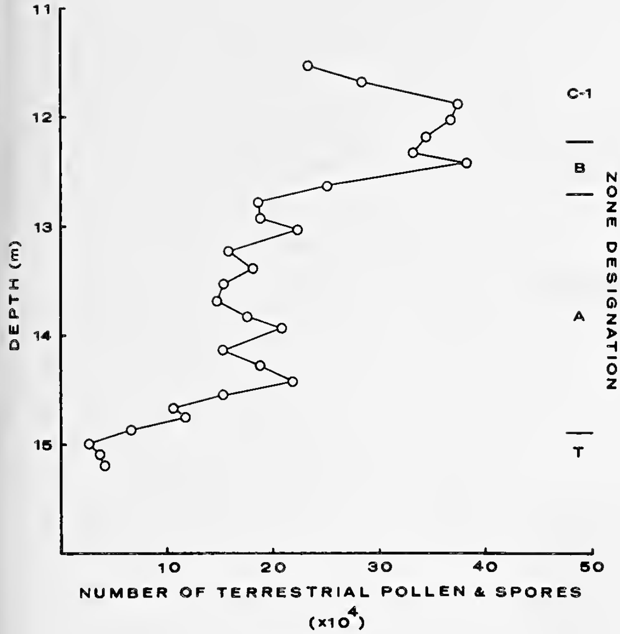


Figure 8

sediments above, the absolute number rises gradually to about 200,000 at 14.425 m near the bottom of the A zone, and it remains near this figure to the end of the zone, at which point the number of grains again increases until the maximum of about 380,000 is reached at 12.425 m. Assuming a constant rate of sedimentation, diagram 8 shows that in relation to the A zone relatively few pollen grains of any type were deposited during the accumulation of T zone sediments. The change upward into the A zone is marked not only by an increase of the percentage of spruce pollen, but also by a sixfold increase in the numbers of spruce grains being deposited. Contrary to the implication of the relative percentage diagram, larger numbers of Cyperaceae pollen occur above the T zone than within.

Zone A. Spruce pollen dominates slightly over 2 m of sediments at Allenberg Bog. It accounts for about 40 percent of the total in nearly all spectra except those near the bottom of the zone, where at one level over 60 percent was found. This peak is associated with lows in the *Pinus* total and *Pinus* diploxylon curves and high (but not the highest) percentages of *Quercus* and *Fraxinus* 3-colpate. The absolute pollen frequency diagram, however, does not show these fluctuations, although lower numbers of *Pinus* grains occur below the level of the *Picea* peak than above it.

Except near the T/A transition, *Pinus* accounts for about 20 to 25 percent of the total in all A zone spectra. Nearly half can be assigned to the diploxylon type. Haploxylon grains also occur, and, in the upper two-thirds of the zone, they account for about 5 percent of the total. Nearer the bottom, lower percentages are found.

With the exception of somewhat higher percentages in the lower part of the zone, *Quercus* averages about 7 percent of the total in all A zone spectra. Highs in *Carpinus-Ostrya, Fraxinus* 3-colpate, and Polypodiaceae curves are also present near the bottom of the zone. Two peaks in the *Abies* curve occur near the beginning (14.425 m) and end (13.075 m) of the zone. From 2 to 5 percent *Ulmus, Betula, Corylus,* and *Populus* pollen is present throughout. *Larix,* although poorly represented in lowest A zone spectra, increases to about 5 percent just below the middle of the zone and remains near this level upward to Zone B.

Above the T/A zone transition, total NAP percentages are about one-third of what they were in zone T. *Alnus,* Cyperaceae, and Gramineae have the highest percentages among NAP types identified. *Salix* is more weakly represented in zone A than below and it finally drops out upward in Zone B (diagram 7) or near the bottom of zone C-1 (diagram 6). High-spine Compositae, *Ambrosia,* and *Artemisia* are present in nearly all spectra. The curve for *Artemisia* has three highs at various points throughout the zone.

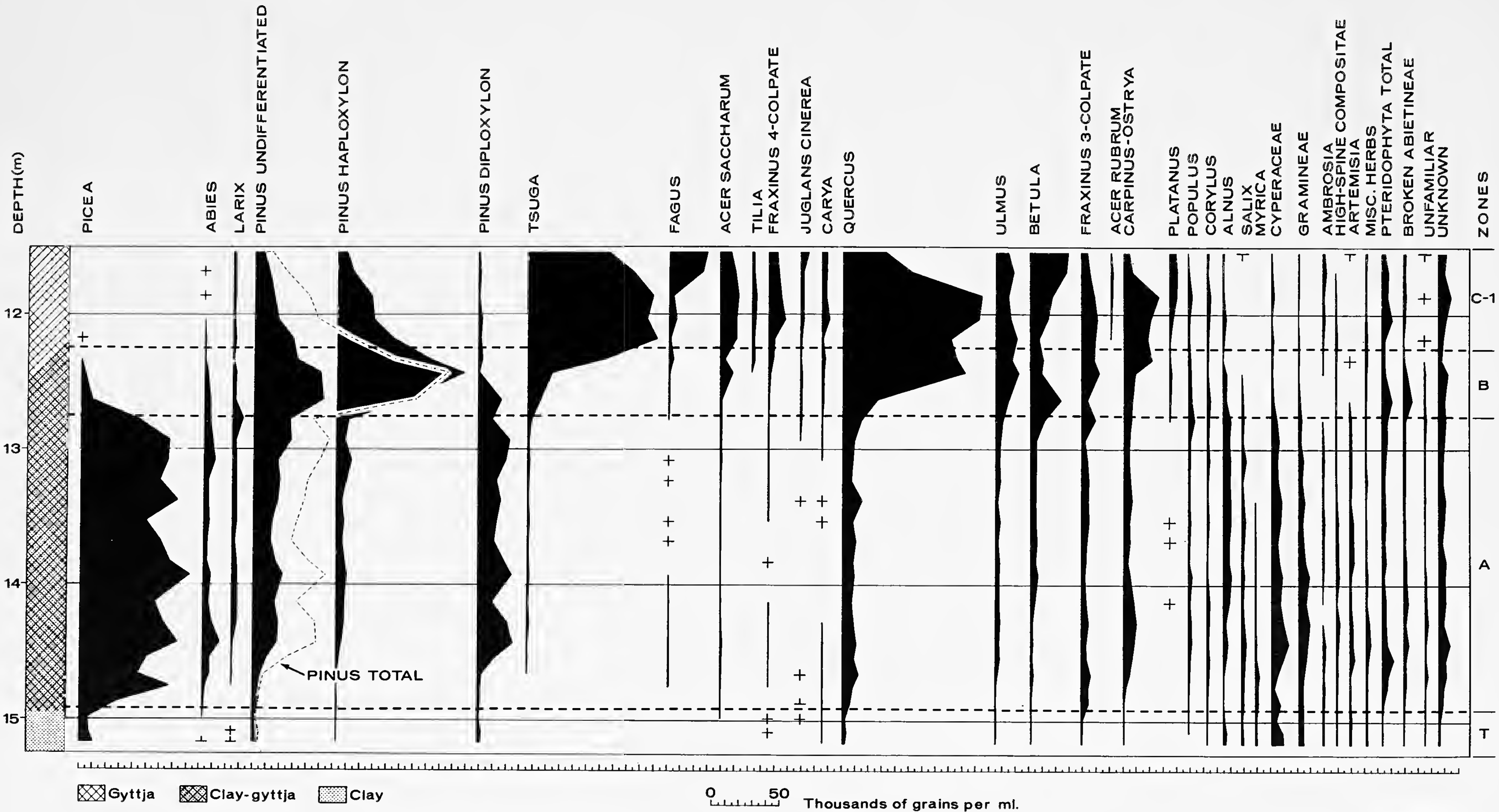
The relative and absolute pollen frequency diagrams agree closely across zone A.

Zone B. The change from zone A to zone B is shown in diagrams 6 and 7. In spite of the close proximity of both sample series, zone B begins 30 cm lower in diagram 7. However, percentages in both match well. Only the zone A top occurs in diagram 6.

The A/B zone transition is marked by several important changes in pollen percentages. In a span of 25 cm, *Picea* decreases from 35 to 5 percent, and it finally drops out near the end of zone B. The boundary between the two zones was drawn at the middle of the *Picea* decline which also corresponds to about the middle of the *Pinus* increase. This transition is characterized by peaks in the curves for *Betula, Fraxinus* 3-colpate, *Larix,* and *Populus. Quercus* percentages steadily increase in the lower half of zone B and reach a high of 25 percent near the end of the zone. Associated is an increase in *Carpinus-Ostrya* percentages, which remain high, but decrease somewhat in the lower part of zone C-1 over a peak reached near the end of zone B.

Total NAP percentages again decrease at the A/B zone transition and remain relatively low throughout zone B. *Alnus,* Cyperaceae, *Ambrosia, Artemisia,* high-spine Compositae, and *Thalictrum* occur most regularly.

ALLENBERG BOG-SECTION C: ABSOLUTE POLLEN FREQUENCY



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In no B zone spectrum do NAP percentages rise above 2 to 3 percent of the total.

Both absolute and relative pollen frequency diagrams are similar across zone B. The high numbers of total pine pollen, which occur across a broader interval than is evident in the corresponding relative frequency diagram, help to define the zone. *Pinus* and *Quercus* are the two taxa that contributed the greatest number of grains in zone B at Allenberg Bog, as was the case at the two Valley Heads bogs discussed previously. The total number of *Pinus* grains at 12.425 m, the peak of the pine curve, is 145,000. At the same level, *Quercus* is represented by 91,000 grains.

The highs in curves for *Betula, Carpinus-Ostrya, Fraxinus* 3-colpate, and *Populus,* shown in the relative frequency diagram, also appear when the data are plotted on an absolute basis. If the sedimentation rate was constant across the A/B zone transition, these peaks occur at a time of high pollen delivery to the basin, which presumably reflects a greater abundance of plants producing these pollen types in the region neighboring the basin.

Zone C-1. Zone C-1 is completely shown in diagram 6, and, in diagram 7, the lower third is present. The B/C-1 transition is marked by rapidly increasing percentages of *Tsuga* pollen, coordinated with decreasing percentages of *Pinus* grains. However, the *Pinus* decline is not as abrupt as the increase in *Tsuga,* and there is a small interval across which the percentages of both are high. *Quercus* remains strongly represented across the transition and high percentages persist through the lower third of the zone. Near 11 m (diagram 6), *Quercus* decreases from 20 to 10 percent, while *Fagus* and *Betula* percentages increase. *Quercus* continues to decline upward through the C-1 until just below the 9 m level where only 7 percent occurs, its lowest postglacial percentage at this site. *Fagus* is weakly represented in B and lower C-1 spectra, but it begins to increase above 11.675 m after *Tsuga* becomes stabilized at near 30 percent of the sum. Near the middle of the zone, *Fagus* accounts for 13 percent of the total, but in the upper one-third of the zone, it comprises 27 percent. The curves for *Acer saccharum, Betula,* and *Juglans cinerea* show highs near the middle of the zone.

Although *Fraxinus* 4-colpate and *Tilia* first appear in zone B, the former reaches a high in the lower third of the C-1, while in the same interval *Tilia* has two minor maxima, one near the beginning and one near the end of the zone. From 3 to 5 percent *Fraxinus* 3-colpate pollen occurs regularly in the lower two-thirds of the C-1. In the rest of the zone, only about 1 percent is present. A parallel change occurs in the *Carpinus-Ostrya* curve. *Ulmus* is uniformly present in all C-1 spectra and accounts for about 7 percent of the sum. The C zone maximum for *Platanus* is reached at the end of the C-1. Percentages of *Carya* pollen, which are low at the beginning of the C-1, increase slightly upward in the zone. Except for sporadic grains in lower levels, *Castanea* occurs regularly from the upper one-third of the zone to the topmost spectrum.

Total NAP percentages vary from 1.2 to 3.6 in zone C-1. Cyperaceae and high-spine Compositae are most consistently present. Less frequently encountered pollen types are graphed in diagrams 6 and 7 or listed in appendixes L and M.

As in zone B, the relative and absolute frequency curves parallel one another (cf. diagrams 7 and 8). In that portion of the C-1 studied, the largest numbers of grains belong to *Tsuga* and *Quercus. Pinus* is also an important component of lower C-1 spectra.

Zone C-2. The boundary between this zone and C-1 can be placed readily at about the midpoint of the *Tsuga* decline, but the upper boundary of the C-2 is more difficult to locate. The gradually increasing *Tsuga* percentages which characterize the C-2/C-3 transition in the Valley Heads bogs are not evident in diagram 6, although they do occur in diagram 5. As shown in diagram 6, *Tsuga* percentages increase somewhat in the upper 0.5 m and for this reason the zone boundary made for locating it beneath the 8 m level, at which point percentages of *Quercus* and *Betula* pollen have decreased somewhat over their previous highs. However, this creates an unusually thin C-2 zone, especially when the amount of sediment above this level and a comparison between diagram 6 and the complete Protection Bog profile are taken into account. Similar reasoning suggests a part of zone C-2 may be represented in diagram 5.

At the C-1/C-2 transition, across an interval of 50 cm, *Tsuga* pollen drops from 38 to 7 percent. A small decrease in the percentage of *Ulmus* pollen is apparent across this interval also. These reductions are compensated for mainly by increases in *Acer saccharum, Betula,* and *Quercus,* and to a lesser degree by *Carya, Fagus, Fraxinus* 3- and 4-colpate, *Pinus* undifferentiated, and *Pinus* haploxylon. The *Fagus* curve shows a gradual increase from 22 percent near the end of the C-1 to 30 percent at 6 m just below the C-2/C-3 boundary. Higher percentages of *Acer saccharum, Betula,* and *Quercus* are maintained throughout the C-2 than occur in upper C-1 spectra. *Castanea* is weakly represented across the C-1/C-2 transition, but it reaches a maximum of 4 percent at 7.175 m well into zone C-2.

Two *Tsuga* highs, each about 15 percent, occur near the middle of the C-2. These represent an increase over a low of 7 percent present near the beginning of the C-2 and a 9 percent low occurring near the end of the zone. After a sporadic presence across much of the C-1, *Larix* regularly occurs from the beginning of the C-1 to the uppermost spectrum in diagram 6. Similarly, *Picea* pollen, after an absence from all C-1 spectra except the lowest, is present in low percentages from near the beginning of the C-2 upward.

Total NAP remains low throughout the C-2. One or two percent *Alnus, Ambrosia, Artemisia,* Cyperaceae, and Gramineae pollen is most regularly present. The peak in the Cyperaceae curve just above the 7 m level may be associated with intrabasinal succession since sedge peat, which is evidence of the presence of a sedge mat at the surface, occurs just below it. The associated *Ambrosia* high is more difficult to explain, although contamination during sampling may be the cause.

Zone C-3. Zone C-3 is completely shown in diagram 5; percentages of minor pollen types are listed in appendix K. At Allenberg Bog, subzone C-3a is characterized by increasing *Tsuga* percentages which are associated with decreasing values for *Fagus.* As at the Valley Heads bogs, upper NAP rich sediments are placed in subzone C-3b; NAP percentages are minimal in subzone C-3a.

Except for minor fluctuations, percentages of most pollen types remain more or less constant across the C-3a. The percentage of *Betula* pollen increases below the C-3a/C-3b boundary and remains higher in the C-3b than in the C-3a. Together, *Picea* and *Larix* account for about 4 percent of the sum in most C-3 spectra. NAP percentages are low in subzone C-3a and average about 3 percent of the total. *Alnus, Ambrosia,* Cyperaceae, and high-spine Compositae are regularly present.

The higher percentages of Cyperaceae in the lower half of the C-3a, rather than in the upper, seem to be related to intrabasinal succession. Upward from the lowest spectrum in diagram 5, the aquatics, *Brasenia, Nuphar,* and *Nymphaea,* abruptly drop out of the counts. Above the level of their disappearance, Cyperaceae percentages increase, and above this, increases occur in the curves for Ericaceae and Osmundaceae. These changes match those expected during succession from open water to an ericaceous shrub association of the type which occurs on the surface today. Pollen typical of the terminal stage, a bog forest, does not replace the Ericaceae upward, but the occurrence of *Larix* and *Picea* pollen throughout zone C-3 is evidence for its presence somewhere on the bog mat. A few spruce needles recovered from the peat in the lower C-3b spectra imply the presence of spruce trees near the sampling point at the time this part of the zone was deposited. No doubt these were produced by black spruce, which is found on the bog mat today.

The C-3a/C-3b transition is abrupt and clearly marked by a decrease in AP and an increase in NAP. The largest reductions in tree pollen percentages occur in *Fagus, Pinus* haploxylon, *Quercus,* and *Tsuga. Acer saccharum* percentages drop somewhat but generally remain high, as do those for *Betula.* Only *Acer rubrum* and *Populus* show a marked increase in C-3b spectra.

At 2.5 cm beneath the surface, total NAP reaches 57 percent of the sum, the highest value reached in subzone C-3b at Allenberg Bog. Pollen from herbs, which today grow mostly in disturbed habitats, is abundant. As at the Valley Heads bogs, *Ambrosia* has higher percentages than any other NAP type. Pollen from Cheno-Ams., Cichorioideae, Gramineae *p. p., Plantago,* and *Rumex,* probably produced by weedy species, also occurs. *Fagopyrum,* Gramineae *p. p.* (incl. Cerealia), and *Zea* pollen, representing cultivated plants, is present but in much lower percentages than the weeds. Highs in the Cyperaceae, Ericaceae, high-spine Compositae, *Nemopanthus,* and Polypodiaceae curves probably reflect conditions on the bog mat favorable to the growth of local species.

Pollen Size-Frequency Measurements

Size may be a useful species character in pollen which on other morphological grounds can be identified to genus only (Cain, 1940; Cain & Cain, 1948; Leopold, 1956a). For this reason, measurements were made of as many well-preserved *Betula, Picea,* and *Pinus* diploxylon grains as possible while counting the Allenberg Bog sections. Silicone oil is a particularly effective mounting medium in such studies because gentle tapping of the cover slip rotates grains permitting access to the length chosen to be measured. The data collected have been plotted in size-frequency graphs (figures 9, 10, and 11).

Some difficulties inherent in size-frequency data have been reviewed by Whitehead (1964). The maceration procedure employed to isolate pollen from sediments, the nature of these sediments, and the medium in which the pollen is mounted for microscopic study apparently affect grain size. When these sources of variability are

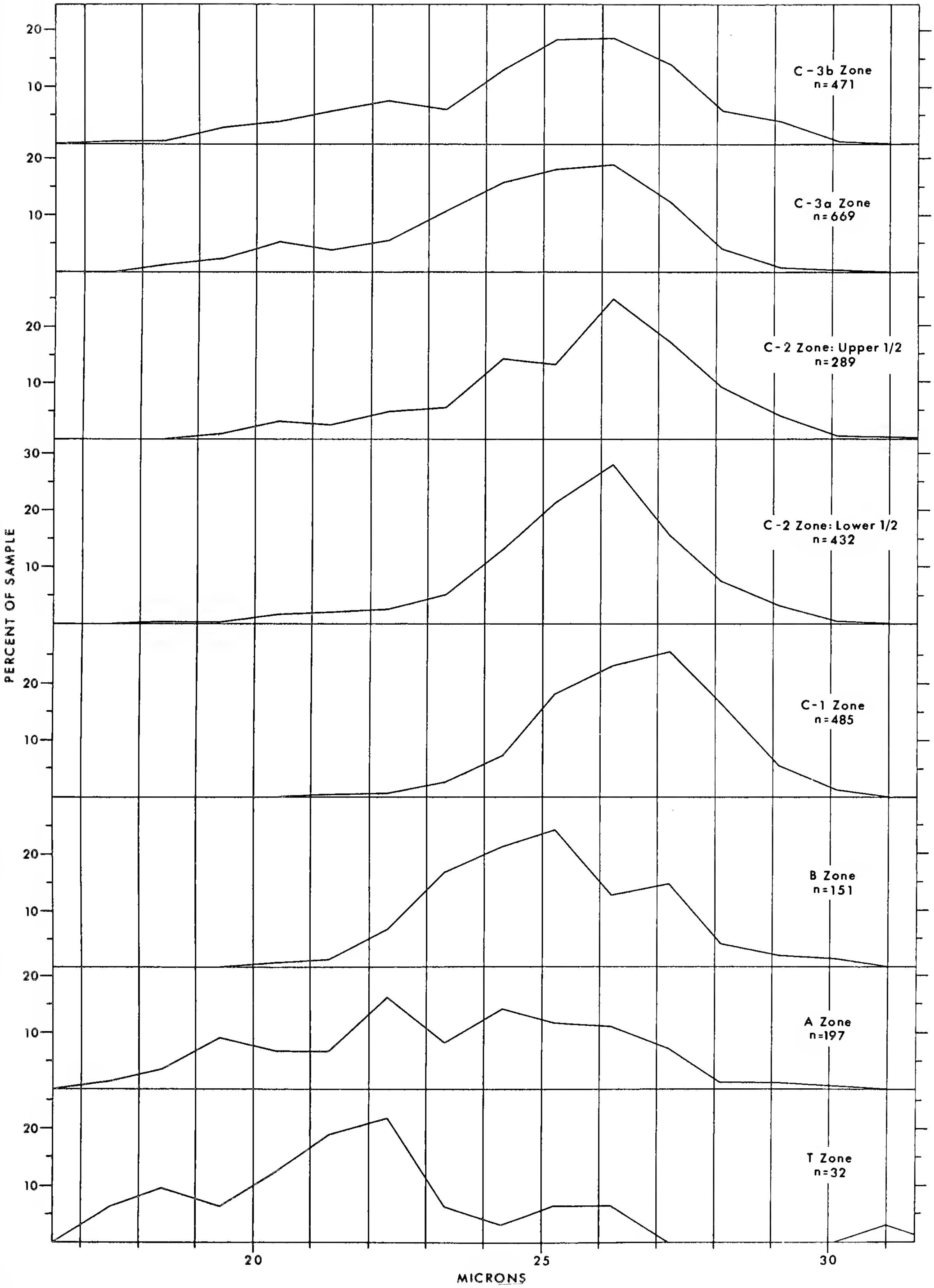

PERCENT OF SAMPLE
20
10
C-3b Zone
n=471
20
10
C-3a Zone
n=669
20
10
C-2 Zone: Upper 1/2
n=289
30
20
10
C-2 Zone: Lower 1/2
n=432
20
10
C-1 Zone
n=485
20
10
B Zone
n=151
20
10
A Zone
n=197
20
10
T Zone
n=32
20
25
30
MICRONS

Figure 9

coupled to the fact that in only a few cases has an analysis been made of the geographical variation in pollen size of a given species, not to mention the absence of an evaluation of differences within populations or within a single individual, fossil size-frequency data must be interpreted cautiously. However, certain of these factors have been studied and in some cases variability of pollen size is less than anticipated. For example, Faegri and Deuse (1960) exposed *Betula tortuosa* pollen to different lengths of treatment in boiling 10 percent KOH and did not find a significant size change with longer treatment, although they did observe an increase in size when acetolysis followed exposure to KOH. These authors have also shown negligible changes over a period of 5.5 years in pollen preparations mounted in water, glycerol, and glycerine jelly. Clausen (1960), who studied fresh pollen removed from different sectors of *Betula* catkins located on various parts of two birch species, was unable to demonstrate any significant size variations within a single species. Similar studies need to be extended to all species identified on size characteristics alone, but, if the same maceration procedure and mounting medium are used for the fossil samples and the modern preparations employed to identify peak frequencies within a fossil spectrum, variability caused by these factors can be minimized.

Betula. The most extensive study of size variation in pollen of the North American species of *Betula* has been published by Leopold (1956a). Birch pollen is triporate and the dimension usually measured extends from the tip of a pore across the grain to the edge of the exine in the interporal area on the opposite side. This, the maximum diameter of the grain, can be measured at three places. The grain diameter:pore depth ratio, used recently by Birks (1968) to identify *Betula nana* pollen, may also be useful in working with temperate North American species.

Measurements collected from individual spectra were lumped by zones or major portions thereof to increase sample size and to produce graphs that are characteristic of the main subdivisions of the pollen diagram (figure 9). As only one mode occurs in nearly all parts of zone C, one or possibly two birch species with pollen grains of similar size seem to have been dominant during C zone time. Today, only *Betula lenta* and *B. alleghaniensis* occur in southwestern New York State (Zenkert, 1934) and, although the former is not listed by Schick and Eaton (1963) as growing within the Allenberg Bog-Waterman Swamp area itself, it is reasonable to conclude that one or both of these species contributed most of the birch pollen to C-3b spectra. The gross volume data collected by the U.S. Forest Service show both species to be about equally abundant in Cattaraugus County (Northeastern Forest Experiment Station, 1967). Because nearly identical modes occur throughout zone C, *B. lenta* and *B. alleghaniensis* are likely to have been the only species present.

The highest size-frequencies occur over a 1 to 2 μ interval with the mode at 26 μ in zones C-3b, C-3a and the upper and lower halves of C-2. In zone C-1, however, the mode shifts to 27 μ. Leopold (1956a) has reported the mode for *Betula lenta* pollen to be 28 μ in acetolyzed samples and to be near 24 μ in those treated only with KOH. In *B. alleghaniensis,* the mode for KOH treated samples is 28 μ, but it is 45 μ for acetolyzed ones. My samples were exposed to both KOH and acetolysis, so it is expected that the modal class would be near the larger figures. The fact that they are smaller may be related to the shrinkage phenomenon reported to occur during fossilization in peat by Buell (1946), Praglowski (1966), and others. The shift in the position of the mode in zone C-1 to slightly larger grains may indicate the presence of *Betula papyrifera,* a species which, although now rare in western New York, may have been more abundant in the past.

The modes shift to smaller size classes in zone B and below. The presence of at least some grains greater than 25 μ suggests that *Betula lenta, B. alleghaniensis,* and perhaps *B. papyrifera* grew at an unspecifiable distance from the basin during the period of time represented by these zones. However, it is difficult to identify the main birch species contributing pollen to zone B sediments because none of the taxa studied by Leopold (1956a) has a mode at 25 μ. Perhaps some aspect of the depositional environment caused pollen from the three tree species to shrink more in zone B than in those zones above or possibly another species was present. If so, it may have been the shrub, *Betula pumila,* which has been found only once in western New York but may have had a wider distribution in the past. Leopold (*ibid.*) considers the pollen of this species to be smaller than that of the tree birches mentioned above, but the mode at 30 μ for the acetolyzed sample she reports does not match the mode in the fossil material. *Betula pumila* pollen treated with KOH only is smaller, however, and six samples prepared this way have a mean size of 24 μ.

The modes at 22 μ in zones A and T can be identified with more certainty. Leopold (1956a) has found

Betula glandulosa, an arctic-alpine species native as far south as the Adirondack Mountains in eastern North America (Fernald, 1950), to have small pollen with modes at 20, 22, and 23 μ in the three acetolyzed modern samples she studied. These comfortably overlap the mode for fossil grains in both zones at Allenberg Bog.

Picea. The technique of using size-frequency measurements from the surface of a deposit to interpret levels beneath can also be used for *Picea* (figure 10). There are three species of spruce that could have been members of the late and postglacial vegetation of western New York, *Picea glauca, P. mariana,* and *P. rubens.* The last named is now found mainly in mountain forests stretching from the southern Appalachians to New Brunswick and Nova Scotia (Fowells, 1965), but, in spite of some evidence that it may have occurred as far west as Michigan during the lateglacial (Cain, 1948), the distributional history of the species is largely unknown.

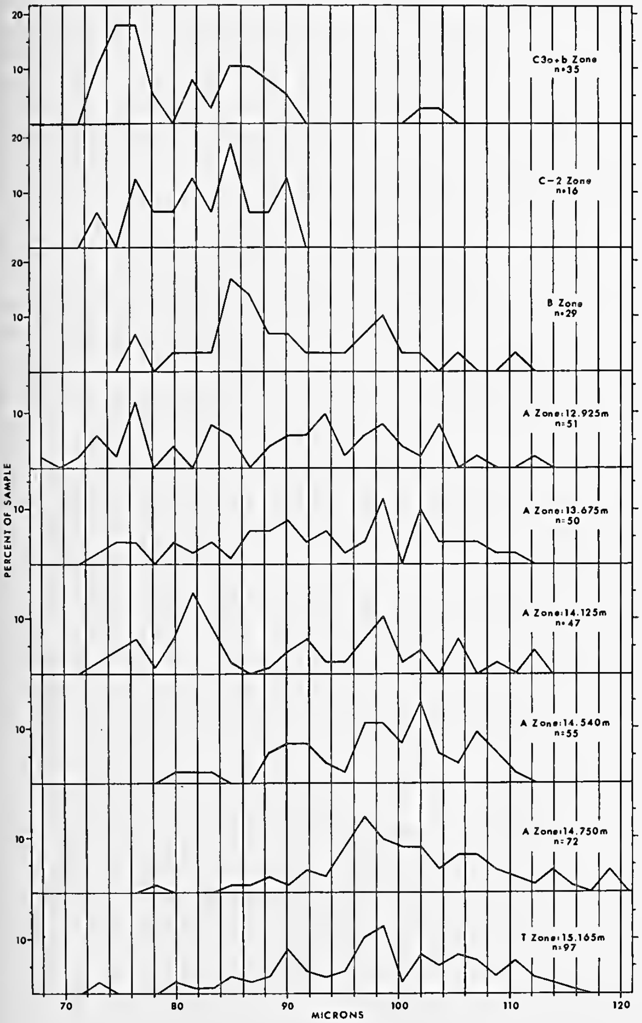


Figure 10

A number of recent workers have consistently separated the pollen of *Picea glauca* and *P. mariana.* Most use only size characteristics, but there seem also to be morphological differences between these species (*ibid.*). Size-frequency measurements indicate that the smaller grains generally belong to *P. mariana* and larger ones to *P. glauca* (Cain, *ibid.;* Davis & Goodlett, 1960; Heusser, 1960). West (1961) has used 100 μ based on wingtip-to-wingtip measurements as the point of separation between them in his work in eastern Wisconsin. Unpublished measurements of this dimension made by J. H. Anderson (personal comm.) on three collections of *P. glauca* treated with 10 percent KOH and acetolyzed have the following means: 116 μ (Arnold Arboretum, Massachusetts), 104 μ (Cheboygan County, Michigan), and 99 μ (Neultin Lake, N.W.T.). Similarly treated samples of *P. mariana* have smaller means: 85 μ (Ingham County, Michigan) and 79 μ (Thunder Bay District, Ontario). Since these data indicate that a total length greater or lesser than 100 μ is a reasonable point of division between the pollen of these species, this figure was used in the present study.

Measurements of maximum internal diameter (excluding the wings) for five collections of *Picea rubens* pollen show that the average of the means is about 3 μ greater in this species than an average of the same dimension in *P. glauca* (Davis & Goodlett, 1960). Wingtip-to-wingtip measurements are unfortunately not available for *P. rubens.*

The size-frequency graphs are readily interpreted with this information. We can be fairly certain that *Picea mariana* was the only species present in zones C-3 (including subzones b and a) and C-2 because of the probable absence of habitats for the two other species near Allenberg Bog during the past 4,000 years. Only two grains larger than 100 μ were found in these zones, and it is likely that these originated from introduced species because they occur in postsettlement spectra. As mature *Picea Abies* trees are common near farm dwellings and in cemeteries in the area, this species is a possible source. The mean grain size in the C-3a + b is 81 μ; in the C-2 it is 82 μ. Spruce pollen is practically absent in zone C-1 at Allenberg Bog. It also occurs in low percentages in the C-1 at other sites included in this study.

In zone B, the mean grain size is 91 μ and 87 percent of the grains are less than 100 μ in length. Progressively lower in the bog, the mean size becomes larger and a maximum of 101 μ is reached at 14.750 m near the bottom of zone A. At this level, 53 percent of the grains are greater than 100 μ. In zone T at 15.175 m, the mean size decreases slightly to 98 μ but 43 percent of the sample is greater than 100 μ. In zones A and T the maximum wingtip-to-wingtip length found was 120 μ. Whether such grains belong to *Picea rubens* cannot be determined, but occasional grains of *P. glauca* attain this size.

Pinus. Early work on size-frequency distributions of *Pinus* pollen suggested the feasibility of species identification on this basis. Cain (1940), for example, demonstrated three modes in a size-frequency curve of fossil pine pollen extracted from the Spartanburg buried soils on the Piedmont of western South Carolina. He related the smallest mode to *P. Banksiana* and the larger ones to *P. glabra* and *P. rigida* or *P. palustris.* In a study of pine pollen from sediments in a southeastern Michigan lake, Cain & Cain (1948) found bimodal and trimodal distributions which they considered evidence for the occurrence of *P. Banksiana, P. resinosa,* and *P. Strobus.*

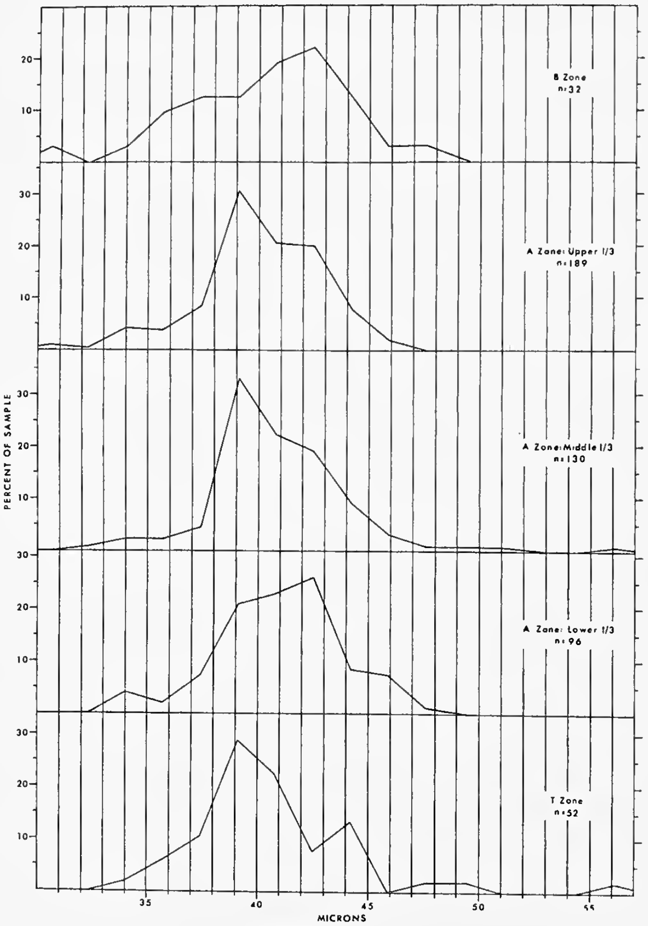


Figure 11

A simple but only recently demonstrated morphological trait, the presence of a verrucose furrow (Ueno, 1958), now allows pollen of *Pinus Strobus,* the only member of subg. Strobus in eastern North America, to be tabulated separately from smooth-furrowed pollen belonging to members of subg. Pinus. Size measurements can thus be directed at identifying the occurrence of species excluding *P. Strobus.*

Three pines with smooth-furrowed pollen, *Pinus Banksiana, P. resinosa,* and *P. rigida,* are expected in western New York pollen profiles on the basis of modern distribution patterns. Whitehead (1964) has studied pollen from all of them, and since our maceration techniques are similar, his data should be comparable to mine. Whitehead shows *P. rigida* to have the largest grains (mean size 44.95 μ based on 9 collections) and pollen of *P. Banksiana* (mean size 37.01 μ based on 24 collections) and *P. resinosa* (40.11 μ based on 12 samples) to be considerably smaller. Whitehead concludes, " it is . . . doubtful if one could separate grains of *Pinus Banksiana* and *P. resinosa* in size-frequency analysis even though the means differ by 3.10 μ . . . [and] . . . a size-frequency curve for fossil grains to which both species contributed would be perfectly unimodal " (p. 772). His measurements are of internal body diameter.

Measurements of fossil *Pinus* subg. Pinus pollen from Allenberg Bog are shown in figure 11. Since I measured external body diameter, 2 μ should be subtracted from my data to obtain figures which are equivalent to those of Whitehead (*ibid.*). In zone B, the modal class at 42.5 μ minus the 2 μ correction factor gives a figure which compares well with the mean size of *Pinus resinosa* pollen determined by Whitehead. In the upper two-thirds of zone A, the mode for the Allenberg data shifts to 39 μ (37 μ) suggesting dominance by *P. Banksiana.* A fairly prominent shoulder at 42.5 μ (40.5 μ) corresponding to the mode in the B zone also occurs in these graphs. In the lower third of zone A, the mode again shifts to the larger size class. None of my size-frequency graphs is strictly bimodal, but the correlation in size implies the presence of both species in zones A and B.

In zone T, two modes occur, one at 39 μ (37 μ) and another at 44 μ (42 μ). The lesser corresponds to the two upper A zone modes and presumably reflects the presence of *Pinus Banksiana* while the greater has no precise counterpart elsewhere in figure 11. Since the T zone was apparently a time of low pollen delivery to the basin by the regional vegetation, the probability of finding far-traveled pollen types in T zone spectra

Figure 12

is greater than elsewhere in the profile. Perhaps the higher frequency of larger grains is related to input by one of several possible pine species such as *P. rigida* which occurred at some distance south of the glacial boundary. However, no clear evidence of the presence of *P. rigida* is shown in the pre-C zone samples graphed in figure 11.

Genesee Valley Peat Works

This site occurs in an area mapped by Connally (1964) as part of the pre-Kent Olean moraine. Similarly, MacClintock and Apfel (1944) and Muller (1960) place the Kent terminal moraine north of the locality. The peat and associated sediments, which have accumulated in what seems to have been originally a shallow 10-acre lake in a pitted valley train, is being actively mined by the owner, Paul Button of Belmont, New York. The site is located in Allegany County in the Town of Amity, 2.6 mi. northeast of Belmont on the north side of NYS 244 about 0.3 mi west of Baker Valley Rd. at 42° 15′ 10″ N. lat. and 78° 59′ 37″ W. long. The surface of the peat deposit lies near the 1,620 ft contour line. The peat works is shown as an area devoid of vegetation with three small ponds marking the periphery of the peat deposit in the northwest quarter of the Wellsville North 7½′ quadrangle. The basin occurs on a flat terrace about 100 ft above Phillips Creek which flows to the southwest and empties 3 mi downstream into the Genesee River. Local relief is about 350 ft, and many of the surrounding hills reach 2,000 ft in elevation.

The peat deposit was wooded when Button purchased it in 1951, and, at this time, no outlet or inlet existed. He removed the trees and built a dike at the west end of the basin to flood it for use as a trout pond. During the ensuing years, the stumps and root mat became freed from the underlying peat and Button decided to drain the pond and excavate the peat. The surface was bulldozed clear, a channel was cut through the drift at the west end to facilitate drainage, and the peat along the south rim of the basin was removed and dragged up onto the land for drying (figure 12). Mining has continued along this edge.

According to Button, the bog surface was covered with a forest of *Acer rubrum, Betula alleghaniensis, Pinus Strobus,* and *Tsuga canadensis.* At the basin edge, *Prunus serotina* and *Ulmus* sp. occurred. Apparently *Picea mariana* and *Larix laricina* were absent. In a somewhat open area near the east end, cranberries (either *Vaccinium macrocarpon* or *V. Oxycoccos*) grew and *Arisaema* sp., *Cypripedium acaule,* and *C. Calceolus* were mentioned as noteworthy for their abundance on the forested mat.

At the present time, the site is entirely surrounded by fields or secondary forests. To the north, and contiguous with the basin margin, is a highly disturbed forest remnant, long cut over and now dominated by trees of small diameter. The following species were noted in the summer of 1967: *Acer rubrum, Crataegus* sp., *Pinus Strobus, Populus grandidentata, Prunus pensylvanica, P. serotina, Quercus alba,* and *Tsuga canadensis.* Cultivated land occurs on the east and south sides, and a plantation of small conifers in an abandoned field is located immediately to the west of the basin. In general, a large percentage of the surrounding hill tops are forested but valley floors and lower slopes are mostly fields or under cultivation. Oak-rich forests are more abundant in this area than to the west in Cattaraugus and southern Erie Counties.

Sediment Stratigraphy

The deposit was sampled on September 12, 1966, near the west end of the basin at a point where Button said that the maximum depth occurred. The Hiller borer was used from the surface to 3.25 m. The Livingstone sampler equipped with a 1-in. diameter barrel was employed beyond this depth. The stratigraphy at the sampling point is:

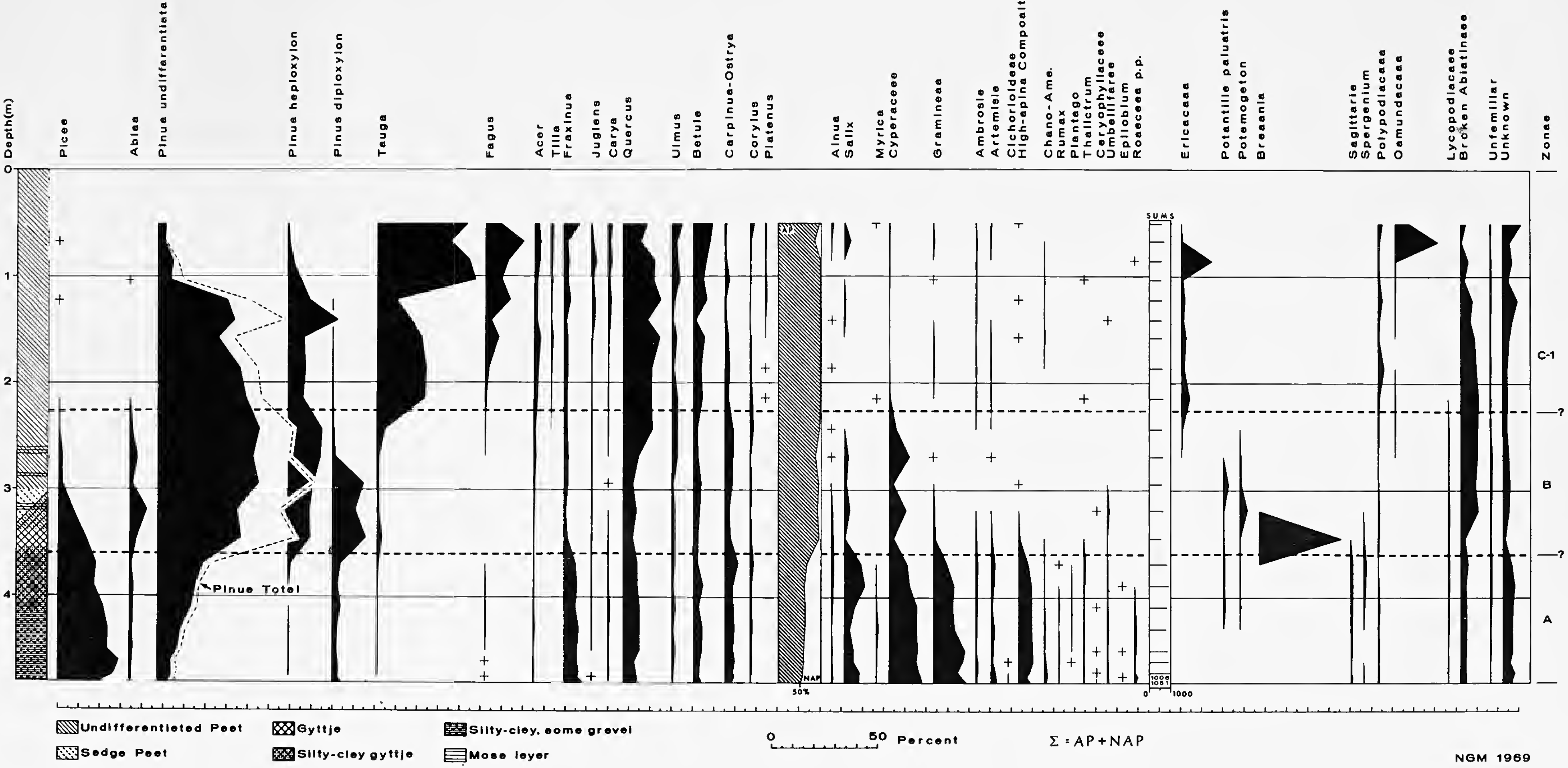
Diagram 9

Genesee Valley Peat Works: Relative Pollen Frequency

0.00–0.50 m : peat, undifferentiated, humified, dark brown, no samples taken because of disturbance;

0.50–3.00 m : peat, undifferentiated, mostly coarse near top, finer at bottom, well compacted, *Meesia trifaria* layers at 2.63 and 2.83 m, dark brown and humified at top, reddish brown commencing at 0.75 m;

GENESEE VALLEY PEAT WORKS: RELATIVE POLLEN FREQUENCY



3.00–3.25 m : peat, mostly sedge leaf debris, with *Meesia trifaria* layer at 3.18 m, light brown;
3.25–3.35 m : gyttja, brown;
3.35–4.16 m : gyttja, with silt and clay;
4.16–4.80 m : silty-clay, compact, with shale fragments and quartz sand and granules throughout but most significant near bottom, layer of gastropod shells at 4.60 m, small vivianite nodules from 4.70 m, mostly greenish gray. Further sampling not possible because of the compactness of the sediment.

Pollen Stratigraphy

The pollen zonation at the Genesee Valley Peat Works is similar to that found in the three bog deposits discussed previously. However, several important differences are apparent: the tripartite C zone does not occur, pine pollen is predominant over an exceptionally broad interval, and very high NAP percentages are associated with rather low percentages of spruce pollen in the sediments beneath zone B. These divergences from the basic pattern have made the placement of zone boundaries difficult and those shown on diagram 9 have been placed with question.

The precise age of the Olean drift on which the present site is located is unknown, but it generally is considered to be older than the Kent glaciation dated at 23,250 B.P. near Cleveland, Ohio (White, 1968). The temporal equivalence of the A and B zones at the Genesee Valley site and similar zones elsewhere in southwestern New York cannot be exact because of differences in basin age. Radiocarbon dates for all the boundaries are needed to determine precise relationships of the Genesee Valley profile.

Zone A. Spruce pollen reaches a maximum of 29 percent in one level near the bottom of the zone, but in general percentages are half what they are at the other sites in the study area. Spruce gradually decreases in abundance upward and is replaced mainly by *Pinus*. About 5 percent *Pinus* subg. Pinus pollen occurs; *Pinus* subg. Strobus pollen is only sparsely represented. Also present in A zone spectra is 2 percent *Abies* pollen.

Pollen from broadleaf deciduous trees consistently occurs in the A zone. *Fraxinus* and *Quercus* each account for about 8 percent of the sum, and lesser, but nonetheless substantial, percentages of *Betula* and *Carpinus-Ostrya* also are found. In addition, *Acer, Carya, Corylus, Fagus, Juglans, Ulmus,* and *Tsuga* pollen are present, but in very low percentages. Typically, these taxa amount to 15–20 percent of the total.

The most unusual aspect of the A zone is high percentages of NAP. In similar stratigraphic positions at the other sites, total NAP reached only 10 percent, but here it accounts for over 30 percent of the sum and reaches 48 percent in the bottom spectrum. Between 3.45 and 3.19 m, near the A/B transition, NAP decreases from 33 to 5 percent. Pollen from a variety of herbs was identified throughout zone A. Cyperaceae, Gramineae, high-spine Compositae, and *Salix* have by far the highest percentages. Total grass and sedge pollen varies from 25 to 30 percent. Lesser amounts of *Alnus, Ambrosia, Artemisia,* Cheno-Am., *Myrica, Plantago,* Rosaceae, *Thalictrum,* and Umbelliferae occur, and, of the minor types listed in diagram 9 and appendix N, the most ecologically significant are grains similar to *Empetrum* sp., *Dryas* spp., and *Saxifraga* spp., which are found in spectra below 4.5 m.

The number of pollen and spores per ml of sediment does not help to further define the A zone. Below 3.19 m, the absolute numbers vary from 42,000 per ml at 4.8 m to 85,000 at 3.45 m, with most spectra having about 50,000 grains. The increase in the number of pollen and spores upward is not great enough to overcome the decrease in spruce percentages, so similar curves are obtained whether the data are plotted on an absolute basis or not.

Zone B. The A/B zone boundary was located at the middle of the increase in the *Pinus* total curve. Greater *Pinus* percentages are compensated for by a decrease in *Picea* and nonarboreal pollen. Pollen of *Pinus* subg. Strobus and subg. Pinus are both present, and, while the former continues to occur in abundance upward, the latter falls to less than 1 percent near the middle of the zone and stays at this level until it drops completely out of the counts in zone C-1. In some spectra, total *Pinus* accounts for 70 percent of the sum. *Abies* percentages reach a peak just below the middle of zone B.

High percentages of *Quercus* pollen which occur with pine in zone B at the other sites are not present until near the end of the zone. In the bottom half of zone B, *Quercus* is found in slightly lower percentages than were present throughout zone A, but above the middle of zone B, *Quercus* increases from 7 to about 15 percent.

The B/C-1 boundary was placed at the middle of the interval where total *Pinus* percentages decrease and *Tsuga* percentages reciprocally increase. The abrupt rise in the *Tsuga* curve marks the beginning of zone C-1 at this site as at others in southwestern New York. A slight increase in percentages of *Ulmus* and *Carpinus-Ostrya* is apparent near the end of zone B, but percentages of other AP types remain fairly constant across the zone.

NAP percentages in zone B are about one-fourth of lower spectra. Cyperaceae and *Salix* pollen are the two most abundant types.

Intrabasinal succession is well defined by peak pollen frequencies of bog and lake indicator species at various levels in the sediments which themselves are evidence for such change. Pollen from *Sagittaria* and *Sparganium,* two shallow water, near-strand aquatics, occur in the lowest spectrum and upward for over 1.5 m. They imply that the water was probably too deep during most of this interval to permit other aquatics to grow near the sampling point. Somewhat higher in the sediments, *Potamogeton* makes its first appearance, and later *Brasenia* occurs in abundance. These are rooted, open water aquatics which generally grow in shallow ponds. Both have peak frequencies higher in the section, near the level where *Sagittaria* and *Sparganium* drop out of the counts. *Potentilla palustris* and *Potamogeton* first appear together, but the peak percentage of the former is slightly above that of the latter, a situation perhaps caused by the occurrence of *Potentilla palustris* at the leading edge of an advancing bog mat. High percentages of Cyperaceae pollen occur in these levels and in those immediately above, at which point both *Potentilla* and *Potamogeton* have nearly dropped out of the counts. The Cyperaceae high occurs precisely between the last occurrence of *Potentilla palustris* and the first occurrence of Ericaceae pollen. In absolute numbers of pollen per ml of sediment, sedge pollen is more than twice as abundant in this part of the profile than in the A zone. Within this interval occur three separate horizons of the moss *Meesia trifaria,* a predominantly boreal forest species with disjunct stations throughout the Great Lakes states. It grows in bogs and swampy woods, often in somewhat calcareous situations. Upward, Cyperaceae percentages decrease and percentages of Ericaceae and Polypodiaceae rise. Ericaceae reach a peak near the top of the profile, and, slightly above this, maximum Osmundaceae percentages occur.

These changes record the presence of several distinct plant communities which probably occurred largely in response to the degree of basin infilling. In a developmental sequence, open water, sedge mat, ericaceous shrub heath, and bog forest are the main ones indicated. The bog forest is the least clearly defined, but evidence of its presence is afforded by high percentages of Osmundaceae spores similar to those produced by *Osmunda cinnamomea* and *O. regalis,* species characteristic of this habitat.

Zone C. The entire C zone is truncated and no subdivisions as defined in previous profiles can be discerned. *Tsuga* and *Fagus* pollen curves indicate that only zone C-1 is present. The *Tsuga* curve is unparalleled elsewhere in the study area. High *Pinus* percentages persist well above the B/C-1 boundary, and *Pinus* subg. Strobus pollen is the predominant type present. Between 0.5 and 1 m, *Pinus* drops below 10 percent of the total.

Pollen from deciduous tree species show a gradual increase in the upper C-1 spectra. *Acer, Betula, Carya, Fagus, Fraxinus, Juglans, Tilia,* and *Ulmus* have higher percentages at the end of the zone than at the beginning. The temporary decrease in the *Betula, Fagus,* and *Quercus* curves at 1.41 m is associated with a reciprocal increase in *Pinus.* This probably reflects a short term change during which *Pinus* became more abundant locally, perhaps due to disturbance.

Total NAP percentages are low and account for less than 2 percent of the sum in all C-1 spectra except at 0.67 m where *Nemopanthus, Rhus, Salix,* and *Viburnum* pollen, probably from species growing on the bog mat, account for over 12 percent of the sum.

Interpretation

ZONE T

Among the sites included in this study, pre-A zone spectra with total NAP amounting to 50 percent or more of the sum occur only at Allenberg Bog, although the lowest spectra from the two Valley Heads bogs contain enough nonarboreal pollen to indicate they are transitional between the NAP-rich T zone and the comparatively NAP-poor A zone. The large nonarboreal pollen content in what I have called the A zone at the Genesee Valley Peat Works is difficult to interpret and will be discussed under zone A. Herb-rich pollen spectra have been reported previously from two sites in upstate New York: Crusoe Lake near Syracuse (Cox & Lewis, 1965) and Kernochan Bog southwest of the Catskill Mountains near the Pennsylvania border (Stingelin, 1965). Erratic fluctuations of tree and herb pollen percentages in the basal gravelly clay at Crusoe Lake and then unknown age of the sediments make interpretation difficult, but the authors tentatively suggest correlation with the Port Huron (Mankato)–Two Creeks–Valders sequence recognized in pollen diagrams from northern Maine (Deevey, 1951). At Kernochan Bog, from 15 to 45 percent NAP occurs in a 2.5 m section of silty clay differentiated as zone T. The entire interval is taken as evidence of a period during which the vegetation near the site was taiga-like. It is of interest that *Quercus* pollen is nearly absent from the bottom 1.5 m of zone T at Kernochan Bog.

T zones, or Herb Pollen Zones as they have come to be called more recently, have otherwise been found in various parts of glaciated eastern North America (Davis, 1967a; Sirkin, 1967), Michigan (Andersen, 1954), Minnesota (Cushing, 1967), and elsewhere. Zone T pollen assemblages from Allenberg Bog have much in common with comparable spectra from these regions, but, in general, sites in New England have less spruce and more sedge pollen, while at Minnesota and Wisconsin localities, more spruce but about the same percentage of sedge pollen occurs.

In recent years, pollen diagrams have been most effectively interpreted by relating the pollen rain in regions of known vegetation to fossil pollen spectra. If fossil and modern pollen assemblages are similar, a high probability exists that the vegetation producing them was analogous, and, as an extension of this, it can be further reasoned that the climate controlling the vegetation was similar at both points in time. The pollen content of uppermost lake sediments, moss polsters, and other surficial pollen traps has been determined at many localities across northern North America.

Among the surface counts compiled by Davis (1967a), none is exactly like zone T pollen assemblages at Allenberg Bog, although certain spectra from tundra and boreal forest regions of Laborador are more or less similar. The pollen rain in the boreal forest-tundra ecotone at Fort Churchill, Manitoba (Ritchie & Lichti-Federovich, 1967) also more or less resembles Allenberg Bog T zone pollen assemblages. Major pollen types found at the surface at Fort Churchill include *Picea* (13 percent), *Pinus* (25 percent), *Betula* (11 percent), Gramineae (6 percent), and Cyperaceae (24 percent). Lesser amounts of *Larix, Alnus, Salix, Myrica,* and pollen of a number of herbaceous species are also present. At this particular site, only 0.1 percent *Artemisia* pollen occurs (*vs.* 5 to 8 percent at Allenberg Bog), but at other sampling localities in the same vegetation type, up to 17 percent is present. The vegetation near Fort Churchill today appears to be a fairly close analogue to that which existed near Allenberg Bog during accumulation of zone T sediments, although as Davis (1967a) points out, the current pollen rain in the tundra and tundra-forest ecotone is too similar to permit distinguishing these vegetation types in the fossil record.

The density of trees across the landscape near Allenberg Bog during zone T time is difficult to estimate. Pollen of *Picea* (20 percent) and *Pinus* (10 percent) indicates that spruce and pine grew within pollen dispersal distance but not necessarily close to the basin. For example, Ritchie and Lichti-Federovich (1967) report 4 to 35 percent spruce pollen from various parts of subarctic Canada where spruce trees occur in widely scattered stands surrounded by extensive heaths and dwarf-birch tundra. Hafsten (1961), working in the southwestern United States, found pine pollen (up to 10 percent) 150 mi from its nearest source, and over 10 percent has been reported from surfaces at three high-arctic sites (Ritchie & Lichti-Federovich, 1967). As these findings indicate, pine and spruce pollen can be blown into areas where the parent plants either do not occur or are of patchy distribution.

Among other arboreal pollen types identified in zone A, those of thermophilic, Temperate Zone genera and species are anomalous in a pollen assemblage which otherwise indicates the vegetation surrounding the site was similar to that in the boreal forest-tundra ecotone. These include *Fraxinus nigra* (from 3 to 5 percent), *Quercus* (from 3 to 8 percent), and a few grains (2 percent and less) of *Carpinus-Ostrya, Carya, Corylus, Fraxinus americana* and/or *F. pennsylvanica, Juglans cinerea,* and *Ulmus.* Such pollen frequently occurs in late glacial T and A zone spectra throughout glaciated eastern North America. Its presence has been explained by claiming redeposition from older sediments (Andersen, 1954) and long-distance wind transport (Deevey, 1951). For climatic reasons, a third alternative, that species producing these types actually grew nearby, seems less likely, at least during accumulation of zone T sediments.

No source near Allenberg Bog for rebedded pollen is known. Pollen in zone T at this site is extremely well preserved and shows little evidence of abrasion. However, a strong case can be made for wind transport using data published by Ritchie and Lichti-Federovich (1967) who measured the pollen rain at Fort Churchill for 6 days in early May, a time when local plants had not begun to flower. During each 24-hour period at least one *Quercus* grain was trapped and a maximum of four grains was collected on one of the 6 days. Other types were recovered less frequently, but were often more abundant. For example, pollen of *Ulmus* (17 grains), *Corylus* (15 grains), *Fraxinus* (5 grains; pollen with three and four colpi not separated) were trapped in one 24-hour period. All anomalous pollen types occurring in zone T at Allenberg Bog except *Carpinus-Ostrya* were found capable of being carried to Fort Churchill from sources 500 to 1000 mi away. Furthermore, because absolute pollen frequency data indicate a low delivery rate of pollen and spores to basins during the T zone interval, the area contributing to the pollen rain may have been much larger at this time than during any subsequent period. Fewer than 1000 grains/cm^2/year were deposited during the T zone interval at Rogers Lake, Connecticut, in sediments older than 12,000 B.P. (Davis, 1967b). The absence of radiocarbon dates from Allenberg Bog makes similar calculations impossible, but the number of grains/ml of sediment is nearly equal in pre-A zone spectra at both sites. With a relatively small number of grains reaching a basin every year, the few grains occasionally shed in the air by local entomophilous species and those derived from distant sources would have an increased chance of being expressed in pollen counts. This also is borne out by data from Fort Churchill where a deposition rate of 1400 grains/cm^2/year has been measured and pollen from both entomophilous taxa and distant trees occur (Ritchie & Lichti-Federovich, 1967).

Calculated as a percent of the sum of all other trapped pollen and spores, however, pollen of Temperate Zone tree species at Fort Churchill amounts to only 0.6 percent of the total. Since higher percentages of *Quercus* and *Fraxinus* pollen occur at Allenberg Bog, species of oak and ash perhaps grew much closer to the site than did species of *Carya, Corylus, Juglans,* and *Ulmus.* The nearness of Allenberg Bog to the unglaciated Salamanca reentrant and other ice-free areas further south suggests that black ash and at least one species of oak may have occupied favorable habitats some tens of miles beyond the terminal moraine. Of the ashes in eastern North America, *Fraxinus nigra* currently has the most northern distribution, so it seems likely that individuals may have been able to survive fairly close to the ice front. Similarly, *Quercus macrocarpa* and *Q. rubra,* which occur northward to the edge of the boreal forest, are the most probable members of the late glacial T zone vegetation near Allenberg Bog.

Davis (1958) has pointed out that T zone herb pollen assemblages are mixtures of taxa which have both northern and southern affinities. Allenberg Bog samples yield pollen of *Artemisia,* Caryophyllaceae, Rosaceae, *Ranunculus, Salix,* Cichorioideae, and Asteroideae (= high-spine Compositae *p. p.*), all of which have species in both arctic and temperate regions. Other pollen types identified in T zone sediments are from taxa which are mainly temperate in distribution. At Allenberg Bog these include *Ambrosia,* Chenopodiaceae-Amaranthaceae, Labiatae, and Umbelliferae. Taxa found exclusively in arctic and subarctic regions have not been identified in the basal layers at Allenberg Bog. However, the presence of *Betula glandulosa* is indicated by size-frequency measurements of *Betula* pollen. This birch is an arctic-alpine species which today is widespread in the North American subarctic and extends southward in eastern North America to the Adirondack Mountains (Fernald, 1950). Microspores of *Selaginella selaginoides,* a species that grows at exposed calcareous sites in boreal forest and subarctic regions across North America as far south as the upper Great Lakes and northern Maine (*ibid.*), are found also in zone T sediments at Allenberg Bog. The presence of these species and pollen from other taxa with high light requirements, supports an interpretation involving the existence of an open or semiopen tundra-like vegetation.

In the absence of radiocarbon dates, it cannot be determined if the semitreeless landscape which occurred adjacent to Allenberg Bog was a successional stage transitional to a spruce forest, or whether a climatically-controlled group of communities equivalent to several of the many expressions of tundra vegetation was present. In southern New England, where tundra persisted several millenia prior to 12,000 B.P. (Davis, 1967b), the treeless interval probably represents a period during which the climate was too severe to allow the development of spruce forest, although trees may also have been absent because they had not migrated to the region.

To summarize, Allenberg Bog T zone pollen assemblages seem clearly to imply the occurrence of park-tundra vegetation prior to development of A zone spruce communities. Size-frequency measurements indicate that *Picea glauca* was the main species of spruce present, although *P. mariana* undoubtedly occurred to some extent also. Spruce trees may have been sparsely scattered across the landscape or occurred some tens of miles away. Also present were *Pinus Banksiana* and/or *P. resinosa,* although these species may have grown far south of the site because pine pollen in the amount present may result from long-distance transport. Plant communities rich in sedges, grasses, and heliophytic herbs probably dominated much of the region. Apparently, few true tundra species were present, although a dwarf birch, *Betula glandulosa,* and *Selaginella Selaginoides,* both of which are northern in distribution, are represented in the deposit.

ZONE A

One of the most consistent stratigraphic features in basal lake and bog sediments across glaciated eastern North America is a zone in which spruce pollen accounts for 30 to 70 percent of the sum. In New York State, the presence of a spruce or A zone was early established by McCulloch (1939) from a bog near Syracuse, and other workers have since demonstrated similar zones from sedimentary basins throughout central and eastern New York (Cox, 1959; Durkee, 1960). A zone rich in spruce pollen also occurs at the four sites in southwestern New York I studied, but because the zone differs from basin to basin, it will be discussed in reference to each of the localities.

Genesee Valley Peat Works

Low spruce percentages and high values for total NAP set zone A at the Genesee Valley Peat Works apart from the others. Most A zone spectra at this locality contain less than 25 percent spruce pollen, although a maximum of 29 percent occurs at one level. By comparison, from 40 to 65 percent is present in equivalent stratigraphic positions at the three other sites. Associated with spruce pollen at the Peat Works are unusually high percentages of Cyperaceae, Gramineae, high-spine Compositae, *Salix,* and other NAP types. Replotting A zone spectra on an absolute basis does not greatly change the form of the curves. Although the overall pollen stratigraphy of the entire diagram is basically similar to the other profiles from the region, the unusual character of the spruce zone makes its interpretation difficult.

Nearly equal representation of AP and NAP throughout zone A at the Peat Works, and particularly near the bottom where *Pinus* percentages are low, implies that the regional vegetation was open and perhaps similar to that which occurred near Allenberg Bog while pre-A zone sediments accumulated there. Somewhat larger spruce percentages in the lower part of the zone may indicate that spruce trees were more abundant around the site early in the depositional history of the basin. Pine pollen increases at the expense of spruce higher in zone A, suggesting that pines became more frequent in the surrounding vegetation with the passage of time. *Pinus Banksiana* and/or *P. resinosa* seem to have been the only species present because *P. Strobus* pollen is only sparsely represented. However, because at least some pine pollen could have been blown in from a distance, the actual abundance of pine in the vegetation around the site must remain conjectural for the lowest part of the profile.

A climate too cold to permit development of more dense spruce and pine communities may have been the controlling factor in the lower part of zone A where pollen identified as *Dryas* sp., *Empetrum nigrum,* and *Saxifraga* sp. is found. The proximity of an ice front may have induced conditions favorable for tundra communities and at the same time might have kept *Picea* from becoming more abundant across the landscape. High frequencies of sedge, grass, and forb pollen are expected in vegetation of this type. A warming trend that aided the colonization of the region by *Pinus Banksiana* and/or *P. resinosa* may have occurred in the upper 1.25 m of zone A. The NAP contribution remains more or less constant during this interval implying persistence of open vegetation.

Incomplete knowledge of the current pollen rain in many sections of northern North America hampers search for a modern analogue of the A zone vegetation near the Peat Works. If pollen spectra from this zone truly represent the regional pollen rain, they cannot be matched with any of the surface samples reviewed by Davis (1967a) because modern pollen assemblages in which *Carpinus-Ostrya, Fraxinus, Quercus,* and *Ulmus* pollen are minor but significant components of spectra otherwise dominated by *Picea, Pinus,* and NAP are unknown. The possibility of a southern source for pollen of these predominantly Temperate Zone genera has already been discussed.

Since the Peat Works is situated on Tazewell or pre-Tazewell Olean drift (Muller, 1965), the lowest part of the profile may antedate most other pollen records in eastern North America. Parallel data are not present at other sites investigated in southwestern New York because they had their inception following subsequent glacial advances. Elsewhere in eastern North America, however, several deposits on Olean drift have been studied previously. Highland Lake south of the Catskill Mountains (Cox, 1959) is truncated basally due to incomplete sampling, as is the Cranberry Bog profile from eastern Pennsylvania (see Stingelin, 1965; Gehris, 1965), but the long sedimentary record at Kernochan Bog (Stingelin, 1965), located near Highland Lake about 150 mi east of central Allegany County, contains spectra roughly similar to those at the Peat Works. At Kernochan Bog, below a point where spruce reaches the A zone maximum (35 percent), there is a long, undated interval of lower spruce percentages and high *Pinus* values which does not occur at the Peat Works. Although total NAP values at Kernochan Bog are less than those at the Peat Works, the pine and spruce curves at both sites are essentially identical above the maxima, which suggests these spectra may have regional significance. This may indicate that for an unknown period following Tazewell(?) glaciation and perhaps contemporaneous with subsequent ice advances, a more or less open park-tundra or a sparse spruce-pine woodland existed on the Allegheny Plateau of southern New York and adjacent regions. Pollen analyses of sediments from unglaciated southeastern Pennsylvania below a radiocarbon date of 13,360 ± 230 B.P. (Y-479; Martin, 1958b) have produced spectra somewhat similar to zone A samples at the Genesee Valley Peat Works, but the contemporaneity of the deposits cannot be proved because the age of the Peat Work's sediment is not known. At the Pennsylvania locality, the main differences include larger total NAP percentages (50 to 75 percent) and a weaker expression of *Picea* (ca. 5 percent); *Pinus* comprises from 15 to 25 percent of the total. In light of the uncertain age of the various drift sheets east of the Salamanca reentrant, and of the Genesee Valley and Kernochan Bog pollen profiles, and in the absence of radiocarbon-dated profiles between these two localities, the park-tundra hypothesis is presented as one of several explanations of existing data.

If, however, the NAP was derived mainly from a source near the basin, an alternate interpretation is possible. In this case, the regional vegetation contributing pollen to A zone sediments at the Peat Works may not have been an open park-tundra, but perhaps a more dense spruce-pine woodland, possibly equivalent to zone A vegetation at Allenberg, Houghton, and Protection bogs. As a correction for possible local overrepresentation, A zone pollen percentages can be recalculated eliminating NAP from the counts and using the total number of arboreal pollen at a given level for the percentage base rather than the sum of AP and NAP. The new curves will show the same trends because total NAP is more or less constant throughout the interval. However, the percentage of major arboreal components in the counts increases, and spruce, for example, attains a maximum of nearly 50 percent. The overall transition from the Spruce-dominated basal sediments to pine-dominated sediments above is not unlike the A/B zone transition at other sites in western New York with the exception that it is more gradual.

Several lines of evidence point toward the possibility of local overrepresentation. The slopes above and leading to the center of the basin are gentle and the depression itself is large and relatively shallow. Therefore, an abundance of habitats for marsh plants could have existed around the margin of the basin during its early history. The presence of *Sagittaria* and *Sparganium* pollen throughout zone A indicates that marshy shallows existed at or near the basin. Both genera are not represented in counts higher in the deposit, perhaps because littoral habitats were eliminated by development of a bog mat. While other parts of the valley floor on which the depression is located may have supported marsh communities also, bedrock highs are abundant in the area and well-drained upland sites must have been a regular feature of the landscape.

The spectra may also be contaminated by redeposited pollen. I have not demonstrated that rebedding has occurred since a source of older pollen is unknown in the area, but presence of *Fagus* pollen in the silty clay at the bottom of the deposit and its absence from the more organic sediment immediately above suggest that pollen eroded from nearby drift may have been carried to the basin with inorganic sediment. Andersen (1954) has asserted that the optimum time for redeposition is during an ice advance when frost activity would be continuously exposing potential pollen-bearing deposits. The occurrence of *Fagus* grains together with pollen of *Dryas, Empetrum,* and *Saxifraga* might be explained by claiming a climate favorable for solifluction. Since there is no objective way to determine what part of a pollen spectrum is composed of redeposited pollen or pollen from local, onsite sources, modified spectra, which might compare more favorable with one or more of the surface pollen assemblages now known, cannot be obtained.

Allenberg Bog

At this site, zone A overlies an interval which I interpret as a record of a more or less treeless landscape with herb communities covering much of the region near the basin. Above this, a rapid increase of spruce percentages occurs and high spruce values are maintained for about 2 m of sediment. Fluctuations in relative numbers of subdominant AP types, however, allow the interval to be divided into several subzones reminiscent of those reported from southern New England (Leopold, 1956b; Leopold & Scott, 1958; Davis, 1958). The correspondence of the subzones in the two areas is not exact, and percentage changes in the Allenberg Bog profile are poor evidence of modification of forest composition induced by advance and withdrawal of an ice sheet.

Four divisions of zone A are recognized at sites studied by Davis (1958) in southern New England. At Tom Swamp, Massachusetts, the *Picea* curve increases in the lowest subzone (A-1), while *Pinus* values decrease slightly over the same interval. These changes are also present across a comparable stratigraphic interval in the Allenberg Bog profile. However, high values for *Betula* and *Populus* pollen (ca. 10 percent each) which characterize subzone A-1 at Tom Swamp are absent from Allenberg Bog, and without other stratigraphic markers, an A-1 cannot be defined readily at Allenberg Bog. At Tom Swamp, *Betula* and *Populus* values drop to 5 percent or less of the total in the next highest subzone (A-2), and a pronounced maximum of relative numbers of *Picea* pollen is present also. Somewhat lower *Quercus* percentages occur in this subzone than are present in the A-1 or in the A-3 above. At Allenberg Bog, a spruce peak occurs between 14.70 and 14.94 m, but in contrast to the New England locality, maximum percentages of *Quercus* and *Fraxinus nigra* pollen also occur in this interval. The Allenberg *Quercus* curve shows no important fluctuations below the *Picea* peak, but the maximum A zone percentage of *Fraxinus nigra* pollen occurs just beneath it. Subzone A-3 at Tom Swamp has somewhat lower *Picea* percentages and increased values for *Pinus, Quercus,* and other AP types. At Allenberg Bog spectra between 14.22 and 14.70 m can be assigned to subzone A-3. Higher percentages of *Carpinus-Ostrya* occur in this interval than elsewhere in zone A, although a maximum for this pollen type is reached just above the *Picea* peak. Spruce percentages increase in subzone A-4 which, at Allenberg Bog, occurs in the upper two-thirds of zone A between 12.80 and 14.22 m. *Pinus* values are lower at the middle of A-4 than in A-3, but the curve of the sum of the three pine categories increases gradually across the upper part of A-4. In contrast to the New England diagrams, *Carpinus-Ostrya, Fraxinus nigra,* and *Quercus* percentages do not decline in A-4.

Interpretation of the New England A zone sequence has been related to late Wisconsin glacial events (see Beetham & Niering, 1961; Davis, 1965b). For example, the climate following retreat of Port Huron ice presumably improved, permitting spruce to increase and attain maximum abundance (subzones A-1 and A-2). Lower relative numbers of *Picea* and increased percentages of *Pinus* and deciduous tree pollen types implied further warming during the A-3. Several radiocarbon age determinations permitted initial correlation of the A-3 with the Two Creeks Interstade (see Leopold, 1956b). A return to higher spruce percentages and a drop in oak and pine values in the A-4 were taken as a record of a spruce-dominated forest developing in response to colder climate thought to have prevailed during the ensuing Valders Stade. However, recent dating of the Two Creeks forest at 11,850 ± 140 B.P. (Broecker & Farrand, 1963) makes its correlation with the New England A-3 doubtful.

The similarity between the Allenberg Bog profile and certain New England pollen diagrams may be fortuitous. The lower part of zone A at Allenberg Bog is perhaps not temporally equivalent to spectra with comparable pollen assemblages in diagrams from New England. Accepting 23,250 B.P. (White, 1968) as the age of the Kent drift upon which Allenberg Bog is situated, not only Valders-Two Creeks climatic changes may have influenced the vegetation surrounding the site, but also those associated with the preceding Cary and Port Huron glaciations. Records of these events in the pollen profile may be in part preserved beneath zone A lower in the incompletely sampled clay deposit, but the A zone itself seems not to show any well-defined changes that might be related to them. At Houghton Bog, 25 mi northeast of Allenberg Bog, wood from near the bottom of zone A is of Two Creeks age (11,880 ± 730 B.P., I-3290). The sample occurs with *Picea*-dominated pollen spectra which are similar to those in the upper part of zone A at Allenberg Bog. Between the dated level and the end of the spruce zone at Houghton Bog, which encompasses the time of the Valders re-advance, changes in pollen percentages similar to those just reviewed from southern New England profiles do not occur. Vegetation in southwestern New York State does not seem to have been affected by climatic changes accompanying the Valders readvance. The maximum southward extension of Valders ice was more than 100 mi north of southwestern New York, apparently never reaching the Lake Ontario basin (Karrow *et al.,* 1961) which was then occupied by Glacial Lake Iroquois.

Replotting section C of the Allenberg Bog profile on an absolute basis permits a different approach to interpretation of the A zone sequence (cf. diagrams 7 and 8). Variations in absolute numbers of different pollen types per unit volume of sediment through time are meaningful, however, only if the sedimentation rate was more or less constant across the interval being considered. Although changes in pollen deposition rates are useful data for assessing vegetation change, if sediment accumulation is constant, variations in absolute numbers of types of pollen with depth will show the same trends. The sedimentation rate at Allenberg Bog should be determined by C-14 dating as has been done at Rogers Lake where, between 14,000 and 10,000 B.P., a more or less constant rate of 0.037 cm/year has been measured (Davis, 1967b; cf. Davis & Deevey, 1964).

In the absence of the necessary age determinations, however, the following paragraph is based on the assumption that the time taken to accumulate a unit volume of sediment was the same in all divisions of zone A.

At Allenberg Bog across the interval in which A zone percentages of *Quercus* and *Fraxinus nigra* pollen are high, the number of grains per ml of sediment increases (figure 8). Between 14.540 and 14.425 m, the pollen and spore total stabilizes near 200,000 grains per ml where it remains until the end of zone A. The increase probably is due mostly to a greater number of spruce and pine pollen being deposited in the basin and this may indicate an increase in the number of spruce and pine trees in the region. By 14.425 m, the maximum attainable density of spruce-pine forest may have been reached, and, above this level, no important changes are evident in *Quercus* and *Fraxinus nigra* percentages. Higher relative pollen frequencies just above the T/A zone boundary may reflect the openness of the developing spruce forest when fewer numbers of *Picea* pollen relative to *Quercus* pollen were being deposited. If the input of *Quercus* remained constant, as was the case according to diagram 8, an increase in the absolute numbers of spruce and pine pollen being deposited would reduce percentage values for *Quercus.*

A similar situation prevails at Rogers Lake where zone A begins at 12,000 B.P. and ends about 9,500 B.P. (Davis, 1967b). *Quercus* pollen is present during the entire interval, but 10,500 years ago it fell from about 15 to 5 percent. Less pronounced reductions also occur in *Carpinus-Ostrya* and *Fraxinus* curves at this site. These changes, clearly expressed in the relative frequency diagram, are not maintained when the data are converted to numbers of pollen and spores accumulating per unit area per year. The pollen input from *Quercus* and other temperate deciduous trees remains relatively constant during the entire interval, and the maximum and minimum of oak pollen at 11,000 and 10,000 years, respectively, that occur in the percentage diagram, no longer exist. Davis (*ibid.*) concludes that fluctuations of *Quercus* percentages reflect increasing deposition rates for coniferous tree pollen 10,000 years ago, not a climatic oscillation correlated with the Allerod–Younger *Dryas* sequence.

Upper A zone spectra at Allenberg Bog, with the exception of somewhat higher percentages of *Carpinus-Ostrya* and *Fraxinus,* agree fairly well with southern New England spectra from equivalent stratigraphic positions. Davis (1967a) considers the New England fossil pollen assemblages to be similar to surface samples deposited today in the Nichicun Lake area west of Schefferville, Quebec (ca. 53° N. lat.). This region has been characterized as an open, park-like woodland in which closed black spruce forests, with an admixture of larch, are present at wet lowland localities while black and white spruce and balsam fir occur in open stands interspersed with lichen communities on the better drained, upland sites (Terasmae & Mott, 1965). Davis (1967a) suggests that the lower part of the New England A zone represents tundra-forest transitional vegetation which developed into a boreal woodland later in the zone. Such a change is evidence of gradual climatic warming. The data from Allenberg Bog would seem to fit this interpretation, but it is to be treated as tentative until confirmatory information is obtained from other sites in southwestern New York State.

The gradual increase in the number of *Quercus* grains in the sediment from zone T to the beginning of zone A may represent northward migration of oaks to positions nearer the basin. The occurrence of from 5 to 7 percent oak pollen throughout the upper part of zone A may indicate that oaks were present somewhere within 100 mi or less of the bog. *Quercus* percentages of this magnitude have not been calculated for sites in the boreal forest or in the more open subarctic woodland to the north, either of which, on other evidence, is the closest analogue of the A zone vegetation. In eastern North America near the northern distributional limit of the genus (ca. 46° N. lat.), similar percentages occur. But since this is located in the mixed coniferous-deciduous forest of mid-Ontario, significant percentages of *Acer*, *Ulmus*, and other temperate AP types are present also. These are present in zone A at Allenberg Bog, but in much lower amounts. Less than 1 percent *Quercus* pollen, calculated using the sum AP as the percentage base, was found by King and Kapp (1963) at the southern edge of the boreal forest north of Georgian Bay.

A relatively high representation of temperate tree pollen in existing vegetation dominated by spruce and larch has been found by Janssen (1967) at Myrtle Lake on the Lake Agassiz plain of north-central Minnesota. By comparing an estimate of the original forest composition derived from the General Land Office Survey notes with pollen deposited on the surface at a number of points along transects at the lake, he showed *Picea* and *Larix* to have high importance values in the surrounding vegetation, but to be relatively poorly represented in surface pollen spectra. On the other hand, *Fraxinus, Quercus,* and *Ulmus* pollen were distinctly overrepresented in reference to the regional vegetation. If spruce and larch had a similarly low " delivery capacity " during late glacial time, they would be underrepresented in pollen profiles while higher percentages for certain extra-regional deciduous trees with greater "delivery capacity" would be expected in spite of the probability that they composed only a minor part of the regional vegetation. This situation may apply to A zone pollen assemblages at Allenberg Bog.

Using 100 μ as the dividing point between the smaller pollen of *Picea mariana* and the larger *P. glauca* grains, size-frequency measurements of A zone spruce pollen at Allenberg Bog confirm the presence of both species (figure 10). *Picea rubens* may or may not have been present also. At 14.750 m near the bottom of the zone, the mean size of measured spruce grains was 101 μ; wingtip-to-wingtip measurements were greater than 100 μ in 53 percent of the sample. Higher in the profile, the mean size decreases. Near the end of the zone at 12.925 m, it is 89.2 μ and only 17.6 percent of the measured sample was over 100 μ. Gradual loss of *P. glauca* upward and, probably, replacement by *P. mariana* is implied.

Most of the pine pollen in the Allenberg A zone is the *Pinus* subg. Pinus type. The configuration of the modes in the size-frequency curves for this pollen type (figure 11) may indicate that both *Pinus Banksiana* and *P. resinosa* contributed to zone A sediments. In view of the similarity in pollen size of these species (Whitehead, 1964), however, conclusive identification of species is not possible. The occurrence of about 20 percent of pine pollen throughout the zone definitely establishes that one or both of these pines grew near the basin. This is in contrast to the situation in the western Great Lakes region where significant amounts of pine pollen are not found in the profile until near the end or following the spruce zone (Wright, 1964, 1968b). Judging from the present day habitat preferences, both *P. Banksiana* and *P. resinosa* grew on dry sandy soils, although the former was probably restricted to the driest sites. The low relative frequency of *Pinus* subg. Strobus pollen indicates that *P. Strobus* was not a part of the regional vegetation because the relatively small amount of white pine pollen present in the counts could have been blown to the basin from afar.

The broad size class spread and the occurrence of several modes in the A zone size-frequency curve of *Betula* pollen indicates that more than one species was present near Allenberg Bog (figure 9). The smallest grains, 20 μ or less, may have been produced by the arctic-alpine dwarf birch, *B. glandulosa.* This species was apparently also present during accumulation of underlying T zone sediments. The modal classes centering near 22 and 24 μ, however, have no exact counterparts among the nine out of eleven native northeastern North American birches studied by Leopold (1956a). Although it could be postulated that extinct species contributed to the modal classes, it is more likely that the maceration technique or some aspect of the depositional environment modified grain size. In the upper part of zone C, for example, where the principal contributors to the pollen rain were *B. lenta* and *B. alleghaniensis,* the modal class is smaller than that reported for pollen from herbarium specimens of either species (*ibid.*). On the basis of modern distribution patterns and pollen size-frequency characteristics, two additional birches may have been members of the late glacial flora near Allenberg Bog. One of these, *B. populifolia,* has small pollen (mode 27 μ in three acetolyzed preparations; *ibid.*). Davis (1958) suggests that it may have occurred in the New England A zone vegetation where it likely occupied disturbed sites. *Betula papyrifera* is also expected because it now grows mainly in the boreal forest. However, the relatively large pollen of this species (mode 33 μ in one acetolyzed preparation; Leopold, 1956a) does not correspond to measurements of fossil grains at Allenberg Bog.

Reviewing briefly the nature of the zone A vegetation at Allenberg Bog as it is has been interpreted here, the lower third of the zone seems to record the development of a more or less open boreal woodland similar to that which today occurs in the subarctic of northern Quebec. This appears to have persisted throughout most of the zone because few meaningful changes occur in zone A above 14.5 m. The woodland was preceded by a transitional vegetation type in which spruce and pine greatly increased in abundance. These changes may have been in response to a warming trend in the climate, as zone A overlies an interval of tundra-like vegetation apparently dominated by herbaceous communities with spruce probably infrequent in the entire region. Without information on the duration of the tundra, however, a simple successional change may be represented instead. The density of *Picea* and *Pinus* in various parts of zone A must remain conjectural until additional surface samples prove that the pollen rain in an open woodland is different from that in a more closed forest. If the landscape contributing to the regional pollen rain was incompletely covered by stands of *Picea glauca* and *P. mariana*, the latter being more abundant at wetter sites, various nontree communities dominated by sedges, grasses, *Artemisia*, other Compositae, and additional herbs occupied the openings. *Alnus* and *Myrica* were probably present at the lake edge and in other nearby wet habitats. *Salix* was also part of the vegetation, but it is not known whether dwarf or shrub species are represented. *Pinus Banksiana* and/or *P. resinosa* probably grew at dry sandy sites in the vicinity, and both *Abies balsamea* and *Larix laricina* were members of the regional vegetation although it is not possible to tell in what proportion they occurred in the forest because their pollen is usually underrepresented. *Carpinus caroliniana* and/or *Ostrya virginiana, Fraxinus nigra*, and *Quercus* spp. occurred at some distance from the basin, perhaps within 100 mi, but this is difficult to document with certainty.

Houghton and Protection Bogs

The two sites that remain to be discussed are associated with the Valley Heads moraine. Both have relatively thin A zones in comparison to the long interval of spruce domination at Allenberg Bog. In neither of them is there clear indication of a zone with high NAP percentages. The lowest spectra in each contain from 15 to 24 percent herb and shrub pollen, but this is in association with high values for *Picea* (40 to 50 percent). The absence of zone T at both localities may be a sampling deficiency although the samplers were pushed as deeply as possible. Pollen is present in the basal clay at Protection Bog, but is absent from similar sediments at Houghton Bog.

Zone A pollen spectra from both Valley Heads bogs compare favorably with upper A zone spectra Allenbreg Bog. The vegetation that presumably produced these pollen assemblages has just been reviewed and little additional information can be added here. In common with the other sites in southwestern New York, *Carpinus-Ostrya, Fraxinus,* and *Quercus* pollen occur in the A zone of both profiles. Lesser amounts of *Carya, Corylus,* and *Ulmus* pollen are present also. Low relative numbers of *Tsuga* pollen first appear in zone A at the two bogs and also near the beginning of this zone at Allenberg Bog. It is probable that hemlock was an extraregional species at this time because the few grains present could have been wind carried to the site from a distant source. All of these are minor pollen types, however, and the zone is clearly dominated by spruce and pine. *Pinus Banksiana* and/or *P. resinosa* were present. Except for the pollen of temperate tree species, the assemblages match the modern pollen rain accumulating today in the open, boreal woodland of subarctic northern Quebec and at points to the south within the boreal forest itself.

A maximum in the *Abies* curve occurs near the end of zone A in all four profiles but is best developed at Protection Bog. At this locality, and perhaps at the others as well, the maximum may represent an actual increase in the number of balsam fir near the basins. Rapidly declining spruce percentages associated with the fir maximum imply an abrupt and perhaps catastrophic change in the vegetation. If balsam fir was growing suppressed in a spruce-dominated woodland, deterioration of the spruce overstory might have released fir seedlings and saplings in the understory. The period during which fir thrived must have been relatively short because its pollen drops out of the counts soon after the maximum is reached. At present, *Abies balsamea* persists under dense forest cover but nearly full sunlight is needed for best development (Fowells, 1965). This is in agreement with its known quick response to release. High fir percentages near the end of the spruce zone occur over a wide area in the Northeast, although the peak is sometimes just within the zone and other times at its end (Cox, 1959; Deevey, 1943; and others).

Deevey (1943) suggests that high fir values, which often occur with a spruce maximum at New England sites, may represent a change in the vegetation brought about by the last major glacial advance. As such it would correlate with subzone A-4 discussed previously. Since the Protection Bog fir peak occurs in sediments accumulated about 10,500 B.P. (extrapolating from the two higher dates at this site assuming a constant sedimentation rate), considerably after the last or Valders glaciation, it seems best to view the peak as a successional event.

The radiocarbon dated Valley Heads profiles enable time stratigraphic correlations to be made between these sites and others in eastern North America. In New York State, few published pollen spectra are comparable in age to the late glacial A zone assemblage at Houghton Bog dated at 11,880 ± 730 B.P. (I-3290). Pollen spectra above and below sediments dated at 12,850 ± 250 B.P. from a bog in eastern New York (Connally & Sirkin, 1970) contain less spruce and more pine and birch pollen than equivalent spectra at sites in southwestern New York. At the King Ferry site in the Finger Lakes region of central New York (Cox, 1959; Brown *in* Deevey *et al.,* 1959) spruce wood, 11,410 ± 410 years old (Y-460), associated with a mastodon skeleton, was embedded in sediments dominated by spruce and pine pollen. Spruce accounts for over 80 percent of total AP; NAP, unfortunately, was not tallied. The microfossil flora was taken to record the presence of a boreal, coniferous forest in central New York (*ibid.*).

Spruce wood dated at 12,100 ± 400 B.P. (I-838; Buckley *et al.,* 1968) from along the Glacial Lake Iroquois strand in central Niagara County near Lockport, N.Y., is approximately the same age as the lower part of the Houghton Bog A zone. A pollen assemblage from silty clay associated with the organic bed from which the wood was taken (N. G. Miller, in prep.) is similar to Houghton Bog spectra of the same age. The main difference is the relative frequency of Cyperaceae pollen: 34 percent is found at the former site, while only 4 to 8 percent occurs at Houghton Bog. If all of the sedge pollen is considered to have been produced by the upland vegetation, it is likely that a considerably less dense spruce woodland occurred near Lockport than existed 50 mi south near Houghton Bog. If, on the other hand, habitats near the strand were especially favorable to aquatic, lowland members of the family, local overrepresentation could explain the difference. Seeds of *Eleocharis* cf. *palustris* are abundant in the organic bed and substantiate a case for a near-site origin of much of the " sedge " pollen. Species of *Eleocharis* probably grew in beach pools at the Lake Iroquois strand and along streams draining Lake Tonawanda which at this time occupied a portion of the lowland between the Niagara and Onondaga escarpments. Since pollen recovered from the lake sediments was carried there by both wind and moving water, near-site aquatic and semiaquatic species shedding pollen into the water would have an excellent chance of being strongly represented in the counts.

Cones of black spruce occur in the Lockport deposit and perhaps one other species of spruce is also represented. Spruce needles, seeds, and twigs are exceptionally abundant. Cone fragments and a single seed of *Larix laricina* establish the presence of this species. But apart from these fossils which indicate the presence of trees, a rich assemblage of mosses recovered from the organic bed permits recognition of several distinct, nonforest plant communities (N. G. Miller, in prep.). Rich fens must have been relatively common because both fen and fen edge mosses are abundant. Drier habitats, perhaps beach ridges, were present, and species which may have grown on or among the calcareous rocks of the nearby Niagara escarpment also occur. Only one species which today typically grows in shaded spruce forests was identified. Other species which sometimes grow in this habitat were found also, but these are less useful indicators because they occur at open sites as well. The absence of a dominant forest element in the moss flora probably means that the landscape along this part of the Iroquois strand was occupied by a patchwork of dry- and wet-site herb and moss communities and that spruce occurred some distance behind the beach. Most of the spruce macrofossils were probably carried to the site by drainage from the inland as is shown by their abraded nature. Nearly all the fossil mosses are characteristic boreal forest species. Most range northward to the arctic tundra, but many also occur in the Great Lakes states. The species of greatest phytogeographic interest are *Aulacomnium acuminatum* and *A. turgidum* whose present North American ranges center on the arctic and subarctic. The southernmost station for the former is along the north shore of Lake Superior, an area well-known for its relict, arctic-alpine plants. *Aulacomnium turgidum* has a greater number of occurrences along the southern edge of its range, but it also is widespread in the subarctic and arctic. In the East, disjunct stations are known from the high peak region in the Adirondack Mountains and from the White Mountains. These taxa indicate that arctic-alpine vascular plants may also have grown near Lockport 12,000 years ago and raise the possibility that limited areas of tundra may have occurred in the region at this time.

Beyond New York State, but within glaciated eastern North America, spruce-rich forests were widely distributed 12,000 years ago. Their presence in southern New England (see Davis, 1965b) has already been mentioned. To the west in southern Ontario, the beginning of organic sedimentation and the upper part of zone A at Crieff Kettle Bog near Hamilton has been dated at 11,950 ± 350 B.P. (Karrow, 1963). Spruce pollen accounts for about 80 percent of total AP (Terasmae *in* Karrow, 1963), and the proportion of white to black spruce pollen is approximately six to one. *Abies, Betula, Pinus Banksiana,* and *Quercus* are the other main tree pollen types present. From 15 to 45 percent NAP occurs in the zone (based on sum AP), and *Ambrosia, Artemisia,* other Compositae, Cyperaceae, and Gramineae are the principal types identified. *Dryas* pollen occurs near the bottom of the zone.

The correspondence of the Houghton Bog date and the newly determined age of the Two Creeks forest bed (11,850 ± 100 B.P.; Broecker & Farrand, 1963) has been noted. West's reanalysis (1961) of the type Two Creeks locality in eastern Wisconsin produced spectra dominated in all levels except the bottom by up to 90 percent spruce pollen (based on AP + NAP sum). In the lowest spectrum, *Shepherdia canadensis* accounts for over 95 percent of total pollen. This heliophytic shrub may have been one of the first colonizers of surfaces freed for plant occupation in the area. One out of every six spruce grains was identified as *Picea mariana.* Spruce forest was also present farther westward in southeastern Minnesota at this time (the *Picea-Larix* Assemblage Zone of Cushing, 1967).

The spruce-dominated vegetation 12,000 years ago, however, was clearly not of uniform composition across the region from New England to Minnesota. The most obvious difference is the presence of high values for *Pinus* pollen in western New York and New England and their absence from sites in Michigan, Wisconsin, and Minnesota. Apparently, pines were a part of the late glacial A zone vegetation in the East, but did not occur in the contemporaneous vegetation of the Midwest. The available data (Wright, 1964; 1968b) indicate that the Appalachian region served as a full and late glacial refugium for the three main pine species, *P. Banksiana, P. resinosa,* and *P. Strobus,* which participated in the revegetation of the glaciated Northeast. The relative numbers of temperate deciduous tree pollen types also vary from site to site within the region. An accurate assessment of the variability in terms of climate, however, depends in part on a detailed knowledge of the pollen rain in existing boreal forest and woodland, the forest-tundra transition, and the tundra itself. This is not available at the present time. Also, it must be kept in mind that modern analogues for certain late glacial pollen assemblages may never be found because the vegetation which produced them may have been a mixture of species brought together by differing migration rates and may thus represent chance combinations of species which coexisted for varying periods of time following the withdrawal and disappearance of the ice.

South of the glacial boundary in Pennsylvania the vegetation 12,000 years ago was apparently much different from that found at this time in western New York. At Bear Meadows in central Pennsylvania (Kovar, 1964; Stingelin, 1965), pollen analysis of sediments below a radiocarbon date of 10,320 ± 290 B.P. (Westerfeld, 1961) produced spectra dominated by pine pollen (60 to 70 percent). Spruce is weakly represented (10 to 15 percent) and NAP totals about 10 percent of the sum. Similar spectra have been obtained by P. S. Martin from sediments below a C-14 date of 11,300 ± 1000 B.P. (Y-727; Guilday *et al.,* 1964) at the New Paris Sinkhole No. 4 in south-central Pennsylvania, 65 mi from Bear Meadows. The 3 m of cave filling beneath the dated horizon is dominated by *Pinus* pollen, which accounts for about 60 percent of the sum (AP + NAP). From 6 to 15 percent *Picea* pollen occurs across the same interval, and the rest of the sum from 20 to 30 percent, is comprised of Cichorioideae, other Compositae, Cyperaceae, and Gramineae pollen. Near-site and onsite plants likely produced much of the pollen in the nonarboreal category. The vegetation producing this assemblage may have resembled an open boreal woodland with spruce and jack(?) pine stands separated by open ground (*ibid.*). Above the dated level, *Pinus* remains dominant, but *Picea* drops to less than 5 percent of the sum, and Betulaceae, *Quercus,* and other temperate arboreal pollen taxa become strongly represented. This apparently records the movement of temperate forest elements into the area.

Sediments below the date contain bones of a large number of vertebrates whose modern ranges center southeast and west of Hudson Bay in boreal Canada. Of particular interest are the remains of at least three Labrador collared lemmings, a species that today occurs mainly within the tundra of northern Quebec. Also found were the bones of the 13-lined ground squirrel and the sharp-tailed grouse, two prairie species whose occurrence substantiates the contention (Schmidt, 1938; see also Benninghoff, 1963) that an eastward extension of prairie elements occurred in late rather than postglacial time.

If the vegetation in central and southern Pennsylvania indeed was an open, boreal woodland like that existing beyond the north edge of the boreal forest today, an interpretation which is in part substantiated by the fossil vertebrates, the presence of a more closed spruce-pine forest to the north on glaciated terrain is difficult to understand because this zonation is the reverse of the current arrangement of these vegetation types in North America. Existing data are too sparse to establish the presence of the boreal forest in the region south of Pennsylvania and a taiga-tundra in a wide band between the ice margin and the forest during full glacial times, 18,000 years ago (cf. Martin, 1958a). If such a zonation existed, however, low relative numbers of spruce pollen in Pennsylvania about 11,500 years ago might have been produced by stragglers of the spruce migration that characterized this phase of revegetation of the glaciated region to the north. The apparent abundance of pine in Pennsylvania at this time, as shown by the work of Martin (Guilday *et al.*, 1964; Kovar, 1964), indicates that certain species of this genus may have dominated the landscape northward toward New York State. A floristic boundary separating spruce- and pine-rich forests must have existed somewhere between the two areas. If pines indeed were dominant behind the spruce forest during A zone time, this would help explain the rapid development of the B or pine zone following the disappearance of spruce from the region. In western New York, *Pinus Strobus* was the principal B zone pine. How early it was present in central Pennsylvania during late glacial time is not known.

The end of the A zone at both Houghton and Protection bogs can be dated by extrapolation. At the former locality, assuming that the pine peak occurred at the same time as it did at nearby Protection Bog and that the sedimentation rate was constant, the midpoint of the *Picea* decline is about 9500 B.P. Since the basal marl at Houghton Bog may have accumulated at a more rapid rate than the silty gyttja at Protection Bog, this date may be somewhat too young. The same type of calculation applied to data from Protection Bog yields an age of 10,500 B.P. for the same point in the spruce decline. Both age determinations are in accord with those listed by Ogden (1967b) who has concluded that the approximate synchroneity of the extinction of spruce forest across midlatitude eastern North America points toward a sudden climatic change at this time.

ZONE B

As the spruce-dominated A zone vegetation near the two Valley Heads sites disappeared 10,500 to 9500 years ago, the pollen record indicates that pines became increasingly abundant in the region. At Houghton, Protection, and Allenberg bogs the transition was abrupt. In contrast, spruce percentages at the Genesee Valley Peat Works gradually decline, although *Pinus* values increase rapidly. This is achieved mainly at the expense of various nonarboreal pollen types. High *Pinus* values are maintained upward well into spectra which seem equivalent to those in zone C-1 at the three other sites. Although *Pinus* drops to about 7 percent of the sum in the Genesee Valley profile above a depth of 1 m, that portion of the diagram in which percentages of both *Pinus* and *Tsuga* are high may be strongly influenced by onsite pine trees. *Pinus Strobus* pollen was the main type identified from this interval and the occurrence of white pine cones at various levels in the peat implies that white pine was growing locally. For this reason, the end of zone B was placed at 2.25 m near the midpoint of the *Tsuga* increase, even though above this level, *Pinus* percentages are still high. The A to B zone transition has not been dated at either Allenberg Bog or the Genesee Valley Peat Works, but, considering the proximity of all four sites, the disappearance of spruce may have been synchronous across the entire region.

The interval over which maximum zone B pine percentages occur in sediments at Protection Bog was dated at 9030 ± 150 B.P. (I-3551). This compares well with a date of 9310 ± 150 B.P. from an equivalent stratigraphic position at Crystal Lake in northwestern Pennsylvania (Walker & Hartman, 1960) where the entire postglacial pollen sequence parallels that in my profiles from western New York. The dated sample at Crystal Lake was taken from the level at which maximum *Pinus* values occur, although at this depth *Picea* still amounts to 10 percent of the sum. In southern New England, maximum relative and absolute numbers of pine pollen have been found in sediments about 9000 years old (Davis, 1967b; see also Davis, 1965b).

The ecological meaning of zone B has been discussed at length by Dansereau (1953) who presents a number of hypotheses to explain the widespread occurrence of maximum pine values following the disappearance of the A zone spruce forests. A part of the difficulty in interpreting zone B lies in the well-known overrepresentation of pine pollen in sediments. With this in mind, Davis (1963, 1965b) has applied correction factors derived from a comparison of surface pollen accumulation and vegetation composition to a profile from northern Vermont. Her data indicate that maximum B zone pine percentages are an artifact caused by the low pollen productivity of the rest of the B zone vegetation. Pine trees were thought to have been rare in the region surrounding the basin in spite of the high relative pine pollen frequencies. This interpretation was later revised, however, when absolute pollen frequency data from Rogers Lake in southern Connecticut became available (Davis, 1967b). The deposition rate of oak, pine, and other arboreal pollen types was found to actually increase in zone B, and at certain levels the rate for pine was 18 times greater than later in postglacial time, implying that pines were truly abundant in the region during zone B time. Absolute pollen frequency determinations from Allenberg and Houghton bogs corroborate these findings, assuming that the sedimentation rate was uniform across zone B at these sites.

Either *Pinus Banksiana* or *P. resinosa* or both appear to have been members of the regional vegetation that contributed pollen to zone A sediments in western New York. Fairly high values for these species, members of *Pinus* subg. Pinus, persist through the lower part of zone B at all sites, but by the end of zone B time, only 1 to 3 percent occurs. Similar values are found in early postsettlement spectra before extensive plantings of pines belonging to subg. Pinus were made in the area. At this time, presumably, only *P. resinosa* was contributing subg. Pinus type pollen to the sediments. Today in western New York, native red pine is restricted to stations along the Genesee River (Zenkert, 1934).

Utilizing data provided by Whitehead (1964), a shift of the mode to a larger size class (figure 11), may indicate that *Pinus resinosa* was the principal B zone pine of subg. Pinus, while both *P. Banksiana* and *P. resinosa* may have been members of the zone A vegetation. However, the closeness in pollen size of these two species, as Whitehead emphasizes, makes positive identification impossible. Pines of subg. Pinus were infrequent in the regional vegetation at the west end of New York State after about 9000 B.P., while they appear to have been more abundant throughout the state before this date (see Cox, 1959). Prior to 10,500 B.P., red or jack pine or both were absent from Minnesota, but about this time they arrived at the southeast corner of the state, having migrated, probably north of the Great Lakes, from their refugium in the Appalachian Highlands of eastern North America (Wright, 1968b; Yeatman, 1967). Jack pine does not seem to have persisted south or west of the upper Great Lakes.

The relatively few *Pinus Strobus* grains which occur in the lower half of zone A imply that white pine was initially not near any of the basins. However, higher in zone A sediments, *P. Strobus* percentages increase indicating that white pine became more abundant regionally. This is most clearly seen in the Allenberg Bog section C diagram. It is certain, however, that white pine was present near Protection Bog during the A to B zone transition because a white pine cone was recovered from silty-clay gyttja at a depth of 5.75 m. Extrapolating from the two higher radiocarbon dates at this site, assuming a constant sedimentation rate, the cone was deposited approximately 10,000 years ago. At 5.75 m, pine pollen accounts for 35 percent of the sum. *Pinus* subg. Strobus and subg. Pinus types each amount to 6 percent; the remainder could not be identified to subgenus. Higher in zone B, a maximum of 25 percent *P. Strobus* pollen is reached and the dominant species of pine throughout B zone time at Protection Bog was clearly white pine. At other sites in southwestern New York, white pine also appears to have been one of the principal species which replaced spruce.

Pinus Strobus arrived in eastern Minnesota 7000 years ago from the east (Wright, 1968b). Its further migration was limited by eastward expansion of the prairie and oak savanna which began 8000 years ago in the upper Midwest. About 4000 years ago, prairie expansion ceased, and white pine began again to migrate westward reaching the northwest part of Minnesota about 2700 B.P., the western edge of its present distribution in North America. White pine in western New York 10,000 years ago supports Wright's contention that the species survived full glacial conditions in eastern North America.

Studies in the Allegheny National Forest of northwestern Pennsylvania (Hough & Forbes, 1943) indicate that *Pinus Strobus* may have played a successional role in the change from spruce to pine forest. Even-aged pine stands whose origin, in many cases, has been traced to an event that opened a part of the forest to seeding from nearby mature individuals occur in this region today. Understory white pines are absent because its seedlings do not survive in the shade. It is easy to visualize white pine seeding into openings created in the deteriorating spruce forest 10,500 years ago. We know that mature, seed-producing white pines were established at this time near Protection Bog and probably elsewhere in the region. They seem to have coexisted temporarily with spruce whose actual abundance in the total vegetation at this time is not precisely known. Size-frequency measurements indicate that *Picea mariana* was the main spruce near Allenberg Bog at the end of zone A. Because this is principally a lowland, wet-site species, upland forests containing *Picea glauca,* which according to pollen size data was present earlier in zone A, may have been replaced by other communities. Considering the narrow stratigraphic interval across which spruce drops from high to low values, spruce forests must have rapidly disappeared, freeing more and more surfaces for occupation by pine and other B zone species. Wright (1964) suggests that spruce regeneration at this time was limited by summer temperatures which exceeded the tolerance of the species.

Extrapolating from the Protection Bog age determinations, the total duration of zone B in western New York seems to have been between 1500 and 2000 years. This is equivalent to about four white pine lifetimes, if we accept 450 years as the normal life span of the species (see Fowells, 1965). The occupation of a given site by successive generations of white pine may mean that other species (e.g., *Tsuga canadensis*) that normally would replace it in the region today had not yet migrated to the area. Since hemlock pollen does not occur in large numbers until some time after the B zone peak at 9030 ± 150 B.P., this hypothesis seems supported by my data. There was at least a four millenium lag in the migration of hemlock northward from somewhere in the unglaciated Appalachians following ice withdrawal from the Valley Heads moraine 13,000 years ago or earlier. In part, this was probably climatically controlled, but differential migration rates of species back onto glaciated terrain may explain the basic pattern of early postglacial pollen succession in western New York State.

In some of my profiles, zone B can be divided into a lower pine-birch subzone and an upper pine-oak subzone. A birch peak in the lower part of the zone is best developed at Allenberg Bog where it is associated with highs in the curves of *Carpinus-Ostrya, Fraxinus nigra,* and *Populus.* These features are less apparent at the other sites, although at Houghton Bog high percentages of *Betula* and *Carpinus-Ostrya* occur in the equivalent stratigraphic interval. Whether these changes have regional significance is doubtful, however, because they are less clearly defined at nearby Protection Bog where no peak is discernable in the *Betula* curve. *Ulmus* is well represented at most sites, suggesting that elms were an important part of the regional vegetation. In fact, the magnitude of elm percentages in zone B is only slightly less than that present in later postglacial time.

The presence of high birch values is not unique to western New York. Similar findings from southern New England have been reported by Davis (1958) and by Whitehead and Bentley (1963). These authors refer to the interval as subzone B-1. Since the peak occurs across the A/B zone boundary, birches may have been locally important members of the vegetation that existed during the transition from spruce to pine domination. In western New York, *Carpinus caroliniana* and/or *Ostrya virginiana, Fraxinus nigra,* and *Populus* spp. appear to have been present during this interval as well. Davis (1967a) mentions that the New England B-1 pollen assemblages compare well with modern surface samples from northern Minnesota and from the Lake Timagami region of Ontario. These localities are in the mixed coniferous-deciduous forest formation about 60 mi south of the boreal forest and may indicate that the climate of southern New England during B-1 time was cooler and drier than it is at present. Slightly lower *Betula* percentages and higher *Quercus* and *Ulmus* values characterize western New York State sites, but, otherwise, B-1 assemblages from this region agree with those from New England.

At Allenberg Bog where size measurements are available for zone B birch pollen, the configuration of the size-frequency curve shows that two species may have been present (figure 9). However, these cannot be identified with size data currently available from herbarium speciments of eastern North American birch species. Possibly *Betula populifolia, B. pumila,* or both were present, as these species have pollen intermediate in size between the small grains of the shrub birch, *B. glandulosa,* and the larger pollen of the tree species, *B. lenta* and *B. alleghaniensis.* If *B. populifolia* and *B. pumila* produced the mode at 25 μ, then the larger modal class near 27 μ may indicate the presence of one of the tree birches during the deposition of zone B. In zone C-1, the mode also occurs at 27 μ, but higher in the section it shifts to 26 μ. Although apparently only *B. lenta* and *B. alleghaniensis* produced the mode at 26 μ in upper C zone spectra, the meaning of the modes at 25 and 27 μ in zone B is obscure.

The upper portion of zone B in western New York is dominated by *Pinus Strobus* and *Quercus* pollen. In some of the profiles, *Betula, Carpinus-Ostrya, Fraxinus,* and *Populus* values are lower than they were near the bottom of zone B. *Acer saccharum* was likely established in the region by the end of zone B. Arrival of oaks and expansion of the area occupied by them at locations near the basins is indicated by rapidly increasing relative numbers of oak pollen, although before this time some oaks were probably growing within 50 to 100 mi of the basins. The species involved are unknown, and either macrofossil evidence or improved pollen identification techniques are needed for specific determinations. However, *Quercus rubra* is one good candidate because of its current " northern " distribution and pioneer status, but other species could have been present also.

The entire B zone seems to record development of a white pine-oak forest. However, it is likely that the vegetation was quite complex at this time. Because of its broad ecological tolerances, white pine probably occurred in lowland valleys with elm and black ash and, in the upland, with oaks and/or sugar maple. The former community may have been similar to the White pine-American elm swamp forest that originally occupied the axes of some of the major valleys in Cattaraugus County (Gordon, 1940). Forest types containing white pine and oak species are also known from western New York at the present time. White pine and red, black, and white oak originally occupied dry sites on about 2 percent of Monroe County (Shanks, 1966), and similar stands undoubtedly occurred elsewhere in the Erie-Ontario Lowland. *Castanea dentata* and, at certain places, *Pinus rigida* were additional important members of this community. The pollen rain of this forest type has not been determined, and, considering the present distribution of vegetation in the lowland, it seems unlikely that a sample which was not influenced by pollen output from the surrounding mesophytic forests could be obtained for comparative purposes. In any case, neither *Castanea* nor *Pinus rigida* appear to have been members of the B zone vegetation according to pollen data currently available. Forests containing white pine and oak species are also known from well-drained sites, usually S-facing slopes, on the Allegheny Plateau.

The pine-oak subzone pollen assemblages seem to have no exact modern analogue, but Davis (1967a) points out they are closest to the modern pollen rain in southern Ontario near the boundary between the deciduous and coniferous-deciduous forest (see King & Kapp, 1963, sample 4). However, an important difference is the higher pine and oak percentages found in upper B zone spectra from southwestern New York State. Although the suggestion that an analogue of the pine-oak subzone is not in existence today seems premature, it is possible that a unique assemblage of species brought together by differential migration rates was present in western New York 9000 years ago.

ZONE C–1

Post-zone B sediments contain a record of the development and persistence of forests which contain the same species that now dominate existing forest types in western New York. Hemlock is an important tree in this region today and its pollen record is especially interesting and significant. The C-1 is set apart from the zones above it by high relative numbers of hemlock pollen and gradually increasing beech values. These features are retained when the relative frequency data from Houghton and Allenberg bogs are replotted on an absolute basis. *Tsuga* percentages increase markedly at the B/C-1 boundary and total *Pinus* values, with *P. Strobus* pollen predominating, reciprocally decline. Across a 30 cm interval at Protection Bog, *Tsuga* increases from 2 to 25 percent. Assuming that it took 26 years to deposit 1 cm of gyttja in the basin (the sedimentation rate between the two radiocarbon dates immediately higher in the section), about 800 years was needed to accumulate this thickness of sediment.

The abrupt nature of the increase and the weak expression of *Tsuga* in zone B suggests that the beginning of zone C-1 records initial invasion and expansion of hemlock in the region. At most of the sites, low relative numbers of hemlock pollen found in zones A and B probably represent grains blown in from distant sources. Unfortunately, detailed information on the dispersal of hemlock pollen is not available, but up to 7 percent has been found in surface sediments near Lansing, Michigan (Parmelee, 1947) at locations about 75 mi south of the limit of more or less continuous hemlock distribution in the State as mapped by E. L. Little, Jr. (*in* Fowells, 1965). According to the R values which I have calculated using several estimates of forest composition, hemlock pollen is somewhat overrepresented in both surface and presettlement spectra. This may also have been true during earlier postglacial time indicating that hemlock trees were actually somewhat less abundant in the total vegetation than the pollen record implies.

The ultimate cause of replacement of white pine is speculative. Arrival of hemlock in the region during its migration northward onto glaciated terrain has already been mentioned as one possibility, but whether hemlock was migrating at its fullest potential during the time preceding its arrival in western New York or whether its movement was held in check by climate or soil development is not known. The latter would seem not to have been too critical because hemlock seeds are able to germinate on a variety of substrata; e.g., moist, well-decomposed litter, rotted wood, mineral soil, and moss mats or soil and rocks (Hough, 1960). Once hemlock was present, however, white pine replacement can be viewed as a successional event. Although in existing forests both white pine and hemlock are often periodic in occurrence, studies in the Allegheny National Forest (Hough & Forbes, 1943) have shown that when both are found together, white pine will drop out of the association as time passes because its seedlings do not become established under a dense canopy, while those of hemlock can.

At the present time hemlock occurs from the southern Appalachians northward across the glacial boundary to northern Maine, New Brunswick, and Nova Scotia. Westward it extends to eastern Kentucky, central Ohio, and through southern Ontario and northern Michigan to northeastern Wisconsin (Little *in* Fowells, 1965). The pollen record for *Tsuga* is not identical across this region, however, and although the main difference is the absence of two hemlock maxima from certain areas, a feature which will be discussed more fully under the heading Zone C-2, another variable is the magnitude of hemlock representation in sediments deposited immediately following high B zone pine percentages. In glaciated eastern North America from northwestern Pennsylvania to northern Maine (see Cox, 1959; Davis, 1965b; Deevey, 1951; Krauss & Kent, 1944; Potzger & Otto, 1943; Terasmae *in* Karrow, 1963; Walker & Hartman, 1960), maximum hemlock values appear early in pollen profiles, and at several sites in the southern part of this region where radiocarbon dates are available, the appearance of hemlock can be estimated at between 9300 and 8500 B.P. (Davis, 1967b; Walker & Hartman, 1960). Hemlock first appears near Halifax, Nova Scotia about this time as well, although maximum values were not reached until about 7100 years ago (Livingstone, 1968). In general, at sites in eastern North America which fall within the present limits of the Hemlock-white pine-northern hardwood forest region (Nichols, 1935), *Tsuga* accounts for 25 to 35 per cent of the sum directly above zone B. However, in southern New England, south of the forest boundary but still within the total range of hemlock, maximum C-1 hemlock values reach only 10 percent (Davis, 1967b). To the west in the Hemlock-white pine northern hardwood forest region of Michigan and Wisconsin, *Tsuga* pollen is also weakly represented in the equivalent stratigraphic interval. Unfortunately few C-14 dated pollen profiles are available from either state, but hemlock would seem to have reached the Douglas Lake region of Michigan (Wilson & Potzger, 1942) early in the period of oak-hardwood domination which probably is temporally equivalent to zone C-1 in the East. About 5 percent or less is present until some point later in postglacial time when an increase to 20 percent took place. In central Michigan, hemlock is consistently a part of the pollen record above a C-14 date of 7982 ± 250 B.P., but it accounts for only 5 percent or less of the sum (Gilliam *et al.,* 1966). West's diagram (1961) from Seidel Lake in eastern Wisconsin similarly shows that *Tsuga* appeared fairly early during the period of oak domination that followed the *Pinus* maximum, but hemlock never exceeded about 3 percent of the total until much higher in the section. Increasing *Tsuga* percentages in later postglacial sediments from this lake (= C-3 in western New York?), parallels the same trend at sites in northern Michigan. This change can also be observed in profiles from many other sites in the region (Messenger, 1966; Potzger, 1946).

Hemlock appears to have entered Michigan from the east, north of Lake Erie, and not from the south across the Prairie Peninsula, which apparently acted as an effective barrier to migration of hemlock, beech, and perhaps other species from the central Appalachians (Benninghoff, 1963). For example, in the diagram from Silver Lake in western Ohio (Ogden, 1966), low relative numbers of hemlock pollen (<5 percent) first occur 9800 years ago, but at several points higher in the section it completely drops out of the counts. Whenever hemlock pollen is found, it comprises only 2 to 3 percent of the sum, indicating that *Tsuga* was never very abundant in western Ohio. During postglacial time in this region, hemlock likely occurred intermittently in small, isolated stands, perhaps on N-facing slopes or in other suitable edaphic situations. At the present time Silver Lake is about 50 mi west of the limit of continuous hemlock distribution in Ohio.

Although hemlock first appeared at about the same time in western New York, Michigan, and northern Wisconsin, the early postglacial period of hemlock dominance characteristic of my western New York profiles is absent from sites to the west. In western New York where this occurs between about 8500 and 4300 B.P., the vegetation appears to have been remarkably stable. The only significant changes occur in the *Fagus* and *Quercus* curves. The former shows a long-term increase, while the latter undergoes a corresponding decline. However, during the same period, the prairie and oak savanna expanded eastward in Minnesota (Wright, 1968a). It has not yet been established whether Wisconsin and Michigan were affected by the drier and warmer climate that probably induced this vegetation change, but if they were this might explain the meager representation of hemlock pollen in sediments accumulated during zone C-1 time at sites in the northern part of these states. Hemlock is known to grow best in a humid, cool climate and to be sensitive to drought which, when excessive, will result in death of the trees. It also follows that western New York State, where hemlock pollen is abundantly represented between 8500 and 4300 years ago, was cooler and more moist than the Midwest. When Minnesota and perhaps surrounding areas were undergoing a " xerothermic " interval, western New York State it appears was not.

Too few pollen profiles are available from the Erie-Ontario Lowland in central and western New York to determine whether the vegetation during zone C-1 time was the same on both sides of the tension zone which now exists in the area, or whether beech-maple and oak forests dominated the lowland vegetation as they did immediately preceding settlement of the region. Prior to settlement, hemlock apparently was much less abundant in the lowland than in the upland. Because development of this difference should be apparent in the pollen record, weaker representation of hemlock pollen in the lowland than the upland during the C-1 might indicate that the tension zone was established fairly early in postglacial time. Little difference is apparent in C-1 *Tsuga* values between available profiles from lowland and upland sites, however. For example, at Bullhead Pond (Cox, 1959), a small lake in central New York, 20 mi south of Lake Ontario, *Tsuga* accounts for about 20 percent of the sum, although generally less than 10 percent is present at Kennedys Bog near Rochester (Yeager, 1969). Somewhat higher percentages of hemlock pollen occur at some of my upland sites, but the difference hardly seems significant. At Cicero Swamp (Cox, 1959) and Pennellville Hidden Lake (Durkee, 1960), about 40 mi further east and near the present edge of the lowland deciduous forest region, *Tsuga* reaches about 40 percent of the sum in zone C-1. In general, pollen diagrams from both the upland and the lowland are enough alike to indicate that only minor differences occurred across the entire region, but further data are needed to treat this problem more adequately.

Forest vegetation developing during zone C-1 time in southwestern New York was very similar to that present in the region just prior to colonial settlement. Upper C-1 spectra closely match pollen assemblages which accumulated in the region from 1000 to 2000 years ago. This means that the regional vegetation, and very likely the climate, during both periods were the same. *Tsuga* and *Fagus* did not arrive in western New York at the same time and communities containing hemlock must have been well-developed when beech entered the region and began to expand. The long-term increase in *Fagus* values, which take place mainly at the expense of *Quercus,* can be interpreted as a trend toward increased mesophytism in the total vegetation. The prominence of beech in postglacial sediments from western New York is scarcely surprising in view of the important position this species holds in the Allegheny National Forest where it ranks highest of all forest species in establishment capacity, survival, and competition. Beech is even less dependent on certain kinds of seedbeds, soil moisture, or light than hemlock (Hough & Forbes, 1943). During zone B time, oak forest types may have occurred at a variety of sites, although at present they are found mostly on S- and SW-facing slopes in southern Cattaraugus County and in limited areas to the north. The pollen record indicates that with the passage of time these forests shrank in size and were in part replaced by more mesophytic associations containing hemlock, beech, sugar maple, and other northern hardwoods.

Overall, the C-1 vegetation was probably a mixture of forest types as complex as now occurs in the region. Pollen from most of the important tree species which at present exist in the area are variously represented in the zone; those that are not, such as *Prunus serotina* and *Magnolia acuminata,* are mainly insect-pollinated and therefore are rarely found as fossils. Both *Tilia* and *Fraxinus americana* and/or *F. pennsylvanica* (4-colpate *Fraxinus* grains) first appear at the beginning of the C-1 and are as well represented in this zone as higher in the profiles. Likewise, pollen from *Platanus occidentalis* was first encountered at about this time in the two Valley Heads bogs; however, to the south at Allenberg Bog small percentages are present throughout zone B. High *Platanus* values are prominent in zone C-1 at Houghton Bog where the outwash plain surrounding the bog may have been an especially favorable habitat for this species. *Juglans cinerea* first occurs in low relative numbers in the upper part of zone A and a few grains were encountered in zone B sediments, but at all sites the postglacial maximum is reached at some point within the C-1. *Ulmus* and *Betula* continue to hold prominent positions in the vegetation of the region. At Allenberg and Protection bogs, birch values are somewhat higher near the middle of the zone than at either beginning or end. Size-frequency measurements of birch pollen at the former location indicate that the tree birches, *B. lenta* and *B. alleghaniensis* were the main species present. Low relative numbers of *Castanea dentata* pollen first appear in zone C-1 at Allenberg and Houghton bogs, although this species regularly occurs from near the beginning of the C-2 upward at Protection Bog. Local habitat differences near the basins probably explain the disparity.

ZONE C–2

In southwestern New York zone C-2 is characterized by low hemlock percentages and increased values for broadleaf deciduous tree taxa. It is an interval between two successive hemlock maxima. The zone is represented in the Houghton, Protection, and Allenberg Bog profiles, but is absent from the Genesee Valley Peat Works diagram because the bulldozed uppermost sediments at this site were not sampled. In my profiles the lower zone boundary can be readily located at the midpoint of the abrupt hemlock decline which, at Protection Bog, has been dated at 4390 ± 110 B.P. (I–3550). However, placement of the upper boundary is arbitrary because of the absence of any clear stratigraphic markers. I have chosen a point where percentages of deciduous tree taxa are reduced over their C-2 maxima and where hemlock just begins to exceed 10 to 15 percent of the sum. Accepting this placement, zone C-2 ended 1270 ± 95 years ago (I–3549) at Protection Bog. This is from 500 to 800 years younger than other age determinations of the C–2/C-3 transition from eastern North America (see Davis, 1965b) but the difference may not be significant due to variability inherent in radiocarbon dates. Using the rate of sediment accumulation between the two highest C-14 dates at Protection Bog (0.069 cm/year), hemlock percentages decrease from 23 to 8 percent in about 350 years. This is only an estimation, however, because the sedimentation rate may have been less in the upper part of the gyttja than between the dated levels in the gyttja and peat. Furthermore, the 25 cm over which the reduction in hemlock percentages takes place reflects the sampling interval used in this part of the profile. Since the same change could have taken place in less than 25 cm the time interval may actually have been shorter. Pollen stratigraphy across the transition should be determined in detail in future studies.

In relative frequency diagrams, the *Tsuga* reduction is compensated for by increases in a number of other arboreal pollen types, principally *Fagus, Acer saccharum, Betula, Quercus,* and *Carya.* Lesser increases also occur in *Pinus Strobus, Fraxinus americana* and/or *F. pennsylvanica, F. nigra,* and at one site, *Carpinus-Ostrya.* In no case is any increase as prominent as the *Tsuga* decline. Size-frequency measurements from the upper and lower halves of zone C-2 at Allenberg Bog indicate that *Betula lenta* and/or *B. alleghaniensis* were the main birches contributing to the pollen rain, but possibly a third species was present during the deposition of the upper part of the zone.

These changes indicate modifications in the regional vegetation which simultaneously favored the expansion of dry site oak and hickory forests and mesic communities containing beech, sugar maple, and birch. Traditionally zone C-2 in eastern North America has been interpreted as a xerothermic interval, a period of warm and dry climate during which oak and hickory forests expanded at the expense of more mesophytic associations (see Deevey, 1949). Although a decrease in the representation of hemlock, a strongly mesophytic species, and the corresponding increase in oak and hickory in western New York State is the expected pattern, if the xerothermic interpretation is accepted, coordinated increases in *Acer saccharum, Betula lenta* and/or *B. alleghaniensis,* and *Fagus grandifolia,* all of which also are mesophytes, are contradictory.

A drier, more continental climate during the C-2 would be better documented if an analogue for the vegetation could be found where such a climate prevails at the present time. The Beech-maple forest region of central Ohio and Indiana is a logical place to look for surface pollen assemblages similar to C-2 spectra from southwestern New York, but unfortunately no systematic study of the recent or subrecent pollen rain in Ohio and Indiana has been made. Pollen profiles from this area provide some comparative data, however. The topmost spectra in diagrams from north-central and northeastern Ohio presented by Sears (1942), which in most cases probably represent the subrecent pollen rain, do not match any of my C-2 assemblages, nor do spectra from just beneath the post-settlement *Ambrosia* peak at Silver Lake in western Ohio (Ogden, 1966). In both areas, *Quercus* and *Carya* values are larger and *Fagus* representation is much weaker than at any of my southwestern New York sites. However, the lack of correspondence is not conclusive proof of the absence of a relationship because the pollen rain has been determined at so few sites in this part of the Midwest. Until such information is forthcoming, it seems best to reserve judgment on the current existence of a probable analogue for the C-2 vegetation.

It has been postulated that a wedge of prairie vegetation extended through central Indiana and Ohio during the putative mid-postglacial xerothermic interval (see Benninghoff, 1963). This hypothesis was used by Shanks (1966) to explain the origin of prairie remnants in oak openings in the Erie-Ontario Lowland of western New York. There is, however, no C-2 increase in grass pollen at any of the sites studied in this area. All C-2 spectra are dominated by arboreal pollen and in only a few cases does nonarboreal pollen account for more than 3 percent of the sum. In these instances, NAP is clearly of local derivation. Of some interest in this regard, however, is the presence of *Ephedra* pollen in zone C-2 at Protection Bog. If it could be established that *Ephedra* species were growing in the region during zone C-2 time, the argument for an interval of xeric, continental climate would be improved. However, Maher's recent review (1964) has shown that *Ephedra* pollen, which has been found widely in the Great Lakes region, is not limited to any one stratigraphic interval, but rather its pollen occurs sporadically in both late and postglacial deposits. This fact and the presence of *Ephedra* pollen in surface samples near Lake Simcoe, north of Lake Ontario (King & Kapp, 1963) and elsewhere, implies that an extraregional origin, through long-distance wind transport from the southwestern United States, is the most likely explanation for the presence of *Ephedra* pollen in western New York. The occurrence of *Liquidambar* pollen in both late and postglacial sediments in this region can be explained in the same way. At present the northern limit of sweet gum is southern Ohio and central West Virginia about 300 mi south and southwest of the sites included in this study.

In eastern North America, pollen profiles with two hemlock maxima separated by a single interval of low hemlock percentages are known from a broad area including northwestern Pennsylvania (Walker & Hartman, 1960), New York State (Cox, 1959; McCulloch, 1939; Dunham, 1965; Durkee, 1960), northern Vermont (Davis, 1965b), southern Vermont (Whitehead & Bentley, 1963), southern New England (Davis, 1967b; Deevey, 1939, 1943), and Maine (Deevey, 1951). In Canada, a hemlock decline is present in what appears to be a top-truncated profile at a site west of Hamilton, Ontario (Terasmae *in* Karrow, 1963). A *Tsuga* minimum also occurs in profiles from north of Toronto (McAndrews, 1970), from the Gatineau Valley region of Quebec, 30 to 60 mi north of Ottawa (Potzger & Courtemanche, 1956), and farther east in Nova Scotia (Livingstone, 1968). South of the glacial boundary at Bear Meadows Bog in central Pennsylvania, (Kovar, 1964) a mid-postglacial *Tsuga* minimum also occurs. It remains to be established, however, whether the hemlock decline is strictly synchronous over the entire region just discussed. Radiocarbon dates are available from only scattered localities but they show a surprising degree of accordance. The Protection Bog date of 4390 ± 110 B.P. agrees favorably with the *Tsuga* minimum which started at Rogers Lake, Connecticut about 4100 years ago (Davis, 1967b) and with the abrupt *Tsuga* decline dated at 4540 ± 140 B.P. at Crystal Lake near Halifax, Nova Scotia (Livingstone, 1968).

Can the hemlock decline be explained in any other way than by postulating a xerothermic interval? Viewing the tripartite C zone as a unit, the decline seems to occur at a time when soil development had progressed to a point where, by late C-1 time, the soil supported the same forest types that exist in the area today. Furthermore, the pollen diagrams indicate that with the possible exception of *Castanea,* no new taxa entered the region following deposition of the lower third of zone C-1, although data are not available on the immigration of *Liriodendron tulipifera, Magnolia acuminata, Prunus serotina,* and a few others which, while not important species regionally, are nonetheless significant members of some forest communities. Whatever was responsible for modifications in the mid-postglacial vegetation of southwestern New York seems to have changed what had become a fairly stable situation, at least with respect to entry of new species into the area.

In any event, hemlock appears to be the key to the interpretation of zone C-2. The relative frequency diagrams clearly depict a reduction in *Tsuga* percentages and an enlargement of values for temperate deciduous tree pollen types. It is difficult, however, to determine which was cause and which effect because of the nature of expressing data in percentages; *i.e.,* when the relative numbers of one category increase, a concomitant reduction in one or several others must occur. Therefore, the hemlock decline could represent an actual reduction in the number of *Tusga* grains being deposited per year or an increase in the deposition rates of *Fagus, Acer saccharum, Quercus,* and other pollen types while deposition of *Tsuga* pollen remained constant. In the former case, increases in relative numbers of deciduous tree taxa would be artifacts of the percentage system providing their deposition rates remained constant; in the latter, the converse would pertain.

Insofar as absolute pollen frequency or the number of grains/unit volume of sediment represents actual deposition rates of the various pollen types, the absolute frequency diagram from Houghton Bog shows that a significant reduction in the numbers of *Tsuga* pollen /ml took place across the C-1/C-2 boundary, and that low absolute numbers persist throughout zone C-2. Of interest also is the fact that *Fagus, Acer saccharum, Quercus,* and *Betula,* which show the greatest increase in relative frequency during the change from zone C-1 to zone C-2, are not any more strongly represented in the C-2 than in the upper part of the C-1. Although these features are meaningful only if the rate of sediment accumulation was constant across the interval (and unfortunately radiocarbon dates which would enable its determination at Houghton Bog are not available), at sites in eastern North America where sedimentation rates have been determined (Davis, 1967b; Ogden, 1967a), it was more or less constant between late C-1 and late C-2 time. This may not be universally true in all small lake basins, but, in the absence of differences in sediment lithology, it seems reasonable to extend the assumption of a uniform sedimentation rate to Houghton Bog.

The absolute pollen frequency data indicate that the C-2 modifications in the relative frequency diagrams were produced mainly by a decrease in the absolute numbers of hemlock, a species whose silvical characteristics are fairly well known (Fowells, 1965; Hough, 1960). Hemlock mortality can be caused by a variety of environmental factors, but drought is most important because of hemlock's shallow root system. Severe damage to hemlock stands over a broad area following the droughts of the early 1930's is well documented in the literature. For example, Secrest *et al.* (1941) estimate that 50 million board feet of hemlock died in the 230,000-acre Menominee Indian Reservation in Wisconsin during the 3 years between 1931 and 1933. These authorities demonstrated that under drought conditions root tips are rapidly killed and gradually larger roots become weakened leaving affected trees open to fungus and insect attack. To the east, hemlock mortality during the same drought period has been recorded at the Allegheny National Forest (Hough, 1936b) and near New Haven, Connecticut, where, in a 0.1 acre plot, dead hemlock saplings and trees comprised 75 percent of the total sample (Stickel, 1933). Near New Haven, hemlock seedlings were killed outright and mortality in all size classes probably was enhanced by shallow soils developed directly over bedrock.

Data from a more detailed study on the effect of the 1930 drought on different forest types in central Pennsylvania (McIntyre & Schnur, 1936) supplies additional pertinent information. Examination of 23 plots spread among chestnut oak, hemlock, scarlet oak-black oak, and white pine-chestnut oak forest types showed that 84 percent of the total basal area of hemlock was lost from the sample. By comparison, black oak lost 52 percent, chestnut oak 28 percent, red oak 26 percent, and sugar maple 11 percent. Before the drought, the four hemlock-type plots contained abundant *Tsuga canadensis*, 60, 67, 78, and 80 percent expressed as a percentage of total basal area, while, after the drought, the relative dominance of hemlock was reduced to 2, 6, 66, and 24 percent in the same plots. The hemlock-type changed from one dominated by this species to one of mixed composition, mainly chestnut and red oak with much smaller amounts of hemlock. In a general way, this change parallels that observed in zone C-2 sediments from western New York with the exception of the importance of beech, sugar maple, and yellow and/or sweet birch in C-2 sediments from this region.

I suggest, therefore, that the hemlock decline can be viewed as a response to several severe drought years. The recorded devastation of hemlock during the 1930 drought from Wisconsin to southern Connecticut, and the accordance of the dates of the hemlock decline between western New York, New England, and Nova Scotia furnish the basis for postulating that widespread droughts might also have occurred about 4400 years ago. This new hypothesis, which can be partly tested by obtaining additional radiocarbon dates, to further check the synchroneity of the mid-postglacial hemlock decline, differs from the xerothermic interpretation in the nature and duration of the warm-dry climatic optimum. I feel that the modifications in the pollen record can be as well explained by postulating a series of severe droughts, perhaps distributed over several centuries or even over much less time, as by postulating an interval of xeric, continental climate lasting several millenia.

The return of *Tsuga* to a position of prominence in the pollen diagrams by zone C-3 time may represent the orderly and gradual succession of hemlock back into communities where it was at one time present. Competition between hemlock and other mesophytes, particularly beech, would accompany this change and would affect the speed of hemlock reestablishment. *Tsuga* was never completely eliminated from the region because its pollen was continuously being deposited, even though in one instance it dropped as low as 4 percent of the sum. *Tsuga* likely survived in especially favorable edaphic situations, perhaps in deep gullies that were cooler and more moist than the surrounding upland.

If the decline in hemlock alone produced the C-2 modifications in pollen diagrams from southwestern New York, biotic factors rather than climate must also be considered as possible causative agents. Certain insects, including two species of hemlock loopers and the hemlock borer, are known to cause local mortality, as are foraging deer, porcupines, and rabbits (Fowells, 1965). Man may also have played a role. The Protection Bog date for the C-1/C-2 boundary corresponds to a period during which central and western New York was occupied by Indians of the Lamoka culture (Ritchie, 1969). They subsisted by hunting, fishing, and gathering; agriculture came somewhat later, perhaps about 1000 B.C. Little is known about the hunting techniques of these Indians, but apparently they secured large game, mostly white-tailed deer, with javelins propelled by throwing boards. They probably used dogs during the hunt and it is not inconceivable that fire was used to drive game. Hemlock is known to be vulnerable to fire damage, and, although old trees may survive light surface fires because of their thick bark, the roots are easily damaged by a burn that extends deeper than loose surface litter.

I attempted to measure the influence and periodicity of past fires in southwestern New York by recording the number of charcoal fragments over 30 μ in size while counting to the basic pollen sum, but charcoal frequency does not seem to have been any greater in zone C-2 than in C-1. However, the counting technique needs refinement before fire damage can be ruled out completely. For one thing, charcoal is brittle and larger pieces probably fragment during maceration, indicating that a smaller minimum size should have been established before counting. Of more serious consequence is the 25 cm sampling interval which is too great to regularly document such catastrophic events as fires. While I cannot rule out direct or indirect biotic interaction as the cause of hemlock decline, it seems unlikely that a biological agent would have led to a reduction in hemlock percentages over the broad area in which they occur. Locally biological agents may have been important, but certainly not across many hundreds of miles.

In some regions of northeastern North America, two *Fagus* maxima occur in sediments which are approximately contemporaneous with those of zone C-2 in western New York. For example at Silver Lake in western Ohio, Ogden (1966) considers the xerothermic interval to be represented by a minimum in beech pollen covering the interval between 3600 and 1300 B.P. This is about the same time period during which a *Fagus* minimum has been found in southern New England deposits (Davis, 1967b; see also Deevey, 1943). The only diagram from New York State in which a similar change occurs is Cox's undated Consaulus Bog profile (1959) from eastern New York near Albany. In this profile, the *Fagus* and *Tsuga* minima are not coordinated as they are in southern New England, but rather the former occurs slightly above the latter. Although *Fagus* is characterized by erratic fluctuations in certain other of Cox's diagrams, it is strongly represented in zone C-2 in all of them. The significance of the bimodal *Fagus* curve in deposits to the east and west of southwestern New York is not known. Since *Fagus* and *Tsuga* minima are not entirely synchronous, it seems likely that different factors were responsible in each case. The relationship between the two should be pursued.

ZONE C–3

Two important changes in the pollen record characterize this zone, the most recent in origin. These are the return of *Tsuga* (subzone C-3a) and the occurrence of high percentages of NAP above the presettlement /postsettlement boundary (subzone C-3b). Following the C-2 *Tsuga* minimum, hemlock values steadily increase higher in the profiles until near the end of the C-3a, the lower of the two subzones, where they are of similar magnitude to those of zone C-1. Percentages of deciduous tree taxa are reduced over their C-2 maxima, but they still remain strongly represented upward to the C-3a/C-3b boundary. Across this interval at the three sites where zone C-3 sediments were sampled, *Tsuga* increases mainly at the expense of *Fagus,* indicating an increased role for the former in the regional vegetation. This may have been enhanced by a trend toward a moister and a somewhat cooler climate which many feel has prevailed during the past several millenia (Sears, 1932) and may represent a continuation of succession begun during zone C-2 time.

This climatic trend seems confirmed at sites in northern New York (Durkee, 1960) and Canada (Potzger & Courtemanche, 1956) by a *Picea* increase in sediments that appear equivalent to zone C-3 sediments in western New York. Spruce, although sparsely represented in the upper 25 cm in Houghton and Protection Bogs, shows a distinct increase upward in zone C-3 at Allenberg Bog. Spruce pollen in this zone at the two Valley Heads bogs is mostly restricted to postsettlement spectra and, therefore, probably originated mainly from planted trees. At Allenberg Bog, however, spruce occurs regularly throughout zones C-2 and C-3 but apparently was absent near the sampling point during the deposition of zone C-1. The small size of spruce pollen (generally <92 µ) in both the C-2 and C-3 indicates the presence of only *Picea mariana* which likely grew on the bog mat. Two grains larger than 100 µ found in zone C-3b at Allenberg Bog probably were contributed by introduced cultivated species. The Allenberg Bog spruce increase needs further documentation in western New York because, rather than indicating a climatic trend, changes in the hydrology of the peat deposit, induced by either physiographic modifications or biotic factors (e.g., beavers), may explain what at the present time appears to be only a localized increase.

In New England, *Castanea* pollen shows a decided increase in the C-3 (Davis, 1969; Deevey, 1939), but this is not true in southwestern New York. Although regularly present upward from either zones C-1 or C-2 in the deposits I have studied, maximum *Castanea* values are reached near the end of the C-2 at Houghton Bog (1.8 percent) and near the middle of this zone at Allenberg Bog (4.2 percent). Less than 1 percent occurs at equivalent positions in the Protection Bog profile. *Castanea* was recorded in the original lot survey data only around Allenberg Bog, and, according to Gordon (1940), presettlement distribution of chestnut mainly included the southern part of Cattaraugus County where it grew with oak on dry upper plateau slopes and tops and in mixed mesophytic forests. Since Allenberg Bog is near the area of maximum chestnut occurrence while the two Valley Heads sites are about 25 mi to the north, my profiles, taken at face value, indicate that chestnut was never very abundant north of central Cattaraugus County in the Allegheny Plateau region of western New York.

Increasing *Tsuga* percentages in sediments that appear stratigraphically equivalent to the C-3a in western New York occur across an area that approximately coincides with the Hemlock-white pine-northern hardwood forest region. A clearly defined hemlock increase is not apparent in profiles from Nova Scotia, however. As was the case in zone C-1, maximum values attained by *Tsuga* vary from district to district. For example, hemlock does not exceed 10 percent in the C-3 just south of the forest region at Rogers Lake, Connecticut, while in western New York it reaches over 25 percent. At Rogers Lake, the highest C-3 hemlock percentages occur between about 1500 B.P. and the *Ambrosia* peak, which marks the advent of European settlement.

To the west but still within the forest region, the hemlock increase is more pronounced and parallels my findings in western New York. The C-14-dated Maple River Township Bog diagram prepared by Hushen and Benninghoff (unpublished ms.) from Emmet County near the northern tip of the Lower Peninsula of Michigan shows hemlock weakly represented (10 percent or less of the sum) between 4000 and about 3200 B.P., at which time an increase began. After several erratic fluctuations upward in the profile, hemlock accounts for 50 percent of the sum in two spectra just beneath the presettlement/postsettlement boundary. This change is accomplished largely at the expense of *Pinus*. Hemlock is weakly represented during C-1 and C-2 time in profiles from Michigan and Wisconsin, but a few *Tsuga* stands probably existed at favorable sites in these states. The *Tsuga* increase can be viewed as an expansion of these colonies, or, alternately, immigration from some source area may be represented. In all, the pollen record for hemlock is worthy of continued study. As more C-14-dated profiles become available from southern Ontario, which appears to have been the principal westward migration route for hemlock, a more critical analysis of its postglacial history will be possible.

The settlement of western New York, which began about 1800, and the attendant forest clearance is sharply marked by increasing NAP percentages and by the presence of wind-blown silt and clay in the Allenberg, Houghton, and Protection Bog profiles. Arboreal pollen drops to 50 percent or less of the sum over a very narrow interval indicating the castastrophic effect of European settlement on the natural vegetation. Although there is no clear evidence of Indian agriculture in any of my diagrams, low but perhaps significant percentages of *Ambrosia* and *Rumex* pollen which expand upward from zone C-3a below the presettlement/postsettlement boundary, may have originated from weeds occupying cleared areas where corn, squash, and beans were being grown by the Indians. It might be claimed that pollen of these types originated from more recent sediments, but *Plantago* pollen, which would be expected to show the same behavior in the pollen diagrams, does not occur below the boundary except for occasional, single grain occurrences. Rayback's map (1966) of known Indian settlements shows a concentration of villages just west of Allenberg Bog in eastern Chautauqua and western Cattaraugus Counties. Other villages are known from near the head of Cattaraugus Creek fairly close to both Houghton and Protection Bogs. I do not know how many of these sites were inhabited by agricultural Indians or exactly at what times they were occupied, but the high incidence of Indian habitation in certain parts of southwestern New York indicates that any associated agricultural activities could be recorded in zone C-3 sediments.

Pollen from cultivated species is found from the beginning of subzone C-3b to the surface. Agriculture indicators, including *Zea* and pollen from other cereals (counted as Gramineae), occur at Protection, Houghton, and Allenberg Bogs, while *Fagopyrum,* buckwheat, is found only at the two last named sites. *Ambrosia* pollen is the dominant NAP type in the subzone and reflects the high incidence of disturbed, nonforest habitats where the common *A. artemisiifolia* and *A. trifida,* and the less frequent adventive, *A. psilostachya,* continue to flourish today. Maximum *Plantago, Rumex,* Cheno-Am, and Cichorioideae values are further evidence of the abundance of surfaces occupied by weedy species. Peak high-spine Compositae percentages may be in part due to increased frequencies of weedy species, but they could also reflect a local change in bog surface conditions favoring an increase in onsite taxa such as certain species of *Bidens.*

Summary and Conclusions

1. All of western New York except the Salamanca re-entrant, a semicircular area approximately bounded by the present course of the Allegheny River, was apparently ice-covered sometime during the Wisconsin glaciation. The various drift sheets in the region lack definitive dates, but the following correlations have been used in a recent review of the Pleistocene geology of New York State (Muller, 1965):

   Lake Escarpment-Valley Heads moraine: assigned to the Port Huron (Mankato) Substage, ca. 13,000 B.P.;
   Kent (Binghamton) moraine: assigned to Cary Substage, minimum date 14,000 B.P.;
   Olean moraine: pre-Cary (may be Tazewell or earlier).

   Other moraines associated with these are considered short recessional still-stands or minor readvances of the ice margin. Recently obtained C-14 age determinations, which indicate the Kent ice overrode the area around Cleveland, Ohio, about 23,250 years ago (White, 1968), and studies by Calkin (1970) will necessitate some revision in the above chronology. Recession to a point north of the Niagara escarpment in northwestern New York State was complete by 12,500 B.P. and ice apparently never again readvanced into western New York.
2. Pollen succession was studied in sediments from four basins located on drift sheets of different age; viz., Houghton and Protection Bogs associated with the Valley Heads moraine, Allenberg Bog on Kent drift, and the Genesee Valley Peat Works on Olean drift. Houghton and Protection Bogs are 10 mi apart, and Allenberg Bog is about 30 mi southwest of these. The Peat Works is 35 mi southeast of the former two sites and 50 mi east of Allenberg Bog.
3. The Portage escarpment separates western New York into two physiographic divisions: the Allegheny Plateau in the south and the Erie-Onatrio Lowland in the north. At the time of arrival of European settlers, the entire region was forested except for limited areas of prairie-like openings in the lowland. Forests of the Hemlock-white pine-northern hardwood Formation covered the upland, while beech-sugar maple and oak-hickory communities belonging to the Deciduous forest Formation occurred in the lowland. The ecotone between the two was not sharp and large inclusions of hemlock-hardwoods have been identified in the lowland. Upland oak forests are mainly limited to dry plateau tops and S-facing slopes near the Pennsylvania border.
4. An analysis of the bearing-trees recorded in the original lot survey notes for areas around Houghton, Protection, and Allenberg Bogs shows *Fagus grandifolia,* followed by *Acer saccharum,* to have the largest importance values. *Tsuga canadensis* is third in importance in two of the three areas. When frequency of mention data were computed from the same survey notes, *Fagus* continues to head the list. Second and third in frequency are *Acer saccharum* and *Tsuga canadensis* around Allenberg Bog, *Acer saccharum* and *Tilia americana* about Houghton Bog, and *Tsuga canadensis* and *Acer saccharum* around Protection Bog. Point-quarter sampling of three existing forest stands shows dominance by the same three leading species but with a change in the order of decreasing importance values. At all three sites, *Acer saccharum* heads the list followed by *Fagus grandifolia* and *Tsuga canadensis.*
5. The relative frequency of different pollen types in surface and presettlement spectra, divided by a percentage estimate of the importance of species in a vegetation sample contributing a given pollen type, provides a measure of the degree of representation of these pollen types in relation to the vegetation surrounding a depositional basin. These ratios or R values were calculated in several ways using surface pollen spectra compared with composition data collected by the U.S. Forest Service in existing forests and presettlement spectra compared with importance percentages and frequency of mention values derived from the original lot survey data. The computations indicate that in recent and subrecent sediment samples from western New York, pollen from *Betula* spp., *Pinus* spp., *Quercus* spp., *Tsuga canadensis,* and *Ulmus* spp. are overrepre-

sented, *Carpinus caroliniana* and/or *Ostrya virginiana, Fagus grandifolia,* and *Juglans cinerea* are proportionately represented, and that *Acer rubrum, A. saccharum, Castanea dentata, Carya* spp., *Fraxinus americana* and/or *F. pennsylvanica, F. nigra, Populus* spp., and *Tilia americana* are underrepresented.

6. A clearly defined T zone characterized by 50 percent or more nonarboreal pollen underlying a zone of spruce pollen domination was found in basal inorganic sediments only at Allenberg Bog. T zone pollen assemblages contain 20 percent *Picea,* 10 percent *Pinus,* 3 to 8 percent *Quercus,* 3 to 5 percent *Fraxinus nigra,* 15 to 25 percent Cyperaceae, about 10 percent Gramineae, and numerous other NAP types, and closely match the pollen rain today in the boreal forest-tundra ecotone at Fort Churchill, Manitoba where discontinuous spruce stands occur interspersed with herbaceous communities in a park-tundra. This implies that the climate in southwestern New York during the deposition of zone T was probably similar to that in this part of the subarctic today. No positive tundra indicator pollen types were found, although microspores of a subarctic and boreal species, *Selaginella selaginoides*, occur in several spectra.

7. Abundant herb pollen was present in basal sediments at the Genesee Valley Peat Works, but a zone in which spruce dominates is not present higher in the profile, making the meaning of the basal herb-spruce-pine assemblage at this site somewhat obscure. If local overrepresentation and redeposition were not operative, then an open vegetation perhaps similar to the park-tundra of T zone time at Allenberg Bog existed around the Genesee Valley site. However, there is some evidence that the pollen rain was influenced by near- and onsite herbs and, therefore, that the regional vegetation was a denser spruce-pine forest. Since the peat works are on the oldest drift sheet in western New York, the basal sediments may antedate comparable deposits elsewhere in eastern North America. If subsequent C-14 dating bears out their antiquity and if the pollen assemblage is taken at face value, a park-tundra may have covered the Allegheny Plateau in southern New York during the " classical " Wisconsin glaciations. More data are needed from additional sites in the region to further document this hypothesis.

8. Zone A at Allenberg Bog shows a long interval of domination by spruce and pine pollen. Changes in *Fraxinus nigra, Quercus, Pinus,* and *Picea* percentages permit subdivision of the zone following the sequence recognized in certain profiles from southern New England where such changes have been interpreted as vegetation modifications in response to the Two Creeks-Valders climatic changes. However, absolute pollen frequency data from Allenberg Bog indicate that an increase in the absolute numbers of spruce and pine pollen being deposited per unit volume of sediment — evidence of an increased abundance of spruce-pine forests on the landscape — was responsible for changes in the *Quercus* and *Fraxinus nigra* curves at this site. Absolute numbers of these pollen types remained more or less constant across the interval.

9. Zone A pollen assemblages from Allenberg, Houghton, and Protection Bogs contain both *Picea glauca* and *P. mariana* and are similar to existing surface pollen accumulations in the open boreal woodland of central Quebec. In contrast to the situation in Michigan, Wisconsin, and Minnesota, *Pinus Banksiana* and/or *P. resinosa* grew in southwestern New York during zone A time. *Abies balsamea* and *Larix laricina* were members of the A zone forests, and deciduous trees, whose pollen consistently occurs in the zone, may have occupied favorable sites within some tens of miles from the basins. This is particularly true of *Quercus* spp. and *Fraxinus nigra*, and perhaps *Carpinus caroliniana* and/or *Ostrya virginiana* also. The presence of *Acer, Carya, Juglans, Tsuga,* and *Ulmus* pollen probably reflects wind transport from distant sources. The bottom of zone A at Houghton Bog has been dated at 11,800 ± 730 B.P.

10. Mosses from an organic bed deposited 12,100 ± 400 years ago along the southern edge of Lake Iroquois near Lockport, N.Y., and a pollen spectrum from associated lacustrine sediments indicate the existence of a mosaic of plant communities in northwestern New York at this time. Species characteristic of dry dune sand, rich fens, and better drained fen edges probably occupied the area between the lake edge and a spruce-fir-larch forest occurring some distance inland. Exposed rocky habitats may have existed also. The occurrence of two typical arctic and subarctic mosses, *Aulacomnium acuminatum* and *A. turgidum,* indicates the possible presence of limited patches of tundra vegetation.

11. The spruce-pine woodland disappeared from 9500 to 10,500 years ago near the Valley Heads sites and was succeeded by zone B forests in which *Pinus*

Strobus held a dominant position. *Abies balsamea* flourished briefly during the transition. At some sites, lower pine-birch and upper pine-oak subzones can be distinguished. A *Pinus Strobus* cone was recovered from sediments about 10,500 years old at Protection Bog and clearly establishes the presence of this species in southwestern New York during the deterioration of the spruce-pine woodland. The B zone pine peak was dated at 9030 ± 150 B.P. at Protection Bog.

12. Zone C-1 is characterized by high percentages of *Tsuga canadensis* and increasing values for *Fagus grandifolia.* Other species which grow on the Allegheny Plateau at the present time are also represented in this zone. The similarity of the pollen assemblages near the end of zone C-1 and those found immediately beneath the presettlement/postsettlement boundary indicate that the zone records the regional development of forests of the hemlock-northern hardwoods type. Forest composition likely was as complex as now occurs in the upland. No major changes took place in the vegetation of southwestern New York during the duration of the C-1, although the *Fagus* increase may indicate a trend toward increased mesophytism.
13. An abrupt hemlock decline at Allenberg, Houghton, and Protection Bogs, which has been dated at 4390 ± 110 B.P. at the last named site, marks the beginning of zone C-2. The relative frequency of *Acer saccharum, Betula, Carya, Fagus, Fraxinus, Pinus Strobus, and Quercus* pollen show small increases in this zone. However, absolute pollen frequency data imply that these changes were induced by a decrease in the total number of hemlock grains being deposited per unit volume. Rather than a long interval of xeric, continental climate, the C-2 in southwestern New York seems to be a result of differences in hemlock abundance alone. Severe drought, which is known to cause heavy hemlock mortality in existing stands, occurring during several successive years or tens of years is postulated as the cause of the hemlock decline. Biotic factors, including man, may or may not have played a secondary role. Hemlock was never completely eliminated from southwestern New York during the C-2.
14. Subzone C-3a began 1270 ± 95 years ago at Protection Bog and records the return of hemlock to a position of prominence in the regional vegetation. This change may have been influenced by a climatic trend toward greater moisture during the past several millenia, but the hemlock return following the low early in C-2 time may represent successional recovery. There is some evidence that Indian agriculture is recorded in the upper half of this subzone.
15. European settlement and forest clearance occurred during the deposition of the topmost pollen assemblages belonging to subzone C-3b. Pollen from agricultural indicators, including *Fagopyrum, Zea,* and other cereals, was found in this subzone and the high frequencies of *Ambrosia,* Cheno-Am., *Plantago,* and *Rumex* pollen, species which grow in disturbed habitats, are characteristic. Subzone C-3b sediments contain large quantities of silt and clay blown in from bare areas around the basins.

Literature Cited

Adams, W. (Ed.). 1893. Historical gazetteer and biographical memorial of Cattaraugus County, N.Y. vi + 1164 pp. Lyman, Horton and Co. Syracuse, N.Y.

Andersen, S. Th. 1954. A late-glacial pollen diagram from southern Michigan, U.S.A. Danmarks Geol. Undersøg. II. 80: 140–155.

Armstrong, G. R., & J. C. Bjorkbom. 1956. The timber resources of New York. U.S. Dept. Agr. Forest Service Northeast. Forest Exper. Sta. unnumbered publication. 37 pp.

Beetham, Nellie, & W. A. Niering. 1961. A pollen diagram from southeastern Connecticut. Amer. Jour. Sci. 259: 69–75.

Benninghoff, W. S. 1963 [1964]. The Prairie Peninsula as a filter barrier to postglacial plant migration. Proc. Indiana Acad. Sci. 72: 116–124.

——— **& R. O. Kapp.** 1962. Suggested notations to indicate identification status of fossil pollen (Abstr.). Pollen Spores 4: 332.

Bickford, C. A., C. E. Mayer, & K. D. Ware. 1963. An efficient sampling design for forest inventory: The northeastern forest resurvey. Jour. Forestry 61: 826–833.

Birks, H. J. B. 1968. The identification of *Betula nana* pollen. New Phytol. 67: 309–314.

Bourdo, E. A., Jr. 1956. A review of the general land office survey and of its use in quantitative studies of former forests. Ecology 37: 754–768.

Braun, E. Lucy. 1937. Some relationships of the flora of the Cumberland Plateau and Cumberland Mountains in Kentucky. Rhodora 39: 193–208.

———. 1950. Deciduous forests of eastern North America. xiv + 596 pp. *1 map.* Blakiston. Philadelphia.

Bray, W. L. 1915. The development of the vegetation of New York State. N.Y.S. Coll. Forestry Tech. Publ. 3. 186 pp.

Broecker, W. S., & W. R. Farrand. 1963. Radiocarbon age of the Two Creeks forest bed, Wisconsin. Bull. Geol. Soc. Amer. 74: 795–802.

Brosius, N. 1953. Study of present conditions in an ice age kettle hole. Sanctuary News, Sept. 1953 Suppl. pp. 3–38. [Mimeo.; published by the Nature Sanctuary Society of Western New York, Inc., Buffalo, N.Y.]

Buckley, J. D., M. A. Trautman, & E. H. Willis. 1968. Isotopes' radiocarbon measurements VI. Amer. Jour. Sci. Radiocarbon Suppl. 10: 246–294.

Buehler, E. J., & I. H. Tesmer. 1963. Geology of Erie County, New York. Bull. Buffalo Soc. Nat. Sci. 21(3). 118 pp. *1 map.*

Buell, M. F. 1946. Size-frequency study of fossil pine pollen compared with herbarium preserved pollen. Amer. Jour. Bot. 33: 510–516.

Cain, S. A. 1940. The identification of species in fossil pollen of *Pinus* by size-frequency determinations. Amer. Jour. Bot. 27: 301–308.

———. 1944. Foundations of plant geography. xiv + 556 pp. Harper & Brothers. New York.

———. 1948. Palynological studies at Sodon Lake: I. Size-frequency study of fossil spruce pollen. Science 108: 115–117.

——— **& Louise G. Cain.** 1948. Palynological studies at Sodon Lake. II. Size-frequency studies of pine pollen, fossil and modern. Amer. Jour. Bot. 35: 583–591.

Calkin, P. E. 1970. Strand lines and chronology of the glacial Great Lakes in northwestern New York. Ohio Jour. Sci. 70: 78–96. *1 map.*

——— **& J. H. McAndrews.** 1969. Dating late glacial recession and vegetation in the Erie basin, northwestern New York. (Abstr.). Fourth Ann. Meeting Northeast. Sect. Geol. Soc. Amer. Abstr. Pt. 1. p. 5.

Carter, D. B. 1966. Climate, pp. 54–78. *In*: J. H. Thompson (Ed.). Geography of New York State. 543 pp. *4 maps.* Syracuse Univ. Press. Syracuse, N.Y.

Clausen, K. E. 1960. A survey of variation in pollen size within individual plants and catkins of three taxa of *Betula*. Pollen Spores 2: 299–304.

Cline, M. G. 1955. Soils and soil associations of New York. N.Y.S. Coll. Agr. Ext. Bull. 930. 64 pp.

Comanor, P. L. 1968. Forest vegetation and the pollen spectrum: An examination of the usefulness of the R value. Bull. New Jersey Acad. 5: 86–98.

Connally, G. G. 1964. The Almond moraine of the western Finger Lakes region, New York. Ph.D. Thesis, 102 pp. Michigan State Univ. East Lansing. [Abstr. in Diss. Abstr. 25: 6532,6533. 1965.]

——— **& L. A. Sirkin.** 1970. Late glacial history of the Upper Wallkill valley, New York. Bull. Geol. Soc. Amer. 81: 3297–3305.

Cottam, G., & J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

Cox, D. D. 1959. Some postglacial forests in central and eastern New York State as determined by the method of pollen analysis. Bull. N.Y.S. Mus. Sci. Service 377. 52 pp.

——— **& D. M. Lewis.** 1965. Pollen studies in the Crusoe Lake area of prehistoric Indian occupation. *Ibid.* 387. 29 pp.

Curtis, J. T. 1956. Plant ecology workbook, laboratory, field and reference manual. Rev. Ed. 86 pp. Burgess. Minneapolis.

———. 1959. The vegetation of Wisconsin. xi + 657 pp. Univ. Wisconsin Press. Madison.

——— **& R. P. McIntosh.** 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476–496.

Cushing, E. J. 1967. Late-Wisconsin pollen stratigraphy and the glacial sequence in Minnesota, pp. 59–88. *In*: E. J. Cushing & H. E. Wright, Jr. (Eds.). Quaternary Paleoecology. vii + 433 pp. Yale Univ. Press. New Haven, Conn.

——— **& H. E. Wright, Jr.** 1965. Hand-operated piston corers for lake sediments. Ecology 46: 380–384.

Daily, Fay K. 1961. Glacial and post-glacial charophytes from New York and Indiana. Butler Univ. Bot. Stud. 14: 39–72.

———. 1968 [1969]. Some late glacial charophytes compared to modern species. Proc. Indiana Acad. Sci. 78: 406–412.

Dansereau, P. 1953. The postglacial pine period. Trans. Roy. Soc. Canada 47. Ser. 3 Sect. 5: 23–38.

Davis, Margaret B. 1958. Three pollen diagrams from central Massachusetts. Amer. Jour. Sci. 256: 540–570.

———. 1963. On the theory of pollen analysis. Amer. Jour. Sci. 261: 897–912.

———. 1965a. A method for determination of absolute pollen frequency, pp. 674–686. *In*: B. Kummel & D. Raup (Eds.). Handbook of paleontological techniques. xiii + 852 pp. W. H. Freeman Co. San Francisco.

———. 1965b. Phytogeography and palynology of northeastern United States, pp. 377–401. *In*: H. E. Wright, Jr., & D. G. Frey (Eds.). The Quaternary of the United States. x + 922 pp. Princeton Univ. Press. Princeton, N.J.

———. 1966. Determination of absolute pollen frequency. Ecology 47: 310, 311.

———. 1967a. Late-glacial climate in northern United Sates: A comparison of New England and the Great Lakes region, pp. 11–43. *In*: E. J. Cushing & H. E. Wright, Jr. (Eds.). Quaternary paleoecology. vii + 433 pp. Yale Univ. Press. New Haven, Conn.

———. 1967b. Pollen accumulation rates at Rogers Lake, Connecticut, during late- and postglacial time. Rev. Palaeobot. Palynol. 2: 219–230.

———. 1969. Climatic changes in southern Connecticut recorded by pollen deposition at Rogers Lake. Ecology 50: 409–422.

——— **& E. S. Deevey, Jr.** 1964. Pollen accumulation rates: Estimates from late-glacial sediment of Rogers Lake. Science 145: 1293–1295.

——— **& J. C. Goodlett.** 1960. Comparison of the present vegetation with pollen-spectra in surface samples from Brownington Pond, Vermont. Ecology 41: 346–357.

Deevey, E. S., Jr. 1939. Studies on Connecticut lake sediments. I. A postglacial climatic chronology for southern New England. Amer. Jour. Sci. 237: 691–724.

———. 1943. Additional pollen analyses from southern New England. *Ibid.* 241: 717–752.

———. 1949. Biogeography of the Pleistocene. Bull. Geol. Soc. Amer. 60: 1315–1416.

———. 1951. Late-glacial and postglacial pollen diagrams from Maine. Amer. Jour. Sci. 249: 177–207.

———. 1957. Typical pollen-stratigraphic sequences in northeastern North America, p. 351. *In*: R. F. Flint. Glacial and Pleistocene geology. xiii + 553 pp. *5 pls.* John Wiley and Sons, Inc. New York.

———**, L. J. Gralenski, & Vaino Hoffern.** 1959. Yale natural radiocarbon measurements IV. Amer. Jour. Sci. Radiocarbon Suppl. 1: 144–172.

Denny, C. S., & W. H. Lyford. 1963. Surficial geology and soils of the Elmira-Williamsport region, New York and Pennsylvania. U.S. Geol. Sur. Prof. Pap. 379. iv + 60 pp.

Dow, C. M. 1921. Anthology and bibliography of Niagara Falls. 2 vols. 1423 pp. State of New York. Albany.

Droste, J. B., M. Rubin, & G. W. White. 1959. Age of marginal Wisconsin drift at Corry, northwestern Pennsylvania. Science 130: 1760.

Dunham, V. L. 1965. A general ecological study of Moss Lake Nature Sanctuary. Unpublished pollen diagram. Science Teaching Library. Syracuse University. Syracuse, N.Y.

Durkee, L. H. 1960. Pollen profiles from five bog lakes in New York State. Ph.D. Thesis. ii + 60 pp. Syracuse Univ. Syracuse, N.Y. [Abstr. in Diss. Abstr. 21: 2446, 2447. 1961.]

Erdtman, G. 1943. An introduction to pollen analysis. Chron. Bot. 12. xv + 239 pp.

———. 1957. Pollen and spore morphology/plant taxonomy. Gymnospermae, Pteridophyta, Bryophyta (illustrations). 151 pp. *5 pls.* Almqvist and Wiksell. Stockholm.

———. 1960. The acetolysis method. A revised description. Sv. Bot. Tidskr. 54: 561–564.

———. 1965. Pollen and spore morphology/plant taxonomy. Gymnospermae, Bryophyta (text). 191 pp. *24 pls.* Almqvist and Wiksell. Stockholm.

———. 1966. Pollen morphology and plant taxonomy. Angiosperms. Corrected reprint and new addendum. xii + 553 pp. Hafner. New York.

Evans, P. D. 1924. The Holland Land Company. Publ. Buffalo Hist. Soc. 28. xiv + 469 pp.

Faegri, K., & P. Deuse. 1960. Size variations in pollen grains with different treatments. Pollen Spores 2: 293–298.

——— **& J. Iversen.** 1964. Textbook of pollen analysis. 237 pp. Munksgaard. Copenhagen.

Fernald, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Amer. Acad. Arts Sci. 15: 239–342.

———. 1950. Gray's manual of botany, 8th edition. lxiv + 1632 pp. American Book Company. New York.

Feuer, R., W. L. Garmon, & M. G. Cline. 1955. Chautauqua County soils. N.Y.S. Coll. Agr. Soil Assoc. Leaflet 3. 6 pp.

Fisher, D. W., I. W. Isachsen, L. V. Rickard, J. G. Broughton, & T. W. Offield. 1961 [1962]. Geologic map of New York. N.Y.S. Mus. Sci. Service Map Chart Ser. 5. 5 sheets.

Fowells, H. A. (Ed.). 1965. Silvics of forest trees of the United States. U.S. Dept. Agr. Forest Service Agr. Handb. 271. vi + 762 pp.

Gehris, C. W. 1965. Pollen analysis of the Cranberry Bog Preserve, Tannersville, Monroe County, Pennsylvania (Abstr.). Diss. Abstr. 25: 4372.

Gilliam, Jeanne A., R. O. Kapp, & R. D. Bogue. 1966 [1967]. A post-Wisconsin pollen sequence from Vestaburg Bog, Montcalm County, Michigan. Pap. Mich. Acad. Sci. Arts Lett. 52: 3–17.

Goldthwait, R. P., A. Dreimanis, Jane L. Forsyth, P. F. Karrow, & G. W. White. 1965. Pleistocene deposits of the Erie lobe, pp. 85–97. *In*: H. E. Wright, Jr., & D. G. Frey (Eds.). The Quaternary of the United States. x + 922 pp. Princeton Univ. Press. Princeton, N.J.

Goodlett, J. C., & W. H. Lyford. 1963. Forest regions and great soil groups, pp. 54, 55. *In*: C. S. Denny & W. H. Lyford. Surficial geology and soils of the Elmira-Williamsport region, New York and Pennsylvania. U.S. Geol. Sur. Prof. Pap. 379. iv + 60 pp.

Gordon, R. B. 1937. The botanical survey of the Allegany State Park. N.Y.S. Mus. Handb. 17: 23–88.

———. 1940. The primeval forest types of southwestern New York. Bull. N.Y.S. Mus. 321. 102 pp.

Graustein, Jeannette E. 1967. Thomas Nuttall, naturalist, explorations in America, 1808–1841. xii + 481 pp. Harvard Univ. Press. Cambridge, Mass.

Guilday, J. E., P. S. Martin, & A. D. McCrady. 1964. New Paris No. 4: A Pleistocene cave deposit in Bedford County, Pennsylvania. Bull. Natl. Speleological Soc. 26: 121–194.

Hafsten, U. 1961. Pleistocene development of vegetation and climate in the southern High Plains as evidenced by pollen analysis, pp. 59–91. *In*: F. Wendorf (Ed.). Paleoecology of the Llano Estacado. Fort Burgwin Res. Center Publ. 1. 144 pp.

Heusser, C. J. 1960. Late-Pleistocene environments of North Pacific North America. Amer. Geogr. Soc. Special Publ. 35 xiii + 308 p. *25 pls.*

Hill, E. J. 1895. Notes on western New York woodlands. I. Garden Forest 8: 342, 343; II. *Ibid.* 382, 383.

Hough, A. F. 1936a. A climax community on East Tionesta Creek in northwestern Pennsylvania. Ecology 17: 9–28.

———. 1936b. The dying of hemlock and other species in the Allegheny National Forest. U.S. Dept. Agr. Forest Service Allegheny (Northeast.) Forest Exper. Sta. Tech. Note 9. 2 pp.

———. 1960. Silvical characteristics of eastern hemlock (*Tsuga canadensis*). U.S. Dept. Agr.. Forest Service Northeast. Forest Sta. Pap. 132. 23 pp.

——— **& R. D. Forbes.** 1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. Ecol. Monogr. 13: 299–320.

Hough, J. L. 1958. Geology of the Great Lakes. xviii + 313 pp. Univ. Illinois Press. Urbana.

———. 1963. The prehistoric Great Lakes of North America. Amer. Scientist 51: 84–109.

Illick, J. S., & L. Frontz. 1928. The beech-birch-maple forest type in Pennsylvania. Bull. Penn. Dept. Forests Waters 46. 40 pp.

Iltis, H. H. 1965. The genus *Gentianopsis* (Gentianaceae): transfers and phytogeographic comments. Sida 2: 129–153.

———. 1966. The western element in the eastern North American flora and its phytogeographic implications (Abstr.). Amer. Jour. Bot. 53: 634.

Janssen, C. R. 1967. A comparison between the recent regional pollen rain and the sub-recent vegetation in four major vegetation types in Minnesota (U.S.A.). Rev. Palaeobot. Palynol. 2:331–342.

Johnson, E. D. 1960. Climate of the states — New York. U.S. Dept. Comm. Climatog. U.S. No. 60–30. 20 pp.

Kalm, P. 1751. Cataracts at Niagara, pp. 79–94. *In*: J. Bartram. Travels from Pensilvania to Onondago, Oswego and the Lake Ontario in Canada. 94 pp. Whiston and White. London. [Facsimile ed., March of America Facsimile Ser. No. 41, Univ. Microfilms, Ann Arbor, Mich. 1966.]

Karrow, P. F. 1963. Pleistocene geology of the Hamilton-Galt area. Ontario Dept. Mines Geol. Rept. 16. vi + 68 pp.

———**, J. R. Clark, & J. Terasmae.** 1961. The age of Lake Iroquois and Lake Ontario. Jour. Geol. 69: 659–667.

King, J. E., & R. O. Kapp. 1963. Modern pollen rain studies in eastern Ontario. Can. Jour. Bot. 41: 243–252.

Kovar, A. J. 1964. Pollen analysis of the Bear Meadows Bog of central Pennsylvania. Proc. Penn. Acad. Sci. 1964: 16–24.

Krauss, R. W., & G. N. Kent. 1944. Analysis and correlation of four New Hampshire bogs. Ohio Jour. Sci. 44: 11–17.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geogr. Soc. Special Publ. 36. v + 116 pp.

Leopold, Estella B. 1956a. Pollen size-frequency in New England species of the genus *Betula.* Grana Palynol. (n.s.) 1:140–147.

———. 1956b. Two late-glacial deposits in southern Connecticut. Proc. Natl. Acad. Sci. (U.S.) 52: 863–867.

——— **& R. A. Scott.** 1958. Pollen and spores and their use in geology. Rep. Smithsonian Inst. 1957: 303–323.

Leverett, F. 1902. Glacial formations and drainage features of the Erie and Ohio basins. U.S. Geol. Sur. Monogr. 41. 802 pp.

Little, E. L., Jr., & W. B. Critchfield. 1969. Subdivisions of the genus *Pinus* (pines). U.S. Dept. Agr. Forest Service Misc. Publ. 1144. iv + 51 pp.

Livingstone, D. A. 1968. Some interstadial and postglacial pollen diagrams from eastern Canada. Ecol. Monogr. 38: 87–125.

Lull, H. W. 1968. A forest atlas of the Northeast. U.S. Dept. Agr. Forest Service Northeast. Forest Exper. Sta. unnumbered publ. 46 pp.

Lutz, H. J. 1930a. Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. Jour. Forestry 28: 1098–1103.

———. 1930b. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. Ecology 11:1–29.

MacClintock, P., & E. T. Apfel. 1944. Correlations of the drifts of the Salamanca re-entrant, New York. Bull. Geol. Soc. Amer. 55: 1143–1164.

——— **& J. Terasmae.** 1960. Glacial history of Covey Hill. Jour. Geol. 68: 232–241.

Maher, L. J., Jr. 1964. *Ephedra* pollen in sediments of the Great Lakes region. Ecology 45: 391–395.

Martin, P. S. 1958a. Pleistocene ecology and biogeography of North America, pp. 375–420. *In*: C. L. Hubbs (Ed.). Zoogeography. Amer. Assoc. Advanc. Sci. Publ. 51. x + 509 pp.

———. 1958b. Taiga-tundra and the full-glacial period in Chester County, Pennsylvania. Amer. Jour. Sci. 256: 470–502.

McAndrews, J. H. 1966. Postglacial history of prairie, savanna, and forest in northwestern Minnesota. Mem. Torrey Bot. Club 22(2). 72 pp.

———. 1970. Fossil pollen and our changing landscape and climate. Rotunda 3(2): 30–37.

McCulloch, W. F. 1939. A postglacial forest in central New York. Ecology 20: 264–271.

McIntyre, A. C., & G. L. Schnur. 1936. Effects of drought on oak forests. Penn. State Coll. Exper. Sta. Bull. 325. 43 pp.

Meinig, D. W. 1966. Geography of expansion, 1785–1855, pp. 140–171. *In*: J. H. Thompson (Ed.). Geography of New York State. 543 pp. *4 maps.* Syracuse Univ. Press. Syracuse, N.Y.

Messenger, A. S. 1966. Climate, time and organisms in relation to podzol development in Michigan sands.

Ph.D. Thesis. 241 pp. Michigan State Univ. East Lansing.

Miller, N. G. 1969. Late- and postglacial vegetation change in southwestern New York State (Abstr.). Diss. Abstr. Intern. 30B: 2565.

Mordoff, R. A. 1949. The climate of New York State. N.Y.S. Coll. Agr. Ext. Bull. 764. 72 pp.

Morey, H. F. 1936. A comparison of two virgin forests in northwestern Pennsylvania. Ecology 17: 43–55.

Morrison, T. M., C. C. Engle, & G. L. Fuller. 1919. Soil survey of Chautauqua County, New York. U.S. Dept. Agr. Field Oper. Bur. Soils (16th Rept.) 1914: 271–326.

Muller, E. H. 1960. Glacial geology of Cattaraugus County, New York. Friends of Pleistocene Geology, Eastern Section, 23d Reunion, Guidebook. 33 pp. Dept. of Geology. Syracuse Univ.

———. 1963. Geology of Chautauqua County, New York. Part II. Pleistocene geology. Bull. N.Y.S. Mus. Sci. Service 392. 60 pp.

———. 1964a. Quaternary geology in New York State. Empire State Geogram 2: 12–16.

———. 1964b. Quaternary section at Otto, New York. Amer. Jour. Sci. 262: 461–478.

———. 1965. Quaternary geology of New York, pp. 99–112. *In:* H. E. Wright, Jr., & D. G. Frey (Eds.). The Quaternary of the United States. x + 922 pp. Princeton Univ. Press. Princeton, N.J.

Munro, R. 1804. A description of the Genesee Country in the State of New York. Reprinted *in*: E. B. O'Callaghan (Ed.). 1849. The documentary history of the State of New York. Vol. 2. pp. 1168–1188. Weed, Parsons and Co. Albany.

Nichols, G. E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. Ecology 16: 403–422.

Northeastern Forest Experiment Station. 1967. Preliminary forest survey statistics, New York — 1967. U.S. Dept. Agr. Forest Service Northeast. Forest Exper. Sta. unnumbered unpaged publ.

Ogden, E. C., & D. M. Lewis. 1960. Airborne pollen and fungus spores of New York State. Bull. N.Y.S. Mus. Sci. Service 378. 104 pp.

Ogden, J. G., III. 1966. Forest history of Ohio. I. Radiocarbon dates and pollen stratigraphy of Silver Lake, Logan County. Ohio Jour. Sci. 66: 387–400.

———. 1967a. Radiocarbon determinations of sedimentation rates from hard and soft-water lakes in northeastern North America, pp. 175–183. *In*: E. J. Cushing & H. E. Wright, Jr. (Eds.). Quaternary paleoecology. vii + 433 pp. Yale Univ. Press. New Haven, Conn.

———. 1967b. Radiocarbon and pollen evidence for a sudden change in climate in the Great Lakes region approximately 10,000 years ago, pp. 117–127. *In*: E. J. Cushing & H. E. Wright, Jr. (Eds.). Quaternary paleoecology. vii + 433 pp. Yale Univ. Press. New Haven, Conn.

Parker, Dorothy. 1936. Affinities of the flora of Indiana: Part I. Amer. Midl. Nat. 17: 700–724.

Parmelee, G. W. 1947. Postglacial forest succession in the Lansing area of Michigan: A study of pollen spectra. M.S. Thesis. 74 pp. Michigan State Univ. East Lansing.

Peattie, D. C. 1922. The Atlantic coastal plain element in the flora of the Great Lakes. Rhodora 24: 57–70, 80–88.

Potzger, J. E. 1946. Phytosociology of the primeval forest in central-northern Wisconsin and upper Michigan, and a brief post-glacial history of the Lake Forest Formation. Ecol. Monogr. 16: 211–250.

——— **& A. Courtemanche.** 1956. Pollen study in the Gatineau Valley, Quebec. Butler Univ. Bot. Stud. 13: 12–23.

——— **& J. H. Otto.** 1943. Post-glacial forest succession in northern New Jersey as shown by pollen records from five bogs. Amer. Jour. Bot. 30: 83–87.

Praglowski, J. 1966. On pollen size variations and the occurrence of *Betula nana* in different layers of a bog. Grana Palynol. 6: 528–543.

Rayback, R. J. 1966. The Indian, pp. 113–120. *In*: J. H. Thompson (Ed.). Geography of New York State. 543 pp. *4 maps.* Syracuse Univ. Press. Syracuse, N.Y.

Ritchie, J. C., & Sigrid Lichti-Federovich. 1967. Pollen dispersal phenomena in arctic-subarctic Canada. Rev. Palaeobot. Palynol. 3: 255–266.

Ritchie, W. A. 1969. The archeology of New York State. Rev. ed. xxxiv + 357 pp. Natural History Press. Garden City, N.Y.

Rowe, J. S. 1959. Forest regions of Canada. Forestry Branch Dept. North. Affairs Natl. Resources Canada Bull. 123. 71 pp.

Rubin, M., & Corrinne Alexander. 1960. U.S. Geological Survey radiocarbon dates V. Amer. Jour. Sci. Radiocarbon Suppl. 2: 129–185.

Sangster, A. G., & H. M. Dale. 1961. A preliminary study of differential pollen grain preservation. Can. Jour. Bot. 39: 35–43.

——— & ———. 1964. Pollen grain preservation of underrepresented species in fossil spectra. *Ibid.* 42: 437–449.

Schick, Sister Mary Salesia, & S. W. Eaton. 1963. Liverworts, mosses and vascular plants of Waterman Swamp and Allenberg Bog. St. Bonaventure Univ. Sci. Studies 21: 5–51.

Schmidt, K. P. 1938. Herpetological evidence for the postglacial eastward extension of the steppe in North America. Ecology 19: 396–407.

Sears, P. B. 1932. Postglacial climate in eastern North America. Ecology 13: 1–6.

———. 1942. Forest sequences in the north central States. Bot. Gaz. 103: 751–761.

Secrest, H. C., H. J. MacAloney, & R. C. Lorenz. 1941. Causes of decadence of hemlock at Menominee Indian Reservation, Wisconsin. Jour. Forestry 39: 3–12.

Shanks, R. E. 1966. An ecological survey of the vegetation of Monroe County, New York. Proc. Rochester Acad. Sci. 11: 108–252.

Shantz, H. L., & R. Zon. 1924. Natural vegetation, 29 pp. *In*: Atlas of American agriculture, Physical basis. 1936. U.S. Government Printing Office. Washington.

Sirkin, L. A. 1967. Correlation of late glacial pollen stratigraphy and environments in the northeastern U.S.A. Rev. Palaeobot. Palynol. 2: 205–218.

Soil Survey Division. 1938. Soils of the United States, pp. 1019–1161. *In*: Yearbook of Agriculture, 1938. 1232 pp. U.S. Government Printing Office. Washington.

Steyermark, J. A. 1939. Some features of the flora of the Ozark region in Missouri. Rhodora 36: 214–233.

Stickel, P. W. 1933. Drought injury in hemlock-hardwood stands in Connecticut. Jour. Forestry 31: 573–577.

Stingelin, R. W. 1965. Late-glacial and post-glacial vegetational history in the north central Appalachian region. Ph.D. Thesis. 191 pp. The Pennsylvania State Univ. University Park. [Abstr. in Diss. Abstr. 26: 6650. 1966.]

Suess, H. E. 1954. U.S. Geological Survey radiocarbon dates I. Science 120: 467–473.

Tauber, H. 1967. Differential pollen dispersion and filtering, pp. 131–141. *In*: E. J. Cushing & H. E. Wright, Jr. Quaternary paleoecology. vii + 433 pp. Yale Univ. Press. New Haven, Conn.

Taylor, A. E., F. B. Howe, C. S. Pearson, & W. J. Moran. 1929. Soil survey of Erie County, New York. U.S. Dept. Agr. Bur. Chem. Soils Ser. 1929. 14. 52 pp.

Terasmae, J. 1958. Non-glacial deposits in the St. Lawrence lowlands, Quebec, pp. 13–28. *In*: J. Terasmae. Contributions to Canadian palynology. Bull. Geol. Surv. Canada 46. 35 pp.

———. 1959. Notes on the Champlain Sea episode in the St. Lawrence lowland, Quebec. Science 130: 334–336.

——— **& R. J. Mott.** 1965. Modern pollen deposition in the Nichicun Lake area, Quebec. Can. Jour. Bot. 43: 393–404.

Tesmer, I. H. 1963. Geology of Chautauqua County, New York, Part I. Stratigraphy and paleontology (Upper Devonian). Bull. N.Y.S. Mus. Sci. Service 391. 65 pp.

Thomas, A. 1871. Pioneer history of Orleans County, New York. xii + 463 pp. H. A. Bruner. Albion, N.Y.

Thompson, Isabel. 1939. Geographical affinities of the flora of Ohio. Amer. Midl. Nat. 21: 730–751.

Thompson, J. H. 1966. The primary sector, pp. 201–231. *In*: J. H. Thompson (Ed.). The geography of New York State. 543 pp. *4 maps.* Syracuse Univ. Press. Syracuse, N.Y.

Turner, O. 1850. Pioneer history of the Holland purchase of western New York. xvi + 670 pp. Jewett, Thomas and Co. Buffalo.

Ueno, Jitsuro. 1958. Some palynological observations of Pinaceae. Jour. Inst. Polytech. Osaka City Univ. Ser. D. 9: 163–187.

Walker, P. C., & R. T. Hartman. 1960. The forest sequence of the Hartstown Bog area in western Pennsylvania. Ecology 41: 461–474.

Wall, R. E. 1968. A sub-bottom reflection survey in the central basin of Lake Erie. Bull. Geol. Soc. Amer. 79: 91–106.

Weaver, J. E., & F. E. Clements. 1938. Plant ecology (ed. 2). xxii + 601 pp. McGraw-Hill. New York.

West, R. G. 1961. Late- and postglacial vegetational history in Wisconsin, particularly changes associated with the Valders readvance. Amer. Jour. Sci. 259: 766–783.

Westerfeld, W. F. 1961. An annotated list of vascular plants of Centre and Huntington Counties, Pennsylvania. Castanea 26: 1–80.

White, G. W. 1968. Age and correlation of Pleistocene deposits at Garfield Heights (Cleveland), Ohio. Bull. Geol. Soc. Amer. 79: 749–752.

———**, S. M. Totten, & D. L. Gross.** 1969. Pleistocene stratigraphy of northwestern Pennsylvania. Bull. Penn. Geol. Sur. G 55. x + 88 pp.

Whitehead, D. R. 1964. Fossil pine pollen and full-glacial vegetation in southeastern North Carolina. Ecology 45: 767–777.

——— **& D. R. Bentley.** 1963. A post-glacial pollen diagram from southwestern Vermont. Pollen Spores 5: 115–127.

Williams, E. T. 1947. Niagara County, pp. 1–448. *In*: J. T. Horton *et al.* History of northwestern New York. Vol. 2. 599 pp. Lewis Historical Publ. Co. New York.

Wilson, I. T., & J. E. Potzger. 1942 [1943]. Pollen study of sediments from Douglas Lake, Cheboygan County and Middle Fish Lake, Montmorency County, Michigan. Proc. Indiana Acad. Sci. 52: 87–92.

Wodehouse, R. P. 1935. Pollen grains, their structure, identification and significance in science and medicine. xv + 574 pp. McGraw Hill. New York.

Wood, R. D. 1965. Monograph of the Characeae. *In*: R. D. Wood & K. Imahori. A revision of the Characeae. xxiv + 904 pp. Vol. 1. Cramer. Weinheim.

——— **& W. C. Muenscher.** 1956. The Characeae of the State of New York. N.Y.S. Coll. Agr. Exper. Sta. Mem. 338. 77 pp.

Wright, H. E., Jr. 1964. Aspects of the early post-glacial forest succession in the Great Lakes region. Ecology 45: 439–448.

———. 1968a. History of the Prairie Peninsula, pp. 78–88. *In*: R. E. Bergstrom (Ed.). The Quaternary of Illinois. Univ. Illinois Coll. Agr. Special Publ. 14. 179 pp.

———. 1968b. The roles of pine and spruce in the forest history of Minnesota and adjacent areas. Ecology 49: 937–955.

——— **& H. L. Patten.** 1963. The pollen sum. Pollen Spores 5: 445–450.

Yeager, D. 1969. A pollen profile from Kennedys Bog in Mendon Ponds Park. Proc. Rochester Acad. Sci. 12: 24–45.

Yeatman, C. W. 1967. Biogeography of jack pine. Can. Jour. Bot. 45: 2201–2211.

Young, A. W. 1875. History of Chautauqua County, New York. xvi + 672 pp. Matthews and Warren. Buffalo, N.Y.

Zenkert, C. A. 1934. The flora of the Niagara Frontier region. Bull. Buffalo Soc. Nat. Sci. 16. x + 328 pp. *1 map.*

APPENDIX A

FOREST STAND DATA: TREES AND SAPLINGS, CANADAWAY CREEK GAME MANAGEMENT AREA,* CHAUTAUQUA COUNTY, NEW YORK

Species and Size Class	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Absolute Density/Acre	Absolute Dominance/Acre
Acer saccharum						
Trees	58.5%	76.6%	80.1%	215.2	76.4	19,596.6
Saplings	60.0%	79.8%	70.6%	210.4	315.0	768.6
Fagus grandifolia						
Trees	22.0%	12.5%	16.4%	50.9	12.5	3,982.9
Saplings	18.6%	11.2%	11.9%	41.7	44.1	129.2
Tsuga canadensis						
Trees	17.1%	9.9%	3.4%	30.4	9.9	844.5
Saplings	8.6%	3.7%	8.0%	20.3	14.7	87.2
Prunus serotina						
Trees	1.2%	0.5%	0.1%	1.8	0.5	11.9
Magnolia acuminata						
Trees	1.2%	0.5%	0.1%	1.8	0.5	14.2
Fraxinus americana						
Saplings	5.7%	2.7%	5.4%	13.8	10.5	58.9
Betula alleghaniensis						
Saplings	4.3%	1.6%	3.0%	8.9	6.3	32.3
Ostrya virginiana						
Saplings	1.4%	0.5%	0.6%	2.5	2.1	6.6
Cornus alternifolia						
Saplings	1.4%	0.5%	0.6%	2.5	2.1	6.6

* New York State Department of Environmental Conservation.

APPENDIX B

FOREST STAND DATA: HERBS AND SEEDLINGS, CANADAWAY CREEK GAME MANAGEMENT AREA,* CHAUTAUQUA COUNTY, NEW YORK

Species and Size Class	Relative Frequency
Acer saccharum	
under 12 inches	24.2%
over 12 inches	9.2%
Arisaema triphyllum	18.3%
Viola incognita	9.2%
Fraxinus americana	
under 12 inches	6.5%
Dryopteris spinulosa var. *intermedia*	5.9%
Euonymus obovatus	5.9%
Dennstaedtia punctilobula	3.3%
Epifagus virginiana	2.6%
Phytolacca americana	2.6%
Aster divaricatus	1.9%
Viola canadensis	1.9%

Species and Size Class	Relative Frequency
Allium tricoccum	0.7%
Asarum canadensis	0.7%
Caulophyllum thalictroides	0.7%
Disporum lanuginosum	0.7%
Fagus grandifolia	
under 12 inches	0.7%
over 12 inches	1.9%
Galium sp.	0.7%
Hepatica acutiloba	0.7%
Monotropa uniflora	0.7%
Rhus radicans	0.7%
Viola rotundifolia	0.7%

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* New York State Department of Environmental Conservation.

APPENDIX C

FOREST STAND DATA: TREES AND SAPLINGS, FORESTRY DEPARTMENT* PLANTATION #11, ERIE COUNTY, NEW YORK

Species and Size Class	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Absolute Density/Acre	Absolute Dominance/Acre
Acer saccharum						
Trees	24.8%	24.0%	34.0%	82.8	66.9	11,694.1
Saplings	41.3%	49.2%	51.7%	142.2	63.0	264.6
Fagus grandifolia						
Trees	23.3%	26.0%	26.6%	75.9	72.5	9,113.3
Saplings	33.3%	26.2%	26.9%	86.4	33.6	137.8
Tsuga canadensis						
Trees	21.7%	24.5%	13.6%	59.8	68.3	4,671.7
Saplings	20.0%	21.3%	15.6%	56.9	27.3	79.2
Prunus serotina						
Trees	16.3%	16.1%	19.7%	52.1	44.9	6,735.0
Tilia americana						
Trees	6.2%	4.2%	2.3%	12.7	11.7	812.0
Saplings	2.7%	1.6%	2.9%	7.2	2.1	14.9
Ostrya virginiana						
Trees	2.3%	1.6%	0.9%	4.8	4.5	332.6
Fraxinus americana						
Trees	1.6%	1.0%	0.5%	3.1	2.8	149.5
Betula alleghaniensis						
Trees	1.6%	1.0%	0.3%	2.9	1.4	46.3
Saplings	2.7%	1.6%	2.9%	7.2	2.1	14.9
Juglans cinerea						
Trees	0.8%	0.5%	1.1%	2.4	1.4	376.3
Ulmus americana						
Trees	0.8%	0.5%	0.6%	1.9	1.4	215.5
Acer rubrum						
Trees	0.8%	0.5%	0.4%	1.7	1.4	121.3

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* County of Erie.

APPENDIX D

FOREST STAND DATA: HERBS AND SEEDLINGS, FORESTRY DEPARTMENT* PLANTATION ♯11, ERIE COUNTY, NEW YORK

Species and Size Class	Relative Frequency
Acer saccharum	
under 12 inches	15.7%
over 12 inches	8.9%
Prunus serotina	
under 12 inches	11.7%
Acer rubrum	
under 12 inches	10.1%
over 12 inches	0.4%
Fraxinus americana	
under 12 inches	6.5%
Viola sp.	4.0%
V. incognita	3.2%
Arisaema triphyllum	2.4%
Geranium Robertianum	2.4%
Ulmus americana	
under 12 inches	2.4%
Dentaria diphylla	2.0%
Dryopteris spinulosa var. *intermedia*	2.0%
Fagus grandifolia	
under 12 inches	2.0%
over 12 inches	0.4%
Tilia americana	
under 12 inches	2.0%
Trillium grandiflorum	2.0%
Ostrya virginiana	
under 12 inches	1.6%
Botrychium virginianum	1.2%
Polygonatum pubescens	1.2%
Actaea pachypoda	0.8%
Carex sp.	0.8%
Caulophyllum thalictroides	0.8%
Circaea quadrisulcata	0.8%
Cornus alternifolia	0.8%
Epifagus virginiana	0.8%
Impatiens sp.	0.8%
Lycopodium complanatum var. *flabelliforme*	0.8%
Mitchella repens	0.8%
Ribes sp.	0.8%
Tiarella cordifolia	0.8%
Viola canadensis	0.8%
V. rotundifolia	0.8%
Athyrium Felix-femina	0.4%
A. thelypterioides	0.4%
Botrychium sp.	0.4%
Carex plantaginea	0.4%
Carya cordiformis	
under 12 inches	0.4%
Dicentra sp.	0.4%
Epipactis Helleborine	0.4%
Hepatica acutiloba	0.4%
Hieracium sp.	0.4%
Maianthemum canadense	0.4%
Mitella diphylla	0.4%
Osmorhiza Claytoni	0.4%
Oxalis montana	0.4%
Phlox divaricata	0.4%
Podophyllum peltatum	0.4%
Polystichum acrostichoides	0.4%
Tsuga canadensis	
over 12 inches	0.4%
Veronica officinalis	0.4%

* County of Erie.

APPENDIX E

FOREST STAND DATA: TREES AND SAPLINGS, ZOAR VALLEY PROPERTY ♯12,* ERIE COUNTY, NEW YORK

Species and Size class	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Absolute Density/Acre	Absolute Dominance/Acre
Acer saccharum						
Trees	48.0%	68.2%	52.9%	169.1	78.9	13,789.4
Saplings	20.5%	22.2%	27.4%	70.1	33.6	131.7
Fagus grandifolia						
Trees	26.0%	16.2%	35.7%	77.9	18.7	9,313.7
Saplings	43.2%	51.4%	31.1%	125.7	77.7	149.2
Tsuga canadensis						
Trees	16.0%	10.4%	2.7%	29.1	12.0	692.3
Saplings	29.5%	22.2%	35.9%	87.6	33.6	172.3
Tilia americana						
Trees	4.0%	2.1%	3.2%	9.3	2.4	838.5
Fraxinus americana						
Trees	3.0%	1.6%	2.6%	7.2	1.9	699.5
Betula alleghaniensis						
Trees	1.0%	0.5%	0.1%	1.6	0.6	38.2
Ostrya virginiana						
Saplings	4.5%	2.8%	5.3%	12.6	4.2	25.3
Carpinus caroliniana						
Saplings	2.3%	1.4%	0.3%	4.0	2.1	1.6

* New York State Department of Environmental Conservation, Multiple Use Land, Acquisition ♯ Catt. 8.3.9.

APPENDIX F

FOREST STAND DATA: HERBS AND SEEDLINGS, ZOAR VALLEY PROPERTY #12,* ERIE COUNTY, NEW YORK

Species and Size Class	Relative Frequency	Species and Size Class	Relative Frequency	Species and Size Class	Relative Frequency
Acer saccharum		*Athyrium thelypterioides*	1.1%	*Acer rubrum*	
under 12 inches	13.4%	*Carya cordiformis*		under 12 inches	0.4%
over 12 inches	12.4%	under 12 inches	0.7%	*Actaea* sp.	0.4%
Arisaema triphyllum	10.2%	over 12 inches	0.4%	*Adiantum pedatum*	0.4%
Fraxinus americana		*Dennstaedtia punctilobula*	1.1%	*Aster divaricatus*	0.4%
under 12 inches	9.2%	*Galium* sp.	1.1%	*A. lateriflorus*	0.4%
over 12 inches	2.1%	*Geranium Robertianum*	1.1%	*Athyrium Felix-femina*	0.4%
Fagus grandifolia		*Prunus serotina*		*Carex plantaginea*	0.4%
under 12 inches	2.5%	under 12 inches	0.4%	*C.* sp.	0.4%
over 12 inches	6.0%	over 12 inches	0.7%	*Circaea alpina*	0.4%
Viola incognita	4.9%	*Botrychium virginianum*	0.7%	*Eupatorium rugosum*	0.4%
Dryopteris spinulosa		*Cornus alternifolia*	0.7%	*Impatiens* sp.	0.4%
var. *intermedia*	3.9%	*Epipactis Helleborine*	0.7%	*Lycopodium lucidulum*	0.4%
Caulophyllum thalictroides	2.8%	*Monotropa uniflora*	0.7%	*Potentilla* sp.	0.4%
Hepatica acutiloba	2.8%	*Osmorhiza Claytoni*	0.7%	*Ribes* sp.	0.4%
Viola rotundifolia	2.5%	*Tilia americana*		*Sambucus canadensis*	0.4%
V. pensylvanica	2.5%	under 12 inches	0.7%	*Tiarella cordifolia*	0.4%
V. canadensis	2.1%	*Ulmus americana*		*Trillium erectum*	0.4%
Circaea quadrisulcata	1.4%	under 12 inches	0.7%	*T.* sp.	0.4%
Maianthemum canadense	1.4%	*Viola* sp.	0.7%	*Urtica procera*	0.4%
Actaea pachypoda	1.1%				

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* New York State Department of Environmental Conservation, Multiple Use Land, Acquisition # Catt. 8.3.9.

APPENDIX G

POLLEN SPECTRA ABOVE AND BELOW GYTTJA SAMPLES USED FOR C-14 AGE DETERMINATION AT PROTECTION BOG

	Depths (m)			
Taxa	3.56	3.66	5.35	5.45
Arboreal Pollen (AP)*				
Picea	——	——	0.7	——
Abies	——	——	0.6	0.4
Larix	——	——	0.3	——
Pinus undifferentiated	0.9	0.5	20.9	21.2
P. haploxylon	1.4	1.4	22.6	23.6
P. diploxylon	0.2	0.2	3.2	2.9
Juniperus	——	——	——	0.1
Tsuga	16.7	23.2	2.1	1.5
Fagus	35.4	38.2	0.7	0.3
Acer saccharum	8.6	7.7	1.5	1.3
Tilia	0.9	0.6	0.3	——
Fraxinus 4-colpate	3.9	1.8	0.6	0.6
Juglans cinerea	1.3	0.3	0.1	0.3
Carya	1.4	1.1	1.0	0.6
Quercus	6.8	7.5	22.3	19.5
Ulmus	5.0	6.4	6.0	6.0
Betula	11.0	5.4	6.2	8.8
Fraxinus 3-colpate	2.0	1.9	1.2	2.3
Acer rubrum	——	0.3	——	——
Carpinus-Ostrya	0.8	0.6	6.0	7.2
Corylus	——	——	0.4	0.7
Platanus	0.9	1.4	0.4	0.4
% AP	97.3	98.7	97.3	97.8

	Depths (m)			
Taxa	3.56	3.66	5.35	5.45
Nonarboreal Pollen (NAP)*				
Alnus	0.6	0.3	0.7	0.5
Salix	0.3	——	0.7	0.1
Viburnum	0.3	——	——	——
Rosaceae	0.2	——	——	——
Cyperaceae	0.3	0.2	0.3	0.7
Gramineae	——	——	0.1	0.4
Ambrosia	0.3	0.2	0.1	——
Artemisia	0.2	0.2	0.3	0.1
Xanthium	0.3	——	——	0.1
High-spine Compositae	——	0.2	0.3	——
Cheno-Am.	0.2	——	——	——
Ranunculus	——	0.2	——	——
Thalictrum	——	0.2	——	——
% NAP	2.7	1.3	2.7	2.2
Misc. Pollen and Spores (MP)†				
Ericaceae	0.5	0.2	——	——
Nuphar	——	——	0.4	——
Sarracenia	0.2	0.2	——	——
Polypodiaceae	——	0.2	3.0	3.3
Osmundaceae	0.5	0.5	——	——
broken Abietineae	——	——	1.1	0.4
unfamiliar	——	——	0.1	——
unknown	2.7	4.0	3.4	1.7

* Percentage base: sum AP + NAP.

† Percentage base: sum AP + NAP + MP.

APPENDIX H

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: PROTECTION BOG

Taxa Depths (m)	*Ephedra*	*Juniperus*	*Liquidambar*	*Nyssa sylvatica*	*Cephalanthus*	*Myrica*	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	*Gentiana* comp.*	Labiatae	Leguminosae	*Polygonum*	*Potentilla palustris*	*Ranunculus*	Umbelliferae	Urticaceae	*Vitis*	*Xanthium*	*Myriophyllum*	*Sagittaria*	*Sarracenia*	*Sparganium*	*Utricularia*	Ophioglossaceae
0.000	—	0.1	0.1	—	—	—	0.3	0.1	—	—	—	—	—	—	—	0.1	0.2	0.1	0.2	—	—	0.1	—	—	—	—
0.025	—	—	—	—	—	—	0.7	—	—	—	—	—	0.1	—	—	0.1	0.2	—	—	—	—	0.3	—	—	—	—
0.075	—	—	0.1	—	—	—	0.2	0.2	—	—	—	—	—	—	—	0.1	0.2	—	—	—	—	—	0.1	—	—	—
0.125	—	—	0.1	—	—	—	0.4	—	0.1	—	—	—	0.6	—	—	—	—	—	—	—	—	0.2	0.1	—	—	—
0.175	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	0.2	—	—	—	—
0.225	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.275	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.325	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
0.425	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—
0.575	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—
0.725	—	—	—	—	—	—	—	—	—	0.5	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
0.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.225	—	—	—	0.3	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.475	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.725	0.2	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.975	—	—	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
2.225	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
2.475	0.2	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
2.725	—	—	—	0.3	—	—	—	0.2	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	0.2	—	—	0.2
2.975	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
3.225	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—
3.475	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1
3.725	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.975	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—
4.225	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4.475	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4.725	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
4.875	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—
5.025	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
5.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.325	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.475	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.625	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
5.775	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—
5.925	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—	0.1	—	—	—	—	—	—	0.1	—	0.1
6.035	—	—	0.1	—	—	0.1	0.1	—	—	—	—	—	—	—	—	0.1	—	—	—	0.1	—	—	—	0.5	—	0.1
6.115	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	—	—	—	—	0.1
6.195	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.6	—	0.1
6.265	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—
6.325	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	0.1	—

* The notation "comp." after certain pollen taxa indicates the degree of certainty in the identification of difficult pollen grains (Benninghoff & Kapp, 1962). It is used when a grain is provisionally assigned to a taxon and to convey that uncertainty exists about the conclusiveness of identification. If no notation follows a taxon, the identification is considered positive.

APPENDIX I

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: HOUGHTON BOG — SECTION A

Depths (m) \ Taxa	*Cephalanthus*	*Rhamnus* comp.	*Rhus*	Rosaceae	*Sambucus*	*Viburnum*	Caryophyllaceae	*Coptis*	Labiatae	Leguminosae	*Ranunculus*	Rubiaceae	*Thalictrum*	Umbelliferae	*Sagittaria*	*Sparganium*	*Typha*	*Utricularia*	Ophioglossaceae
0.000	—	—	—	0.6	—	0.5	—	—	—	0.2	—	—	—	0.2	0.1	—	0.1	—	—
0.025	0.2	0.1	0.1	0.3	0.2	—	0.1	—	—	—	—	—	0.1	0.3	—	—	—	—	0.2
0.075	0.1	—	—	—	—	—	0.1	—	0.1	0.2	0.1	0.1	—	—	0.3	0.1	0.1	—	0.1
0.125	—	—	—	0.3	—	—	—	—	—	—	0.1	—	—	—	—	—	—	—	0.1
0.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.225	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.375	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
0.725	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—
0.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
1.225	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.425	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.725	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2
1.925	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—
2.225	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
2.475	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.725	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
2.975	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.225	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.425	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
3.725	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—
3.925	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—

APPENDIX J

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: HOUGHTON BOG — SECTION B

Taxa Depths (m)	*Celtis*	*Liquidambar*	*Nyssa sylvatica*	Ericaceae	*Nemopanthus*	*Rhamnus* comp.	*Rosaceae*	Caryophyllaceae	*Coptis*	*Gentiana* comp.	*Impatiens* comp.	Rubiaceae	*Rumex*	*Thalictrum*	Umbelliferae	*Xanthium*	*Brasenia*	*Nuphar*	*Nymphaea*	*Menyanthes*	*Proserpinaca*	*Sagittaria*	*Sarracenia*	*Typha*	*Utricularia*
4.13	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.3	0.2	—	—	—	—	—	—
4.38	—	—	—	—	0.7	—	0.2	—	—	—	—	—	0.4	0.4	—	—	—	—	—	—	—	—	—	—	—
4.63	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	0.3	0.2	—	—	—	—	—	—
4.88	—	—	—	—	0.2	—	—	—	—	0.4	—	—	—	0.2	—	—	—	0.6	0.2	—	—	—	0.4	—	—
5.13	—	—	—	—	0.4	0.2	—	—	—	—	—	—	—	—	—	—	—	0.6	0.4	—	—	—	—	0.1	—
5.38	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—	—	—	—
5.63	0.2	—	—	—	—	0.4	—	—	—	—	—	—	—	0.2	—	—	0.2	0.2	0.3	—	—	—	—	0.2	—
5.88	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
6.13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.38	0.2	—	—	—	0.2	—	0.2	—	—	—	0.2	0.2	—	0.2	—	—	—	0.3	—	—	—	—	—	—	—
6.63	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.88	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.1	—	—	—	—	—	—	—
7.06	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.21	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—
7.36	—	—	0.2	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.3	—	—	—	—	—	—	—
7.56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
7.71	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—	—	—	—	—
7.86	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.01	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—
8.25	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
8.37	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.49	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.61	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.73	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	0.2
8.84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2
8.96	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—
9.01	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3
9.07	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—
9.13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.31	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.5	0.2	—	—	—	—	—	—	0.3	—	—	—
9.41	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	0.5	—	—	—	—	—	—	—	—	—	—	—
9.55	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.67	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—
9.79	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.3	0.3	—	0.2	—
9.91	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

APPENDIX K

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: ALLENBERG BOG — SECTION A

Taxa / Depths (m)	*Juglans nigra*	*Liquidambar*	*Magnolia acuminata*	*Cephalanthus*	*Myrica*	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	Labiatae	Leguminosae	*Ranunculus*	*Thalictrum*	Umbelliferae	Urticaceae	*Vitis*	*Xanthium*	*Sagittaria*	*Sarracenia*	*Sparganium*	*Utricularia*	*Equisetum*	Ophioglossaceae
0.000	0.2	0.1	—	—	—	2.6	0.1	—	—	—	—	—	—	—	0.1	—	0.1	—	—	—	—	—	—
0.025	—	—	—	0.1	—	1.1	0.3	—	—	0.3	0.2	—	—	0.5	—	0.2	0.1	0.3	—	0.1	—	—	0.1
0.075	0.2	0.1	—	—	—	0.7	0.3	—	—	—	0.2	—	—	0.2	0.2	—	0.1	—	—	0.1	—	—	—
0.125	0.2	0.1	—	0.1	0.1	1.1	2.3	—	—	0.1	0.1	0.4	—	—	—	—	—	0.1	0.1	—	—	0.1	—
0.175	0.3	0.2	—	—	—	0.3	1.2	—	—	—	—	—	—	—	0.2	—	—	—	0.1	—	—	—	—
0.225	0.2	—	0.3	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—
0.275	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	1.6	—	—	—	—
0.325	—	0.2	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	0.7	—	—	—	—
0.375	0.3	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—	—
0.425	0.2	—	—	—	—	0.2	0.2	—	—	—	—	—	0.3	—	—	—	—	—	0.4	—	—	—	—
0.475	0.2	—	—	—	0.2	—	0.5	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—
0.675	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
0.925	—	—	—	—	—	—	0.9	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.117	—	—	—	—	—	0.3	0.2	—	0.3	—	—	—	0.2	—	—	—	—	—	0.7	—	—	—	—
1.425	—	—	0.2	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	0.3	—	—	—	—
1.675	0.2	—	—	—	—	1.1	0.5	—	0.2	—	—	—	0.2	—	—	—	—	—	0.4	—	—	—	—
1.925	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	0.3	—	—	—	0.2	—	0.2	—	—
2.175	0.2	—	—	—	—	0.3	0.5	—	—	—	—	—	0.5	—	—	—	—	—	0.3	—	0.1	0.1	—
2.425	—	—	—	—	—	0.5	0.3	—	—	—	—	—	0.2	—	—	—	—	—	0.1	—	0.1	—	—
2.675	—	—	—	—	0.2	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.925	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	—

APPENDIX L

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: ALLENBERG BOG — SECTION B

Depths (m) \ Taxa	*Juglans nigra*	*Liquidambar*	*Magnolia acuminata*	*Nyssa sylvatica*	*Cephalanthus*	*Myrica*	*Rhus*	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	*Epilobium*	Cichorioideae	Umbelliferae	Urticaceae	*Xanthium*	*Myriophyllum*	*Potamogeton*	*Sarracenia*	*Utricularia*	*Equisetum*	Ophioglossaceae
4.525	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4.675	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—
4.925	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.6	—	—	—
5.175	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—
5.425	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—
5.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
5.925	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—
6.175	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.425	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—
6.675	0.3	—	0.2	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—
6.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.1	0.1	0.1	—
7.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
7.425	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—
7.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
7.925	0.2	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	4.1	—	—	—	—
8.175	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	0.1	—	0.1	—	—	—	—
8.425	—	0.3	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
8.925	0.2	—	—	—	—	—	—	—	0.2	—	0.3	—	—	—	—	—	—	—	—	—	—	—
9.175	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.425	0.3	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.1	—	—	—
10.425	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10.675	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
10.925	—	—	—	—	—	0.2	—	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—
11.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
11.425	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2
11.675	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	0.2	—	—	0.2	—	—	—
11.925	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
12.175	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	0.2	0.2	—	0.1	—	—	0.1	—	—
12.425	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	0.2	—	—	—	—

APPENDIX M

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: ALLENBERG BOG — SECTION C

Taxa Depths (m)	*Nyssa sylvatica*	*Rhus* comp.	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	*Epilobium*	*Galium* comp.	*Gentiana* comp.	Labiatae	*Polygonum*	*Ranunculus*	Umbelliferae	Urticaceae	*Xanthium*	*Eriocaulon*	*Menyanthes*	*Sagittaria*	*Sparganium*	*Isoëtes*	Ophioglossaceae	*Selaginella selaginoides*
11.525	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—
11.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11.875	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.025	—	—	—	0.3	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
12.175	—	—	0.4	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—	—	—	—	—
12.325	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.425	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.625	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.775	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	0.3	0.3	—	—	—
12.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	0.1	—
13.075	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.3	0.1	—	—	—
13.225	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	0.1	0.3	—	0.1	—
13.375	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.7	—	—	—
13.525	—	—	0.3	—	—	—	—	—	—	—	—	—	—	0.1	0.1	—	—	—	0.3	—	0.1	—
13.675	—	—	0.1	—	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—	0.3	—
13.825	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—
13.925	—	—	0.1	—	—	—	—	0.1	—	0.1	—	—	—	—	—	—	—	—	—	—	0.1	—
14.125	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.5	0.1	—	—
14.275	—	0.1	—	—	—	—	—	0.1	—	—	—	—	0.1	—	—	—	0.1	—	—	—	0.1	—
14.425	—	—	0.1	—	—	—	—	—	—	—	—	0.3	—	—	0.1	—	—	0.1	0.4	—	0.3	—
14.540	0.1	—	0.3	—	—	—	—	—	—	0.3	—	0.1	—	—	—	—	—	—	0.4	—	0.1	—
14.660	—	—	—	—	—	—	—	—	—	—	—	0.3	—	0.3	—	—	—	0.1	0.1	—	—	—
14.750	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.3	—	—	—	0.1	0.1	—	—	—
14.870	—	—	—	—	—	—	—	—	—	0.1	—	0.1	—	0.3	—	—	—	—	—	—	—	—
14.985	—	—	0.3	—	0.1	—	—	—	0.3	—	—	0.4	0.3	—	—	—	—	—	—	—	0.3	0.1
15.085	—	—	0.2	—	0.4	—	—	—	—	0.1	—	0.1	—	—	—	—	—	—	—	—	—	0.1
15.165	—	—	—	—	0.1	—	—	—	—	0.1	0.1	0.2	—	—	—	0.1	—	—	—	—	—	—

APPENDIX N

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: GENESEE VALLEY PEAT WORKS

Depths (m) \ Taxa	*Juglans nigra*	*Larix*	*Liquidambar*	*Nyssa sylvatica*	*Populus*	*Cephalanthus*	*Nemopanthus*	*Rhus* comp.	*Sambucus*	*Viburnum*	*Arceuthobium*	*Campanula rotundifolia*	*Coptis*	*Cornus canadensis*	*Dryas* comp.	*Empetrum* comp.	*Gentiana* comp.	Labiatae	*Lysimachia* comp.	*Polemonium* comp.	*Ranunculus*	*Saxifraga* comp.	Urticaceae	*Menyanthes*	*Myriophyllum*	*Proserpinaca*	*Sagittaria*	*Scheuchzeria*	*Typha*	*Utricularia*	Ophioglossaceae	unfamiliar spore type A
0.51	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.67	—	—	—	0.1	0.3	—	1.5	2.8	0.3	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—	—
0.85	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—
1.03	—	0.1	0.4	—	0.4	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.22	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.41	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.57	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.86	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—
2.43	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.69	—	—	—	—	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—
2.94	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—
3.19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
3.45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
3.69	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.1	0.6	—	0.1	—	—	—	—	—	—	—	—	0.1	0.6	0.1	—
3.89	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	0.1	—	—	—	—	—	—	—	—	—	—	0.3	—	—
4.09	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—
4.30	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—
4.50	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—	0.1	—	—	—	—	—	—	—	0.1	—	—	—	—	0.1	—
4.60	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	0.3	0.1	—	—	—	0.1	—	—	—	—	—	—
4.70	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	0.6	—	0.3	—	—	—	—	0.1	—	—	0.3	0.4
4.74	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	0.4	0.2
4.80	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	0.5	—	0.1	—	0.2	—	—	—	—	0.1	0.4	0.6

Pollen Diagrams

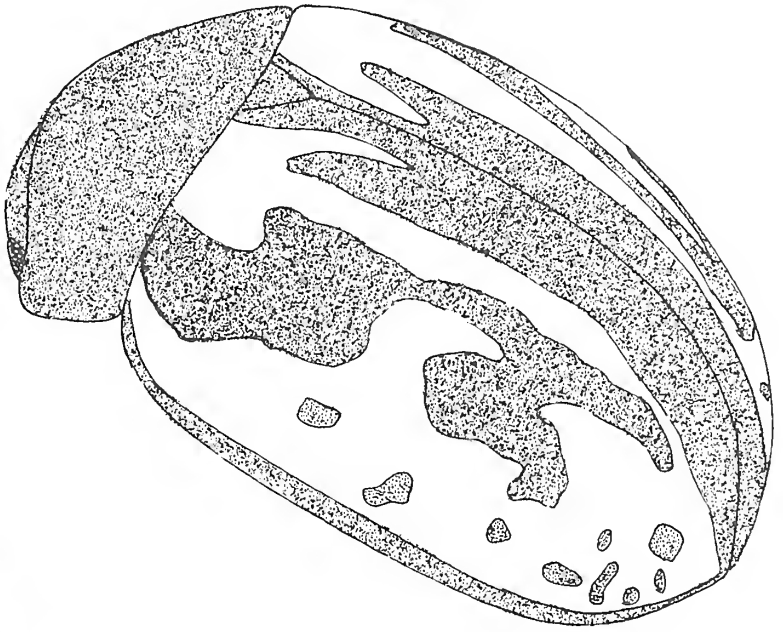
1. Percentages of all pollen taxa on the left side of the sums column were computed using the sum of the arboreal and nonarboreal pollen excluding aquatics and pteridophytes.
2. Only major pollen taxa are included in the following diagrams. See Appendices H to N for a listing of minor types.
3. When a given pollen type occurs with regularity across some interval, but elsewhere is represented by only one or two grains, which may be stratigraphically isolated from other occurrences immediately above and below, a + symbol is used.

A f the
North American Chrysomeline Leaf Beetles
(Coleoptera: Chrysomelidae)

by JOHN A. WILCOX

Senior Scientist (Entomology)

BULLETIN 421



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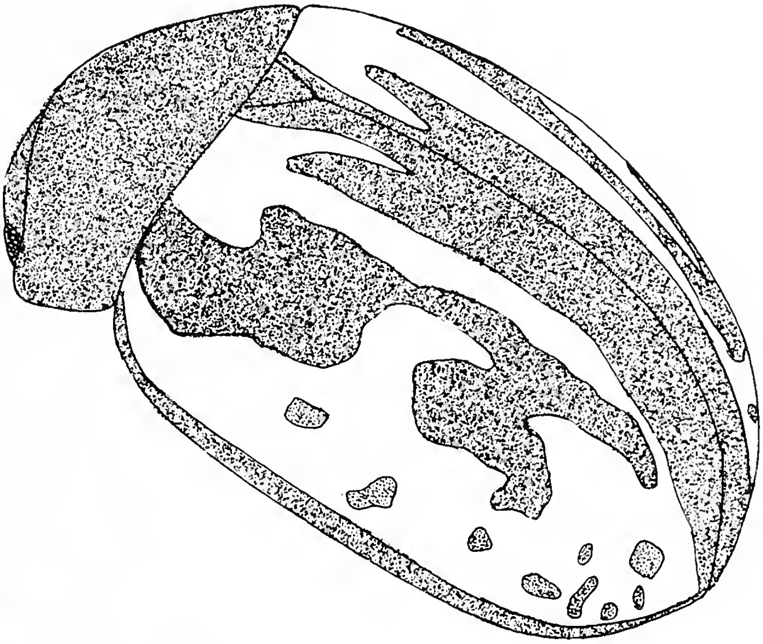

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A Review of the North American Chrysomeline Leaf Beetles (Coleoptera: Chrysomelidae)[1]

by JOHN A. WILCOX[2]

Introduction

This publication, a review of the Chrysomelinae of the United States and Canada, includes a checklist and compilation of keys to the 136 species. One new species, *Leptinotarsa collinsi,* is described. This is one of the larger subfamilies with about 3,000 species represented in all areas of the world. The North American species are here grouped into seven tribes, although Entomolscelini, Prasocurini, and Phratorini are of doubtful validity. I follow Crowson and Arnett in using the subfamily name Chrysomelinae in the broad sense, equal in rank to Chriocerinae and Eumolpinae which I leave in Chrysomelidae.

Both larvae and adults live openly on plants, feeding on leaves or flowers. The larvae enter the ground for pupation, or sometimes remain attached to their food plant, the pupa then being attached at its posterior extremity.

A number of species in this subfamily, Chrysomelinae, are of economic importance, including the Colorado potato beetle (*Leptinotarsa decemlineata*), the poplar leaf beetle (*Chrysomela scripta*), the imported willow leaf beetle (*Plagiodera versicolor*), the red turnip beetle (*Entomoscelis americana*), and the yellow-margined leaf beetle (*Microtheca ochroloma*). On the other hand, two species of *Chrysolina* (*quadrigemina* and *hpyerici*) have been well established in America to help control Klamath weed in the Pacific Northwest.

These typical members of the family Chrysomelidae are 3 to 16 mm. long; broadly oval to elongate; often brightly colored. Head inserted into the prothorax to the eyes, only partly visible dorsally. Antennae with 11 segments, moderately long, the apical segments somewhat enlarged. Antennal insertions widely separated, between eye and mandible, not on tubercles. Prothorax usually broad and somewhat convex; side margins well defined; frequently emarginate in front. Front coxae transverse, widely separated. Elytra convex, covering the abdomen; epipleura well defined. Tarsal formula apparently 4–4–4 but actually 5–5–5, the fourth segment minute and hidden in the bilobed third segment.

Labrum distinct. Mandibles short, stout, curved; apices acute, blunt, or dentate. Maxillary palpi four-segmented, the segments usually enlarged, but not strongly dilated or elongate. Gular sutures usually absent. Labial palpi three-segmented, the segments short, apically acute. Eyes lateral, moderate, round or emarginate on the inner side. Pronotum broader than the head, quadrate or oval; lateral borders margined; pleural region broad. Legs usually short to moderately long; trochantins not exposed. Metacoxae transverse. Trochanters small, triangular. Femora usually without apical spurs. Wing venation with the basal part of the anal area reduced; folding pattern with the fold below Cu approaching the Haplogastra type. Abdomen with five visible sternites. Male genitalia with the aedeagus stout, curved; parameres distinct or absent; pars basalis ring-shaped, with long slender basal struts, ventrally fused. Female genitalia with the paraprocts and valvifers with baculi closely articulating; coxite simple, sometimes very large.

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[1] Manuscript submitted for publication May 8, 1972.

[2] Senior Scientist, Entomology, New York State Museum and Science Service.

Subfamily Chrysomelinae

Key to the North American genera of Chrysomelinae

1\. Front coxal cavities closed behind (figure 2)....2

— Front coxal cavities open behind (figure 17)....3

2\. Upper surface uniformly brown, bronze or black (figure 1); prosternum, between coxae, longer than metasternum (figure 2); British Columbia—California .... *Timarcha* Latr.

— Upper surface bicolored, at least elytra with pale margin; prosternum, between coxae, shorter than metasternum (figure 17); on Cruciferae........14

3\. Tarsal claws appendiculate (figure 23); on willow, poplar, and birch..........................15

— Tarsal claws simple (figures 9, 25)...........4

4\. Claws connate, that is parallel and contiguous at base (figure 4); elytra striped or spotted (figures 5, 72–80, 88–91)............*Zygogramma* Chev.

— Claws divergent or at least separated at base (figure 9) 5

5\. Last segment of maxillary palp attenuate toward apex, cylindrical or oval (figure 83); third tarsal segment usually bilobed or emarginate (figure 8), sometimes simple (figure 7)................14

— Apical segment of maxillary palp broadly truncate at tip, subquadrangular or dilated (figures 3, 14); third tarsal segment entire or slightly emarginate (figure 7) 6

6\. Apical segment of maxillary palp shorter than the preceding, truncate (figures 81, 82)..........7

— Apical segment of maxillary palp as long as or longer than the preceding, dilated, truncate (figure 14) 8

7\. Front femur of male strongly toothed (figure 10), normal in female; mesosternum forming a blunt tubercle between the middle coxae, raised above the level of the prosternum; (figure 11) [Species in key to *Leptinotarsa* also]....*Labidomera* Chev.

— Front femur of male and female normal; mesosternum not raised above the level of the prosternum; (figure 6)..........*Leptinotarsa* Stal

8\. Elytra with spots or stripes delimited by punctures (figures 12–13, 35–71); pronotum not thickened at sides, without distinct longitudinal impressions .... *Calligrapha* Chev.

— Elytra entirely dark or dark with pale lateral margins (figure 15); elytral punctures usually in irregular rows; sides of pronotum thickened, the thickened portion separated from disc by a longitudinal impression..........*Chrysolina* Motsch.

9\. Shining black, usually with bronze or green luster; lateral margins of pronotum and elytra and a narrow discal stripe on each elytron pale yellow (figures 27, 28)............................13

— Color pattern of pronotum and elytra different from that described above; elytral stripes, if present, very short 10

10\. Larger elytral punctures in regular rows which are separated by a distance equal to at least four times the diameter of the punctures in them; upper surface entirely dark blue, green, bronze, purple or black; 3–4.3 mm. long; on water cress or other Cruciferae; (figure 20)..........*Phaedon* Latr.

— Elytral punctation confused, or if in rows then the rows are separated by a distance not greater than two times the diameter of the punctures.......11

11\. Pronotum with a distinct longitudinal impression on each side (figures 16, 18); elytra usually pale with dark markings but may be entirely dark in some species; 4.3–9.5 mm. long; on willow, poplar or alder.......................*Chrysomela* L.

— Pronotum without distinct longitudinal impressions; elytra brown with pale margins or entirely dark blue, green, or purple..................12

12\. Prosternum, between coxae, narrower than third antennal segment; body strongly convex, hemispherical in cross section; sides of elytra nearly parallel (figure 19); elytra entirely dark although some species may have strong coppery or golden luster; 4–6.2 mm. long; on Polygonaceae (*Rumex* or *Polygonum*).............*Gastrophysa* Chev.

— Prosternum, between coxae, much broader than the third antennal segment; body less convex, not hemispherical in cross section; sides of elytra strongly curved; elytra brown with pale margins or entirely dark blue, green, or purple; 3.5–5 mm. long; on willow (*Salix*); (figure 21)........... .... *Plagiodera* Chev.

13\. Basal margin of pronotum with a fine elevated bead; sutural dark stripe not much wider around scutellum (figure 27); form very elongate; length at least 2.5 times width; Quebec-Ohio-Colorado-British Columbia; on water parsnip (*Sium*) [*P. phelandrii* (L.)]..............*Prasocuris* Latr.

— Basal margin of pronotum without such a bead; form broader, length less than 2.5 times width; sutural dark stripe abruptly widened around scutellum (figure 28); on *Ranunculus*............ .... *Hydrothassa* Thoms.

14. Elytral punctation confused; pronotum black with pale margins; each elytron red with suture and a discal stripe black (figure 22); 6.5–10 mm. long; Minnesota-Washington-Alaska [*E. americana* Brown] .... *Entomoscelis* Chev.

— Punctures of each elytron in four regular rows; pronotum entirely dark; elytra dark brown except for pale margins (figure 26); 4.5 mm. long; Alabama-Louisiana [*M. ochroloma* Stal] .... *Microtheca* Stal

15. Tibiae dilated and toothed near apex (figure 30); upper surface usually partly pale, never with metallic luster (figure 29); on willow and poplar .... *Gonioctena* Chev.

— Tibiae not dilated nor toothed near apex; upper surface entirely dark with metallic blue, green, bronze, or purple luster (figure 24); on willow, poplar, and birch................ *Phratora* Chev.

Tribe Timarchini

Genus *Timarcha* Latreille 1829:150

(Subgenus *Americanotimarcha* Jolivet 1948:4)

vandykei Jolivet 1948:6	Wash.
intricata Haldeman 1853:363	B.C.-Idaho-Calif.
violacea Jolivet 1948:7	
adusta Jolivet 1948:7	
viridis Jolivet 1948:7	
s. *intertexta* Haldeman 1853:364	Oreg.
yvettae Jolivet 1948:7	
cerdo Stal 1863:8	Wash.-Oreg.
intenta Jolivet 1948:8	
nigra Jolivet 1948:6	
aenea Jolivet 1948:8	
s. *leechi* Jolivet 1948:8	Oreg.

Key to the North American species of *Timarcha* Latr. (Translated from Jolivet 1948:5)

1\. Upper surface of body smooth, not wrinkled, feebly punctuate; bronze; 7–9 mm. long; Wash. (figures 1, 2) .... *vandykei* Jolivet

— Upper surface of body strongly alutaceous...... 2

2\. Size large, 7–11 mm. long; color generally black; California to British Columbia.... *intricata* Hald.

— Size small, 5–8 mm. long; color reddish or coppery brown, shining in general; Calif.-B.C... *cerdo* Stal

Tribe Doryphorini

Zygogrammini

Genus *Zygogramma* Chevrolat 1837:422
Zygospila Achard 1923:53

exclamationis (Fabricius) 1798:86	Dak.-Utah-Ariz.-Tex.
conjuncta (Rogers) 1856:34	Minn.-Kans.-Mont.-Ariz.
s. *pallida* (Bland) 1864:71	
? *stolata* (Suffrian) 1858:271	
amoena: (Sturm) 1843:288	
continua (Leconte) 1868:57	Ariz.-Utah-Tex.
fasciatipennis Jacoby 1891:249	
suturalis (Fabricius) 1775:95	Me.-N.C.-Colo.-Canada
pulcra (Fabricius) 1792:313	
s. *casta* (Rogers) 1856:33	Mich.-Nebr.-N.Dak.
? *festiva* (Fabricius) 1775:100	
pulchra: (Coquebert) 1804:123	
disrupta (Rogers) 1856:34	Kans.-Ariz.-Tex.
heterothecae Linell 1896:197	Tex.-Colo.-Ariz.
tortuosa (Rogers) 1856:32	Tex.-Ariz.
malvae (Stal) 1859:322	Tex.-Ariz.-Mex.
signifera: (Sturm) 1843:288	
opifera (Stal) 1860:460	Tex.-Ariz.-Mex.
piceicollis (Stal) 1859:322	Tex.-Ariz.
aggregata (Stal) 1860:461	
signatipennis (Stal) 1859:321	Ariz.-Mex.
arizonica Schaeffer 1906:240	Ariz.
estriata Schaeffer 1919:322	Ariz.

Key to the North American species of
Zygogramma Chev.

(Modified from Linell 1896:196)

1. Pronotum brown with anterior angles pale or entirely pale 2

— Pronotum unicolorous, brown, or aeneous......5

2. Fourth discal vitta absent, vittae wide and regular; subsutural and sutural vittae confluent (figure 72); 6.3–7.3 mm. long; Ariz...........*continua* (Lec.)

— Fourth discal vitta present though not extending much beyond the middle....................3

3. Sutural and subsutural vittae dark, reaching apex (figure 89); larger, 7 mm. long; Kans.-Mont.-Ariz......................*exclamationis* (Fab.)

— Sutural and subsutural vittae pale, becoming obsolete behind the middle; smaller, 6 mm. long; Kans.-Mont.-Ariz...............................4

4. Vittae entire (figure 90).....................
.................*conjuncta conjuncta* (Rogers)

— Vittae broken into spots (figure 86)...........
.....................*conjuncta pallida* (Bland)

5. Elytral vittae sinuous, interrupted, or irregular...7

— Elytral vittae regular, more or less entire.......6

6. Each elytron with a single broad vitta on the disc (figure 73); N.H.-N.C.-Colo.................
....................*suturalis suturalis* (Fab.)

— Each elytron with two narrow vittae on the disc (figure 74); Mich.-Nebr. *suturalis casta* (Rogers)

7. Subsutural vittae free, narrow................8

— Subsutural and sutural vittae confluent, at least in apical third 9

8. Second vitta twice interrupted, fourth represented by a spot only (figure 88); 4–6 mm. long; Tex.-Colo.; on *Heterotheca scabra*..*heterothecae* Linell

— Second vitta not interrupted; fourth short, confluent at base with third (figure 91); 5–7 mm. long; Kans.-Ariz. .... *disrupta* (Rogers)

9\. Epipleura of elytra pale 10

— Epipleura of elytra dark 12

10\. Each elytron with a very sinuous stripe; Tex.-Ariz. 11

— Elytra with numerous spots, not forming stripes (figure 77); body and dark markings reddish brown; 6 mm. long; Ariz. .... *estriata* Schaef.

11\. Rusty red-brown; epipleura margined with brown; subsutural stripe free for at least half the length; 6 mm. long; Tex.-Ariz. (figure 78) .... *tortuosa* (Rogers)

— Dark brassy or golden green; elytral epipleura entirely pale; sutural stripe trifid at base; 6 mm. long; Tex.-Ariz. (may not be distinct from *tortuosa*) .... *malvae* (Stal)

12\. Lateral margin of elytra dark in posterior half .. 14

— Lateral margin pale in posterior half, epipleura may be dark 13

13\. Elytra with an elongate spot on lateral margin behind middle; discal stripe very sinuous, margins regular (figure 75); 6.3–6.8 mm. long; Ariz..... .... *opifera* (Stal)

— Lateral margin of elytra without spots; discal stripe more or less straight, margins of stripe very irregular (figure 76); 5.7–6.5 mm. long; Ariz. .... *arizonica* Schaef.

14\. Head and pronotum greenish black; humeral stripe confluent with sutural stripe at middle (figure 80); body elongate oval, moderately convex; 2.5–7.3 mm. long; Ariz.-Mex........ *signatipennis* (Stal)

— Head and pronotum brown, may be slightly bronzed 15

15\. Humeral and sutural stripes not confluent (figure 79); body elongate oval, moderately convex; 6.5 mm. long; Tex.-Ariz.-Mex...... *piccicollis* (Stal)

— Humeral and sutural vittae confluent at middle (figure 5); body oval, more strongly convex; 6.2–6.8 mm. long; Ariz. (figures 3, 4, 98) .... *opifera* (Stal)

Genus *Calligrapha* Chevrolat 1837:422

Subgenus *Graphicallo* Monros 1955:57

lunata (Fabricius) 1787:69	Me.-Mass.-Colo.
brunnea (Thunberg) 1787:43	
mediorupta (Achard) 1923:69	
medionota Schaeffer 1933:478	
bowditchi (Achard) 1923:69	
s. *hybrida* (Say) 1824:449	Mo.-Colo.-Manit.-Alta.
lativittata (Achard) 1923:69	
lativittis Schaeffer 1933:478	

Subgenus *Bidensomela* Monros 1955:54

bidenticola Brown 1945:122	N.B.-Fla.-Colo.-Tex.
similis (Rogers) 1856:35	
intermedia (Achard) 1923:69	
hilaris (Achard) 1923:69	
s. *meridionalis* (Monros) 1955:54	Fla.

Subgenus *Calligramma* Monros 1955:56

cephalanthi Schwarz 1878:366	Fla.
cephalanti: Monros 1955:56	

Subgenus *Acalligrapha* Monros 1955:55

praecelsis (Rogers) 1856:35	Ohio-Nebr.-Kans.

Subgenus *Coreopsomela* Monros 1955:55

californica Linell 1896:198	Calif.-B.C.
s. *coreopsivora* Brown 1945:122	Me.-Dak.
elegans (Olivier) 1808:532	

Subgenus *Calligrapha* Chevrolat 1837:422

Polyspila Hope 1840:165
Metallographa Motschulsky 1860:198
Boliographa Motschulsky 1860:198

incisa (Rogers) 1856:34	Kans.-Manit.-Ill.
verrucosa (Suffrian) 1858:266	Mo.-Manit.-B.C.
multipunctata (Say) 1824:451	Conn.-Ga.-Alta.-Wash.
v. *bigsbyana* (Kirby) 1837:212	N.S.-Ga.-B.C.-Oreg.
v. *suturella* Schaeffer 1933:478	N.H.
philadelphica (Linnaeus) 1758:372	N.B.-Ga.-Nebr.-B.C.
decipiens (Weber) 1801:52	
ruficornis (Olivier) 1791:703	
vicina Schaeffer 1933:476	N.Y.
alni Schaeffer 1928:290	N.S.-W.Va.-Mich.
confinis (Kirby) 1837:211	
alnicola Brown 1945:124	Que.-Ont.

apicalis Notman 1919:139	Que.-N.Y.-Mich.
spiraeae (Say) 1826:297	Me.-Pa.-Mich.
rowena Knab 1909:85	Que.-Ga.-Mich.
knabi Brown 1940:166	Que.
rhoda Knab 1909:83	N.H.-Md.-Wis.-Kans.
v. *walshiana* Blatch. 1910:1157	Ind.-Mo.
amelia Knab 1909:86	N.J.-Va.-Ohio
confluens Schaef. 1928:290	N.S.-Mass.
dolosa Brown 1945:126	Ont.
ostryae Brown 1945:126	Ont.-N.Y.-Mich.
ignota Brown 1945:127	N.S.-Minn.-Tenn.
pruni Brown 1945:127	Ont.-Ohio
scalaris (Leconte) 1824:173	Que.-Ga.-Tex.
multiguttis Stal 1865:261	
floridana Schaeffer 1933:476	Fla.
virginea Brown 1945:130	Que.-Ont.
tiliae Brown 1945:130	Ont.
amator Brown 1945:132	Ont.
pnirsa (Stal) 1860:462	Que.-Minn.-N.C.-Ind.
labyrinthica: Horn 1884:128	
dislocata (Rogers) 1856:32	Tex.-Calif.-Mex.
sigmoidea (Leconte) 1859:285	Nebr.-Utah-Calif.
serpentina (Rogers) 1856:32	Tex.-Ariz.-Mex.
mexicana (Stal) 1859:323	
multiguttata (Stal) 1859:326	Kans.-Ariz.-Mex.
sylvia (Stal) 1860:462	Ariz.-Mex.
fulvipes (Stal) 1859:323	Tex.-Mex.
wickhami Bowditch 1911:325	Tex.

Key to the North American species of *Calligrapha* Chev. (Modified from Monros 1955, Brown 1945, and Linell 1896)

1\. Elytra with longitudinal dark stripes, without numerous spots 2

— Elytra pale with numerous small dark spots (figure 12); spots may rarely form irregular stripes but these forms also have separate spots; spots may also coalesce, in which case the elytra are black with pale spots; aedeagus with lateral apical spines and without apical truncate projection (figure 94) (subgenus *Calligrapha*) 10

2\. Elytra with a scutellar row of punctures 3

— Elytra without a scutellar row of punctures; pronotum entirely brown, each elytron with a sutural and two regular brown stripes (figures 38, 94); Florida; on *Cephalanthus* . . . . . . (subgenus *Calligramma* Monros) . . . . *cephalanthi* (Schwarz)

3\. Pronotum entirely dark; apex of aedeagus with small lateral spines 4

— Pronotum with pale lateral and apical margins; apex of aedeagus without small lateral spines 7

4\. Length 7–9 mm.; elytral epipleura at least partly pale; lateral margin of discal stripe not notched; color of the stripes usually reddish brown; aedeagus with small spines on apical projection . . . (subgenus *Graphicallo* Monros) 5

— Length 4–6.5 mm.; elytral epipleura dark; lateral margin of discal dark stripe with a notch near the middle (figure 13); stripes usually dark brown; apical spines on aedeagus itself . . . . (subgenus *Bidensomela* Monros) 6

5\. Discal brown stripe of elytra with a single yellow longitudinal stripe immediately outside 4th row of punctures; punctures between rows 4 and 9 completely irregular; Me.-Mass.-Colo.; on *Rosa* (figure 95) . . . . *lunata lunata* (Fab.)

— Discal brown pattern consisting of three more or less longitudinal stripes separated by pale ones (figure 36); punctures between rows 4 and 9 tending to be arranged in rows; Mo.-Colo.-Manit.-Alta. on *Rosa* . . . . *lunata hybrida* (Say)

6\. Discal elytral dark stripe entire, not divided by a longitudinal stripe 7

— Discal elytral dark stripe divided by a pale longitudinal stripe in the space between the 4th and 5th rows of puntcures; Fla. . . . . *bidenticola meridionalis* (Monros)

7\. Apex of aedeagus with a small, truncate, apical lobe (figure 96); sutural dark stripe not distinctly widened at apex; N.B.-Ala.-Colo.-Tex; on *Bidens, Coreopsis, Ambrosia* . . . . *bidenticola bidenticola* Brown

— Apex of aedeagus broadly, evenly rounded, without an apical lobe (figure 99); sutural dark stripe abruptly, distinctly widened near apex of elytra (figure 40); Kans.-Ill.-Manit. . . . . *incisa* (Rogers)

8\. Basal margin of pronotum dark; with a small tooth between the claws; elytra more convex than the protonum; elytra yellowish white with suture and a broad discal stripe brown (figures 37, 92) . . (subgenus *Acalligrapha* Monros) . . *praecelsis* (Rogers)

— Basal margin of pronotum usually pale (figure 35); without a tooth between the claws; elytral convexity follows that of pronotum.........(subgenus *Coreopsomela* Monros) 9

9. Dark discal stripe of elytra entire or weakly notched (figure 35); 5–6.5 mm. long; Atlantic to Pacific; on *Coreopsis, Bidens, Ambrosia*......... ....*californica coreopsivora* Brown

— Dark discal stripe of elytra divided by an oblique pale transverse band (figure 93); Calif.-B.C...... ....*californica californica* Linell

10. Pronotum at least partly pale................11

— Pronotum entirely dark.....................17

11. Subsutural stripe of elytra confluent with sutural one 12

— Subsutural stripe of elytra free from sutural one 13

12. Dark markings of elytra black with metallic green or bronze luster..........................15

— Dark markings of elytra and pronotum reddish brown, same color as legs (figure 43); 7.5 mm. long; Tex....................*wickhami* Bowd.

13. Sutural and subsutural stripes pale reddish brown, much lighter in color than other elytral markings (figure 41); 8–9 mm. long; Mo.-Manit.-B.C.-Oreg.; on willow (*Salix*)......*verrucosa* (Suff.)

— Subsutural and usually sutural stripes as dark as other elytral marking......................14

14. Dark markings of pronotum reddish brown, without green luster (figure 42); 6.5–8 mm. long; Conn.-Ga.-Alta.-Wash.; on willow (*Salix*)...... ....*multipunctata multipunctata* (Say)

— Dark markings of pronotum with distinct green luster; 6.5–8 mm. long; N.S.-Ga.-Oreg.; on willow (*Salix*) and aspen (*Populus*)................ ....*multipunctata bigsbyana* (Kirby)

15. Anterior margin of pronotum pale; elytra without midlateral spot; 7.5 mm. long; N.H.; on willow (*Salix*).........*multipunctata suturella* Schaef.

— Anterior margin of pronotum dark; pale pronotal areas limited to sides and apical angles; elytra with a mid lateral spot........................16

16. On Alder (*Alnus*); 7.5–9.5 mm. long; Que.-N.Y.-Mich. (figure 45)..............*apicalis* Notm.

— On hawthorn (*Crataegus*); 9–9.3 mm. long; Ont. ....*dolosa* Brown

17. Legs black or dark metallic.................18

— Legs red 22

18. Elytral epipleura black or dark metallic.......20

— Elytral epipleura pale.....................19

19. Subsutural stripe confluent with sutural stripe (figure 68); 8.5–10 mm. long; Nebr.-Alta.-B.C.-Calif.; on mallow (*Malva*) and hollyhock (*Althaea*) ....*sigmoidea* (Lec.)

— Subsutural stripe free from sutural one (figure 39); 9 mm. long; Tex.-Ariz.-Mex............. ....*dislocata* (Rogers)

20. Humeral lunule confluent with arcuate band and the spot enclosed by lunule (figure 65)........21

— Humeral lunule not confluent with arcuate band or the spot enclosed by lunule; color pattern as in *scalaris* group (figure 71); 8.5 mm. long;? Ariz.-Mex. ....*sylvia* (Stal)

21. Large, 7.5–9 mm. long; color pattern basically as in *scalaris* group but with most spots confluent (figure 69); Que.-Minn.-N.C.-Ind.; on basswood (*Tilia*) ....*pnirsa* (Stal)

— Small, 6.5 mm. long; color pattern very irregular, variable (figure 44); Kans.-Ariz.-Mex.......... ....*multiguttata* (Stal)

22. Elytral epipleura black or dark metallic.......23

— Elytral epipleura pale or reddish brown.......25

23. Arcuate band free from subsutural stripe, may be greatly reduced to one or two small spots (figure 65); found in the arid southwest............24

— Arcuate band confluent with sutural and subsutural stripes (figure 62); 7.8–9 mm. long; N.S.-Pa.; on birch (*Betula*)...........*ignota* Brown

24. Arcuate band entire, joined to lunule anteriorly and to lateral spots posteriorly, forming a long sinuous stripe (figure 70); 10–12 mm. long; Ariz.-N.Mex.-Mex. ....*serpentina* (Rogers)

— Arcuate band interrupted, absent or reduced to small spots (figure 46); 7–9 mm. long; Tex.-Mex. .... *fulvipes* (Stal)

25. Elytral epipleura, in large part, as pale as the palest areas on elytra......................26

— Elytral epipleura reddish brown, distinctly darker than the palest areas of elytra...............27

26. Subsutural elytral stripe free from the sutural one (figure 65) (*philadelphica* group)............30

— Subsutural elytral stripe confluent with the sutural one (figure 59) (*scalaris* group)............31

27. Subsutural stripe free from the sutural one (figure 65) 28

— Sutural and subsutural stripes confluent (figure 60) 29

28\. Much of the pale elytral area darkened, reddish brown; 7–8.5 mm. long; on alder (*Alnus*) (figure 49) ....*alni* Schaef.

— Pale areas of elytra without or with very little reddish brown color; 7.5–8.5 mm. long; Que.-Ont.; on alder (*Alnus*) (figure 143)....*alnicola* Brown

29\. On nine-bark (*Physocarpus*); 6.2–7 mm. long: Conn.-Pa.-Mich. (figure 50).....*spiraeae* (Say)

— On hop-hornbeam (*Ostrya*); 6.6–9.5 mm. long; Ont.-N.Y.-Mich. (figure 60).....*ostryae* Brown

30\. On dogwood (*Cornus*); 7–9 mm. long; N.B.-Ga.-Nebr.-B.C. (figure 47).......*philadelphica* (L.)

— On dogwood (*Cornus*); 8 mm. long; N.Y. (figure 48)........................*vicina* Schaef.

— On alder (*Alnus*); 7–8.5 mm. long; N.S.-N.J.-Mich. (figure 49)..................*alni* Schaef.

— On alder (*Alnus*); 7.5–8.5 mm. long; Que.-Ont. (figure 12)....................*alnicola* Brown

— On alder (*Alnus*); 6.5–9 mm. long; N.Y.-Va.-Ohio (figure 54).................*amelia* Knab

31\. Food plant elm, *Ulmus americana* L.; body and elytral markings blue-green; subsutural spot of the apical declivity of each elytron nearly always joined to the sutural stripe; the latter, except rarely, strongly and abruptly narrowed immediately before the apex; posterior portion of the arcuate band seldom strongly angulate on its hind margin (figures 56, 59); 7.4–9.3 mm. long; Que.-Ga.-Tex. ....*scalaris* (Lec.)

— Food plant basswood, *Tilia americana* L.; body and elytral markings blue-green; subsutural spot of the apical declivity seldom joined to the sutural stripe, the latter always gradually narrowed before the apex; posterior portion of the arcuate band nearly always strongly angulate on its hind margin (figures 58, 61); 8.6–10 mm. long; Que.-Ont.. *virginea* Brown

— Food plant basswood, *Tilia americana* L.; body and elytral markings green; subsutural spot of the apical declivity usually joined to the sutural stripe, the latter always gradually narrowed before the apex; posterior portion of the arcuate band usually strongly angulate on its hind margin (figure 67) 8–9.2 mm. long; Ont..............*tiliae* Brown

— Food plant basswood, *Tilia americana* L.; body and elytral markings blue-green; subsutural spot of the apical declivity usually free but frequently joined to the sutural stripe, the latter usually gradually, sometimes abruptly, narrowed before the apex; posterior portion of the arcuate band variable, sometimes strongly angled on its hind margin (figure 64); 6.7–9.2 mm. long; Ont.. *amator* Brown

— Food plant cherry, *Prunus americana* Marsh.; body and elytral markings green, bluish reflections usually feeble or lacking; posterior markings of the elytra extremely variable (figure 63); body slightly less elongate and averaging much smaller than in any of the other species; 6–7.7 mm. long; Ont.-Ohio ....*pruni* Brown

— Florida; on (?) star anise (*Illicium*); 7–8.2 mm. long (figure 66).............*floridana* Schaef.

— On alder (*Alnus*); 8 mm. long; N.Y. (figure 48) .... *vicina* Schaef.

— On alder (*Alnus*); 7–8 mm. long; N.S.-Mass. (figure 55)..................*confluens* Schaef.

— On hawthorn (*Crataegus*); 9–9.3 mm. long; Ont. (figure 57) .... *dolosa* Brown

— On nine-bark (*Physocarpus*); 6.2–7 mm. long; Conn.-Pa.-Mich. (figure 50)......*spiraeae* (Say)

— On dogwood (*Cornus*); 6.5–8.5 mm. long; Que.-Ga.-Mich. (figure 51)...........*rowena* Knab

— On dogwood (*Cornus*); 6.3-8 mm. long; Que. (figure 52) ....*knabi* Brown

— On hazel (*Corylus*); 7–8 mm. long; N.H.-Wis.-Kans. (figure 53)................*rhoda* Knab

— Host unknown; 7–8 mm. long;.................................... *rhoda* v. *walshiana* Blatch.

Genus *Leptinotarsa* Stal 1858:475

Polygramma Chevrolat 1837:421

Mycoryna Stal 1858:475

collinsi, new species	Ariz.
dahlbomi (Stal) 1859:317	Tex.-Mex.
haldemani (Rogers) 1856:30	Tex.-Mex.
libatrix (Suffrian) 1858:248	Ariz.-Guat.
violascens (Stal) 1859:317	
violacea: (Sturm) 1843:287	
behrensi (Harold) 1877:16	Calif.-Mex.
modesta Jacoby 1883:229	
puncticollis Jacoby 1883:228	
rubiginosa (Rogers) 1856:30	Tex.-Ariz.-Mex.
lineolata (Stal) 1863:159	Tex.-Ariz.-Mex.
peninsularis (Horn) 1894:407	Ariz.-Mex.

juncta (Germar) 1824:590	Pa.-Ohio-La.-Fla.
s. *texana* (Schaeffer) 1906:239	Tex.-Ariz.
tumamoca Tower 1918:68	
defecta: Linell 1896:196	
defecta (Stal) 1859:317	Tex.
decemlineata (Say) 1824:453	N. Amer., Europe
albida Tower 1918:64	
melanicum Tower 1918:63	
minuta Tower 1918:64	
pallida Tower 1918:62	
rubrivittata Tower 1918:63	
tortuosa Tower 1918:64	
s. *multitaeniata* (Stal) 1859:317	Tex.-Mex.
intermedia Tower 1903:7	
obscura Tower 1918:50	
melanothorax (Stal) 1859:317	
tacubayaenis Tower 1918:48	
variabilis Tower 1918:52	
multilineata (Stal) 1859:316	
undecimlineata (Stal) 1859:316	Mex.-?Calif.

Key to the North American species of *Leptinotarsa* Stal

1\. Elytra unicolorous 2
— Elytra with stripes or spots 5
2\. Elytra red or yellowish brown; antennae, palpi, legs, and scutellum black; Tex.-Ariz.-Mex. .... *rubiginosa* (Rogers)
— Elytra dark green, blue or black 3
3\. Dark coppery green; very large, 13–16 mm. long; Calif.-Mex. .... *behrensi* (Harold)
— Black; elytra dark blue or green 4
4\. Head and pronotum dull black; form less convex; Tex.-Mex. .... *haldemani* (Rogers)
— Head and pronotum dark metallic green; form more convex; Ariz.-Mex. .... *libatrix* (Suff.)
5\. Pronotum without markings 6
— Pronotum with distinct markings; on *Solanum* spp. 10
6\. Dark markings of elytra consist of unbroken stripes; the humeral stripe may be very short but there are no separate spots 8
— At least some of the elytral stripes broken; small dark spots also present on elytra 7
7\. Each elytron with four longitudinal stripes, all of which are broken just before the middle; 7–7.7 mm. long; Tex.-Ariz.-Mex. .... *lineolata* (Stal)
— First two elytral stripes (counting from suture) unbroken; lateral half of elytron marked with irregular spots; 6.2 mm. long; Arizona (figures 81, 87, 100) .... *collinsi*, new species
8\. Each elytron black with two narrow, pale, longitudinal stripes; Tex.-Mex. .... *dahlbomi* (Stal)
— Each elytron pale with four or more dark stripes .. 9
9\. Each elytron with suture and five complete stripes black; pronotum black; 6–13 mm. long 12
— Each elytron with suture, three complete discal stripes and a very short humeral stripe dark brown; The first discal stripe is joined to the dark sutural marking and the short humeral stripe is joined to the third discal stripe; pronotum brown (figure 6); 7 mm. long; Ariz.-Mex. .... *peninsularis* (Horn)
10\. Ventral surface of body entirely dark metallic green or black; Calif.-Mex. .... *undecimlineata* (Stal)
— Ventral surface of body at least partly pale 11
11\. Elytral markings bordered by a single, regular row of punctures 13
— Elytral markings bordered by an irregular double row of punctures 12
12\. Elytral epipleura pale; United States, Canada, and Europe .... *decemlineata decemlineata* (Say)
— Elytral epipleura usually dark; Mexico and Big Bend region of Texas (characters separating these two subspecies are variable and inconsistent) .... *decemlineata multitaeniata* (Stal)
13\. Elytral suture pale brown or yellow 14
— Suture black; Tex.-Mex. .... *defecta* (Stal)
14\. Space between elytral epipleura and 9th row of punctures black; Pa.-Fla.-La.-Ohio .... *juncta juncta* (Germar)
— Marginal interspace of elytra pale; 8–9.5 mm. long; Texas (? Arizona) *juncta texana* (Schaef.)

Leptinotarsa collinsi, new species

Figures 81, 87, 100

Oval, strongly convex; entirely dark reddish brown except for portions of elytra. Elytra very pale yellow with the following black or dark brown markings: epipleura; lateral margin between marginal bead and last row of elytral punctures; sutural and subsutural stripes complete and united; second stripe narrow but complete, free from subsutural stripe except at apical fifth, neither of these stripes reaching base of elytra; third stripe broader, starting at base in depression between humerus and disc of elytra, covering only inner portion of humerus, interrupted at basal third, continued at middle as a rather elongate, irregular spot, more or less united with second stripe. There are also six to eight small dark spots between this third stripe and the lateral and apical margins.

Eyes small, separated by a little more than two thirds the width of the head across the eyes. Vertex alutaceous, moderately, sparsely punctate; clypeal suture evenly arcuate; clypeus a little more closely punctate. Antennae short, reaching humerus. Segments 2 and 4 equal, 3 is one and one half times as long as 2. Terminal segment of maxillary palp distinctly narrower and shorter than penultimate segment, narrower at apex than at base; apex truncate.

Width of prothorax at base almost twice length at middle. Pronotum moderately convex, somewhat flattened at sides. Base strongly curved; sides nearly straight though convergent in basal third then strongly rounded to apex; apical angles produced forward, acute at apex. Surface of pronotum alutaceous; moderately, sparsely punctate at middle; coarsely, closely punctate at sides.

Elytra strongly, evenly convex; surface finely alutaceous, shining. Punctures moderate in size, regularly arranged around first two elytral stripes, irregular beyond second stripe.

Metasternum finely punctate, metasternal episternum coarsely and closely punctate. Tarsal claws moderately divaricate.

Aedeagus produced at apex into a rather long lobe with sides parallel and apex slightly wider but evenly rounded. Stylet irregularly spatulate at apex with very broad membranous margins.

Length 6.2 mm.

Holotype: ♂, Sabino Can., Arizona, VIII–5–55, D. J. and J. N. Knull (Ohio). Paratype: ♂ same date (W577).

This species is similar to *Zygospila tortuosa* (Rogers) and *Z. opifera* (Stal) in size, color, and form and was at first confused with them. However, the divergent tarsal claws and complete, wide marginal dark stripe will serve to identify it. *Calligrapha subdenticulata* Bechyné, from Costa Rica is similarly marked, but in that species the dark areas have a more distinct metallic luster and the discal dark patches are more completely joined to the subsutural stripe. Of the United States species, *L. peninsularis* Horn seems to be most closely related to this species, especially so in the form of the aedeagus. In *peninsularis* the elytral stripes are very regular and complete.

Leptinotarsa collinsi is named in honor of Dr. Donald L. Collins, New York State Entomologist.

Genus *Labidomera* Chevrolat 1837:421
Paropsimena Motschulsky 1860:186

clivicollis (Kirby) 1837:213	Me.-Fla.-Iowa
? *trimaculata* (Fabricius) 1775:95	
s. *rogersi* Leconte 1858:26	Manit.-Tex.
mimica Brown 1961:973	Tex.

Key to the species of *Labidomera* Chev.

1. Elytra orange or orange-brown except the suture, which is very narrowly dark on the apical third or two-thirds; this narrow stripe not widened at the apex; 10.4–10.8 mm. long; each anterior femur of the male with two subapical teeth; Texas .... *mimica* Brown

— Elytra yellow or orange with dark blue, purple or black spots; the rest of the body entirely dark...2

2. Each elytron with two to four large dark spots; 9–11 mm. long; eastern U.S.A.; on swamp milkweed (*Asclepias incarnata* L.), hedge bindweed (*Convolvulus sepium* var. *fraterniflorus* M. & B.) .... *clivicollis clivicollis* (Kirby)

— Dark spots reduced and fragmented so there are more than four on each elytron (figure 11).....3

3. Large, 10.4–10.8 mm. long; elytral punctures fine, Texas ....*mimica* Brown

— Smaller, 8.0–9.3 mm. long; elytral punctures moderate; Manitoba to Texas; on *Asclepias* sp....... .... *clivicollis rogersi* Lec.

Genus *Chrysolina* Motschulsky 1860:210
Chrysomela auct.

subsulcata (Mannerheim) 1853:254	Alaska
cavigera (J. Sahlberg) 1885:35	Alaska
tolli (Jacobson) 1910:54	
magniceps (J. Sahlberg) 1885:38	Alaska
caurina Brown 1962:64	Alaska
flavomarginata (Say) 1824:452	Ohio-Alta.-Ariz.
s. *vidua* (Rogers) 1856:36	Idaho-Alta.-B.C.-Oreg.
subseriata (Leconte) 1860:321	
extorris Brown 1962:65	Calif.
hudsonica Brown 1938:35	Nfld.-Que.-Manit.-N.W.T.

finitima Brown 1962:67	Alaska
basilaris (Say) 1824:451	Colo.-Yukon
montivagans (Leconte) 1878:463	
auripennis (Say) 1824:452	Ind.-Ala.-N.Mex.-Colo.-Iowa
inornata (Rogers) 1856:36	
schaefferi Brown 1962:70	Utah-Ariz.-N.Mex.
cyanea (Schaeffer) 1933:479	
subopaca (Rogers) 1856:36	N.Y.-Fla.-Tex.-Ill.
cribraria (Rogers) 1856:36	
staphylea (Linnaeus) 1758:370	Nfld.-N.S. (Eur.)
hyperici (Forster) 1771:20	B.C.-Colo.-Calif. (Eur.)
quadrigemina (Suffrian) 1851:125	B.C.-Colo.-Calif. (Eur., Australia)
geminata auct.	
gemellata auct.	
varians (Schaller) 1783:271	B.C. (Eur.)

Key to the American species of *Chrysolina* Motsch.
(Modified from Brown 1962:59–61)

1. Elytra punctate-striate; the intervals lacking coarse punctures, usually more or less convex or variably elevated into ridges; the strial punctures occasionally obsolete in specimens with elevated intervals; the elytral epipleura not paler than the disc; flightless species restricted to treeless areas of Alaska . . 2

— Elytra usually with the punctures confused or seriate in part and then lacking impressed striae and convex or ridged intervals; the elytra tending to be punctate-striate only when the epipleura, and often the lateral margins, are reddish and paler than the disc 5

2. Apical abdominal segment transversely impressed and declivous before the apex, very strongly so in males, not strongly but distinctly so in females; legs and apical half of the apical ventral segment usually reddish-yellow or reddish-brown, sometimes blackish (figure 102) . . . *cavigera* (J. Sahlb.)

— Apical abdominal segment flattened or feebly depressed at middle (♂) or unmodified (♀), with a strongly impressed marginal line but not declivous before the apex; legs and abdomen entirely blackish 3

3. Elytral intervals feebly convex and the length 5 to 5.8 mm. in the four specimens known; apex of the male genital organ very broadly rounded (figure 104) .... *caurina* Brown

— Elytra extremely variable, with some of the intervals at least moderately convex except rarely; apex of the male genital organ attenuated into a blunt point 4

4. Length 5.5 to 6.8 mm., usually about 6.2 mm.; elytral intervals 3, 5, 7, and 9 usually strongly elevated into ridges, sometimes not or only moderately elevated above the others; male genital organ feebly recurved before the apex (figure 103) .... *magniceps* (J. Sahlb.)

— Length 5.0 to 8.1 mm., usually about 7.0 mm.; elytra with the intervals similar to one another or with the alternate intervals only moderately elevated above the others; male genital organ evenly curved (figure 101) . . . . *subsulcata* (Mann.)

5. Pronotum not sulcate although usually with a feeble impression on each side at base; strongly metallic; elytra never with the epipleura or lateral margins pale; the elytral punctures not at all seriate; body broadly oval, the width 7/10 as great as the length; length 4.6–5.5 mm.; B.C.; on *Hypericum* (figure 114) . . . . *varians* (Schall.)

— Pronotum with a distinct sulcus on each side, at least basally, except in some specimens with blackish or bicolored elytra. Elytral punctures usually subseriate in part; body more elongate; the size usually greater 6

6. The coarse punctures of each elytron arranged in a subsutural row and in four pairs of irregular rows; pronotal sulci strongly impressed basally, not or scarcely impressed at middle and apically; metallic above, the elytra not paler at the margins or black; B.C.-Colo.-Calif.; on *Hypericum*. 7

— Elytral punctures rarely arranged in paired rows; pronotal sulci usually moderately or strongly impressed at middle and apically. 8

7. Length 5.3 to 6.1 mm., apical ventral segment of male not distinctly impressed (figure 112)...... .... *hyperici* (Forst.)

— Length 6.0 to 7.1 mm.; apical ventral segment of male not deeply but broadly and very distinctly impressed (figures 15, 113) . . *quadrigemina* (Suff.)

8. Pronotum with the sulci at least moderately impressed from base to apex; lateral margins of elytra not paler than the disc. 9

— Pronotum with the sulci feebly to moderately impressed basally, feebly impressed or obsolete at middle and apically. 13

9. Entirely reddish-brown; restricted to Newfoundland and Nova Scotia (figure 111) . *staphylea* (L.)

— Not reddish-brown 10

10. Pronotum slightly wider at middle than at base; Northern Yukon Territory to the high altitudes of southeastern British Columbia and Colorado (figure 108) .... *basilaris* (Say)

— Pronotum widest at base 11

11. Entirely dark blue, sometimes faintly violaceous; southwestern Utah, Ariz., and N. Mex. .... *schaefferi* Brown

— Blackish or bicolored species 12

12. Elytra green, brassy green, or coppery red, or black-brown and feebly bronzed but not concolorous with the darker pronotum; underside and legs usually very dark blue; pronotal sulci not deeper basally; Ind.-Iowa,-Ala.-N.Mex.; the blackish form restricted to south-central Texas (figure 109) .... *auripennis* (Say)

— The entire insect black or black-brown; elytra and pronotum very feebly bronzed, concolorous; pronotal sulci at least slightly deeper near the base: Pa.-Fla.-Ill.-Tex. (?N.Y.) (figure 110) .... *subopaca* (Rogers)

13. Length 4.2–6.2 mm.; bronze-green or bronze above; elytra with the epipleura and usually, the lateral margins dull red or reddish-yellow; arctic and subarctic species 14

— Length 5.8 to 7.4 mm.; black or blue-black, very rarely feebly bronzed above; elytra sometimes with pale margins; occurring from central Alberta southward 15

14. Elytra with the coarse punctures confused in part; first segment of each anterior tarsus longer than wide; elytra lacking convex intervals; transcontinental at and near the northern limit of trees; on *Achillea* and *Tanacetum* (and ? willow) .... *hudsonica* Brown

— Elytra with the coarse punctures arranged in well-defined, regular series; first segment of each anterior tarsus not longer than wide (♂) or with the elytral intervals feebly to moderately convex (♀); arctic Alaska (figure 107) .... *finitima* Brown

15. Elytra lacking conspicuous pale margins; entirely blackish, or with the epipleura more or less obscurely rufescent and then sometimes with each lateral interval pale or rufescent in part; Alberta, B.C.-Idaho-Oregon; on *Artemisia* and *Aster*.... .... *flavomarginata vidua* (Rogers)

— Elytra with the epipleura and lateral margins pale reddish-yellow; this pale band covering at least each lateral interval, often extended onto or beyond the next interval 16

16. Male genital organ abruptly narrowed before the apex (figure 106); San Bernardino Co., California .... *extorris* Brown

— Male genital organ less abruptly narrowed apically (figure 105); southern Alberta to Iowa, N. Mexico, and Arizona; on *Artemisia* .... *flavomarginata flavomarginata* (Say)

Tribe Chrysomelini

Genus *Chrysomela* Linnaeus 1758:368

Gymnota Gistl 1837:403
Strickerus Lucas 1920:413

Subgenus *Chrysomela* s. str.

Lina Dejean 1837:402
Melasoma Stephens 1831:349

crotchi group: Brown 1956:21

crotchi Brown 1956:24	N.S.-Va.-Alaska-N.Mex.
tremulae: auct. Amer.	
saliceti: auct. Amer.	
invicta Brown 1956:25	Alta.-Mont.

Subgenus *Microdera* Stephens 1834:351

Macrolina Motschulsky 1860:198

interrupta group: Brown 1956:22

interrupta Fabricius 1801:438	Pa.-Fla.
mainensis Bechyné 1954:670	Nfld.-N.J.-Alta.
alnicola Brown 1956:27	
s. *interna* Brown 1956:29	Alaska-Oreg.
s. *littorea* Brown 1956:31	Alaska-B.C.
walshi Brown 1956:32	Que.-Ont.
knabi Brown 1956:34	N.H.-N.C.-Alta.-N.Mex.
s. *hesperia* Brown 1961:974	Alta.
falsa Brown 1956:36	Nfld.-Lab.-B.C.-Alaska
quadriguttata (Schaeffer) 1928:43	
aeneicollis (Schaeffer) 1928:43	Alta.-Colo.-B.C.-Calif.
quadriguttoides Beller & Hatch 1932:98	

scripta group: Brown 1956:22

scripta Fabricius 1801:438	Mass.-Fla.-B.C.-Mex.
laurentia Brown 1956:42	Me.-N.W.T.-Mich.
confluens Rogers 1856:37	Utah-Wash.-Calif.
maculicollis (Schaeffer) 1928:44	
semota Brown 1956:45	Mont.-N.W.T.
lineatopunctata (Forster) 1771:22	Que.-N.J.-N.W.T.-Idaho
novaboracensis (Gmelin) 1790:1689	
obsoleta (Say) 1824:453	
scriptoides (Schaeffer) 1928:44	
texana (Schaeffer) 1919:331	Tex.

schaefferi group, new group

schaefferi Brown 1956:50	Manit.-Alaska-Calif.
immaculata (Schaeffer) 1919:330	

blaisdelli group, new group

braisdelli (VanDyke) 1938:48	Alaska-N.W.T.
engelhardti (Hatch) 1939:49	Alaska-N.W.T.

Key to the North American species of *Chrysomela* L.
(Modified from Brown 1956:21–23.)

1. Elytra immaculate, pale brown or brownish yellow; pronotum with the sides not or scarcely paler than the disc; tibiae unicolorous; usually larger, the males 7.0–8.0 mm. long, females 7.2–9.7 mm.; apex of aedeagus neither attenuate nor evenly rounded, angulate on each side (*Chrysomela s. str.,* = *crotchi* group) 2

— Elytra maculate or entirely dark; or with the pronotal sides broadly pale and the disc dark; or with the tibiae distinctly bicolored; or with the body smaller; apex of aedeagus somewhat attenuate or broadly rounded, lacking lateral angles (subgenus *Microdera*) 3

2. Except for the elytra, darker; usually blackish with strong green reflections and rufescent areas; the pronotum often rufescent laterally or throughout but rarely strongly so; body beneath usually reddish or rufescent in part; abdomen and legs nearly always largely or entirely dark; elytral

apices of the female distinctly produced, more strongly acute than in the male; apex of aedeagus produced on each side into a blunt tooth (figure 152); northern Virginia and Nova Scotia to Idaho and Alaska; New Mexico........*crotchi* Brown

— Except for the elytra, paler; brownish-red, often with greenish reflections in certain lights, the metasternum and legs sometimes slightly darker in part; elytral apices of the female not or scarcely produced, usually more strongly acute than in the male; apex of aedeagus not produced on the sides (figure 151); southwestern Alberta and northwestern Montana ....*invicta* Brown

3. Elytra without traces of striae except for the stria that limits the external ridge of each; the punctures not arranged in series except near the suture....4

— Elytra distinctly substriate; occasionally with the punctures confused as in the other species and with the intervals subequal; usually with the discal punctures subseriate in part and with the third, fifth, and seventh intervals largely impunctate and more convex; elytra entirely black or dark brown; Alaska and North West Territories (*blaisdelli* group) 18

4. Elytra entirely pale, or entirely blackish and somewhat bronzed; never with bluish reflections; less than 6.5 mm. long; lateral ridge of each elytron feebly delimited; western (*schaefferi* group)..... ....*schaefferi* Brown

— Elytra with the standard pattern of dark spots, or entirely dark blue or blue-green or dark and with the lateral margin or some discal spots pale (rarely obscurely pale in *lineatopunctata*); lateral ridge of each elytron strongly delimited...............5

5. Each elytron, when pale and maculate, with a basic pattern of seven dark spots of which two are median (figures 115–137); these spots never elongate, often joined together and to the suture to produce an irregular transverse band; the elytra sometimes largely dark due to fusion of the spots, the pale areas then reduced to small spots and, nearly always, very irregular transverse lines; the elytra very rarely entirely pale, sometimes with only the two median spots on each, usually with the spots more or less fused, never entirely dark; the pale ground of the elytra sometimes yellowish but always red in breeding individuals; apex of aedeagus somewhat attenuate and rather narrowly rounded (figure 150) (*interrupta* group). This group consists of eight sibling species and subspecies, which cannot be keyed. The following couplets give their food plants and distributions. When two or more species occur in one locality, they breed on different hosts and are sometimes separable by color.....6

— Each elytron, when pale and maculate, with a basic pattern of seven dark spots of which three are median (figures 138–148); these median spots always elongate, never joined to produce a transverse band; the elytra, when largely dark, with pale areas reduced to longitudinal streaks; the elytra sometimes entirely pale (*schaefferi*), rarely with the median and posterior spots lacking in part, sometimes with the spots more or less fused, sometimes entirely blackish or bluish; the pale ground of the elytra is pale yellow in pinned specimens, often silvery in breeding individuals; apex of aedeagus broadly and evenly rounded (figure 149) (*scripta* group) 13

6. Breeding on *Alnus*; the adults of *mainensis* very rarely on *Salix* in early spring................7

— Breeding on *Salix* or *Populus*................10

7. Occurring east of the Rocky Mountains........8

— Occurring in the Rocky Mountains and westward 9

8. Occurring from southeastern Pennsylvania to Florida; larger; each elytron with the basal spots usually joined, the median spots often joined and nearly always attaining the suture (figures 115–117), the posterior markings nearly always fused into a blotch which always attains the suture; underside and legs largely dark; on alder (*Alnus serrulata*) .... *interrupta* Fab.

— Occurring from northern New Jersey, Newfoundland, and the interior of Labrador to Alberta and Great Slave Lake; smaller; each elytron usually with seven discrete spots and with the suture entirely pale (figures 118–119); underside and legs largely or entirely pale except in some specimens from Labrador.......*mainensis mainensis* Bech.

9. Occurring on the coasts of British Columbia and southernmost Alaska; darker (figures 122–123); frequently with the pronotal sides largely or entirely dark and with the elytra entirely dark; the underside and legs largely dark................ ....*mainensis littorea* Brown

— Occurring in inland regions; Oregon to south-central Alaska; paler above (figures 120–121) and sometimes beneath ......*mainensis interna* Brown

10. Restricted to *Populus balsamifera;* occurring in eastern and southernmost Ontario and in south-

western Quebec; very variable but intermediate in color and size between *m. mainensis* and *knabi* (figures 124–127) . . . . *walshi* Brown

— Sometimes occurring on, but not restricted to, *Populus* 11

11. Breeding on both *Populus* and *Salix;* northern, occurring from Newfoundland and Labrador to British Columbia and Alaksa; extremely variable in color (figures 132–134) . . . . *falsa* Brown

— Breeding only on *Salix;* adults of *knabi* frequently on *Populus* in the spring 12

12. Occurring in the mountains of southern Alberta and southern British Columbia to southwestern Colorado and Tulare Co., California; smaller; pronotum entirely dark or virtually so; the dark areas of the elytra usually covering more than half of the disc (figures 135–137) . . . . . *aeneicollis* (Schaeff.)

— Occurring from southernmost Ontario, southernmost New Hampshire, and western North Carolina to southern Alberta and New Mexico; larger; the pronotal sides broadly pale, the dark areas of the elytra less extensive (figures 128–131) . . . . *knabi* Brown

13. Body elongate, the width from 50 to 55 percent as great as the length; the standard elytral pattern of dark spots well defined except rarely in *laurentia*; the three median spots of each elytron very elongate, the intermediate of these usually from six to seven times as long as wide (figures 138–142) . . 14

— Body usually less elongate, the width at least 53 percent as great as the length; elytra largely or entirely dark, or with the median spots shorter and with the intermediate of these very rarely more than five times as long as wide (figures 145–147) 15

14. Usually larger; the elytral spots usually relatively smaller, discrete or virtually so (figures 138–139); on *Salix* and *Populus*; southern New England, southernmost Ontario, and the southern parts of the Prairie Provinces and British Columbia to southernmost United States and Mexico . . . . *scripta* Fab.

— Usually smaller and with the dark areas of the elytra more extensive; the elytral spots sometimes more or less confluent (figures 140–142); more northern; south-central Quebec and central New England to eastern Ontario, Lake Superior and Great Slave Lake . . . . *laurentia* Brown

15. Head, pronotum, underside, and legs entirely reddish-yellow or virtually so; central and southern Texas (figure 147) . . . . *texana* (Schaeff.)

— Head, pronotum, underside, and legs dark or bicolored except in some specimens of the more northern *lineatopunctata* 16

16. Body more convex and less elongate, the width from 57 to 59 percent as great as the length; extremely variable in color (figures 145–146) . . . . *lineatopunctata* Forst.

— Body slightly less convex and slightly more elongate; the width 54 to 58 percent as great as the length; western species 17

17. Elytra virtually dichromatic; either entirely deep blue or blue-green, or pale and maculate with the standard pattern (figure 143), the intermediate condition very rare; the spots usually bluish, sometimes black, rarely confluent; more southern, western Washington to central Utah and central California . . . . *confluens* Rogers

— Elytra always maculate with the standard pattern (figure 144): the markings always blackish, virtually always discrete; more northern, northwestern Montana, southeastern British Columbia, and northward . . . . *semota* Brown

18. Pronotum bicolored, the sides broadly red . . . . *blaisdelli* (Van Dyke)

— Pronotum entirely black . . . . . . *engelhardti* (Hatch)

Genus *Phaedon* Latreille 1829:151

***Emmetrus* Motschulsky 1860:221**

***Orthosticha* Motschulsky 1860:196**

prasinella (Leconte) 1861:358	Wash.-Calif.
punctatus Hatch 1928:46	
vandykei Hatch 1928:61	
purpurea (Linell) 1898:482	Utah-Ariz.
purpurescens Hatch 1928:61	
oviformis (Leconte) 1861:357	N.Eng.-Alaska
?*vancouverensis* Hatch 1928:62	
viridis (Melsheimer) 1847:175	Que.-Fla.-N.Mex.
aeruginosus Suffrian 1858:395	
microreticulatus Hatch 1928:46	

dietrichi Hatch 1928:46	
?*oklahomensis* Hatch 1931:103	
americanus Schaeffer 1929:287	Eastern U.S.A.
armoraciae auct. Amer.	
niger Hatch 1928:47	Wash.
planus Hatch 1931:104	
carri Hatch 1928:46	Que.-Alta.
cochleariae auct. Amer.	
uniformis Fall 1929:150	Mass.-Ga.-Miss.-Ohio
cyanescens Stal 1860:470	Colo.-Ariz.-Mex.
huachucae Hatch 1928:62	

Key to the North American species of *Phaedon* Latr. (Fall 1929:148–149)

1. Second elytral interval without a subbasal series of widely spaced larger punctures.............2
— Second elytral interval with a widely spaced subbasal series of larger punctures...............6
2. Head and pronotum finely alutaceous or microreticulate; tarsal claws smaller than elsewhere in the genus 3
— Head and pronotum not perceptibly alutaceous, usually visibly but very finely punctulate between the larger punctures 4
3. Head coarsely punctate, punctures distinctly larger than those of the median parts of the pronotum; ventral segments coarsely punctate; size larger, about 3.5 mm. long; Que.-Fla.-N.Mex.......... .... *viridis* (Melsh.)
— Head more finely and sparsely punctate, punctures not or but very slightly coarser than those of the pronotum, which are nearly uniform in size from side to side; ventral segments more sparsely and very finely punctate; size usually less than 3 mm. long; Mass.-Ga. .... *uniformis* Fall
4. Form oblong oval 5
— Form distinctly rotundate, deep purple or violaceous varying to greenish; ventral surface very finely punctate; Ariz............. *cyanescens* Stal
5. Interstitial punctures of elytra sparse and very minute; color purpureo-violaceous, the pronotum usually green; ventral surface coarsely punctured; size large, over 4 mm. long; Utah-Ariz.......... .... *purpurea* (Linell)
— Interstitial punctures of elytra always strong and distinct, may be nearly as large as those of the striae; smaller, usually less than 3.5 mm. long; Wash.-Calif. (figure 20)........ *prasinella* (Lec.)
6. Elytra not perceptibly transversely subrugulose..7
— Elytral intervals transversely subrugulose in varying degree, as a rule more distinctly so toward the sides; New England-Alaska.... *oviformis* (Lec.)
7. Clypeal suture nearly equally impressed throughout; antennae entirely black; humeral callus stronger, ventral surface distinctly microreticulate, the last segment commonly entirely pale; eastern U.S. .... *americanus* Schaef.
— Clypeal suture feeble at middle, more strongly impressed at sides; basal two segments of antennae more or less pale beneath; humeral callus less strong; ventral surface not or scarcely visibly microreticulate; the last ventral segment black usually with a narrow pale apical border; Que.-Alta.-N.Y. .... *carri* Hatch

Genus *Gastrophysa* Chevrolat 1837:405

Gastroeidea Hope 1840:164

Gastroidea Gemminger & Harold 1874:3403

cyanea Melsheimer 1847:175	Conn.-N.Dak.-Calif.-Tex.
s. caesia (Rogers) 1856:38	Calif.
dissimilis (Say) 1824:450	Mo.-Kans.-Utah
formosa (Say) 1824:451	Kans.-Mont.-Ariz.
polygoni (Linnaeus) 1758:370	Eur.-Sib., N.S.-N.Y.-Sask.-Mo.
caerulipennis (Say) 1826:297	

Key to the species of *Gastrophysa* Chev.

1. Entirely metallic, prothorax not testaceous or orange 2
— Legs and prothorax reddish orange; elytra metallic blue; 4–4.5 mm. long; eastern U.S.A. and Canada; on *Polygonum aviculare*.......... *polygoni* (L.)
2. Suture purple, rest of elytra green with golden or coppery luster; 4–4.5 mm. long; Kansas-Montana-Arizona; on *Rumex venosus* (figure 19)........ .... *formosa* (Say)
— Elytra uniformly green, blue or purple.........3
3. Elytra with a submarginal carina; head sulcate; body larger, 5.5–6.2 mm. long; Kansas-Missouri-Utah; on *Polygonum* sp. (? *punctatum*)........ .... *dissimilis* (Say)
— Elytra not distinctly carinate; head flat; size smaller, 4–5.3 mm. long; on *Rumex* spp........4

4. Moderately convex, sides not usually parallel; eastern U.S.A. . . . . *cyanea cyanea* Melsh.
— Strongly convex, sides parallel; California . . . . *cyanea caesia* (Rogers)

Genus *Plagiodera* Chevrolat 1837:404

Linamorpha Motschulsky 1860:197
Plagiosterna Motschulsky 1860:190
Plagiomorpha Motschulsky 1860:197
Melasomida Schaeffer 1920:117
Pseudolina Schaeffer 1919:331

arizonae (Crotch) 1874:53	Tex.-Ariz.-Colo.-Utah
californica (Rogers) 1856:37	Calif.
thymaloides Stal 1860:468	Tex.-Mex.
versicolora (Laicharting) 1781:148	Eur., Me.-N.J.-Ohio
armoraciae (Fabricius) 1787:103	

Key to the species of *Plagiodera* Chev.

1. Elytra uniformly dark metallic blue, green or purple 2
— Elytra brown without metallic luster, lateral and apical margins paler, testaceous; 4.25 mm. long; Texas-Mexico . . . . *thymaloides* Stal
2. Prothorax and legs black with metallic blue, green or purple luster 3
— Prothorax and legs pale, orange or testaceous; 4.7 mm. long; southwestern U.S.A. (figure 21) . . . . *arizonae* (Crotch)
3. Punctures of pronotum coarse, about as large as those on elytra; color of elytra dark green with very faint bronze luster; 4.2–5.2 mm. long; California; on willow (*Salix* sp.) . . . . *californica* (Rogers)
— Pronotal punctures fine, distinctly smaller than those on the elytra; color of elytra dark blue or purple; 3.3–4.5 mm. long; eastern U.S.A.; on willow (*Salix* sp.) . . . . *versicolora* (Laich.)

Tribe Phratorini

Genus *Phratora* Chevrolat 1837:429
Phyllodecta Kirby 1837:216

interstitialis Mannerheim 1853:259	B.C.-Alaska
aklaviki (Carr) 1932:192	
purpurea Brown 1951:124	N.S.-Mass.-B.C.-Yukon
americana: (Schaeffer) in part	
?*vitellinae*: Blatch. 1910:1161	
s. *novae-terrae* Brown 1951:125	Nfld.
kenaiensis Brown 1952:339	Alaska
californica Brown 1961:976	Calif.
americana (Schaeffer) 1928:46	Me.-Ga.-Ohio
pallipes (Schaeffer) 1928:47	
vitellinae: auct. Amer.	
vulgatissima: auct. Amer.	
s. *canadensis* Brown 1951:126	N.B.-N.H.
hudsonia Brown 1951:128	Que.-Manit.-Alaska
frosti Brown 1951:129	N.S.
americana: (Schaeffer) in part	
s. *remissa* Brown 1951:129	Labr.-Alaska-Colo.

Key to the North American species of *Phratora* Chev.
(Modified from Brown 1951:122)

1. Anterior margins of antennal segments four to six with a fringe of long hairs in males and some females; males with first segments of all tarsi equally dilated 2

— Antennal segments four to six lacking long hairs, except near their apices in both sexes, males with first segment of each hind tarsus two-thirds as wide as the third segment and first segment of each front and middle tarsus three-fourths as wide as third segment 6

2. Lateral declivities of elytra very irregularly punctate, usually with striae not or scarcely traceable; blue-green, blue, or green above; male with first segment of each tarsus nearly equal in width to third segment; female with a fringe of long hairs on the anterior margins of antennal segments four to six; B.C. and northward (figure 162) .... *interstitialis* (Mann.)

— Lateral declivities of the elytra less irregularly punctate, the striae usually defined; males with first segment of each tarsus about three-fourths as wide as the third segment; females lacking, or virtually lacking, long hairs except apically on antennal segments four to six 3

3. Purple or coppery above, internal sac of male copulatory organ lacking large teeth; on *Populus* and *Salix* 4

— Color above variable; internal sac with two large, spiniform, heavily sclerotized teeth; on *Salix*; eastern 5

4. Usually deep purple above, sometimes bright purple, rarely coppery and then usually with purple reflections; Mass.-B.C.-Yukon (figure 161)..... .... *purpurea purpurea* Brown

— Coppery above, the reddish reflections always evident, sometimes with purple reflections that rarely are strong; Newfoundland .... *purpurea novae-terrae* Brown

5. Deep purple above or dark blue or blue-green and then usually with purple reflections; tibiae normally dark, their extreme apices usually obscurely pale; New England-Ohio-Georgia (figure 160) .... *americana americana* (Schaef.)

— Dark blue, blue-green, green, bronze or coppery above; sometimes reddish above but then lacking the deep purple color or reflections usual in *americana americana*; tibiae sometimes dark, sometimes partly or entirely reddish-yellow; color of both dorsum and tibiae varying individually and geographically; northern New England-Nova Scotia-Ontario .... *americana canadensis* Brown

6. Black or greenish above, lacking coppery or bluish reflections; on *Betula papyrifera*; Hudson Bay-Manitoba-Alaska .... *hudsonia* Brown

— Blue or greenish-blue above; on *Salix*; Nova Scotia (figure 159) .... *frosti frosti* Brown

— Coppery above, the reddish reflections strong and sometimes tending to purple; rarely blue above; on *Salix* and perhaps *Populus tremuloides*.......... .... *frosti remissa* Brown

Tribe Entomoscelini

Genus *Entomoscelis* Chevrolat 1837:426

americana Brown 1942:172	Minn.-Wash.-Alaska
adonidis auct. Amer.	

Genus *Microtheca* Stal 1860:464

ochroloma Stal 1860:464	Ala.-La., S. Amer.

Tribe Prasocurini

Genus *Prasocuris* Latreille 1802:224

phellandrii (Linnaeus) 1758:376	Eur.-Sib., Que.-B.C.-Colo.-Ohio

Genus *Hydrothassa* Thomson 1866:279

boreela Schaeffer 1928:289	N.Y.-Alta.
ovalis (Blatchley) 1910:1151	Ind.-Mich.
vittata (Olivier) 1808:595	Me.-Pa.-Alta.
trivittata (Say) 1826:289	
varipes (Leconte) 1866:9	
obliquata (Leconte) 1866:9	N.Y.-Ind.

Key to the North American species of *Hydrothassa* Thoms.

(Modified from Schaeffer 1928)

1\. Row of punctures on the pale, last elytral interval entire from base to apex; black lateral vitta on each elytron not reaching the base, discal and marginal pale vittae united at base....................2

— Row of punctures on last elytral interval obliterated at or slightly behind middle; black lateral stripe on each elytron reaching the base; subsutural and marginal pale stripes not united at base.........3

2\. All elytral intervals impunctuate; form narrower and relatively more elongate; size smaller, 3–4 mm. long; eastern U.S. and Canada; larva on flowers of *Ranunculus acris* L.....*vittata* (Oliv.)

— Some of the elytral intervals more or less distinctly punctate; form broader, size larger, 4.5–4.75 mm. long; N.Y.-Ind..............*obliquata* (Crotch)

3\. Elytral epipleura with a single row of punctures close to the internal margin and occasionally a few scattered punctures near the base; sides of prothorax nearly parallel or slightly convergent from about apical third to base; form more elongate oval; 3.5–4 mm. long; N.Y.-Alta. (figure 28).... .... *boreela* Schaef.

— Elytral epipleura with confused double rows of punctures; prothorax wider, sides distinctly divergent from about apical third to base; form more regularly oval; 3.5–4 mm. long; Mich.-Ind....... .... *ovalis* (Blatch.)

Tribe Gonioctenini

Genus *Gonioctena* Chevrolat 1837:427

Phytodecta Kirby 1837:213

nivosa (Suffrian) 1851:222	Eur.
affinis (Gyllenhal) 1808:257	
s. *arctica* (Mannerheim) 1852:3	Alaska-Manit.-Siberia
s. *alberta* Brown 1952:340	Alta.-Mont.
notmani (Schaeffer) 1924:140	N.Y.-N.W.T.
americana (Schaeffer) 1924:139	N.Y.-Alta.
arctica: Bechyné 1948:118	
guttifer Bechyné 1948:128	
occidentalis (Brown) 1942:104	B.C.-Alta.-Yukon

Key to the North American species of *Gonioctena* Chev.

(Modified from Brown 1942:100)

1. Tenth antennal segment distinctly longer than wide; antennae attaining posterior coxae in male and middle of metasternum in female; males with first segment of each front and middle tarsus a little wider than the third segment; elytra often distinctly alutaceous and rather dull; the striae terminating on the humeral umbone more or less irregular at middle; on willow; arctic and mountainous regions of the west (figure 155) .... ***nivosa*** **(Suff.)**

— Tenth antennal segment not longer than wide; antennae similar in the sexes, not extending beyond middle coxae; tarsi never with the first segments wider than third; elytra polished, never alutaceous; sublateral striae normally regular ***2***

2. Pronotum and elytra immaculate or with small black spots, spots of pronotum not extending onto anterior half of disc (figure 29); individuals with maculate elytra have clypeus black; aedeagus attenuate apically, with a feeble notch at apex (figure 158); N.Y.-Que.-Alta.; on willow .... ***notmani*** **(Schaef.)**

— Pronotum and elytra rarely immaculate (*americana*), pronotal spots usually extending onto the anterior half of disc; clypeus always pale **3**

3. Aedeagus short, apex truncate and bilobed (figure 156); from Atlantic to Pacific; on the aspen poplar .... ***americana*** **(Schaef.)**

— Aedeagus attenuate apically, apex deeply cleft (figure 157); on willow; Alta.-B.C. .... ***occidentalis*** **Brown**

Selected References

Achard, Julien. 1923. Étude sur le genre *Zygogramma* Chevr. (Col. Chrysomelidae). Fragments entomologiques, 4:51–64; 5:65.

Arnett, Ross H., Jr. 1960. The Beetles of the United States. Catholic University of America Press, Washington, D.C., 1112 pages.

Bechyné, Jan. 1952. Nachtrage zu den Katalogen von Blackwelder und Junk-Schenkling der neotropischen echten Chrysomeliden. Ent. Arb. Mus. Frey 3:1–62.

Brown, W. J. 1945. Food-plants and distribution of species of *Calligrapha* in Canada with descriptions of new species. Canadian Ent. 77:117–133.

——— 1942. The American species of *Phytodecta* Kby. Canadian Ent. 74:99–105.

——— 1951. The American species of *Phratora* Chev. Canadian Ent. 83:121–130.

——— 1956. The New World species of *Chrysomela* L. Canadian Ent. 88 (Suppl. 3):1–54.

——— 1962. The American species of *Chrysolina* Mots. Canadian Ent. 94:58–74.

Crowson, R. A. 1955. The natural classification of the families of Coleoptera. Nathaniel Lloyd & Co., London, 189 pages.

Fall, H. C. 1929. On the genus *Phaedon*. Pan-Pacific Ent. 5:145–152.

Jacoby, Martin. 1882–1883. Biologia Centrali-Americana, Coleoptera 6(1): 182–262.

Jolivet, Pierre. 1948. Contribution a l'étude des *Americanotimarcha* new subgenus (Col. Chrysomelidae). Bull. Mus. Roy. Hist. Nat. Belgique 24 (54):1–2.

Linell, Martin L. 1896. A short review of the Chrysomelas of North America. J. New York Ent. Soc. 4:195–200.

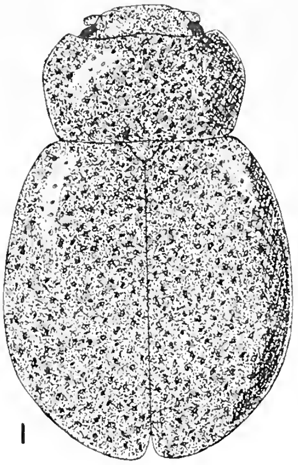
Monros, F. 1954. Notes and synonyms in Chrysomelidae. Proc. Ent. Soc. Washington 56:23–26.

——— **& Jan Bechyné.** 1956. Über einige verkannte Chrysomeliden-Namen. Ent. Arb. Mus. Frey 7:1118–1137.

Tower, William L. 1906. An investigation of evolution in Chrysomelid beetles of the genus *Leptinotarsa*. Carnegie Inst. Washington, Publ. 48, p. 1–320.

——— 1918. The mechanism of evolution in *Leptinotarsa*. Carnegie Inst. Washington, Publ. 263, p. 1–384.

Weise, J. 1916. Coleopterorum Catalogus, pars 68 (Chrysomelinae), p. 1–255.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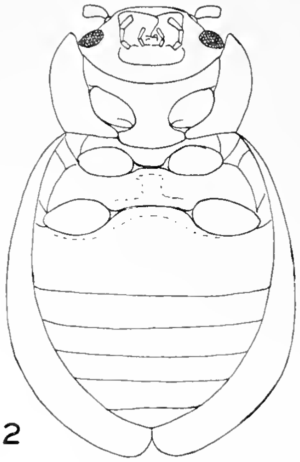
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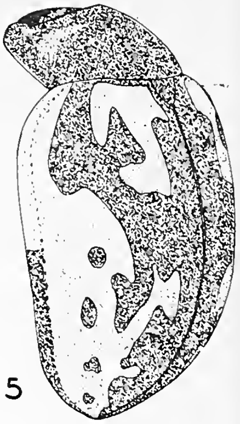
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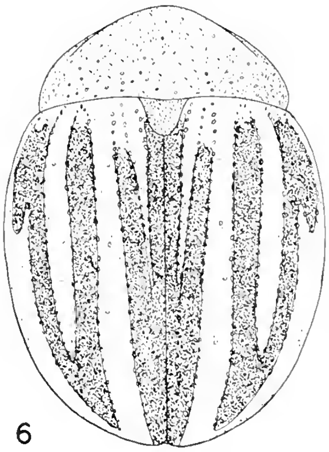
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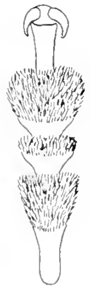
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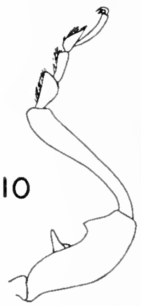
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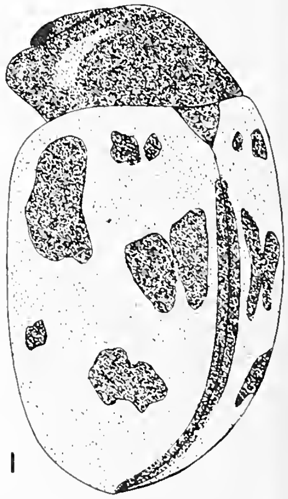
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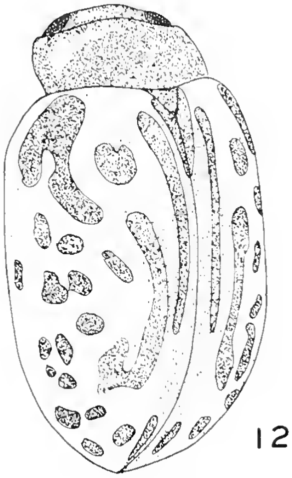
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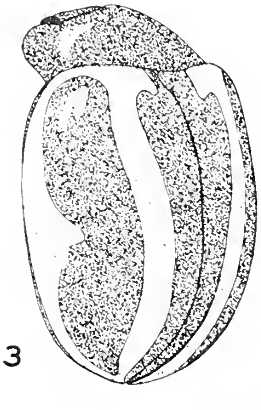
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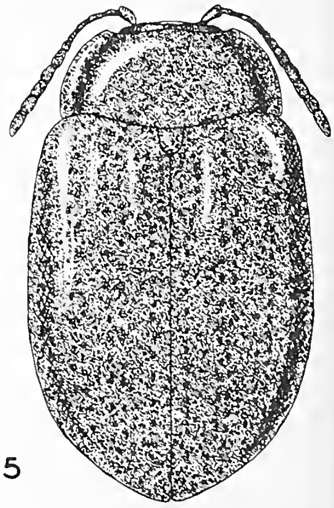
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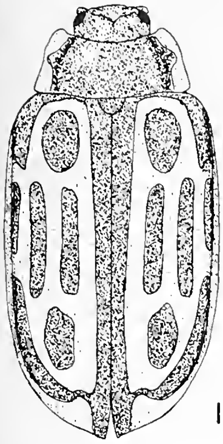
Legend for plate 1

1. *Timarcha vandykei* (?), dorsal view.
2. *Timarcha vandykei* (?), ventral view.
3. *Zygogramma opifera*, palp.
4. *Zygogramma opifera*, claws.
5. *Zygogramma opifera*, dorso-lateral view.
6. *Leptinotarsa peninsularis*, dorsal view.
7. *Leptinotarsa peninsularis*, ventral view of posterior tarsus.
8. *Chrysomela crotchi*, ventral view of posterior tarsus.
9. *Labidomera clivicollis*, claws.
10. *Labidomera clivicollis*, front leg of male.
11. *Labidomera clivicollis rogersi*, dorso-lateral view.
12. *Calligrapha alnicola*, dorso-lateral view.
13. *Calligrapha* (*Bidensomela*) *bidenticola*, dorso-lateral view.
14. *Chrysolina quadrigemina*, palp.
15. *Chrysolina quadrigemina*, dorsal view.



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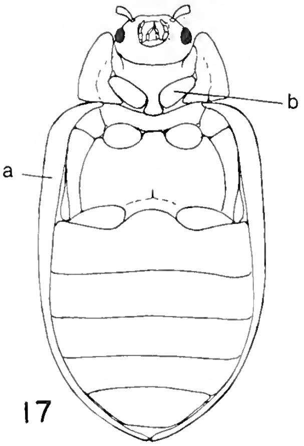

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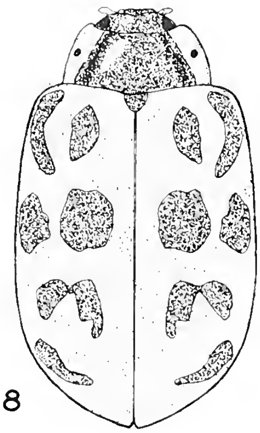

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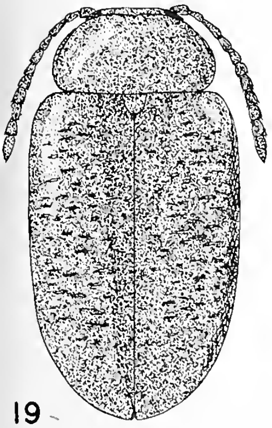

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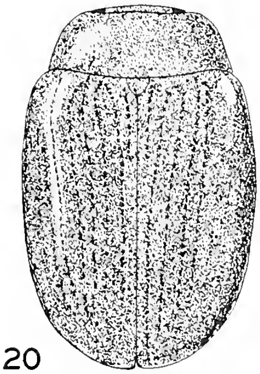

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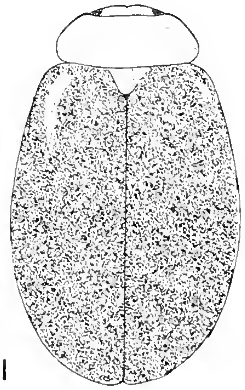

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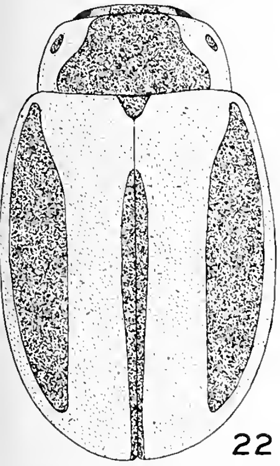

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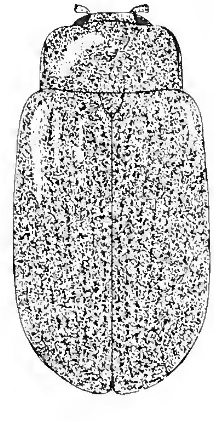

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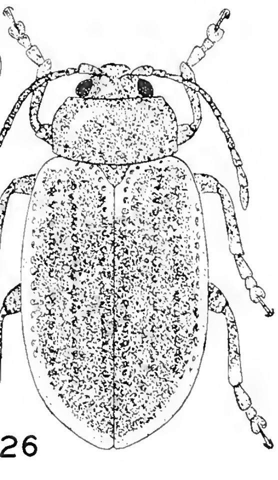

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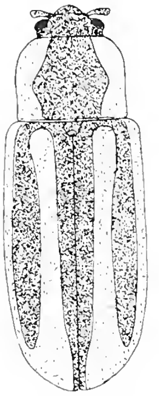
Legend for plate 2

16. *Chrysomela laurentia.*
17. *Chrysomela mainensis,* ventral view; a. epipleuron; b. front coxal cavity.
18. *Chrysomela mainensis.*
19. *Gastrophysa formosa.*
20. *Phaedon prasinella.*
21. *Plagiomorpha arizonae.*
22. *Entomoscelis americana.*
23. *Phratora purpurea,* claws.
24. *Phratora purpurea.*
25. *Microtheca ochroloma,* claws.
26. *Microtheca ochroloma.*



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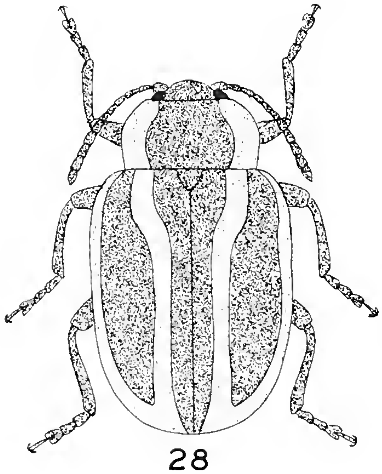

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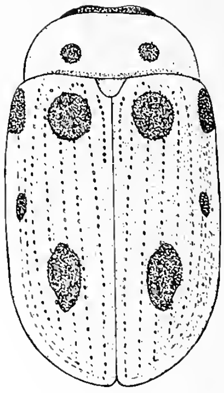

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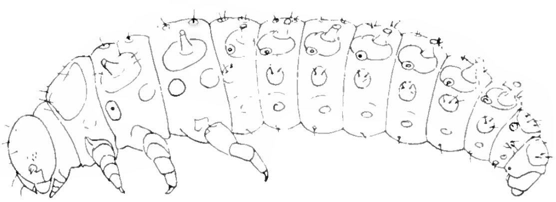

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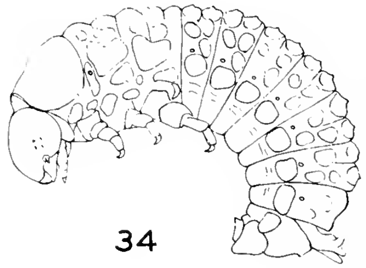

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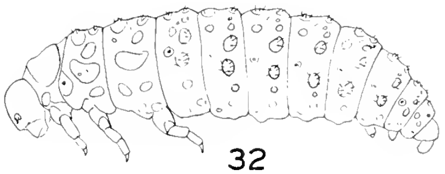

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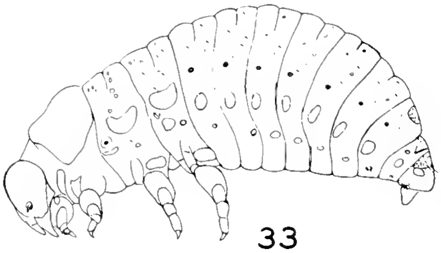

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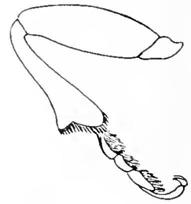

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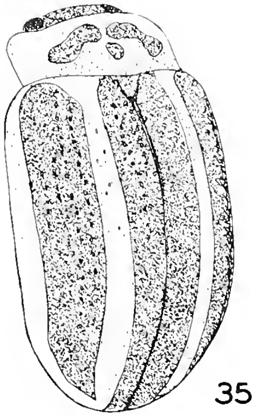

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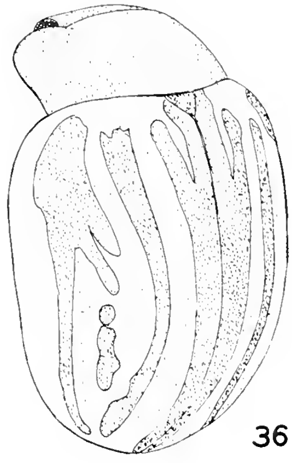

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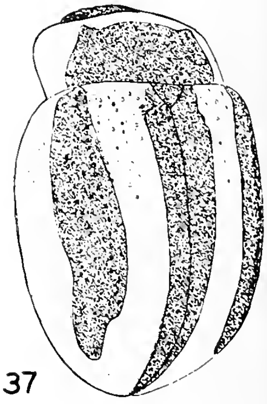

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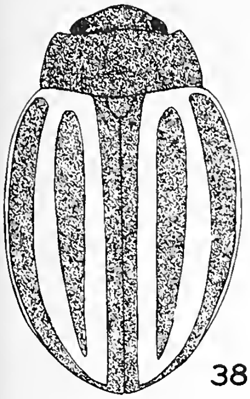
Legend for plate 3

27. *Prasocuris phellandrii.*
28. *Hydrothassa boreela.*
29. *Gonioctena notmani.*
30. *Gonioctena notmani,* middle leg.
31. *Phratora americana,* larva.
32. *Microtheca ochroloma,* larva.
33. *Calligrapha* (*Coreopsimela*) *californica coreopsivora,* larva.
34. *Gonioctena americana,* larva.
35. *Calligrapha* (*Coreopsimela*) *californica coreopsivora.*
36. *Calligrapha* (*Graphicallo*) *lunata hybrida.*
37. *Calligrapha* (*Acalligrapha*) *praecelsis.*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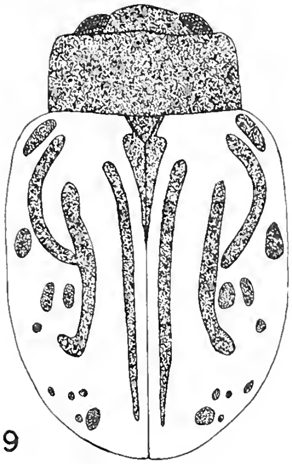
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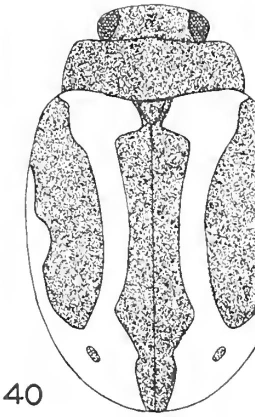
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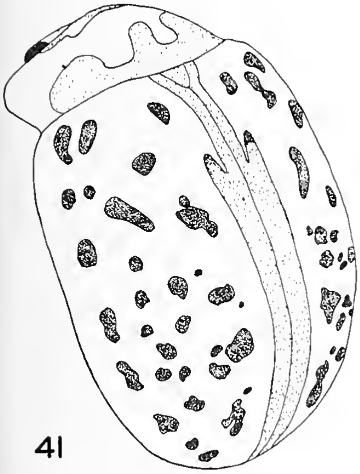
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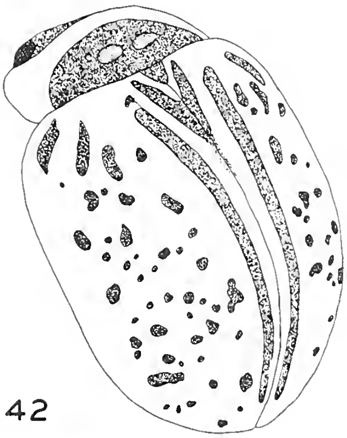
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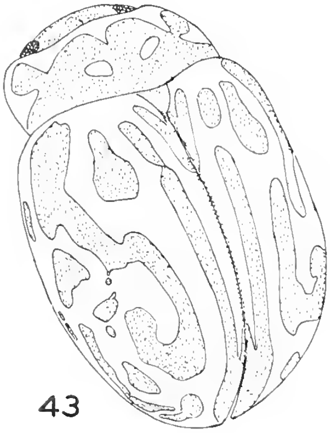
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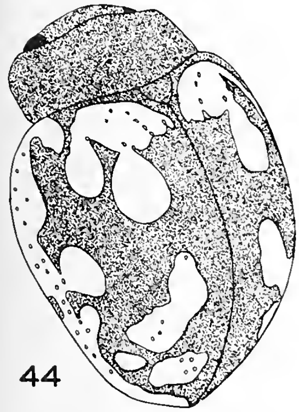
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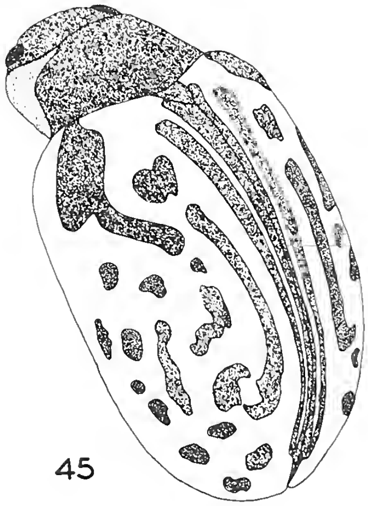
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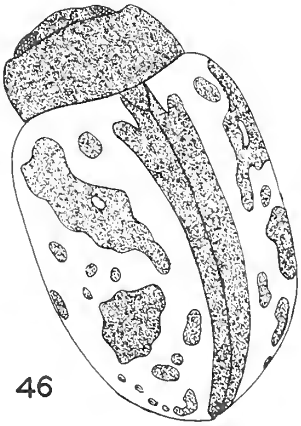
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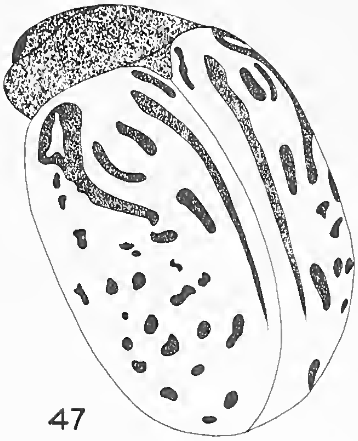
Legend for plate 4

38. *Calligrapha cephalanthi* Schwarz, redrawn from Monros 1955.
39. *Calligrapha dislocata* (Rogers), redrawn from Rogers 1856.
40. *Calligrapha incisa* (Rogers), redrawn from Rogers 1856.
41. *Calligrapha verrucosa* (Suff.)
42. *Calligrapha multipunctata* (Say)
43. *Calligrapha wickhami* Bowd.
44. *Calligrapha multiguttata* (Stal)
45. *Calligrapha apicalis* Notm.
46. *Calligrapha fulvipes*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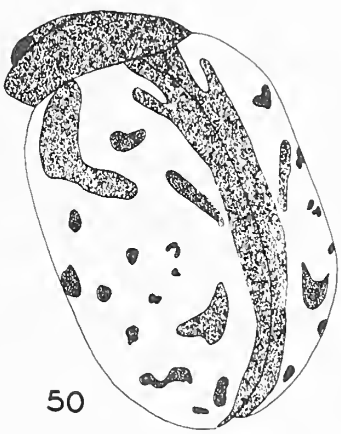
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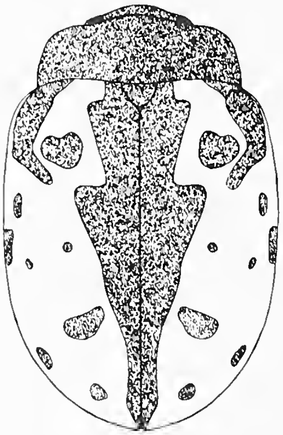
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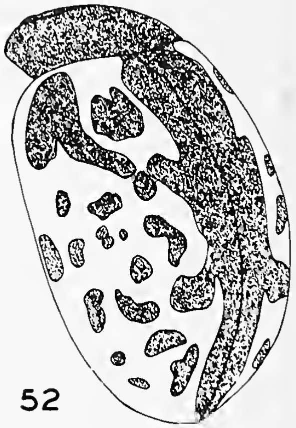
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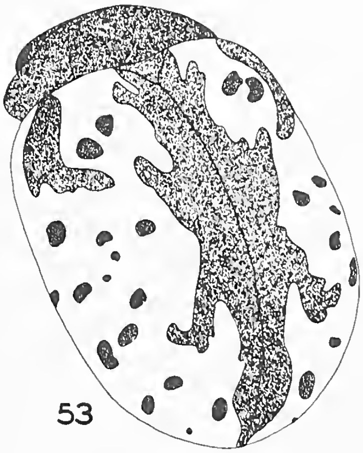
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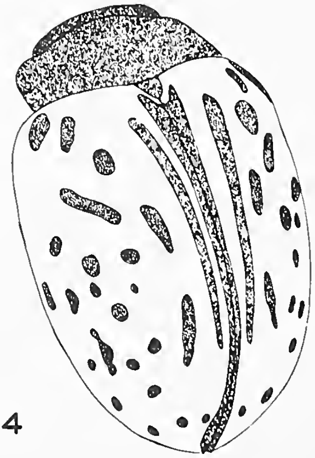
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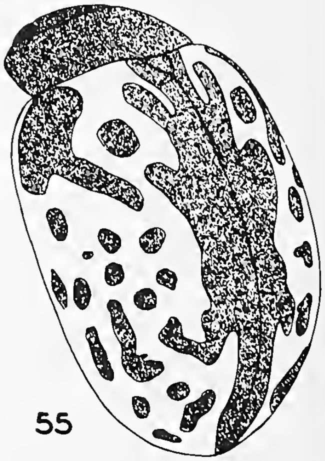
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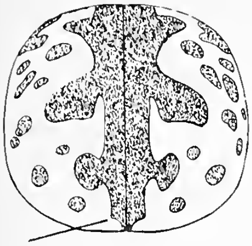
Legend for plate 5

47. *Calligrapha philadelphica* (L.)
48. *Calligrapha vicina* Schaef.
49. *Calligrapha alni* Schaef.
50. *Calligrapha spiraeae* (Say)
51. *Calligrapha rowena* Knab
52. *Calligrapha knabi* Brown
53. *Calligrapha rhoda* Knab
54. *Calligrapha amelia* Knab
55. *Calligrapha confluens* Schaef.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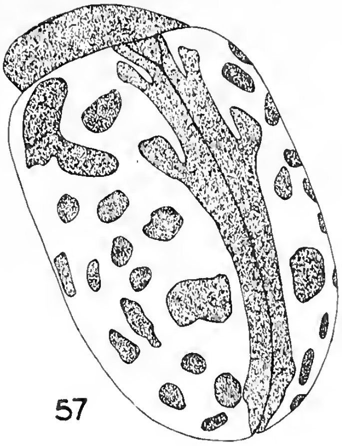
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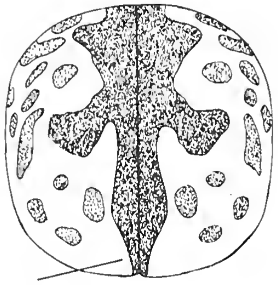
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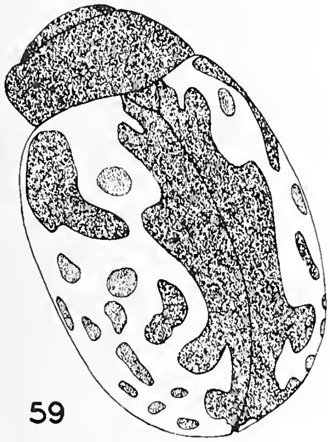
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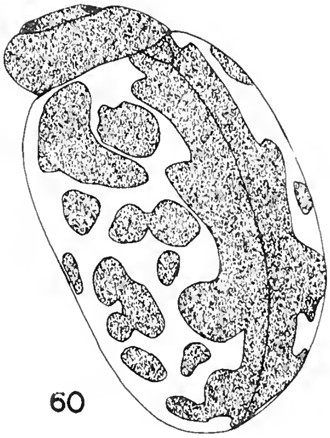
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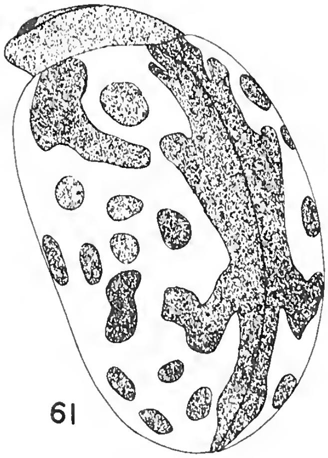
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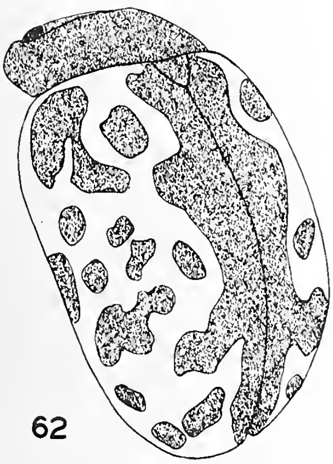
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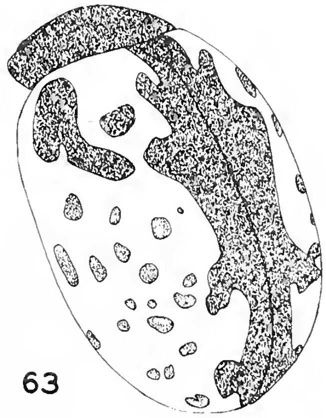
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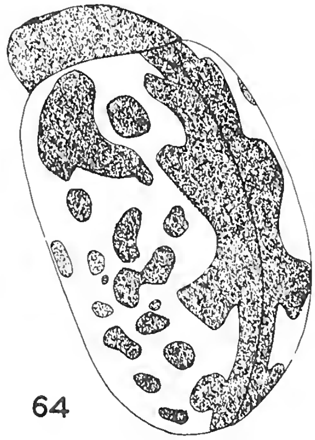
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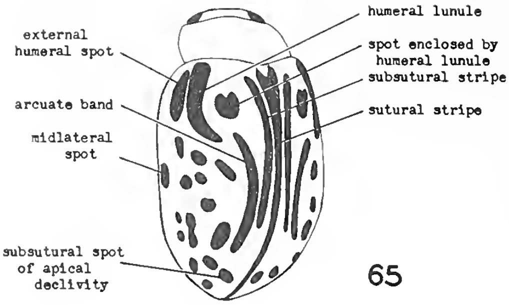
Legend for plate 6

56. *Calligrapha scalaris* (Lec.), caudal view.
57. *Calligrapha dolosa* Brown
58. *Calligrapha virginea* Brown, caudal view.
59. *Calligrapha scalaris* (Lec.)
60. *Calligrapha ostryae* Brown
61. *Calligrapha virginea* Brown
62. *Calligrapha ignota* Brown
63. *Calligrapha pruni* Brown
64. *Calligrapha amator* Brown



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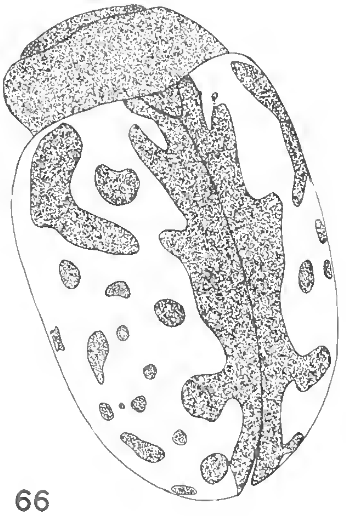

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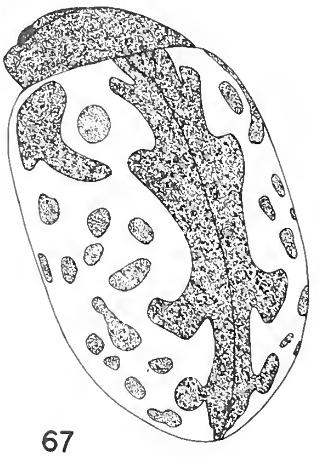

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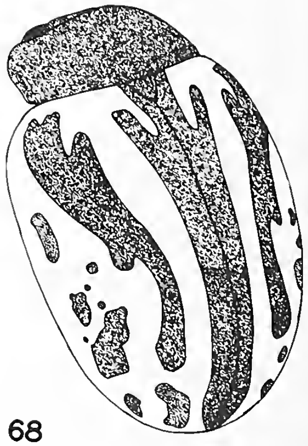

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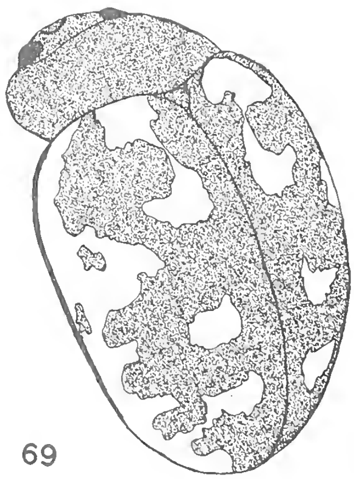

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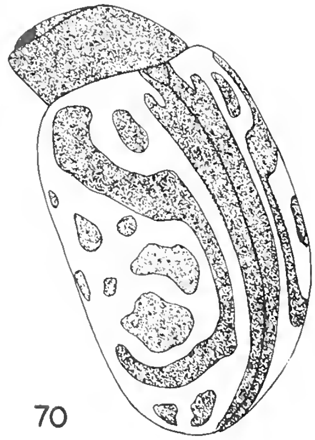

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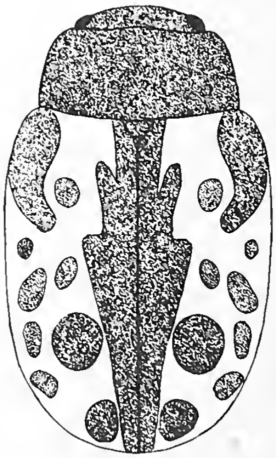

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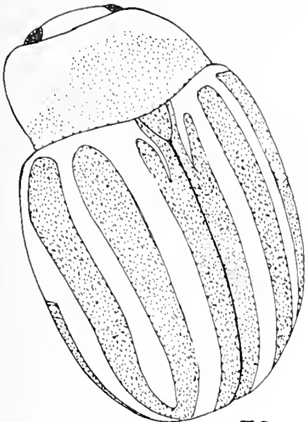
Legend for plate *7*

65. *Calligrapha,* identification of elytral markings
66. *Calligrapha floridana* Schaef.
67. *Calligrapha tiliae* Brown
68. *Calligrapha sigmoidea* (Lec.)
69. *Calligrapha pnirsa* (Stal)
70. *Calligrapha serpentina* (Rogers)
71. *Calligrapha sylvia* (Stal)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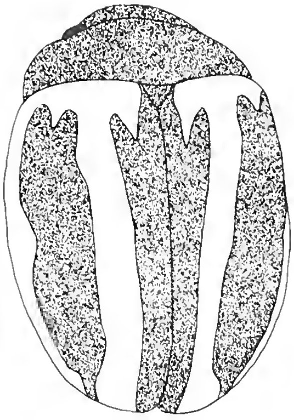
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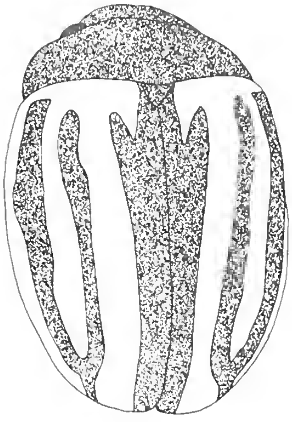
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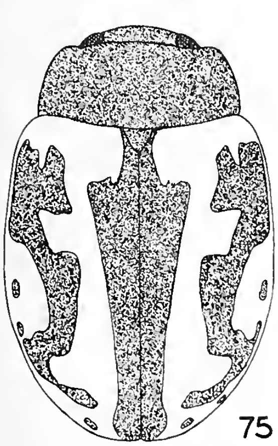
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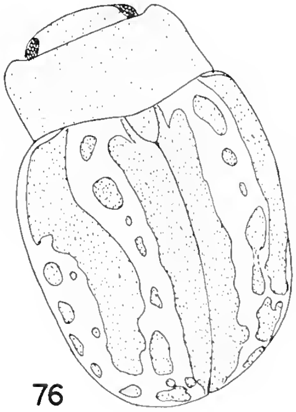
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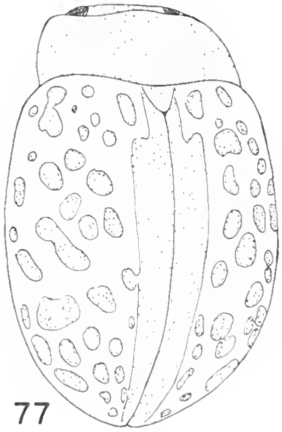
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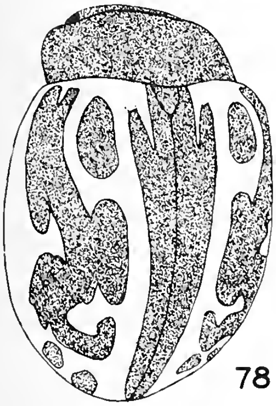
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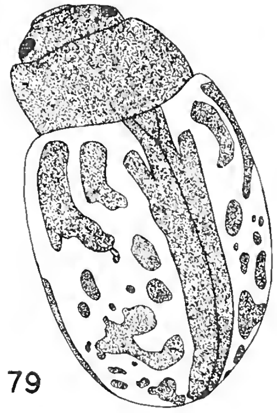
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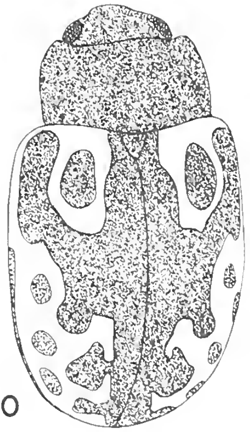
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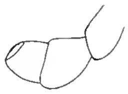
Legend for plate 8

72. *Zygogramma continua* (Lec.)
73. *Zygogramma suturalis* (Fab.)
74. *Zygogramma suturalis casta* (Rogers)
75. *Zygogramma opifera* (Stal)
76. *Zygogramma arizonica* Schaef.
77. *Zygogramma estriata* Schaef.
78. *Zygogramma tortuosa* (Rogers)
79. *Zygogramma piceicollis* (Stal)
80. *Zygogramma signatipennis* (Stal)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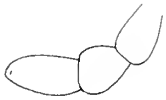
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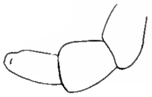
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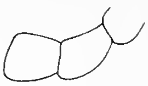
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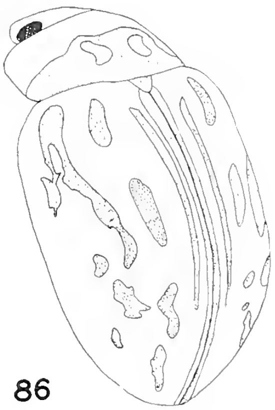
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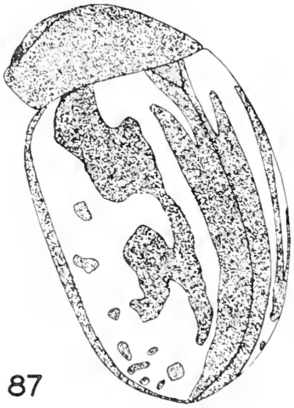
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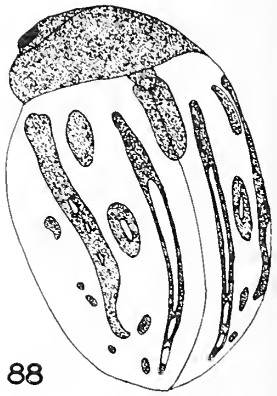
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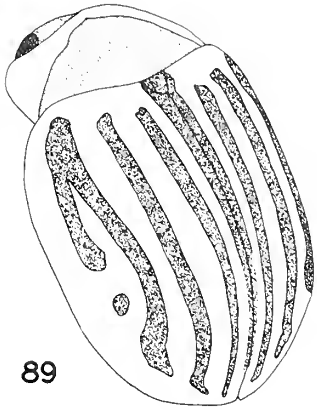
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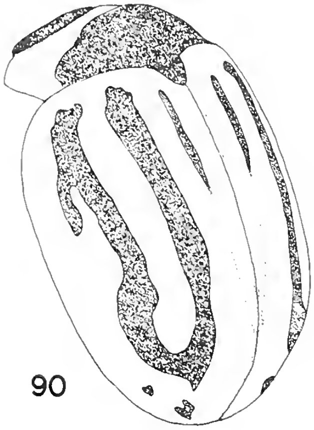
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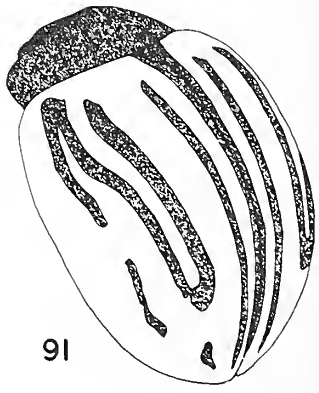
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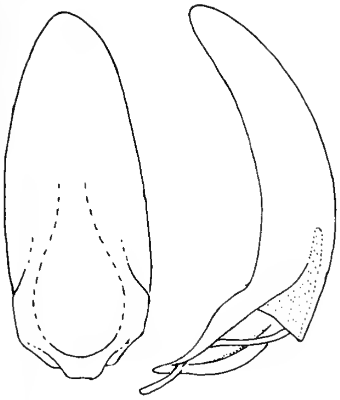
Legend for plate 9

81. *Leptinotarsa collinsi,* new species, maxillary palp.
82. *Leptinotarsa decemlineata* (Say), maxillary palp.
83. *Chrysomela mainensis* Bechyné, maxillary palp.
84. *Gastrophysa dissimilis* (Say), maxillary palp.
85. *Calligrapha rowena* Knab, maxillary palp.
86. *Zygogramma conjuncta pallida* (Bland).
87. *Leptinotarsa collinsi,* new species.
88. *Zygogramma heterothecae* (Rogers).
89. *Zygogramma exclamationis* (Fab.).
90. *Zygogramma conjuncta* (Rogers).
91. *Zygogramma disrupta* (Rogers).



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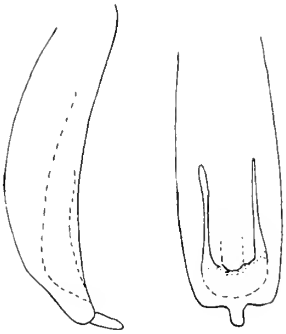

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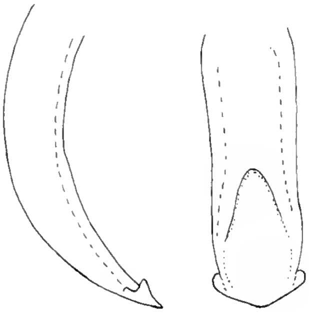

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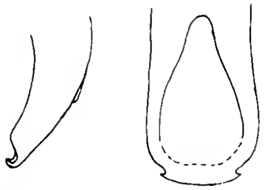

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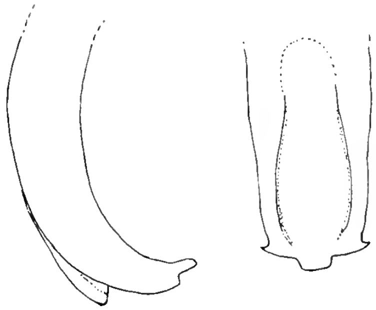

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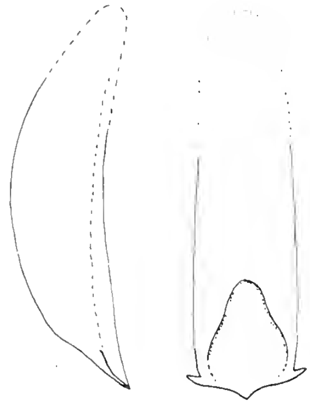

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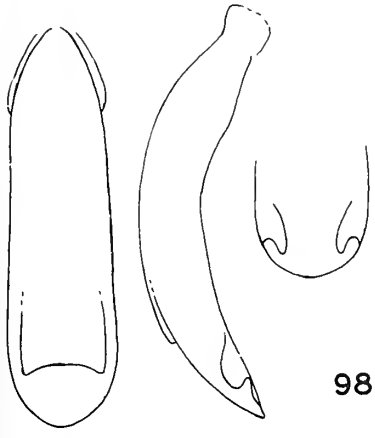

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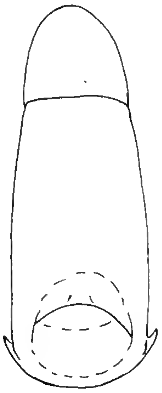

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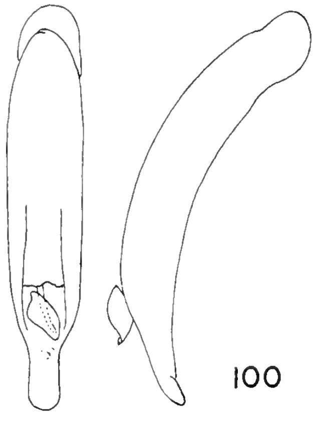

100

Legend for plate 10

92. *Calligrapha* (*Acalligrapha*) *praecelsis* (Rogers), aedeagus.*
93. *Calligrapha* (*Coreopsomela*) *californica* Linell, aedeagus.*
94. *Calligrapha* (*Calligramma*) *cephalanthi* Schwarz, aedeagus.*
95. *Calligrapha* (*Graphicallo*) *lunata* (Fab.), aedeagus.*
96. *Calligrapha* (*Bidensomela*) *bidenticola* Brown, aedeagus.*
97. *Calligrapha* (*Calligrapha*) *polyspila* (Germar), aedeagus.* This South American species is the type species of Calligrapha.
98. *Zygogramma opifera* (Stal).
99. *Calligrapha incisa* (Rogers), aedeagus.
100. *Leptinotarsa collinsi,* new species, aedeagus.

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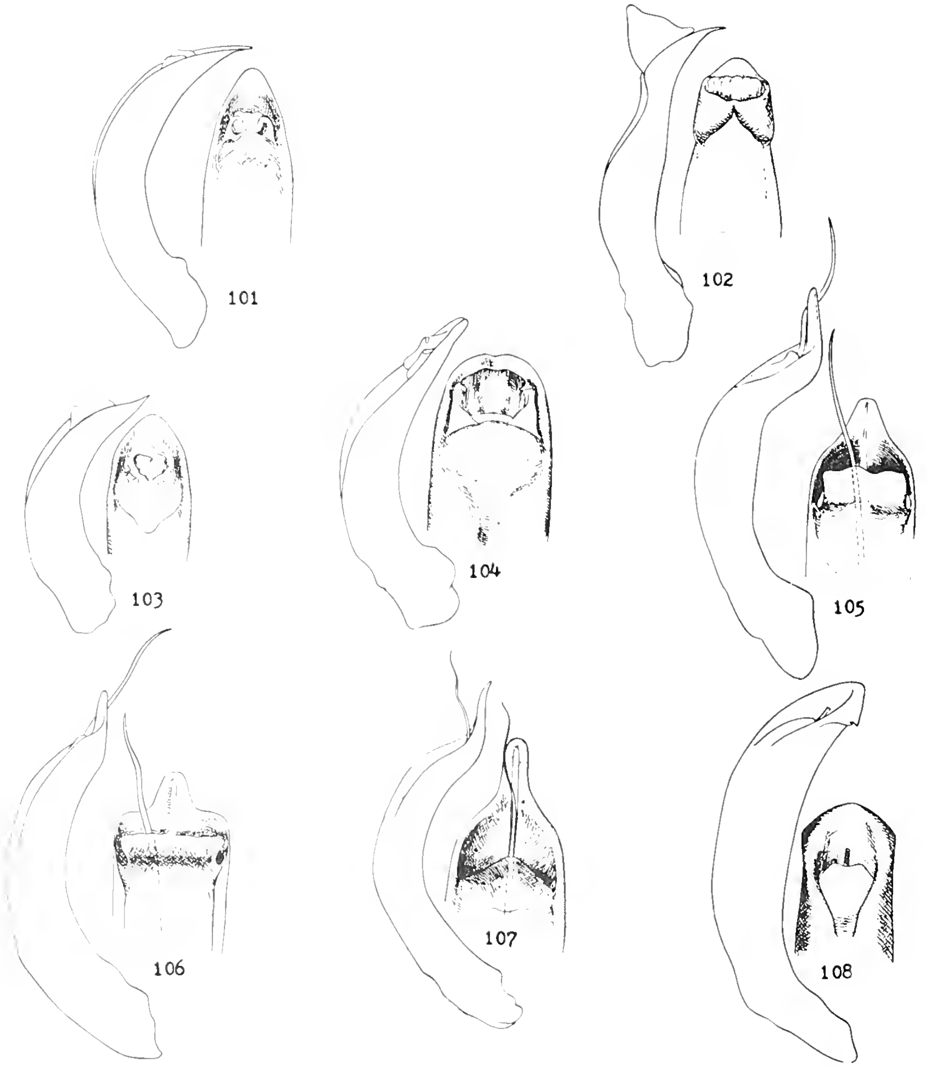
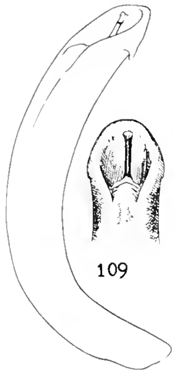
* Redrawn from Monros 1955.



Legend for plate 11

Illustrations of aedeagi after Brown, 1962, Canadian Ent. 94:63

101. *Chrysolina subsulcata* (Mann.)
102. *Chrysolina cavigera* (Sahl.)
103. *Chrysolina magniceps* (Sahl.)
104. *Chrysolina caurina* Brown
105. *Chrysolina flavomarginata flavomarginata* (Say)
106. *Chrysolina extorris* Brown
107. *Chrysolina finitima* Brown
108. *Chrysolina basilaris* (Say)



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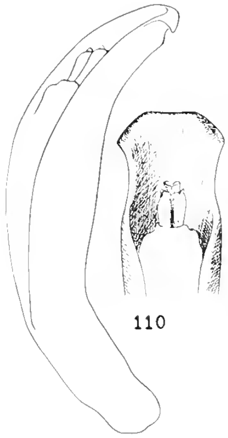

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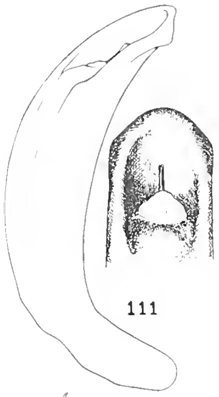

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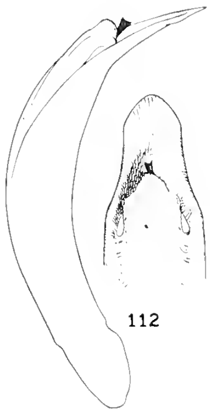

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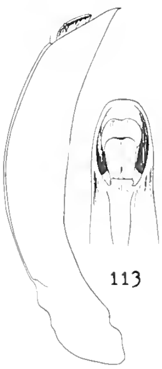

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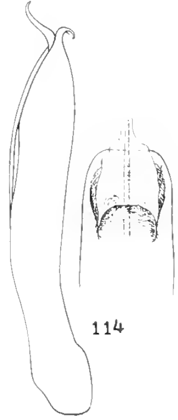

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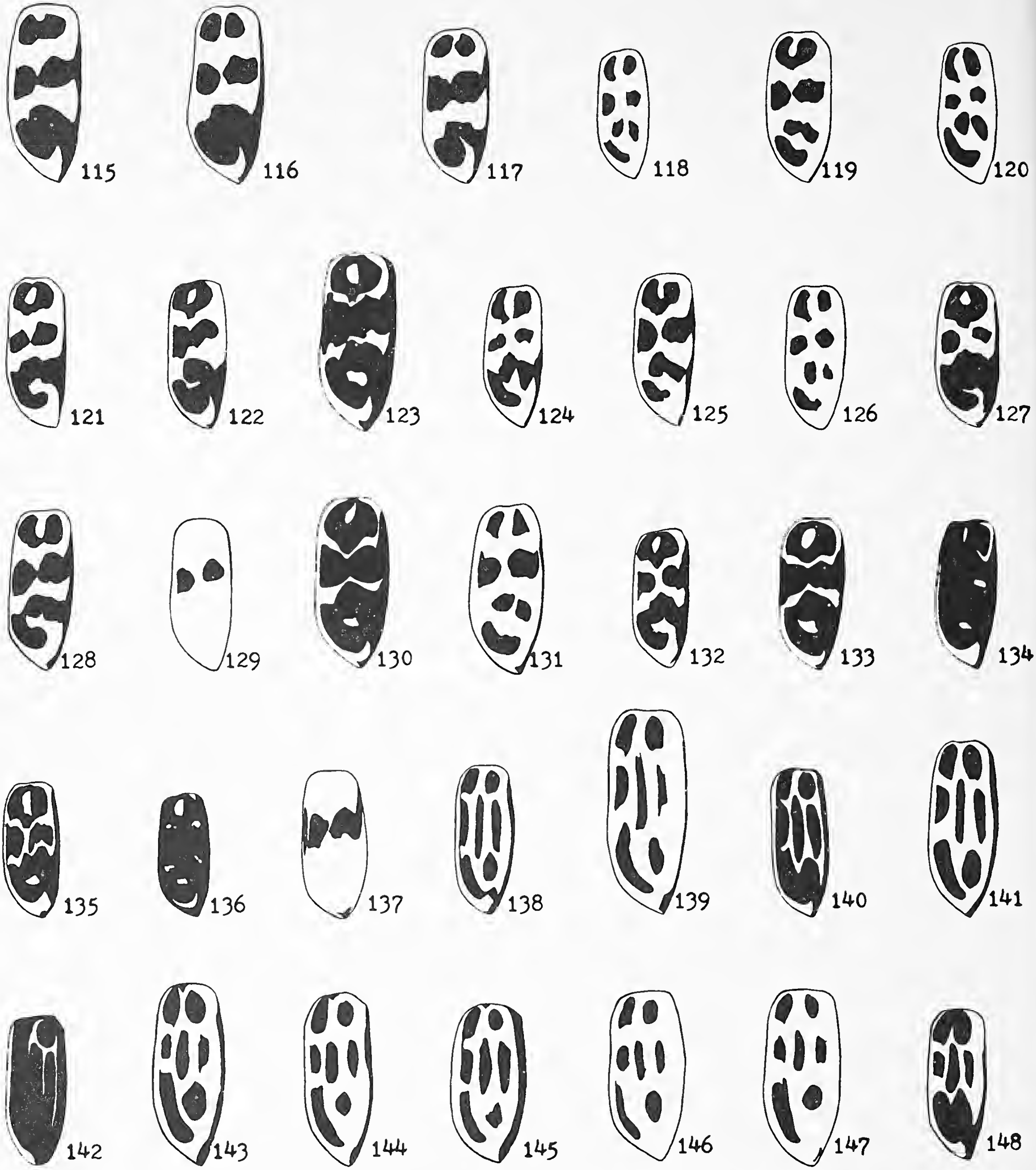
Legend for plate 12

Illustrations of aedeagi, after Brown, 1962
Canadian Ent. 94:69

109. *Chrysolina auripennis* (Say)
110. *Chrysolina subopaca* (Rogers)
111. *Chrysolina staphylea* (L.)
112. *Chrysolina hyperici* (Forst.)
113. *Chrysolina quadrigemina* (Suff.)
114. *Chrysolina varians* (Schaller)

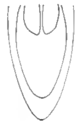


Legend for plate 13

Chrysomela, color pattern of left elytron, after Brown, 1956, Canadian, Ent. 88(suppl.) :19

115–117. *Chrysomela interrupta* Fab.
118–119. *Chrysomela mainensis mainensis* Bechyné
120–121. *Chrysomela mainensis interna* Brown
122–123. *Chrysomela mainensis littorea* Brown
124–127. *Chrysomela walshi* Brown
128–131. *Chrysomela knabi* Brown
132–134. *Chrysomela falsa* Brown
135–137. *Chrysomela aeneicollis* (Schaef.)
138–139. *Chrysomela scripta* Fab.
140–142. *Chrysomela laurentia* Brown
143. *Chrysomela confluens* Rogers
144. *Chrysomela semota* Brown
145–146. *Chrysomela lineatopunctata* Forst.
147. *Chrysomela texana* (Schaef.)
148. *Chrysomela cruentipennis* (Duv.), from Cuba


149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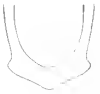
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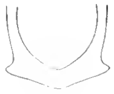
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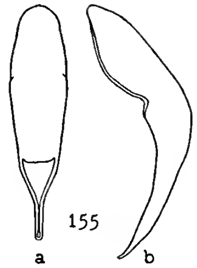

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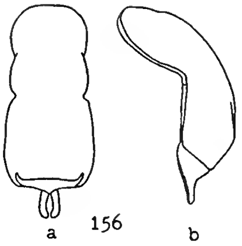

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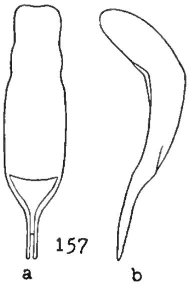

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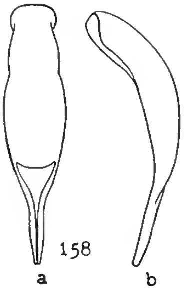

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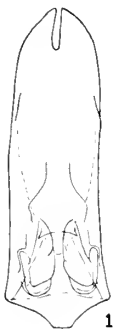
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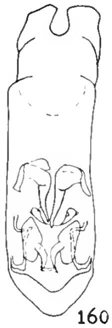
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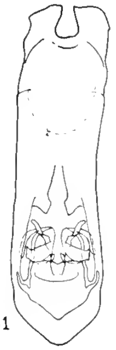
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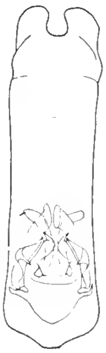
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Legend for plate 14

Chrysomela, apex of aedeagi, after Brown, 1956, Canadian Ent. 88(suppl.) :17

149. *Chrysomela scripta* Fab.
150. *Chrysomela knabi* Brown
151. *Chrysomela invicta* Brown
152. *Chrysomela crotchi* Brown
153. *Chrysomela tremula* Fab., from Europe
154. *Chrysomela saliceti* (Weise), from Europe

Gonioctena, aedeagi, after Brown, 1942 Canadian Ent. 74:101.

155. *Gonioctena nivosa* (Suff.)
156. *Gonioctena americana* (Schaef.)
157. *Gonioctena occidentalis* (Brown)
158. *Gonioctena notmani* (Schaef.)

Phratora, aedeagi, after Brown, 1951, Canadian Ent. 83:125

159. *Phratora frosti frosti* Brown
160. *Phratora americana* (Schaef.)
161. *Phratora purpurea* Brown
162. *Phratora interstitialis* Mann.

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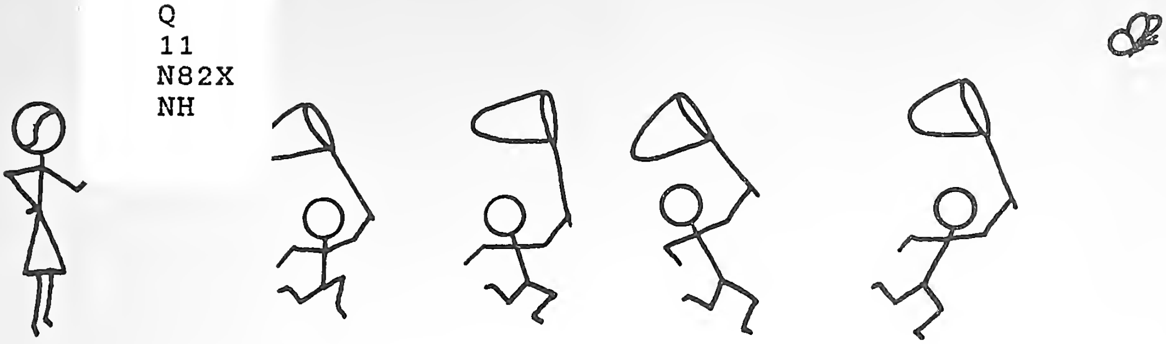

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for Elementary and Secondary Schools

By John A. Wilcox
Senior Scientist, Entomology

BULLETIN 422
New York State Museum
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SEPTEMBER

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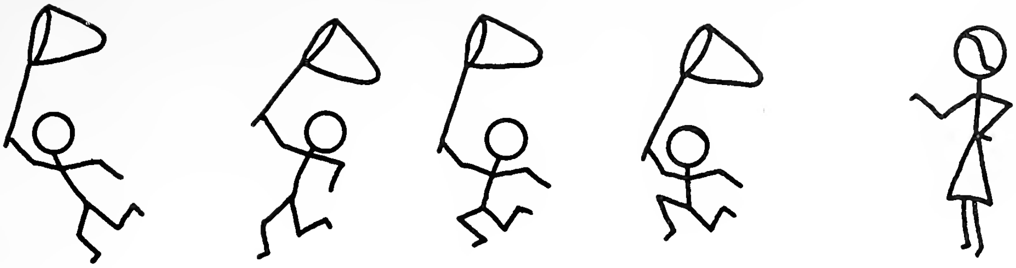

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ENTOMOLOGY PROJECTS[1]
for Elementary and Secondary Schools

By John A. Wilcox [2]

Introduction

Insect study has a host of proponents, from the amateur collecting butterflies to the scientist researching pest control, to the teachers using insects to demonstrate biological and ecological principles.

Insects are numerous, varied in form and habit, and small enough to bring into the classroom to be watched more closely. Since they can be killed and easily preserved, it is not difficult to prepare a permanent collection. Most youngsters are familiar with some insects and, with a little encouragement, will show considerable interest in any directed insect study.

For several reasons, insects have never been popular with teachers. The many different kinds of insects, most of them small, make identification difficult; also, it is discouraging to tell an eager child you don't know the name of the specimen he brought to class. Insects in general are esthetically displeasing to many people, and many are afraid of being stung or bitten. Wasps, hornets, bees, waterbugs, assassin bugs, three or four species of fuzzy caterpillars, all bite or sting a careless collector. If these insects can be recognized there will be little to worry about from the others.

A field trip often makes a subject exciting when classroom discussion and demonstration is lifeless. Active participation and a chance of finding something different often engender interest in the most unlikely pupil. However, to make a field trip more than just a picnic, planning and preparation are necessary. The major portion of this bulletin consists of an outline and suggestions for a field trip to collect insects, the subsequent classroom work of mounting specimens, and recording information and conclusions. Other projects in rearing and collecting are also suggested.

Pages 3, 10, 15, 22, 23, 37, 38 have been designed to be photocopied for distribution to all class members.

Some of the chemicals mentioned in this publication are dangerous if not handled properly. Supervision of younger children is advisable.

---

[1] Submitted for publication May 9, 1972.

[2] Senior Scientist, Entomology, New York State Museum and Science Service.

Project A. Make an insect collection from a single habitat.

Select a particular habitat and examine the wildlife community living there. Collect insects, return to the classroom and mount, label, and identify specimens. Indicate how each insect fits into the food chain, and its relationship to other members of the wildlife community. Working time required: approximately 2½ hours.

A1. Preliminary activities. Select goals for the field trip. Decide exactly what you want to find and plan in detail what you will do. For example: (1) travel to field; (2) distribute nets and collector's kits; (3) for the first 15 minutes observe the insects on the plants to see what they are doing; (4) collect as many different species as you can (20 minutes); (5) return to classroom; (6) mount, label, and identify one or more of each kind; (7) determine their places in the food chain.

Select an area where you can collect fairly large numbers of insects; open fields are usually best. A goldenrod field is very good in autumn, and in spring, an open field is satisfactory if the leaves are fairly well developed. Thickets of small willow, poplar, or cherry trees are also good. The trip leader should, of course, visit the trip destination to know what to expect and be sure the trip goals can be met.

Select a date for the field trip. Insect collecting is a fair weather activity. A trip on a wet day will offer little unless the class is specifically looking for aquatic insects, so an alternative rain date should be picked. Make transportation arrangements if the group is to travel beyond walking distance.

Prepare and distribute notices to parents of each member of the class. These notices should include permission slips to be returned to the trip leader, description of the field trip, and a list of things to bring or to consider before attending the trip (see page 3). Be sure the permission slips are returned and on file.

Become familiar with some of the insects you may find. Study books or other references so you can recognize some of the commoner kinds (see bibliography on pages 44 and 45). Know what is meant by herbivore, parasite, predator, scavenger, and pollinator. If an insect collection is available, look it over carefully.

Round up the field equipment you will need. Obtain or make nets (see figures 1–5), killing jars (figure 6), and storage boxes (figure 7). Prepare a collector's kit for each member of the class or for each group of four or five. The collector's kit is a cloth, plastic, or paper bag containing the following items which must be returned to the trip leader at the end of the project.

(1) A trail guide pamphlet if one is available for the area.
(2) One reference book.
(3) One magnifying glass or hand lens.
(4) One knife.
(5) One pencil.
(6) 3 x 5 file cards or paper for notes.
(7) One killing jar for insects to be preserved.
(8) One or two empty jars or five small vials for living insects.

Envelopes or paper or plastic bags may be provided at the end of the trip to carry insects or other items home.

COME PREPARED FOR A FIELD TRIP

What should you bring with you on a field trip? Here are a few things you should have for a successful trip.

Collecting jars — a killing jar or two, and two empties for livestock.

A net if you have one (not absolutely necessary).

A knife or hand axe (only if you have had training in their use and can refrain from cutting live trees).

Mosquito repellent.

A bottle of water to drink (a canteen or a cleaned, plastic bleach bottle).

First aid kit (at least a couple of band-aids). Special medication if you are allergic to bees or wasps, or susceptible to asthma.

Food (a snack for mid-afternoon, and lunch if you will be out during the noon or evening meal).

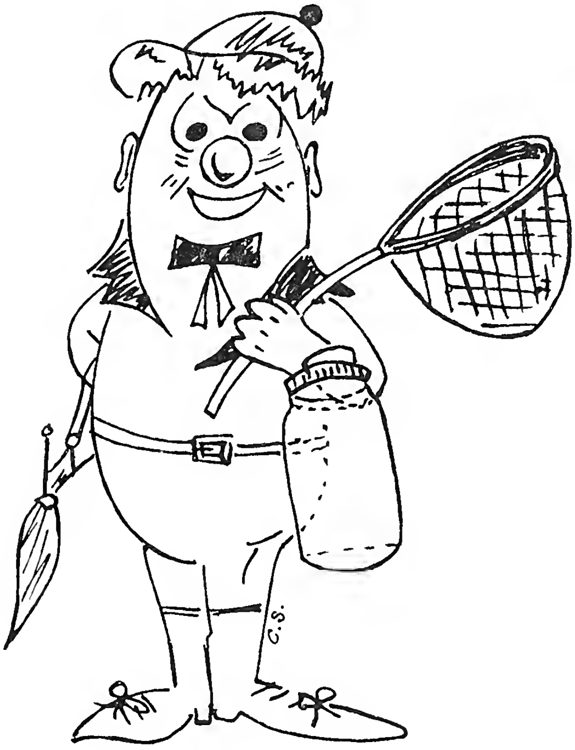
A pack or cloth bag with shoulder or belt straps to carry equipment so your hands will be free.

Proper clothing: a hat to shade your eyes; good shoes, well broken in; old clothes (slacks or jeans to protect you from the berry bushes); jacket or raincoat, depending on the weather.

If you are going to collect host plant specimens, you will need a vasculum or plastic bag for carrying the plants.

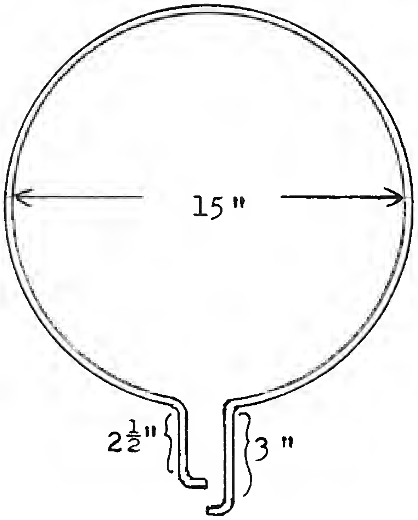
Make sure you know where you are going and how to get back before you leave the starting point. Anyone, even an experienced woodsman, can get lost. The trick is to find your way before you hike an extra hour or two. So look at a map and carry a compass, especially if you are going into hilly or wooded areas.

Know what the dangers are: poison ivy, snakes, poisonous spiders. If you are not familiar with them, ask your trip leader if there are any in the area, how to recognize and avoid them, and what to do if you encounter any of them.



This is a model page which can be photocopied and distributed to members of the class.

INSECT COLLECTING NET



52 inch piece of
No. 8 iron wire

Figure 1

Figure 2

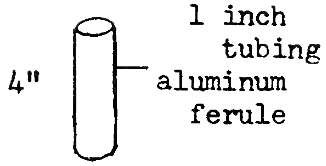


Figure 3

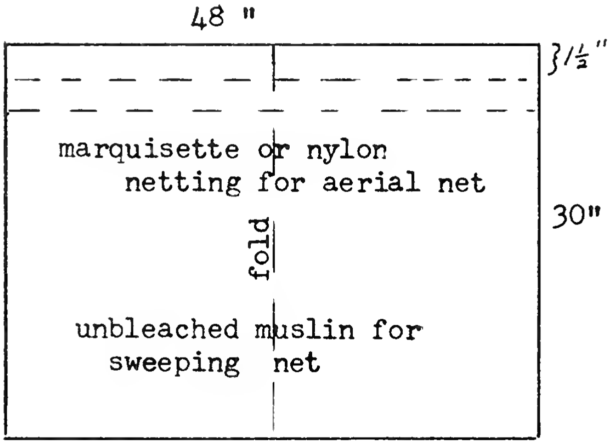


Figure 4

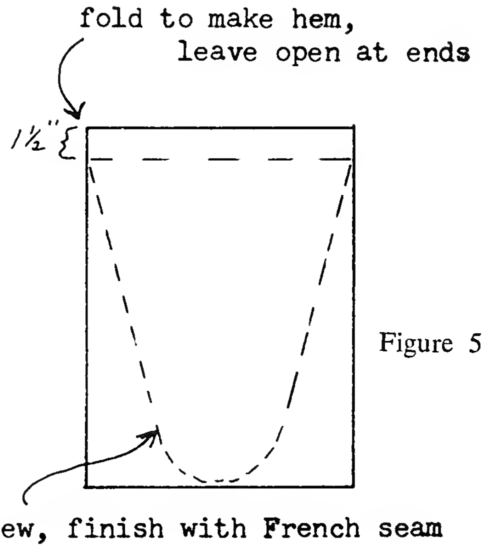


Figure 5

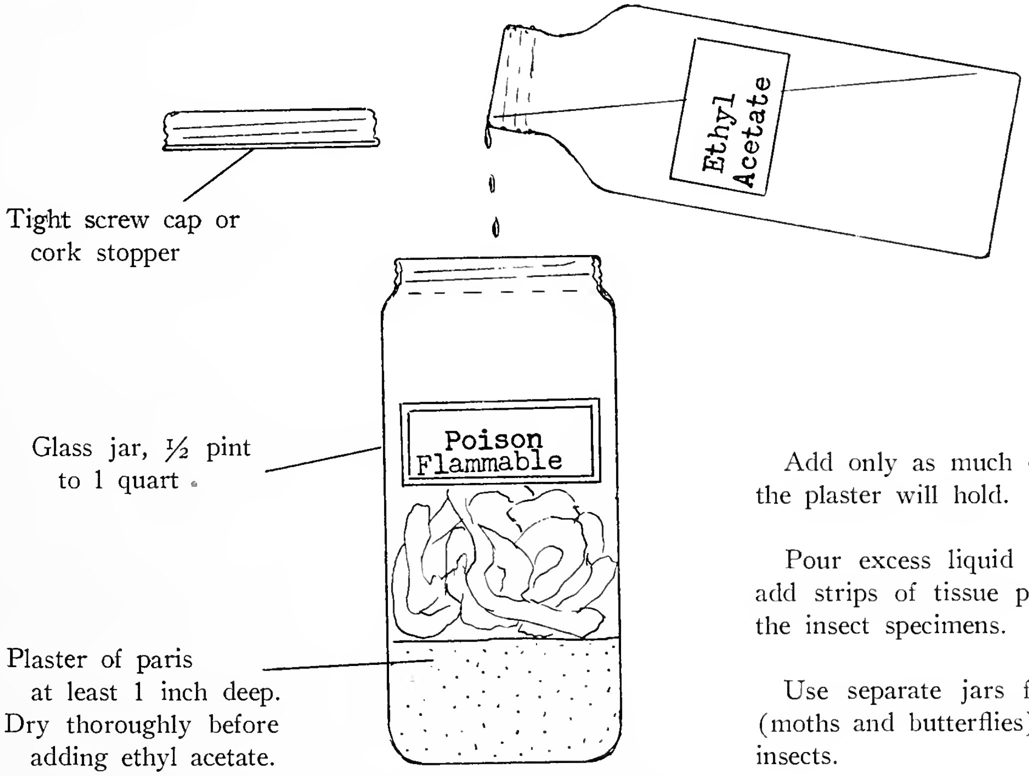
A2. The field trip. Killing jars should be charged before use (figure 6). Place about two teaspoonfuls of ethyl acetate in each jar containing plaster of paris and tightly cap the jar. Allow the ethyl acetate to soak into the plaster for 5 to 10 minutes. This can be done in the classroom just before the class leaves for the field. When the jars are ready for use, pour excess acetate back into its original container and leave the jars open for a couple of minutes to allow plaster to dry. Add a few strips of tissue paper or paper towelling to absorb moisture and protect the insects from damage.

Unless you have enough equipment for all members of the class, use the following system of distributing equipment and responsibility. Break the class into groups of four members each. Designate each group by letter (Group A, Group B, etc.). Within each group, designate each student by number (Student No. 1, Student No. 2, etc.). Assign supplies and equipment as follows to reduce confusion. Student No. 1 of each group is to pick up one collector's kit and write his name on the card inside. Student No. 2 — pick up one killing jar if there is no jar in the kit. Student No. 3 — pick up one net. Student No. 4 — pick up one clip board or notebook, and instruction sheet.

Spend the first 15 minutes in demonstrating the use of the nets and killing jars. Move to the collecting area and quietly observe any insects, birds, and other animals in the field. Record observations of insect activity. Note the number of insects which can be found this way. Look especially for predators (such as spiders, mantids, and stink bugs) which have caught their prey.

Spend the next 20 minutes (or more, depending on the time available) collecting as many different kinds of insects as possible. The sweeping net, with a heavy frame and muslin bag, provides the best method of collecting large numbers of insects in the field. It is brushed through weeds, bushes, and branches of trees, sweeping insects off the plants. Some damage is done to the plants so this method of collecting should not be used where the plants are valuable. The sweeping net is not satisfactory for capturing such flying insects as butter-

Killing Jar for Insects Figure 6



Add only as much ethyl acetate as the plaster will hold.

Pour excess liquid out of jar and add strips of tissue paper to protect the insect specimens.

Use separate jars for Lepidoptera (moths and butterflies) and for other insects.

flies and dragonflies because the tight mesh of the bag fails to let the air through and the butterfly may be blown out of the way by the net itself. A light weight net bag is necessary for capturing butterflies, but will be torn by weeds or branches. After a few sweeps, flip the end of the net over the rim to trap the insects. Flip the sweeping net again to force them down to the bottom of the net and examine your catch. Trap the insects you wish to keep in the killing jar or live jar. Flies, wasps, and bees are very quick, so watch for them first. They can be trapped in the bottom of the net by encircling the net loosely with your hand a few inches from the bottom, then gradually opening your hand and allowing the insects to come out through a small opening. Capture them in the jar as they emerge. There is some risk of bee or wasp stings if you hold the net at the tip or too tightly.

Share the sweeping nets and other equipment. Group collecting is an exercise in cooperation. The person who has the net is expected to take four or five sweeps, collect the insects from the net, then give the net to the member of his group with the next number. Two students, working together until they are experienced, may be necessary to get specimens from net to jar.

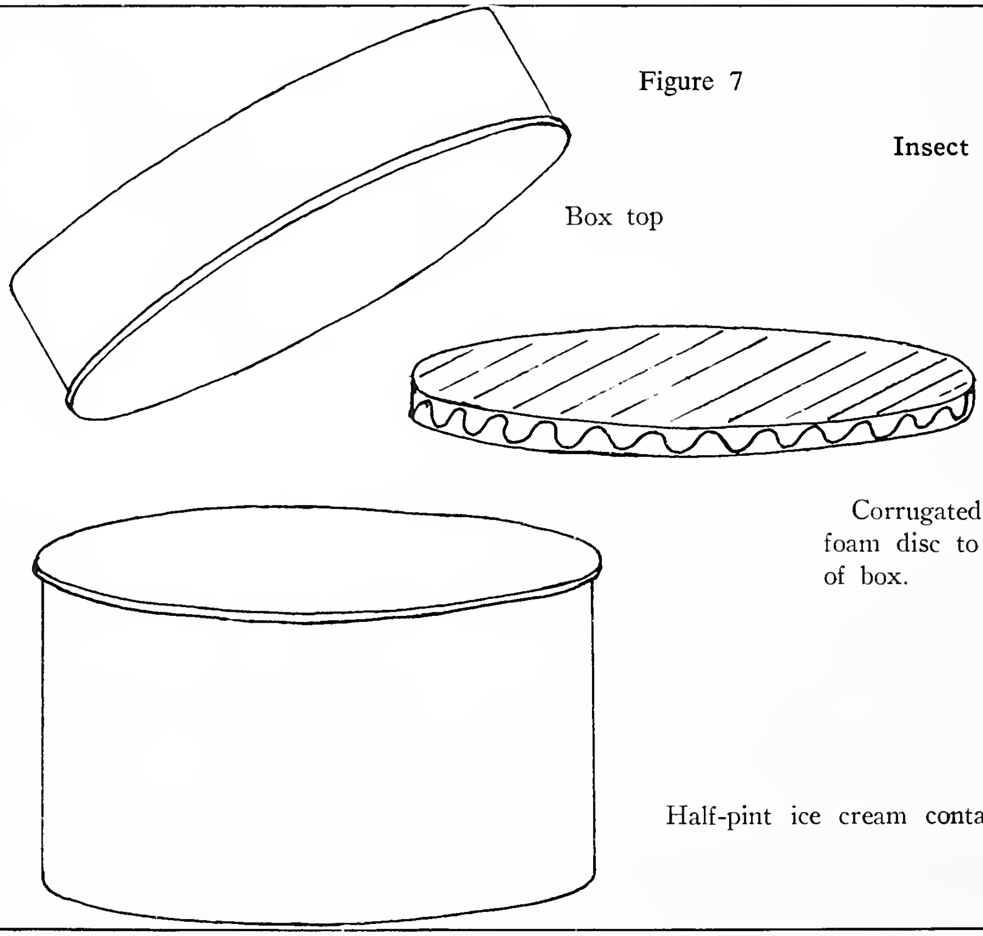
Collect only winged insects for this project. They are rigid enough to hold shape when dried, and are usually much easier to identify. Note that adult beetles and bugs have wings even though the wings may be hard to recognize. Spiders, caterpillars, and other soft-bodied insects can be dried by a special method (section A13) but are usually preserved in 70 percent ethyl alcohol (section A12). Butterflies and dragonflies are not satisfactory specimens for this type of exercise or project because about a week is required to dry on special mounting boards (section A11).

If you have studied insects before going to the field, look for some which are herbivores, predators, parasites, scavengers, and pollinators. A variety will add to the value of your collection.

At the end of the collecting period return to the starting point and return your nets to the trip leader. Place your killing and collecting jars in your collector's kit.

Figure 7

Insect box for small collection



Write your name or group name on a card and place it in the collector's kit to prevent confusion. Live insects should be turned loose, or made comfortable if you are taking them back to the classroom. Don't smother them in jars which are too small or too tightly capped.

A3. Classroom laboratory. Use the following procedure in the classroom. Maintain the same group organization as in the field. Student No. 1 can pick up one storage box for each member of his group. Student No. 2 should get 10 insect pins for each member. Student No. 3 — pick up foam plastic or corrugated cardboard to be cut and fitted into the bottom of the storage boxes. Student No. 4 can pick up one insect mounting kit.

A4. Storage boxes. First prepare the storage boxes which will hold the mounted insects. Cigar boxes are an old standby for entomologists, but any box at least 2½ inches deep, with firm sides and good cover will do. Half pint, rolled edge, liquid tight, paper containers normally used for ice cream serve very well for small collections such as those made in the school exercise described here (figure 7). A soft material must be placed in the bottom of the box to hold the pin. The best material is polyethylene plastic foam. Polystyrene plastic foam commonly used as Christmas decorating material or as packing containers for small radios and other appliances will do if paradichlorobenzene moth crystals are not used to protect your collection. Polystyrene becomes a liquid in the fumes of paradichlorbenzene. Soft corrugated cardboard used in packing boxes can be used if plastic is not available, but you may have difficulty in finding boxes which are soft enough for the pins. Cut the bottom material so it fits tightly into the box, or glue it to the bottom. Put your name on the bottom or side of your box. For larger collections, use cigar boxes or the large, glass-topped display case described in section A15.

A5. Collection protection. Carpet beetles and their relatives are always a threat to dried insect collections. The larvae naturally feed on dead insects and will soon destroy a collection unless you take protective measures. Keep it continually fumigated by placing moth crystals (paradichlorbenzene) or moth flakes (naphthalene) in small boxes or packets in the storage box. An alternative method is storing storage boxes in an airtight cabinet or box and placing the moth balls in it. An unprotected insect collection has a very short life expectancy.

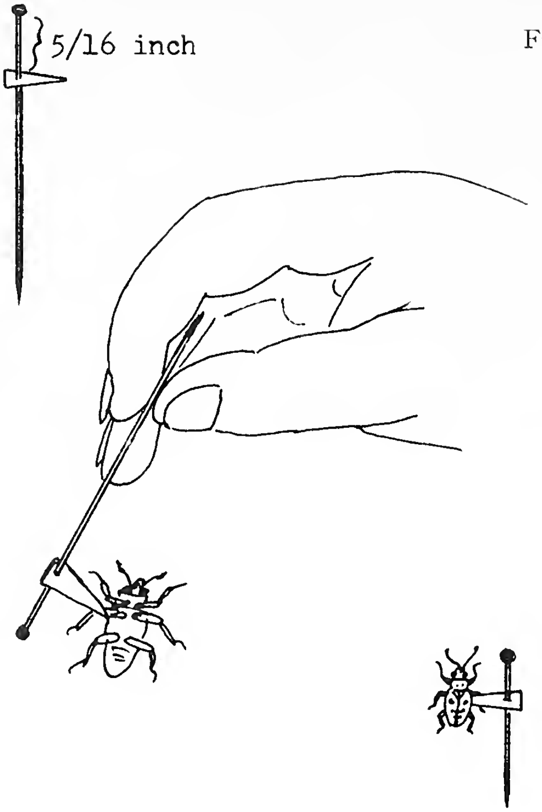
A6. Pinning insect specimens. Pin the insects so you can examine them. The pin serves as a handle and the insects can be manipulated without breakage. They can be turned upside down and the characters on the ventral side can be seen. Purchase special insect pins made of good rust proof steel, that bends slightly but will not stay bent under ordinary use; and long enough to hold several labels as well as the insect. Ordinary sewing pins are too short, too thick, and very often will corrode enough in a year to destroy the insect specimen. Pin sizes ranging from 000 to 6 are available. Size 3 is satisfactory for all but the most specialized collections. (Size 1 is very thin but can be used by the beginner. Size 3 is large enough for any but the largest tropical beetles.) Insects too small to be mounted on No. 3 pins can be glued to pinned paper triangles. Generally speaking, the pin is run through the insect somewhere near the middle, at the widest part of the body between the hind wings. Pin the insect just a little to the right of the midline. The dot (•) on figures 91 through 113 indicates the recommended pin position. Leave about $\frac{5}{16}$ inch of the pin above the insect (figures 8, 10).

A7. Reports, records, and labels indicating biology of the specimens. The value of an insect collection lies in the biological information associated with the specimens. Food plant or prey is of great interest. The particular habitat, time of day, weather, and temperature at time of capture may be useful. The entomologists have now named almost every insect in the eastern United States, and are now becoming more interested in what the insect does rather than what it is. Such information can be placed in the catalog, or put on labels attached to the pin (figures 10 and 11).

A8. There are more than 20,000 species of insects in New York State. Since most species transform through four or more different stages, there may be almost 100,000 different insect forms. Identification, therefore, is one of the most disconcerting aspects of insect study. Since most books deal almost exclusively with adults, the beginner should collect only winged insects. These are adults and you will have a better chance of putting the correct names on them.

Insects, the Little Golden Guide by Zim & Cottam, is useful for the beginning collector. However, it deals with only 225 species and even the beginner will pick up many kinds not included. *A Field Guide to the Insects* by Borror and White (1,300 illustrations), and the *Field Book of Insects* by Lutz (800 illustrations) are much more useful, both for identification and for interesting information about the insects. The *Field Guide* is most complete and up-to-date at present time and should be available for anyone doing serious work

Figure 8



To mount a tiny insect on a paper point when it is too small to pin directly:

1. Cut and pin a small paper triangle as shown at left.
2. Place the insect on its back, legs up, with the head away from you.
3. Hold the point of the pin in your right hand.
4. Touch the tip of the paper point to a drop of glue (Duco cement, clear nail polish, etc.) so there is a small drop of glue on the paper point.
5. Reach over the insect and touch the glued tip of the point to the underside of the insect between the middle and hind legs.
6. Arrange the insect in proper position with another pin or forceps.

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with insects. Comparison between a specimen and the illustrations in one of these books is usually the first step in naming your captures. An accurately named collection will provide an easier tool for identification, but is rarely available, although any school can maintain such a collection built up by student activities.

Several college text books in entomology are available. *An Introduction to the Study of Insects* by Borror and DeLong is most complete. This type of book has keys to the identification of insect families, thus making is possible to put at least a family name on nearly every specimen in your collection. The keys, however, may be difficult, and require experience for satisfactory use. A key to the orders is provided on page 40. It would be to your advantage to run several different, well-known insects through the key just to learn its use.

A key to the identification of an insect is a series of paired descriptive statements. The two descriptions in each couplet are mutually exclusive — only one of them will apply to the specimen you wish to identify. Always start with couplet 1, decide which statement agrees with the specimen and note the number at the end of that statement on the right margin of the text. This number indicates the next couplet to be checked. Go to this couplet, again decide which statement describes your specimen and again note the number of the next couplet to be checked. Continue in this manner until a decision leads you to a name. This is the name of your specimen if you have made no mistakes and if your unknown has been included in the key.

As an example try to run a grasshopper through the key on page 40. In the first couplet you must decide that the front wings of the grasshopper are tough and leathery or parchment-like in comparison with the hind wings. This decision leads to couplet 2. Grasshoppers have jaws (mandibles) for chewing food so go next to couplet 4. The specimen does not have forcepslike cerci at the end of the body as shown in figure 98 so move on to couplet 5. Since a grasshopper fits the description in 5b rather than 5a apply the name Orthoptera to it.

The following data should be recorded.

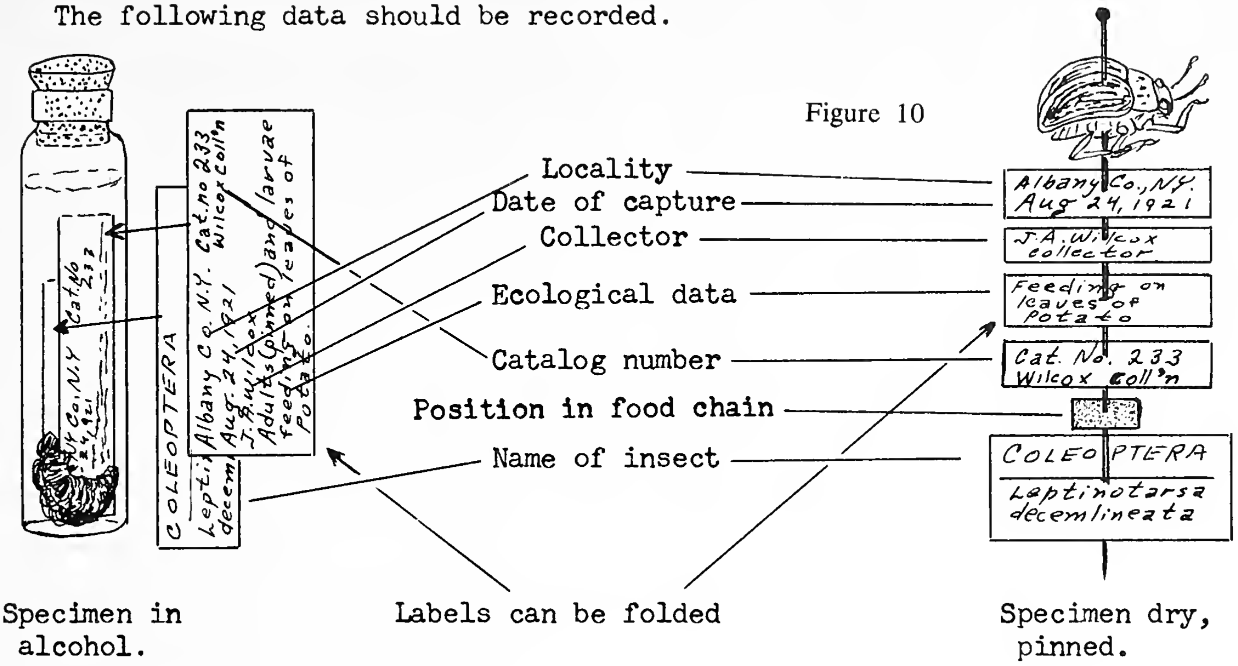
Figure 9

Figure 10

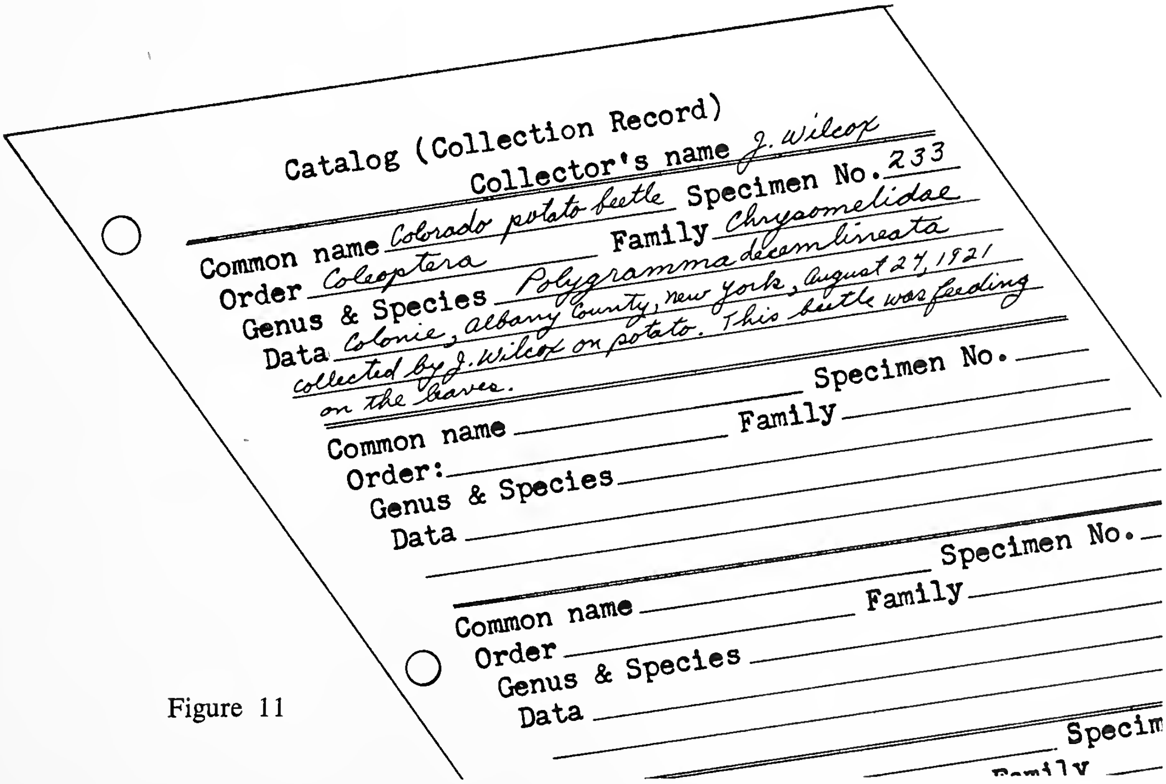
Figure 11

Catalog (Collection Record)

Collector's name J. Wilcox

Common name Colorado potato beetle Specimen No. 233

Order Coleoptera Family Chrysomelidae

Genus & Species Polygramma decemlineata

Data Colonie, Albany County, New York, August 27, 1921 collected by J. Wilcox on potato. This beetle was feeding on the leaves.

Common name ____ Specimen No. ____

Order: ____ Family ____

Genus & Species ____

Data ____

Common name ____ Specimen No. ____

Order ____ Family ____

Genus & Species ____

Data ____

Specim

Catalog (Collection Record)

Collector's name:

Common name: .... Specimen number........................

Order:.................................... Family: ....

Genus & Species: ....

Data: ....

....

....

Common name: .... Specimen number........................

Order:.................................... Family: ....

Genus & Species: ....

Data: ....

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Common name: .... Specimen number........................

Order:.................................... Family: ....

Genus & Species: ....

Data: ....

....

....

Common name: .... Specimen number........................

Order:.................................... Family: ....

Genus & Species: ....

Data: ....

....

....

Anthropods frequently seen on land or in fresh water

Order	**Common Names**
Class Crustacea	Crustaceans
Branchiopoda	Fairy Shrimps, Water-Fleas
Copepoda	Copepods
Ostracoda	Ostracods
Amphipoda	Beach-Fleas, Sand-Fleas
Isopoda	Sowbugs, Pillbugs
Decapoda	Lobsters, Crayfish, Crabs, Shrimps
Class Diplopoda	Millipedes
Class Chilopoda	Centipedes
Class Symphyla	Symphylids (rarely seen)
Class Tardigrada	Water-Bears, Tardigrades (rarely seen)
Class Arachnida	
Scorpionida	Scorpions
Chelonethida	Pseudoscorpions
Phalangida	Harvestmen, Daddy-Longlegs
Acarina	Mites, Ticks, Chiggers
Araneida	Spiders, Tarantulas
Class Insecta	
Thysanura	Bristletails, Silverfish, Firebrats
Collembola	Springtails, Snowfleas
Ephemeroptera	Mayflies
Odonata	Dragonflies, Damselflies
Orthoptera	Grasshoppers, Locusts, Katydids, Crickets, Mantids, Walking Sticks, Cockroaches
Isoptera	Termites
Plecoptera	Stoneflies
Dermaptera	Earwigs
Psocoptera	Psocids, Booklice, Barklice (=Corrodentia)
Mallophaga	Chewing Lice, Biting Lice
Anoplura	Sucking Lice
Thysanoptera	Thrips
Hemiptera	True Bugs, Water Striders, Water Scorpions, Back Swimmers, Water Boatmen
Homoptera	Cicadas, Froghoppers, Treehoppers, Leafhoppers, Aphids, Plant-Lice, Whiteflies, Scale Insects
Neuroptera	Lacewings, Ant Lions, Dobsonflies, Alderflies
Coleoptera	Beetles, Weevils
Strepsiptera	Twisted-Winged Insects (rarely seen)
Mecoptera	Scorpionflies
Trichoptera	Caddisflies
Lepidoptera	Moths, Butterflies, Skippers
Diptera	True Flies, Midges, Mosquitoes, Gnats, Sheepticks
Siphonaptera	Fleas
Hymenoptera	Bees, Ants, Wasps, Hornets, Sawflies, Horntails, Ichneumons, Chalcids, Braconids

Families of common and frequently collected insects

This is not a complete list. Numbers indicate page and position on page of the family in the *Field Guide to the Insects,* by Borror and White, which does describe nearly all insect families. H = plant feeder, Pr = predator, Pa = parasite, S = scavenger (most members of a family).

		THYSANURA	
S H	61.4	Lepismatidae	silverfish and firebrat
		COLLEMBOLA	
S	64.3	Poduridae	snowfleas and podurid springtails
S	64.3	Entomobryidae	elongate-bodied springtails
S	64.9	Sminthuridae	globular springtails
		EPHEMEROPTERA	
Pr S	66.4	Ephemeridae	burrowing mayflies
Pr S	66.6	Heptageiniidae	stream mayflies
Pr S	66.8	Baetidae	small mayflies
		ODONATA	
Pr	70.7	Aeshnidae	darners and dragonflies
Pr	72.7	Libellulidae	common skimmers and dragonflies
Pr	74.7	Coenagrionidae	narrow-winged damselflies
		ORTHOPTERA	
H	78.3	Acrididae	short-horned grasshoppers
H	80.3	Tettigoniidae	long-horned grasshoppers
Pr	82.4	Gryllacrididae	camel crickets
H	82.9	Gryllidae	crickets
Pr	86.1	Mantidae	mantids
H	86.5	Phasmatidae	walking sticks
H S	86.7	Blattidae	cockroaches
		ISOPTERA	
H S	90.0	Rhinotermitidae	subterranean termite
		PLECOPTERA	
Pr	93.2	Perlidae	common stoneflies
Pr H	94.0	Isoperlidae	green-winged stoneflies
H	94.8	Pteronarcidae	giant stoneflies
H	96.8	Capnidae	small winter stoneflies
		DERMAPTERA	
H S	98.7	Forficulidae	common earwigs
		HEMIPTERA	
Pr	112.8	Corixidae	water boatmen
Pr	113.1	Notonectidae	back swimmers
Pr	114.0	Nepidae	water scorpions
Pr	114.3	Belostomatidae	giant water bugs
Pr	116.2	Gerridae	water striders
H	118.0	Miridae	leaf bugs and plant bugs
Pr	118.8	Phymatidae	ambush bugs
Pr	119.0	Reduviidae	assassin bugs
Pr	120.2	Nabidae	damsel bugs
H	120.6	Tingidae	lace bugs
H	122.0	Lygaeidae	seed bugs
H	122.3	Pyrrhocoridae	red bugs and stainers
Pr H	122.5	Coreidae	leaf-footed bugs
H	123.0	Coriscidae	broad-headed bugs
H	126.3	Corimelaenidae	negro bugs
H	126.5	Scutelleridae	shield bugs
H Pr	126.8	Petatomidae	stink bugs

HOMOPTERA

H	129.0	Cicadidae	cicadas
H	129.0	Membracidae	treehoppers
H	129.3	Cercopidae	froghoppers and spittlebugs
H	129.6	Cicadellidae	leafhoppers
H	132.2	Acanaloniidae	acanaloniid planthoppers
H	132.4	Flatidae	flatid planthoppers
H	133.2	Dictyopharidae	dictyopharid planthoppers
H	135.0	Aphididae	aphids
H	138.4	Diaspididae	armored scales
H	138.8	Coccidae	wax and tortoise scales

NEUROPTERA

Pr	140.9	Corydalidae	dobsonflies and fishflies
Pr	141.2	Sialidae	alderflies
Pr	144.2	Chrysopidae	green lacewings

COLEOPTERA

Pr	151.3	Cicindelidae	tiger beetles
H Pr	152.1	Carabidae	ground beetles
Pr	154.0	Dytiscidae	predaceous diving beetles
Pr	154.7	Gyrinidae	whirligig beetles
Pr	156.0	Histeridae	hister beetles
S	156.3	Hydrophilidae	water scavenger beetles
S	158.8	Silphidae	carrion beetles
Pr S	160.1	Staphylinidae	rove beetles
Pr	162.5	Cantharidae	soldier beetles
Pr	162.8	Lampyridae	lightningbugs or fireflies
Pr	163.1	Lycidae	net-winged beetles
H S	164.1	Dermestidae	dermestid beetles
Pr	165.1	Cleridae	checkered beetles
H Pr	166.8	Elateridae	click beetles and wireworms
H	169.1	Buprestidae	metallic wood-boring beetles
H	175.3	Languriidae	lizard beetles
H	176.6	Erotylidae	pleasing fungus beetles
H	178.3	Phalacridae	shining flower beetles
Pr H	180.3	Coccinellidae	lady beetles or ladybird beetles
Pa H	184.2	Meloidae	blister beetles
H Pr	185.1	Mordellidae	tumbling flower beetles
H	186.1	Tenebrionidae	darkling beetles
H	190.7	Lucanidae	stag beetles
H S	192.1	Scarabaeidae	scarab beetles
H	196.0	Cerambycidae	long-horned beetles
H	198.0	Chrysomelidae	leaf beetles, flea beetles, and tortoise beetles
H	202.4	Curculionidae	weevils and snout beetles

MECOPTERA

Pr	210.0	Panorpidae	common scorpionflies

TRICHOPTERA

H	214.5	Phryganeidae	large caddisflies
H	214.7	Limnephilidae	northern caddisflies
H	215.1	Hydropsychidae	net-spinning caddisflies
H	216.5	Lepidostomatidae	lepidostomatid caddisflies

LEPIDOPTERA

H	222.4	Papilionidae	swallowtails
H	224.0	Pieridae	whites, sulfurs, cabbage butterflies
Pr H	224.4	Lycaenidae	blues and coppers
H	226.2	Nymphalidae	brush-footed butterflies
H	226.9	Satyridae	nymphs and satyrs
H	228.3	Danaidae	milkweed butterflies

H	228.8	Hesperidae	skippers
H	230.3	Sphingidae	sphinx or hawk moths
H	232.0	Saturniidae	giant silkworm moths
H	232.6	Citheroniidae	royal moths
H	234.0	Geometridae	geometers and inchworm moths
H	234.8	Notodontidae	prominents
H	236.1	Lasiocampidae	tent caterpillars and lappet moths
H	236.8	Ctenuchidae	ctenuchid moths
H	238.0	Arctiidae	tiger moths
H	238.6	Noctuidae	noctuids and cutworm moths
H	246.0	Pyralidae	pyralid moths
H	248.0	Olethreutidae	olethreutid moths
H	248.3	Tortricidae	tortricid moths

DIPTERA

S	262.2	Tipulidae	crane flies
Pa	266.0	Culicidae	mosquitoes
Pa	268.5	Simuliidae	black flies
Pa	274.0	Tabanidae	horse flies and deer flies
Pr	274.7	Rhagionidae	snipe flies
Pr	276.8	Asilidae	robber flies
Pa	278.2	Bombyliidae	bee flies
Pr	278.7	Dolichopodidae	long-legged flies
Pr	281.0	Syrphidae	syrphid flies
H	288.0	Otitidae	picture-winged flies
H	288.8	Tephritidae	fruit flies (part)
H S	298.1	Chloropidae	frit flies
H S	300.8	Drosophilidae	pomace flies and fruit flies (part)
S	306.0	Muscidae	house fly and muscid flies
Pa	306.4	Tachinidae	tachinid flies
S	306.7	Calliphoridae	blow flies
S Pa	307.0	Sarcophagidae	flesh flies

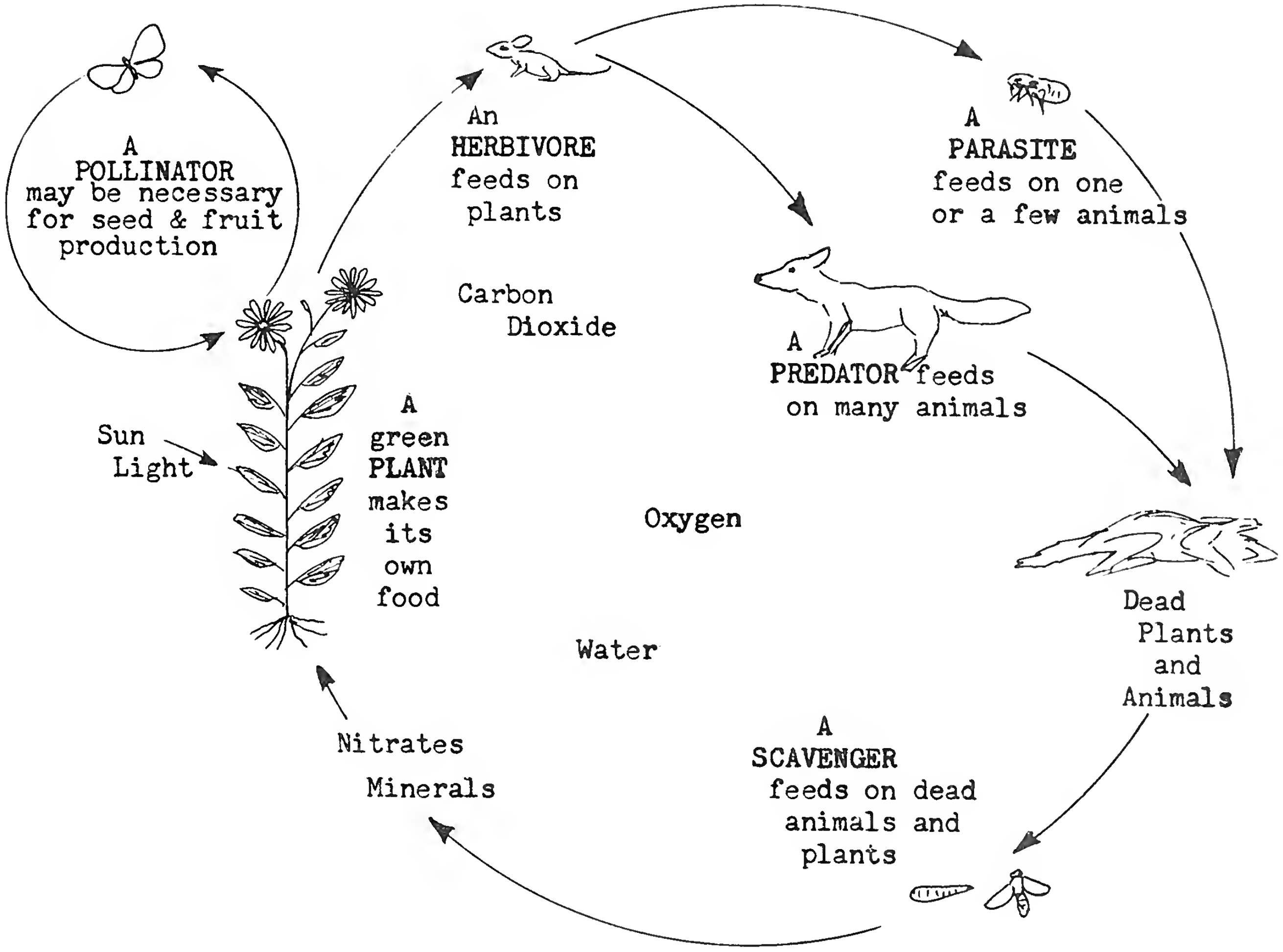
SIPHONAPTERA

Pa	308.8	Pulicidae	common fleas

HYMENOPTERA

H	314.6	Tenthredinidae	common sawflies
Pa	320.8	Braconidae	braconid wasps
Pa	322.0	Ichneumonidae	ichneumonid wasps
Pa	324.9	Eulophidae	eulophid wasps
Pa	328.0	Chalcididae	chalcid wasps
Pa	330.3	Eurytomidae	eurytomid wasps
Pa	330.5	Perilampidae	perilampid wasps
H	332.6	Cynipidae	cynipid wasps and gall wasps
Pa	338.8	Chrysididae	cuckoo wasps
H S Pr	344.5	Formicidae	ants
Pr	346.6	Vespidae	hornets and paper wasps
Pr	350.2	Sphecidae	sphecid wasps
H	356.0	Colletidae	yellow-faced and plasterer bees
H	356.4	Andrenidae	andrenid bees
H	356.8	Halictidae	halictid bees
H	358.0	Melittidae	melittid bees
H	358.1	Megachilidae	leafcutting bees
H	358.4	Apidae	honey bees, bumble bees, digger bees

Figure 12. The Food Chain in a Natural Habitat



A9. Mark specimens in the project A collection to indicate their position in the food chain (figure 12). This can be done by cutting and pinning a small colored tag to each specimen (figure 10). Use a red tag for a predator; orange for a parasite; green for an herbivore; black for a scavenger; and yellow for a pollinator. Almost all pollinators will bear two tags.

Catalog numbers or names

Herbivores (green) ____

Predators (red) ____

Parasites (orange) ____

Scavengers (black) ____

Pollinators (yellow) ____

Additional and Alternative Techniques in Making an Insect Collection

A10. Relaxing an Insect Specimen

Because of their hard exoskeleton, insects can be preserved indefinitely merely by drying. Best results in mounting are obtained by pinning and spreading while the insects are still flexible, immediately after being killed. If impractical to mount them so soon, pack in envelopes or small cardboard boxes and store where carpet beetles and mold cannot attack them. The mold danger is increased if the insects are not perfectly dry when placed in glass or plastic vials. Insects, extremely fragile when dry, should never be handled when dry nor should the envelope be opened.

An insect specimen can later be " relaxed," spread, and mounted in a desired position by placing it (still in its envelope or box) in a moist chamber. The simplest relaxing chamber consists of a large glass with two or three crumpled paper towels in the bottom. Put enough water on the paper to wet it, but not so much that there is any free water in the jar.

Place the storage envelopes in the jar and close the jar. Usually 12 hours is enough time to moisten the insects so the joints are flexible and the legs, antennae, and wings can be moved without breaking. If appendages are still stiff, leave the insect in the relaxing jar for a longer period of time.

Mold is always a threat to any specimen in a moist situation, so steps must be taken to avoid leaving the insect in a relaxing jar for too long a time. Danger from mold can be reduced by placing moth crystals (paradichlorobenzene or naphthalene) or carbolic acid (such as " Lysol ") in the jar. Prevent carbolic acid from getting on the insect.

A11. Mounting Moths and Butterflies

1. Section A6 describes the method for pinning an insect. Do not pin any specimen you plan to mount on cotton, under glass. In either case, moths, butterflies and some other insects should be spread on a board (figure 14) and allowed to dry while the wings are held in the desired position. Three to 10 days may be required, depending on the size of the insect and room humidity.

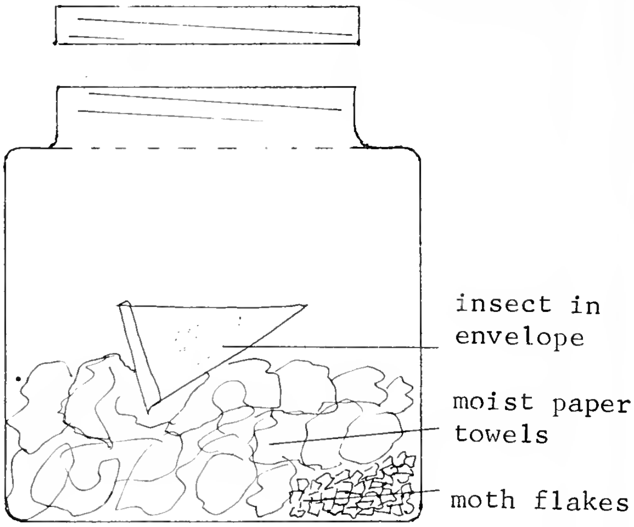


Figure 13

2. Place the body of the specimen in the slot of the spreading board. Hold the body in place with a pin on each side of the head and on each side of the body, just behind the wings (figure 14).

3. Use a very fine pin to move one front wing to the desired position (figure 15). Hook this pin just behind a vein so the wing will not be torn. Do the same with the hind wing on the same side.

4. Cut a thin (¼ inch) strip of heavy paper and pin in over the spread wings (figure 15) to hold the wings in position. Place this strip very close to the body. Remove the pins used to move the wings into position.

5. Repeat this procedure with the wings on the other side. Check to be sure your specimen is symmetrical.

6. Place a broader strip of paper over the rest of the wing surface on each side (figure 16). Arrange legs and antennae and hold in position with pins. Set the board in a safe place to dry.

7. When the specimen is dry, remove the pins and strips of paper and add labels.

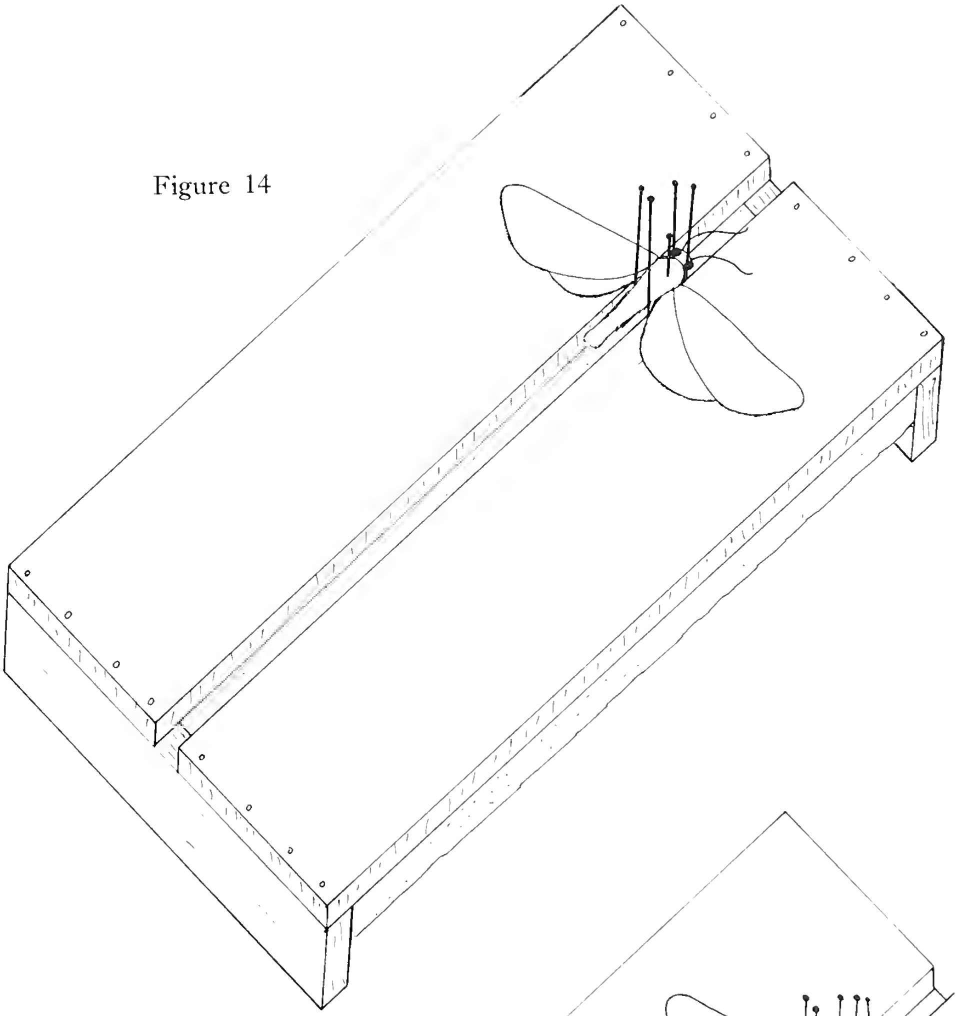


Figure 14

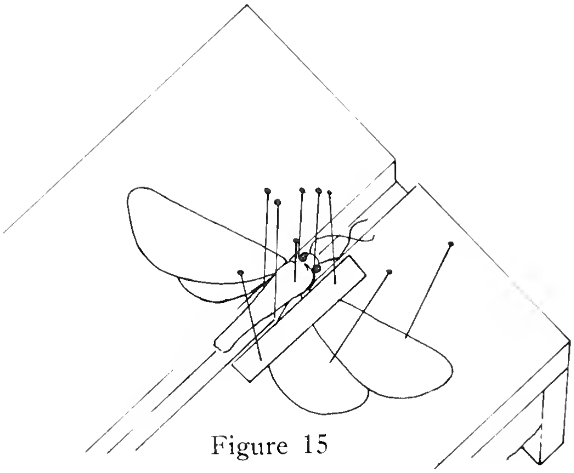


Figure 15

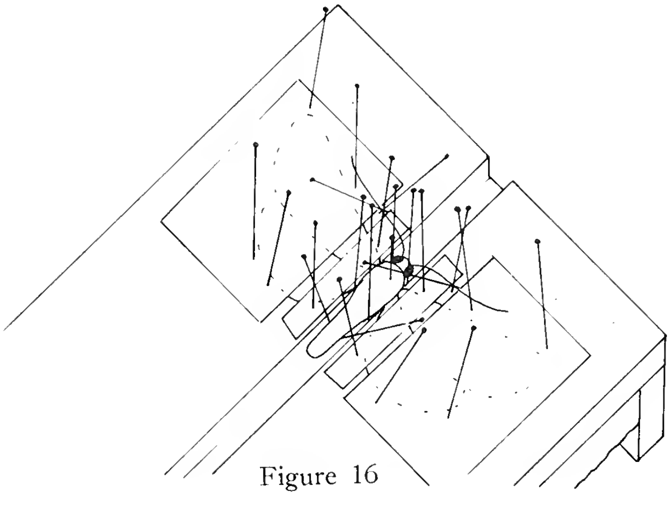
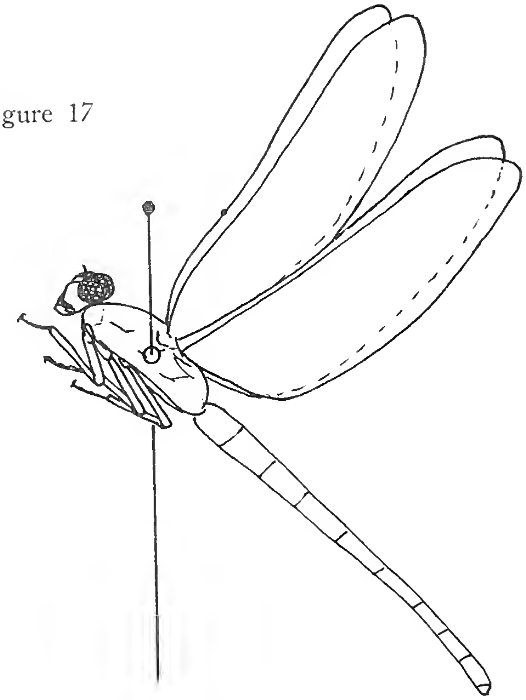


Figure 16

Dragonflies

Dragonflies may be spread and dried with the same method used for butterflies. An alternative method, used more often, is to fold the wings together over the back and pin the insect through the sides.

Figure 17



A12. Killing and Preserving Fluid for Soft-Bodied Insects

Preserve spiders, grubs, caterpillars, maggots, and other soft-bodied insects in 70 percent ethyl alcohol. Frequently specimens become shriveled and sometimes discolored if dropped directly into the alcohol. Kill them in water heated just to boiling, or in a killing fluid mixed as follows.

Kerosene	1 part
Alcohol (95 percent ethyl alcohol)	10 parts
Acetic Acid (glacial)	2 parts
Dioxane (may be omitted if the kerosene mixes with the other ingredients)	1 part

Leave the insect in the K.A.A.D. for several hours and then transfer to 70 percent alcohol for permanent storage. Most "rubbing alcohol" is made of isopropyl alcohol, but ethyl alcohol can usually be found at drug stores in your community.

Any other insects, except moths, butterflies, fuzzy flies, and bees can be stored in alcohol.

Store soft-bodied insects in alcohol in small bottles, vials, or test tubes. Figure 9 shows a 4 dram, homeopathic, glass vial with a neoprene stopper. This type of vial is perhaps the best container for wet collections, although rather expensive (vials are priced at 7¢ and stoppers at 5¢ in current catalogs). Natural cork stoppers are less expensive but sometimes permit the alcohol to evaporate in a few months, thus destroying the specimen. Use of 10 dram, plastic, snap-cap vials is cheaper (figure 18). These plastic vials can be obtained from many drug stores for about $5 per gross. However, fluids escape very quickly. If you wish to use these vials, half fill with alcohol and store in larger glass jars (such as 1 quart mayonnaise jars). Add about a cup of alcohol to the jar and check every few months to prevent drying.

A13. Dry Preservation of Soft-Bodied Insects

Soft-bodied insects such as caterpillars, grubs, and maggots can be preserved by drying using the following method.

1. Kill the insect in hot water or K.A.A.D. to extend it and harden the tissues. Preserve in 70 percent ethyl alcohol indefinitely or until ready to dry.

2. Transfer the specimen to a jar of acetone for ½ to several hours, depending on the size of the specimen. The acetone will remove water and fats or oils from the body. Many specimens or large ones will dilute and contaminate the acetone, so the specimen should be

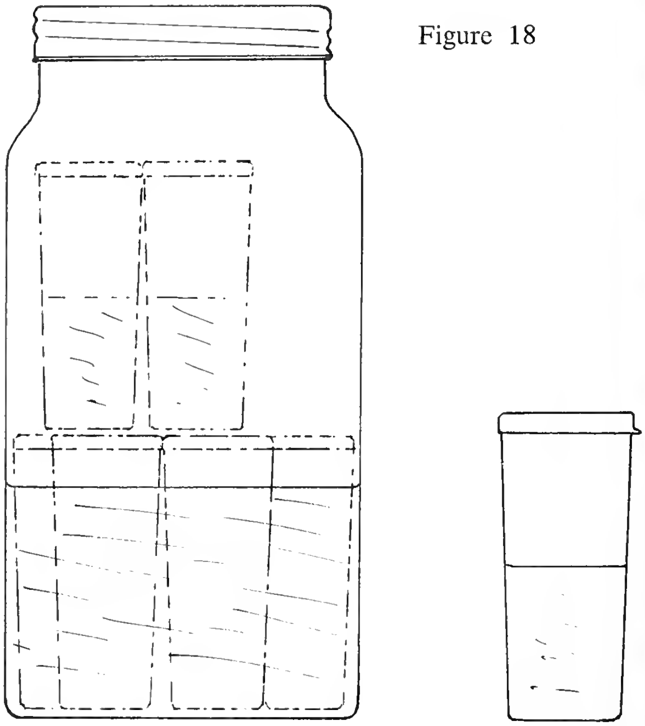


Figure 18

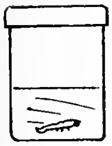


Figure 19

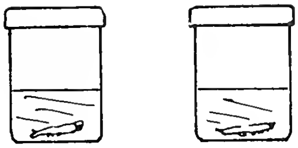


Figure 20

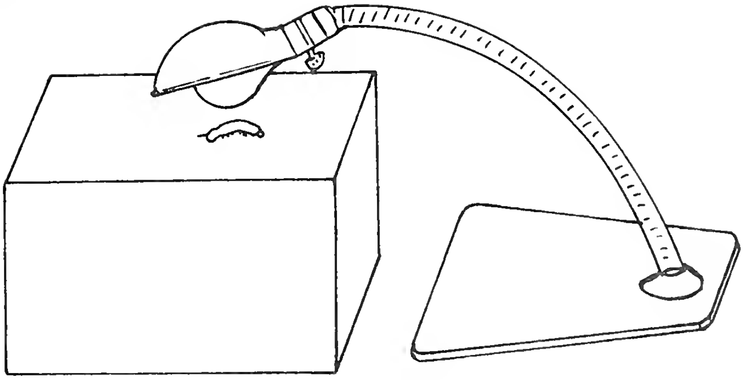


Figure 21

transferred again to another jar of fresh acetone. Unless *all* water and grease is removed, the specimen will not dry properly.

3. Remove the specimen from acetone and place on a paper towel. Put the paper towel and specimen under an electric light to dry. A goose-neck lamp works very well. Tilt the lamp so the bulb is very close to the specimen — 1 to 3 inches if a 60 watt bulb is used. Leave the specimen there until completely dry. This may take a few minutes for small insects or a few hours for large ones such as tomato hornworms.

Acetone evaporates quickly and maintains enough pressure when heated to inflate and keep the body of the insect expanded until dry. The specimen will collapse if the distance to the heat source is too great. Small specimens will burst if placed too close to the light bulb. A little experience will teach you how to adjust specimens to the right temperatures.

4. Dried specimens, extremely fragile, must be handled with great care but can be treated in the same manner as harder-bodied insects. They can be pinned, glued to paper points or wires attached to pins, or placed in Riker mounts.

Unfortunately, specimens dried in this way become faded. Greens and yellows may disappear completely and reds and browns lose their intensity.

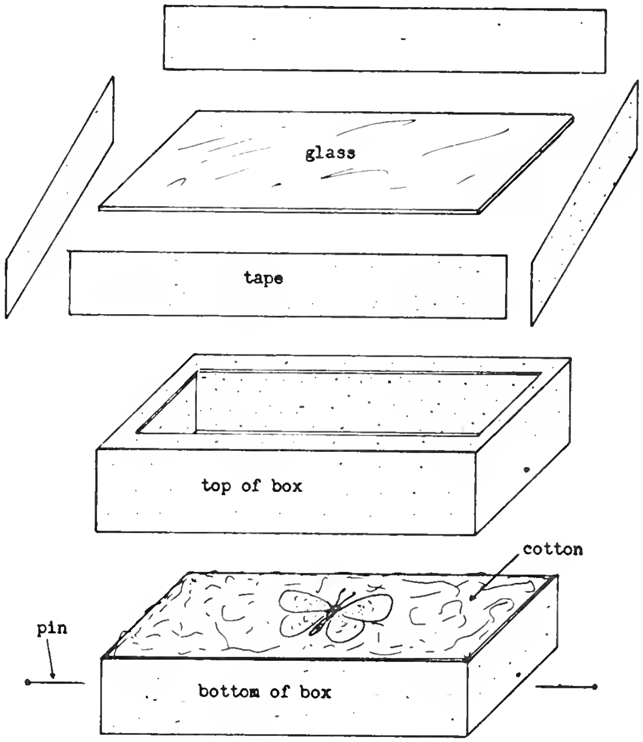


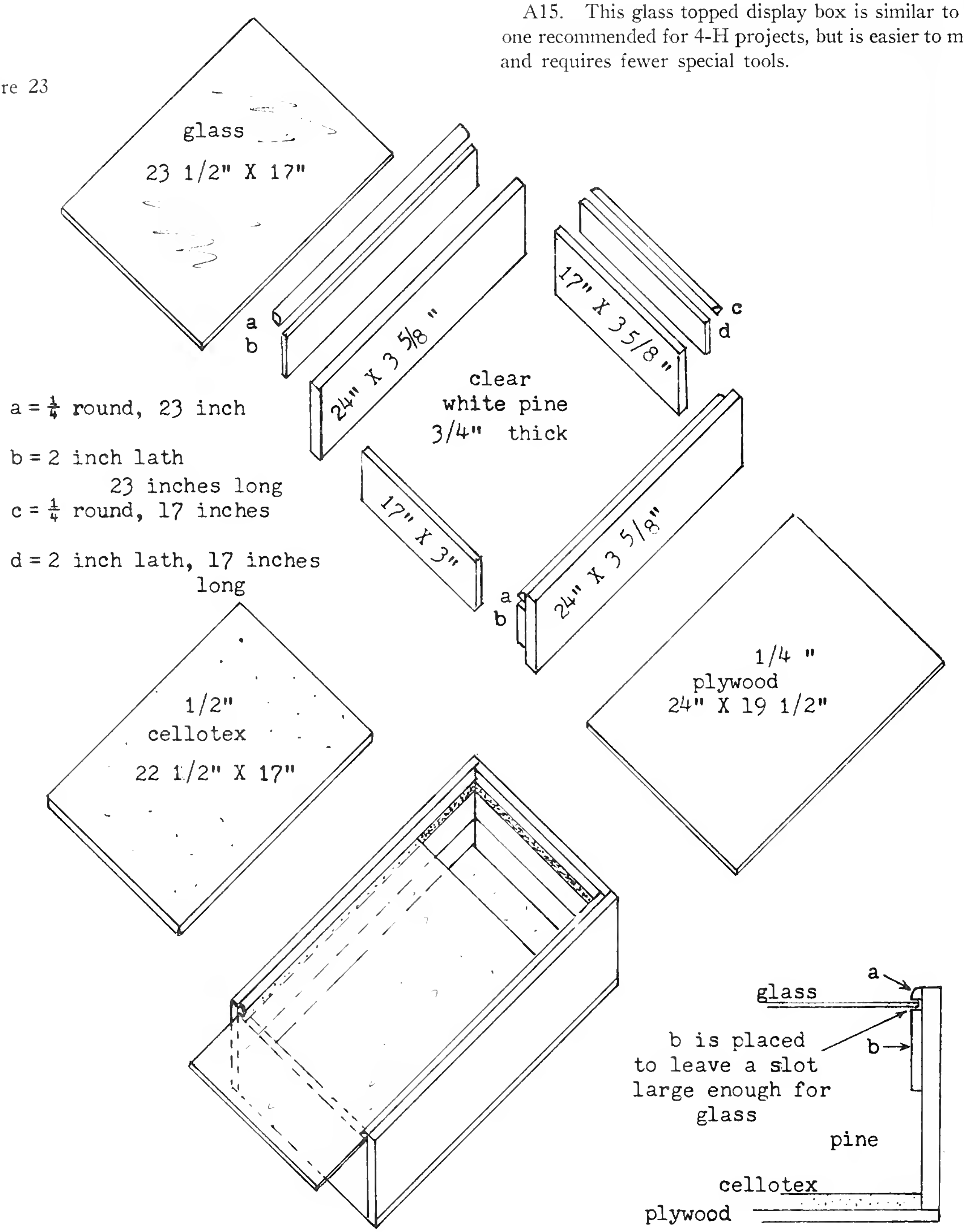
Figure 22

A14. Riker Mount

The Riker mount, another popular type of storage-display box, has the disadvantage of holding the insect specimen in a single position thus preventing examination of the underside. Its advantage lies in the greater protection given the specimens and the reduced space required for a collection. To make a Riker mount, use a flat box about ¾ inch deep. Fill it with cotton. Cut the center of the top out, leaving an edge about ¼ inch. Cut a piece of glass as wide and as long as the box top. Place the glass on top of the box top (outside) and seal down with tape. Place the insects on the cotton in the box and replace the top. Seal by running pins through the sides, or by tape. Store this box in a cabinet or container with moth balls to protect the specimens from carpet beetles.

A15. This glass topped display box is similar to the one recommended for 4-H projects, but is easier to make and requires fewer special tools.

Figure 23



Additional Projects

Project B. Intermediate General Collection.

Make a collection of 50 different species. Notebook records should be prepared as in project A. ( )

Include 10 orders of insects (see next page). ( )

Include 3 orders of arthropods other than insects. ( )

Include 3 species beneficial to man.

catalog
number ____, ______________________ ( )
____, ______________________ ( )
____, ______________________ ( )

Include 3 species harmful to man.

catalog
number ____, ______________________ ( )
____, ______________________ ( )
____, ______________________ ( )

Include three species too small to mount on pins.

catalog
number ____, ______________________ ( )
____, ______________________ ( )
____, ______________________ ( )

Project C. Insect Architects

Make a collection of at least six different kinds of "bug houses," that is, structures made by the insects themselves or produced by insects. How does the insect make each of them? Is the structure made of material from the insect's body, from living plant material, or other material? Know to what order the insect belongs and what stages of its life cycle can be found within.

These structures provide some protection to the insect, its eggs, growing larvae, or pupa. Examples are: wasp nests, caterpillar tents, caddis cases, and insect galls. For further information see *The New York State Conservationist,* April 1962.

Catalog number	Type of structure	Material used
	Insect responsible	Order

Project D. Predators

Make a collection of 10 different insects which capture and feed on other insects (predators). Predators must be captured while still holding their prey. Mount the predator and prey side by side in the collection. Give each a separate catalog number.

predator ______________________ order __________ cat. no. ______
prey ______________________ order __________ cat. no. ______
predator ______________________ order __________ cat. no. ______
prey ______________________ order __________ cat. no. ______
predator ______________________ order __________ cat. no. ______
prey ______________________ order __________ cat. no. ______
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prey ______________________ order __________ cat. no. ______
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prey ______________________ order __________ cat. no. ______
predator ______________________ order __________ cat. no. ______
prey ______________________ order __________ cat. no. ______
predator ______________________ order __________ cat. no. ______
prey ______________________ order __________ cat. no. ______

Project E. Parasites Reared From Insect Hosts

Make a collection of six different kinds of parasites including both Diptera and Hymenoptera. Each specimen should be accompanied by the remains of the insect host on which it developed. Collect also insect specimens diseased by fungi which produce recognizable fruiting bodies.

Capture and rear a large number of nearly full-grown larvae or collect a number of pupae. Treat them as you would for project J. Look especially for those which appear to be sick or dead. Keep them in very tight cages and watch for parasitic flies or wasps which may emerge from the dead bodies 3 or 4 weeks after the host dies. Cocoons which do not hatch may contain parasites so keep them for several weeks after others of the same kind have produced moths.

parasite ________________________________ cat. no. ______
order ____________________ attacking the ______________ stage of
host ________________________ in order ________________
parasite ________________________________ cat. no. ______
order ____________________ attacking the ______________ stage of
host ________________________ in order ________________
parasite ________________________________ cat. no. ______
order ____________________ attacking the ______________ stage of
host ________________________ in order ________________
parasite ________________________________ cat. no. ______
order ____________________ attacking the ______________ stage of
host ________________________ in order ________________
parasite ________________________________ cat. no. ______
order ____________________ attacking the ______________ stage of
host ________________________ in order ________________
parasite ________________________________ cat. no. ______
order ____________________ attacking the ______________ stage of
host ________________________ in order ________________

Project F. Rear Mosquitoes From Larva to Adult

Mosquitoes are very easy to rear. Catch wigglers with a cup or kitchen strainer (fine mesh). Half fill a pint or quart jar with water from the pool in which you found the wigglers and rear the wigglers in it. Cover with a piece of cloth to keep adults from getting loose.

Eggs are laid on water or ground that is likely to be flooded. Most mosquitoes scatter their eggs, but some species lay eggs in small masses (rafts) which float on the surface of the water.

Larvae live in water and can be found from April to October. The manner of swimming has given them the name " wigglers." These wigglers must breathe air, and at the caudal end of the body spiracles thrust up through the water's surface. In most species, larvae feed on algae and organic debris. Usually there is enough such matter in the water in which larvae are found to supply food until maturity is reached. Culicine mosquitoes (*Aedes and Culex*) have spiracles on the end of a long siphon and can be recognized by the presence of the siphon and habit of hanging head down from the surface of the water while breathing. Anopheline mosquitoes (*Anopheles*) do not have a long siphon and rest parallel with, and just below the surface of the water when taking in air.

Mosquito pupae are quite active and different from most other insects. The comma-shaped pupa can be seen swimming to the surface of the water to breathe. In this stage, the air-breathing spiracles are on the thorax.

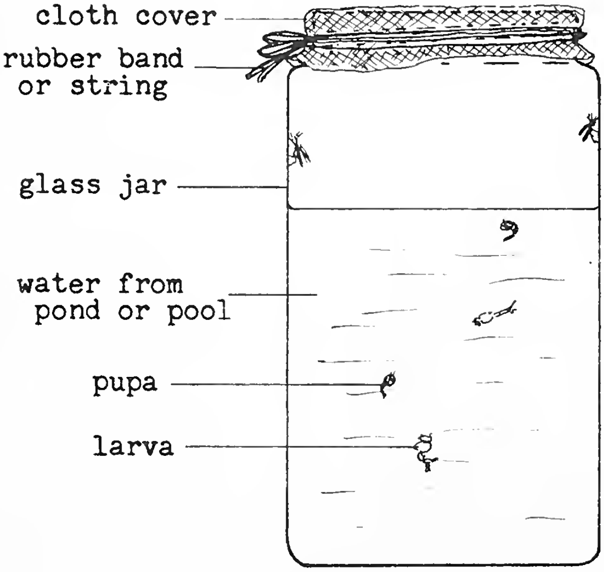


Figure 24

Adults emerge from the pupal skin at the surface of the water, and can alight on the glass sides of the jar or even on the water. Only females can bite, and have relatively thin antennae. Males have bushy antennae. Anophelines, which can carry malaria, have spotted wings and stand on their heads when biting. Culicines, which can sometimes carry yellow fever, do not have spotted wings and rest parallel to the skin surface when biting. Mosquitoes carry disease pathogens only from some human or animal who has the disease.

Project G. Life Cycle of Goldenrod Ball Gall Fly

Observe development of the goldenrod ball gall fly through larval, pupal, and adult stages. Note that the young fly (larva) looks nothing like the adult. Observe parasites and predators and note their effect on the fly population.

Many insects provide shelter by producing plant galls. A gall, typically an abnormally swollen, hollow portion of a living plant, is plant tissue stimulated to unusual growth by some secretion of the insect. Galls produced by various insects vary from a slight swelling to a very ornate structure which does not appear to belong to the plant. However, a single insect species produces only a single type of gall.

One of the most easily found galls is the ball gall of goldenrod. This nearly spherical gall is produced by a dark brown fly with mottled wings. It spends the winter in the larval stage in the gall and can be found as an oval, headless, legless maggot.

When warm weather returns, the larva changes to a pupa and later emerges from the gall as an adult winged fly. Eggs are laid in late May or early June in the terminal buds of goldenrod. After hatching from an egg, the young larva bores through the bud to the

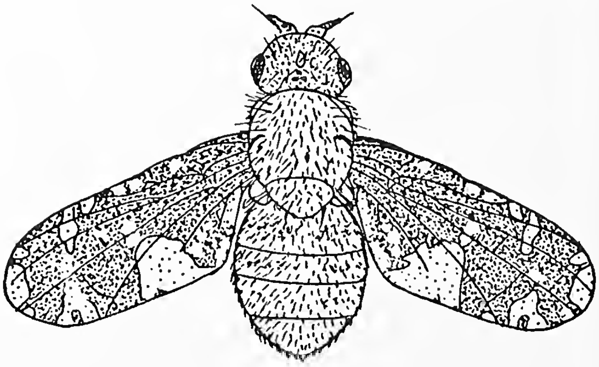
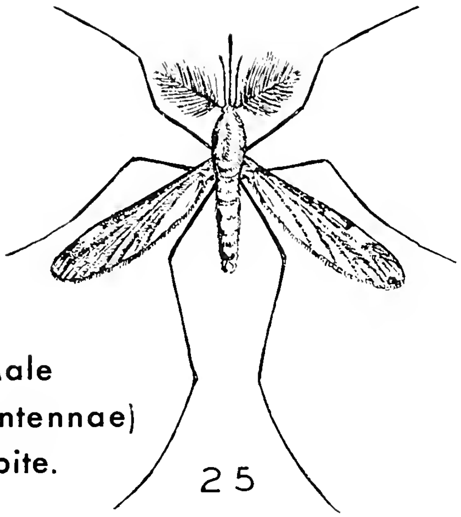


Figure 30

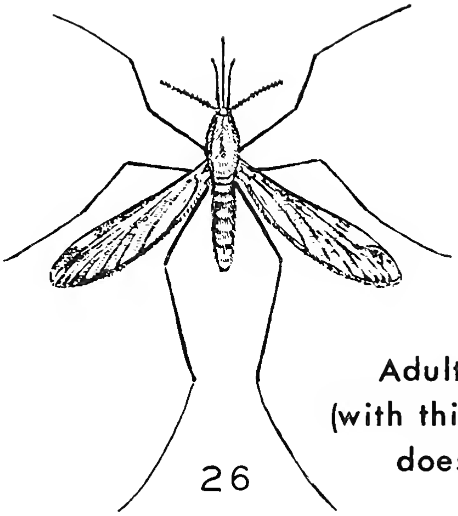
Figures 25–29

MOSQUITO LIFE CYCLE



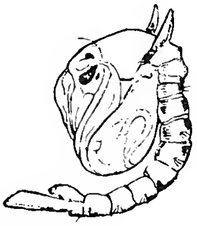
25

Adult Male (with fuzzy antennae) cannot bite.



26

Adult Female (with thin antennae) does bite!



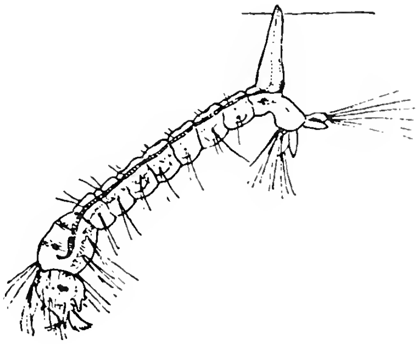
29

Pupae, also found in water, are very active.

27

Eggs are laid on water or on ground likely to be flooded.

28



Mosquito larvae, called wigglers, live in water but must breathe air from the surface.

meristematic tissue. Apparently the gall is produced in response to a chemical in the egg. A similar but more elongate gall is produced by the caterpillar of a small moth (figure 37).

Other insects are sometimes found in these galls. A parasitic wasp, *Eurytoma obtusiventris,* often attacks and kills the gall maker. The larva of this wasp enters the body of the fly maggot, induces it to form a small pupa in the autumn, kills the pupa and then changes to a pupa itself inside the fly puparium. A second species of wasp, *Eurytoma gigantea,* also attacks and kills the gall fly larva. The larva of this wasp does not enter the body of its host, and can also feed on plant tissue of the gall. Therefore, its status as a parasite is in question. The larva of a small mordellid beetle, *Mordellistena unicolor,* is the third type of insect frequently found. This larva normally feeds on plant tissue and can survive on the gall tissue. When this larva does break into the central cavity of the gall, it attacks and destroys the gall fly larva and may, therefore, be considered an " accidental predator " of the gall fly.

For further information see the article by Lowell Uhler, 1951, " Biology and ecology of the goldenrod ball fly, *Eurosta solidaginis.*" Cornell University Agricultural Experiment Station, Memoir 300.

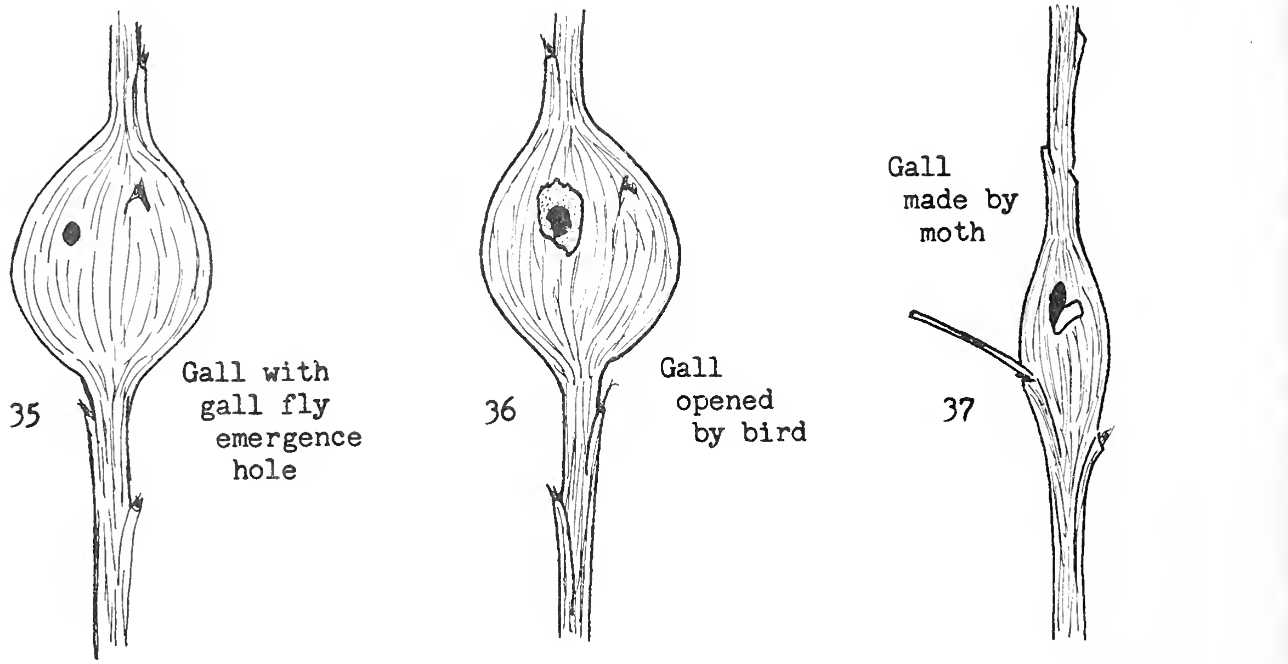
Collect a few galls in late summer or autumn, bring them into the classroom and open them. Observe the larva — color, size, shape. No change takes place during the winter, so the project can be suspended until the following spring. Since the larva may need a period of freezing temperatures before it will develop, the project should be continued (or started) in late winter or spring (February or March). Collect a large number of galls (30 or 40) and bring them into the classroom. Open a few and observe the larva. An empty cell and a rough hole in the gall (figure 36) indicates a bird has eaten the larva. Two or three types of larvae may be found (see discussion above and figures below). Record appearance of gall fly larva, and store the rest of the galls in a cage or large, covered jar. Four or 5 days later open several more galls and record observations. Repeat this procedure until flies begin to emerge from the galls

Gall fly larva natural size

Wasp larva

Normal Gall fly pupa

Parasitized gall fly pupa



Figures 31–37

(approximately 2 or 3 weeks). Leave the rest of the galls in the cage for a few more weeks and watch for tiny black wasps or beetles to emerge.

Insects, other than the gall fly, which may be found in or reared from ball galls of goldenrod. The small figure next to the numeral indicates the natural size of the insect.

38. A eurytomid wasp, *Eurytoma gigantea.* A partial parasite of the gall fly, its larva does not enter the body of the fly larva.
39. A mordellid beetle larva which may be a predator on the gall fly larva.
40. A mordellid beetle adult, *Mordellistena unicolor.*

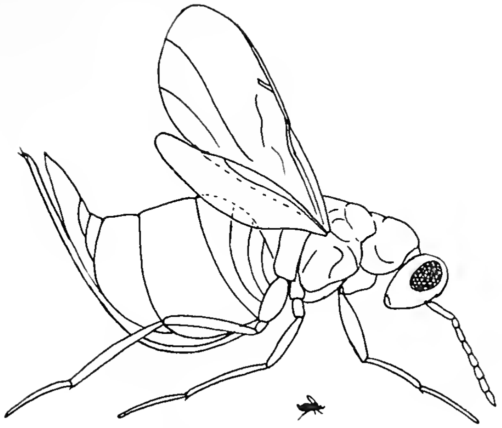


Figure 38

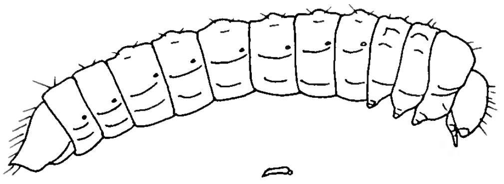


Figure 39

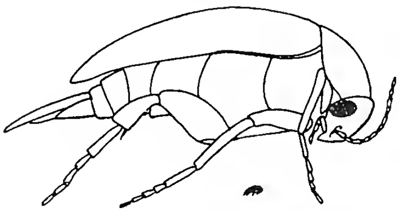


Figure 40

Make observations on the reduction of an insect population by parasites and predators. Select an area with at least 50 goldenrod ball galls in autumn. Divide this area into two sections so each section has about half. Do not disturb section 1 but count the number of galls and mark the section so you can find it in the spring. Collect all the galls in section 2 and bring into the classroom. Do not miss any, even the little ones, but count only those produced by the ball gall fly. Open the collected galls and record the following data:

	Autumn		Spring	
	number	%	number	%
1. number of galls				
2. galls with living gall fly larvae but no other insects				
3. galls with parasitized pupae				
4. galls with free wasp larvae or pupae				
5. galls with mordella beetles				
6. galls with some other insect				
7. galls opened by birds				
8. galls with nothing inside (possibly the larva was killed by disease or a parasite which died)				

Collect and open the galls in section 1 during March or early April. Record data as described above. Compare the recorded data for the two dates. What percentage of the flies survived to start the next generation?

Project H. Identity of a Family and Variation Within a Species

Lady Beetles of New York

Lady bug, lady bug, fly away home,
Your house is on fire, your children will roam,
Except little Nan, who sits in a pan
Weaving gold laces as fast as she can.

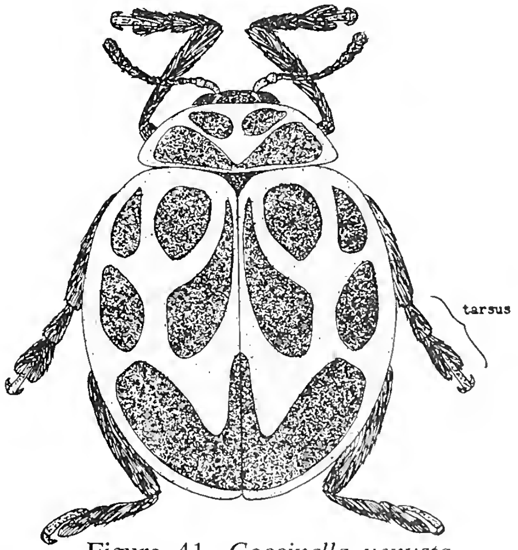


Figure 41. *Coccinella venusta*

Lady Beetles of New York

The following species are figured here:

Figure 42. *Hippodamia glacialis,* the glacial lady beetle.

43. *Hippodamia parenthesis,* the parenthesis lady beetle.

44. *Coleomegilla maculata,* the spotted lady beetle (formerly called *Megilla fuscilabris*).

45. *Hippodamia convergens,* the convergent lady beetle.

46. *Naemia seriata.*

47. *Hippodamia tredecempunctata,* the thirteen-spotted lady beetle.

48. *Coccinella novemnotata,* the nine-spotted lady beetle.

49. *Coccinella trifasciata,* the three-banded lady beetle.

50. *Coccinella transversalis,* the transverse lady beetle.

51. *Epilachna borealis,* the squash beetle, eats leaves of squash plants.

52. *Epilachna varivestis,* the Mexican bean beetle, eats leaves of bean plants.

53. *Exochomus aethiops.*

54. *Adalia bipunctata,* the two-spotted lady beetle.

55. *Psyllobora vigintimaculata,* the twenty-spotted lady beetle, eats fungus spores.

56. *Anatis quindecimpunctata,* the fifteen-spotted lady beetle.

57. *Anatis ocellata mali,* the eye-spotted lady beetle.

58. *Cycloneda munda,* the red lady beetle.

59. *Adalia frigida.*

60. *Adalia frigida.*

61. *Mulsantina picta.*

62. *Mulsantina picta.*

63. *Mulsantina picta.*

64. *Mulsantina hudsonica.*

65. *Coccinella monticola.*

66. *Rodolia cardinalis,* the vedalia, not known from New York but figured here because it is one of the most famous beetles. It was introduced into California and Florida from Australia to help control the cottony cushion scale on citrus trees.

67. *Neomysia pullata.*

68. *Coccidula lepida.*

69. *Scymnus fraternus.* Several other small species of *Scymnus* also occur in New York.

70. *Hippodamia parenthesis* (see also figure 2).

71. *Hippodamia parenthesis.*

72. *Anisosticta strigata.*

73. *Brachyacantha ursina.* Several other species of *Brachyacantha* also occur in New York.

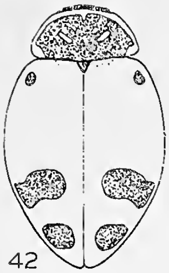
74. *Hippodamia convergens,* larva (adult in figure 4).

75. *Hippodamia convergens,* pupa.

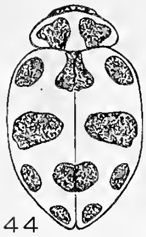
76. *Harmonia similis.*

77. *Chilocorus bivulnerus,* the twice-stabbed lady beetle.

78. *Harmonia similis.*


42
H. glacialis


43
H. parenthesis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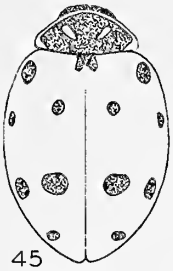
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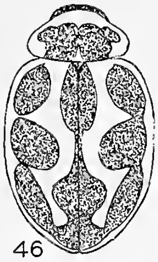
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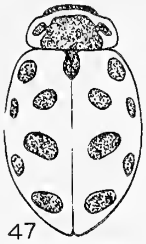
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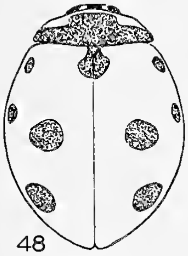
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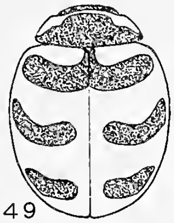
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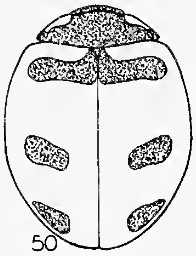
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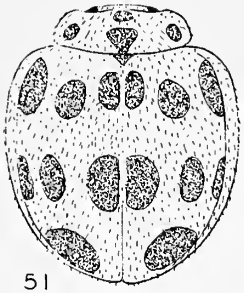
C. transversalis

5 mm.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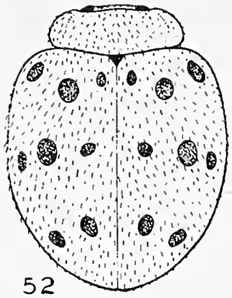
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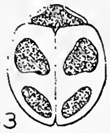
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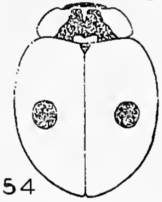
E. aethiops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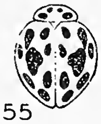
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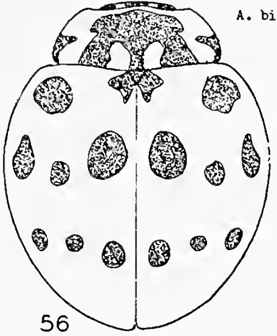
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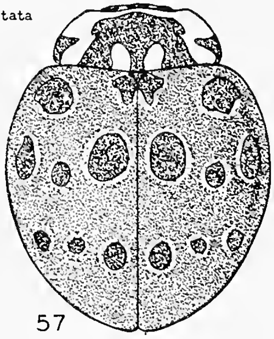
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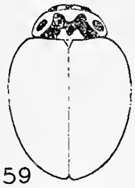
A. ocellata mali


58
C. munda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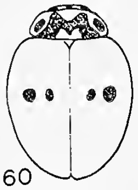
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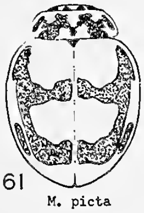
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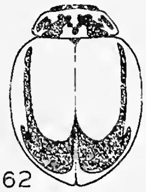
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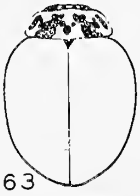
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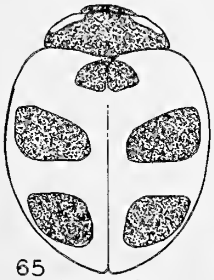
M. picta


64
M. hudsonica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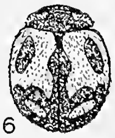
C. monticola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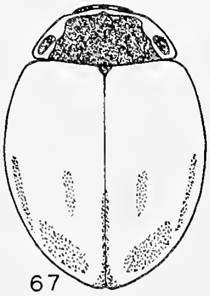
R. cardinalis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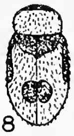
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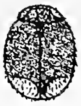
C. lepida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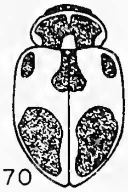
S. fraternus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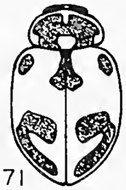
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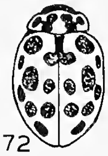
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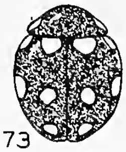
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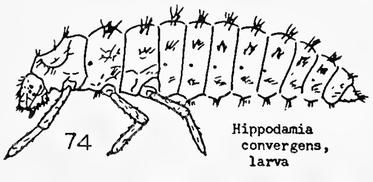
B. ursina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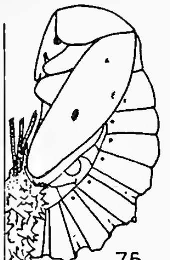
Hippodamia convergens, larva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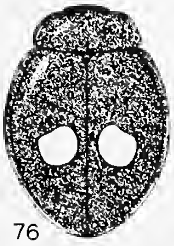
Hippodamia convergens, pupa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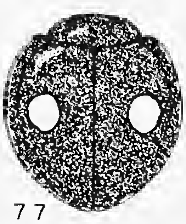
H. similis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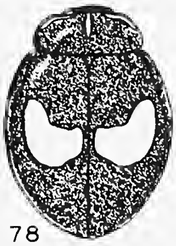
C. bivulnerus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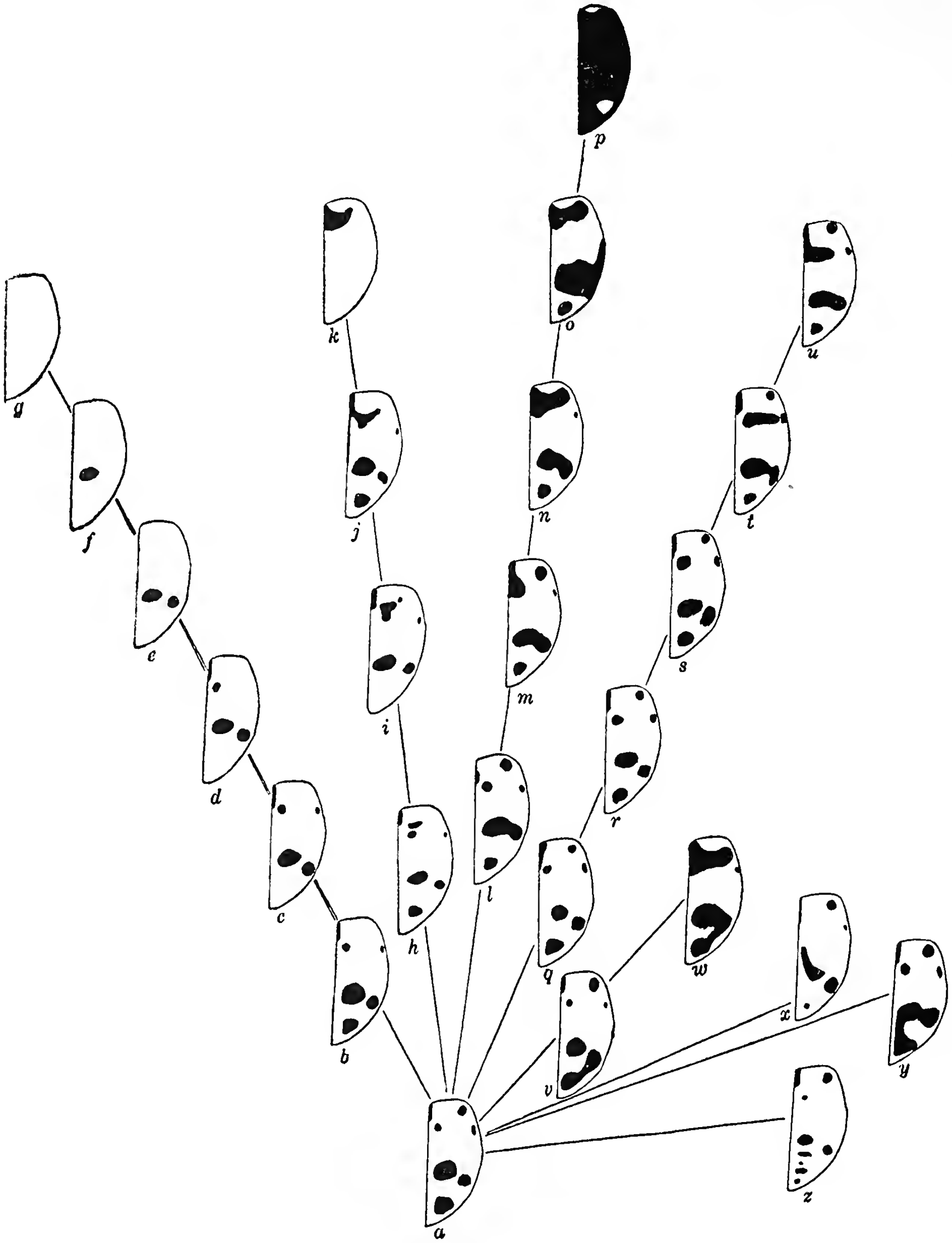


Variation of elytral pattern in *Hippodamia convergens.*

Figure 79

Illustration from *Determinate Evolution in the Color Pattern of the Lady Beetles,* by Roswell H. Johnson, 1910, Carnegie Institution of Washington, Publication No. 122

The lady beetles are probably as familiar to us as any of the beetles. The old nursery rhyme above dates back to the middle ages. Even then the value of lady beetles in destroying harmful insects was realized. The nursery rhyme shows a knowledge too, of the life history of these small creatures, in referring to the time, after harvest, when the hop vines were burned. The lady beetle's children (larvae which look nothing like their parents) would crawl away from the burning vines. The young lady beetles which have reached the yellow pupa stage, of course could not move, for they are fastened to the cast larval skin (the pan) which is, in turn, fastened to the leaf or stem of the plant.

There are only a few species of lady beetles in New York. The larger and more common ones are shown on the following page. All but three are considered to be beneficial, eating such other small insects as aphids and scale insects. Two eat leaves of bean or squash plants and are harmful; and one apparently lives on spores of certain fungi. The name lady beetle can be applied to any of the beetles belonging to the family Coccinellidae (cock-sin-ell′-id-ee). They are sometimes also called ladybird beetles or ladybugs. Some of the species have specific common names, but most have only a Latin or scientific name.

Most species of lady beetles are fairly easy to identify but some other beetles look similar. In members of the Coccinellidae, the tarsus (foot) consists of three segments. The second segment is dilated. Most species can be recognized by the markings on the head, thorax, and elytra, but color and color pattern in some insects and other animals are extremely variable (think of blondes, red heads, and brunettes in the human species).

Information on the use of lady beetles as predators in controlling aphids and scale insects can be found in the book, *Beneficial Insects,* by Lester A. Swan.

Make a collection of lady beetles, identify them to species, and examine a series of one species. Look for differences in color, size, and number of spots or stripes. Note that there is variation within a species as there is in human beings. Place a few of the beetles in a small cage, such as a petri dish or 1-quart glass jar. Locate an aphid colony and place it in the beetle cage. Aphids can usually be found on rose bushes, poplar trees, goldenrod, and other weeds. Cut the twig or leaf and put the base of it in water (figures 81, 82). The aphids drop off the plant when it is cut, so hold a dish or piece of paper under them when collecting the colony. They will crawl back to the twig after you place them in the cage.

Project I. Hornets

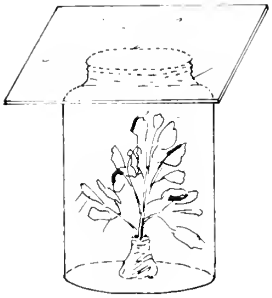
Hornets and yellow jackets are fascinating creatures, although somewhat dangerous. Perhaps this danger makes them so interesting. For most people, the hornet sting is quite painful, remains swollen, and itches for several days. Some individuals develop an allergy to the hornet's venom, and the anaphylactic shock which follows a sting may produce death in a short time. For this reason hornets should be treated with respect.

At times it is desirable to kill the hornets, either because they are a pest in a particular area, or to open and examine the nest. The latter must be done with much circumspection because inhabitants of the nest rush out in fighting form if the nest is disturbed. Insecticides, now being packaged in aerosol type containers, will spray a hornet or wasp nest from a distance of 10 to 15 feet. These sprays will kill the flying insects, although several days may pass before all are dead.

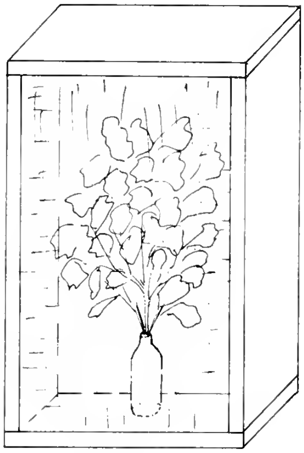
Engine starter is one of the best weapons for combating a nest of hornets or yellow jackets. This is basically ethyl ether in an aerosol spray can, available in auto supply stores. Normal use is to spray the ether into the air intake of an automobile engine for easier engine starting on cold days.

Approach the nest at night, 2 or 3 hours after sunset. By this time all of the insects are usually nested. Approach carefully and check with a flashlight to be sure all are inside. If there are a few still outside the nest, return another night. If all are inside, the operation can begin. Spray the ether into the opening of the nest for 3 or 4 seconds with a steady blast. The cold spray and the anaesthetizing ether will knock the hornets down almost immediately, at least those near the opening. Others will work their way down to the opening and must be sprayed as they appear at the doorway. After 5 to 10 minutes all buzzing sound will stop, indicating the hornets have all been immobilized. The nest can then be cut out of the tree or off the building to which it was attached. Place the nest in a tight can or box and pour on ethyl acetate or gasoline to kill the hornets. Some hornets will recover from the ether in a few hours. Remember: ETHER, ETHYL ACETATE, AND GASOLINE ARE POISONOUS AND FLAMMABLE OR EXPLOSIVE!

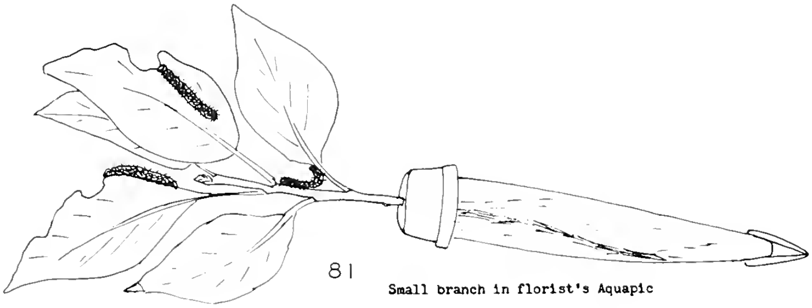
Figures 80–85



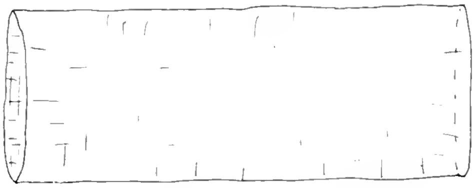
80 Rearing jar



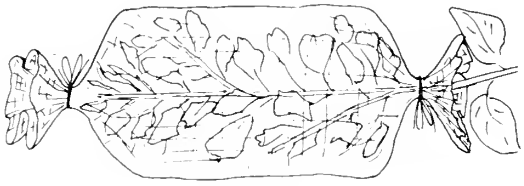
82 Rearing cage



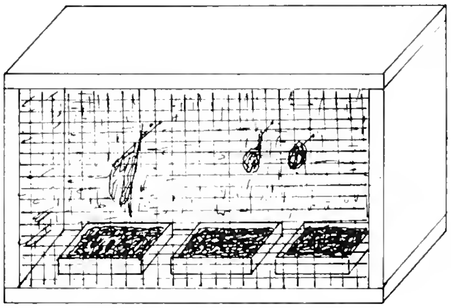
81 Small branch in florist's Aquapic



83 Sleeve cage made of dacron marquisette



84 Sleeve cage tied to tree



85 Emergence cage

Project J. Rearing Moths and Butterflies From Eggs

Max Richter, of the Butterfly Farm and Museum, East Durham, N.Y., suggests the following procedures for rearing caterpillars.

When you obtain eggs of a moth or butterfly, place them on absorbent paper and sprinkle lightly with a fine water sprayer. When dry again, place in a small glass jar lined on the bottom with absorbent paper. Cover the jar with glass or cardboard and put in a warm place (75 to 80 degrees F.). Do not put food into the jar with eggs. When eggs start to hatch, prepare another rearing jar by placing some leaves of the food plant in it. As caterpillars emerge, transfer them to this second jar. Most caterpillars are very particular and will eat leaves of only a very few plants. Be sure to offer the right food.

Separate rearing jars should be used for caterpillars emerging on different days. In other words, do not put caterpillars of different ages together. Larvae which have not started feeding within 12 hours should be given a little sprinkling, but not in the hatching jar. After drinking their fill, they will more readily take to food.

Continue rearing in this manner until the larvae have molted (shed their skins) for the third time, using larger and larger jars as they grow. Use wide mouthed jars and always have paper on the bottom. Never give wet or damp food, too much food in the jar at one time, or set the jar in direct sunlight. Do not overcrowd the caterpillars — the right number will be learned with a little experience. Mold is apt to grow in glass or metal cages so examine frequently and keep cages clean.

After the third molt, transfer the larvae to a large rearing cage. Branches of the food plant can then be set in a bottle of water (figure 82) and placed in the cage. It is recommended, especially when "soft" plants are used, that the branches be replaced every 48 hours. Use the best, cleanest, most mature leaves possible. Only very young caterpillars should be given young plant shoots of food. The later stages can also be reared on the host plants without removing branches by placing caterpillars directly on the leaves and protecting from predators by covering the branch with a sleeve cage. A sleeve cage is a cloth cylinder made of netting slipped over a branch and tied at each end.

A butterfly caterpillar forms a chrysalis above ground. Many moths spin silk cocoons above ground, often incorporating hairs, leaves, or other debris. Most other moths do not make cocoons but change to pupae in cells in the earth. If you do not know which type of insect you are rearing, provide a box of earth.

A caterpillar ready to spin its cocoon usually changes in color, and its excrement changes from dry, hard balls to a half-liquid form. The caterpillar will begin to wander around and shrink markedly. At this time put each one in a separate paper bag with a few leaves of food plant. When a cocoon is complete, remove from the bag and place in an emergence cage. Pin the cocoon to the side of the cage, several inches above the bottom, taking care not to run the pin through the pupa inside the cocoon.

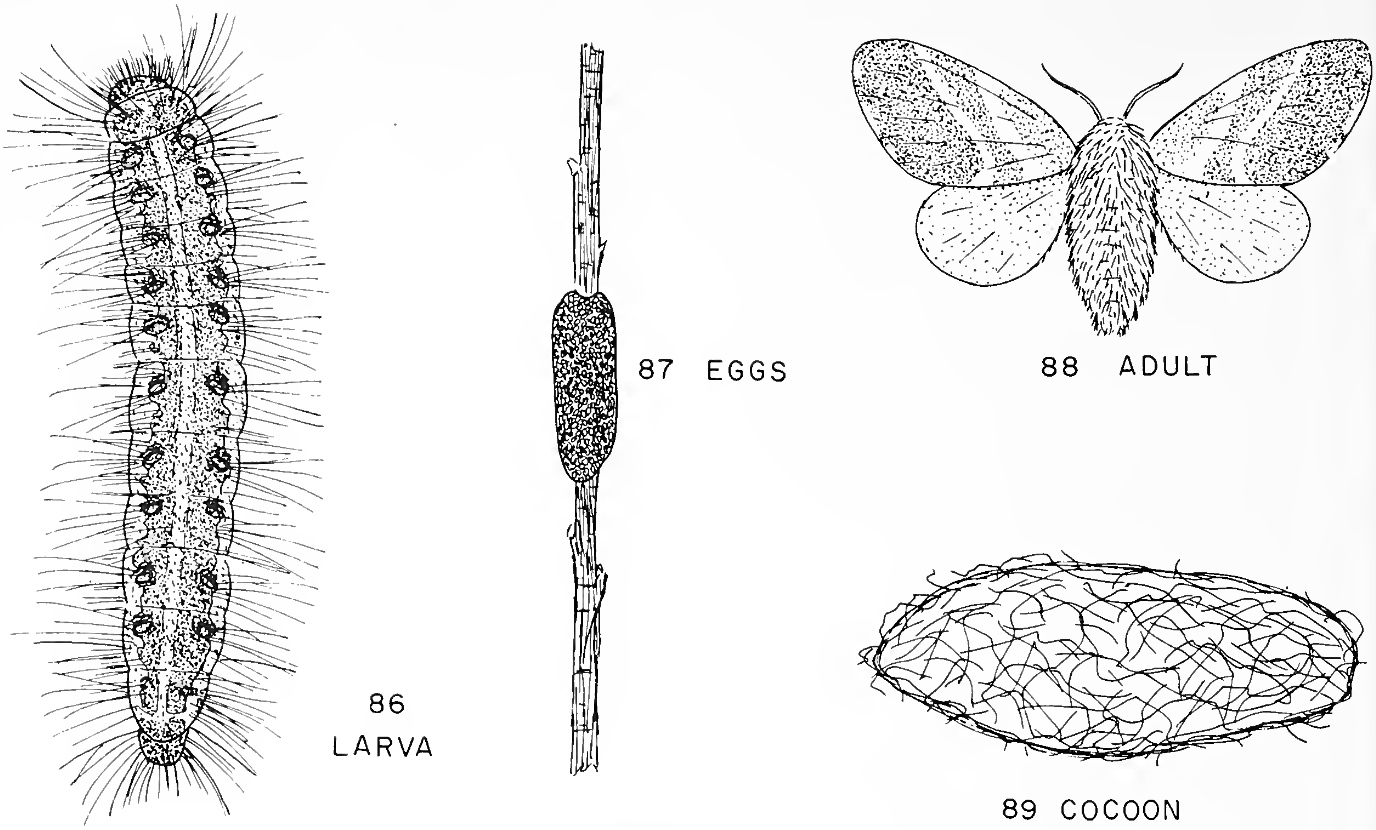
For hawk moths and other insects which pupate in the ground, provide a box with 2 or 3 inches of sifted earth on the bottom. Place dampened moss on the surface and put the caterpillar in the box. Remove the pupa from the earth about 2 weeks after the caterpillar disappeared into it. Roll the pupa in paper, leaving the head end open, and place the rolled pupa on the moss or sawdust in the emergence cage. Dampen it occasionally. A small, open container of water in the emergence cage is desirable to maintain a higher humidity than is usually found in a classroom.

The emergence cage should have sides of rough wood, or covered with coarse cloth or wire screen so the insect can hang on and climb up. Cover the bottom with damp moss or damp sawdust. The cage must be closed so the insect cannot escape.

Project K. Life Cycle and Behavior of Tent Caterpillars

Raise tent caterpillars from egg to adult. Observe growth and development in distinct stages (egg, larva, pupa, and adult, and step by step growth in the larval stage rather than a gradual increase in size). This project extends from April to June.

Obtain an egg mass from the small branches of wild cherry, apple, or peach trees. This mass, found throughout late summer, winter, and early spring, can be located easier in winter when the leaves are off the tree. Eggs hatch when buds open and new spring leaves start to develop. Bring in some branches without eggs a week or more before the eggs are brought indoors, so there will be a supply of food for the young caterpillars. Supplying an adequate amount of food for the caterpillars if they are started early can be a serious problem. Cut branches placed in water as quickly as possible will remain green and fresh longer if the basal 4 or 5 inches of the branch are cut off under water then placed in a jug (figure 90). More than 100 caterpillars may hatch from one egg mass. This number will soon eat



86 LARVA

87 EGGS

88 ADULT

89 COCOON

Figures 86–89

leaves faster than you can provide them, so, as the caterpillars grow, destroy most of them, leaving a population of not more than 15 or 20. Small caterpillars will remain on the branches if the jugs holding branches are set in pans of water, and as long as there is an adequate food supply. After becoming 1½ inches long caterpillars should be kept in a cage to prevent their wandering around the classroom. When fully grown, the caterpillars will naturally wander away from the food supply in search of a good place to spin cocoons.

QUESTIONS TO ANSWER FROM DIRECT OBSERVATION OF TENT CATERPILLARS

Where is the nest made?
Do caterpillars remain in the nest all the time?
Do caterpillars remain in the nest on bright, sunny days?
Do caterpillars remain in the nest on dark, cloudy days?
Do caterpillars make a trail of silk on their route to the leaves where they feed?
What happens if this trail is destroyed (rubbed off) or covered by a branch or leaf?
How do caterpillars act if their nest is removed or access to it broken?
Will caterpillars build a new nest if their old one is removed?
Do caterpillars ever make bridges from one branch to another?
Do caterpillars eat leaves? flowers? bark?
How do caterpillars eat?
Do caterpillars eat all of the leaf?
Do caterpillars drop any parts of a leaf?
How long are caterpillars when just hatched?
How long were caterpillars when you first measured them?
How long were caterpillars a week later?
How long were caterpillars when full grown?
How much did caterpillars grow in a week, in length?
How much did caterpillars grow in a week, in bulk?
How do caterpillars walk?
How many legs do caterpillars have?

How many legs do caterpillars need to hold on to a branch?

Can you watch a caterpillar molt (shed its skin)?

How does it do this?

How does the head compare in size before and after molting?

How does the body compare in size before and after molting?

How does the caterpillar react when slightly disturbed (blow on them at a time when they are eating or moving about)?

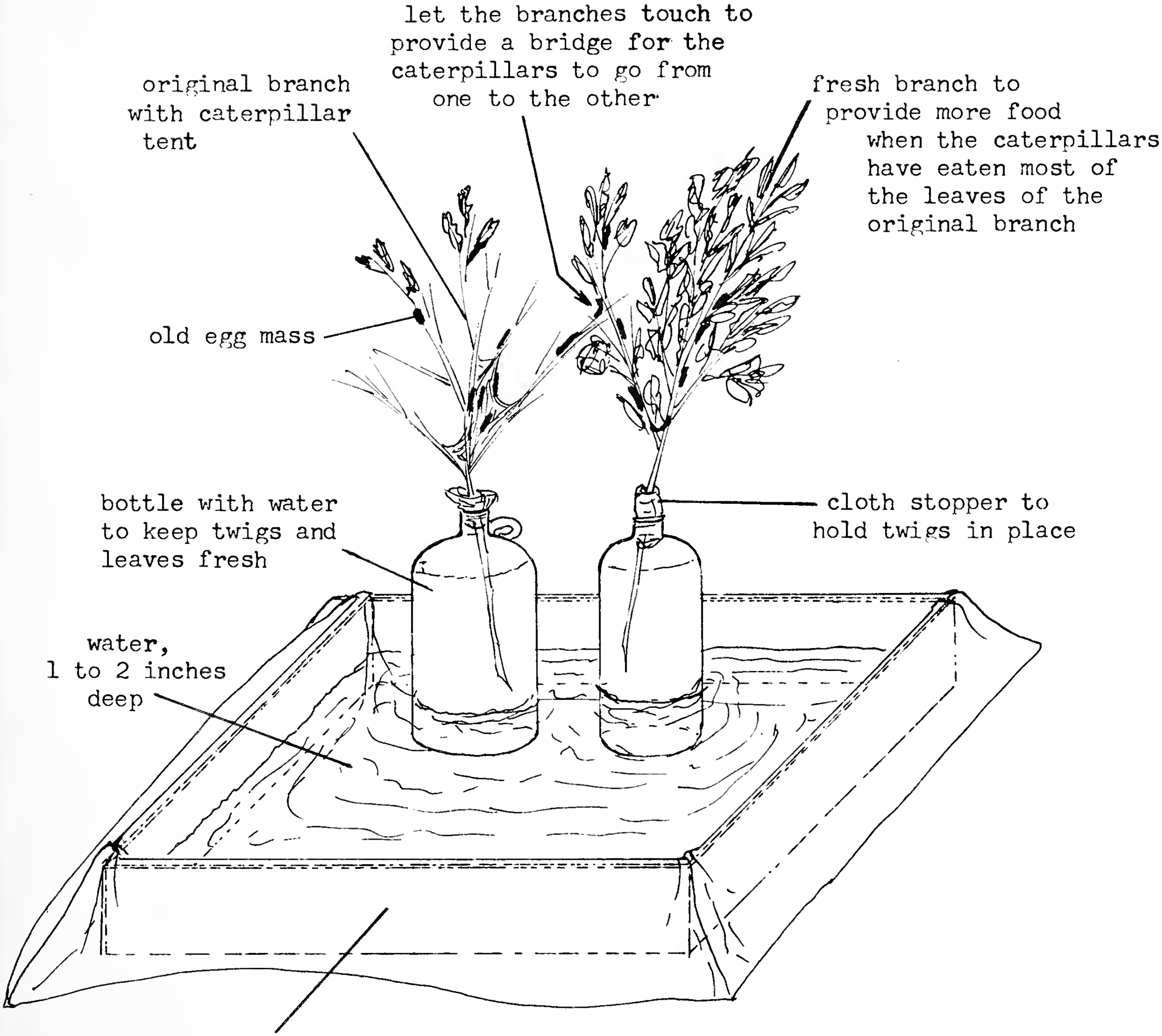
How does the caterpillar react when greatly disturbed (poke one with a pencil)?

Are these reactions apt to be effective?

Are caterpillars gregarious?

Figure 90.

Arrangement for rearing tent caterpillars



Large pan or box with strong plastic liner to hold water, which provides a moat to confine the caterpillars. They will not try to get away unless there is a lack of good fresh leaves.

Activity Outlines and Notices

Entomological Workshop

The next meeting will be a "workshop" meeting. This means that in addition to the formal lecture you will take an active part in the activities of the meeting. You will actually mount insects, label them, prepare a catalog, identify to order (use a key), get some suggestions on storing and exhibiting your collection, and making some pieces of equipment.

The price of admission is some small entomological item for exhibit. This can be an insect, a small collection, work done by insects, photographs, a piece of equipment, some observation you have made, a suggestion on how to work with insects, some article clipped from the newspaper, or any item you find interesting or think might be interesting to someone else. Here is a chance to show what you have been doing in entomology.

Bring your entomological laboratory kit. The equipment needed in studying insects in the laboratory (classroom or at home) includes: insect pins, forceps, spreading board (for Lepidoptera and Odonata), pinning block, labels, cards (to make labels, strips for spreading insects, or points for tiny insects), points, glue (Duco or clear fingernail polish), shears, crow-quill pen and wiper, India ink, observation block, magnifying glass, and storage box (cigar box with soft pinning bottom).

Bring your notebooks. These should contain blank pages for notes, catalog of specimens or field notes, information leaflets distributed previously, and books or pamphlets dealing with insect identification.

Bring some specimens which are either fresh or which have been relaxed and are limber enough to be pinned and spread at the meeting. We shall supply some insects but bring your own for more variety. Also bring some duplicates for trading. When you run across interesting insects which are fairly numerous, be sure to collect a few extra specimens for exchange. Perhaps you can trade them for something you do not have. This is one of the best ways of adding rare or unusual items to your collection.

So remember! Bring to the meeting: an exhibit,
a lab kit,
notebook and references,
specimens for trade and mounting.

An Entomology Field Trip (Outline of Project A)

Preliminary Considerations

Select goals and plan activities.
- Observe the great variety of different species.
- Observe their activities.
- Make a collection of some of them.
- Identify the ones you collect.
- Determine their place in the food cycle.
- Consider their inter-relationships.

Become familiar with some of the insects you may find.
- Study books or other references so you can recognize some of the more common kinds.
- Practice mounting and labeling insect specimens.

Set a date for the trip. Also set an alternate rain date. Arrange for transportation if you plan to go beyond walking distance from the meeting place.

Round up the equipment you will need: killing jars, nets, pins, storage boxes for the final collection, labels, magnifying glasses, and references.

The Field Trip. The trip should run at least 2 hours in the afternoon, on a warm, sunny day.

First few minutes. Review the goals, distribute equipment for collecting, orient yourself in the field.

First 45 minutes. Scatter either in groups or singly and collect the insects you see. Observe some to learn their habits.

Second 45 minutes. Return to starting point. Mount and identify the insects you have collected. Label and number them. Label each insect with a colored tag indicating its place in the food cycle.

Last 30 minutes. Discuss observations; answer questions; draw conclusions about the wildlife community you have just examined.

Followup

Reenforce what has been learned by later discussions of observations made on the trip. Using this wildlife community as an example, go on to consideration of biological principles and applications, to a study of man's place in nature and his effect on his environment.

In this 2-hour period the class will collect insects in the field, return to the classroom, mount, label, and identify each insect by name and indicate its position in the food chain.

The collecting equipment will be assigned to certain members of each group but must be shared equally. For example, the person who has the collecting net is expected to take four or five sweeps, collect the insects from the net and give it to the member of his group with the next number.

Try to collect at least one herbivore, one predator, one parasite, one scavenger and one pollinator for each student. The insects can be first captured in the plastic vials and transferred to the killing jars after examination and identification. Two collections are to be made. Each student should collect and mount two insects of each kind. One of these goes into the school collection and one into the student's own collection.

IN THE FIELD

A. Group Organization.

1. Break the class into groups of four members each.
2. Designate each group by letter (Group A, Group B, etc.).
3. Within each group, designate each student by number (Student Number 1, Student Number 2, etc.).

B. Distribution of collecting equipment.

All equipment must be returned to the instructor at the end of the class period.

1. Student Number 1 of each group is to pick up one collector's kit.
2. Student Number 2 — pick up one killing jar.
3. Student Number 3 — pick up one net.
4. Student Number 4 — pick up one clip board and one food chain notebook page.

C. Spend approximately 40 minutes collecting in the field. Do not kill butterflies, caterpillars, frogs, and other soft-bodied animals.

D. Return nets and clip boards to the instructor.

E. Go to the classroom or assembly area.

IN THE CLASSROOM

Seat the students by group so they can work together. Equipment must be returned to the instructor at the end of the class period. Supplies need not be returned.

F. *Distribution of equipment and supplies.*

1. Student Number 1 — obtain one storage box (supplies) for each member of his group.
2. Student Number 2 — pick up 10 insect pins (supplies) for each member of his group.
3. Student Number 3 — pick up plastic or cardboard (supplies) to be cut and fitted into bottom of storage boxes. Don't waste it but get enough for each member of the group.
4. Student Number — pick up one insect mounting kit (equipment).

G. *Prepare boxes and mount and label insects.*

1. Cut plastic or cardboard pinning bottom to size and fit into box.
2. Put your name on or in the storage box.
3. Pin each insect.
4. Put a locality and date label on each.
5. Put a catalog number on each (your initials and a number, JAW #3).
6. Identify each specimen.
7. Place a colored tag on each specimen to indicate its place in the food chain (red for predator, orange for parasite, green for herbivore, black for scavenger, yellow for pollinator).
8. Put an identification label on each ("Lady Beetle," etc.).
9. Place the pinned and labeled insect in the school collection or in your students' collection.

H. *Cleanup.*

1. Student Number 1 — replace collector's kit items and turn in.
2. Student Number 2 — return killing jars to instructor.
3. Student Number 3 — clean table and throw out waste paper, leaves, and other trash.
4. Student Number 4 — replace equipment of mounting kit and return to the instructor.

EQUIPMENT

Collector's kit:
1 cloth carrying bag
5 plastic vials with cotton stoppers
1 hand lens

sweep net
killing jar
clip board
notebook pages

Mounting kit:
shears
glue
paper points
labels, locality
labels, colored

A Small Game Safari

An Insect-Collecting Competition

Form small groups of approximately five persons in each. Each group is to pick up one collecting kit (1 paper bag containing: 1 killing jar; 1 empty jar; 5 vials, one for each member of the group; 1 collection box with pinning bottom, pins, paper points and labels; a record sheet; an outline of activity; and a net if one is available).

Write your group name or number on the bag, box, and record sheet. Read the papers carefully so you will know what you should do, what to collect, and how to complete your project.

Head for the fields, woods, and streams (open meadows are best). Collect the insects you find. There is only one killing jar for each group, but all members of the group can capture insects in the vials and then dump into the killing jar or into the empty jar. No collecting is allowed within 200 feet of the starting point to reduce confusion. The hunting trip is to last no longer than ½ hour; then return to the starting point to mount trophies.

Prepare your collection box by cutting the plastic foam or corrugated cardboard and fitting it into the ½ pint container. Mount the insects by pinning or gluing to a pinned paper point. Soft bodied insects and spiders should be put into alcohol in the small vials. Put a locality and date label on each (see sample collection). Identify each specimen to order and attach a name label. Books, pamphlets, or exhibit collections may be available to help you in identification. Write the labels with India ink or pencil. DO NOT USE ORDINARY INK!

If you do not wish to kill the insects place specimens in vials or the empty jar. Place one species in each vial. Add labels as you would to the vials with alcohol. The insects can be turned loose after the collection is judged. Stopper the vials with cotton wool.

When your collection is complete or you run out of time, put your name or number on the bag and box and turn in for judging. Turn in the killing jars, vials, nets, etc. The dry pinned collection is yours after grading.

The collections will be judged on the following basis. No specimen will be considered unless correctly mounted, labeled, and identified.

10 points	for each order with at least one representative specimen. [For example: 1 beetle (Coleoptera), 1 fly (Diptera) and 1 bee (Hymenoptera) equal 30 points (3 orders).]
10 points	for each life stage in each order (egg, larva, pupa, adult) in addition to the number one specimen which represents the order. [For example: 1 beetle (Coleoptera adult, 10 points), 1 white grub (Coleoptera larva, 10 points), 1 mass of lady beetle eggs (Coleoptera eggs, 10 points) equal 30 points (3 different stages in one order).]
1 point	for each species collected in addition to the number one specimen representing its order. [For example: 8 different beetles (1st order and 7 additional species) and 4 different bees and wasps (2d order and 3 additional species) equal 30 points (2 orders, 20 points; 10 additional specimens, 10 points).]

Key to the Orders of Winged Insects

1a Front wings horny, leathery, or parchmentlike, at least at base; hind wings membranous..................2

1b Wings entirely membranous, may be covered with scales 6

2a With sucking mouthparts, the beak elongate and usually segmented 3

2b With chewing mouthparts..................4

3a Beak arising from front part of head (figure 92); front wings usually leathery at base and membranous at tip, the tips generally overlapping when at rest (figure 94) (true bugs)..................*Hemiptera*

3b Beak arising from hind part of head, often appearing to arise at base of front legs (figure 95); front wings of uniform texture throughout, the tips not or only slightly overlapping when at rest (figure 91) (hoppers and cicadas)..................*Homoptera*

4a End of abdomen with forcepslike cerci (figure 98); elytra (thickened front wings) short, leaving most of the abdomen exposed (earwigs)..................*Dermaptera*

4b Abdomen without forcepslike cerci, or if cerci appear forcepslike, then the wings cover most of the abdomen 5

5a Front wings without veins and usually meeting in a straight line down the middle of the back (figure 100); antennae usually with 11 or fewer segments; hind wings, if present, narrow, usually longer than the front wings when unfolded and with few veins (beetles and weevils)..................*Coleoptera*

5b Front wings with veins and either held rooflike over the abdomen or overlapping over abdomen when at rest (figures 96, 97); antennae usually with more than 12 segments; hind wings broad, usually shorter than the front wings and with many veins (grasshoppers, crickets, roaches, mantids, katydids) ....*Orthoptera*

6a With two wings..................7

6b With four wings..................10

7a Body shaped like that of a grasshopper; pronotum (upper part of first body segment behind head) extending back over abdomen and pointed at tip (figure 99); hind legs enlarged (grouse or pygmy locusts) ....*Orthoptera*

7b Body not like a grasshopper; pronotum not as above; hind legs not so enlarged..................8

8a Abdomen with threadlike or stylelike tails (figures 103, 103); mouthparts vestigial; halteres present or absent..................9

8b Abdomen without threadlike or stylelike tails; mouthparts usually well developed and forming a sucking proboscis; halteres present (figure 102) (true flies, mosquitoes, midges, gnats, punkies) ....*Diptera*

9a Wings with only a single forked vein; antennae long and conspicuous; halteres present and hooklike; minute insects, usually less than 5 mm. in length (figure 103) (male scale insects).................. *Homoptera*

9b Wings with numerous veins and cross veins; halteres absent; antennae short, bristlelike, and inconspicuous; usually over 5 mm. long (similar to figure 101 but lacking hind wings) (mayflies) .... *Ephemeroptera*

10a Wings largely or entirely covered with scales; mouthparts usually in the form of a coiled proboscis; antennae many-segmented (figure 104) (moths and butterflies)..................*Lepidoptera*

10b Wings not covered with scales although they may be hairy; mouthparts not in the form of a coiled proboscis 11

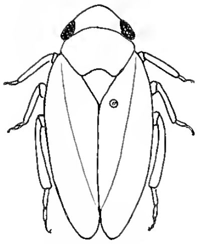
11a Wings narrow, veinless or with only 1 or 2 veins and fringed with long hairs (figure 107); tarsus with only 1 or 2 segments, the last segment swollen; very small insects, usually less than 5 mm. long (thrips) ....*Thysanoptera*

11b Wings not as above..................12

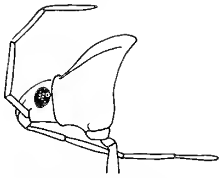
12a Hind wings smaller than front wings (in length and usually also in area) and usually with fewer veins 13

12b Hind wings as large as or larger than front wings and with as many or more veins..................17

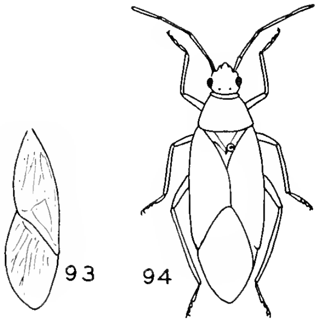
Figures 91–106



91 SPITTLEBUG

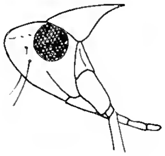


92 HEMIPTERA

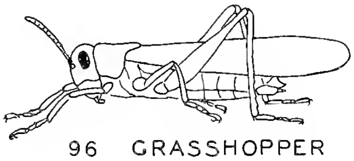


93 94

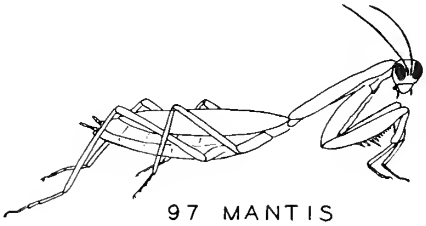
PLANT BUG



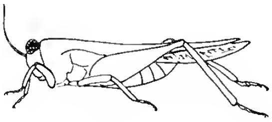
95 HOMOPTERA



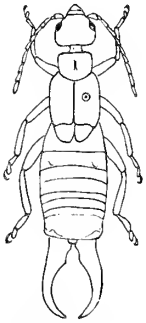
96 GRASSHOPPER



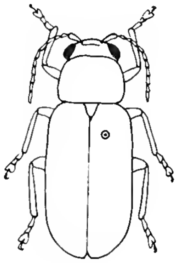
97 MANTIS



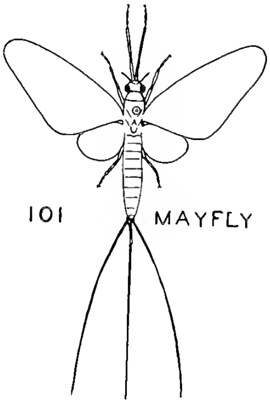
99 PYGMY LOCUST



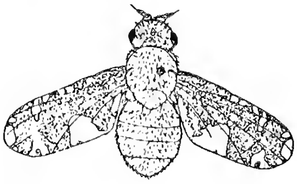
98 EARWIG



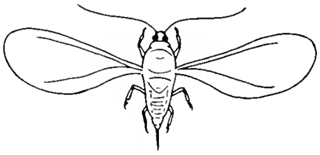
100 BEETLE



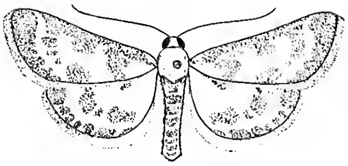
101 MAYFLY



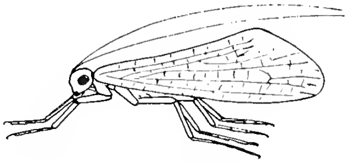
102 FLY



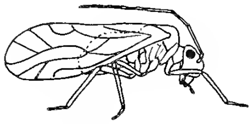
103 SCALE INSECT



104 MOTH



106 CADDISFLY



105 BARK LOUSE

13a Front wings with many cross veins and cells; antennae short, bristlelike, and inconspicuous; abdomen with two or three long threadlike tails (figure 101); delicate, soft-bodied insects similar to figure 101 (mayflies) .... *Ephemeroptera*

13b Front wings with few cross veins and cells; antennae fairly long and conspicuous, or if short and bristlelike then there are no threadlike tails 14

14a With sucking mouthparts (figure 91) (hoppers, cicadas) .... *Homoptera*

14b With chewing mouthparts..15

15a Wings distinctly hairy; mouthparts usually much reduced except for palpi (figure 106) (caddisflies) .... *Trichoptera*

15b Wings not distinctly hairy; mandibles (jaws) well developed 16

16a Tarsus with two segments (figure 105); front wing with a long, more or less curved cell, opening at wing tip; vein forming hind edge of this cell with two shorter veins branching from it (booklice or barklice) .... *Psocoptera*

16b Tarsus with 4 or 5 segments; front wing without a long cell like the one described above (figure 108) (ants, wasps, bees, sawflies)......*Hymenoptera*

17a Antennae short, bristlelike, and inconspicuous; wings with many cross veins, never held flat over abdomen when at rest; body long, slender (figure 110) (dragonflies, damselflies) ....*Odonata*

17b Antennae long and conspicuous...............................18

18a Head prolonged to form a beak (figure 114); costal area of front wings (along the front edge of the wing) with not more than one or two cross veins (scorpionflies) ....*Mecoptera*

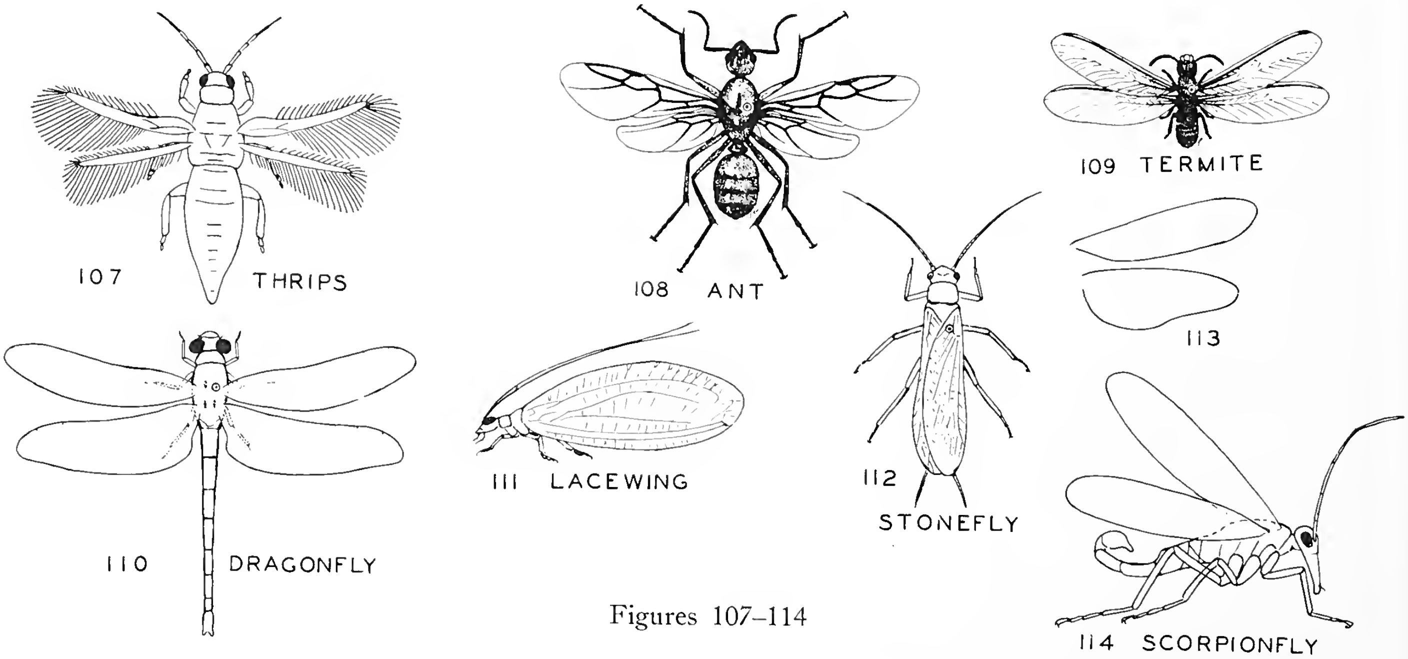
18b Head not prolonged to form a beak.......................19

19a Front and hind wings similar in size and shape, veins not darkened; with very few cross veins or cells in median part of wing (figure 109); body 8 mm. long or less (termite)..........................*Isoptera*

19b Front and hind wings not as described above, if same size and shape then the veins are darkened and there are at least 5 or 6 closed cells in the median part 20

20a Hind wings wider than the front wings, at least in the basal half; wings folded flat over the abdomen when at rest; long hair-like cerci project back from the end of the abdomen (figure 112) (stoneflies) .... *Plecoptera*

20b Hind wings not distinctly wider than front wings; never folded flat over the abdomen when at rest; abdomen without cerci at tip (figure 111) (fishflies, dobsonflies, lacewings, ant-lions)..*Neuroptera*


107 THRIPS

108 ANT

109 TERMITE

110 DRAGONFLY

111 LACEWING

112 STONEFLY

113

114 SCORPIONFLY

Figures 107–114

REFERENCES

Selected References for Insect Collecting and Identification

The following books deal primarily with insect collecting and insect identification. The college texts usually provide little help for specific identification but most have good keys and descriptions of the families of insects. I would recommend Borrer and White's *A Field Guide to the Insects* for the serious beginner.

Some of the list may be out of print and cannot be purchased, but may be consulted in libraries. A book can be borrowed through interlibrary loan if necessary.

General Insect Identification

Zim, H. S. and C. Cottam. *Insects.* (One of the Golden Nature Guide series) Simon & Schuster, Inc., New York, 1951, 160 pp. $1 paper covered. An excellent book for the beginner but describes and illustrates only 225 insect species.

Borror, D. J., and R. E. White. *A Field Guide to the Insects.* (One of the Peterson Field Guide series) Houghton Mifflin Company, Boston, 1970, 404 pp. $5.95. One of the best books for the serious beginner. The 1,300 illustrations are excellent. Most of the insect families are considered. Good for identification and general information.

Lutz, Frank E. *Field Book of Insects.* G. P. Putnam's Sons, New York, 1948, 510 pp. $3.95. Excellent for the beginner although some names are out of date.

Jaques, H. E. *How To Know the Insects.* Wm. C. Brown, Dubuque, Iowa, 1947, 205 pp. $2 (paper cover). A good key to the identification of common insects.

Borror, D. J., and D. M. DeLong. *An Introduction to the Study of Insects.* 3d ed. Holt, Rinehart and Winston, Inc., New York, 1971. $17.50. A college text with descriptions and keys to the identification of almost all North American families of insects. Additional chapters on collecting and studying insects and man's relationship to insects.

Pennak, Robert W. *Fresh-Water Invertebrates of the United States.* The Ronald Press Company, New York, 1953, 769 pp. A very useful book for identifying other invertebrates, as well as adult and larval insects living in fresh water.

Chu, H. F. *How to Know the Immature Insects.* Wm. C. Brown Co., Dubuque, Iowa, 1949, 205 pp. $3. A key to some of the common species of all orders.

Felt, E. P. *Plant Galls and Gall Makers.* Comstock Publ. Co., Ithaca, N.Y., 1940, 364 pp.

General Entomology

Frost, S. W. *Insect Life and Insect Natural History.* Dover Publications, New York, 1959, 526 pp. $42.25. An excellent introduction for more advanced insect studies. Not useful for identification, but provides a wealth of information on insect biology and has a good bibliography.

Klots, Alexander B., and Elsie B. *Living Insects of the World.* Doubleday & Company, Inc., Garden City, N.Y., 1959, 304 pp. An excellent, nontechnical book with many superb photographs. Not useful for identification.

Insects of Economic Importance

Swan, Lester A. *Beneficial Insects.* Harper & Row, Publishers, New York, 1964, 429 pp. $7.95.

Mallis, Arnold. *Handbook of Pest Control.* 4th ed. McNair-Dorland Co., New York, 1964, 1148 pp. Deals exclusively with household pests.

Metcalf, C. L., W. P. Flint (revised by R. L. Metcalf). *Destructive and Useful Insects.* 4th ed. McGraw-Hill Inc., New York, 1962, 1,087 pp. Deal primarily with agricultural crop pests.

Peairs, L. M., and R. H. Davidson. *Insect Pests of Farm, Garden and Orchard.* 5th ed. John Wiley & Sons Inc., New York, 1956, 661 pp.

Horsfall, William R. *Medical Entomology.* The Ronald Press Company, New York, 1962, 467 pp.

Eckert, John E., and Frank R. Shaw. *Beekeeping.* Macmillan & Co. Ltd., New York, 1960, 536 pp.

Collecting Techniques

Teale, Edwin Way. *Insect Life.* Merit Badge Series, Boy Scouts of America, New Brunswick, N.Y., 1944

(reprint 1958), 63 pp. $0.35. This pamphlet is available wherever official boy scout equipment is sold.

Johnson, Warren T. *Know Your Insects.* An extension publication (4-H M-6-1) of the New York State College of Agriculture, Cornell University, Ithaca, N.Y., 1966, 23 pp. Single copies free to residents of New York State; additional copies $0.15. This is the 4-H member's manual telling how to make an insect collection, plus other useful information.

Single Insect Orders

Klots, Alexander B. *Field Guide to the Butterflies.* (One of the Peterson Field Guide series.) Houghton Mifflin Company, Boston, 1951, 349 pp. $3.75.

Mitchell, Robert T., and Herbert S. Zim. *Butterflies and Moths.* Golden Nature Guide. Golden Press, Inc., New York, 1962, 160 pp. $1.20. Elementary but very good.

Holland, W. J. *The Moth Book.* Dover Publications, Inc., 180 Varick St., New York, N.Y. 10014. Reprinted 1968. 479 pp. $5. Excellent. Good color photographs of most of the larger moths of the United States and Canada.

Jaques, H. E. *How To Know the Beetles.* Wm. C. Brown Co., Dubuque, Iowa, 1951, 372 pp. A key to some of the common beetles.

Arnett, Ross H., Jr. *The Beetles of the United States.* Catholic University of America Press, Washington, D. C., 1963, 1,112 pp. Excellent, technical, keys to identification of all beetle genera.

Dillon, Elizabeth, and Lawrence S. *A Manual of Common Beetles of Eastern North America.* Row, Peterson & Co., Elmsford, N.Y., 1961, 884 pp.

Wheeler, William Morton. *Ants: Their Structure, Development and Behavior.* Columbia University Press, New York, 1960 (3d printing), 663 pp.

Michener, Charles D. and Mary H. *American Social Insects.* D. VanNostrand Co., New York, 1951, 267 pp.

Spiders

Levi, Herbert W. and Lorna R. *Spiders and Their Kin.* Golden Nature Guide. Golden Press, Inc., New York, 1968, 160 pp. $1.20. Elementary but very good.

Kaston, Benjamin J. and Elizabeth. *How to Know the Spiders.* Wm. C. Brown, Co., Dubuque, Iowa, 1952, 220 pp. $3. Excellent but rather technical. Identification of common species.

Gertsch, Willis J. *American Spiders.* D. VanNostrand Co., New York, 1949, 285 pp. Excellent for general information on spiders and their biology. Not useful for identification.

Biological Supply Houses

Equipment for collecting, mounting, and preserving insects can sometimes be purchased in hobby stores or from the sales desks in museums, but generally you will have to buy, by mail, from one of the biological supply houses such as those listed below. They will supply a catalog if you write and tell them your interests.

General Biological Supply House, Inc. (Turtox)
8200 South Hoyne Avenue
Chicago, Illinois 60620

Ward's Natural Science Establishment, Inc.
3000 East Ridge Road
Rochester, New York 14603

Carolina Biological Supply Co.
Burlington, North Carolina 27215

New York Scientific Supply Co.
331 East 38th Street
New York, New York 10016

Standard Scientific Supply Co.
808 Broadway
New York, New York 10003

Clay-Adams Co.
141 East 25th Street
New York, New York 10010

Bio Quip Products Division
Bio Metal Associates
P.O. Box 61
Santa Monica, California 90406

VWR Scientific
P.O. Box 23, High Bridge Station
Bronx, N.Y. 10452

Bernel Foam Products Co., Inc.
P.O. Box 655
Buffalo, N.Y. 14240

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in New York

by

EUGENE C. OGDEN, State Botanist

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Albany, New York 1974

THE UNIVERSITY OF THE STATE OF NEW YORK

Perennial aquatic herbs from seeds, winter buds, or rhizomes. Stems simple or branched, terete or compressed, 0.1-5 mm in diameter; nodes sometimes with a pair of glands; internal anatomy of internodes variable but mostly uniform for each species. Leaves alternate, except opposite or subopposite at nodes with a peduncle, all submersed or with both submersed and floating blades. Submersed leaves flaccid, sessile, or petioled, blades linear to ovate, apex acute or obtuse, entire to dentate, sometimes with 1 or more rows of translucent cells (lacunae) each side of midrib; stipules fused to form a single structure with 2 midveins arising from the axil of the stem and leaf, free or adnate to the leaf base, mostly sheathing the stem and sometimes with the outer margins partially fused (connate). Floating leaves coriaceous, petioled, elliptic to ovate; stipules like those of submersed leaves but never adnate nor connate. Inflorescence a spike, sessile, or on a peduncle to 60 cm long, with 1-20 whorls of flowers, capitate, cylindric, or moniliform, with 2-4 flowers in each whorl. Flowers with rounded, short-clawed, greenish sepals, 1-3 mm long; stamens 4, anthers sessile on the sepal claws, 2-celled, extrorse; pollen spherical, inaperturate; carpels 4, free, sessile. Fruits a dryish drupelet (appearing to be an achene on herbarium sheets) with spongy mesocarp and bony endocarp, the latter tissue projecting as a fold (endocarp loop) into the center of the fruit, 1-seeded; embryo coiled, endosperm absent. Winter buds (shortened and hardened tips of branches with crowded leaf blades and stipules) are produced in some species. Chromosomes: $2n = 26, 28, 52, 78$, or 104. There is evidence to indicate that each " flower " may be an inflorescence composed of 1 pistillate and 4 staminate flowers.

USEFUL REFERENCES

Fassett, N. C. 1957. A manual of aquatic plants. 2d. ed. University of Wisconsin Press.

Fernald, M. L. 1932. The linear-leaved North American species of Potamogeton. Mem. Am. Acad. Arts & Sci. 17(1): 1-183.

——— 1950. Gray's manual of botany. 8th ed. American Book Co.

Gleason, H. A. 1952. The new Britton and Brown illustrated flora. Vol. 1. New York Botanical Garden.

Haynes, R. R. 1974. A revision of North American Potamogeton subsection Pusilli (Potamogetonaceae). Rhodora 76: in press.

House, H. D. 1924. Annotated list of the ferns and flowering plants of New York State. New York State Museum Bulletin 254.

Muenscher, W. C. 1944. Aquatic plants of the United States. Comstock Publishing Co.

Ogden, E. C. 1943. The broad-leaved species of Potamogeton of North America north of Mexico. Rhodora 45: 57-105, 119-163, 171-214.

——— 1953. Key to the North American species of Potamogeton. New York State Museum Circ. 31.

St. John, H. 1916. A revision of the North American species of Potamogeton of the section Coleophylli. Rhodora 18: 121-138.

Manuscript submitted for publication May 2, 1974.

Key to Species

1. Leaves all submersed, linear, auricled at base, margins finely denticulate; stipules adnate .... 4. *P. robbinsii*
1. Leaves various, but if linear then not auricled
  2. Stipules adnate to the base of the leaf for a distance of 10 mm or more; floating leaves absent
    3. Leaves acute and sharp pointed at apex; fruits 2.5-4 mm long, with a short beak .... 3. *P. pectinatus*
    3. Leaves obtuse and blunt at apex, or sometimes minutely apiculate; fruits 2-3 mm long, beakless
      4. Primary stems 1-3 mm in diam; lower leaves with blades 1-2 mm wide and with loose inflated sheaths; upper leaves from the branches filiform; spikes with 5–12 whorls of flowers .... 2. *P. vaginatus*
      4. Stems 0.5-1 mm in diam; all leaves filiform, 0.2-0.5 mm wide; sheaths tight; spikes with 2–5 whorls of flowers .... 1. *P. filiformis*
  2. Stipules free or adnate for a distance of less than 10 mm; floating leaves present or absent
    5. Leaf margins serrate .... 5. *P. crispus*
    5. Leaf margins entire
      6. Leaves linear, veins 15–35 .... 7. *P. zosteriformis*
      6. Leaf shape various but, if linear then with less than 15 veins
        7. Submersed leaves linear, less than 10 mm wide, length more than 20 times the width
          8. Submersed leaves ribbonlike, flaccid, 2-10 mm wide, with a prominent, parallel-sided median band of lacunae filling the broad space between the inner veins; fruits (not formed unless floating leaves are present) 2.5-4 mm long, embryo coil more than a complete revolution .... 17. *P. epihydrus*
          8. Submersed leaves 0.1-4 mm wide, lacunae not forming a prominent parallel-sided band; fruits 0.8-3 mm long, embryo coil less than 1 revolution or, if more, then fruits less than 2.5 mm long
            9. Stipules of some or all of the submersed leaves adnate to base of leaf blade; embryo coil more than a complete revolution
              10. Submersed leaves obtuse, usually rounded at apex, space between midrib and lateral veins commonly with lacunae; sheath of stipule longer than the free tip; emersed peduncles 0.5-3 cm long; fruits 1.3-2.2 mm in diam, with lateral keels rounded or absent ..... 15. *P. spirillus*
              10. Submersed leaves subobtuse to acute or setaceous, lacunae absent or nearly so; sheath of stipule shorter than the free tip; emersed peduncles 0.2-1.5 cm long; fruits 0.8-1.5 mm in diam, with lateral keels tiny but evident .... 16. *P. diversifolius*
            9. Stipules free from the leaf blade; embryo coil less than a complete revolution
              11. Floating leaves present, more than 10 mm wide, with (7-) 9-37 veins

12. Floating leaf blades 2.5-6 cm wide, usually cordate; submersed leaves (usually absent at maturity) mostly from the main stem, 0.8-2 mm wide; fruits 3.5-5 mm long, keels obscure, coat wrinkled; apex of embryo pointing toward basal end . . . . 22. *P. natans*

12. Floating leaf blades 1-3 cm wide, rounded or cuneate at base; submersed leaves (usually present) mostly from branches, 0.2-1 mm wide; fruits 2.5-3.5 mm long, keels prominent, coat smooth; apex of embryo pointing a little above the basal end . . . 23. *P. oakesianus*

11. Floating leaves absent or, if present, mostly less than 10 mm wide, with 5–15 veins

13. Leaves all submersed, flaccid, setaceous, 0.1-0.5 mm wide, 10-80 cm long, tapering to a delicate apex; peduncle 1 (rarely 2) from tip of primary stem, 1.5-24 cm long; fruits 2.2-3 mm long . . . . 6. *P. confervoides*

13. Submersed leaves mostly more than 0.5 mm wide (except *P. vaseyi,* which has floating leaves and with submersed leaves less than 10 cm long); peduncles often more than 1 per stem

14. Floating leaves usually present; submersed leaves 0.1-0.5 mm wide, tapering to a sharp pointed apex . . . . 14. *P. vaseyi*

14. Floating leaves absent; submersed leaves (0.3-) 0.5-4 mm wide

15. Leaves (at least some of them) with bristle tips; peduncles 5-15 mm long; spikes capitate, with 1–4 flowers . . . . . . 12. *P. hillii*

15. Leaves obtuse or acute but not ending in a bristle

16. Stipules strongly fibrous, becoming whitish, especially on the winter buds

17. Leaves thin, 1.5-3.5 mm wide, with 5–7 veins, obtuse or rounded at apex; winter buds fan-shaped; peduncles flattened . . . . 9. *P. friesii*

17. Leaves firm, 0.5-2.5 mm wide, with 3–5 veins, acute; winter buds slender; peduncles terete . . . 10. *P. strictifolius*

16. Stipules delicate, greenish or brownish

18. Leaves 2-4 mm wide, rounded at apex; fruits 3-4 mm long; winter buds 20-40 mm long, 3.5-7 mm wide . . . . 13. *P. obtusifolius*

18. Leaves 0.3-3 mm wide, acute to obtuse (if rounded, then with a sharp mucro); fruits 1.8-2.8 mm long; winter buds 7-18 mm long, 0.5-2.5 mm wide

19. Fruits with dorsal keel thin, undulate or dentate; leaves acute . . . . 8. *P. foliosus*

19. Fruits with dorsal keel rounded; leaves acute or obtuse . . . . 11. *P. pusillus*

7. Submersed leaves without parallel sides, 2-70 mm wide (sometimes linear in *P. gramineus*), length less than 20 times the width

20. Submersed leaves petioled or sessile but not clasping; floating leaves often present

21. Submersed leaves sessile, apex obtuse; floating leaves delicate, blade tapering without sharp distinction into the petiole; fruit wall hard and smooth, tawny-olive . . . . 18. *P. alpinus*

21. Submersed leaves sessile or petioled, apex obtuse or acute; floating leaves coriacous, blade distinct from petiole; fruit wall spongy, greenish, brownish, or reddish

22. Submersed leaves with 11–37 veins, margins without denticles; floating leaf blades cuneate to cordate at base, with 19–51 veins

23. Submersed leaves usually arcuate, more than 25 mm wide, veins 19–37; stem not black spotted; floating leaf blades cuneate or rounded at base, veins mostly more than 30; fruits 3.5-4.5 (-5) mm long, cuneate at base . . . . 19. *P. amplifolius*

23. Submersed leaves not arcuate, usually less than 25 mm wide, veins 9–21; stem usually black spotted; floating leaf blades cordate or rounded at base, veins mostly less than 30; fruits 3-3.5 (-4) mm long, rounded or lobed at base . . . . 20. *P. pulcher*

22. Submersed leaves with 7–19 veins, margins with fugaceous 1-celled denticles; floating leaf blades tapering or rounded at base with 9–29 veins

24. Submersed leaves with petioles 4-13 cm long, apex acutish but not sharp pointed; fruits 3.5-4 mm long, usually reddish, seldom developed unless floating leaves are present . . . . . . 21. *P. nodosus*

24. Submersed leaves sessile or with petioles to 4 cm long, apex acutish or sharp pointed, sometimes rounded but with a mucronate tip; fruits 1.7-3.5 mm long, usually greenish

25. Stem usually much branched, 0.5-1 mm in diam; submersed leaves 0.2-1.5 cm wide, sessile, with 3–9 veins; floating leaf petioles mostly longer than the blades; fruiting spikes 1-2.5 cm long; fruits 1.7-2.8 mm long . . . . 24. *P. gramineus*

25. Stem simple or once branched, mostly 1.5-5 mm in diam; submersed leaves 1.5-4 cm wide, sessile or petioled, with 9–17 veins; floating leaf petioles mostly shorter than the blades; fruiting spikes 2.5-6 cm long; fruits 2.5-3.5 mm long . . . . 25. *P. illinoensis*

20. Leaves all submersed, cordate or rounded at base and clasping the stem

26. Leaves ovate-oblong, mostly 10-20 cm long, apex cucullate; stipules persistent and conspicuous; stem often whitish; peduncles mostly 15-60 cm long; fruits more than 4 mm long, dorsal keel strongly developed . . . . 26. *P. praelongus*

26. Leaves roundish, ovate, or elongate-ovate, 1-10 cm long, apex not cucullate; stipules at maturity inconspicuous or disintegrated to fibers; stem greenish; peduncles 1-25 cm long; fruits less than 3.5 mm long, dorsal keel weakly developed

27. Stipules coarse, disintegrating to persistent whitish fibers; peduncles clavate, 1.5-25 cm long; fruits with a cavity in the endocarp loop . . . . 27. *P. richardsonii*

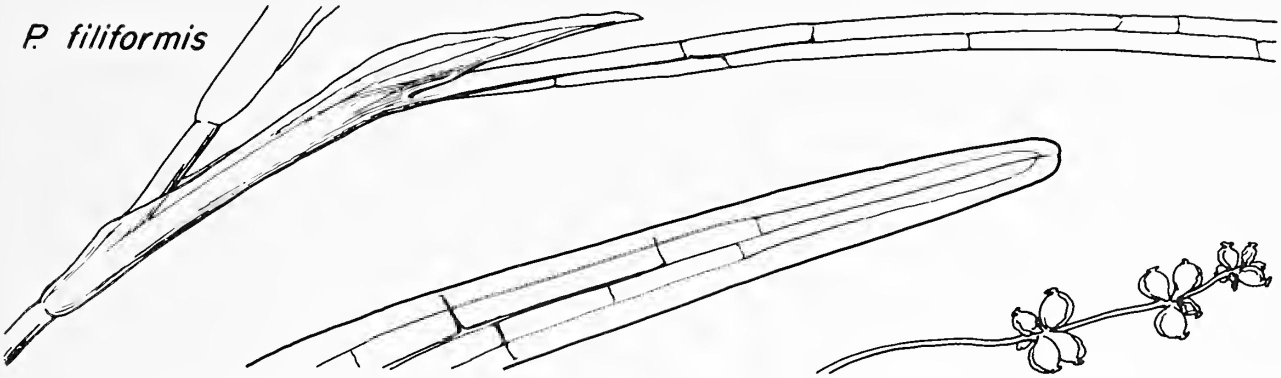
27. Stipules delicate, disappearing with age; peduncles not clavate, 1-9 cm long; fruits without a cavity in the endocarp loop 28. *P. perfoliatus*

1. P. filiformis Persoon

Occasional. Calcareous or brackish, mostly shallow water of lakes and streams.

Ours is var. **borealis** (Raf.) St. John

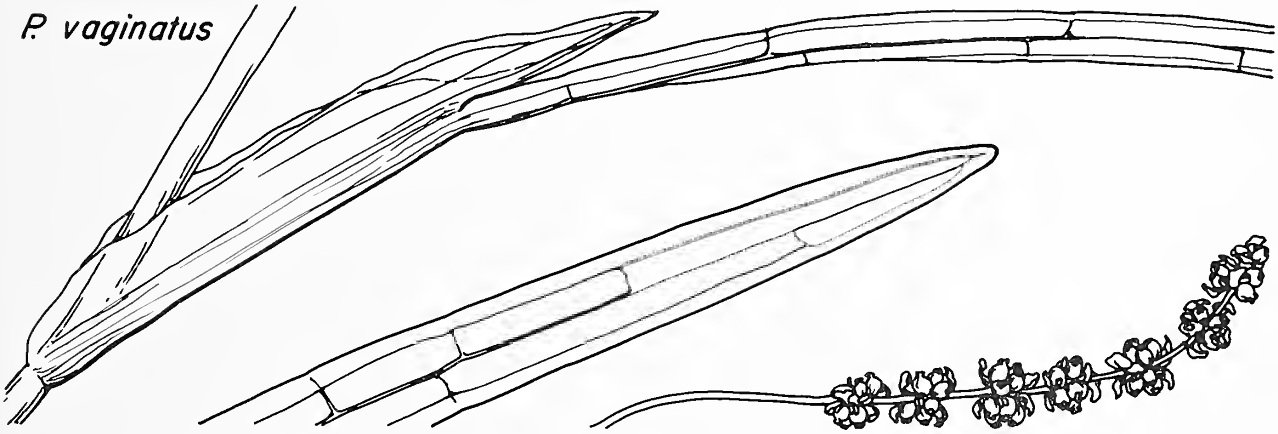
Recognized by the adnate, slender stipular sheaths and obtuse leaf tips.



2. P. vaginatus Turcz.

Rare. Calcareous or brackish water of lakes and streams.

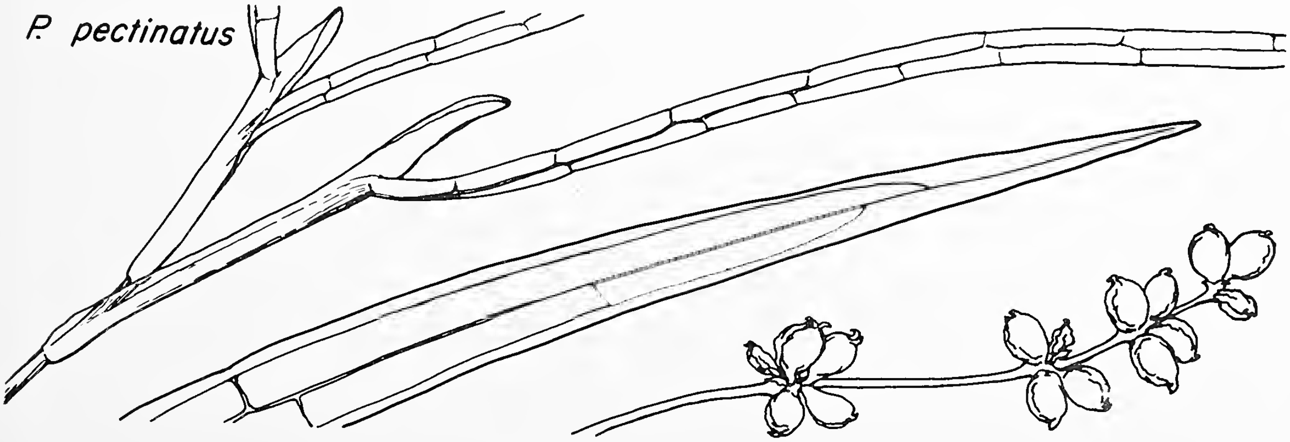
Recognized by the adnate broad stipular sheaths and obtuse leaf tips. Upper sterile branches difficult to distinguish from *P. filiformis*.



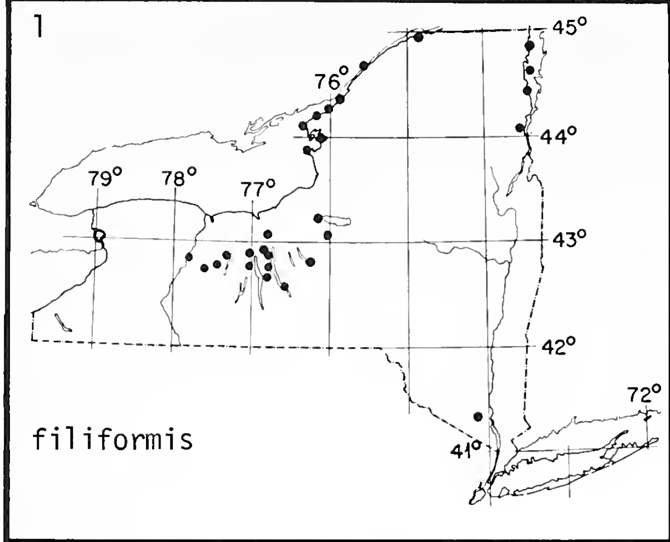
3. P. pectinatus L.

Common. Alkaline or saline water.

Recognized by the adnate, slender stipular sheaths and acute to sharp pointed leaf tips.



POTAMOGETON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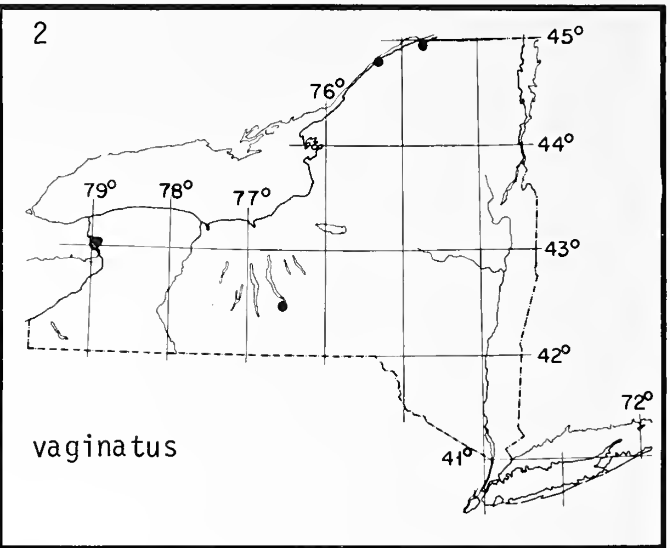
filiformis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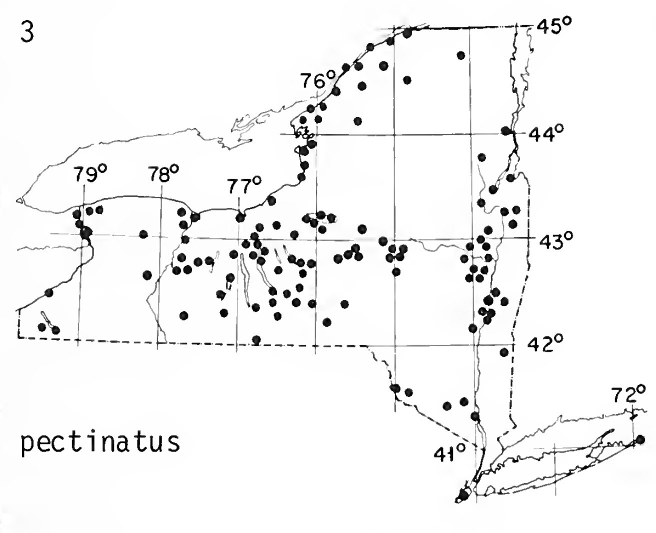
vaginatus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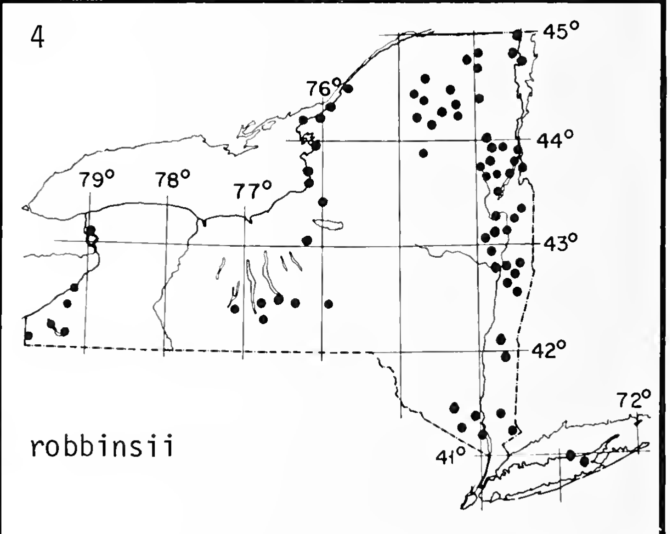
pectinatus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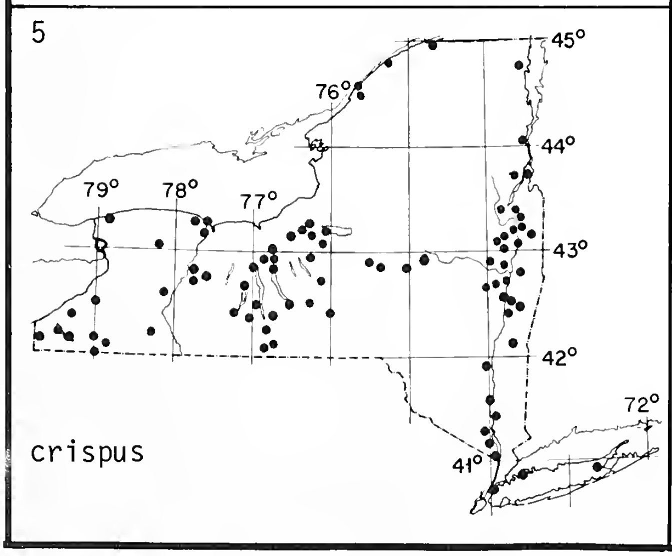
robbinsii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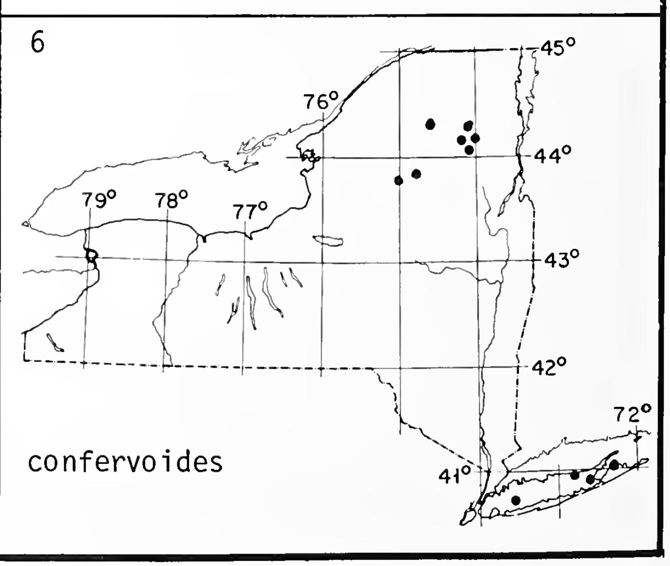
crispus

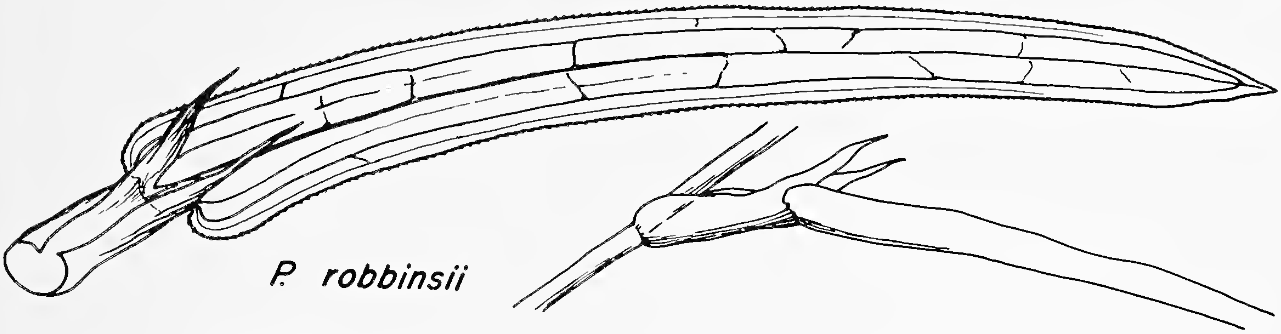

6

confervoides

4. P. robbinsii Oakes

Occasional to common; sometimes locally abundant and weedy.

Recognized by the leaves which are auriculate at base, and by the finely serrulate leaf margins. Also, by the whitish adnate stipular sheaths and acute leaf tips. The leaves are usually stiffly 2-ranked, giving the branches a feathery appearance in the water. Often abundant and weedy but rarely found with fruit. A taxon with entire leaf margins (forma *cultellatus* Fassett) has not been found in New York.

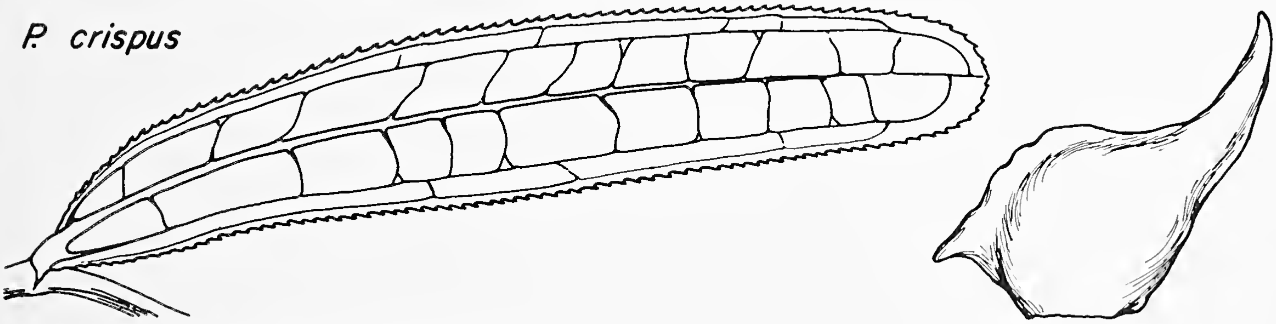

P. robbinsii

5. P. crispus L.

Not native, but now widespread and often an abundant weed. Pools, lakes, and streams.

Our only species with dentate leaf margins.

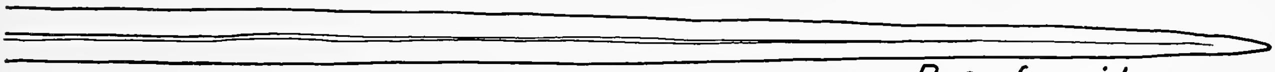
P. crispus



6. P. confervoides Reichenb.

Uncommon. Bog pools and acid lakes.

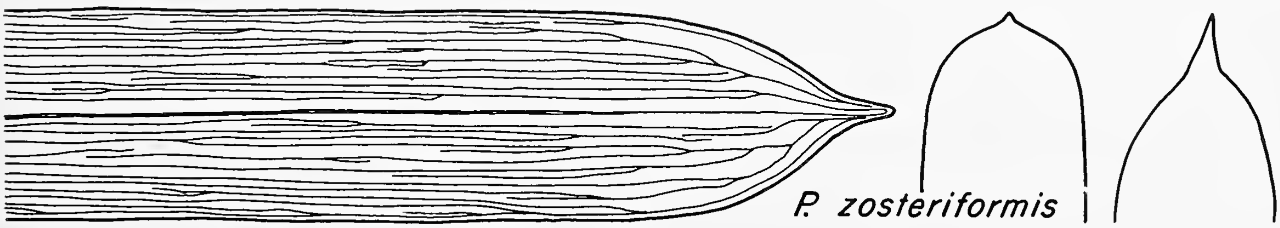
Usually recognized by the slender, delicate, grass-green leaves that gradually taper to a slender apex. The primary branches are much branched, giving a fan-shaped appearance in the water.


P. confervoides

7. P. zosteriformis Fernald

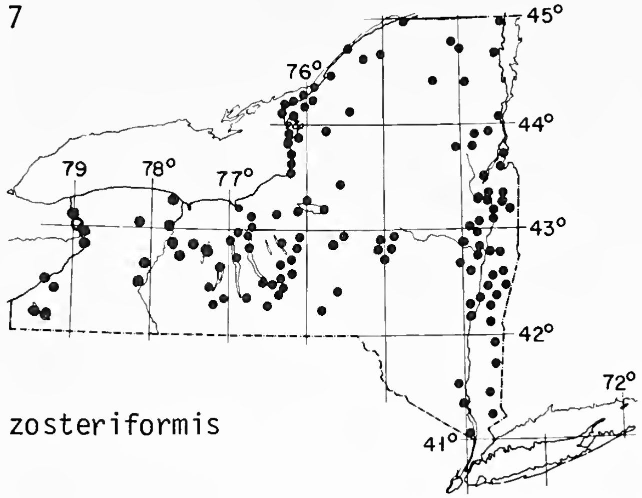
Common. Lakes and quiet streams.

Easily recognized by the laterally flattened stem and linear leaves with 15 or more veins.


P. zosteriformis

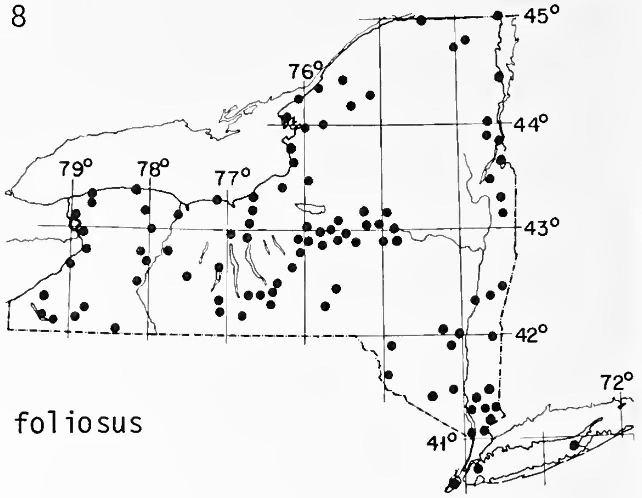
POTAMOGETON

7



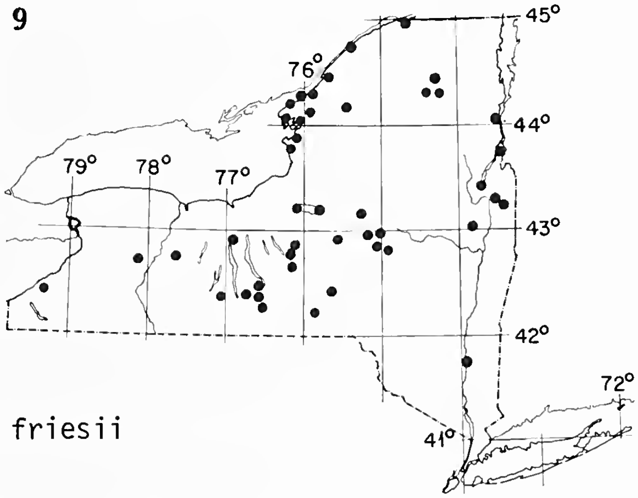
zosteriformis

8



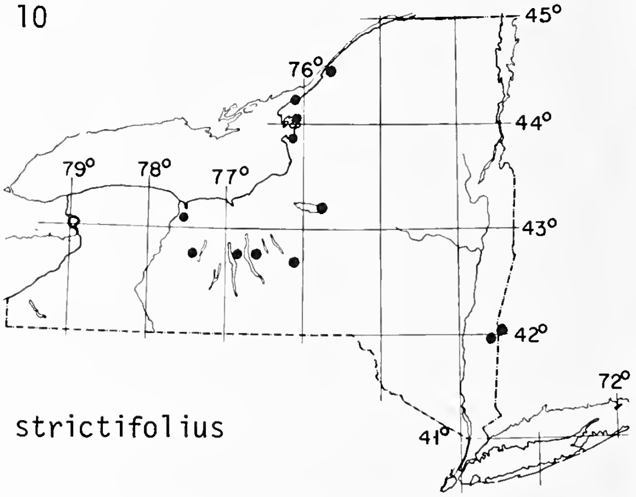
foliosus

9



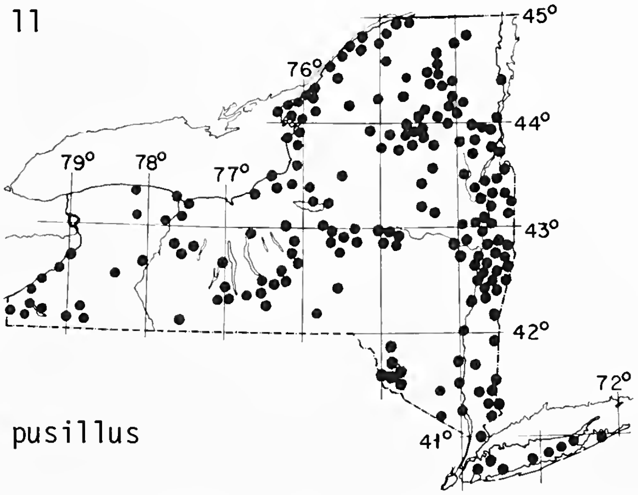
friesii

10



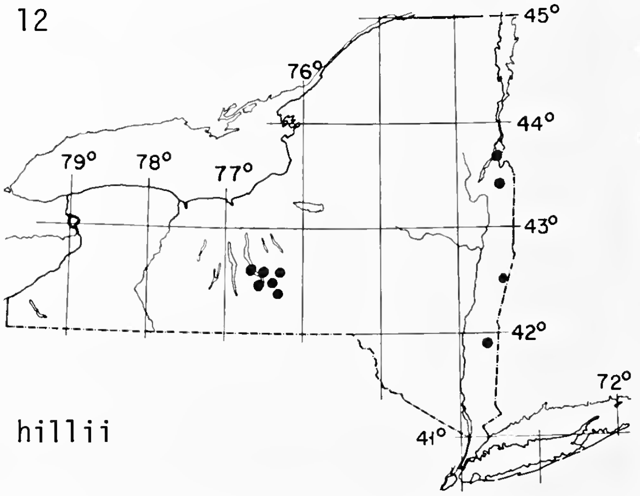
strictifolius

11



pusillus

12



hillii

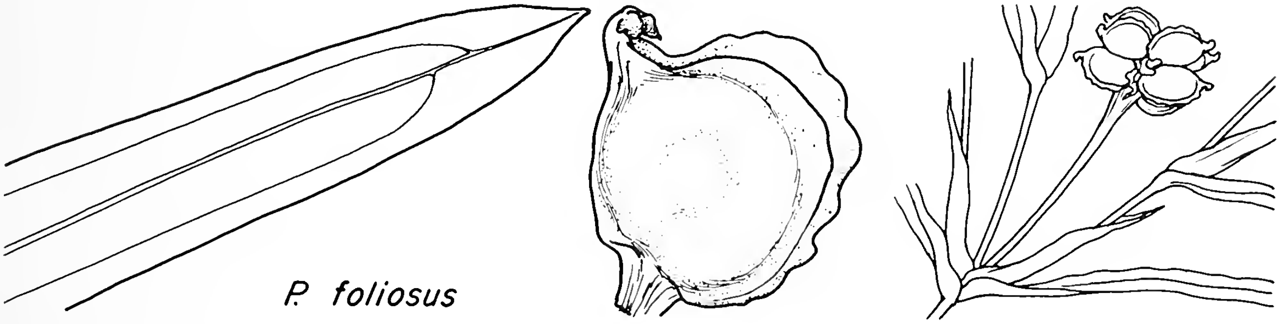
8. P. foliosus Raf.

Frequent. Fresh or brackish water of lakes and streams.

Sterile specimens are difficult to distinguish from *P. pusillus.* With mature fruit there is no question, it being the only species in the State bearing fruit with a thin, winglike dorsal keel and the embryo coil with no more than 1 revolution. The leaves are usually less lacunate and the apex never obtuse, as may occur in the variable *P. pusillus.* Also, the stems are oval to flattened in cross section, in contrast to the terete stems of *P. pusillus.*

Two intergrading varieties, which differ only in size, have been recognized: var. **foliosus** and var. **macellus** Fernald.

1. Stems loosely branched; leaves 1.4-2.7 mm wide, with 3–5 veins; stipules 7-18 mm long . . . . var. *foliosus*
1. Stems bushy-branched; leaves 0.3-1.5 mm wide, with 1–3 veins; stipules 3-11 mm long . . . . var. *macellus*

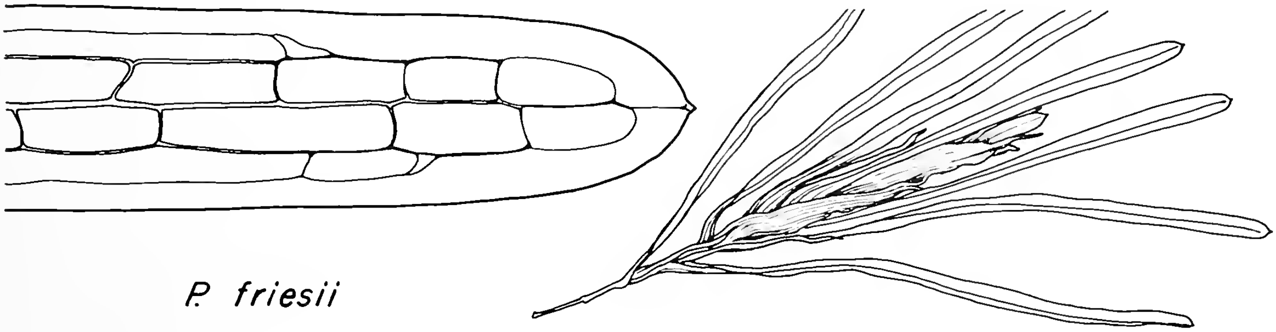


P foliosus

9. P. friesii Rupr.

Frequent. Calcareous or brackish water of lakes and streams.

Similar to *P. strictifolius.* These species are usually distinguished from the other linear-leaved species by the firm, fibrous, whitish stipules.

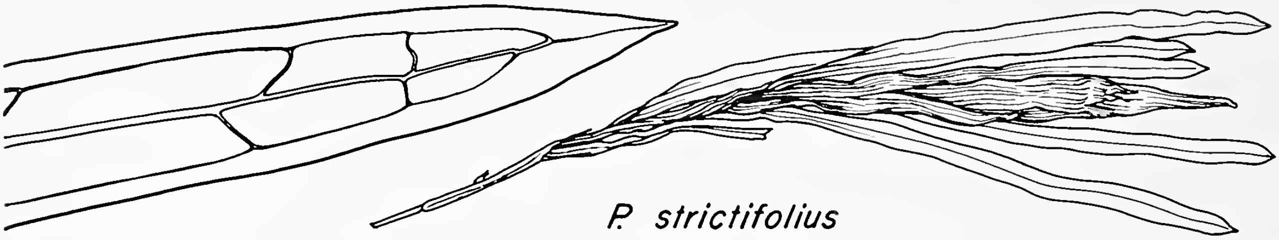


P friesii

10. P. strictifolius Benn.

Frequent. Calcareous water of lakes and streams.

Similar to *P. friesii.* See above.



P strictifolius

11. P. pusillus L.

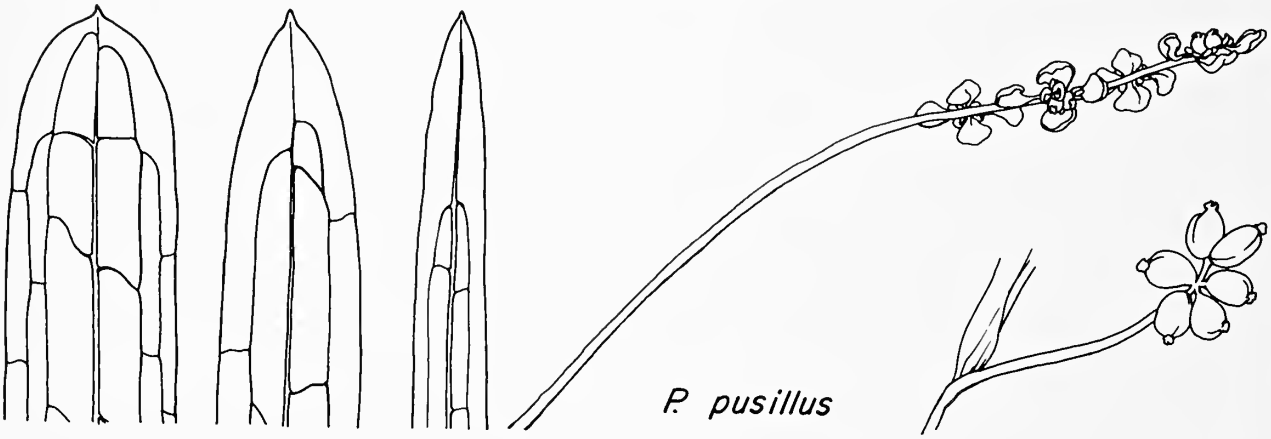
Common and often abundant. Fresh or brackish water of lakes and slow streams.

Sterile material is similar to *P. foliosus;* see discussion under that species.

A highly variable species. We have two varieties which are treated as two species by many authors: var. **pusillus** and var. **tenuissimus** M. & K. (= *P. berchtoldii, P. b.* var. *tenuissimus, P.b.* var. *acuminatus, P.b.* var. *lacunatus, P.b.* var. *polyphyllus*).

1\. Peduncles 1.5-8 cm long; spikes with 3–5 whorls of flowers, the whorls usually separated in fruit; leaves without lacunae along midrib or with a single row each side at base . . . . var. *pusillus*

1\. Peduncles 0.3-3(-4.5) cm long; spikes with 1–3 contiguous whorls; leaves with one or more rows of lacunae each side of midrib . . . . . . var. *tenuissimus*

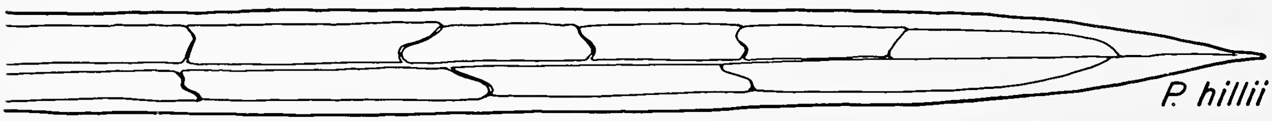


P pusillus

12. P. hillii Morong

Rare, but may be locally abundant. Pools (often stagnant) and slow streams.

Our only species with leaves more than 1 mm wide that have only 3 veins and a bristle-tipped apex. The rare hybrid *P.* × *longiligulatus* also has bristle-tipped leaves but with more veins; it is mostly sterile. *P. hillii* fruits freely. The mucro at the leaf tip of *P. zosteriformis* sometimes appears like a short bristle.

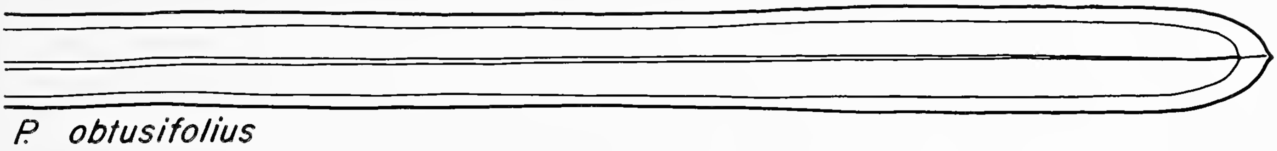


P hillii

13. P. obtusifolius M. & K.

Not common. Ponds and streams.

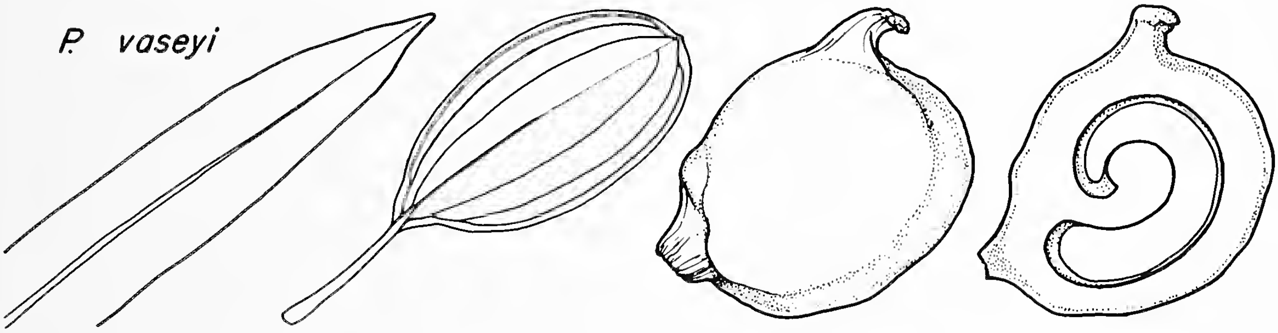
Generally distinguished from the other linear-leaved species by the leaves that are 2-4 mm wide and rounded at apex. Superficially similar to *P. friesii,* from which it differs by leaves with only 3 prominent veins and with nonfibrous stipules.



14. P. vaseyi Robbins

Occasional. Quiet water of lakes.

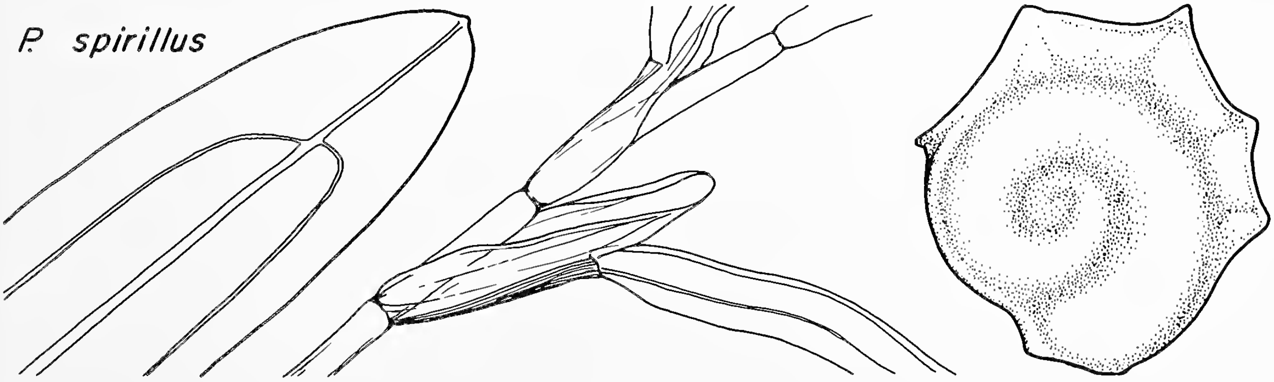
Our only species with the combination of floating leaves less than 9 mm wide, linear submersed leaves less than 1 mm wide, and fruits with embryo coil less than 1 complete revolution. The similar *P. lateralis* Morong is thought not now to be in New York; it may be merely a variant of *P. vaseyi* or a hybrid with *P. vaseyi* being one of the parents.



15. P. spirillus Tuckerman

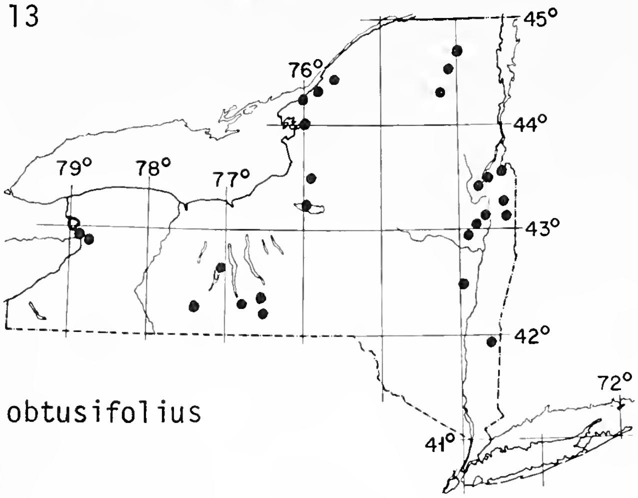
Common. Shallow pools, lake margins, and quiet streams.

Similar to *P. diversifolius.* These two species are recognized by their tiny fruits with walls so thin that the embryo coil is evident.



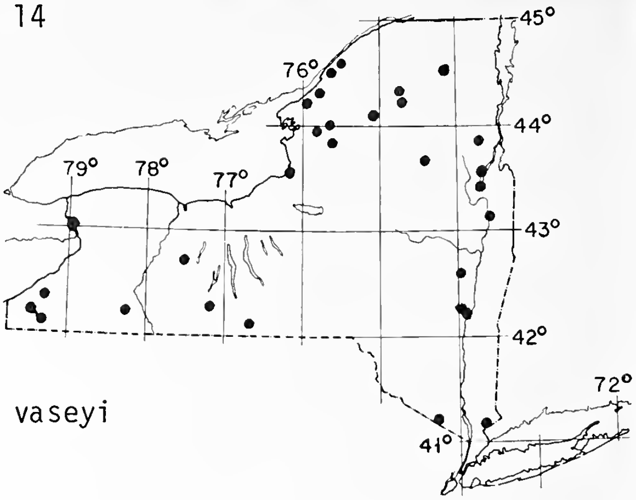
POTAMOGETON

13



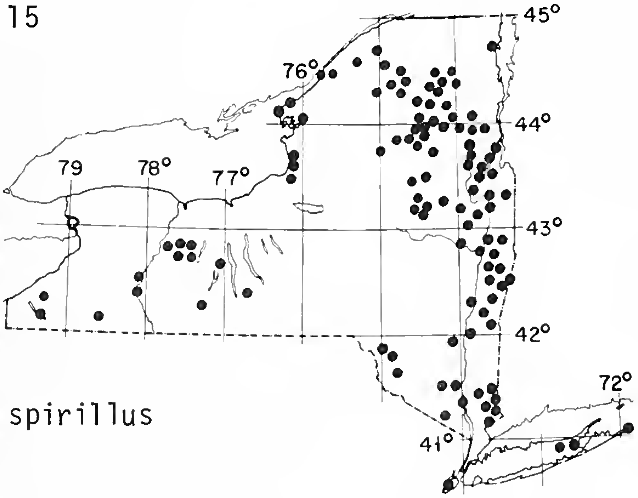
obtusifolius

14



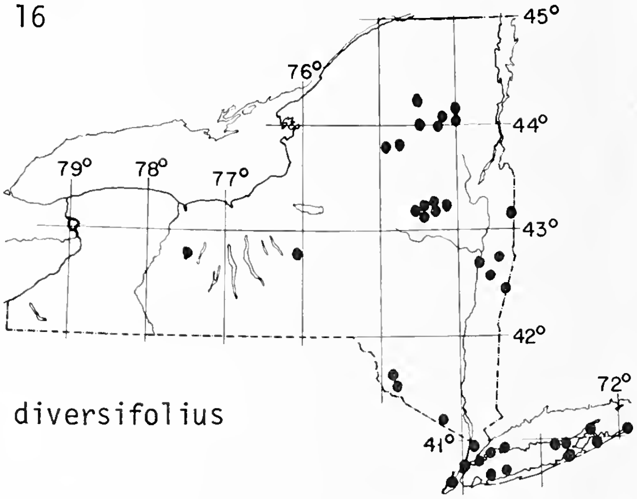
vaseyi

15



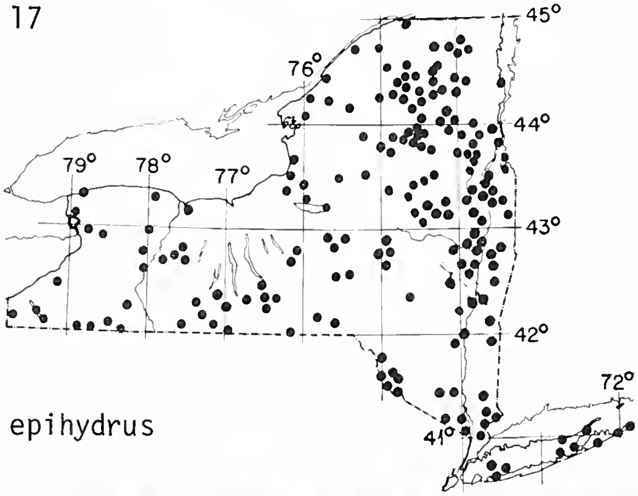
spirillus

16



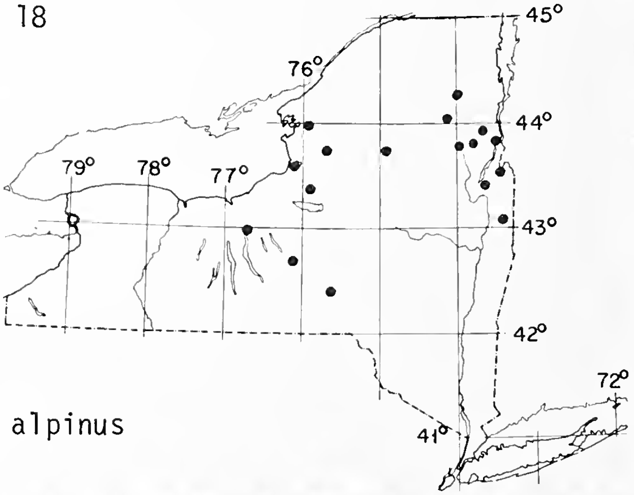
diversifolius

17



epihydrus

18



alpinus

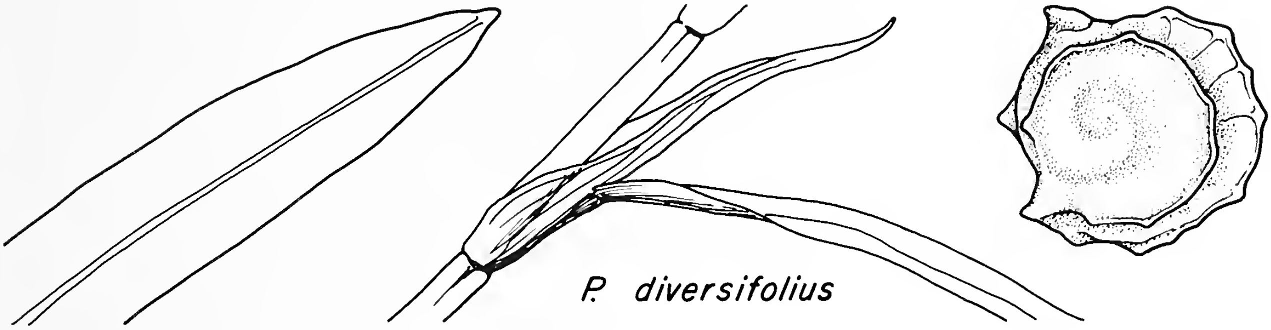
16. P. diversifolius Raf.

Not common, except in the Adirondacks and on Long Island. Pools, lakes, and slow streams.

Similar to *P. spirillus*. We have two varieties, which differ mainly by size: var. **diversifolius** and var. **trichophyllus** Morong *(= P. capillaceus).*

1. Submersed leaves 0.4-1.5 mm wide, subobtuse to acute; stipules 6-30 mm long; floating leaves with 5–15 veins, apex rounded; submersed peduncles 1-4 mm long . . . . var. *diversifolius*

1. Submersed leaves 0.1-0.6 mm wide, apex setaceous, stipules 3-12 mm long; floating leaves with 3–7 veins, apex acutish; submersed peduncles 3-13 mm long . . . . var. *trichophyllus*



P. diversifolius

17. P. epihydrus Raf.

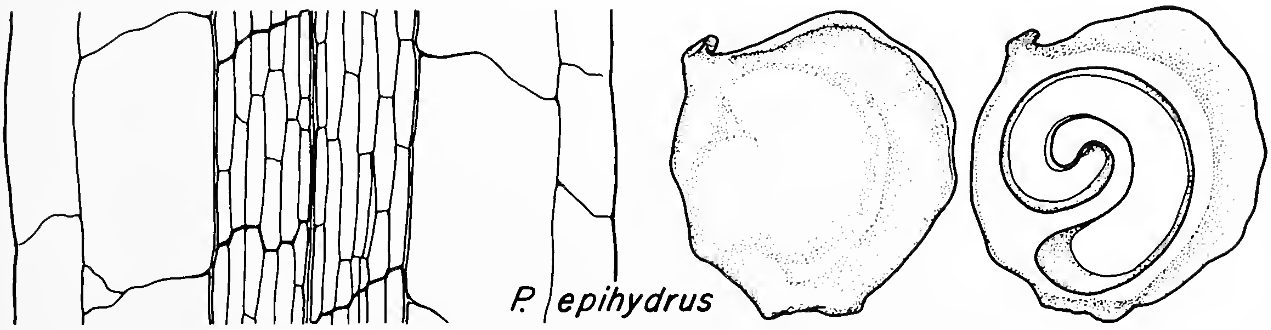
Common and often abundant. Pools, lakes, and streams.

Easily recognized by the ribbonlike submersed leaves with a broad band of lacunae between the 2 veins closest to the midrib and by the large fruits with embryo coiled more than 1 complete revolution.

We have two intergrading varieties: var. **epihydrus** and var. **ramosus** (Peck) House (= var. *nuttallii*).

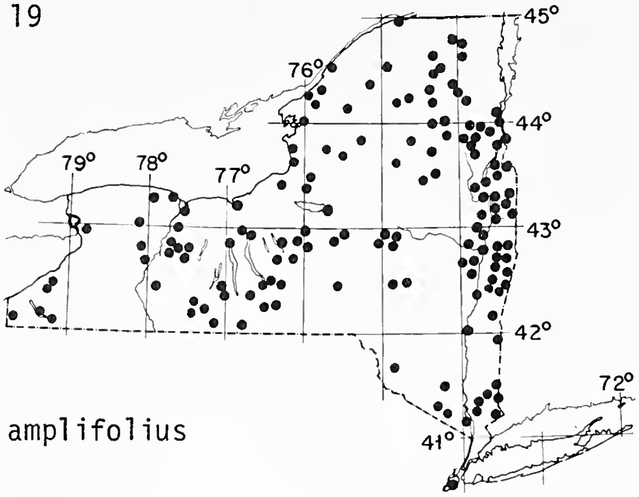
1. Submersed leaves 5-10 mm wide, with 7–13 veins; floating leaves 15-35 mm wide; fruits 3-4.5 mm long, 3-3.6 mm wide . . . . var. *epihydrus*

1. Submersed leaves 2-6 mm wide, with 5–7 veins; floating leaves 4-25 mm wide; fruits 2.5-3.5 mm long, 2-3 mm wide . . . . var. *ramosus*



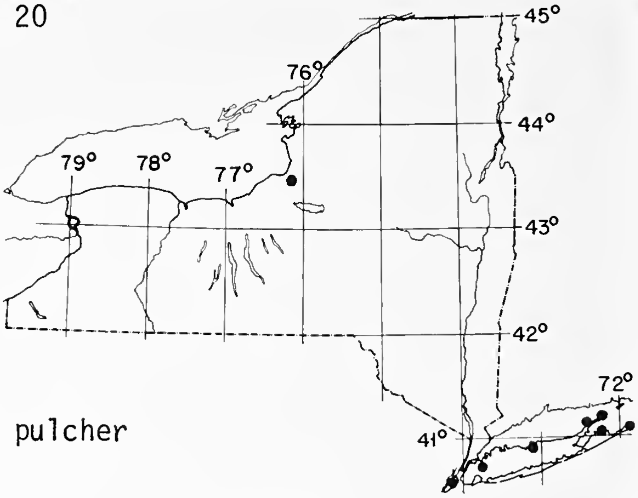
P. epihydrus

19



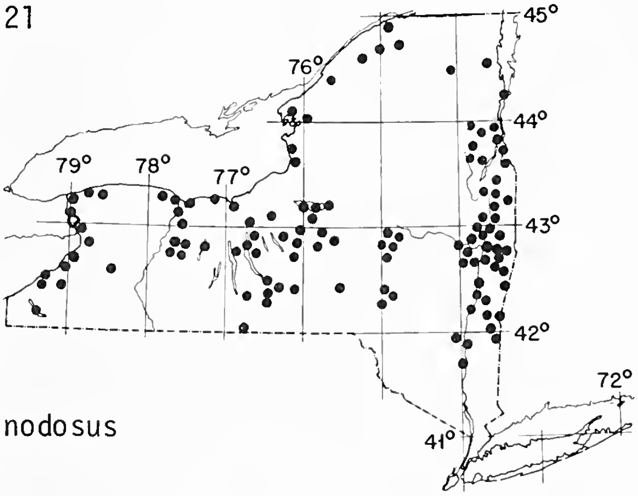
amplifolius

20



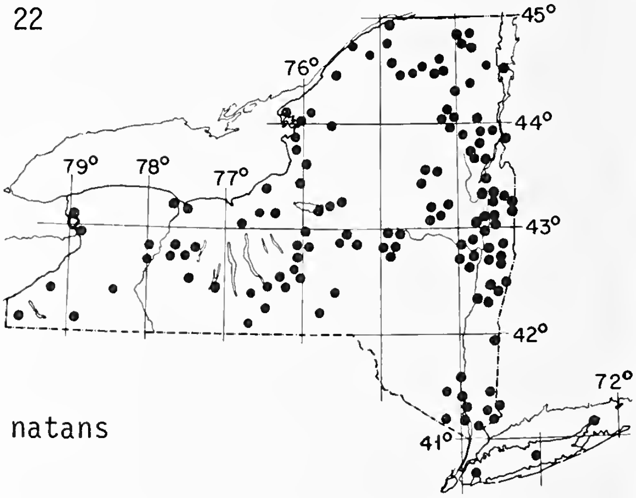
pulcher

21



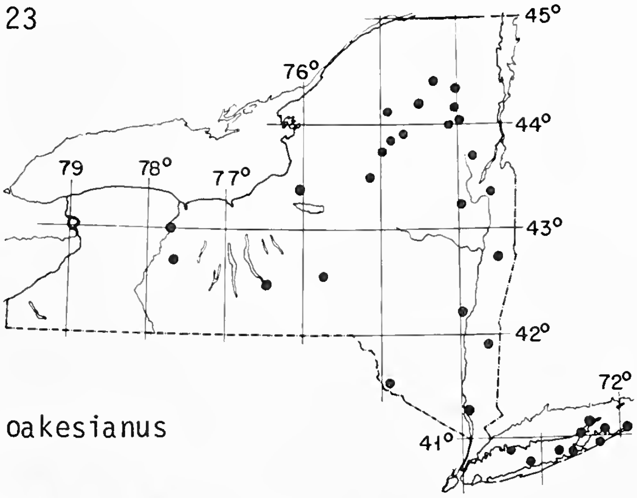
nodosus

22



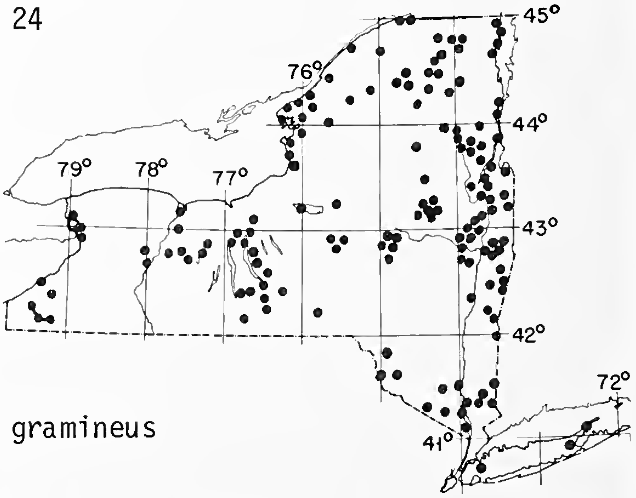
natans

23



oakesianus

24



gramineus

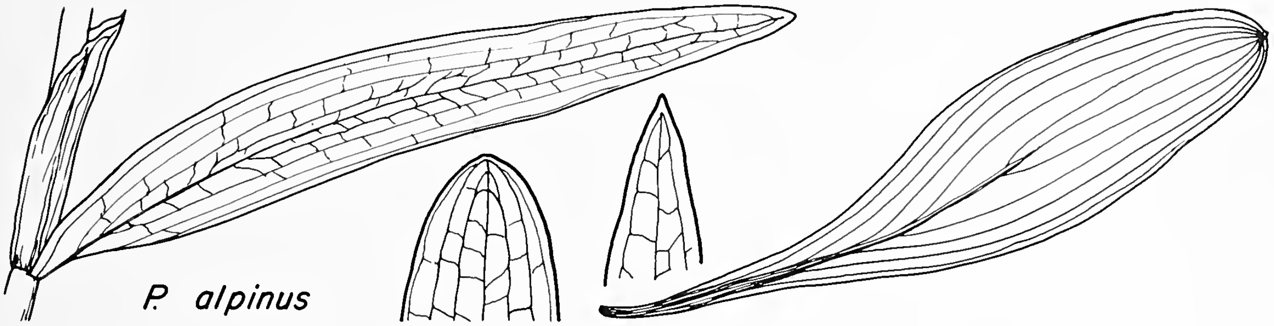
18. P. alpinus Balbis

Uncommon. Cold water of lakes and streams.

Easily recognized by the fruit, which is smooth, hard, and eggshell-like. With sterile specimens, clues are: sessile submersed leaves often with a reddish cast, and floating leaves that are delicate and with blades tapering gradually to the petiole.

We have two intergrading varieties which differ slightly from the European var. **alpinus:** var. **tenuifolius** (Raf.) Ogden, and var. **subellipticus** (Fernald) Ogden.

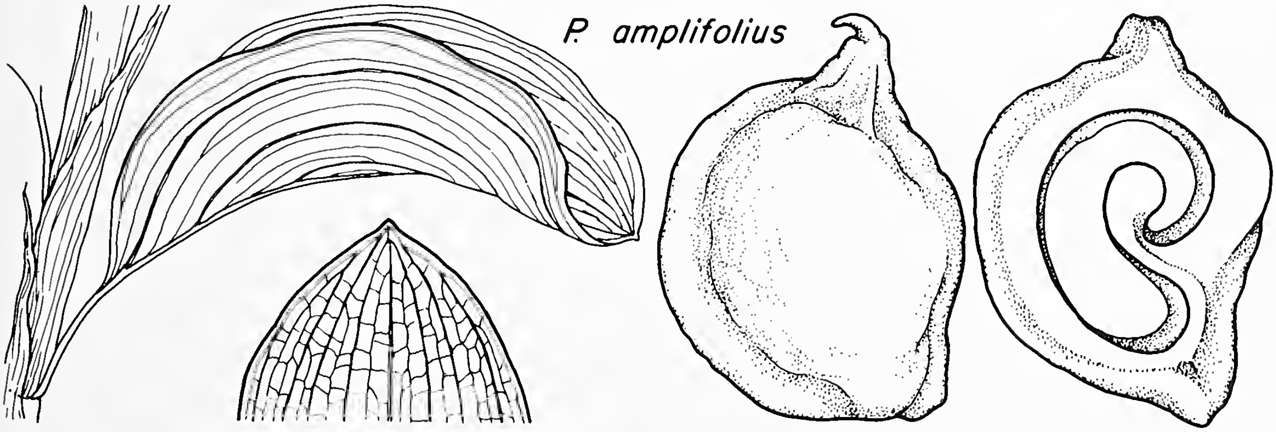
1. Submersed leaves oblong-linear to linear-lanceolate, 7-25 cm long, usually more than 8 times as long as wide, tapering to an obtuse or acutish apex . . . . var. *tenuifolius*
1. Submersed leaves oblong to ovate-oblong, 4-10 cm long, usually less than 8 times as long as wide, with a rounded apex . . . . var. *subellipticus*



19. P. amplifolius Tuckerman

Common and often abundant. Lakes and streams, usually in deep water.

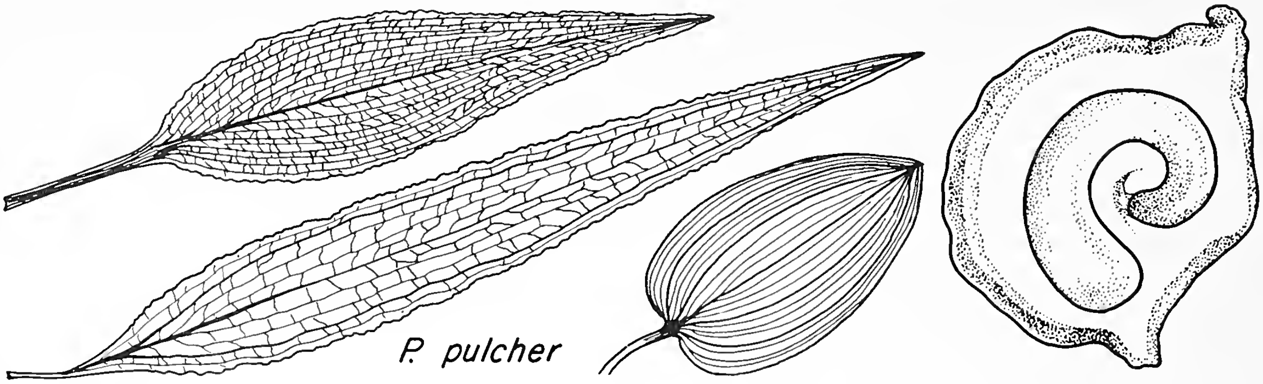
Usually recognized by its many large, arcuate, submersed leaves. It is sometimes confused with *P. pulcher, P. nodosus,* or *P. illinoensis,* but generally has many more veins in the submersed leaves (19–37) and in the floating leaves (29–51). From the highly variable *P. illinoensis,* it is separated by the submersed leaf apex: sharp in *P. illinoensis* and blunt in *P. amplifolius.*



20. P. pulcher Tuckerman

Rare or locally common. Shallow muddy pools and slow streams.

Our only species with cordate floating leaves and broad submersed leaves.

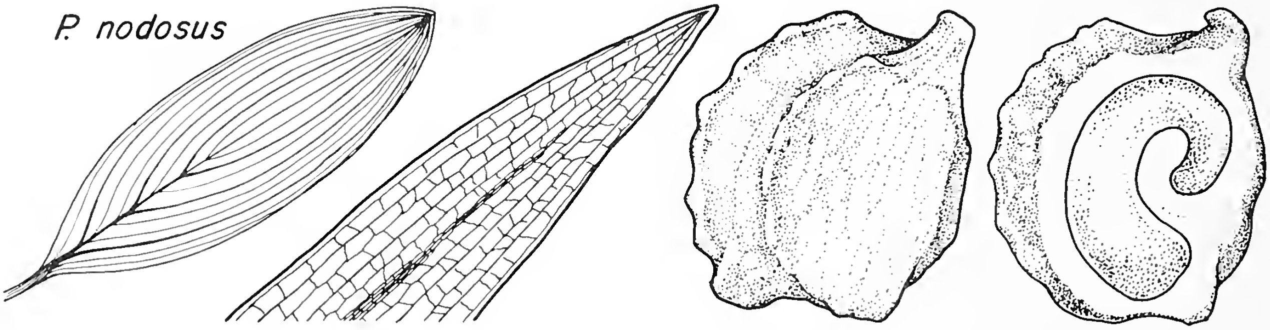


21. P. nodosus Poiret

Synonym: *P. lonchites*

Frequent to common. Lakes and streams.

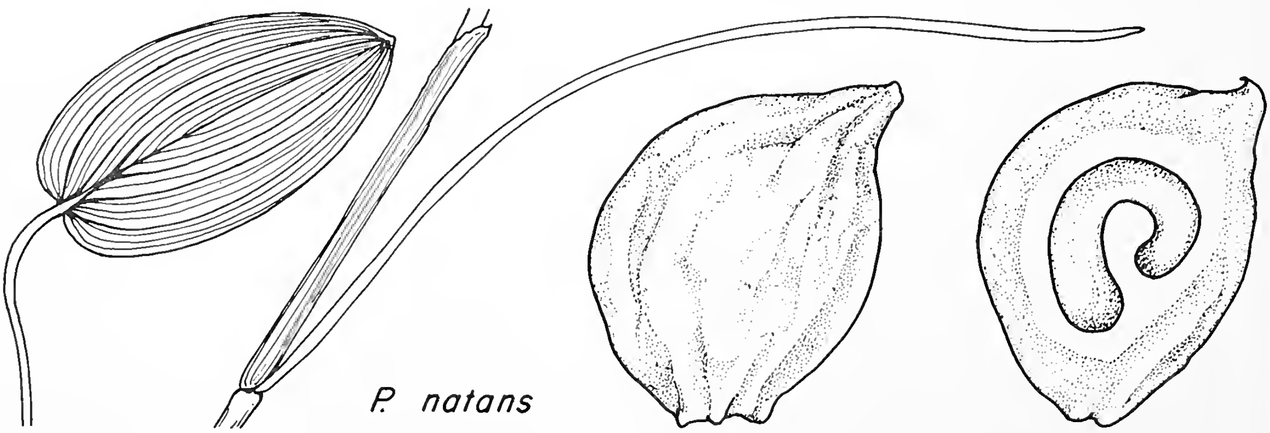
A variable (in vegetative parts) species with floating leaf blades cuneate at base, submersed leaf blades narrowly lanceolate and tapering gradually to each end, and reddish fruits with strongly developed keels.



22. P. natans L.

Common and often abundant. Lakes and streams.

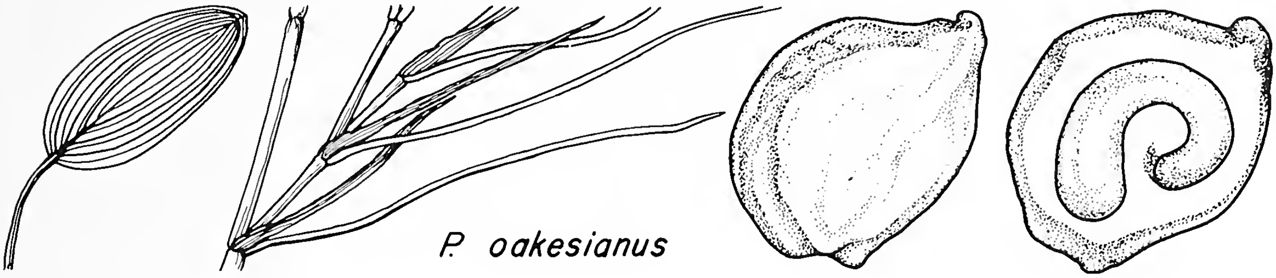
Plants with cordate floating leaves and narrowly linear submersed leaves. The latter decay early and are usually gone by the time the fruits appear.



23. P. oakesianus Robbins

Occasional. Ponds and slow streams.

Similar to *P. natans* but smaller. In North America some bog pool plants have floating leaves that are narrowly elliptic and as narrow as 5 mm, but these have not been found in New York.

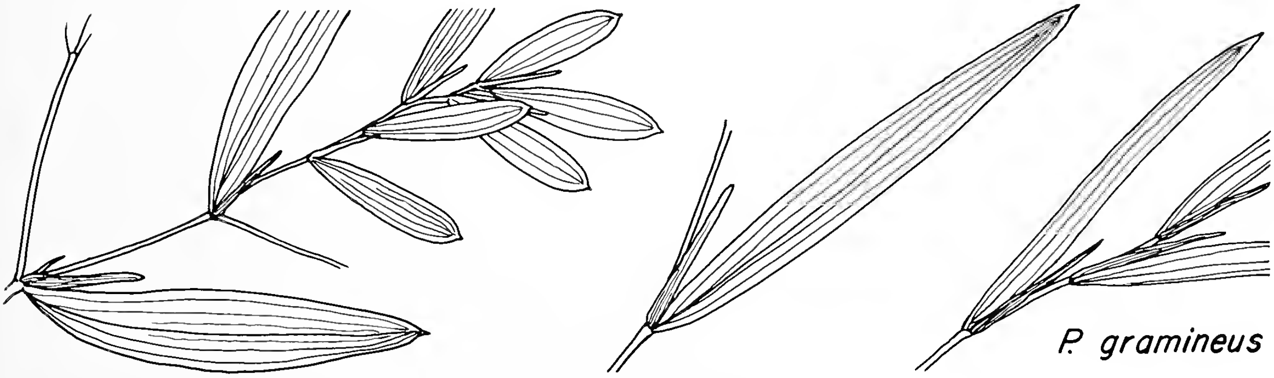


24. P. gramineus L.

Common and often abundant. Lakes and streams.

A variable species with many compound branches bearing sessile lance-elliptic submersed leaves. Var. **gramineus** is the most common, but var. **maximus** Morong ex Bennet and var. **myriophyllus** Robbins occur in the State. It occasionally hybridizes with *P. illinoensis, P. perfoliatus,* and other species.

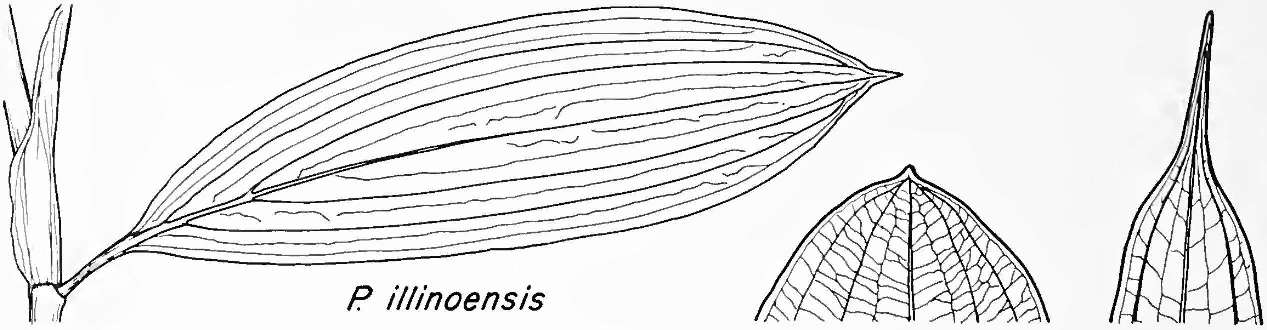
1. Submersed leaves narrowly elliptic to oblanceolate, mostly 2-10 mm wide, 5-10 times as long as wide, veins (3–) 5–9
    2. Submersed leaves of the main stem mostly 15-50 mm long, 2-6 mm wide; veins 5-7 . . . . var. *gramineus*
    2. Submersed leaves of the main stem mostly 60-100 mm long, 6-10 mm wide; veins 7–9 . . . . var. *maximus*
1. Submersed leaves linear, mostly 15-35 mm long, 1-2.5 mm wide, 10-20 times as long as wide; veins 3 . . . . var. *myriophyllus*



25. P. illinoensis Morong

Common and often abundant. Lakes and streams.

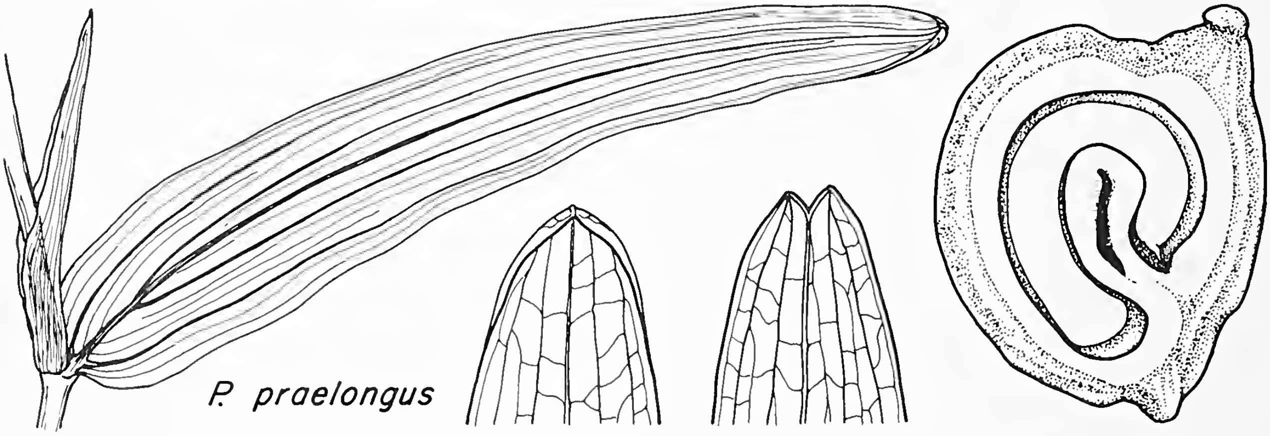
A highly variable species. It sometimes approaches *P. gramineus* (with which it hybridizes) but is coarser and less branched. From other species, it is usually distinguished by the sharp pointed, often mucronate, broad, submersed leaves. It is frequently found, even fruiting, with no floating leaves.



26. P. praelongus Wulfen

Occasional. Lakes and streams, usually in deep water.

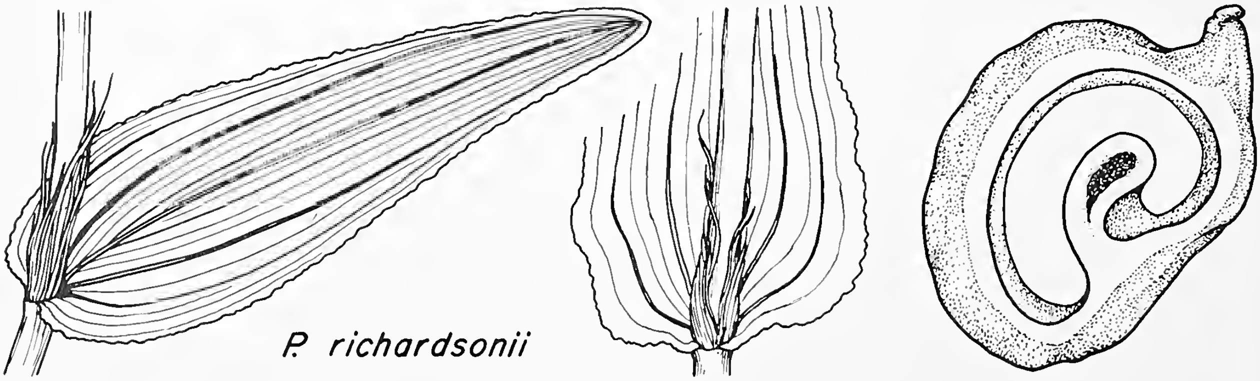
Plants with large, ovate-oblong leaves which are cucullate (boat-shaped) at the apex, whitish stem, large, conspicuous stipules, and long peduncles bearing large fruits. The fruits mature early (June) and sink, so are not seen late in the season. The cucullate leaf apex often splits when flattened.



27. P. richardsonii (Bennett) Rydberg

Common. Lakes and streams.

Similar to *P. perfoliatus,* from which it is distinguished by the cavity in the endocarp loop of the fruit and by the coarse whitish stipules. Sterile hybrids between these two species appear to be common.

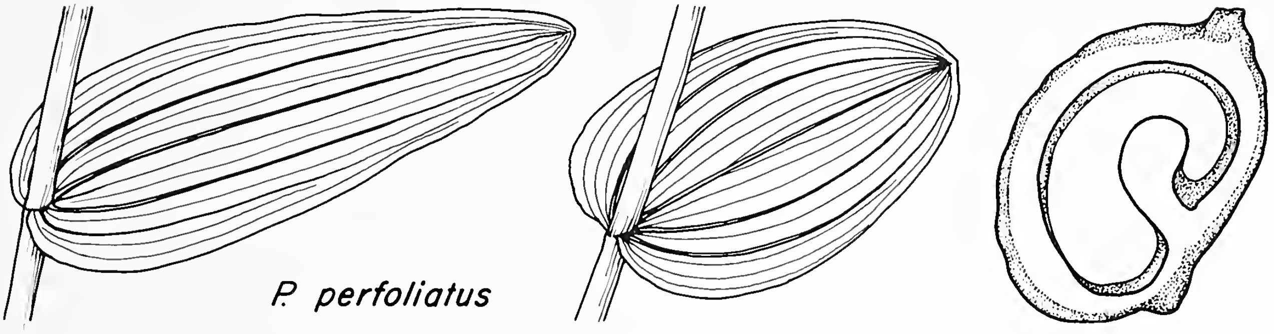


28. P. perfoliatus L.

Common. Lakes and streams.

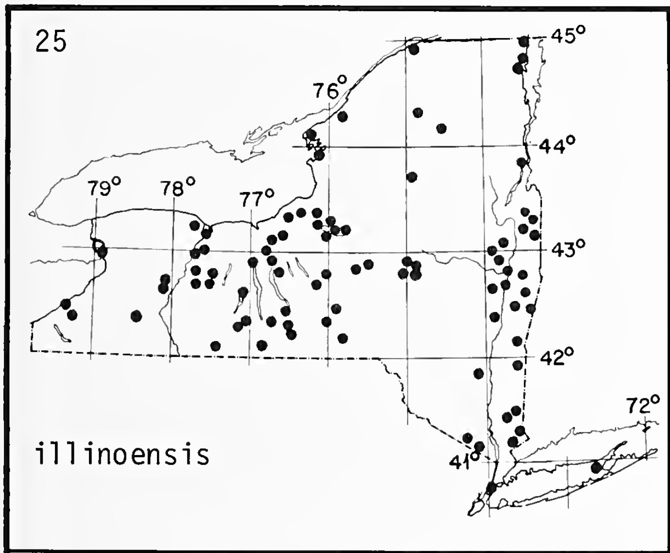
Ours is var. **bupleuroides** (Fernald) Farwell

Plants of brackish water have small ovate leaves but in fresh (especially acid) water the leaves are larger, more elongate, and may simulate those of *P. richardsonii*. In the absence of fruits, the delicate fugaceous stipules yield the best character. Sterile intermediates are common.

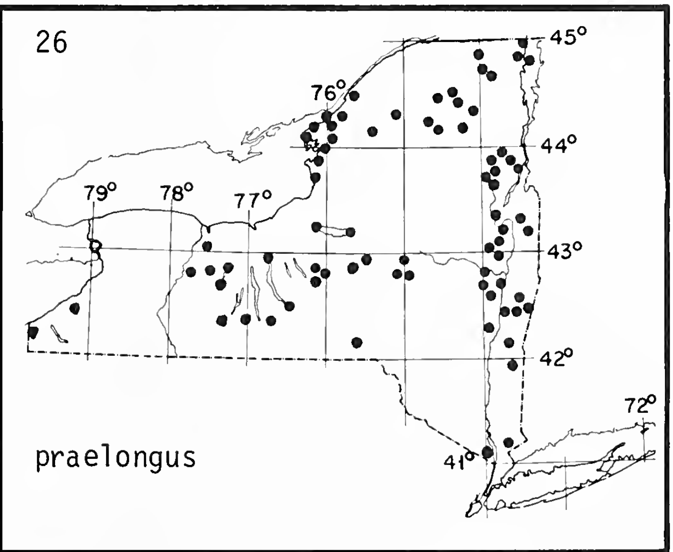


P. perfoliatus

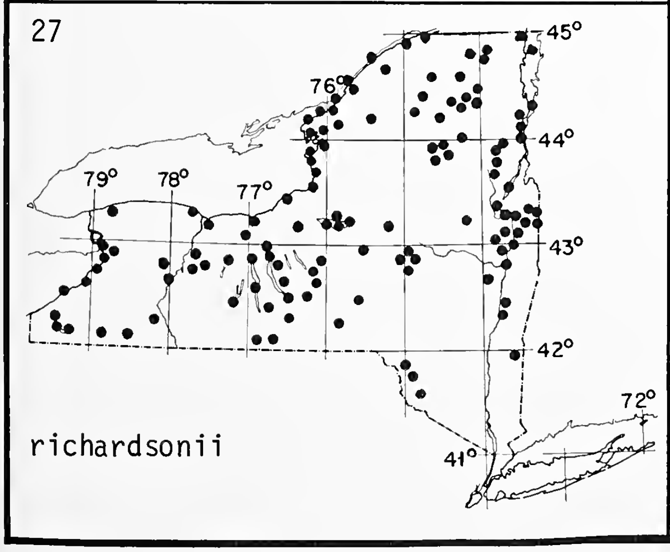
POTAMOGETON



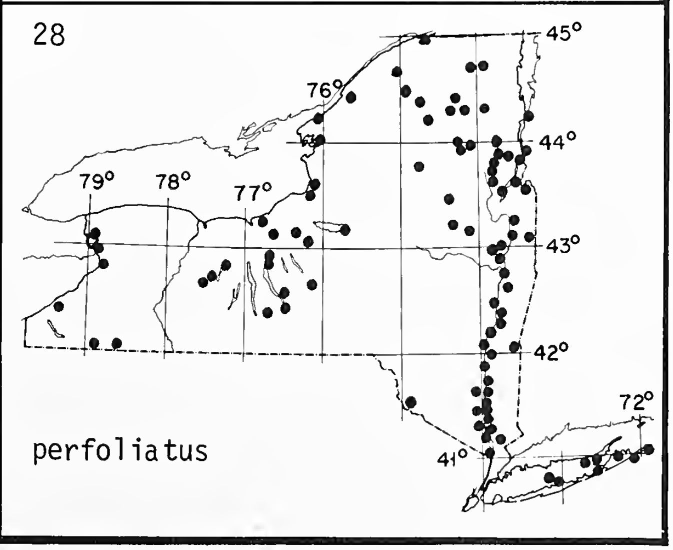
25 illinoensis



26 praelongus



27 richardsonii



28 perfoliatus

Excluded Species

P. lateralis Morong

Collected in Hemlock Lake, Livingston Co. in 1882; not seen since. Apparently closely related to *P. vaseyi,* it may be merely a variant of that species.

P. longiligulatus Fernald

This is probably a hybrid. *P. zosteriformis* is likely one of its parents; the other may be *P. strictifolius* or *P. hillii.* Collected in a few localities in the State. Also collected in Newfoundland, Connecticut, Ontario, Michigan, and Minnesota, but it had not been found in fruit until a single mature fruit was found in 1970 in Columbia Co., New York.

Hybrids

P. perfoliatus × richardsonii, P. gramineus × illinoensis and P. gramineus × perfoliatus are the most frequent hybrids seen in the State. The following have been reported for New York:

alpinus × nodosus
amplifolius × praelongus
amplifolius × richardsonii
epihydrus × nodosus
gramineus × illinoensis
gramineus × natans
gramineus × nodosus
gramineus × perfoliatus
illinoensis × nodosus
illinoensis × perfoliatus
perfoliatus × richardsonii
strictifolius × zosteriformis

Acknowledgments

The original manuscript has been greatly improved by suggestions from Dr. Robert R. Haynes of Ohio State University and Dr. Edward G. Voss of the University of Michigan. The drawings were executed by Richard W. Snook, temporary research assistant. The maps were prepared by J. Kenneth Dean, laboratory technician, from range maps kept current by Stanley J. Smith, senior scientist and curator of the New York State Herbarium.

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State Botanist

BULLETIN 424

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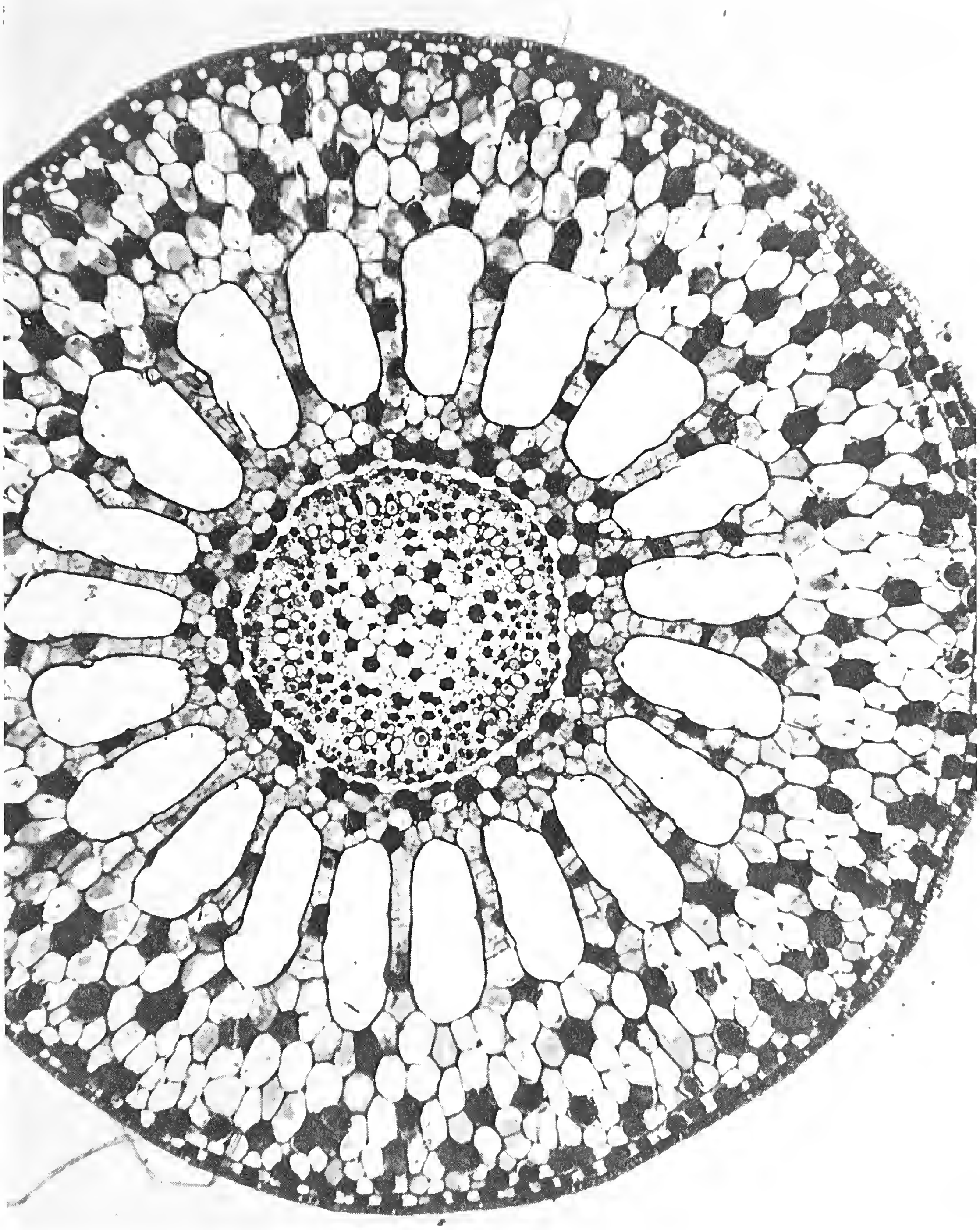

Myriophyllum brasiliense stem × 65

See Plate 54 for comparison of photomicrograph and drawing.

Acknowledgments

Special credit and thanks go to Stanley J. Smith for collections of histological material, for advice regarding classification and nomenclature, and for locations of uncommon species. The maps were prepared from the range maps in his charge and kept current by him.

J. Kenneth Dean prepared many of the permanent microscope slides and the freehand sections for comparisons. His help with the anatomical descriptions is much appreciated. He prepared all of the 208 maps.

Dr. Fay Hyland, University of Maine, reviewed the final manuscript and suggested several improvements. He prepared the slides that were used to illustrate *Najas* and *Sagittaria.*

Richard W. Snook prepared most of the illustrations (62 plates). His training in both botany and art was especially helpful.

Donald J. Moore processed much of the histological collections to microscope slides and prepared four of the plates of illustrations.

Dr. James R. Nolan, State University of New York at Plattsburgh, supplied the microscope slides with interpretive notes from which the illustrations of *Isoetes* were made.

Slocum Water Gardens, Winter Haven, Florida, kindly supplied histological material of *Nelumbo.*

Eileen T. Coulston handled most of the bibliographic work.

Nancy M. Farr saw the manuscript through all of its typing and proofreading stages.

The frontispiece was prepared by John H. Haines.

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Anatomical Patterns of Some Aquatic Vascular Plants of New York[1]

Eugene C. Ogden, State Botanist
New York State Museum and Science Service

INTRODUCTION

In several types of research, it is desirable to determine the identity of aquatic vascular plants that are sterile and fragmentary. Available floristic manuals frequently are not adequate for this. It is often necessary to seek characters not available from external morphology. Internal anatomical patterns of stem internodes offer additional characters. Published information on this is widely scattered or nonexistent. The purpose of this Bulletin is to bring together in convenient form useful anatomical patterns of the frequently encountered vascular plants that grow in water.

The usual definition of aquatic plant (i.e., growing in water) may not be most desirable here. Fragments from the stomachs of wild waterfowl and aquatic mammals may include material that did not grow in water. As most truly aquatic vascular plants are characterized by having much aerenchyma tissue, this character, which is readily seen in cross section, may be chosen for determining if the plant is likely aquatic. Thus, the definition of an aquatic plant, for purposes of this treatment, is one having a stem or stemlike parts in which the cross section area (excluding the pith, if it is hollow) is at least 50 percent lacunate, i.e., noncellular portions cover at least half of the area. Exclusion of the hollow pith is necessary to eliminate large groups of dry area plants as in the Gramineae and Umbelliferae. With this circumscription of " aquatic plants," dry habitat species of *Equisetum* are still included.

Stemlike parts include root, rhizome, stem (used here to exclude rhizome for convenience, brevity, and usefulness), leaf (usually the petiole) and peduncle (including pedicel). In a few cases a young fruit might be stemlike, such as *Vallisneria*. Genera are excluded if only the roots are lacunate. Roots of the aquatic genera are similar and offer little help in identification.

Stemlike shapes in cross section may be circular to triangular or flattened, but with the longest diameter no more than five times the shortest diameter. As extremely slender fragments generally do not have useful discernible anatomical patterns, those less than 1 millimeter in longest diameter are mostly not included. Those greater than 10 mm in shortest diameter are also excluded.

This is a book on anatomical patterns rather than on anatomy. Its slant is taxonomic rather than anatomic.

Preparation of reference slides

Histological material of submersed and emersed stemlike organs was collected from various parts of vascular plants and stored in FAA killing and preserving solution. Standard herbarium collections for vouchers were taken for filing in the herbarium of the New York State Museum and Science Service, unless the species identity was not in question and the species had been sampled previously for anatomical studies and vouchered at least once. Usually an additional collection was taken for making comparative anatomical studies from dried pressed material as found in the usual herbarium. Details of the process of preparation of the microscope slides are unnecessary here. The paraffin method was used. The sections were cut with a rotary microtome at a thickness from 10 to 30 microns. Staining was with safranin and fast green. The tissues were sealed in Canada balsam. For some rare species, which would require an unwarranted amount of effort to obtain as fresh material and in a genus having one or more species in the fresh specimen collections, dried herbarium material was obtained, boiled in water to soften and expand, and then processed by the paraffin method. Because of

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[1] Manuscript submitted for publication April 25, 1974.

the large number of collections to be processed and because fine detail (such as structure of the cell wall and nature of the cell contents) was not needed, rapid methods of slide preparation were employed. Occasionally, when requested, the technicians processed material from vacuumed preserving solution to the stained and mounted slides in 7 or 8 hours.

Preparation of unknowns for comparison

Material for identification may be from sterile specimens, fragments at the shore or on feeding platforms, from animal stomachs, etc. It may be preserved in some fluid or as dried material. It is seldom feasible or necessary to process this material as for research-quality microscope slides. Simpler and quicker methods usually will provide adequate mounts for determining the anatomical patterns. Although any of several methods may be employed, the following is what I use at the present time and have found to be satisfactory during the past 35 years.

Dried material, a few millimeters long, is boiled in water or emersed in a detergent to soften and expand the tissues, then dropped into cold water to reduce flabbiness. Fresh or otherwise soft material need not be boiled. Place the following items near a dissecting microscope: flat paper towel, 3 x 5 index card, sharp safety razor blade, open vial of fountain pen ink (washable blue Skrip), tweezers, two dissecting needles with very slender tips, glass microscope slide (preferable the concavity or depression type), and small container (finger bowl) of cold water. Place a drop of water on the slide. Move the material, without undue crushing, to the towel to remove excess water. Move the material from the towel to the card. Place under the scope. Make a clean transverse cut near one end. Grip the other end with tweezers and dip the cut end into the ink for a few seconds. Rinse briefly in cold water and place on the towel again. It may be rolled a bit or squeezed slightly to remove excess water. It is now moved to the card again and oriented as when the first cut was made. Cut a thin freehand section from the stained end. This should remain attached to the razor blade. Place the microscope slide under the scope and with a needle push the tissue into the drop of water, stained end up. Usually one such section is enough but several of different thicknesses may be helpful, some being stained, some unstained. Under the dissecting scope, at a magnification of 5 to 10, use the two needles to pull the tissue into expanded form. This is done by hooking the needle push the tissue into the drop of water, stained end outward. A small amount of tearing is not objectionable. The gross anatomical pattern can be seen at low magnification. For greater detail, move the slide to a microscope at 100 diameters. The lacunae allow enough light to come through to illuminate most of the cells.

Color differentiation in these mounts varies greatly among the different genera and even with preparations from the same bit of tissue. Ideally the cellulose walls retain the blue stain and those with suberin or lignin appear yellowish.

If these mounts are needed for later observation or for permanent storage, a water-missible mounting fluid (such as glycerin jelly) is placed on the slide instead of water. A freehand, inkstained section of a *Potamogeton* stem sealed on a depression slide with Karo syrup is well preserved 30 years later.

Glycerin jelly mounts are easily made. Commercial glycerin jelly may be used. A formula which we like is: 2 parts gelatin, 12 water, 11 glycerin, 2% phenol (1 part to each 50 parts of the glycerin jelly). Mix the gelatin and water. The mixture may be warmed slightly to dissolve the gelatin faster. When dissolved, add the glycerin and phenol. Let stand overnight. Strain through cheesecloth. Prestained glycerin jelly eliminates the need to stain before mounting. We add a drop of saturated aqueous basic fuchsin to each 15-20 ml of the glycerin jelly. This jelly is stored as a solid and warmed to a liquid (in a water bath) for use. On standard flat microscope slides, as the jelly dries and the cover glass settles, the thick-cut sections may be distorted unless some rim-sealing material (such as epoxy, nail polish, or paraffin) is used. More satisfactory, except for cost, is the commercial depression (concavity) slide.

Arrangement of taxa

The genera are listed in the general sequence in which they appear in currently used floristic manuals: horsetails, quillworts, ferns, monocots, and dicots. The species of each genus are listed in alphabetical order. Each species name encompasses all subspecific taxa in the State. It is expected that users of this Bulletin will have access to one or more of the following five books which include the aquatic vascular plants of New York State.

Fassett, N.C. 1957. A manual of aquatic plants. Revised ed. University of Wisconsin Press, Madison.

Fernald, M.L. 1950. Gray's manual of botany. 8th ed. American Book.

Gleason, H.A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. New York Botanical Garden.

House, H.D. 1924. Annotated list of the ferns and flowering plants of New York State. New York State Museum Bulletin No. 254. 759 p.

Muenscher, W.C. 1944. Aquatic plants of the United States. Comstock.

Excluded genera

Genera with herbaceous species found growing in water but with parts (except roots) not sufficiently lacunate to be included here. Some are listed in the text but not illustrated:

Cicuta
Cyperus
Impatiens
Podostemum
Polygonum
Ranunculus
Rorippa
Samolus
Sium
Typha
Veronica
Zostera

With stemlike parts lacunate but too small. Some of these are listed in the text but are not illustrated:

Callitriche
Echinodorus
Elatine
Limosella
Littorella
Subularia

Plants that generally are not lacunate but may produce some aerenchyma in the cortex of submersed parts when growing in water:

Cardamine
Decodon
Distichlis
Epilobium
Lycopus
Lythrum
Mentha
Peplis
Phragmites
Scutellaria

Plants that are lacunate but rare, and suitable material not available for study:

Hottonia
Limnobium

Nomenclature

The scientific names are chosen according to the most recent and authoritative taxonomic opinions. If the name used in one or more of the above five reference books differs from the one chosen here, that name appears as a synonym. Such names are in parentheses. Some obvious synonyms, as for subspecific taxa, are not included.

Occurrence

Statements about relative abundance refer only to New York and only to those areas in the State where it is found. This varies for different localities and the remarks are, of necessity, generalized.

The maps indicate the areas of occurrence. They were prepared from the range map file in the New York State Herbarium, which is kept current by Stanley J. Smith, Senior Scientist and Curator.

Habitat data refer to the usual situations but are meant to be inclusive for all types of habitat where the species may be found adjusted to its environment.

Anatomical patterns

Generalized descriptions of the patterns are given for each genus, calling attention to characters useful in comparing tissue preparations with the illustrations. For genera with more than one species, the description is under the genus heading with additional remarks under those species that vary sufficiently to warrant them. For genera with but one species, this description appears under the species heading, refers only to this species, and may or may not include patterns of species not found in the State. In general, characters that are obvious from the illustrations and those that are of doubtful value are not described.

Diameter measurements represent what are usually encountered and not the uncommon extremes. All measurements refer to diameters in cross section unless otherwise stated.

References

The references are those that have illustrations of the cross sections of lacunate stemlike parts. They are chosen to indicate availability of illustrations that are useful to supplement those in this Bulletin. Such references under the genus are included even though the species illustrated may not be found in New York. Although they are chosen primarily for their useful illustrations, a few are included because of important descriptive material. Importance, here, refers to their value for making comparisons and as aids in identification of unknowns, rather than learned discussions of anatomical features. Only in rare cases are references included that have no pertinent illustration. References are favored if readily available and in the English language.

Decisions about whether to include certain published illustrations were frequently difficult to make. Many diagrams showing tissue regions and many drawings or photographs of small portions of the plant organ (such as details of a vascular bundle) might be useful, if readily at hand. However, many of these were judged not sufficiently useful to warrant encouraging the user of this Bulletin to take the estimated amount of time necessary to locate them.

If the illustration is of a species found in New York, the plate or figure number is cited under the species entry; if of a species not in the State, it is cited under the genus entry.

Illustrations

The line drawings were made directly with ink on translucent drafting film from projected images of the tissues mounted on microscope slides. A microscope with lenses for a wide range of magnifications, zoom control, and a high intensity light with rheostat, was perched on an adjustable jack in a specially constructed box with a plate glass top. The desired image was focused on the drafting film which allowed each cell wall to be traced with great accuracy. The original plates are 12.5 x 21 inches. All drawings are of transverse (cross section) views. They are drawn from thin sections (mostly 20 microns) even though designed for comparison with thicker freehand sections. The magnification of each drawing is indicated by the length in millimeters of a line, sometimes to be multiplied by the circled factor. The labels are simple and self-explanatory.

Descriptive Text

This, the main portion of the book, will be used in different ways for different requirements. The plates of drawings are purposely placed together to facilitate rapid matching of illustrations with the anatomical preparation of the plant to be identified. After illustrations are chosen which are similar to the unknown, one may locate those genera in the text (by referring to the index) where the characters to observe are given and where the names of other genera that might be possibilities are suggested.

EQUISETUM Maps 1–8, Plates 1–3

Nine species in New York.

Anatomical patterns somewhat variable in the genus but mostly uniform for each species. Stems terete but often with prominent ridges, from less than 1 to 20 mm; usually with one or several large lacunae and many smaller lacunae; outer circle of lacunae (vallecular cavities) alternate with the ridges.

Agashe, S.N. 1968. Phloem studies in the pteridophytes, Part I. *Equisetum*. Am. Fern J. 58:74–77. Pl. 9, fig. 1: stem.

Bierhorst, D.W. 1971. Morphology of vascular plants. Macmillan.

Bold, H.C. 1967. Morphology of plants. 2d ed. Harper & Row.

Eames, A.J., 1936. Morphology of vascular plants: lower groups. McGraw-Hill. Fig. 69: stem.

Fernald, M.L. 1950. Gray's manual of botany. 8th ed. American Book.

Foster, A.S., and E.M. Gifford, Jr. 1959. Comparative morphology of vascular plants. W.H. Freeman, San Francisco, Calif.

Gleason, H.A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Vol. 1. New York Botanical Garden.

Hauke, R. 1963. A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete*. Beihefte zur Nova Hedwigia, Heft 8:1–123.

Haupt, A.W. 1953. Plant morphology. McGraw-Hill.

Holden, R. 1915. The anatomy of a hybrid *Equisetum*. Am. J. Bot. 2(5):225–237.

Jeffrey, E.C. 1899. The development, structure, and affinities of the genus *Equisetum*. Boston Soc. Nat. Hist. Memoir 5:155–190.

Johnson, M.A. 1933. Origin and development of tissues in *Equisetum scirpoides*. Bot. Gaz. 94:469–494.

Korsmo, E. 1954. Anatomy of weeds. Grondahl & Sons, Oslo, Norway.

Milde, J. 1865. Monographia equisetorum. Verhandl. der Kaiserlichen Leopoldino-Carolinischen deutschen Akad. der Naturforscher 32(2):1–605.

Scagel, R.F., R.J. Bandoni, G.E. Rouse, W.B. Schofield, J.R. Stein, and T.M.C. Taylor. 1965. An evolutionary survey of the plant kingdom. Wadsworth, Belmont, Calif. Fig. 20-13: stem.

E. arvense

Common and often abundant. In dry or damp soil.

Main stem 1.5–5 mm, with 8–14 ridges; branch stems with as few as 3 ridges; central cavity small, ± ¼ diam of stem; vallecular cavities large.

References: Bold, fig. 20-5: stem. Fernald, fig. 1: stem. Gleason, p. 15: stem. Jeffrey, pl. 28, fig. 6: node. Milde, pls. 1–3: stem.

E. fluviatile

This is our commonest species in lakes, being found in open quiet water to several feet in depth; also on the shores and in swamps.

Main stem 2–8 mm, shallowly 10–30-ridged; central cavity ⅘ (or more) diam of stem; vallecular cavities absent, except sometimes near base of stem.

References: Fernald, figs. 10, 11: stem. Gleason, p. 17: stem.

E. hyemale (E. laevigatum, E. praealtum)

Common on dry or wet banks and along shores of ponds and streams.

Main stem 2–20 mm, mostly with 14–40 ridges; ridges broad and rounded; central cavity ¾ (or more) diam of stem; vallecular cavities small. Superficially similar to the stem or the connate sheath of some sedges, such as *Dulichium* and *Cladium*.

References: Eames, fig. 69: stem. Fernald, figs. 13, 15: stem. Foster and Gifford, fig. 9-3: stem. Gleason, p. 17: stem. Haupt, fig. 210: stem. Holden, figs. 11, 12, 17: rhizome and stem. Jeffrey, pl. 28, fig. 3: node. Milde, pls. 29, 30: stem.

E. palustre

Local. Marshes and wet shores.

Main stem 1–4 mm, deeply 5–10-ridged; ridges smooth or rough but not spinulose; central cavity small, mostly ± ⅙ diam of stem; vallecular cavities very large.

References: Fernald, fig. 6: stem. Gleason, p. 15: stem. Korsmo, pls. 3, 4: root, rhizome, and stem. Milde, pls. 13, 14: rhizome and stem.

E. pratense

Rare. Moist soil of stream banks and alluvial woods.

Main stem 1–3 mm, with 10–20 ridges; ridges broader than the furrows, slightly roughened; central cavity ± ⅓ diam of stem. Branch stems mostly 3-angled.

References: Fernald, fig. 2: stem. Gleason, p. 15: stem. Korsmo, fig. 8: stem. Milde, pls. 7, 8: stem.

E. scirpoides

Frequent. Moist shady banks.

Stem 0.7–1 mm, 6 (rarely 8)-ridged; central cavity absent; vallecular cavities 3 or 4, large.

References: Bierhorst, fig. 7-3: stem. Fernald, fig. 16: stem. Gleason, p. 17: stem. Johnson, pl. 8, figs. 31–35: root, rhizome, and stem. Milde, pl. 35: stem.

E. sylvaticum

Common. Moist sandy woods.

Main stem 1–4 mm, with 10–18 ridges with vallecular cavities between; central cavity more than ½ diam of stem.

References: Fernald, fig. 5: stem. Gleason, p. 15: stem. Jeffrey, pl. 28, fig. 5: node. Korsmo, pls. 5, 6: root and stem. Milde, pls. 9, 10: stem.

E. variegatum

Local. Moist banks and low woods.

Main stem 1–2 mm, 5–10-ridged, the ridges furrowed, with 2 rows of silicious tubercles; central cavity ¼ to ⅓ diam of stem; vallecular cavities large.

References: Bierhorst, fig. 7-3: stem. Gleason, p. 17: stem. Holden, figs. 7–10, 13–16: rhizome and stem. Milde, pl. 34: stem.

ISOETES — Maps 9–14, Plate 4

Six species in New York, *I. echinospora* being the most common and the only species examined.

Bold, H.C. 1967. Morphology of plants. 2d ed. Harper & Row. Fig. 19-35: root.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin. Fig. 5.15: diagram of leaf.

Smith, G.M. 1955. Cryptogamic botany, 2d ed. Vol. 2. Bryophytes and pteridophytes. McGraw-Hill. Fig. 138: root.

Stokey, A.G. 1909. The anatomy of *Isoetes*. Bot. Gaz. 47:311–335, pl. 20.

I. eatonii

Rare. Shallow water and wet shores.

I. echinospora (I. braunii, I. muricata)

Frequent. Shallow water of lakes and streams.

Stem (rootstock) not lacunate. Roots less than 1 mm, with a small vascular bundle surrounded by a thin-walled endodermis; cortex of large thin-walled cells and with a single large lacuna. Leaves, above the base, terete; from less than 1 to 3 mm, usually 1–2 mm at the middle; in the center is a single small vascular bundle; the cortex may have none or 4 small bundles alternating with the 4 large lacunae; epidermis of emersed portion of leaf with stomata. These leaves might be confused with the tiny leaves (less than 1 mm) of *Littorella* and *Limosella,* which have only 2 lacunae.

Reference: Stokey, pl. 20, fig. 9: leaf.

I. engelmannii

Uncommon. Shallow water and mud of lakes and ditches.

I. macrospora

Rare or overlooked. Shallow to deep water of lakes and streams.

I. riparia

Rare. On muddy soil or in shallow water of river and lake shores.

I. tuckermanii

Occasional. Sandy lake shores.

MARSILEA — Map 15, Plate 5

One species in New York.

Allsopp, A. 1954. Experimental and analytical studies of pteridophytes. XXIV. Investigations on *Marsilea*. 4. Anatomical effects of changes in sugar concentration. Ann. Bot., N.S. 18:449–461. Pls. 23, 24: root, rhizome, and leaf.

Bierhorst, D.W. 1971. Morphology of vascular plants. Macmillan.

Bold, H.C. 1967. Morphology of plants. 2d ed. Harper & Row. Figs. 23-4, 23-5: root, rhizome, and leaf.

Gaudet, J.J. 1964. Morphology of *Marsilea vestita*. II. Morphology of the adult land and submerged leaves. Am. J. Bot. 51:591–597. Figs. 14 to 21: leaf.

Haupt, A.W. 1953. Plant morphology. McGraw-Hill.

Scagel, R.F., R.J. Bandoni, G.E. Rouse, W.B. Schofield, J.R. Stein, and T.M.C. Taylor. 1965. An evolutionary survey of the plant kingdom. Wadsworth, Belmont, Calif. Fig. 21-58: rhizome. (This illustration redrawn from Smith 1955.)

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin. Fig. 6.8: rhizome.

Smith, G.M. 1955. Cryptogamic botany. 2d ed. Vol. 2. Bryophytes and pteridophytes. McGraw-Hill. Fig. 239: rhizome. (This illustration repeated in Scagel et al. 1965.)

M. quadrifolia

Not native, but now found in a few localities where it may be an abundant weed. Lake shores, small pools, and slow streams.

Rhizome terete, 1–2 mm, with a large nonlacunate central area having 2 circles of endodermis; the inner circle may be indistinct in young tissues; cortex with a single circle of lacunae separated by 1-cell-wide chains of cells. The pattern is similar to that of the stems of *Myriophyllum* and *Gratiola,* and sometimes also *Najas, Zannichellia,* and *Ceratophyllum*, but from all these the mature rhizome is distinguished by the 2 circles of endodermis. Petiole mostly less than 1 mm, with a small nonlacunate central portion and a single circle of large lacunae in the cortex.

References: BIERHORST, fig. 17-2: stem. HAUPT, fig. 249: rhizome.

SPARGANIUM Maps 16–22, Plates 6–7

Seven species in New York.

Roots similar in all species; cortex becoming lacunate with large radially arranged lacunae; central area (stele) often with large circular lacunae. Rhizomes, stems, and peduncles similar. Rhizome 2–6 mm; stem 1–10+ mm; peduncle 1–6 mm. Central area of each with numerous bundles, scattered toward the center but forming a ring near the outer portion; ground parenchyma among the bundles not lacunate but becoming lacunate outside the bundle ring (cortex). Submersed stems more lacunate than emersed stems. Somewhat similar to a terete-stemmed *Scirpus*. Peduncles often lacking lacunae. Leaves in cross section triangular to plano-convex to thin, with prominent midrib; lacunae large, separated by 1-cell-wide chains of cells; with bundles at most of the junctures.

Kaul, R.B. 1972. Adaptive leaf architecture in emergent and floating *Sparganium*. Am. J. Bot. 59:270–278.

S. americanum

Frequent. Marshes and margins of lakes. Mostly emersed. Stem 1–3 mm.

Reference: KAUL, fig. 10: leaf.

S. androcladum

Frequent. Shallow water of marshes and bogs. Mostly emersed. Stem 1–3 mm.

S. angustifolium

Common in the Adirondacks, occasional elsewhere. Cold lakes and slow streams. Mostly submersed. Stem 1–2 mm.

S. chlorocarpum

Occasional to frequent. Boggy ponds, marshes, and slow streams. Mostly emersed. Stem 1–3 mm.

S. eurycarpum

Common over most of its range in the State, but infrequent on Long Island. Shallow water of marshes, streams, and lakes. Mostly emersed. Stem 2–10+ mm. Our largest species, but parts vary greatly in size.

Reference: KAUL, fig. 11: leaf.

S. fluctuans

Common in the Adirondacks, occasional elsewhere. Cold lakes. Mostly submersed. Stem 1–2 mm.

Reference: KAUL, fig. 12: leaf.

S. minimum

Frequent in the Adirondacks, rare elsewhere. Ponds and slow streams, usually on a soft bottom. Stem 1–2 mm. Our smallest species.

Reference: KAUL, fig. 13: leaf.

POTAMOGETON Maps 23–50, Plates 8–14

Twenty-eight or 29 species in New York.

Anatomical patterns variable in the genus but mostly uniform for each species.

Stems terete to flattened, from less than 1 to 4 mm in longest diam, with a central stele enclosed by an endodermis and a broad lacunate cortex. Stele composed of fibrovascular bundles, mechanical tissue, and parenchyma cells; xylem of each bundle usually merely a single unwalled opening, often appearing like a lacuna, sometimes remnants of the tracheid wall persist; phloem area of each bundle may or may not be distinct. Arrangement of bundles in the stele varies with different species. Four patterns may be recognized: (1) Proto type. Bundles all free, each having 1 patch of phloem, 4 of them median and with a few smaller bundles on each side (pl. 13). (2) Trio type. Three of the median bundles fused to form a single xylem canal, with 1 patch of phloem on the outer face and 1 or 2 on the inner face of the xylem canal (pls. 10, 12). (3) Oblong type. Median bundles 1 or 2, with no phloem on the inner faces; lateral bundles 1 (or 2) on each side; shape of the stele oblong or elliptical (pls. 9, 14). (4) One-bundled type. Only 1 bundle, with 4 patches of phloem which often are not evident (pl. 8B).

Endodermis usually evident. The cells may have thin walls and appear similar to the cells of the cortex or they may have thick walls and are more clearly evident. Two cell types are recognized: O-cells, having the wall thin or evenly thickened (pls. 12, 13); U-cells, having the wall thickened on the inner and lateral faces but thin on the outer face next to the cortex (pls. 9, 10, 11).

Cortex highly lacunate. This area may be without bundles (pls. 12, 13) or bundles of vascular tissue and fibers or of fibers alone at some of the junctures of the chains of cells separating the lacunae (pls. 9, 10, 11, 14). These are called interlacunar bundles. Cortical bundles adjacent to the epidermis are called subepidermal bundles. They may be present (pls. 10, 14) or absent (pls. 11, 12, 13). In some species, the outermost lacunae are adjacent to the single-layered epidermis (pl. 14); in others, 1 or more layers of cortical cells are between the lacunae and the epidermis (pls. 10, 12, 13). These cells are not thickened but do add support to a highly lacunate stem. This area is the pseudohypodermis.

Rhizome anatomy similar to that of the other stems. Any differences are mentioned under the species descriptions. Rhizomes are absent in many species. Roots less than 1 mm, lacunate or not. Petioles of floating and submersed leaves are described and illustrated where pertinent.

Peduncles lacunate, usually with 2 to 4 large central bundles; other bundles may or may not be present; endodermis mostly absent (pls. 10, 12, 14) but present (pl. 11) in *P. filiformis, P. pectinatus,* and *P. vaginatus.*

The stem of *Hydrocotyle* is similar to some species of *Potamogeton.*

Arber, A. 1920. Water plants. Cambridge University Press.

Arber, A. 1925. Monocotyledons. Cambridge University Press.

Burström, H.G., and C. Odhnoff. 1963. Vegetative anatomy of plants. Svenska Bokförlaget, Stockholm, Sweden. Fig. 79: stem.

Campbell, G. 1936. The anatomy of *Potamogeton pectinatus.* Trans. Bot. Soc. Edinburgh 32:179–186.

Chrysler, M.A. 1907. The structure and relationships of the Potamogetonaceae and allied families. Bot. Gaz. 44(3):161–188.

Eames, A.J., and L.H. MacDaniels. 1947. An introduction to plant anatomy. 2d ed. McGraw-Hill.

Hagström, J.O. 1916. Critical researches on the Potamogetons. Kungl. Svenska Vetenskapsakademiens Handlingar, 55(5):1–281. Numerous illustrations.

Ogden, E.C. 1943. The broad-leaved species of Potamogeton of North America north of Mexico. Rhodora 45:57–105, 119–163, 171–214.

Ogden, E.C. 1953. Key to the North American species of Potamogeton. N.Y. State Mus. Circ. 31.

Ogden, E.C. 1966. Potamogetonaceae. *In* C.L. Lundell, Flora of Texas 1(3):369–382.

Pieters, A.J. 1901. The plants of western Lake Erie, with observations on their distribution. U.S. Fish Comm. Bull. for 1901.

Raunkiaer, C. 1903. Anatomical Potamogeton-Studies and *Potamogeton fluitans.* Botanisk Tidsskrift 25(3):253–280.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin.

Singh, V. 1964. Morphology and anatomical studies in Helobiae. I. Vegetative anatomy of some members of Potamogetonaceae. Proc. Indian Acad. Sci., Ser. B, 60(3):214–231.

P. alpinus (P. tenuifolius)

Uncommon. Cold water of lakes and streams.

Stem terete, 1–2 mm; stele trio type, having 2 patches of phloem on the inner face of the trio bundle; endodermis of O-cells; cortical bundles absent; pseudohypodermis absent.

Reference: HAGSTROM, fig. 63: stem.

P. amplifolius

Common and often abundant. Lakes and streams, usually in deep water.

Stem terete, 1–3.5 mm; stele proto type; endodermis of O-cells; cortex with interlacunar bundles present but subepidermal bundles absent; pseudohypodermis present.

P. confervoides

Uncommon. Bog pools and acid lakes.

Stem terete, less than 1 mm; stele 1-bundled or oblong type with 1 median bundle; endodermis of O- or U-cells; cortical bundles absent; pseudohypodermis present or absent.

Reference: HAGSTROM, fig. 34: stem, leaf, and peduncle.

P. crispus

Not native, but now widespread and often an abundant weed. Pools, lakes, and streams.

Stem oval, 0.5–2 mm; stele oblong type with 1 median bundle; endodermis of O-cells; cortical bundles absent; pseudohypodermis 1 cell thick.

References: ARBER 1920, fig. 40: stem. CHRYSLER, pl. 17: stem. HAGSTROM, figs. 21, 22, 24: rhizome, stem, and leaf. OGDEN 1966, pl. 50: stem. RAUNKIAER, fig. 3: stem. SCULTHORPE, figs. 5.22, 5.23: stem. SINGH, figs. 1, 4, 7: root and stem.

P. diversifolius (P. capillaceus)

Not common, except in the Adirondacks and on Long Island. Pools, lakes, and slow streams.

Stem terete, less than 1 mm; stele oblong type, with 1 or 2 median bundles; endodermis of O-cells; cortical bundles absent or rarely with 1 or 2 tiny ones next to the epidermis; pseudohypodermis present or absent.

P. epihydrus

Common and often abundant. Pools, lakes, and streams.

Stem oval, 0.5–2 mm; stelar pattern variable: proto type, trio type, or oblong type with 2 median bundles; endodermis of O-cells; interlacunar bundles in the outer interlacunar circle; subepidermal bundles present or absent; pseudohypodermis present or absent.

References: EAMES AND MACDANIELS, fig. 139: leaf. HAGSTROM fig. 62: stem (as *P. nuttallii*).

P. filiformis

Occasional. Calcareous or brackish, mostly shallow water of lakes and streams.

Stem terete, less than 1 mm; stele 1-bundled type or oblong type with 1 or 2 median bundles; endodermis of U-cells; presence of cortical bundles variable, interlacunar bundles may be absent or only in the outer interlacunar circle or in several circles; subepidermal bundles are usually absent; pseudohypodermis present. Anatomy of stem and peduncle similar to that of *P. pectinatus.*

Reference: HAGSTROM, fig. 4: stem and leaf.

P. foliosus

Frequent. Fresh or brackish water of lakes and streams.

Stem oval or flattened in cross section, less than 1 mm in longest diam; stele 1-bundled type; endodermis of O-cells; cortex with no interlacunar bundles but usually with subepidermal bundles; pseudohypodermis absent.

References: HAGSTROM, fig 35: leaf and peduncle. OGDEN 1966, pl. 51: stem.

P. friesii

Frequent. Calcareous or brackish water of lakes and streams.

Stem flattened in cross section, less than 1 mm in longest diam; stele 1-bundled type; endodermis of O-cells; cortex with no interlacunar bundles but with subepidermal bundles; pseudohypodermis present or absent.

P. gramineus

Common and often abundant. Lakes and streams.

Stem terete, 0.5–1 mm; stele oblong type with 1 (rarely 2) median bundle and usually only 1 lateral bundle on each side; endodermis of narrow U-cells, strongly thickened on the inner and lateral faces; cortex with interlacunar bundles strongly developed but only in the outer interlacunar circle; subepidermal bundles present or absent; pseudohypodermis absent or 1 cell thick.

References: HAGSTROM, fig. 102: stem. RAUNKIAER, fig. 3: stem.

P. hillii

Rare but may be locally abundant. Pools (often stagnant) and slow streams.

Stem oval or flattened in cross section, 0.5–1 mm in longest diam; stele 1-bundled type or oblong type with 1 median bundle; endodermis of O-cells; cortex with no interlacunar bundles but with subepidermal bundles; pseudohypodermis absent.

Reference: HAGSTROM, fig. 44: leaf and peduncle.

P. illinoensis P. angustifolius, P. lucens

Common and often abundant. Lakes and streams.

Stem terete, 1.5–5 mm; stelar pattern variable, proto type, trio type, or oblong type; endodermis of strongly developed broad U-cells; cortex with bundles strongly developed in the outer interlacunar circle and sometimes a few in the next inner circle; subepidermal bundles present or absent; pseudohypodermis absent or 1 cell thick.

References: HAGSTROM, fig. 99: stem. OGDEN 1966, pl. 56: stem.

P. lateralis

Rare or absent in New York. Collected in Hemlock Lake, Livingston County in 1882; not seen since.

Stem terete, less than 1 mm; stele 1-bundled type; endodermis of O-cells; cortical bundles absent; pseudohypodermis absent.

P. natans

Common and often abundant. Lakes and streams.

Stem terete, 1–2 mm; stele trio type, with 2 patches of phloem on the inner face of the trio bundle; endodermis of strongly developed broad U-cells; cortex with strongly developed bundles throughout the interlacunar and subepidermal circles (these bundles fewer and smaller in the rhizome); pseudohypodermis 1 cell thick. Patterns of submersed leaf and emersed leaf petiole similar.

References: ARBER 1920, fig. 41: root. CHRYSLER, pls. 15, 17: rhizome, stem, leaf, and peduncle. OGDEN 1943, pl. 747: stem. OGDEN 1953, pl. 1: stem. RAUNKIAER, figs. 1, 3: stem. SCULTHORPE, figs. 5.16, 5.19, 5.22–5.25: stem. SINGH, fig. 5: stem.

P. nodosus (P. americanus, P. lonchites)

Frequent to common. Lakes and streams.

Stem terete, 1–1.5 mm; stele trio type with 1 patch of phloem on the inner face of the trio bundle; endodermis of O-cells; cortical bundles absent; pseudohypodermis absent.

References: OGDEN 1966, pl. 55: stem. PIETERS, pl. 13: stem.

P. oakesianus

Occasional. Ponds and slow streams.

Stem terete, 0.5–1 mm. Anatomy as in *P. natans,* except interlacunar bundles in but 1 circle, pseudohypodermis sometimes absent.

P. obtusifolius

Not common. Ponds and slow streams.

Stem oval in cross section, 0.5–1 mm; stele oblong type, with 1 or 2 median bundles; endodermis of O-cells; cortex with no interlacunar bundles but with subepidermal bundles; pseudohypodermis absent.

Reference: HAGSTROM, fig. 51: rhizome, stem, and leaf.

P. pectinatus

Common. Alkaline or saline water.

Stem terete, less than 1 mm; stele 1-bundled type or oblong type with 1 or 2 median bundles; endodermis of U-cells; cortex with bundles in 1, 2, or 3 interlacunar circles; subepidermal bundles usually absent; pseudohypodermis present. Peduncle less than 1 mm, with a prominent endodermis of U-cells; 2 or more poorly developed bundles in the center and none outside the endodermis; pseudohypodermis usually 1 cell thick.

References: ARBER 1920, fig. 40: stem; fig. 41: root. CAMPBELL, fig. 2: stem. CHRYSLER, pl. 16: stem. EAMES AND MACDANIELS, fig. 139: stem. HAGSTROM, fig. 16: stem and leaf. OGDEN 1966, pl. 49: stem. RAUNKIAER, fig. 6: leaf. SCULTHORPE, fig. 5.22: stele. SINGH, figs. 3, 8, 10: stem and leaf.

P. perfoliatus (P. bupleuroides)

Common. Lakes and streams.

Stem terete, 0.5–2 mm; stele trio type, usually with 2 patches of phloem on the inner face of the trio bundle; endodermis of O-cells; cortex with no bundles; pseudohypodermis usually present as a 1-cell layer. Rhizome similar but endodermis not evident.

Reference: RAUNKIAER, figs. 2, 3: stem.

P. praelongus

Occasional. Lakes and streams, usually in deep water.

Stem terete, 1.5–4 mm; stele proto type (see pl. 13); endodermis of U-cells; cortex with many interlacunar and subepidermal bundles; pseudohypodermis 1–3 cells thick.

References: HAGSTROM, fig. 116: diagram of stele. RAUNKIAER, fig. 3: stem. SINGH, fig. 6: stem.

P. pulcher

Rare or locally common. Shallow muddy pools and slow streams.

Stem terete, 0.5–2.5 mm; stele proto type; endodermis of O-cells; cortex with no bundles; pseudohypodermis 1 cell thick.

References: CHRYSLER, pl. 16: stem and rhizome. OGDEN 1966, pl. 54: stem. SCULTHORPE, fig. 5.22: stem and stele.

P. pusillus (P. berchtoldii, P. panormitanus)

Common and often abundant. Quiet water of pools, lakes, and slow streams.

Stem terete, less than 1 mm; stele usually 1-bundled type but robust specimens may have the oblong type with 1 median bundle; endodermis of O-cells; cortex with no interlacunar bundles but with subepidermal bundles; pseudohypodermis absent.

References: HAGSTROM, fig. 24: stem; fig. 38: stem and leaf (as *P. panormitanus*); fig. 53: stem and leaf (as *P. lacunatus*); fig. 54: peduncle; fig. 55: leaf. SCULTHORPE, fig. 5.22: stele. SINGH, fig. 11: leaf.

P. richardsonii

Common. Lakes and streams.

Stem terete, 1–2.5 mm. Anatomy of stem and peduncle identical to *P. perfoliatus.*

P. robbinsii

Occasional to common; sometimes locally abundant and weedy.

Stem terete or oval, 0.5–2 mm; stele oblong type with 1 median bundle; endodermis of O-cells; cortex with bundles in 1 or more interlacunar circles; subepidermal bundles present or absent; pseudohypodermis present or absent.

Reference: HAGSTROM, fig. 19: stem and leaf.

P. spirillus (P. dimorphus)

Common. Shallow pools, lake margins, and quiet streams.

Stem terete, less than 1 mm; stele 1-bundled type or oblong type with 1 or 2 median bundles; endodermis of O-cells; cortex with no bundles or rarely with faint ones; pseudohypodermis absent.

P. strictifolius (P. rutilus)

Frequent. Calcareous water of lakes and streams.

Stem terete to oval in cross section, less than 1 mm in greatest diam; stele 1-bundled type or oblong type with 1 median bundle; endodermis of O-cells; cortex with no interlacunar bundles but with subepidermal bundles; pseudohypodermis present or absent.

P. vaginatus

Rare. Calcareous or brackish water of lakes and streams.

Stem terete or oval, 0.5–4 mm. Anatomy of stem and peduncle essentially the same as *P. pectinatus.*

Reference: HAGSTROM, fig. 12: stem and leaf.

P. vaseyi

Occasional. Quiet water of lakes.

Stem terete, less than 1 mm; stele 1-bundled type or oblong type with 1 median bundle; endodermis of O-cells; cortex with no interlacunar bundles but with subepidermal bundles; pseudohypodermis absent.

Reference: HAGSTROM, fig. 59: leaf and peduncle.

P. zosteriformis (P. compressus)

Common. Lakes and quiet streams.

Stem strongly flattened, 1–3 mm in longest diam; stele oblong type with 1 median bundle; endodermis of O-cells; cortex with interlacunar bundles variable in number from many throughout to none; subepidermal bundles present; pseudohypodermis usually absent.

Reference: PIETERS, pl. 13: stem.

RUPPIA Map 51, Plate 15

One species in New York.

Graves, A.H. 1908. The morphology of *Ruppia maritima.* Trans. Conn. Acad. Arts and Sci. 14:59–170.

R. maritima

Common in suitable habitats. Shallow saline water.

Rhizome, stem, leaf, and peduncle usually less than 1 mm, lacunate. Rhizome, stem, and peduncle essentially the same, all varying in amount of lacunation. Pattern simple and similar to several other tiny stems: *Potamogeton, Zannichellia, Najas, Elodea, Elatine, Callitriche,* and *Utricularia.*

Reference: GRAVES, figs. 8–10; pls. 1, 3, 4, 6: root, rhizome, stem, and peduncle.

ZANNICHELLIA Map 52, Plate 16

One species in New York.

Z. palustris

Common. Fresh or brackish water of lakes, ditches, and slow streams.

Rhizome and stem usually less than 1 mm. Stem with a single central bundle; cells of stele all thin walled; endodermis evident; cortex with 1 or 2 circles of large lacunae. Rhizome similar to stem but usually not lacunate. Stem pattern simple and similar to several other tiny stems: *Potamogeton, Ruppia, Najas, Elodea, Elatine, Callitriche,* and *Utricularia.*

ZOSTERA Map 53

One species in New York.

Arber, A. 1920. Water plants. Cambridge University Press.
Chrysler, M.A. 1907. The structure and relationships of the Potamogetonaceae and allied families. Bot. Gaz. 44(3):161–188.

Z. marina

Common to abundant in suitable habitats. Saline water of the ocean and Hudson River.

Stem terete to flattened, 1–3 mm, not lacunate or with few to many lacunae (to nearly 50 percent); with 3 evident bundles. Leaves flat, lacunate, appearing somewhat stemlike at base owing to the concentric rings of leaf sheaths. Not illustrated.

References: ARBER, figs. 85, 86: leaf. CHRYSLER, pl. 18: stem.

NAJAS Maps 54–59, Plate 17

Seven species in New York.

Roots less than 1 mm, scarcely lacunate. Stems mostly less than 1 mm and with anatomical pattern as illustrated, except for *N. marina,* which is 1–2 mm and scarcely or not at all lacunate. Stem pattern simple and similar to several other tiny stems: *Potamogeton, Ruppia, Zannichellia, Elodea, Elatine, Callitriche,* and *Utricularia.*

Arber, A. 1920. Water plants. Cambridge University Press.
Pieters, A.J. 1901. The plants of western Lake Erie, with observations on their distribution. U.S. Fish Comm. Bull. for 1901.

N. flexilis

Common to abundant. Lakes and streams.

Reference: PIETERS, figs. H, K: stem and leaf.

N. gracillima

Occasional. Shallow water of sandy lakes.

N. guadalupensis

Occasional. Shallow water of lakes.

N. marina

Locally common. Saline water of lakes.

N. minor

Not native. Locally established in brackish and fresh water of river bays and small ponds.

Reference: Arber, fig. 140: root.

N. muenscheri

Local. Brackish tidal margins of Hudson River.

N. olivacea

Rare. Deep water of Cayuga Lake, Seneca County. Not examined.

SCHEUCHZERIA Map 60, Plate 18

One species in New York.

S. palustris

Frequent. Bogs, marshes, and peaty shores.

Rhizome terete, 3–5 mm; pith lacunate, surrounded by a solid ring of bundles and often with a few separate bundles internal to the ring and with a few to many smaller bundles in the lacunate cortex; stelar bundles amphivasal, as in rhizomes of *Acorus* and *Calla*. Stem terete, 1–3 mm, similar to rhizome but bundles not amphivasal, except at base. Leaf, excluding sheath, concavo-convex, 2–4 mm, highly lacunate. Peduncle 1 mm or less, not lacunate. Rhizome similar to that of *Acorus*. Stem similar to rhizome of *Lysimachia*. Leaf similar to petiole of *Alisma* and some species of *Potamogeton* and *Sagittaria*.

ALISMA Maps 61–62, Plate 19

Two or three species in New York. Treated here as two.

Petioles variable in diam, from a few mm to more than 10, semiterete (above the sheathing base), 1 side flattened, with a ridge at each end of the flat side; interlacunar bundles mostly 5–9; subepidermal bundles many. Similar to petiole of *Sagittaria;* see also *Nuphar*. Submersed petioles more lacunate than emersed petioles. Peduncles about same diam as petioles, triangular with broad rounded corners to nearly terete; often not obviously lacunate, except for pith area which becomes hollow. Young peduncles at base may be lacunate between epidermis and ring of bundles. This delicate tissue becomes crushed and folded and the lacunation becomes less up the peduncle until none. The peduncle is somewhat similar to the stem of *Cladium*.

Björkqvist, I. 1967. Studies in *Alisma* L. I. Distribution, variation and germination. Opera Botanica, No. 17.

Stant, M.Y. 1964. Anatomy of the Alismataceae. J. Linn. Soc. (Bot.) 59(376):1–42.

A. gramineum (A. geyeri)

Uncommon. Shallow water and mud.

Petiole similar to *P. plantago-aquatica*, but with fewer and larger lacunae and only 5 interlacunar bundles. Peduncle 1–2 mm.

Reference: Bjorkqvist, fig. 11: petiole.

A. plantago-aquatica (A. subcordatum, A. triviale)

Common. Marshes, muddy shores, and ditches. Considered by many to include two species.

References: Bjorkqvist, fig. 10: petiole. Stant, figs. 53, 54, 57–59, 61: root, petiole, and peduncle (as *A. plantago*).

SAGITTARIA Maps 63–70, Plates 20–21

Eight or nine species in New York.

Anatomical patterns of roots, rhizomes, petioles, and peduncles similar to the illustrations, except that the smaller species have fewer bundles. Sizes, shapes, and amount of lacunation vary somewhat according to the part of the plant organ that is chosen. Petioles vary from plano-convex at base to sharply triangular above. Similar to petioles of *Alisma*. Peduncles circular to triangular.

Arber, A. 1925. Monocotyledons. Cambridge University Press. Figs. 57, 59, 84: leaf.

Stant, M.Y. 1964. Anatomy of the Alismataceae. J. Linn. Soc. (Bot.) 59(376):1–42. Figs. 6–50: root and leaf.

S. calycina (Lophotocarpus c., L. spongiosus)

Rare. Brackish ponds, sloughs, and marshes. Peduncle 1–3 mm. Not examined.

S. cuneata

Occasional. Mud or shallow quiet water of ponds, sloughs, and marshes. Peduncle 1–2 mm.

S. eatonii (S. graminea, in part)

Rare. Tidal river mud and sand. Considered by some to be a distinct species, by others merely a tidewater variant of *S. graminea*. Not examined.

S. engelmanniana

Frequent on Long Island. Acid shallow water of sandy ponds. Peduncle 1–3 mm. Not examined.

S. graminea

Frequent to locally abundant. Peduncle 1–2 mm.

S. latifolia

Common to abundant. Shallow water of mud of ponds, marshes, and bogs. Peduncle 1–10+ mm.

S. rigida

Common to locally abundant. Shallow to deep water of ponds and marshes. Peduncle 1–5 mm.

S. subulata

Local. Fresh to brackish tidal mud. Peduncle ± 1 mm, with large lacunae.

S. teres

Rare. Shallow water of sandy ponds in Suffolk County. Peduncle 1–2 mm, with large lacunae.

Reference: ARBER, fig. 84: leaf.

BUTOMUS Map 71, Plates 22–23

One species in New York.

Arber, A. 1925. Monocotyledons. Cambridge University Press.
Fahn, A. 1967. Plant anatomy. Pergamon.
Stant, M.Y. 1967. Anatomy of the Butomaceae. J. Linn. Soc. (Bot.) 60(381):31–60.

B. umbellatus

Locally common. Shallow to deeper water with muddy or silty bottom.

Root 1–2 mm, with a circle of lacunae in the outer portion; there is a single xylem element in the center. Rhizome mostly more than 10 mm, scarcely lacunate. Leaf 5–10+ mm, strongly 3-angled above, sheathing at base. Peduncle (scape) 3–6 mm, lacunate in the central area; pedicel 1 mm or less, not lacunate when young, becoming lacunate in the central area with age.

References: ARBER, fig. 2: root. FAHN, fig. 96: leaf. STANT, figs. 33–39, 51, 54, 70: root, leaf, and peduncle.

ELODEA Maps 72–73, Plate 24

Three species in New York.

Roots less than 1 mm, not lacunate. Stems terete, 1–3 mm, with 1 or more circles of lacunae; cortical bundles present or absent. Stem pattern simple and similar to several other tiny stems: *Potamogeton, Ruppia, Zannichellia, Najas, Elatine, Callitriche,* and *Utricularia.* Peduncles less than 1 mm, with 3 large lacunae.

Hulbary, R.L. 1944. The influence of air spaces on the three-dimensional shapes of cells in *Elodea* stems, and a comparison with pith cells of *Ailanthus.* Amer. J. Bot. 31:561–580.

E. canadensis (Anacharis c., Philotria c.)

Common and often an abundant weed, especially in alkaline water.

E. densa (Anacharis d., Philotria d.)

This is the common aquarium and laboratory " elodea " that is found occasionally as an introduction and persists in some areas of Long Island.

Reference: HULBARY, fig. 40: stem.

E. nuttallii (Anacharis n., A. occidentalis, Philotria n., P. o.)

Frequent. Fresh, usually acid or slightly brackish water.

VALLISNERIA Map 74, Plate 25

One species in New York.

Arber, A. 1920. Water plants. Cambridge University Press.

V. americana (V. spiralis)

Common and often abundant. Quiet water of ponds and slow streams, usually with muddy bottom or of sand and coarse silt.

Anatomical patterns of male and female plants the same. Root less than 1 mm; stele tiny, simple, with a single central channel and a few surrounding cells; cortex with 1 circle of lacunae. Rhizome or stolon terete, 2–4 mm; peduncle terete: male 0.5–1 mm, female 1.5–3 mm. Fruit terete, 3–5 mm, wall slightly to nearly 50 percent lacunate.

Reference: ARBER, fig. 139: root.

CAREX Maps 75–80, Plate 26

Many species in New York, whose stems (culms) may be somewhat lacunate at base.

Stems sharply triangular above, bluntly triangular below, less than 1–5 mm (excluding enveloping sheaths); bundles in 1 or 2 circles; lacunae small to large, usually covering less than 50 percent of the area, alternating with the outer circle of bundles; central tissue spongy or with large cavities. Stem similar to *Eriophorum* but more evidently triangular. A few species whose stems approach 50 percent lacunation are listed here; others may be similar.

Metcalfe, C.R. 1971. Anatomy of the monocotyledons. Vol. 5. Cyperaceae. Clarendon Press, Oxford, England.

C. aquatilis (C. substricta)

Frequent. Shallow water of cold lakes and streams and in bogs and swamps.

Stem triangular, 1–3 mm. Bundles mostly not contiguous; large ones in a single ring. Lacunae peripheral, in a single circle with smaller bundles between. Pith spongy, becoming partly hollow. The enveloping sheaths are highly lacunate, somewhat similar to those of *Scirpus* and *Cladium*.

C. comosa

Frequent to common. Shallow water of lakes and swamps.

Stem 2–4 mm, similar to *C. aquatilis* but lacunae usually larger.

C. lasiocarpa

Frequent to common. Wet soil to shallow water.

Stem 1–2 mm, similar to *C. comosa,* but usually with 2 distinct circles of large bundles at the base of the stem.

C. limosa

Frequent. Bogs and marshes.

Stem mostly less than 1 mm. Pattern similar to *C. comosa,* but nearly all bundles are between the lacunae.

C. rostrata (C. inflata)

Common. Wet shores, marshes, and swamps.

Stem 1–2 mm (except the spongy base may be up to 15 mm). Similar to *C. comosa.*

C. vesicaria

Common. Wet meadows, marshes, and swamps.

Stem 1–2 mm, similar to *C. lasiocarpa.*

CLADIUM Map 81, Plate 27

One species in New York.

Metcalfe, C.R. 1971. Anatomy of the monocotyledons. Vol. 5. Cyperaceae. Clarendon Press, Oxford, England.

Plowman, A.B. 1906. The comparative anatomy and phylogeny of the Cyperaceae. Ann. Bot. 20:1–33.

C. mariscoides (Mariscus m.)

Common to locally abundant. Fresh or brackish water of marshes and lake shores.

Rhizome terete, with large marginal lacunae. Stem terete to slightly triangular, mostly 1–3 mm; similar to rhizome but with smaller marginal lacunae; somewhat similar to stem of *Eriophorum* and peduncle of *Alisma.* The connate lacunate sheath in freehand sections may appear to be a part of the stem. The sheath alone is similar to the main stem of *Equisetum hyemale*. Leaf horseshoe-shaped at lower portion to nearly terete above, 1–3 mm, highly lacunate. Peduncle scarcely or not lacunate.

Reference: PLOWMAN, fig. 18: rhizome.

CYPERUS Map 82

More than 15 species in New York. One of them, at least, with small lacunae when growing in water, but not covering 50 percent of the area. Not illustrated.

Metcalfe, C.R. 1971. Anatomy of the monocotyledons. Vol. 5. Cyperaceae. Clarendon Press, Oxford, England.

C. esculentus

Stem triangular, 1–4 mm. Similar to *Scirpus americanus* but lacunae much smaller and mostly separated by single-cell chains.

DULICHIUM Map 83, Plate 28

One species in New York.

Plowman, A.B. 1906. The comparative anatomy and phylogeny of the Cyperaceae. Ann. Bot. 20:1–33.

D. arundinaceum

Common. In shallow water and wet shores of ponds, streams, marshes, and bogs.

Rhizome not lacunate, but may develop a circle of small lacunae. Stem terete or nearly so, 2–5 mm; central area very large, soon becoming hollow; outer area with 2 circles of bundles and 1 circle of lacunae; similar to the main stem of *Equisetum hyemale* and also to some species of *Juncus.* Peduncle scarcely or not lacunate.

Reference: PLOWMAN, figs. 13, 14: stem.

ELEOCHARIS Maps 84–104, Plate 29

About two dozen species in New York, of which nine or ten are common and widespread.

Roots not lacunate when young, but in age the cortex breaks down to radial rows of trapezoidal lacunae. Rhizomes variable owing to age and perhaps species. In general there is a ring of bundles, which is discontinuous or continuous, surrounding a small area of parenchyma cells when young. The endodermis is evident. The large cortex is nonlacunate when young, breaking to radially elongated lacunae in age. Stem (scapes) terete or with 3–8 angles; patterns similar among the species but appearing much unlike the rhizomes; central area (inner cortex) very large, with large lacunae; vascular bundles in a discontinuous ring between the inner and outer cortex; outer cortex of 1 or 2 layers (circles) of palisade-shaped cells, with secretory cells usually evident; epidermal bundles present, these are tiny bundles of fibers separating cells of the epidermis and about the size of, or a little larger than, an epidermal cell. There is some variation with habitat, but the general patterns are the same among the species examined.

Metcalfe, C.R. 1971. Anatomy of the monocotyledons. Vol. 5. Cyperaceae. Clarendon Press, Oxford, England.
Plowman, A.B. 1906. The comparative anatomy and phylogeny of the Cyperaceae. Ann. Bot. 20:1–33.

E. acicularis

Common and often abundant. Damp soil, muddy shores, and shallow water. Stem much less than 1 mm, similar to the larger species but with only a few bundles.

E. ambigens

Rare. Wet ground in Suffolk County. Stem ± 1 mm. Not examined.

E. annua (E. ovata in part)

Common. Wet soil of marshes and lake shores. Stem terete, ± 1 mm.

E. compressa (E. acuminata)

Occasional. Marshes and shores. Stem ± 1 mm or less. Not common, but can be distinguished from most other species of the genus by the compressed stem.

E. diandra (E. ovata in part)

Local. River and lake silt. Stem ± 1 mm.

E. elliptica (E. capitata, E. tenuis)

Common. Wet soil. Stem ± 1 mm or less.

E. engelmannii

Rare. Wet soil and muddy shores. Stem ± 1 mm.

E. equisetoides (E. interstincta)

Rare. Shallow water. Stem 4–5 mm; pith very large, soon becoming hollow; cortex with a single circle of large bundles alternating with a single circle of large lacunae. Somewhat similar to the sheath of *Cladium*. If fragment of stem is sufficiently long, this species can be recognized by the cross septations which are ± 2–5 cm apart.

E. erythropoda (E. calva, E. glaucescens)

Common. Marshy and muddy places and lake shores. Stem ± 1 mm or less.

E. halophila (E. uniglumis of New York reports)

Rare. Saline or brackish shores. Stem ± 1 mm. Not examined.

E. intermedia (E. reclinata)

Frequent. Wet soil, marshes, and shallow ponds. Mostly less than 1 mm.

E. melanocarpa

Rare. Wet sandy soil, Suffolk County; reported from Staten Island. Stem 1–2 mm.

E. obtusa

Common to abundant. Wet soil and muddy shores. Stem 1–2 mm.

E. olivacea (E. flavescens)

Occasional. Wet sands, peats, and muddy shores. Stem ± 1 mm or less.

E. palustris

Common. Shallow water of lakes, marshes, and slow streams. Stem 1–3 mm.

Reference: PLOWMAN 1906, figs. 12, 19, 20: rhizome, stem, and peduncle.

E. parvula (Scirpus nanus)

Rare. Wet saline soil. Stem less than 1 mm. Not examined.

E. quadrangulata (E. mutata)

Rare. Shallow water of sandy ponds and peaty shores. Stem square, 3–5 mm, strongly lacunate with large lacunae having bundles on the otherwise 1-cell-wide chains of cells between the lacunae. It may be distinguished from most other species of the genus by its large 4-angled stem.

E. quinqueflora (E. pauciflora, Scirpus pauciflorus)

Rare and local. Wet or boggy soil. Mostly less than 1 mm.

E. robbinsii

Rare. Shallow water and mud. Stem triangular, 1–2 mm. Can be distinguished from most other species of the genus by the 3-angled stem.

E. rostellata

Occasional or locally common. Saline and calcareous marshes and wet meadows. Stem ± 1 mm.

E. smallii (E. palustris in part)

Common. Shallow water and margins of ponds and stream in sandy or peaty soils. Stem 1–4 mm.

E. tenuis (E. capitata in part)

Rare. Wet or dryish sand and peat. Stem 4–8-angled, these angles often obscure on freehand cut sections, ± 1 mm.

E. tortilis (E. simplex)

Rare, one location in Nassau County. Wet soil. Stem sharply 3-angled, ± 1 mm. Not examined.

E. tricostata

Rare. One location in Suffolk County. Wet sandy or peaty soil. Stem compressed or subterete. Not examined.

E. tuberculosa

Rare. Wet sandy soil. Stem oval, ± 1 mm.

ERIOPHORUM Maps 105–107, Plate 30

Six or seven species in New York. Six are frequent to common in bogs. Stems usually with a single circle of lacunae mostly alternating with the bundles. Somewhat similar to the stem of *Cladium* and to the peduncle of *Alisma*; also to some species of *Carex*. Patterns similar among the species, but there is great variation as to amount of lacunation and thickness of tissue between the lacunae.

Metcalfe, C.R. 1971. Anatomy of the monocotyledons. Vol. 5. Cyperaceae. Clarendon Press, Oxford, England.

E. alpinum (Scirpus hudsonianus)

Scarcely lacunate.

Reference: METCALFE, fig. 61: stem.

E. angustifolium

Rare or absent in the State.

Reference: METCALFE, fig. 34: leaf.

E. gracile

Stem 1–2 mm, lacunate.

E. tenellum

Lacunate but less than 1 mm.

E. vaginatum (E. callitrix, E. spissum)

Frequent in open bogs in the northern part of the State. Representative of the usual pattern.

E. virginicum

Scarcely lacunate.

E. viridi-carinatum

Stem 1–3 mm, lacunate.

FUIRENA Map 108, Plate 26

One species in New York.

Metcalfe, C.R. 1971. Anatomy of the monocotyledons. Vol. 5. Cyperaceae. Clarendon Press, Oxford, England.

F. pumila (F. squarrosa)

Not common. Wet meadows and marshes.

Rhizome absent. Stem subterete, 1–3 mm. Vascular bundles in a circle near the epidermis and also scattered in the central area. Lacunae in the central area large and separated by 1-cell-wide chains of cells when young, these collapsing in age to slender strands and losing the cellular appearance. Somewhat similar to *Eleocharis* (which lacks bundles in the central area) and terete-stemmed *Scirpus* (which is usually larger and with bundles more numerous).

RHYNCHOSPORA Maps 109–112, Plate 31

Several species in New York, of which four are common enough to be considered here.

Stem subterete at base, 1–2 mm, not lacunate or with the area surrounding the solid bundle ring slightly to highly lacunate, becoming triangular and less lacunate above. Similar to *Eriophorum* but the lacunae usually smaller and more numerous; also to *Lysimachia*.

R. alba

Frequent. Bogs and marshes.

R. capillacea

Local. Marly bogs and wet limestone.

R. fusca

Frequent to common. Bogs, marshes, and lake shores.

R. glomerata (R. capitellata)

Locally common. Wet soil.

SCIRPUS Maps 113–122, Plates 32–33

About two dozen species in New York, of which some (bulrushes) are highly lacunate and are included here;

others (woolgrasses) growing in water or wet soil may be similar.

Stems variable in size and shape, terete to triangular; vascular bundles usually embedded in the ground tissue but the outermost often at the boundary between the chlorenchyma and ground parenchyma. Rhizomes terete, even with triangular-stemmed species, lacunate but less so than the stem. Peduncles scarcely or not at all lacunate. Patterns of the rhizomes somewhat similar to the stems of *Sparganium.* Patterns of the terete stems somewhat similar to *Calla, Peltandra,* and *Pontederia.*

Kaul, R.B. 1971. Diaphragms and aerenchyma in *Scirpus validus.* Am. J. Bot. 58:808–816.

Levardsen, N.O. 1960. Bulrushes, hard or soft stem. Turtox News 38(8):204–205.

Metcalfe, C.R. 1971. Anatomy of the monocotyledons. Vol. 5. Cyperaceae. Clarendon Press, Oxford, England. Figs. 61, 62: stem.

Plowman, A.B. 1906. The comparative anatomy and phylogeny of the Cyperaceae. Ann. Bot. 20:1–33. Pls. 1, 2.

Smith, S.G. 1969. Natural hybridization in the *Scirpus lacustris* complex in north central United States. Pages 175–200 *in* J.E. Gunckel, ed. Current topics in plant science. Academic Press, New York.

S. acutus

Common and often abundant. Shallow water of lakes and marshes.

Stem terete, 1–10 mm, similar to *S. validus.* Although fresh stems of *S. acutus* are obviously more firm than those of *S. validus* (determined by squeezing), no anatomical characters were detected to cause it.

References: LEVARDSEN: basal sheath. SMITH, fig. 1: stem.

S. americanus

Common. Shallow water and sandy or muddy shores. Most frequent in alkaline, brackish, or saline water.

Stem sharply triangular, 1–5 mm.

S. fluviatilis

Common. Shallow, usually calcareous water of lakes, marshes, and streams.

Stem terete, 3–10+ mm. Pattern similar to that of *S. validus* but lacunae smaller and more numerous.

S. heterochaetus

Local. Shallow water of lakes.

Stem terete, 3–10+ mm. Pattern similar to stem of *S. validus.*

Reference: SMITH, fig. 2: stem.

S. olneyi

Not common. Salt marshes.

Stem sharply 3-angled with concave sides, 4–8 mm, highly lacunate.

S. rubrotinctus

Common. Marshes and swamps.

Stem terete, 3–6 mm. Pattern similar to *S. validus* but less lacunate.

S. smithii

Not common. Sandy or muddy lake shores.

Stem terete, ± 1 mm, highly lacunate; similar to stem of *Fuirena.*

S. subterminalis

Frequent. Sluggish water of lakes, bogs, and slow streams.

Stem terete, ± 1 mm, scarcely lacunate.

S. torreyi

Frequent to locally common. Shallow lakes, marshes, and borders of fresh to brackish ponds and sloughs.

Stem sharply triangular, 1–4 mm, similar to *S. americanus.*

S. validus

Common and often abundant. Shallow water of lakes, marshes, and slow streams.

Stem terete, 2–10+ mm, highly lacunate. See note under *S. acutus.*

References: KAUL, fig. 2: stem and sheath. LEVARDSEN: basal sheath. SMITH, fig. 1: stem.

ACORUS Map 123, Plate 34

One species in New York.

Kaplan, D.R. 1970. Comparative foliar histogenesis in *Acorus calamus* and its bearing on the phyllode theory of monocotyledonous leaves. Amer. J. Bot. 57:331–361.

Molisch, H. 1954. Anatomie der Pflanze. Gustav Fischer, Jena, E. Germany.

Sculthorpe, C.D. 1967. Biology of aquatic vascular plants. St. Martin.

A. calamus

Common and often abundant. Shallow water of marshes and slow streams.

Root 1–2 mm; stele with 5–10 large xylem elements and several smaller ones; pith usually evident but may disappear with enlargement of the xylem; endodermis usually evident; cortex without bundles. Rhizome more than 10 mm; bundles amphivasal (xylem surrounds the phloem) as in rhizomes of *Calla* and *Scheuchzeria*. Peduncle (scape) narrowly to broadly triangular, 3–10+ mm; bundles scattered throughout, not amphivasal (except an occasional small one); all of the large bundles and many small ones completely surrounded by a strong fiber sheath. Leaf (spathe) lenticular; with 3 or more bundles, not amphivasal, these sometimes scarcely evident.

References: KAPLAN, figs. 53, 54: leaf. MOLISCH, fig. 125: root. SCULTHORPE, fig. 6.9: root.

CALLA Map 124, Plate 35

One species in New York.

C. palustris

Common and often abundant. Shallow, mucky water of bogs and marshes.

Root less than 1 mm. Stem (rhizome) terete, 5–10 mm, with scattered bundles, many of them partly or completely amphivasal (xylem surrounds the phloem) as in rhizomes of *Acorus* and *Scheuchzeria*. Petiole similar to stem, terete or semicircular. Peduncle (scape) similar to stem, terete or somewhat cordate, 2–5 mm. Bundles of petiole and peduncle not amphivasal. Patterns of stem, petiole, and peduncle somewhat similar to stem of some species of *Scirpus*, stem of *Pontederia*, petiole of *Peltandra*, and peduncle of *Nuphar*.

ORONTIUM Map 125

One species in New York.

O. aquaticum

Rare to occasional. Shallow water of sandy, muddy, or peaty swamps, ponds, and quiet streams.

Petiole mostly 3–5 mm but broader at base because of the sheath. Peduncle mostly 3–6 mm. Patterns of petiole and peduncle essentially the same and similar to that of *Calla* but without amphivasal bundles. Not illustrated.

PELTANDRA Map 126, Plate 36

One species in New York.

P. virginica

Common in some areas, rare in others. Marshes, lake shores, and quiet streams.

Root 3–6 mm, similar to those of *Acorus* and *Calla*, but larger. Rhizome more than 10 mm. Petiole terete or nearly so above, terete below except for sheath extensions, 5–10+ mm; bundles scattered in the interlacunar areas; pattern similar to stem of *Calla*, *Pontederia*, some species of *Scirpus*, and peduncle of *Nuphar*. Peduncle terete, 5–10+ mm; pattern same as petiole.

ERIOCAULON Maps 127–128, Plate 37

Two species in New York.

Roots less than 1 mm, lacunation variable in amount. Rhizomes not lacunate. Leaves flat, 0.5–1 x 1–4 mm, with 3–9 large lacunae. Peduncles (scapes) terete, with 4–7 low angles, ± 1 mm; with 4–7 large lacunae, these separated by partitions that are several cells wide.

Tomlinson, P.B. 1969. Anatomy of the monocotyledons. Vol. 3. Commelinales — Zingiberales. Clarendon Press, Oxford, England. Figs. 32, 33, 35, 38: leaf and peduncle.

E. parkeri

Local. Tidal mud flats and shallow water of estuaries in the Hudson River. Similar to *E. septangulare* but peduncle with fewer lacunae.

E. septangulare

Common and often abundant. Shallow to deep water of lakes and slow streams.

Peduncle with 6 or 7 large lacunae and, alternating with these, 6 or 7 low angles; upon drying, these angles become more pronounced.

HETERANTHERA Maps 129–130, Plate 38

Two species in New York.

Roots less than 1 mm, becoming lacunate in outer cortex. Stems terete, 2–6 mm. Leaves variable.

H. dubia (Zosterella d.)

Common, often abundant and weedy. Shallow to deep quiet water of streams and lakes.

Stem 2–4 mm. Leaf with no petiole; blade flat. Peduncle seldom produced in New York, less than 1 mm, scarcely lacunate, except for pith which has 1–3 hollow areas; lower portion enclosed by two connate sheaths.

H. reniformis

Rare. Mud and shallow water of tidal Hudson River.

Stem 3–6 mm, similar to *H. dubia* but larger. Petiole terete, oval, or plano-convex, 1–3 mm, with a large hollow central area surrounded by a highly lacunate ring, with 10–15 large bundles and several small ones. Peduncle not examined.

PONTEDERIA Map 131, Plate 39

One species in New York.

Eames, A.J., and L.H. MacDaniels. 1947. An introduction to plant anatomy. 2d ed. McGraw-Hill.

P. cordata

Common and often abundant. Shallow water of marshes and lakes.

Root 1–2 mm; stele with several large conducting elements (vessels); endodermis evident; cortex next to the stele, not lacunate but of closely packed, round, thick-walled cells, outer cortex becoming highly lacunate with cells that are elongate or in the shape of a cross, these eventually appearing as radial lines; epidermis of one layer of cells. Stem, petiole, and peduncle similar to each other, terete or nearly so, from a few mm to more than 10 mm; pith area soon becoming hollow; cortex highly lacunate. Young stem similar to stem of *Calla* and some species of *Scirpus,* to the petiole of *Peltandra,* and the peduncle of *Nuphar.*

Reference: EAMES AND MACDANIELS, fig. 184: submersed leaf.

JUNCUS Maps 132–142, Plates 40–41

Thirty-two species in New York. Most of these are not sufficiently lacunate to be included here. The stems and leaves may have continuous cells or have a few lacunae or have one large lacuna which simulates a hollow pith. In *J. effusus*, the central area of the stem is composed of lobed cells joined to create numerous tiny lacunae (pl. 41). These cells break down in age to form a large central hollow lacuna. Stems of some other species have a nonlacunate central area (but sometimes with a partially hollow pith) and a lacunate surrounding area (pl. 40). Those known to have lacunate stems or to grow in water in the State are listed and mapped.

Cutler, D.F. 1969. Anatomy of the monocotyledons. Vol. 4. Juncales. Clarendon Press, Oxford, England. Many illustrations, mostly diagrams.

Korsmo, E. 1954. Anatomy of weeds. Grondahl & Sons, Oslo, Norway. Pl. 17: root, rhizome, and stem.

J. acuminatus (J. paradoxus)

Frequent to common. Wet soil and marshes.

Stem 1–3 mm; pattern similar to *J. articulatus*; cortex lacunate; pith solid or partly hollow.

J. arcticus (J. balticus)

Locally abundant. Marshes and sandy lake shores.

Stem ± 1 mm; not lacunate; pith hollow or with loose strands of cells.

J. articulatus

Frequent. Wet places.

Stem 1–3 mm; cortex lacunate; pith solid.

Reference: CUTLER, fig. 6: stem and leaf.

J. brevicaudatus

Wet places. Frequent to common.

Stem 1–3 mm, not lacunate, except for a circle of small lacunae near the outer edge; pith usually hollow.

J. canadensis

Marshy places. Frequent to common.

Stem 1–3 mm; not lacunate; pith hollow or essentially so.

J. effusus

Common and often abundant. Wet meadows, swales, and marshes.

Stem 2–5 mm. Our only species of the genus with abundant distinctively lobed pith cells. Portion above inflorescence identical to stem.

Reference: KORSMO, figs. 39, 40: rhizome, stem, and leaf.

J. filiformis

Common in the Adirondacks, local elsewhere. Wet soil, margins of lakes, streams, and bogs.

Stem 1 mm or less; scarcely lacunate, but may have a circle of small lacunae near the outer edge; pith ± ½ diam of stem, becoming hollow in age.

J. militaris

Not common. Shallow water of lakes and streams.

Stem 2–5 mm; anatomical pattern similar to *J. articulatus* but central area mostly hollow; lacunae vary in size and number from none in the emersed part to highly lacunate in the submersed part.

J. nodosus

Frequent to common. Wet places.

Stem 1–2 mm; scarcely lacunate, but often with small lacunae near the outer edge; pith becoming hollow.

J. pelocarpus

Locally common. Shores and shallow water of lakes and streams.

Stem ± 1 mm; pattern similar to *J. articulatus.*

J. torreyi

Not common. Shores and shallow water.

Stem 1–2 mm; not lacunate; pith of round cells, usually mostly hollow.

RUMEX Map 143

Only one or two of the New York species are found in water. Not illustrated.

Korsmo, E. 1954. Anatomy of weeds. Grondahl & Sons, Oslo, Norway. Figs. 50–58, pls. 25–27: root, stem, and petiole.
Metcalfe, C.R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 2. Clarendon Press, Oxford, England. Fig. 265: diagrams of stem and petiole.

R. verticillatus

Frequent or occasional. Wet soil or shallow water of swamps and lakes.

Stem angular-terete, 3–10 mm, sometimes lacunate, especially in the pith area which becomes hollow with age; bundles in a ring which is continuous or nearly so; pith large and without bundles; somewhat similar to stem of *Armoracia.* Petiole plano-convex to lenticular, 2–3 mm; mesophyll lacunate; similar to petiole of *Alisma.*

SALICORNIA Map 144

Three species in New York.

Stems 1–5 mm. These not lacunate except that, when very young, the stems may have 4 large lacunae in the central portion, which become a single lacuna (hollow pith) with age. The cortex has large water storage cells and sometimes also lacunae. Not illustrated.

Fahn, A. 1967. Plant anatomy. Pergamon. Fig. 86: stem.

S. bigelovii

Salt marshes. Long Island and Staten Island.

S. europaea

Common in salt marshes.

S. virginica (S. perennis)

Salt marshes. Long Island and Fisher's Island.

BRASENIA Map 145, Plate 42

One species in New York.

B. schreberi

Common to locally abundant. Ponds and slow streams.

Stem terete or nearly so, 2–3 mm. Petiole terete or oval, 1–2 mm. Peduncle terete, ± 2 mm, usually with 3 or 4 simple bundles but may have 2 double bundles as in the stem. Star-shaped or branched idioblasts, as seen in some genera of this family (Nymphaeaceae), not seen in *Brasenia schreberi*; however, large mucilaginous cells may project into the lacunae and rhombic crystals may occur in and on the surface of any of the tissues. Stem, petiole, and peduncle similar to those in *Cabomba.*

CABOMBA Map 146, Plate 43

One species in New York.

C. caroliniana

Not native but introduced into ponds in some localities where it has become locally abundant.

Rhizome and stem with the same pattern and similar in size, shape, and pattern to that of *Brasenia.* Petiole ± 1 mm, slightly to strongly lacunate, with double bundles. Peduncle ± 1 mm, with 2 or 3 bundles. Idioblasts apparently absent.

NELUMBO Map 147

One species in New York. Not illustrated.

N. lutea (N. pentapetala)

Rare. Lakes.

Rhizome (not examined) said to have a stele with numerous vascular bundles in a concentric ring and with an evident endodermis. Petiole terete, 2–5 mm. Peduncle terete, 4–8 mm. Anatomical patterns of petiole and peduncle essentially the same; pith area hollow, surrounded by a ring of bundles; some of the bundles are normal with phloem on the epidermal side of the xylem, others have the phloem on the pith side of the xylem; cortical lacunae very large and in one circle, except for a few small ones; stellate idioblasts apparently are absent, but cluster crystals may be present.

NUPHAR Map 148, Plate 44

One species in New York; sometimes treated as three or four species.

Metcalfe, C.R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 1. Clarendon Press, Oxford, England.

N. luteum (N. advena, N. microphyllum, N. rubrodiscum, N. variegatum, Nymphaea a., Ny. m., Ny. r.)

Common. Shallow to deeper water of bog pools, lakes, marshes, and slow streams.

Root 1–3 mm, similar to *Nymphaea.* Rhizome 5 mm (ssp. *pumilum*) to several cm, with scattered small lacunae in a reticulate pattern; bundles distributed irregularly. Petiole triangular, plano-convex, or oval, 2–10+ mm in longest diam, with scattered simple bundles. Peduncle terete, 3–10+ mm. Star-shaped or branched idioblasts are common in petiole and peduncle. Vascular bundles in petiole and peduncle have phloem on only 1 side of the xylem canal; in contrast with those of *Nymphaea,* some of which have phloem on 2 sides. The peduncle pattern is somewhat similar to the scape of *Calla,* petiole and peduncle of *Peltandra* and young stem of *Pontederia.* However, the star-shaped idioblasts distinguish it from these genera.

Reference: METCALFE AND CHALK, fig. 19: petiole.

NYMPHAEA Maps 149–150, Plate 45

Two species in New York; treated as one by some authors.

Root 2–5 mm, endodermis absent. Rhizome usually more than 10 mm, less than 50 percent lacunate. Petiole 2–10 mm, with simple and double bundles. Peduncle 3–8 mm, similar to petiole. Idioblasts of various shapes are frequently seen in petiole and peduncle. Vascular bundles in petiole and peduncle occur as singles (phloem on 1 side of xylem canal) and doubles (phloem on 2 sides of xylem canal) in contrast with those of *Nuphar,* which are all single. Patterns distinctive and not easily confused with other genera.

Conard, H.S. 1905. The waterlilies. A monograph of the genus *Nymphaea.* Carnegie Institution of Washington, Washington, D.C.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin. Figs. 5.16, 5.17, 5.21: petiole.

Williams, G.R. 1970. Investigations in the white waterlilies (Nymphaea) of Michigan. Mich. Bot. 9:72–86. Fig. 10: petiole.

N. odorata (Castalia o.)

Common to locally abundant. Shallow to deeper water of bog pools, sloughs, and ponds.

Reference: CONARD, figs. 8, 26: root, petiole, and peduncle.

N. tuberosa (Castalia t.)

Frequent to common. Lakes and slow streams.

Reference: CONARD, fig. 26: petiole and peduncle.

CERATOPHYLLUM Maps 151–152, Plate 46

Two species in New York.

Roots absent. Stems 0.5–2 mm; scarcely lacunate; with a small central xylem canal and tiny cortical lacunae in a single circle in the inner cortex (these lacunae are usually larger than shown in the illustration); endodermis sometimes evident. Leaves less than 1 mm.

Arber, A. 1920. Water plants. Cambridge University Press.

Fahn, A. 1967. Plant anatomy. Pergamon. Fig. 97: leaf.

Pieters, A.H. 1901. The plants of western Lake Erie, with observations on their distribution. U.S. Fish Comm. Bull. for 1901.

C. demersum

Common and often an abundant weed. Shallow ponds and slow streams.

References: ARBER, fig. 56: stem stele. PIETERS, pl. 13: stem.

C. echinatum

Not common. Shallow water of pools and sluggish streams.

CALTHA Map 153, Plate 47

One species in New York.

Korsmo, E. 1954. Anatomy of weeds. Grondahl & Sons, Oslo, Norway.

C. palustris

Common and often abundant. Swamps, marshes, low meadows, ditches, and margins of streams.

Root 2–4 mm, becoming lacunate with age. Stem terete, slightly to strongly furrowed, 3–10+ mm, bundles (about 20) widely separated in a ring, with well-developed xylem elements (vessels); between the xylem and the phloem is a distinct cambium in a curve with the concavity to the phloem; on the internal side of the xylem and on the external side of the phloem are crescent-shaped groups of fiber cells, in older stems these may meet; usually not confused with other genera, but see illustrations of *Armoracia, Nasturtium,* and *Bidens.* Petiole 2–3 mm. Peduncle semiterete, furrowed, 2–3 mm, similar to stem.

Reference: KORSMO, fig. 74: root, stem, and petiole.

RANUNCULUS

Approximately 25 species in New York, of which six or seven grow in water. However, even with those species that grow mostly submersed, the stemlike parts are slightly (if at all) lacunate. Roots of some species (such as *R. ficaria*) may have a circle of lacunae and the petioles may have a lacuna on each side of the central bundle. Not illustrated.

Korsmo, E. 1954. Anatomy of weeds. Grondahl & Sons, Oslo, Norway. Fig. 78: root, petiole, and stem.

Stover, E.L. 1951. An introduction to the anatomy of seed plants. Heath, Boston, Mass. Fig. 7: root.

ARMORACIA Map 154, Plate 48

One species in New York.

Metcalfe, C.R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 1. Clarendon Press, Oxford, England. Fig. 22: diagram of stem.

Stover, E.L. 1951. An introduction to the anatomy of seed plants. Heath, Boston, Mass. Fig. 94: stem (as *Radicula*).

A. aquatica (Neobeckia a., Rorippa a.)

Not common. Ponds and slow streams.

Root less than 1 mm; cortex lacunate. Stem 2–6 mm; generally recognized by the combination of lacunate pith, solid bundle ring, and nonlacunate cortex (submersed stems of *Rumex* and *Rorippa* may have this combination of characters); emersed stem similar to submersed stem but lacunae smaller. Petiole of submersed leaves plano-convex, ± 1 mm; emersed leaf petiole ± 1 x 3 mm. Peduncle 1 or 2 mm, not lacunate except in age as tearing occurs in the pith.

NASTURTIUM Map 155, Plate 49

Two species in New York.

N. officinale (Sisymbrium nasturtium-aquaticum)

Common. Ditches and shallow streams.

Stem 2–5 mm, mostly not lacunate but some cells of the pith and of the cortex may be very large, and there may be torn areas in the cortex. Petiole and peduncle seldom lacunate. Anatomical patterns of *Cardamine* may be similar to those of *Nasturtium*.

N. microphyllum (N. officinale var. m)

Rare or overlooked, Rockland, Delaware, and Suffolk Counties.

Stem 2–3 mm. Not examined.

RORIPPA Map 156

Four species in New York. One is commonly found in wet places and occasionally in shallow water. Not illustrated.

Korsmo, E. 1954. Anatomy of weeds. Grondahl & Sons, Oslo, Norway. Fig. 94, pl. 46.

R. palustris (R. islandica, Radicula p., Radicula hispida)

Stem subterete, often furrowed, 1–10 mm; pattern similar to *Armoracia*.

SUBULARIA Map 157

One species in New York. Not illustrated.

S. aquatica

Local. Shallow water.

Stem more or less lacunate, but only ± 0.5 mm. Leaf less than 1 mm, with a conspicuous central bundle and a strongly lacunate cortex; similar to the simple pattern of several other tiny stems. See statement under *Callitriche*.

CALLITRICHE Maps 158–162

Six species in New York, of which five are found in water.

Stems less than 1 mm; stele simple, being a small ring of xylem surrounded by phloem; there is no cambium; the tiny pith soon becomes hollow; endodermis evident (apparently absent in the root); cortex with a single circle of lacunae separated by 1-cell-wide chains of cells. Stem pattern simple and similar to several other tiny stems: *Potamogeton, Ruppia, Zannichellia, Najas, Elodea,* and *Elatine*. Not illustrated.

Arber, A. 1920. Water plants. Cambridge University Press.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin.

C. anceps (C. heterophylla in part)

Colton Flow, Raquette R., St. Lawrence County. Not examined.

C. hermaphroditica (C. autumnalis)

Occasional. Quiet water.

C. heterophylla

Occasional to common. Quiet shallow water.

C. stagnalis

Rare to locally frequent in quiet or flowing water.

References: ARBER, figs. 114, 138: stem and root steles. SCULTHORPE, fig. 6.10: root stele.

C. terrestris (C. deflexa)

Rare. Damp soil. Not examined.

C. verna (C. palustris)

Common. Pools, springs, and lake shores.

HYPERICUM Map 163, Plate 50

Several species in New York, of which three or four grow in wet places. The roots, and sometimes also the young stems, may be lacunate. Only one species (found growing in shallow water) examined.

H. ellipticum

Common. Swamps, marshes, and shores of ponds and streams.

Rhizome 1–2 mm, more or less lacunate; stem and peduncle not lacunate.

TRIADENUM Map 164, Plate 50

One or two species in New York; treated here as one.

T. virginicum (T. fraseri, Hypericum v.)

Common. Marshes and swamps. Rhizome terete, 1–3 mm. Stem above water and peduncle not lacunate.

ELATINE Maps 165–166

Two species in New York. Not illustrated.

Eames, A.J., and L.H. MacDaniels. 1967. An introduction to plant anatomy. 2d ed. McGraw-Hill. Fig. 183: stem stele.

E. americana (E. triandra)

Occasional. Shallow water of ponds and slow streams. Not examined.

E. minima

Rare to locally frequent. Shallow water of ponds and slow streams.

Stem terete, ± 1 mm, with a small central stele; pith absent; endodermis evident; cortex with a circle of large lacunae, separated by 1-cell-wide chains of cells. Stem pattern simple and similar to several other tiny stems: *Potamogeton, Ruppia, Zannichellia, Najas, Elodea, Callitriche,* and *Utricularia.*

LUDWIGIA Map 167, Plate 51

Four species in New York, but only one is commonly found submersed.

L. palustris

Common. Shallow water of ponds, streams, and marshes. Often completely submersed or forming floating mats.

Stem 1–2 mm. Rhizome, stem, and petiole patterns similar; with a single central bundle. Petiole sometimes with 1 or 2 accessory bundle strands. Somewhat similar to rhizome of *Triadenum* and stem of *Hippuris.*

TRAPA Map 168, Plates 52–53

One species in New York.

T. natans

Not native but locally abundant and weedy. Quiet water of rivers and lakes.

Root less than 1 mm with a single central bundle. Stem 2–4 mm, anatomical pattern similar for submersed and emersed parts. Petiole 1–3 mm (below floater) to 5 mm (above floater) to 10 mm (floater), lacunate but variable in amount. Peduncle 2–10 mm, smallest near the lower portion (illustrated), largest in the upper portion and with larger lacunae in the cortex. The stem is not easily confused with other genera, but the peduncle is somewhat similar to the stems of *Lysimachia* and *Menyanthes.*

MYRIOPHYLLUM Maps 169–176, Plates 54–55

Nine species in New York.

Rhizomes, stems, and peduncle terete, 1–3 mm. Patterns essentially the same; with a nonlacunate stele, with or without a pith area (considered to be not a true pith but undeveloped xylem); with a large cortex having an evident endodermis and a single circle of large lacunae separated by 1-cell-wide chains of cells, strongly appearing as spokes in a wheel. This pattern is also seen in *Marsilea, Gratiola,* and *Utricularia.* Perhaps also in the rare *Hottonia.* Also some other genera whose stems are usually less than 1 mm. Spherical, spiny, asterisk-shaped cluster crystals, 0.02–0.03 mm are frequently seen in freehand sections but only occasionally seen in the microtome-cut, chemically treated tissues in our permanent slide collection. Leaves less than 1 mm, often with radially arranged lacunae. This pattern is also found in leaves of *Ceratophyllum, Utricularia,* and *Littorella.* Peduncles absent or similar to stem.

Arber, A. 1920. Water plants. Cambridge University Press.

Burström, H.G., and C. Odhnoff. 1963. Vegetative anatomy of plants. Svenska Bokförlaget, Stockholm, Sweden. Fig. 78: stem.

Molisch, H. 1954. Anatomie der Pflanze. Gustav Fischer, Jena, E. Germany.

M. alterniflorum

Rare. Shallow water. Stem 1–2 mm.

M. brasiliense

Not native but introduced on Long Island into streams and ponds.

Stem 2–3 mm. Central large area appears to be true pith.

Reference: Molisch, fig. 98: stem (as *M. proserpinacoides*).

M. farwellii

Rare. Shallow acid water. Stem ± 1 mm.

M. heterophyllum

Rare to local. Ponds and slow streams. Stem 1–6 mm.

M. humile

Locally common. Shallow water and muddy banks. Stem ± 1 mm.

M. pinnatum (M. scabratum)

Rare. Long Island and Orange County. Shallow acid water. Stem ± 1 mm. Not examined.

M. spicatum (M. exalbescens)

Common and often an abundant weed. Our native plant is *M. spicatum* ssp. *exalbescens,* but apparently the Eurasion ssp. *spicatum* is established and increasing in the State. Both subspecies may be troublesome weeds. Shallow or deep, calcareous or brackish water of ponds and quiet streams. Stem 2–3 mm.

Reference: Arber, fig. 109: leaf; figs. 116, 117: stem.

M. tenellum

Occasional. Sandy ponds and slow streams. Stem 1–2 mm.

M. verticillatum

Frequent. Deep or shallow lakes and streams, often in flowing water. Stem 1–3 mm.

PROSERPINACA Map 177, Plate 56

Two species in New York.

Stover, E.L. 1951. An introduction to the anatomy of seed plants. Heath, Boston, Mass.

P. palustris

Occasional. Temporary pools and shallow margins of ponds.

Stem angular-terete, 1–2 mm. Amount of lacunation varies from submersed to emersed parts. Pattern similar to *Hippuris* but stele much larger in proportion and cortex with 1 or 2 circles of lacunae; also somewhat like stem of *Ludwigia*; cluster crystals occur. Submersed leaf oblong to terete, less than 1 mm, with large cells but not lacunate.

Reference: Stover, fig. 65: leaf.

P. pectinata

Rare. Pond and stream margins. Suffolk and Orange Counties. Stem ± 1 mm, similar to *P. palustris.* Leaf not examined.

HIPPURIS Map 178, Plate 56

One species in New York.

Lloyd, B. 1949. Handbook of botanical diagrams. 2d ed. University of London Press, London, England. Pl. 34: stem.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin.

Tron, E. Zh. 1967. Anatomical structure of the stem of *Hippuris vulgaris* L. [in Russian, English summary]. Bot. Zh. 52:811–819. No illustration.

H. vulgaris

Rare. Shallow water of ditches and marshy ponds.

Submersed stem, 1–2 mm; cortex strongly lacunate; stele similar to that of *Myriophyllum* but usually with more strongly developed xylem; there is no true pith but the central parenchyma cells may appear pithlike in young stems; cortex with more than 1 circle of lacunae; endodermis clearly evident. Similar to stems of *Elodea, Proserpinaca* and *Ludwigia.*

Reference: Sculthorpe, figs. 5.16, 5.26: stem.

HYDROCOTYLE Map 179, Plate 57

Three species in New York. One with lacunate parts.

H. umbellata

Not common. Wet ground and shallow water.

Stem (rhizome) terete, 1–2 mm. Petiole 1–2 mm. Peduncle not examined. The stem is similar to some species of *Potamogeton,* especially *P. perfoliatus* and *P. richardsonii,* but without an inner patch of phloem on any bundle; also similar to *P. alpinus* and *P. nodosus* which have no pseudohypodermis; the stele is similar to that found in some collections of *P. illinoensis,* which species is easily separated by the cortical bundles; *Potamogeton* usually has a more evident endodermis.

LYSIMACHIA Maps 180–181, Plate 58

Several species in New York, of which two may grow in water.

Rhizomes and stems similar, terete, 1–7 mm, lacunate in pith and cortex; secretory cells and cavities present in pith and cortex. Patterns somewhat similar to *Triadenum, Menyanthes, Rhynchospora,* and *Sparganium.* Peduncles terete or squarish, ±1 mm, similar to stem but less lacunate.

L. nummularia

Common. Wet places and occasionally in water. Stem 1–2 mm, pattern similar to *L. terrestris.*

L. terrestris

Common. Low ground and swamps. Stem 1–7 mm.

MENYANTHES Map 182, Plate 59

One species in New York.

Metcalfe, C.R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 2. Clarendon Press, Oxford, England.

M. trifoliata

Rare to locally frequent. Wet bogs and margins of bog streams.

Root ± 1 mm, slightly to highly lacunate. Stem and rhizome similar, 2–8 mm; cortex usually with (but sometimes without) bundles; specimens without bundles in the cortex are somewhat similar to stem of *Lysimachia* and peduncle of *Trapa.* Petiole 2–3 mm, usually with 5 or 6 large bundles and 1 or more small ones in a circle. Peduncle similar to petiole.

Reference: METCALFE AND CHALK, fig. 216: petiole.

NYMPHOIDES Maps 183–184, Plate 60

Two species in New York.

Stems from less than 1 to 3 mm; cortex with 1 to several circles of lacunae; branched idioblasts usually common. Petioles less than 1 to 2 mm, terete or plano-convex; idioblasts common. The idioblasts distinguish this genus from all except *Nuphar* and *Nymphaea,* whose patterns are much different.

Metcalfe, C.R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 2. Clarendon Press, Oxford, England.

N. cordatum (Trachysperma lacunosa)

Occasional to locally common. Open water of lakes. Stem mostly less than 1 mm. Floaters 2 mm, not lacunate. Petiole less than 1 mm.

N. peltatum

Not native but introduced and locally abundant in the Hudson River. Stem ± 3 mm. Floaters absent. Petiole 2–3 mm. Peduncle less than 1 mm.

Reference: METCALFE AND CHALK, fig. 216: petiole (as *Limnanthemum peltatum*).

GRATIOLA Maps 185–186, Plate 61

Two species in New York.

Roots usually less than 1 mm. Stems and rhizomes similar, 1–3 mm; pith small or large, becoming hollow; xylem forming a solid circle; cortical lacunae large, mostly in a single circle. The pattern is superficially similar to *Myriophyllum, Utricularia,* and *Marsilea;* also some other genera whose stems are usually less than 1 mm. Peduncle similar to stem, but usually less than 1 mm.

G. aurea (G. lutea)

Occasional or locally common. Wet sandy or peaty soil and shallow water.

G. neglecta

Common. Wet soil.

LINDERNIA Maps 187–188, Plate 62

Three species in New York, of which two are common.

Stems 1–3 mm; square with 4 small cortical (subepidermal) bundles at the 4 corners. Pith solid, terete, surrounded by a circle of bundles, separate or essentially so. Cortex highly lacunate with large lacunae; these lacunae extending from the stelar bundles nearly to the epidermis.

L. anagallidea (Ilysanthes inaequalis)

Infrequent to locally common. Wet soil.

L. dubia (Ilysanthes d.)

Frequent to locally common. Wet soil or shallow water.

L. pyxidaria

Rare. Jefferson County. Wet soil.

MIMULUS Maps 189–192, Plate 63

Four species in New York.

Stems scarcely 50 percent lacunate; only one species examined in detail.

M. alatus

Occasional. Marshes and swamps.

M. guttatus (M. langsdorfii)

Rare. Low ground.

M. moschatus

Occasional. Wet places.

M. ringens

Common. Marshes, edges of streams and swamps, wet meadows.

Stem subterete at base, 3–8 mm, becoming squarish above and smaller to less than 1 mm; pith of roundish cells, soon becoming hollow; bundle area a solid ring; pericycle with groups of fiber cells; cortex lacunate with 1-cell chains of cells, the lacunae extending to the epidermis.

UTRICULARIA Maps 193–205, Plate 64

Thirteen species in New York.

Stems terete, mostly less than 1 mm, sometimes to 2 mm; stele of 1 or more tracheids surrounded by little groups of phloem; endodermis of thin-walled cells similar to the cells of the cortex and appearing merely as a circle of cortical cells around the thicker walled cells of the stele; cortex of submersed and emersed stems differ in amount of lacunation. Stem pattern simple and similar to several other tiny stems: *Marsilea, Potamogeton, Ruppia, Zannichellia, Najas, Elodea, Elatine, Callitriche.* Leaves with a single simple bundle; mesophyll with large lacunae reaching the epidermis. Peduncles terete, from less than 1 to 3 mm; patterns different from stems; xylem in a ring, discontinuous or continuous; pith solid to partly hollow; cortex lacunate (except *U. cornuta*).

Arber, A. 1920. Water plants. Cambridge University Press.

U. biflora (U. pumila)

Rare. Suffolk County. Shallow water. Not examined.

U. cornuta

Occasional to locally common. Bogs and sandy shores. Stem less than 1 mm. Not examined. Peduncle (scape) not lacunate.

U. fibrosa

Rare to locally frequent. Suffolk County. Shallow water. Not examined.

U. geminiscapa (U. clandestina)

Rare. Shallow water. Not examined.

U. gibba

Rare. Shallow water. Stem less than 1 mm. Peduncle less than 1 mm; xylem in a continuous ring; pith solid.

U. inflata (U. radiata)

Rare. Quiet water. Stem less than 1 mm; peduncle ± 1 mm; pattern similar above and below floaters; pith solid to hollow.

U. intermedia

Occasional to locally common. Shallow water. Stem ± 1 mm. Peduncle less than 1 mm; bundles separate in a ring.

U. juncea (U. virgatula)

Rare. Sandy shores. Not examined.

U. minor

Rare or occasional. Shallow water. Not examined.

Reference: ARBER, fig. 74: leaf.

U. purpurea

Occasional to frequent. Quiet water. Stem ± 1 mm. Peduncle with solid pith containing a few small bundles; cortex with a circle of large lacunae, separated by 1-cell-wide chains of cells, similar to stem of *Myriophyllum.*

U. resupinata

Frequent to common. Shallow water. Stem less than 1 mm. Not examined.

U. subulata

Rare. Wet sandy soil. Not examined.

U. vulgaris (U. macrorhiza)

Common and often abundant. Slow streams and quiet water (often stagnant) of lakes. Stem 1–2 mm. Peduncle 1–3 mm.

JUSTICIA Map 206, Plate 65

One species in New York.

Metcalfe, C.R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 2. Clarendon Press, Oxford, England.

Jones, W.R. 1912. The development of the vascular structure of *Dianthera americana.* Bot. Gaz. 54:1–30.

J. americana (Dianthera a.)

Locally common. Shallow water of lakes and streams. Root ± 2 mm. Rhizome terete, 3–5 mm. Stem angular-terete, 2–3 mm, similar to rhizome but less lacunate; there are 6 bundles (steles) in a circle and a 7th in the center; each has an endodermis; not easily confused with any other genus. Peduncle 1–2 mm, not lacunate; bundle tissue in a continuous ring.

LOBELIA Map 207, Plate 66

Seven species in New York, of which one is commonly found in water.

Armand, M.L. 1912. Recherches morphologiques sur le *Lobelia dortmanna* L. Rev. gén de Botanique 24:465–478.

L. dortmanna

Common. Shallow ponds. Root less than 1 mm. Leaf ± 1.5 x 2.5 mm, with 2 large lacunae as in *Ruppia.* Peduncle (scape) terete, 2–3 mm, scarcely lacunate, with a large hollow pith.

Reference: ARMAND, figs. 4, 11: root and peduncle.

BIDENS Map 208, Plate 67

Sixteen species in New York, of which one is sufficiently lacunate to be included here.

Pieters, A.J. 1901. The plants of western Lake Erie, with observations on their distribution. U.S. Fish Comm. Bull. for 1901.

B. beckii (Megalodonta b.)

Occasional. Lakes and slow streams.

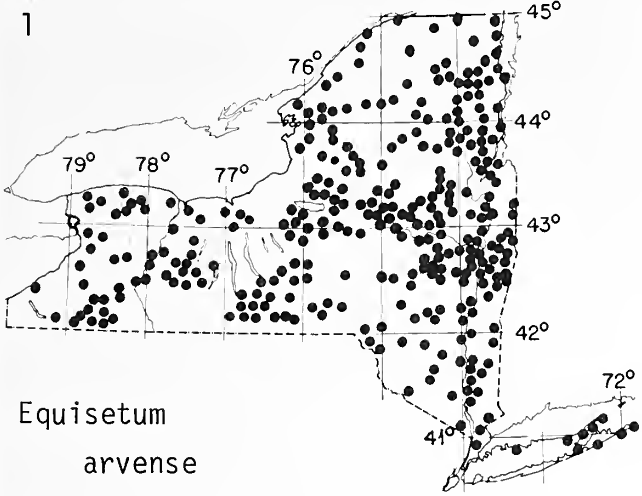
Stem 1–4 mm. Stem between roots with small stele, solid pith, and cortex with large lacunae. Stem between emersed leaves with many bundles in a well-defined ring, pith hollow, and cortex with small lacunae. Middle of stem intermediate, mostly with large solid pith, bundles in a ring, and cortex with large lacunae. In older stems, the area between bundles is filled with fiber cells. Because of variability due to age and position of parts in relation to water, the pith may be solid or hollow, the bundles separate or continuous, and the cortex may be slightly to strongly lacunate. Thus the stem may be similar to several other genera. Peduncle 1–2 mm, similar to stem above water.

Some of the other species of *Bidens* may have a highly lacunate cortex at base, but this area is only a small portion of the stem area.

Reference: PIETERS 1901, pl. 13: stem.

Distribution Maps

1



Equisetum
arvense

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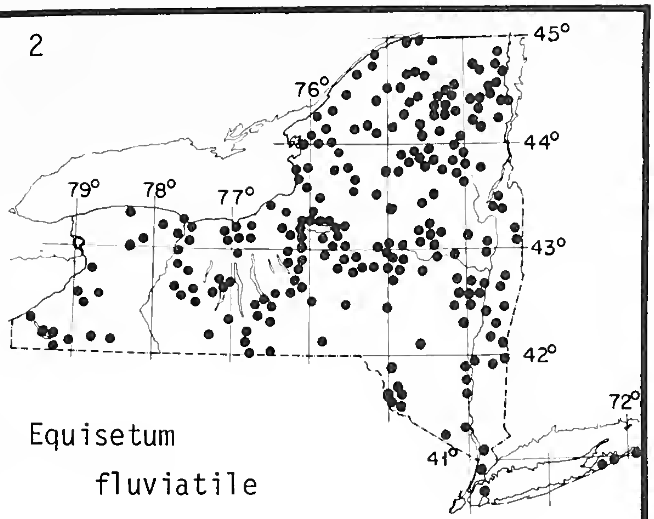

Equisetum
fluviatile

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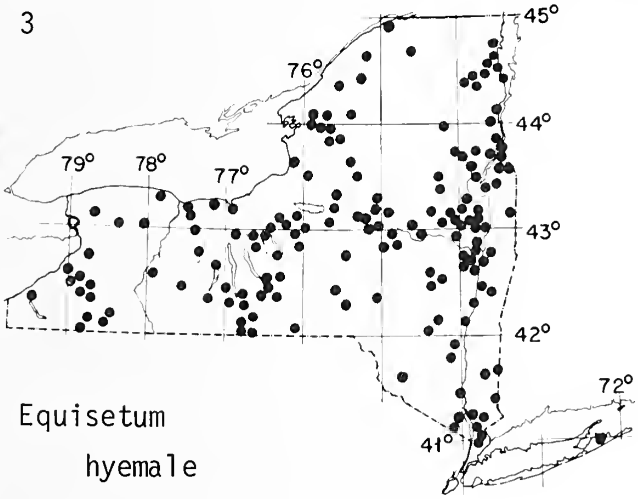

Equisetum
hyemale

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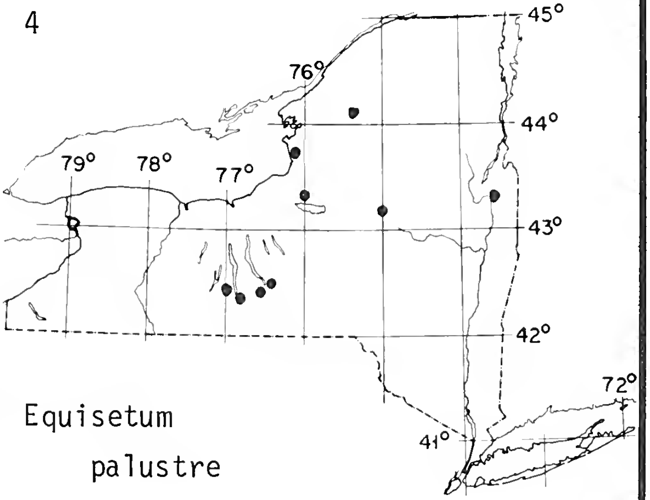

Equisetum
palustre

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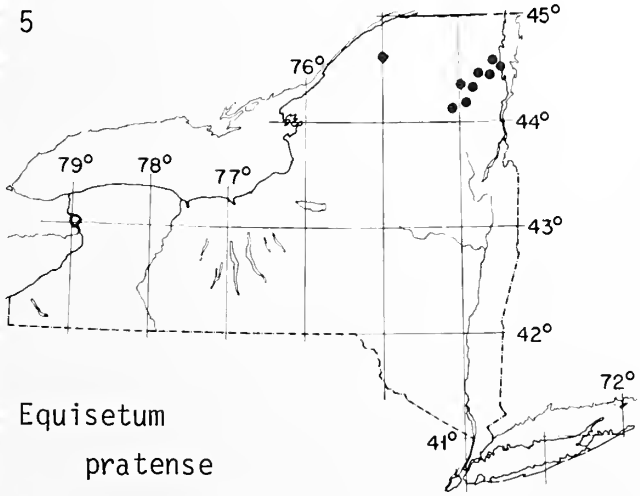

Equisetum
pratense

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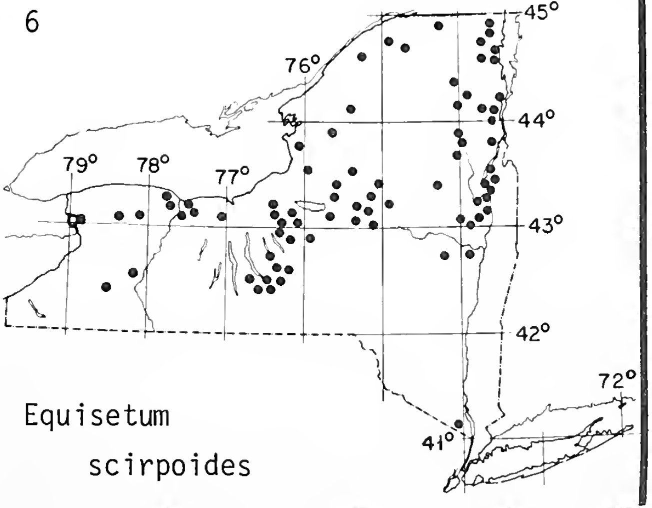
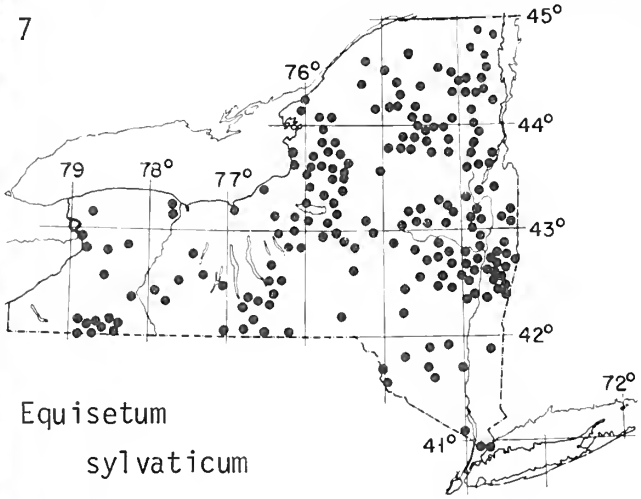


Equisetum
scirpoides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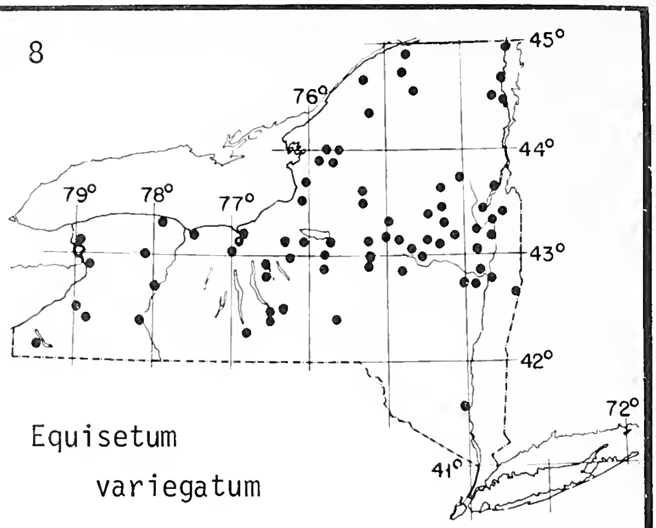
Equisetum sylvaticum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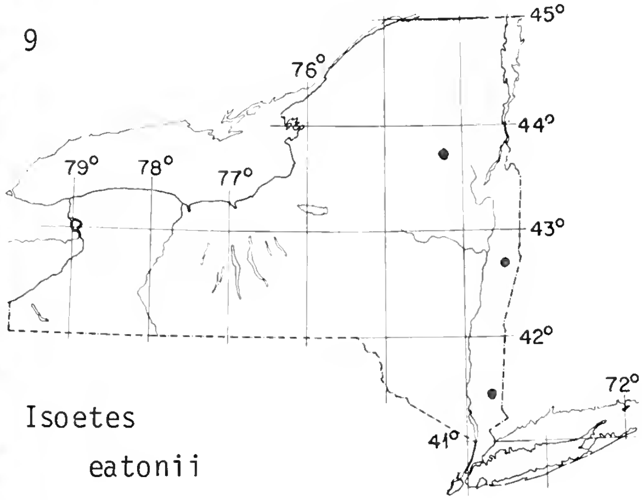
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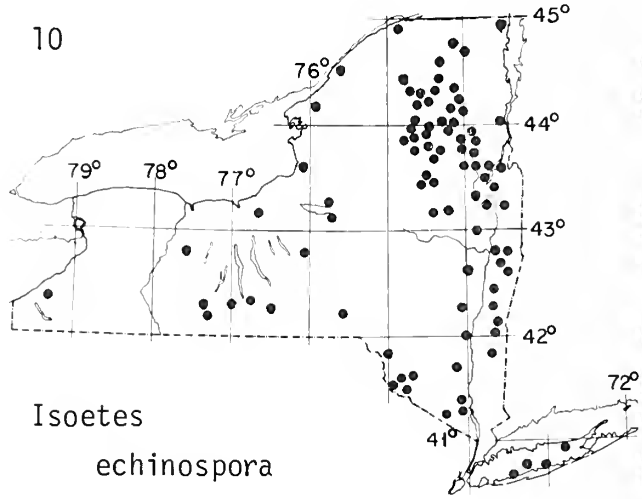
Isoetes eatonii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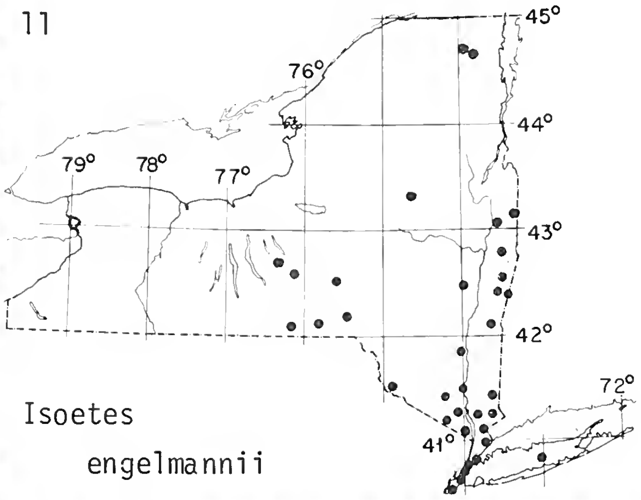
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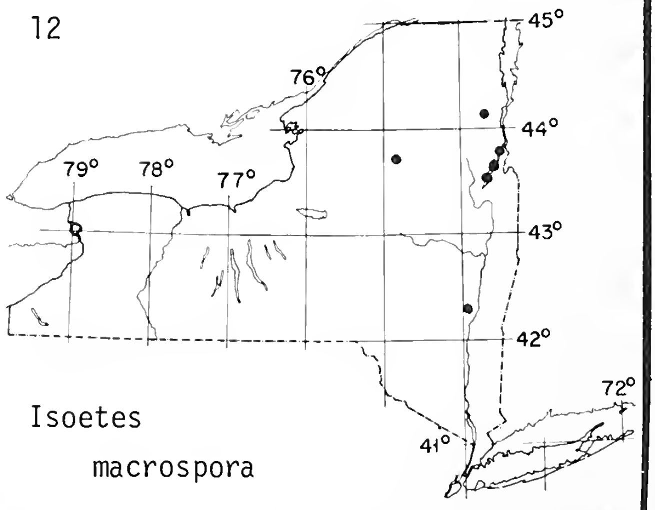
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Isoetes macrospora

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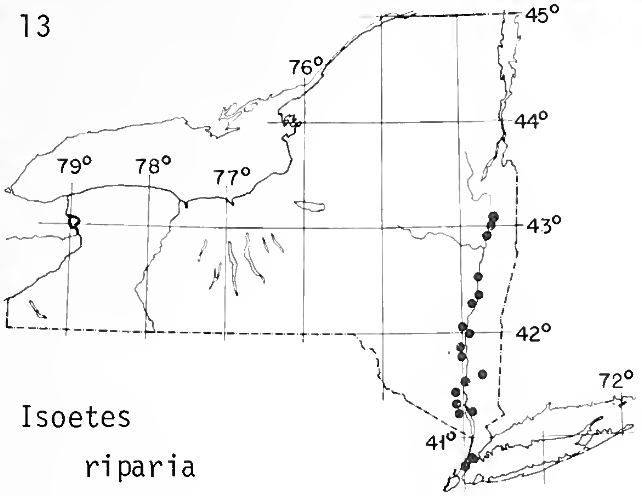

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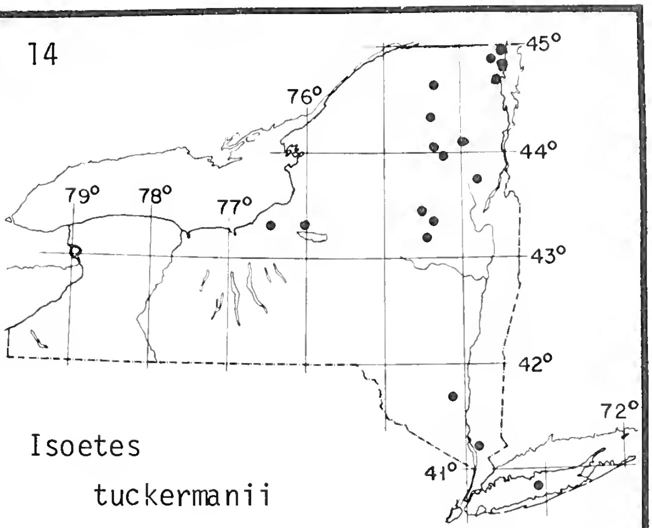

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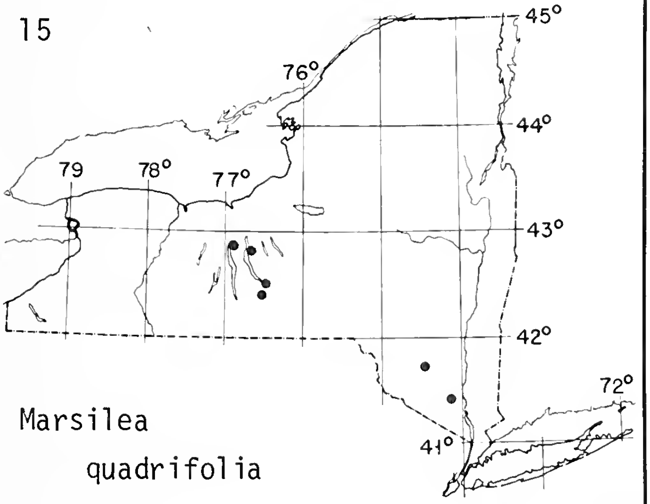

Marsilea quadrifolia

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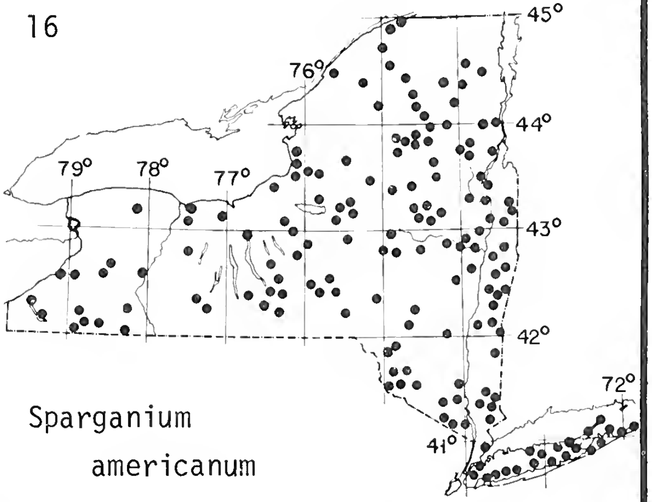

Sparganium americanum

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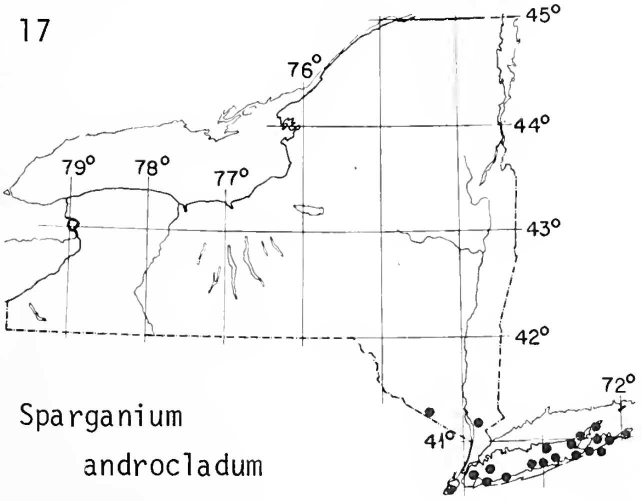

Sparganium androcladum

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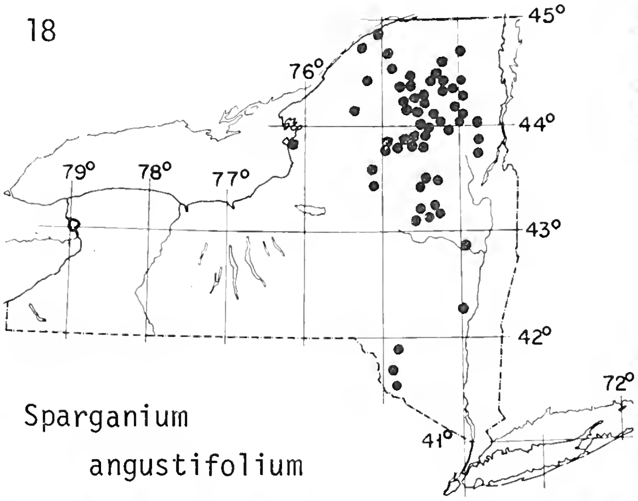

Sparganium angustifolium

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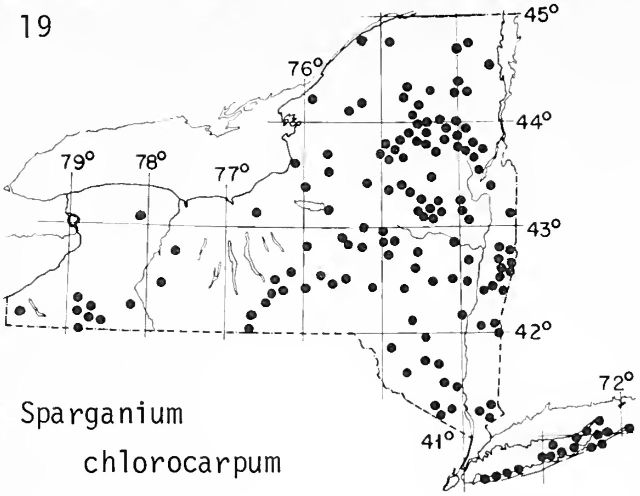

Sparganium chlorocarpum

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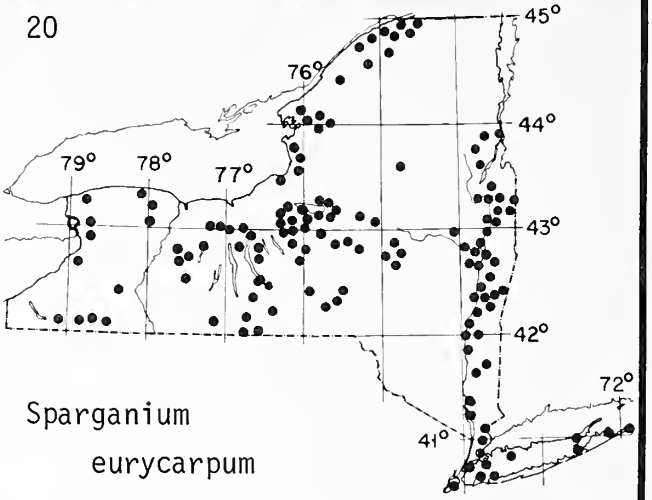

Sparganium eurycarpum

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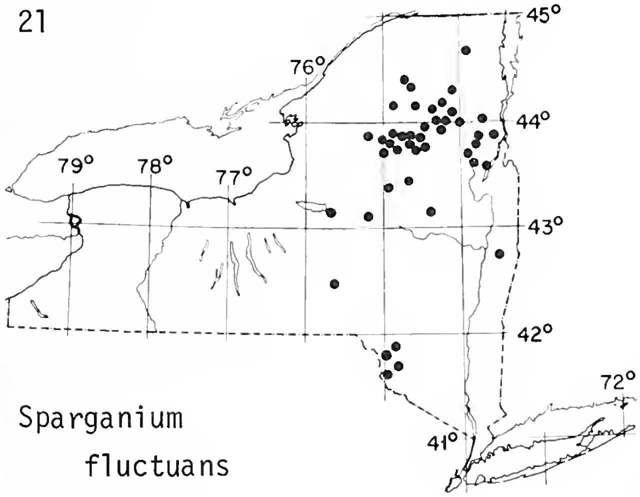

Sparganium fluctuans

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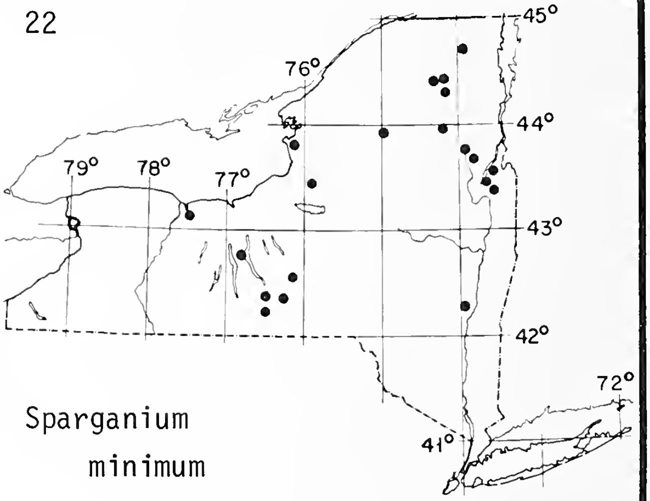

Sparganium minimum

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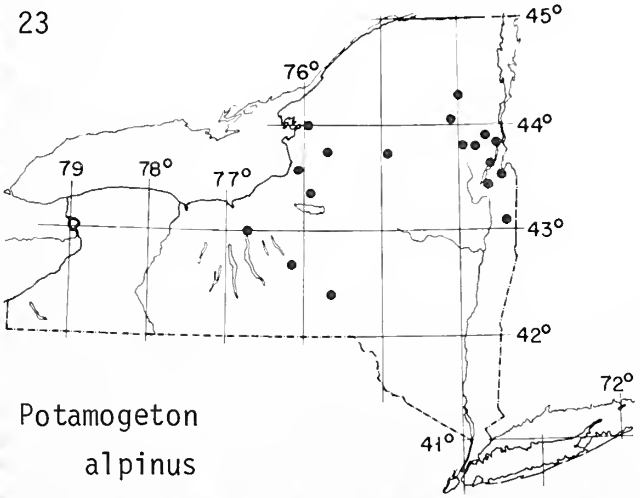

Potamogeton alpinus

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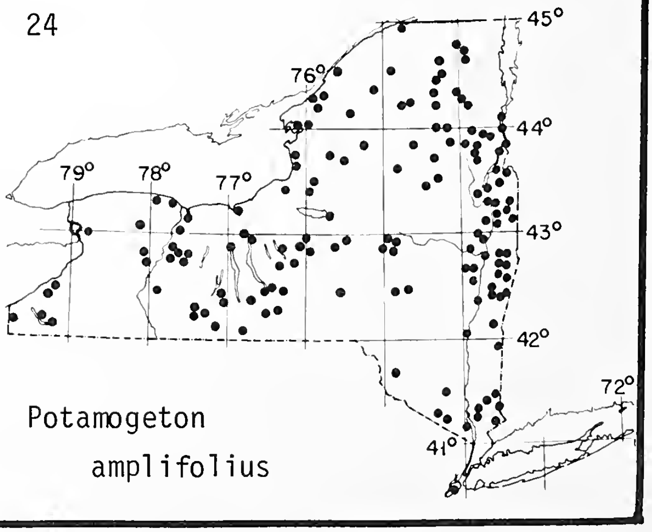

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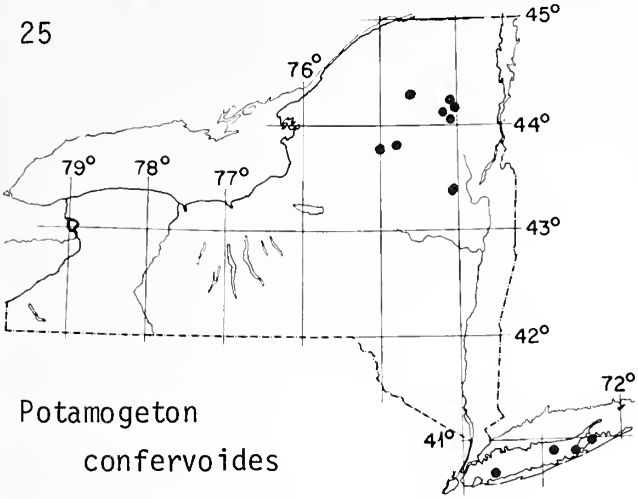

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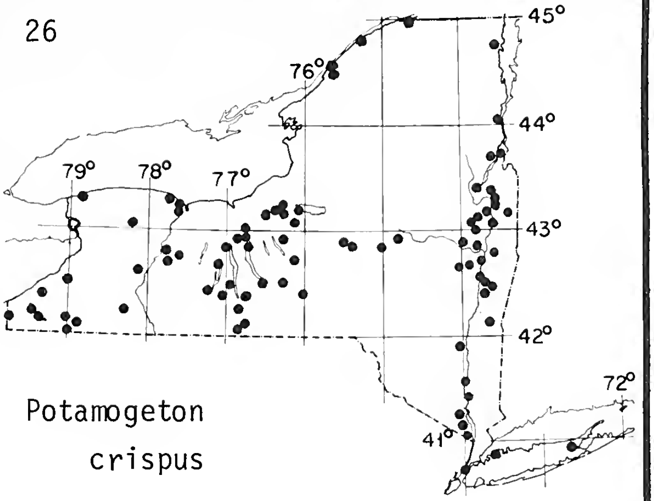

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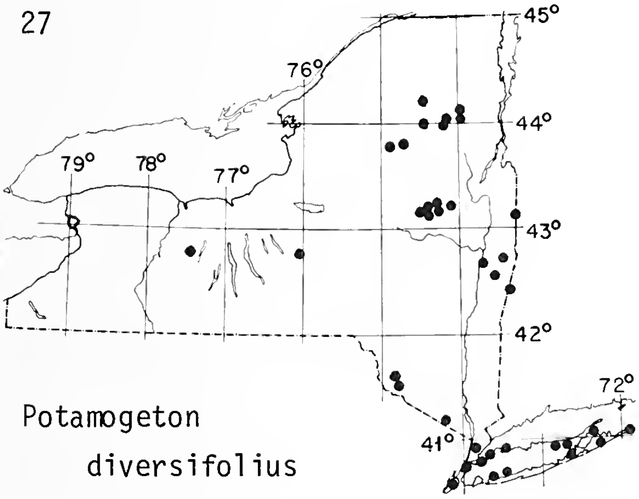

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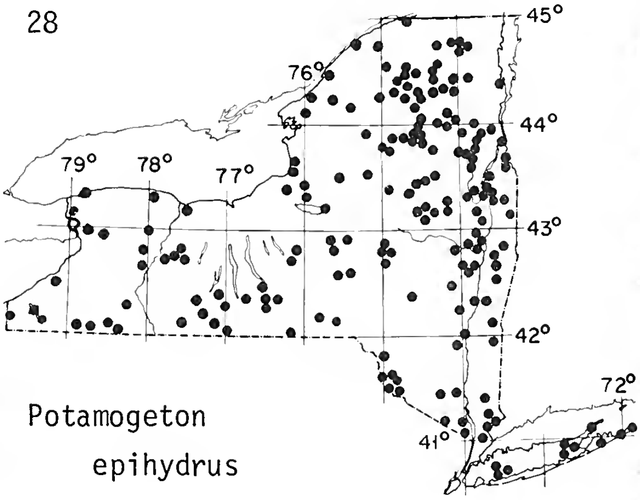

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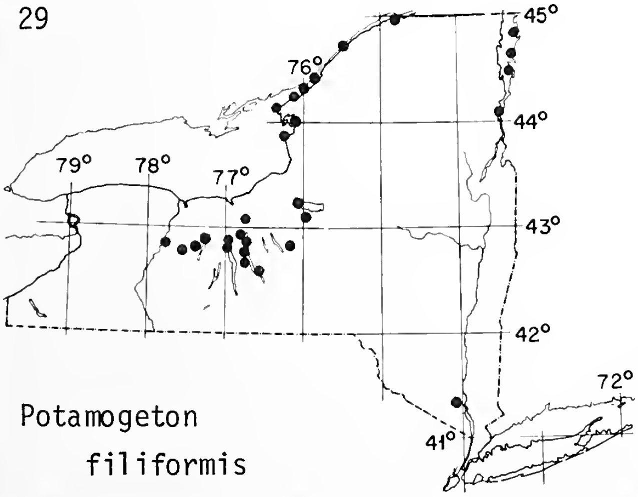

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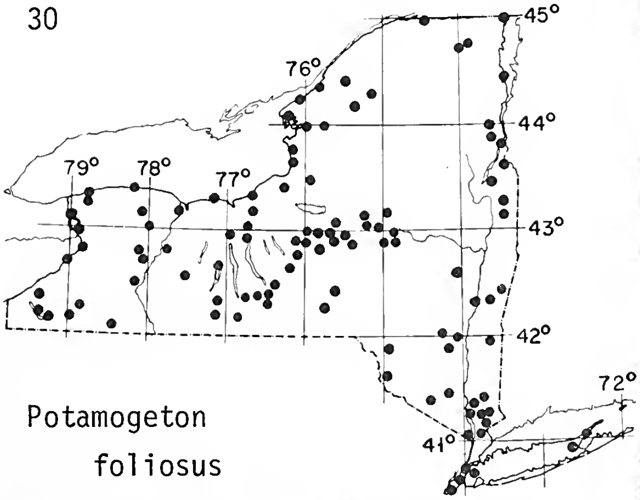

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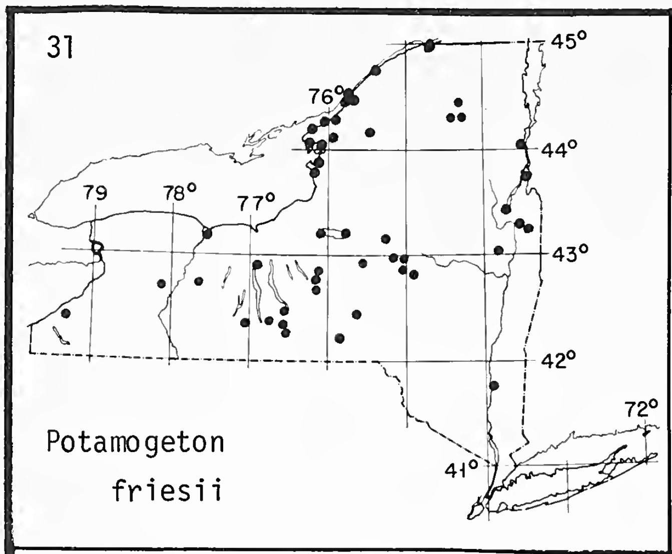
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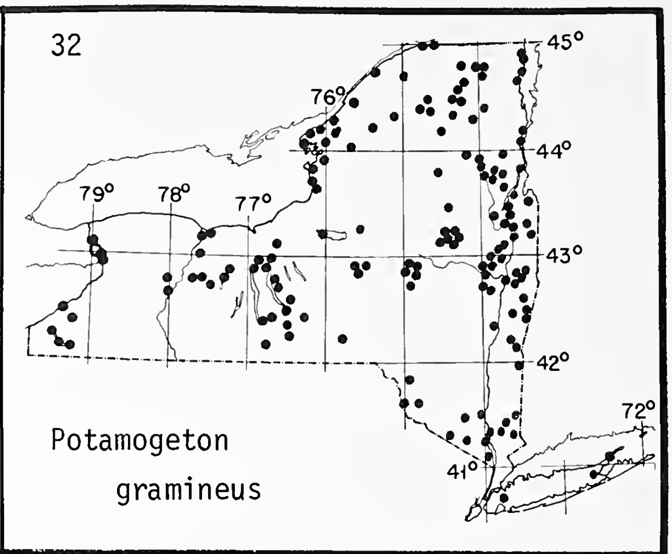
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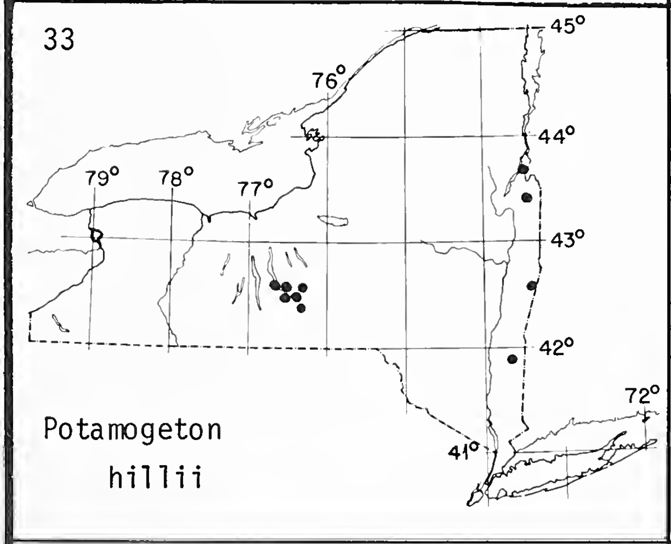
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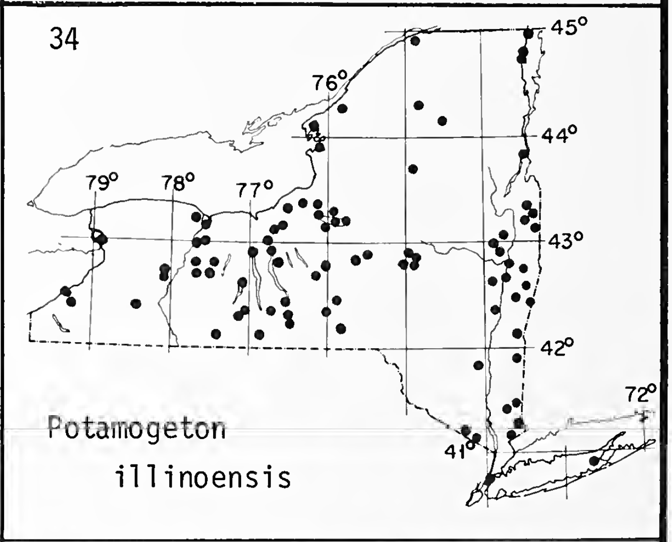
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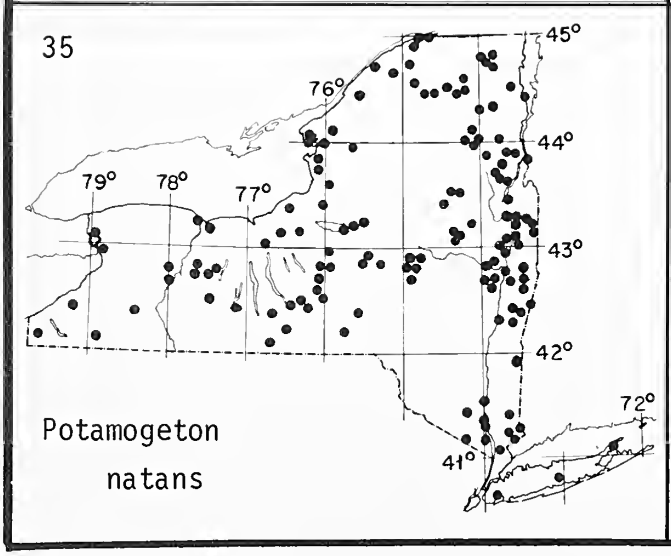
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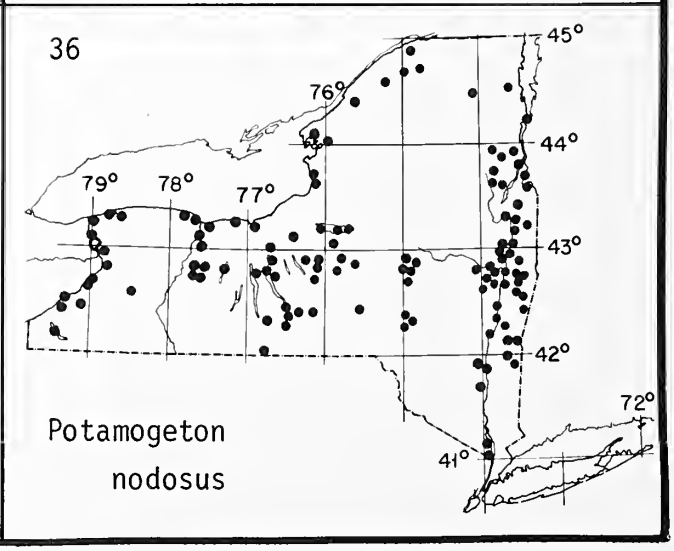
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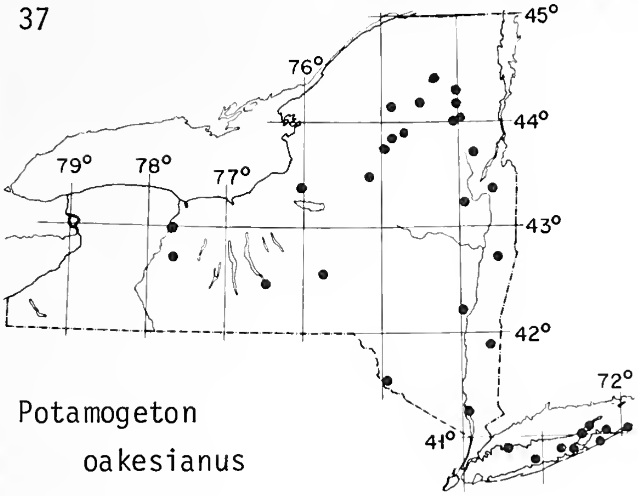

Potamogeton
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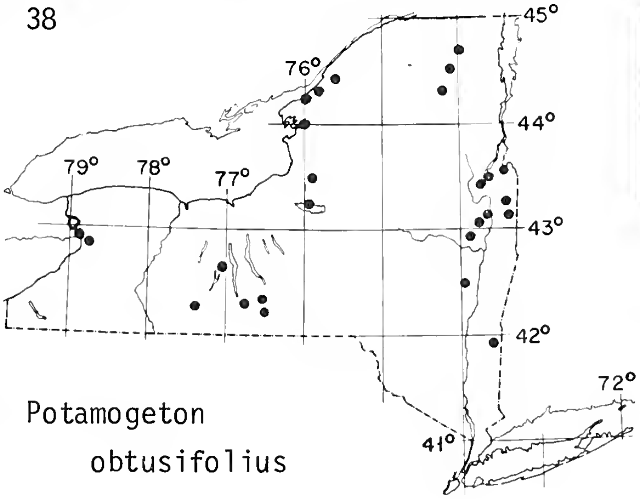

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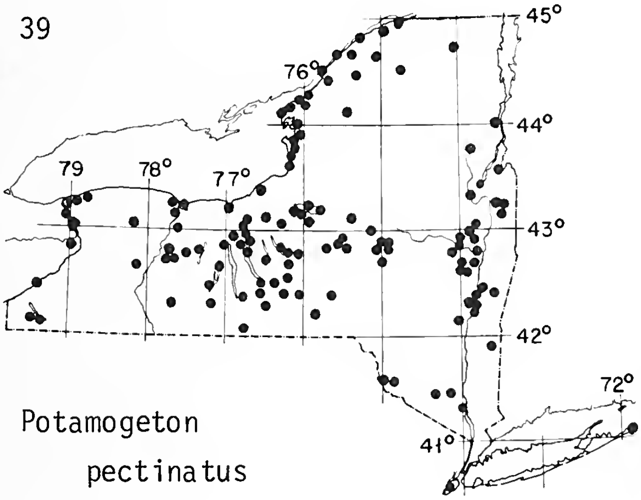

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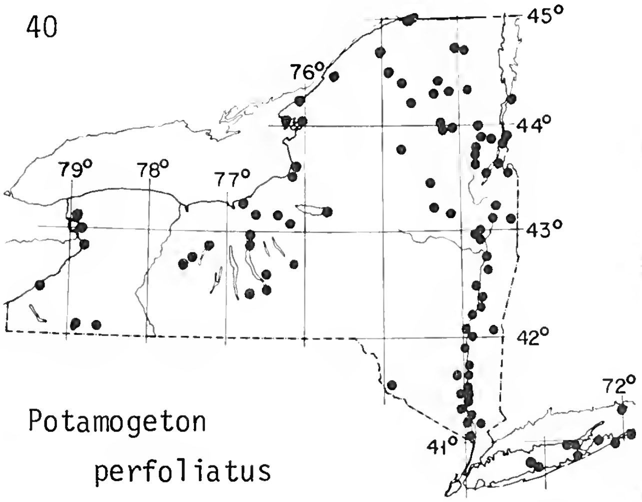

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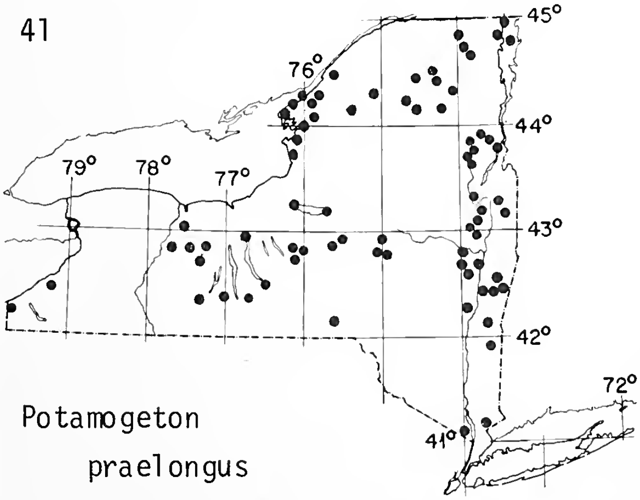

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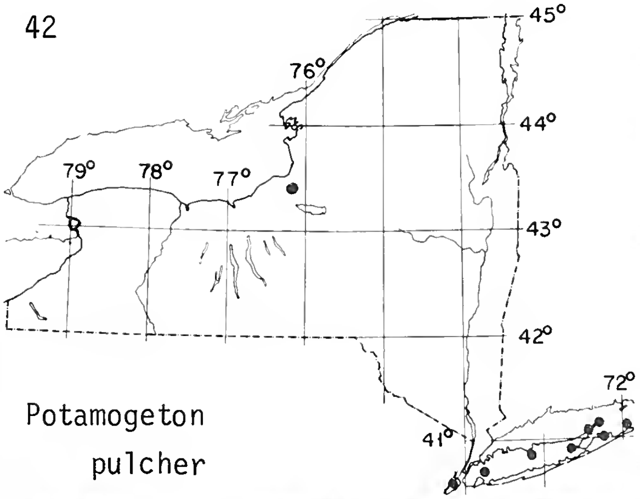

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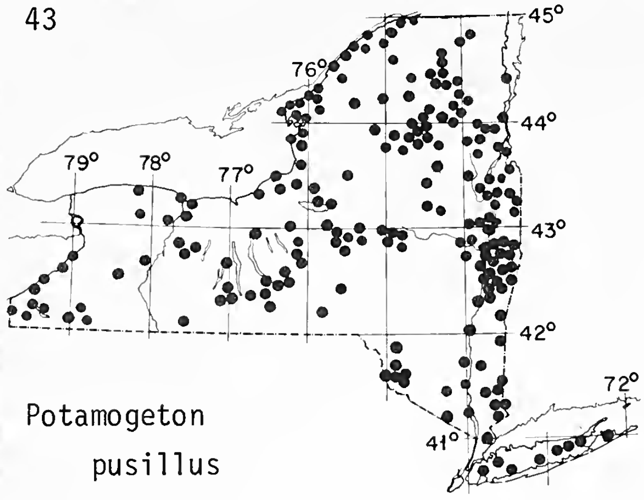

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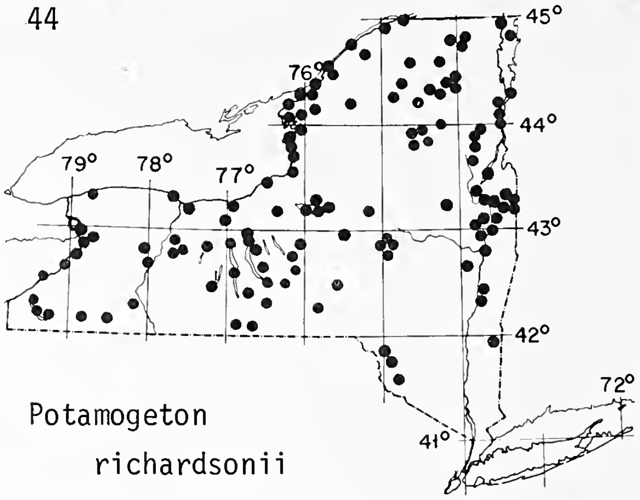

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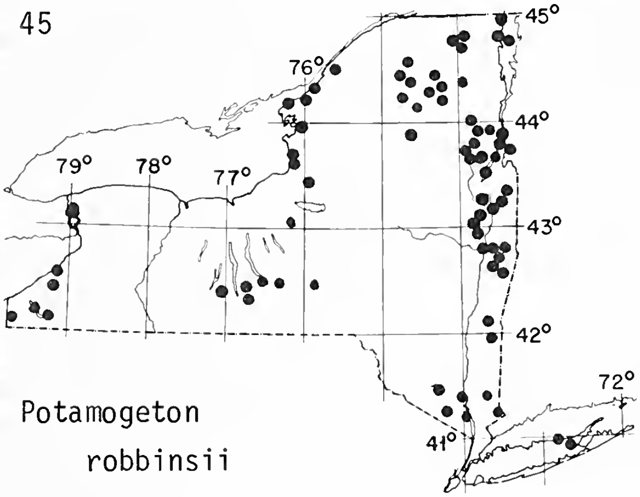

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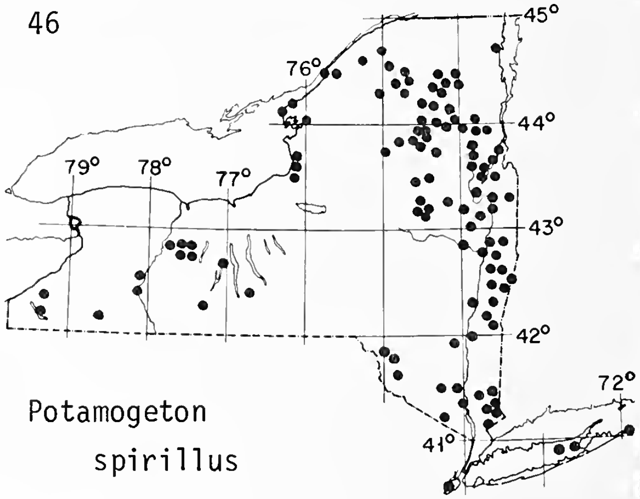

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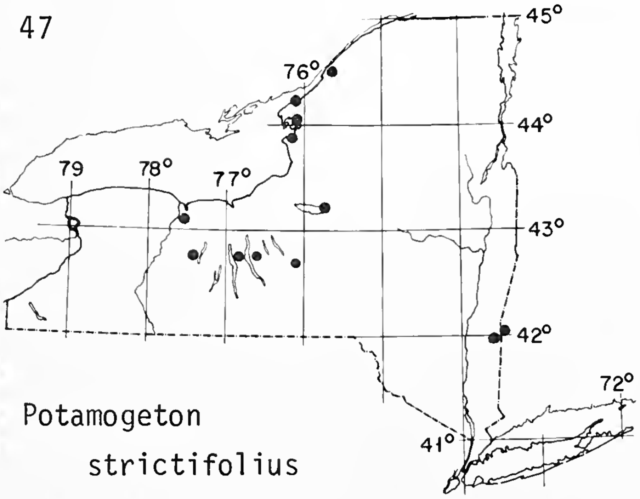

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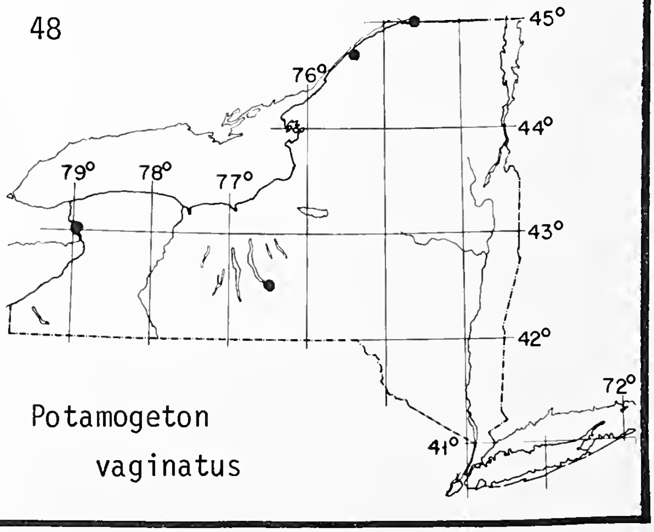
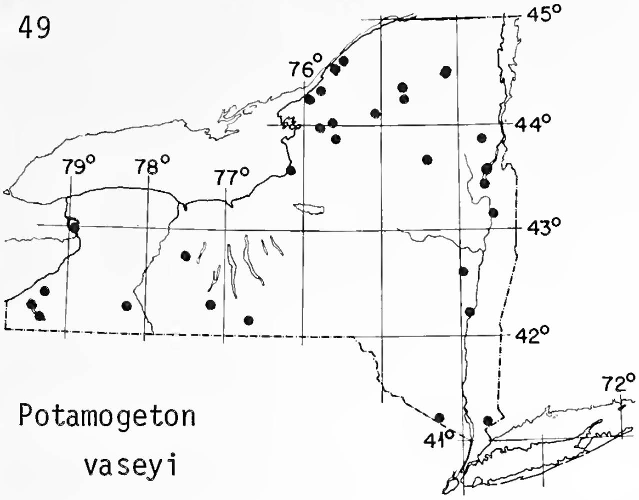


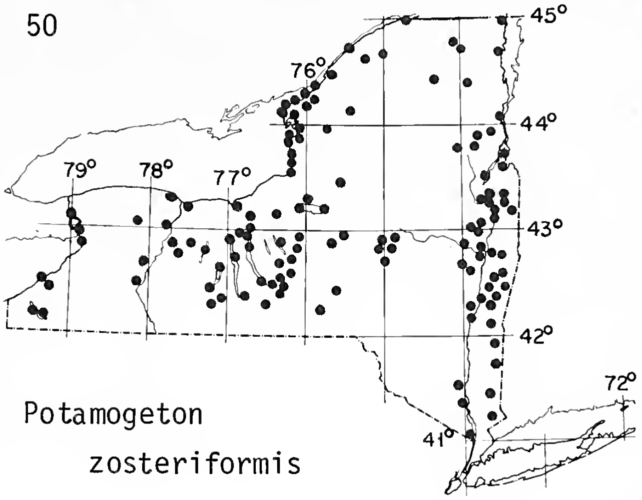
Potamogeton vaginatus

49



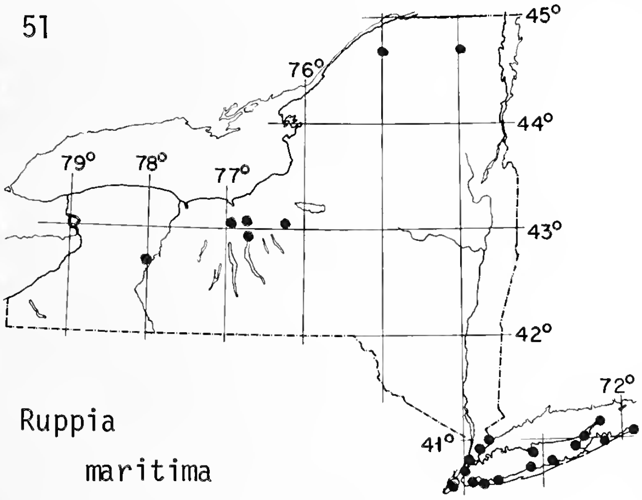
Potamogeton
vaseyi

50



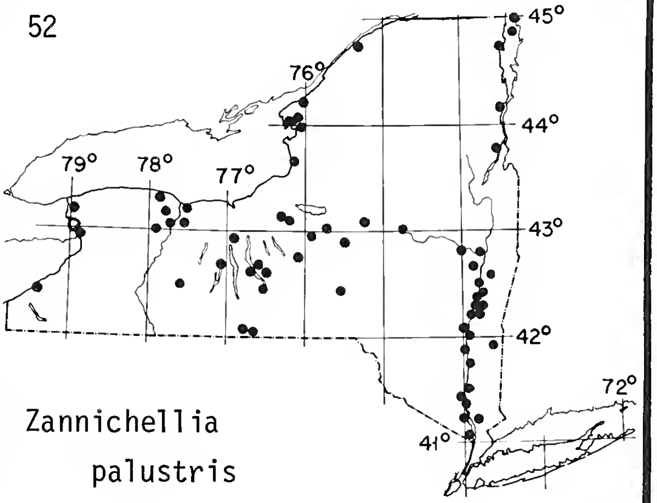
Potamogeton
zosteriformis

51



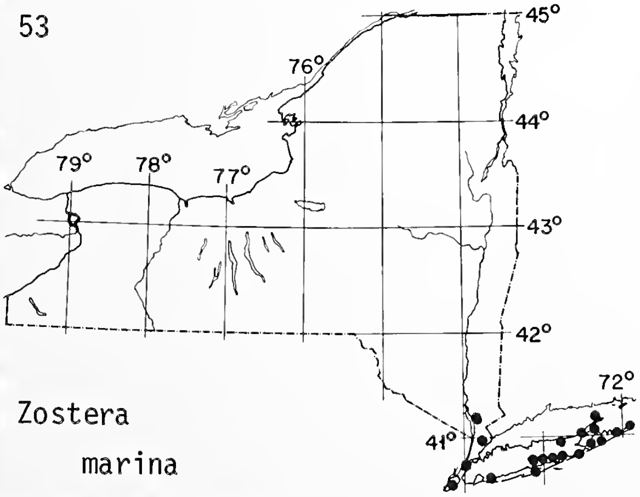
Ruppia
maritima

52



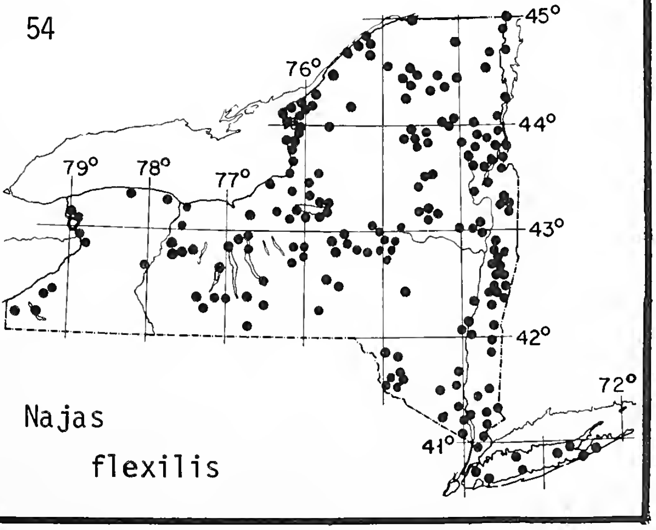
Zannichellia
palustris

53



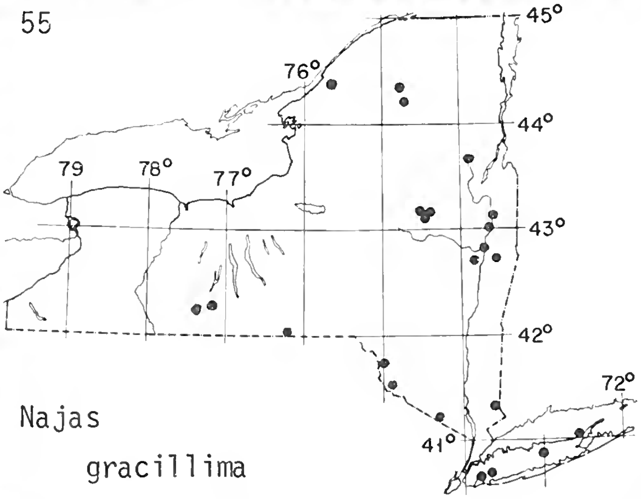
Zostera
marina

54



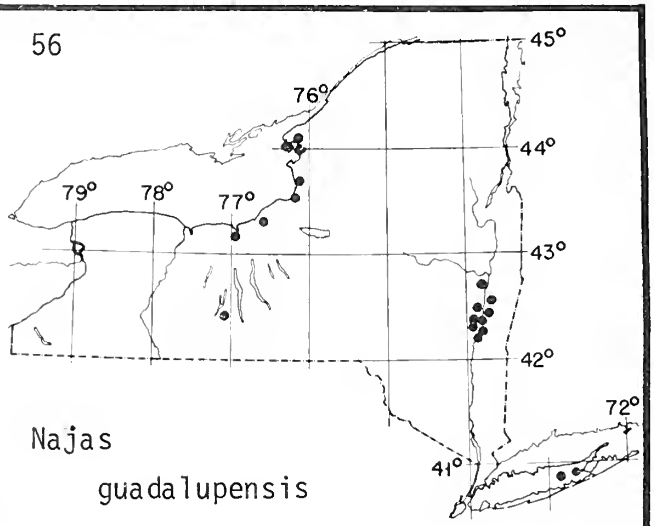
Najas
flexilis

55



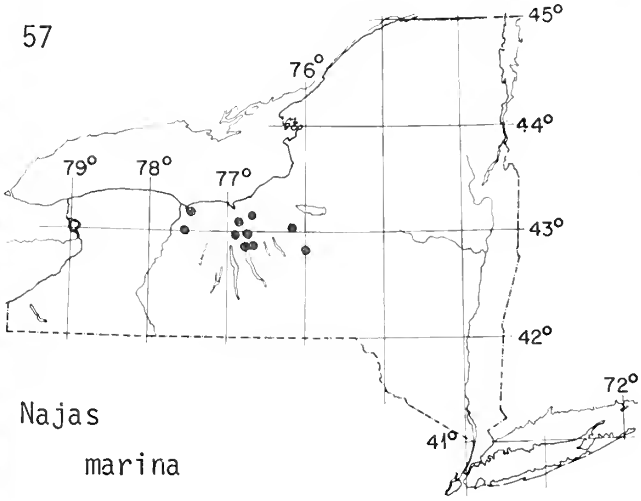
Najas
gracillima

56



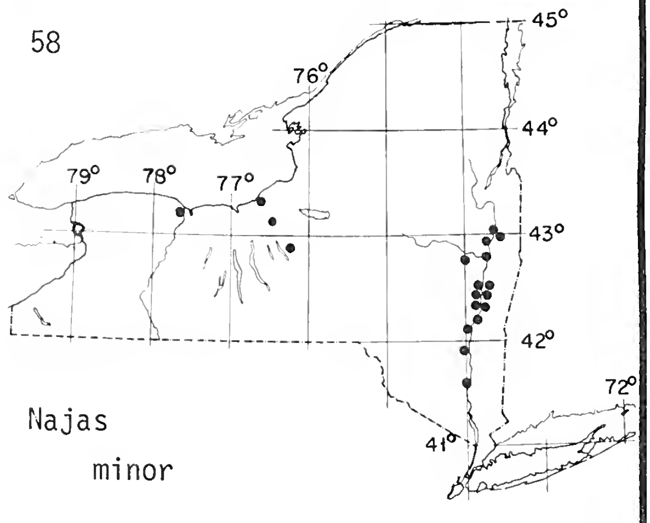
Najas
guadalupensis

57



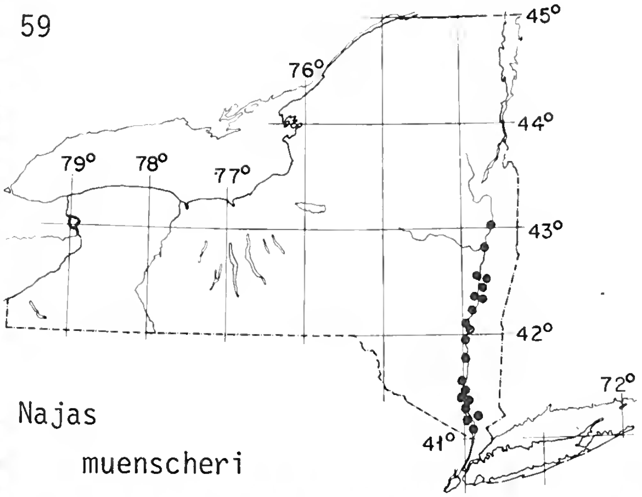
Najas
marina

58



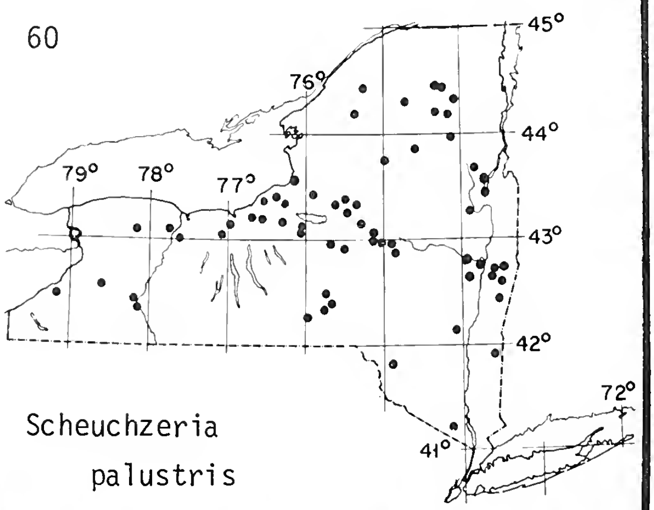
Najas
minor

59

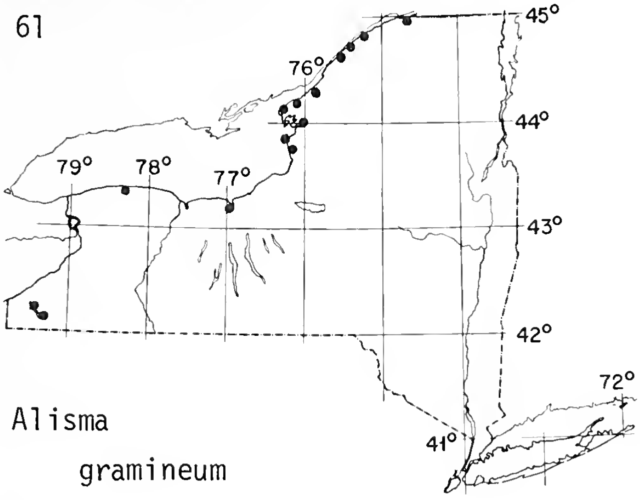


Najas
muenscheri

60

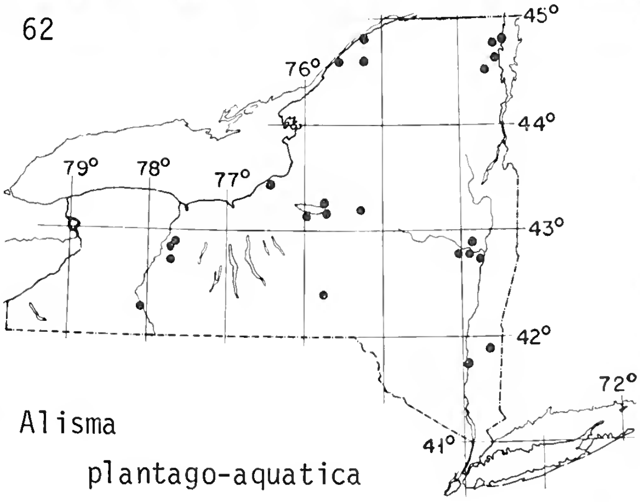


Scheuchzeria
palustris



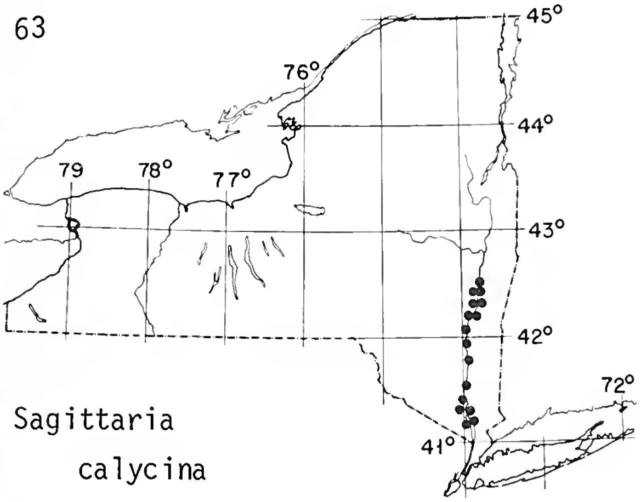
61

Alisma gramineum



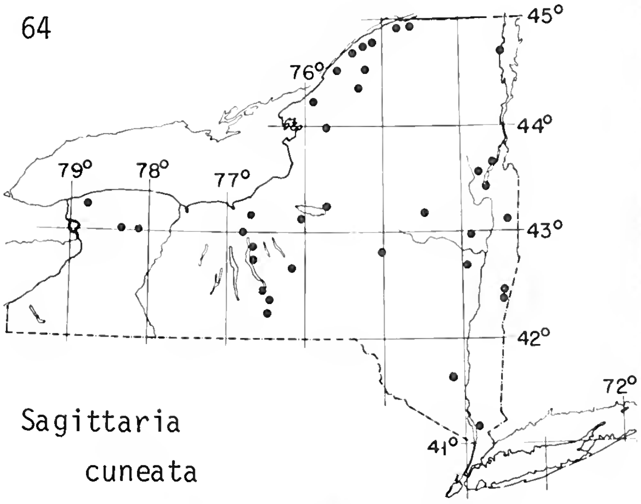
62

Alisma plantago-aquatica



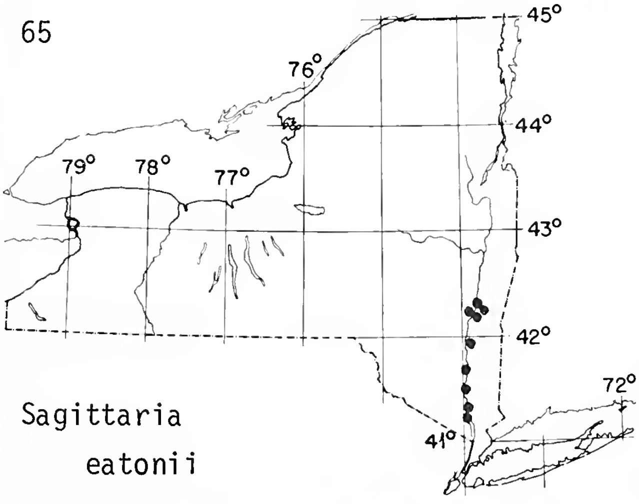
63

Sagittaria calycina



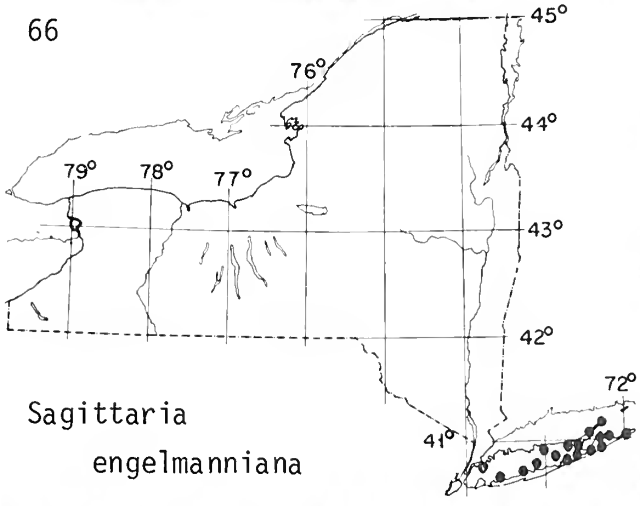
64

Sagittaria cuneata



65

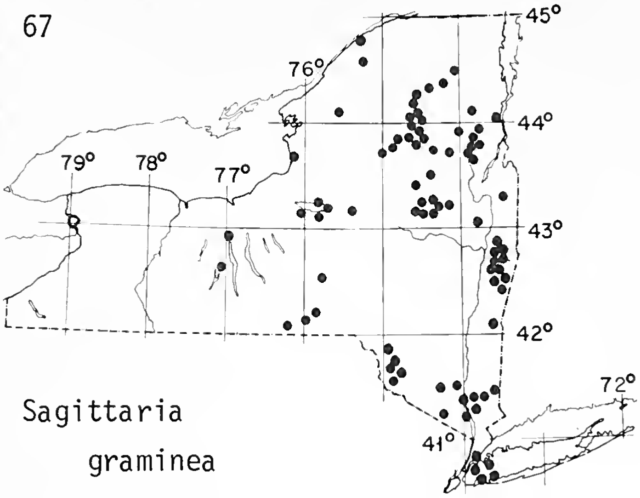
Sagittaria eatonii



66

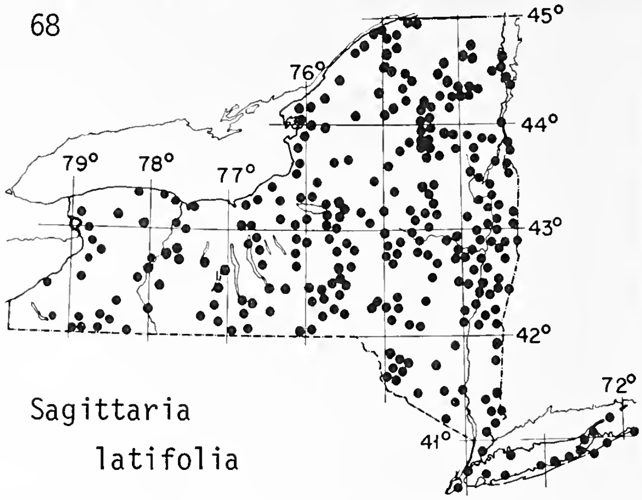
Sagittaria engelmanniana

67



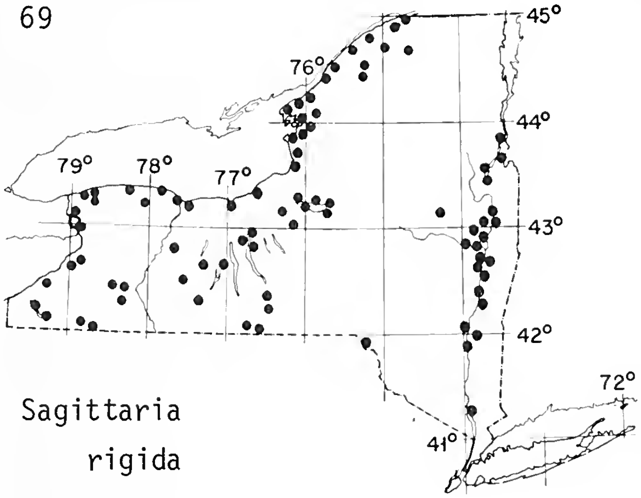
Sagittaria graminea

68



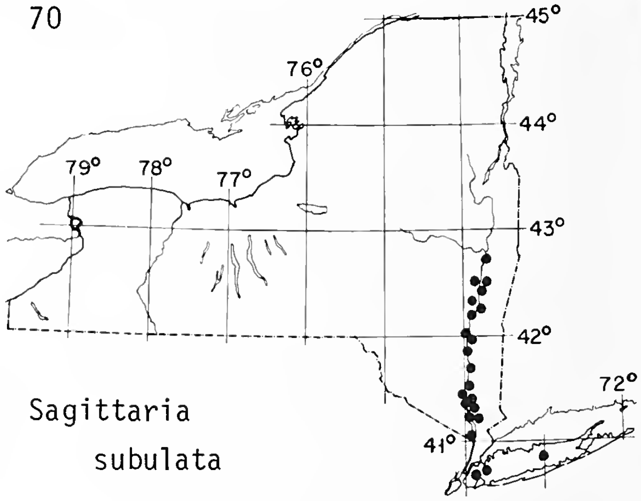
Sagittaria latifolia

69



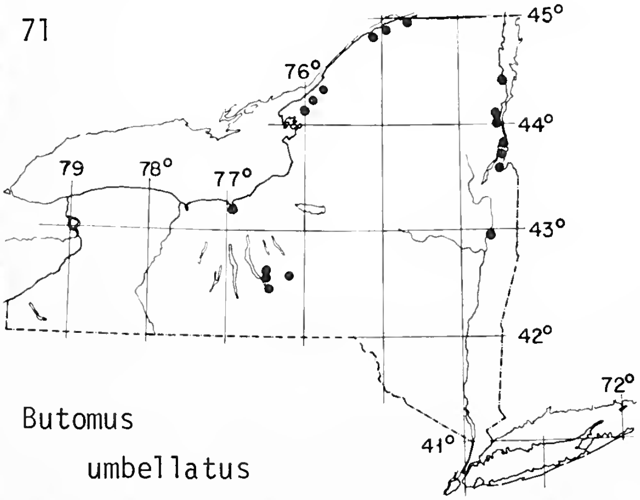
Sagittaria rigida

70



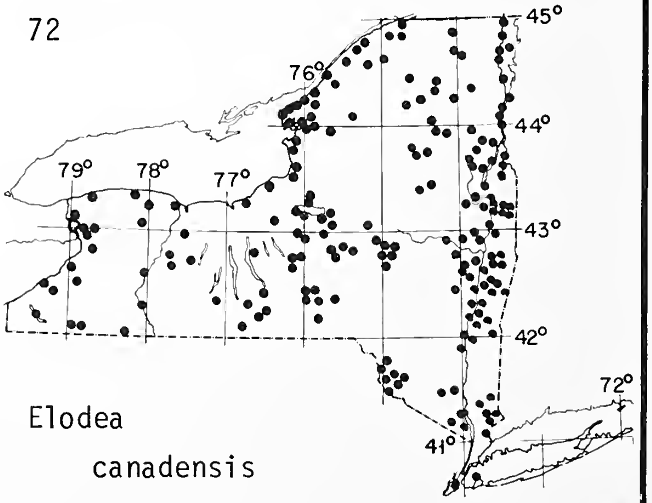
Sagittaria subulata

71



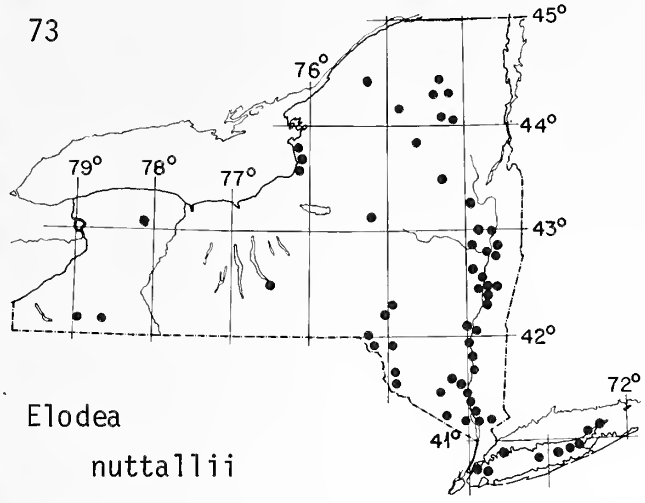
Butomus umbellatus

72



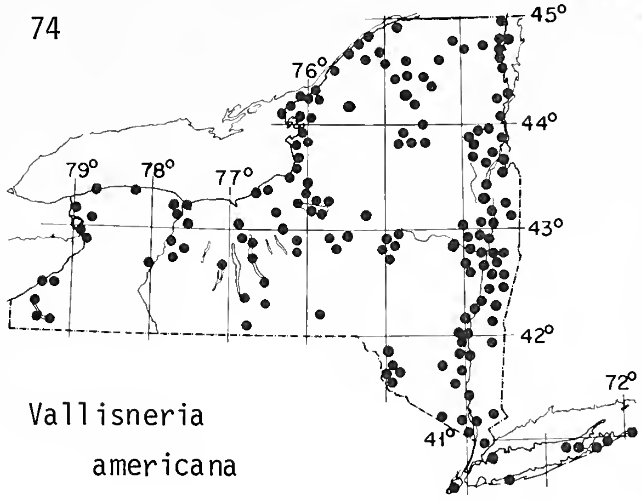
Elodea canadensis

73



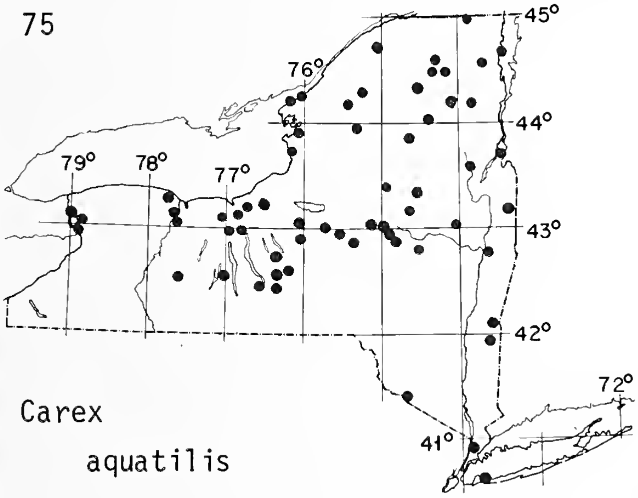
Elodea nuttallii

74



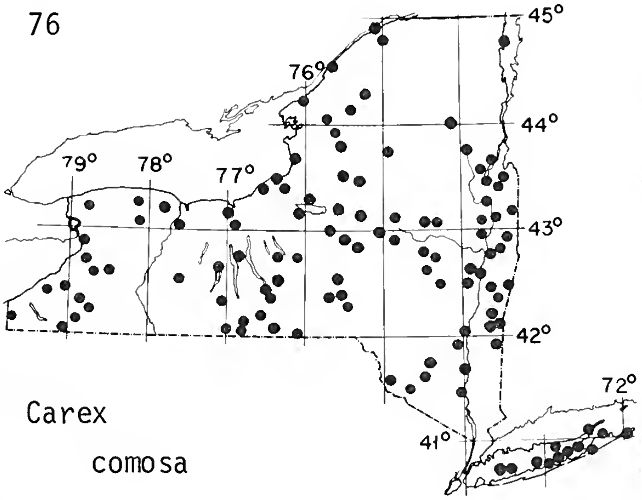
Vallisneria americana

75



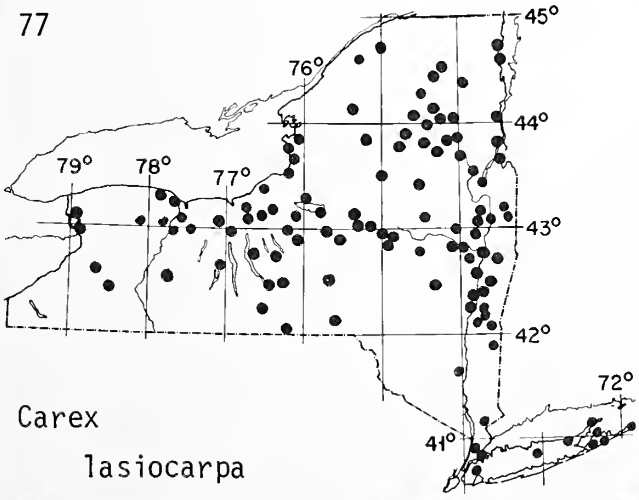
Carex aquatilis

76



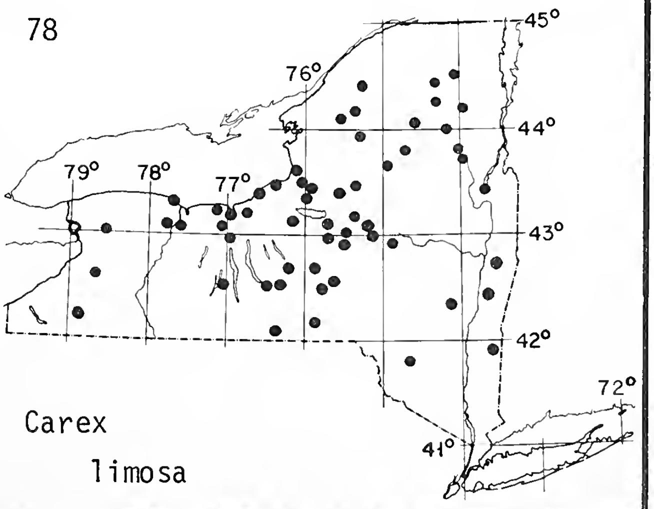
Carex comosa

77



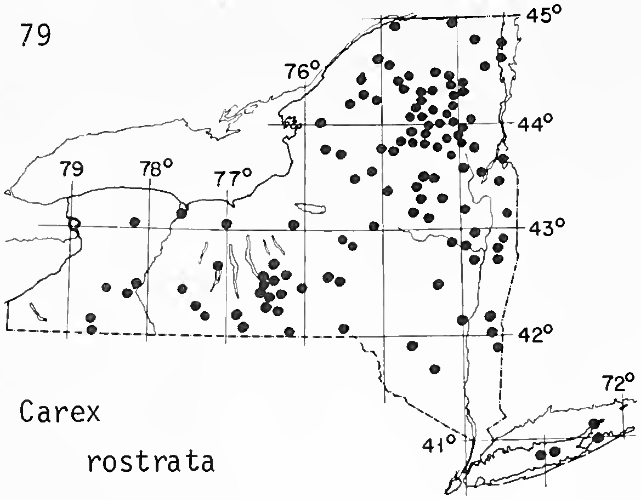
Carex lasiocarpa

78



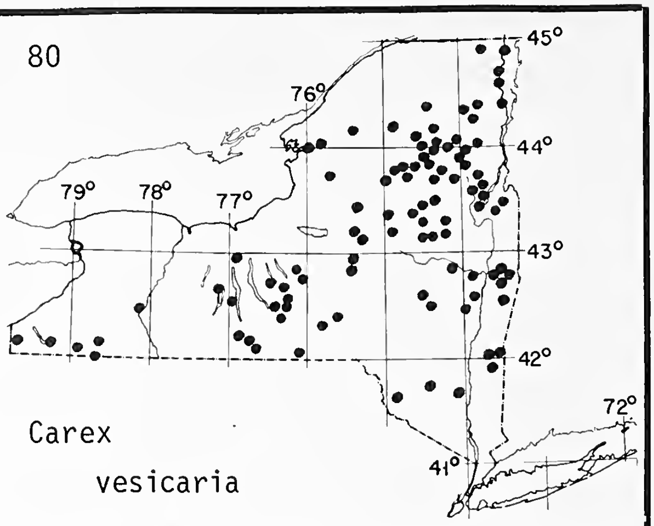
Carex limosa

79



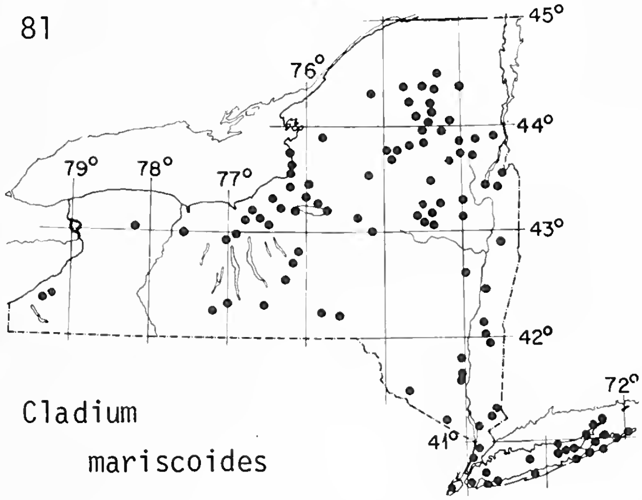
Carex rostrata

80



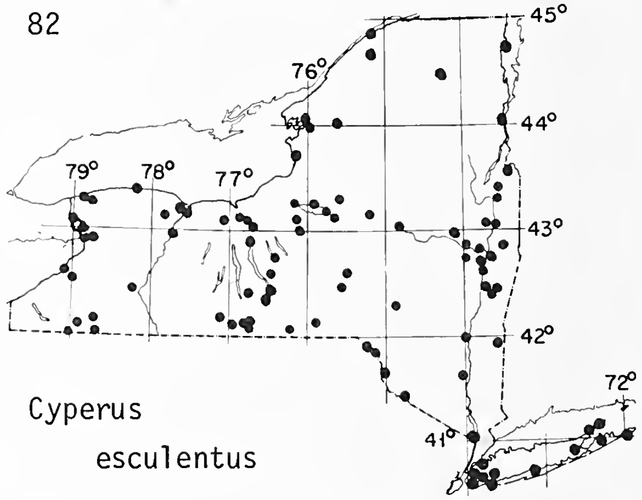
Carex vesicaria

81



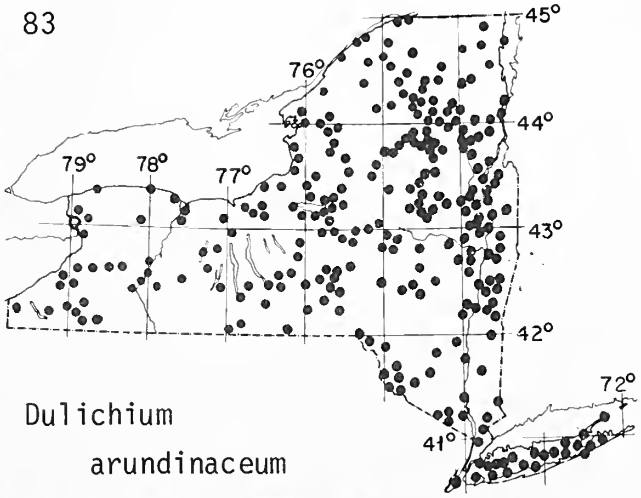
Cladium mariscoides

82



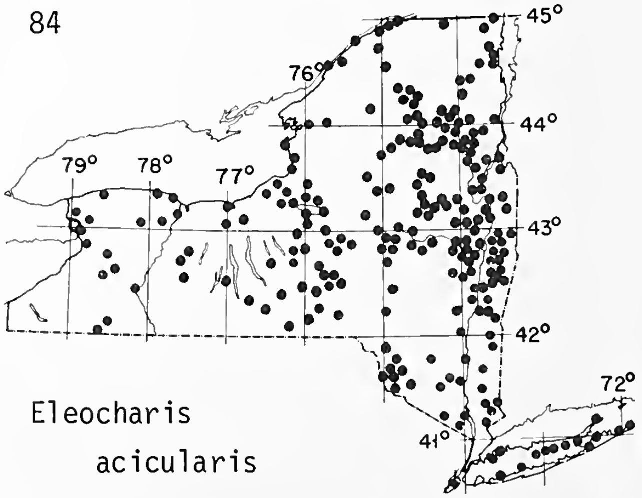
Cyperus esculentus

83



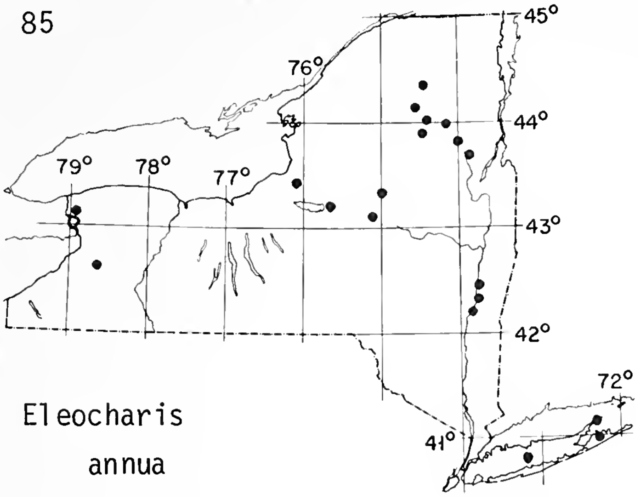
Dulichium arundinaceum

84



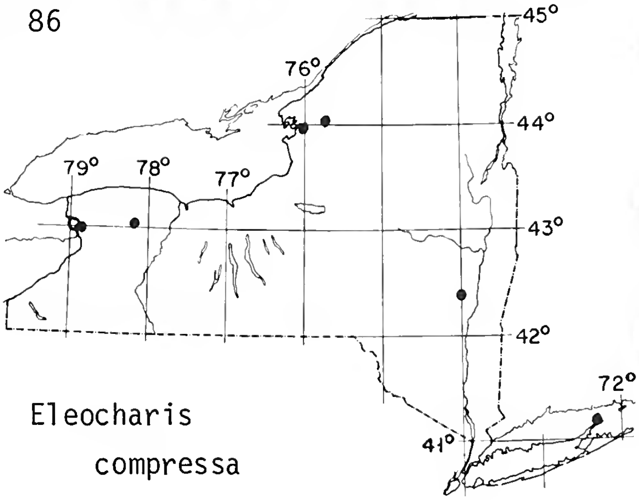
Eleocharis acicularis

85



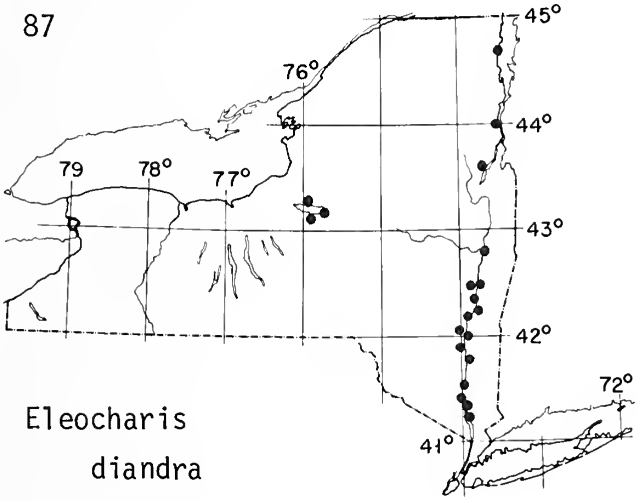
Eleocharis annua

86



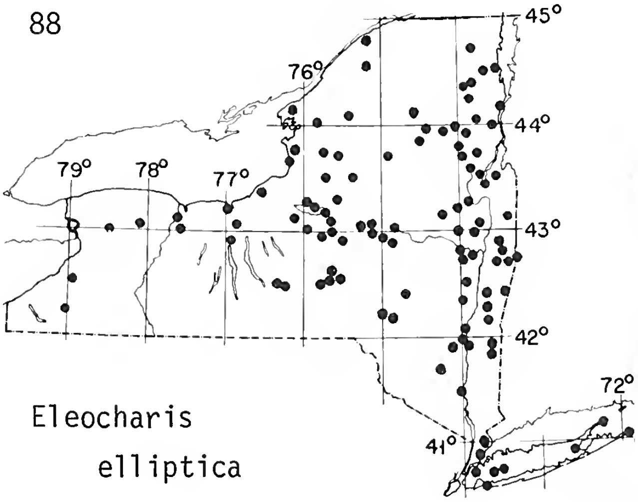
Eleocharis compressa

87



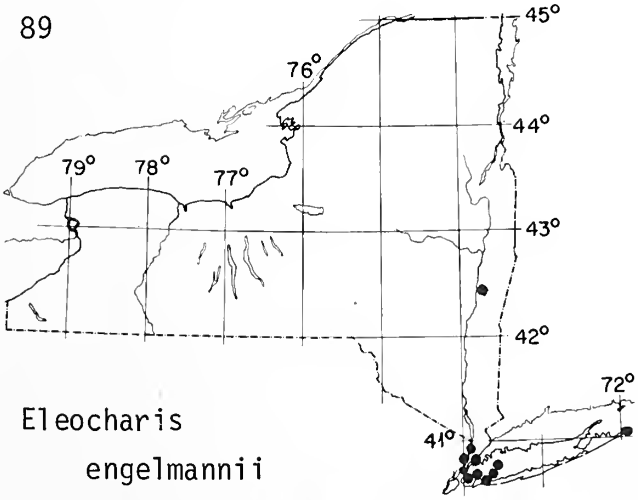
Eleocharis diandra

88



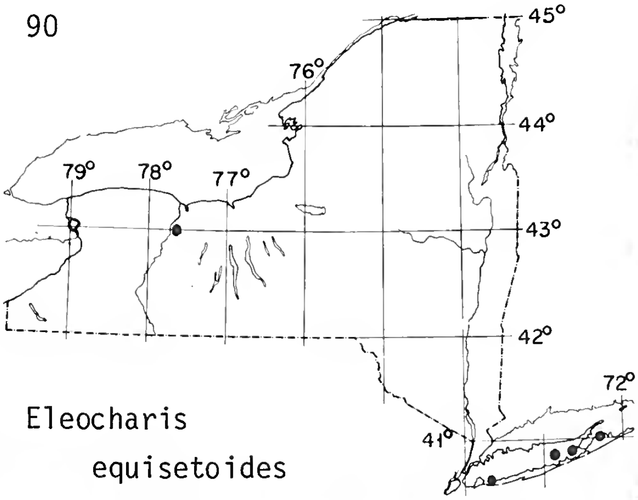
Eleocharis elliptica

89



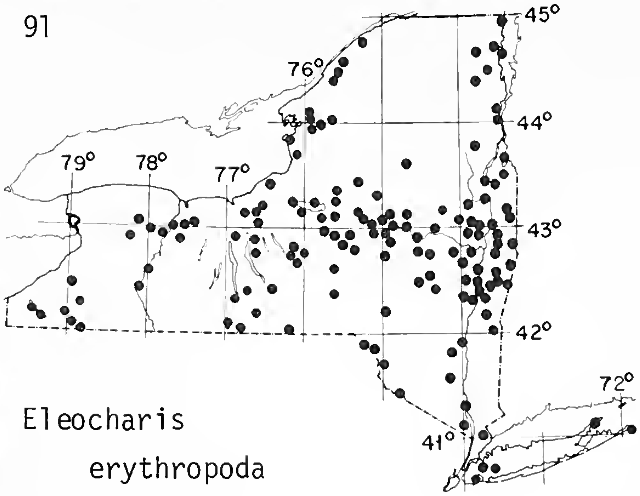
Eleocharis engelmannii

90



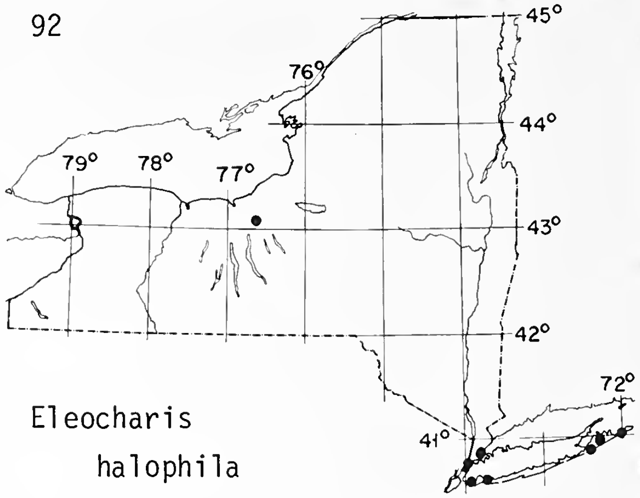
Eleocharis equisetoides

91



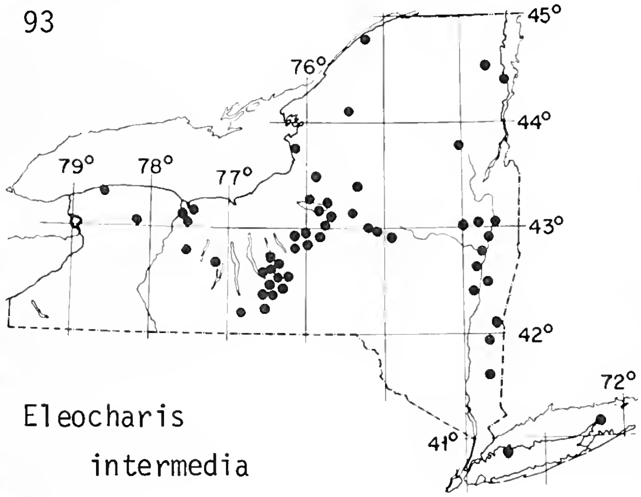
Eleocharis
erythropoda

92



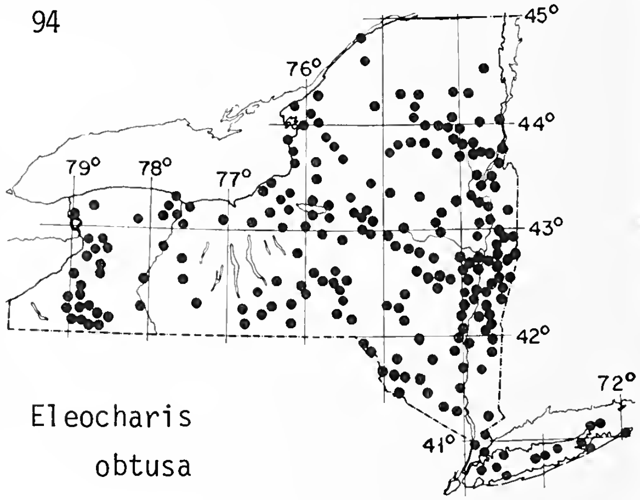
Eleocharis
halophila

93



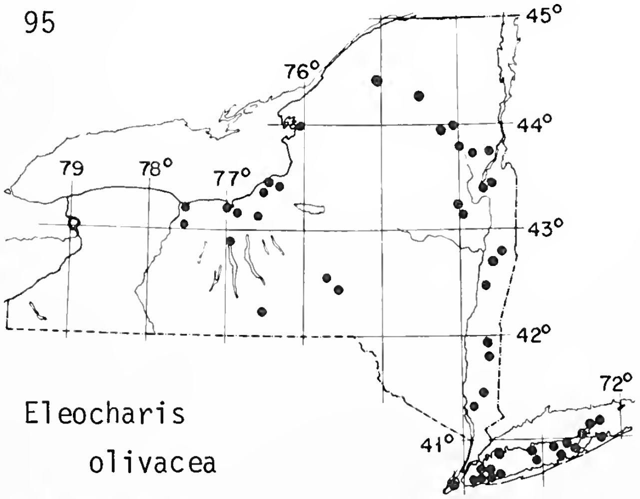
Eleocharis
intermedia

94



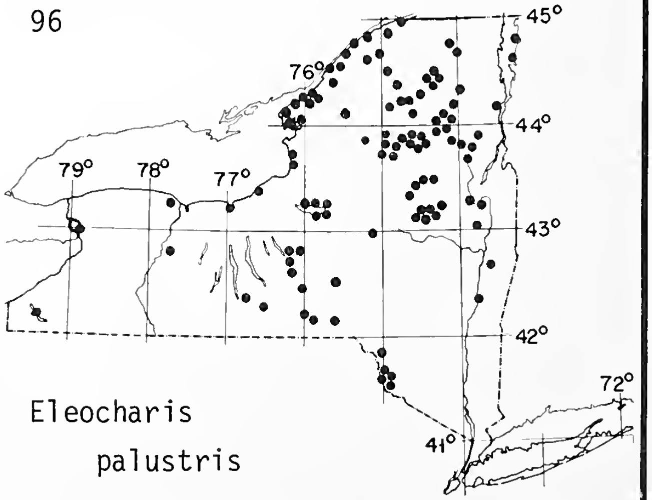
Eleocharis
obtusa

95



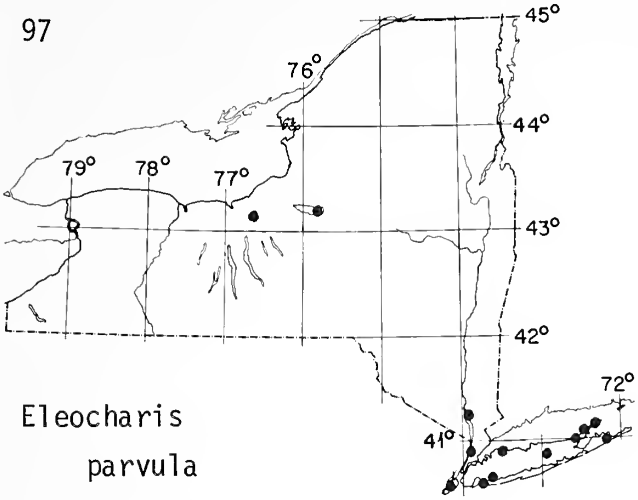
Eleocharis
olivacea

96



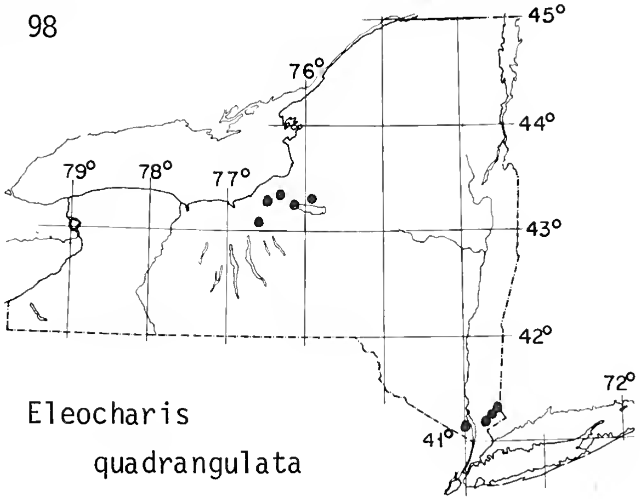
Eleocharis
palustris

97



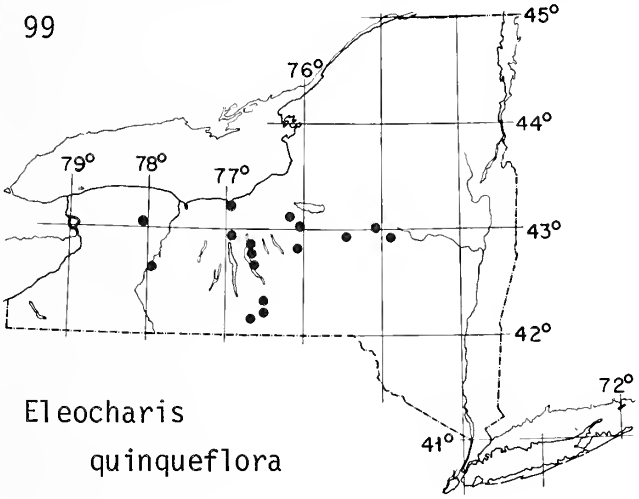
Eleocharis parvula

98



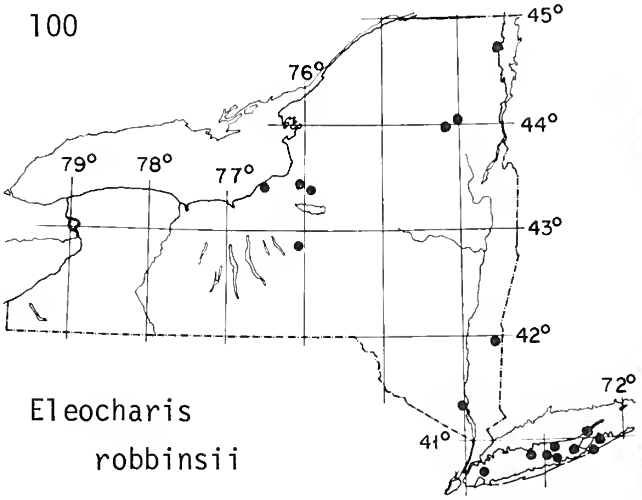
Eleocharis quadrangulata

99



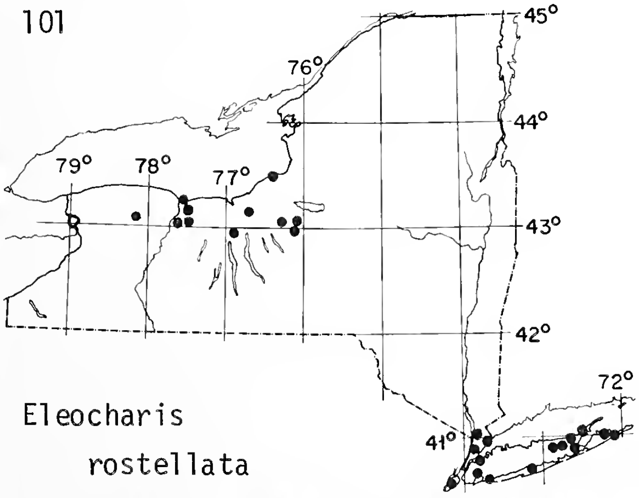
Eleocharis quinqueflora

100



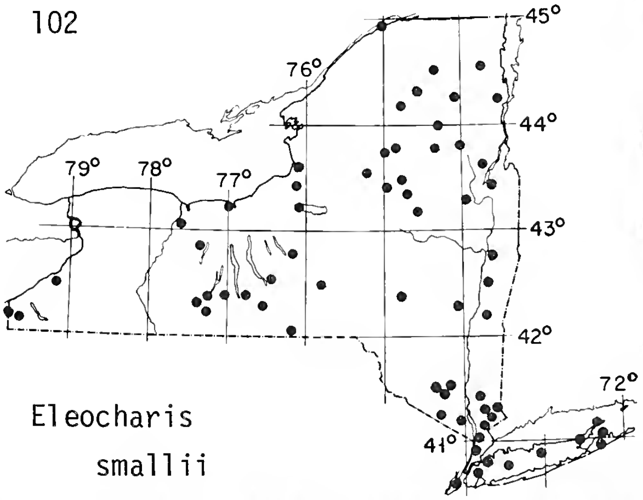
Eleocharis robbinsii

101



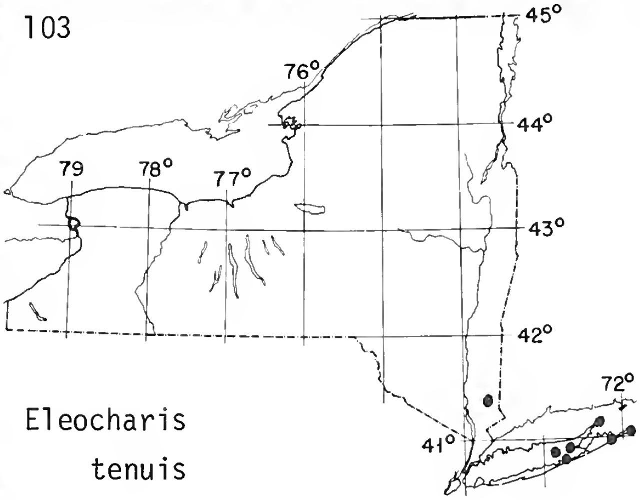
Eleocharis rostellata

102



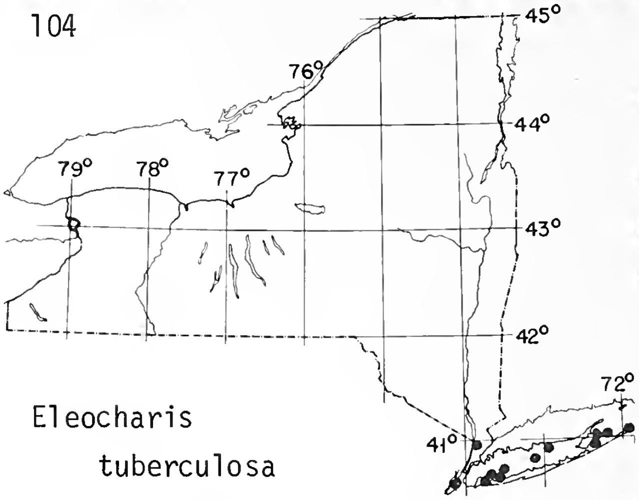
Eleocharis smallii

103



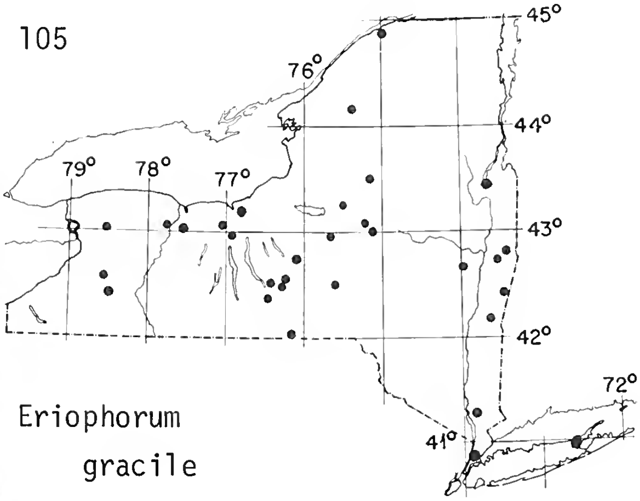
Eleocharis
tenuis

104



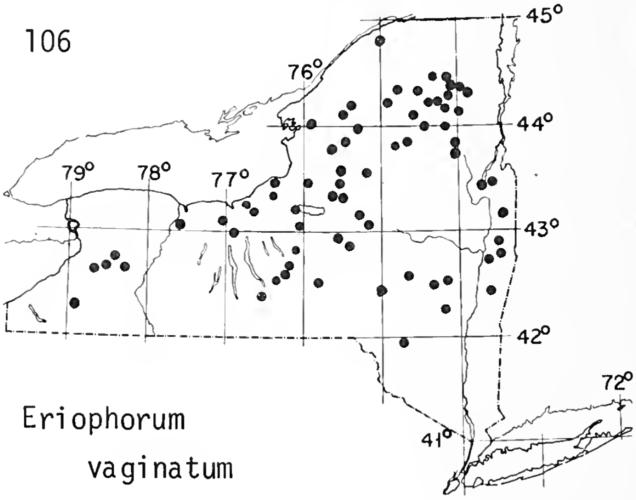
Eleocharis
tuberculosa

105



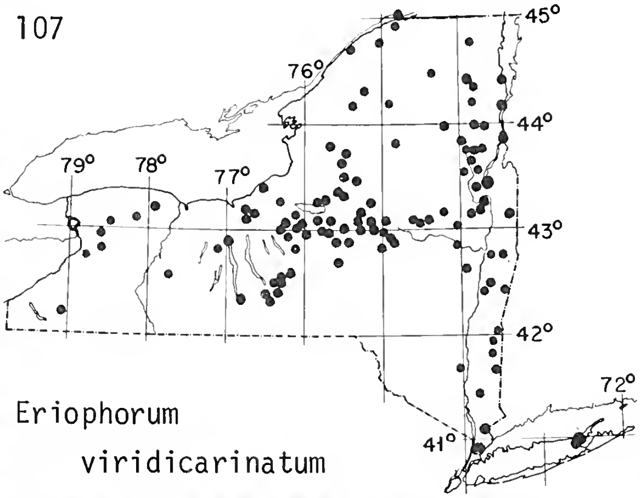
Eriophorum
gracile

106



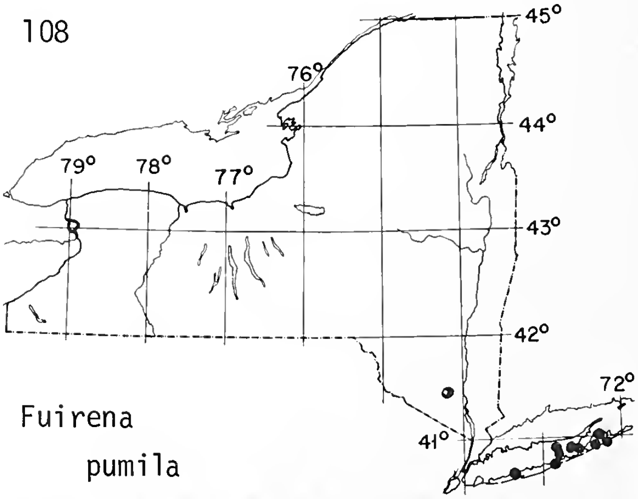
Eriophorum
vaginatum

107



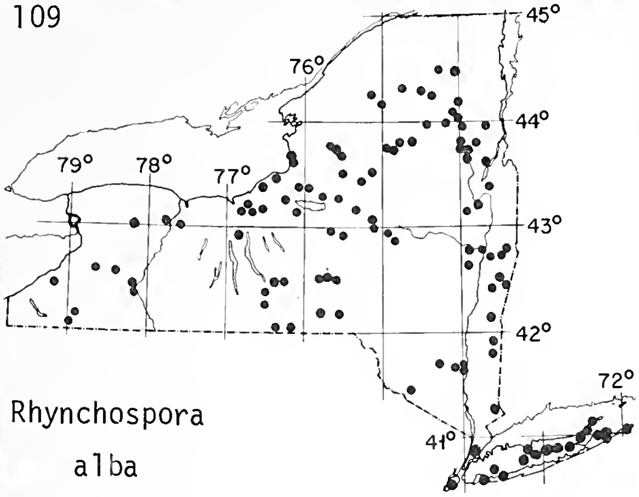
Eriophorum
viridicarinatum

108



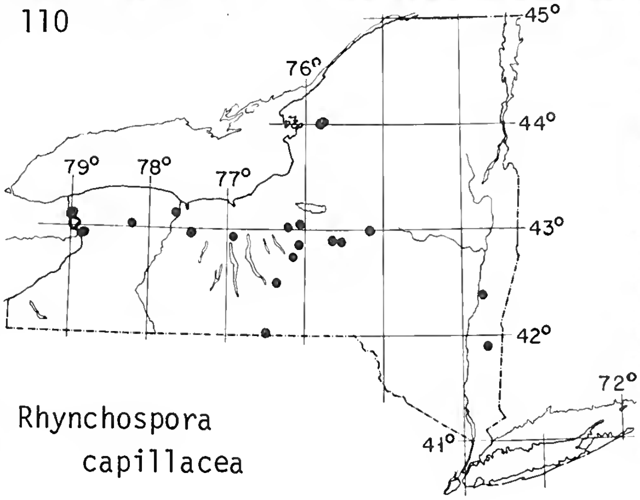
Fuirena
pumila

109



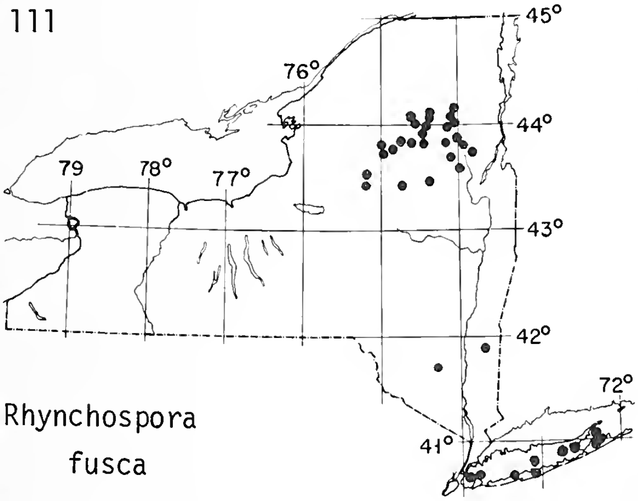
Rhynchospora
alba

110



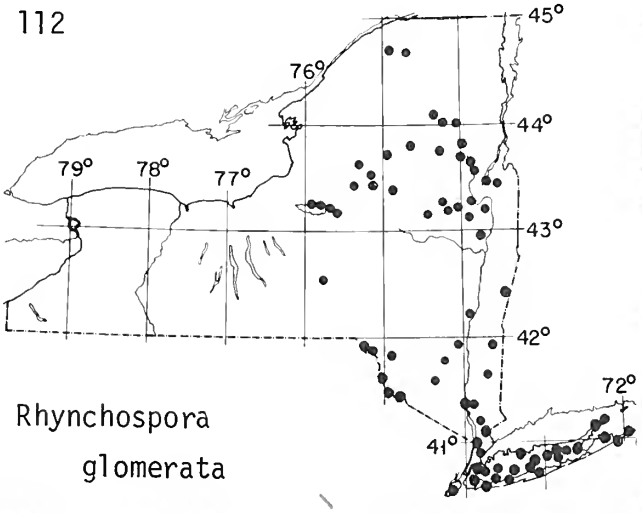
Rhynchospora
capillacea

111



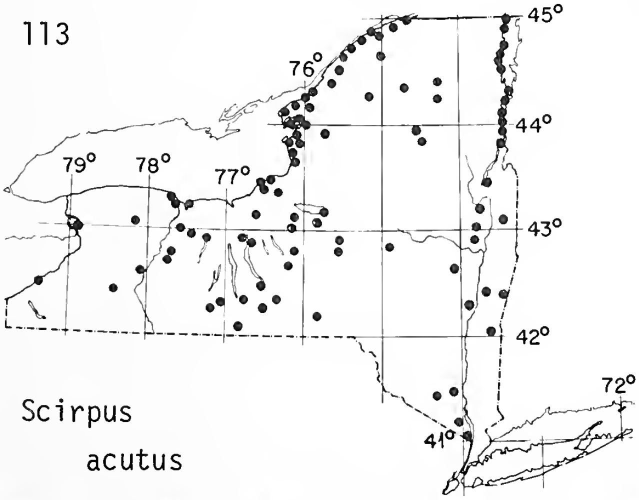
Rhynchospora
fusca

112



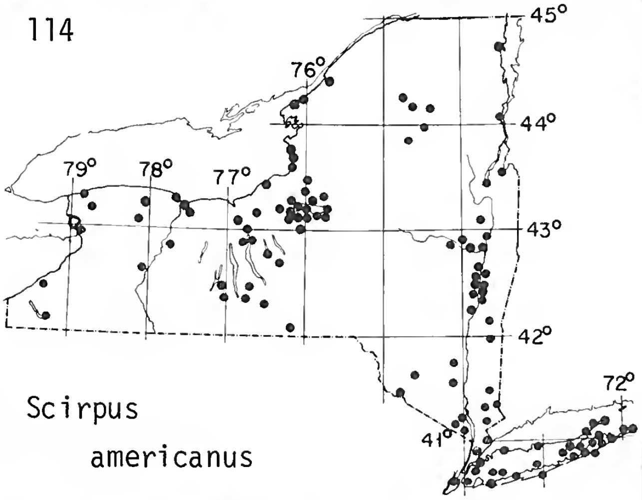
Rhynchospora
glomerata

113



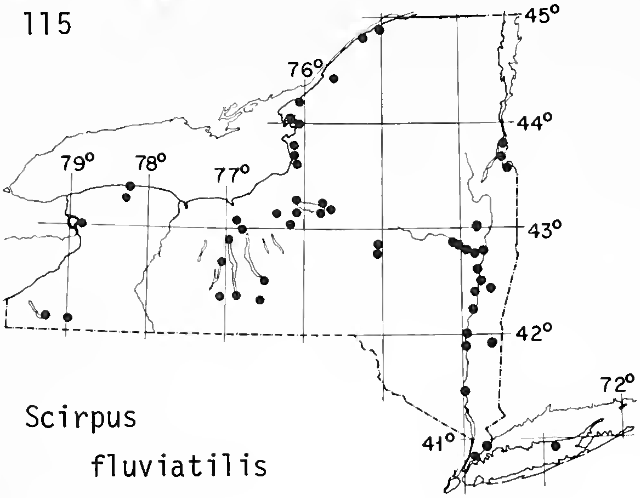
Scirpus
acutus

114



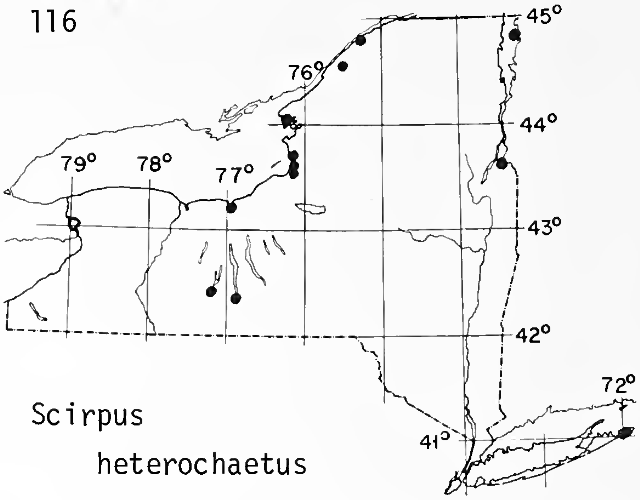
Scirpus
americanus

115



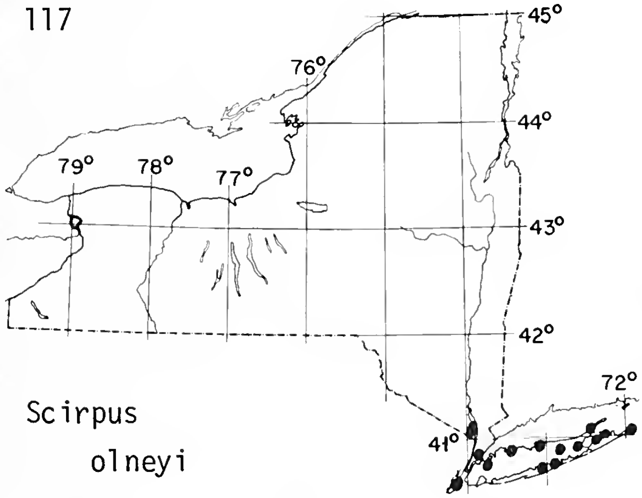
Scirpus fluviatilis

116



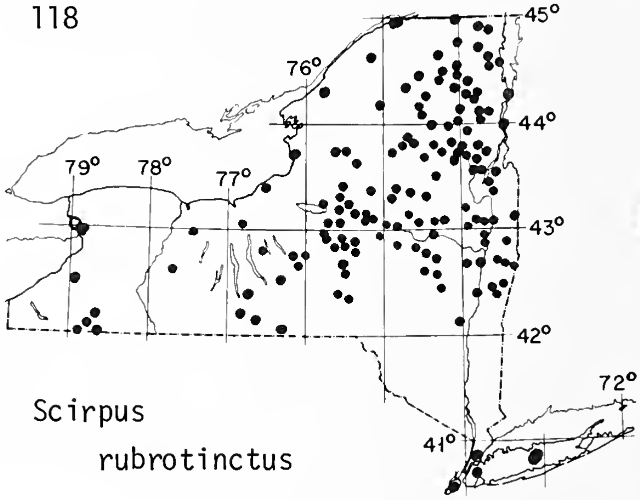
Scirpus heterochaetus

117



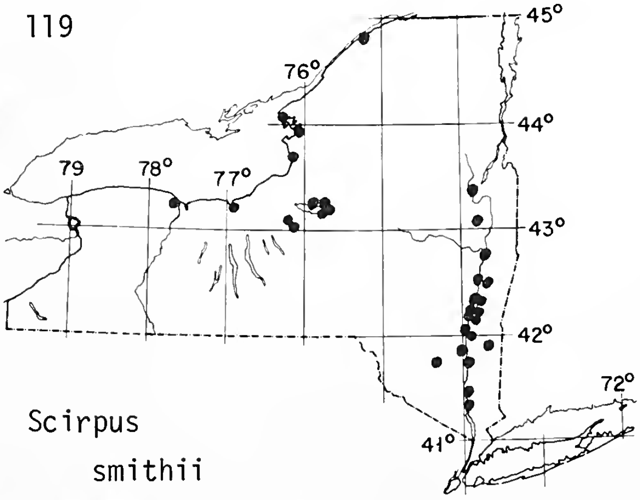
Scirpus olneyi

118



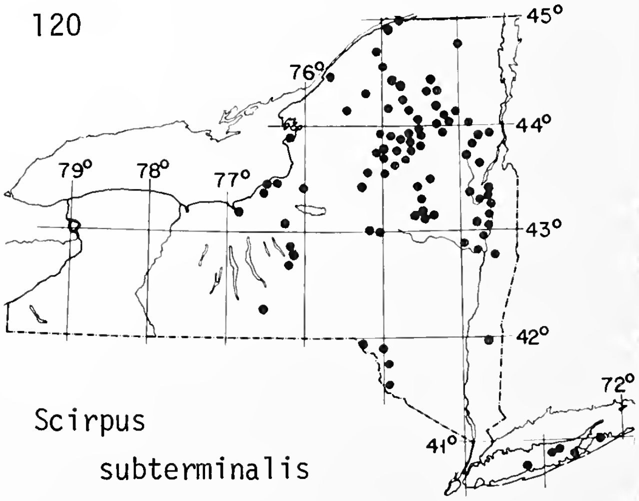
Scirpus rubrotinctus

119



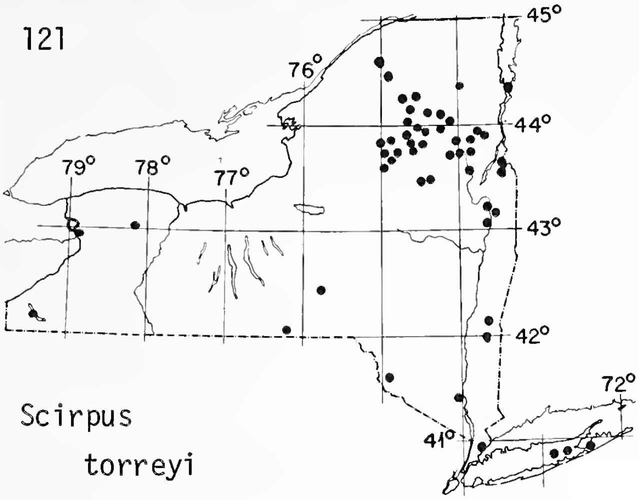
Scirpus smithii

120



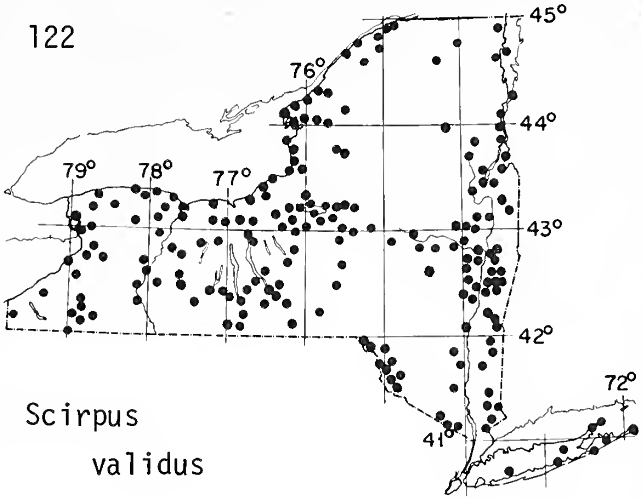
Scirpus subterminalis

121



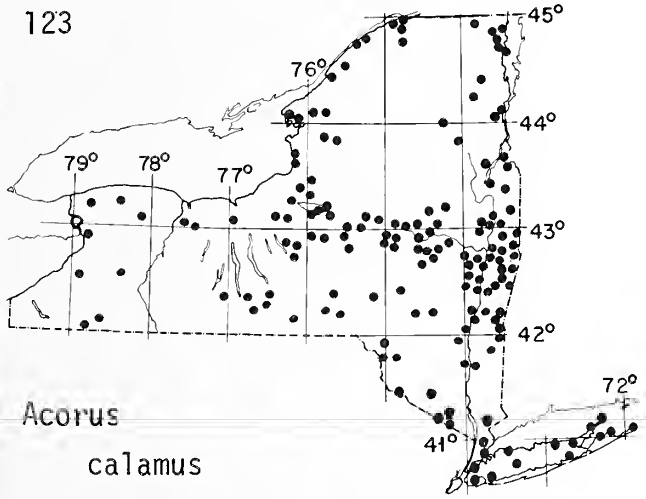
Scirpus
torreyi

122



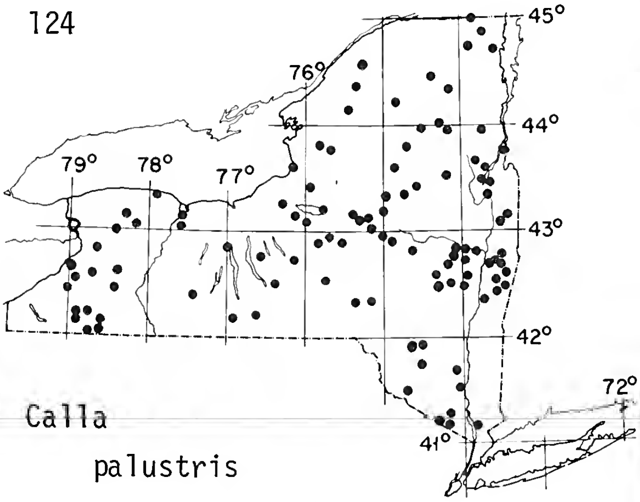
Scirpus
validus

123



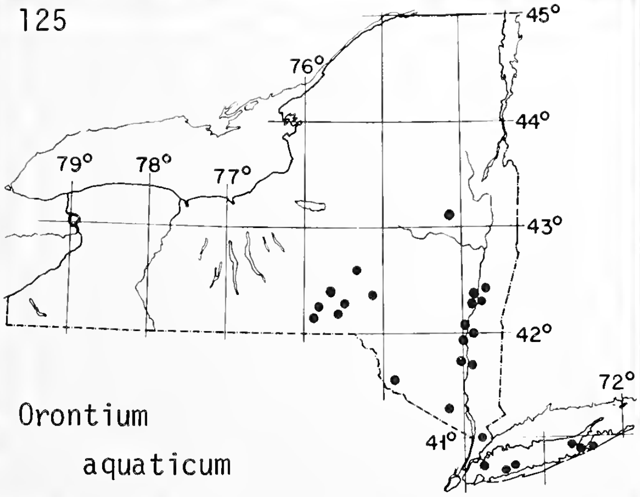
Acorus
calamus

124



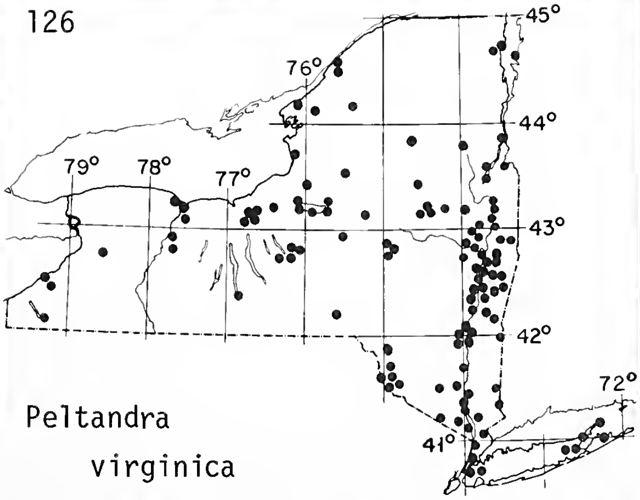
Calla
palustris

125



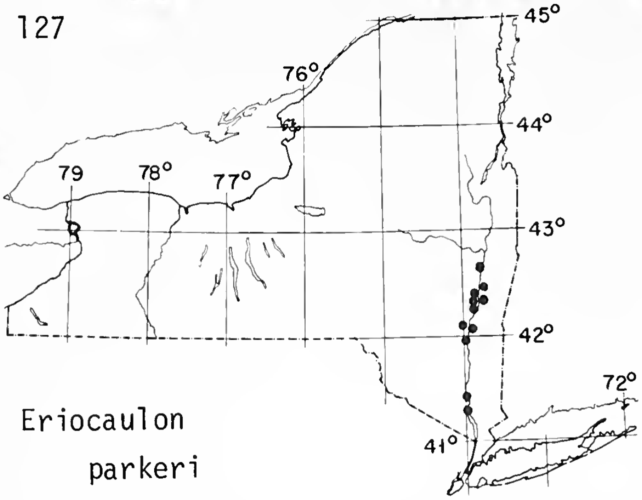
Orontium
aquaticum

126



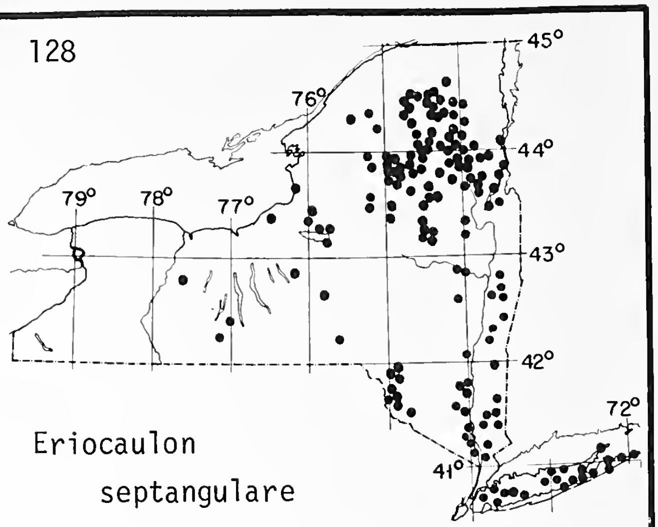
Peltandra
virginica

127



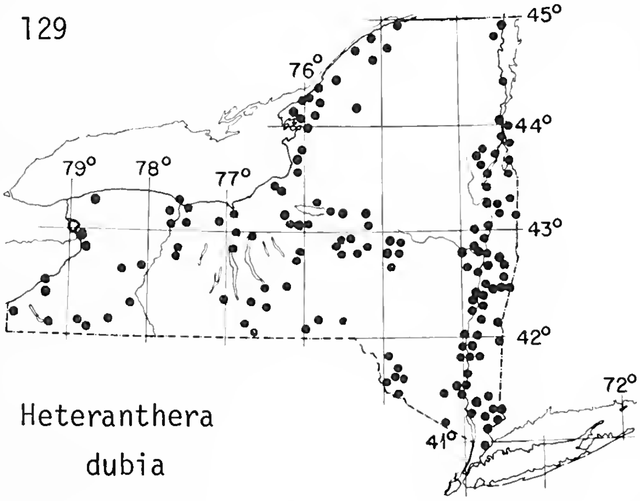
Eriocaulon parkeri

128



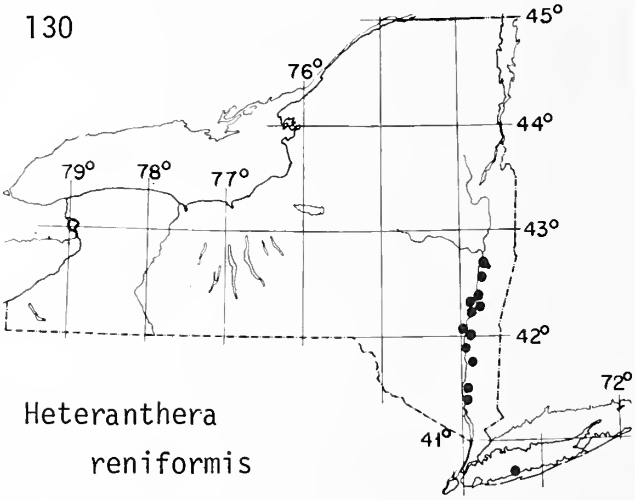
Eriocaulon septangulare

129



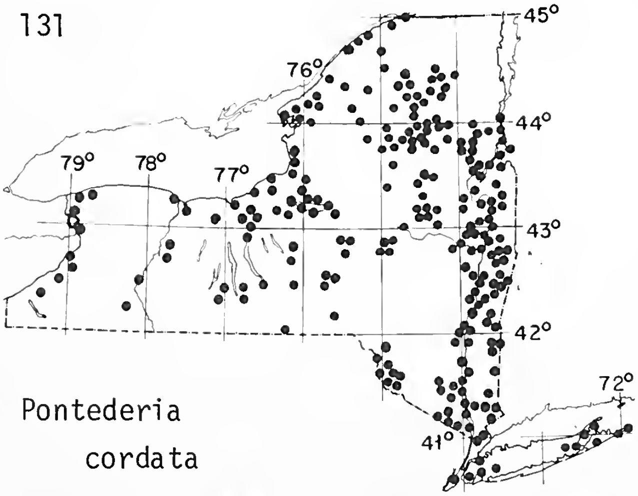
Heteranthera dubia

130



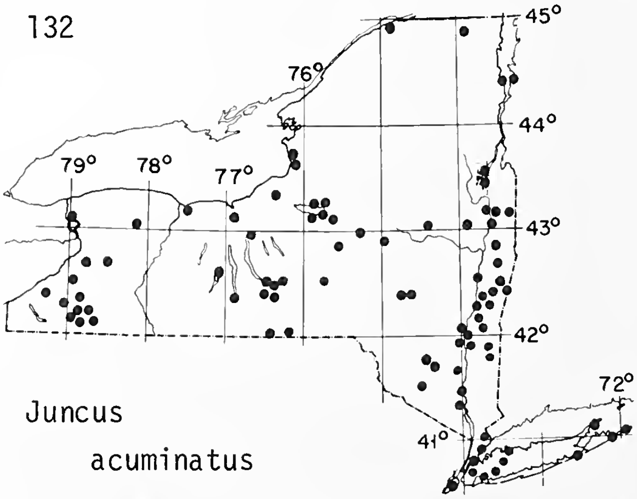
Heteranthera reniformis

131



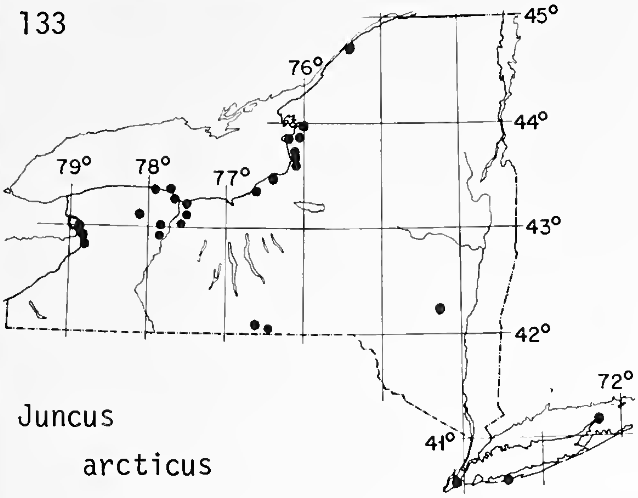
Pontederia cordata

132



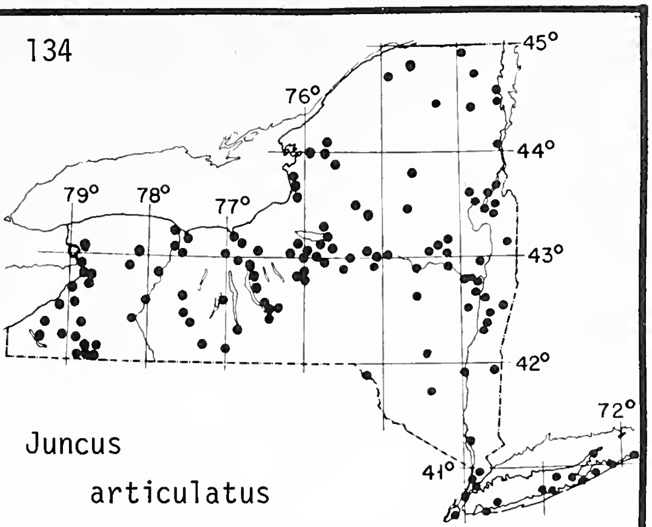
Juncus acuminatus

133



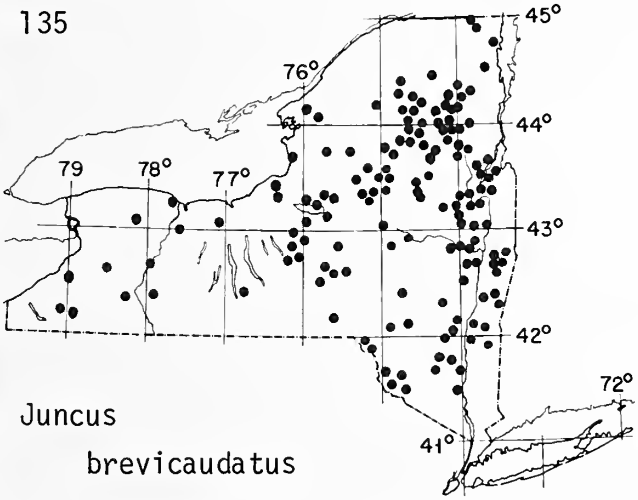
Juncus arcticus

134



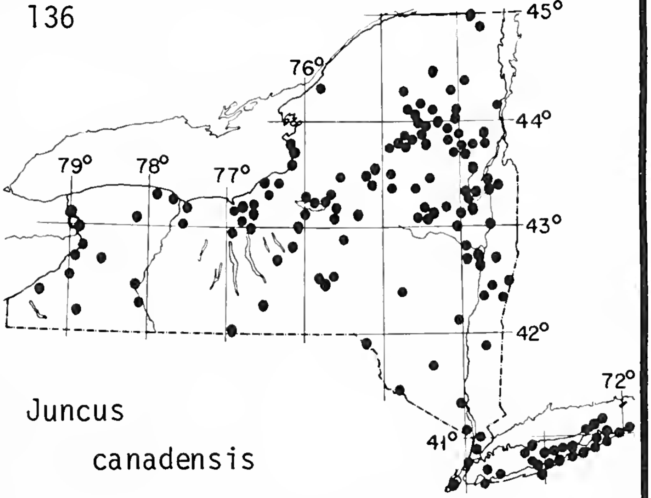
Juncus articulatus

135



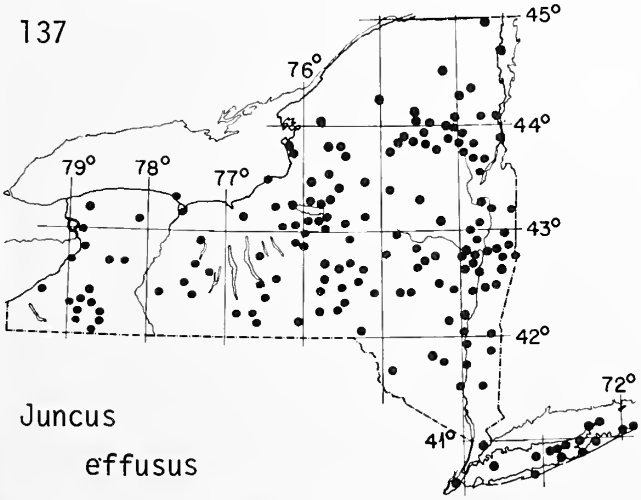
Juncus brevicaudatus

136



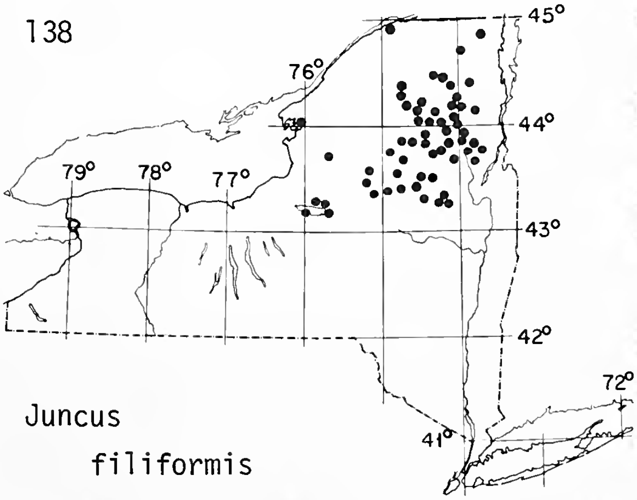
Juncus canadensis

137



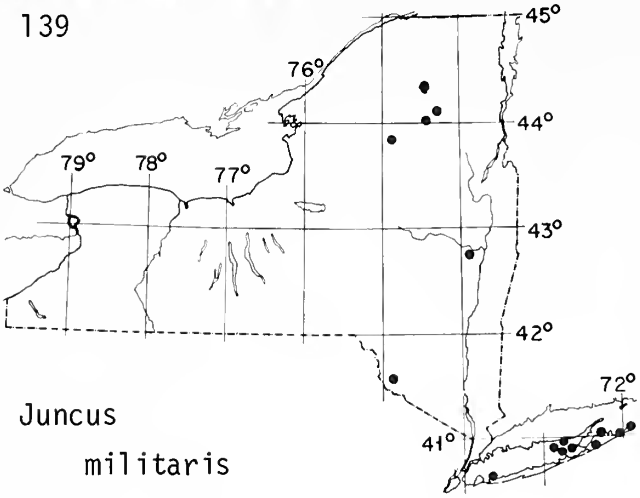
Juncus effusus

138



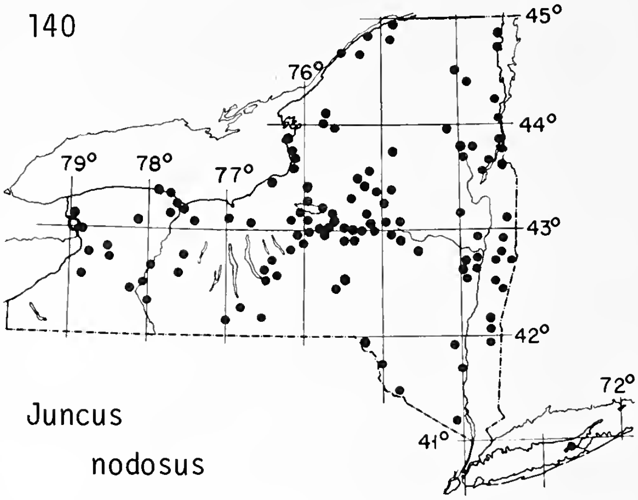
Juncus filiformis

139



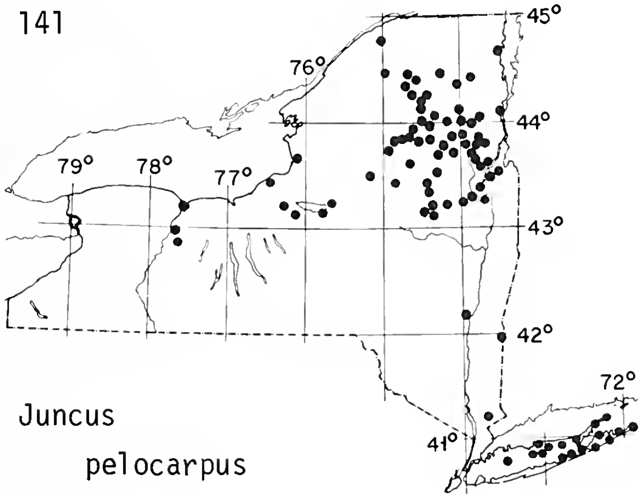
Juncus militaris

140



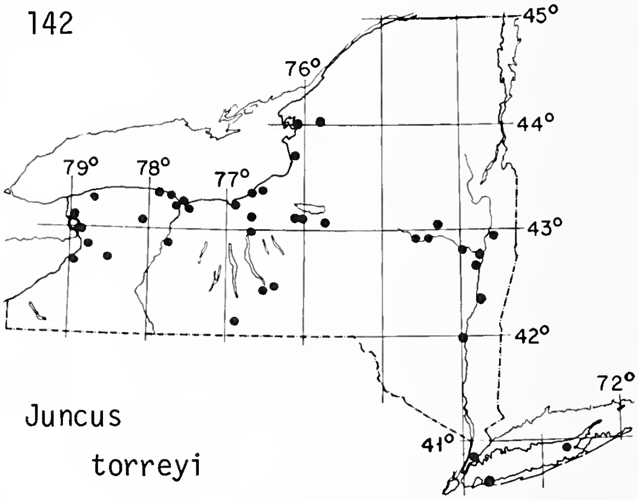
Juncus nodosus

141



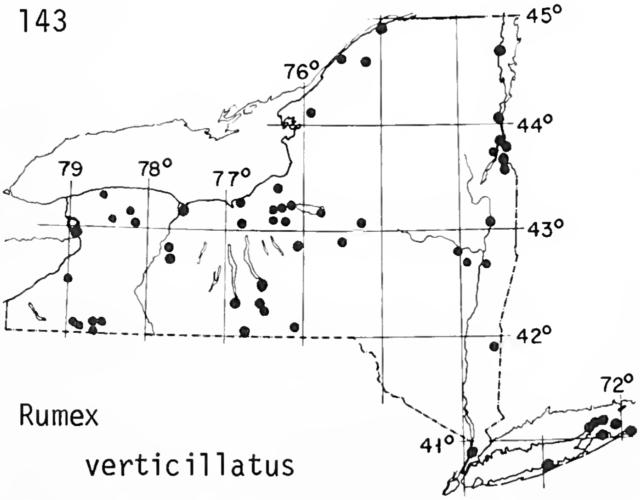
Juncus pelocarpus

142



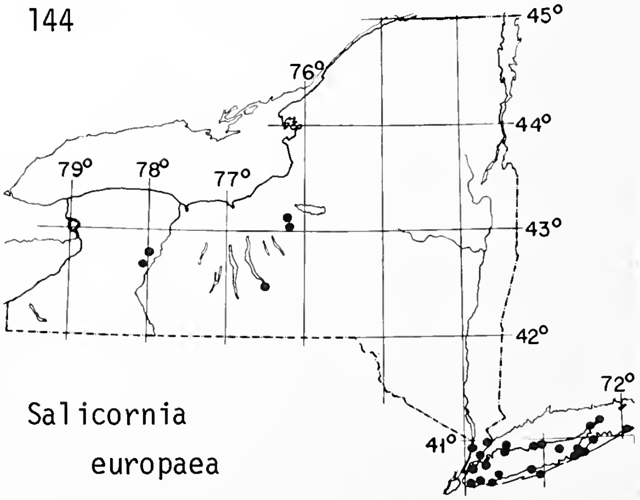
Juncus torreyi

143



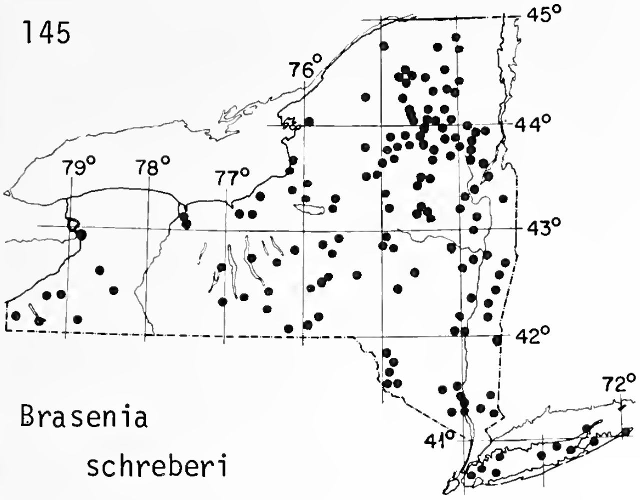
Rumex verticillatus

144



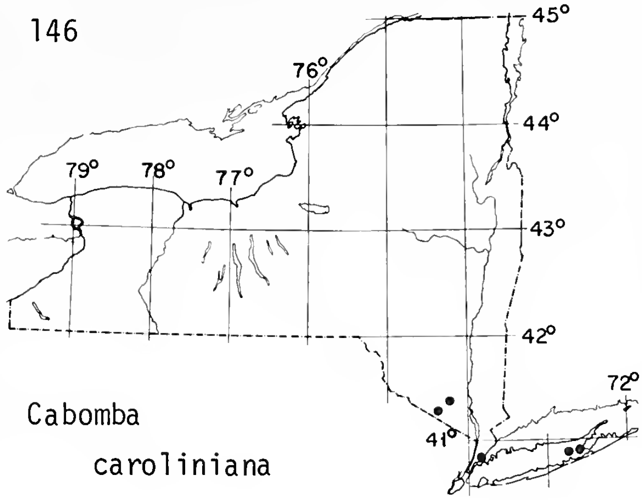
Salicornia europaea

145



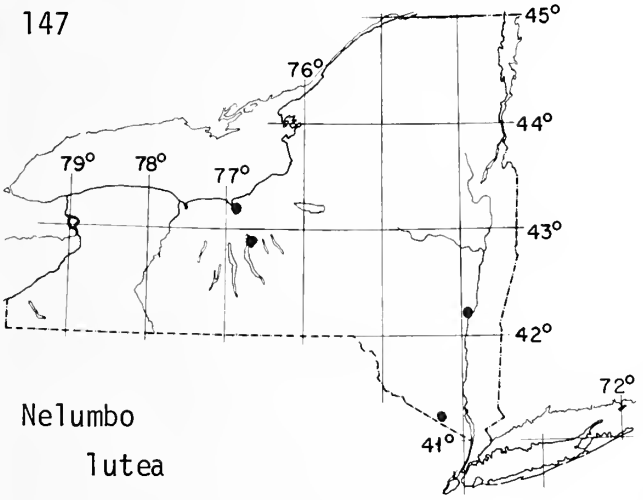
Brasenia
schreberi

146



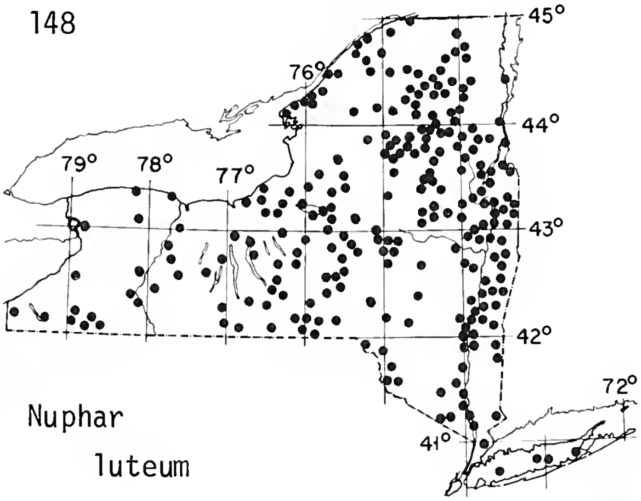
Cabomba
caroliniana

147



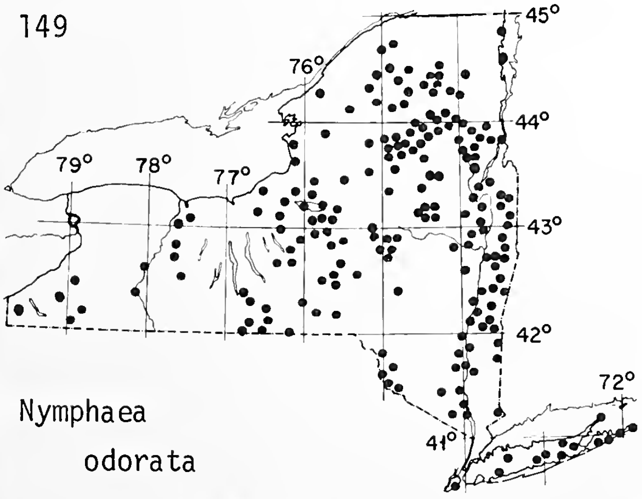
Nelumbo
lutea

148



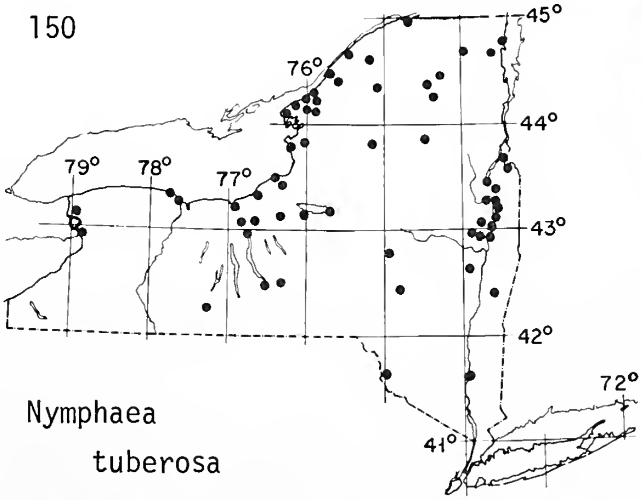
Nuphar
luteum

149



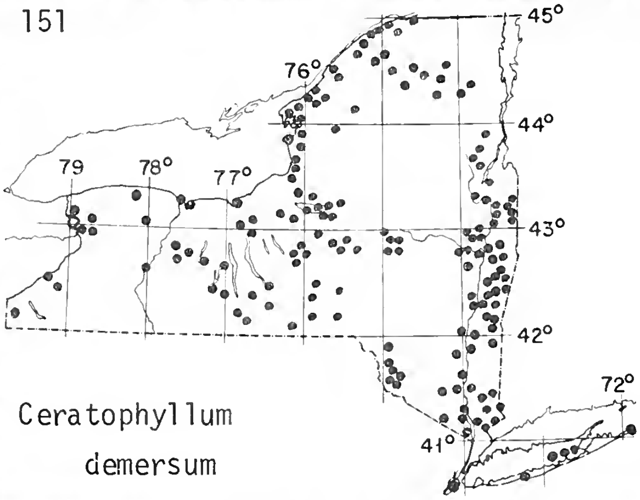
Nymphaea
odorata

150



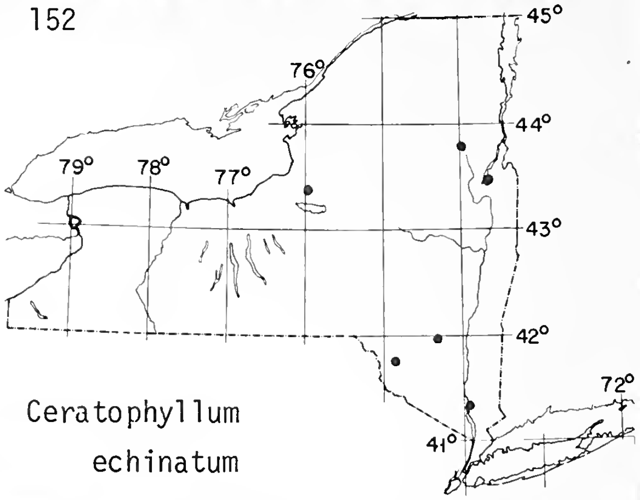
Nymphaea
tuberosa

151



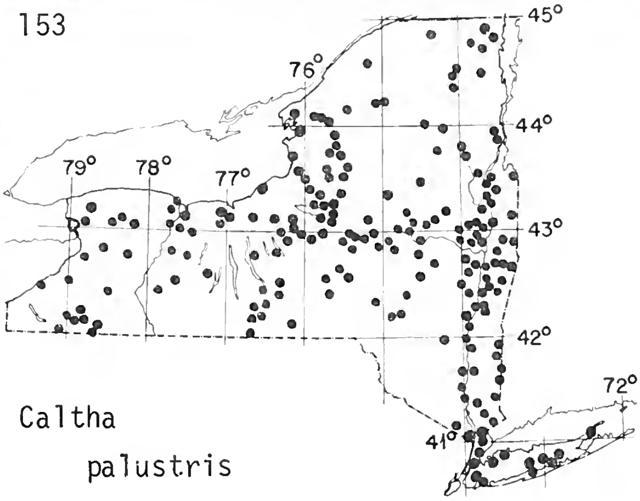
Ceratophyllum demersum

152



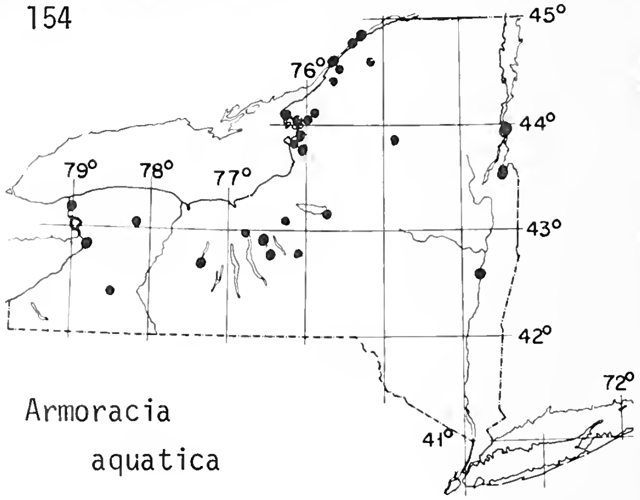
Ceratophyllum echinatum

153



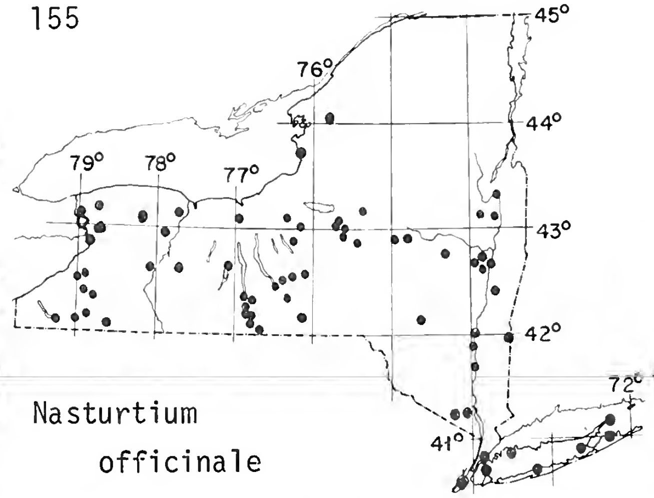
Caltha palustris

154



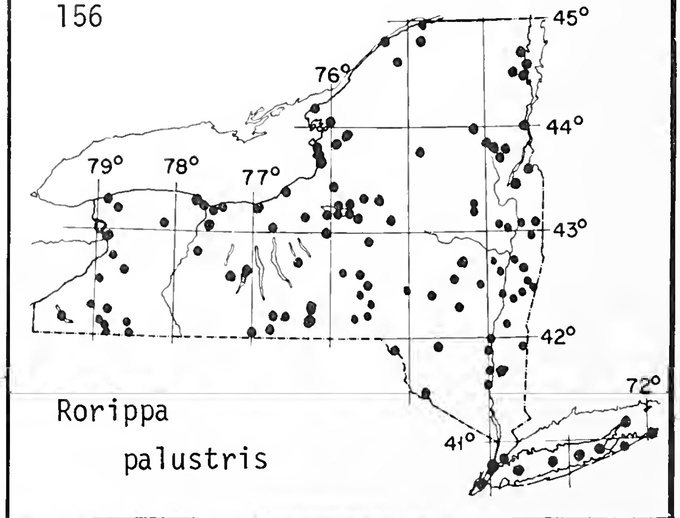
Armoracia aquatica

155

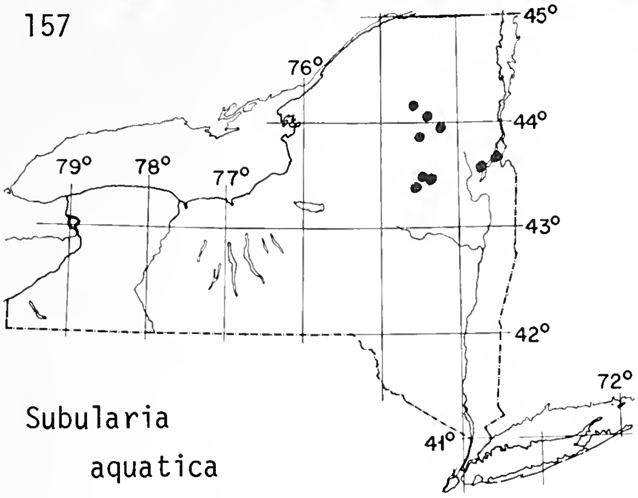


Nasturtium officinale

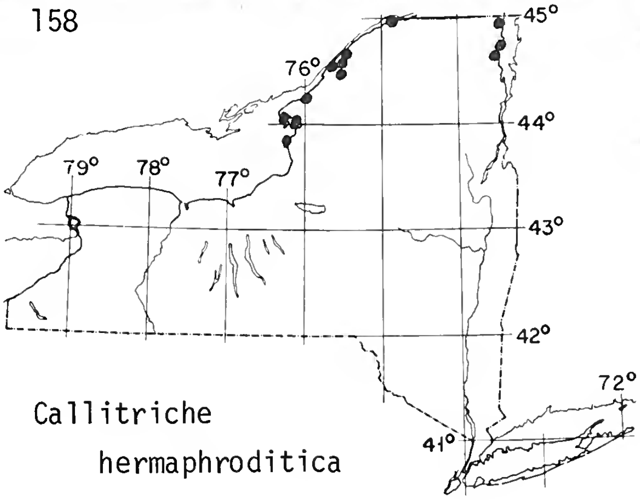
156



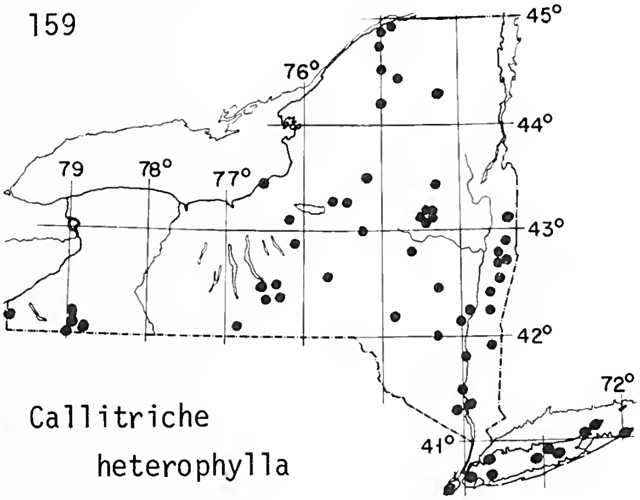
Rorippa palustris


157

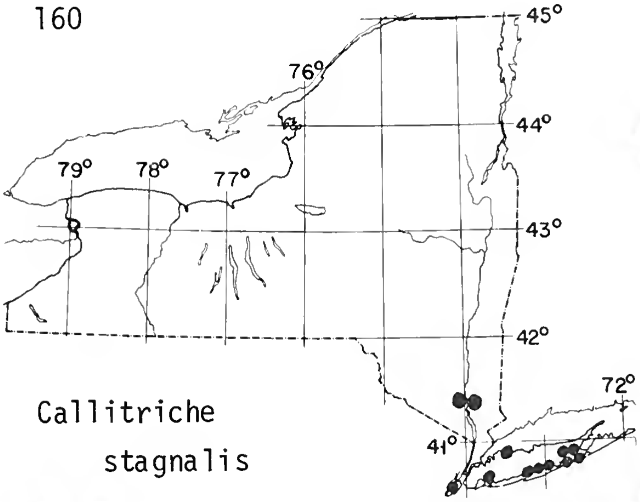
Subularia aquatica


158

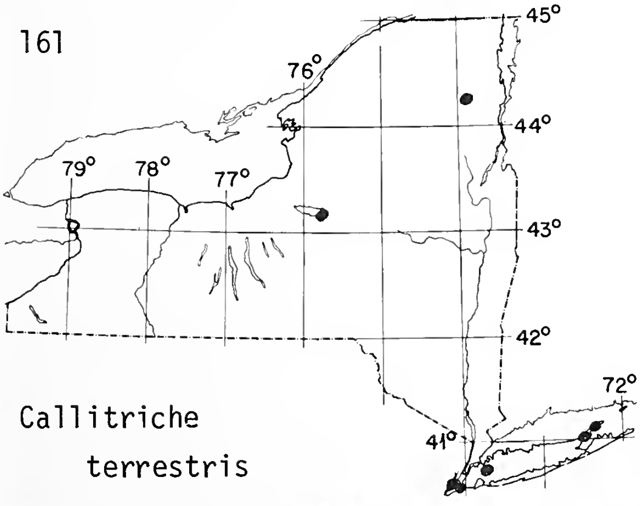
Callitriche hermaphroditica


159

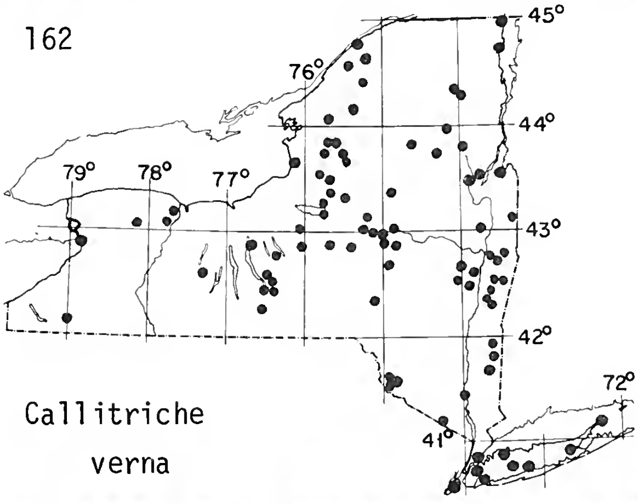
Callitriche heterophylla


160

Callitriche stagnalis

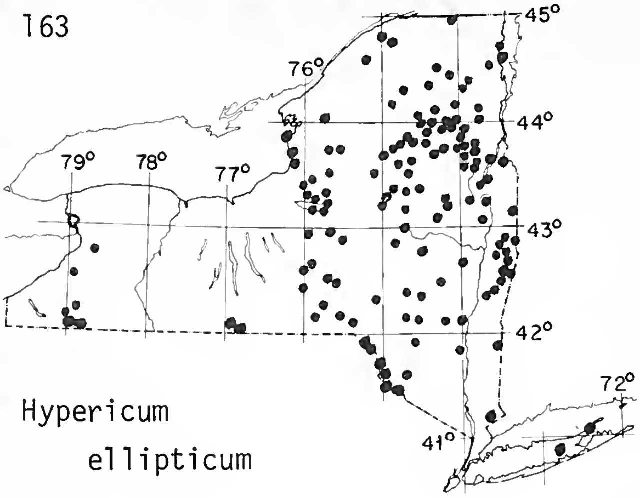

161

Callitriche terrestris


162

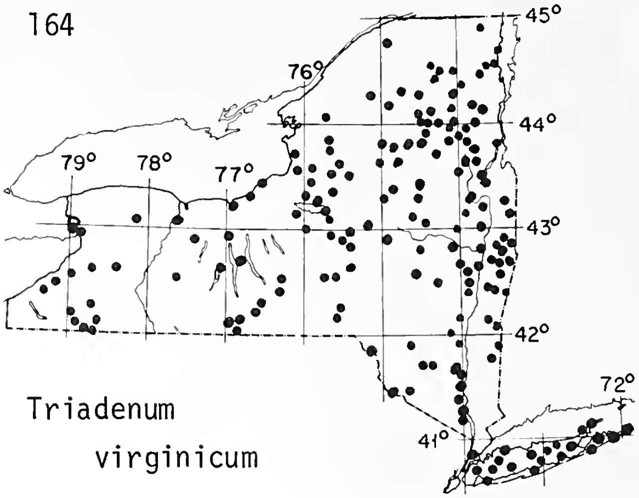
Callitriche verna

163



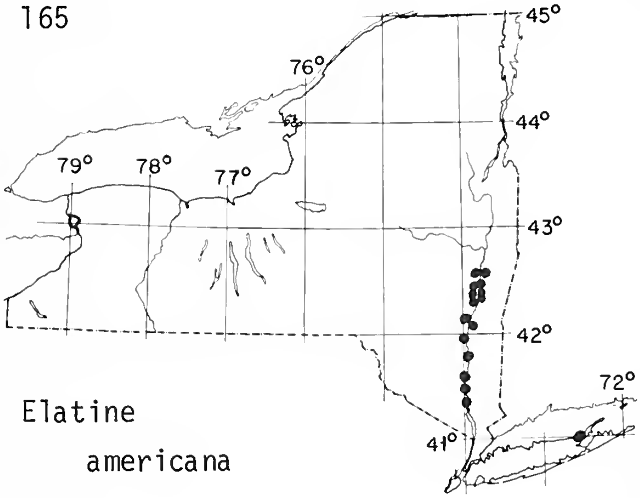
Hypericum ellipticum

164



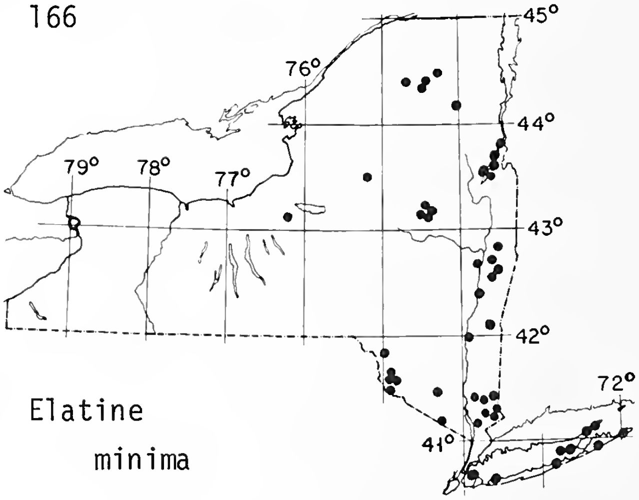
Triadenum virginicum

165



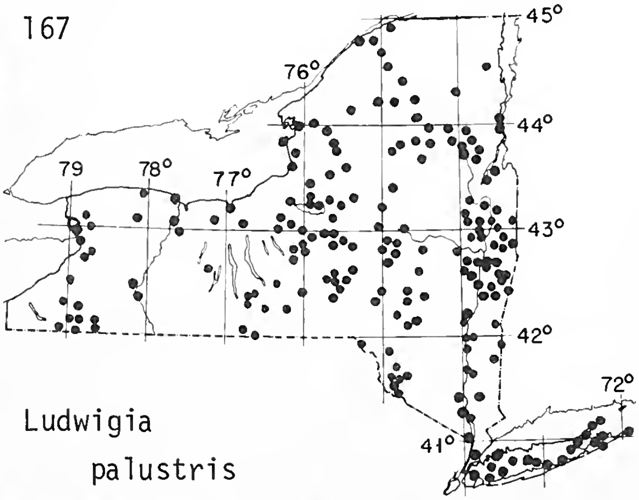
Elatine americana

166



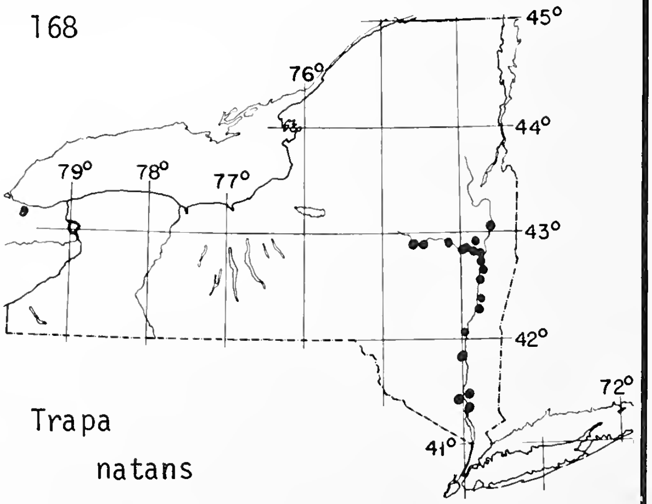
Elatine minima

167



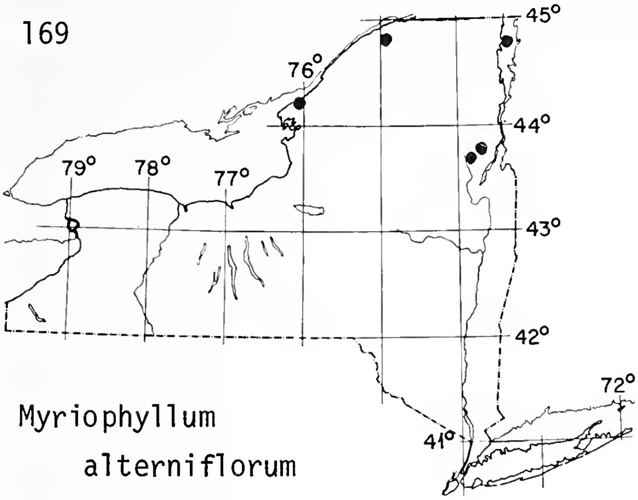
Ludwigia palustris

168



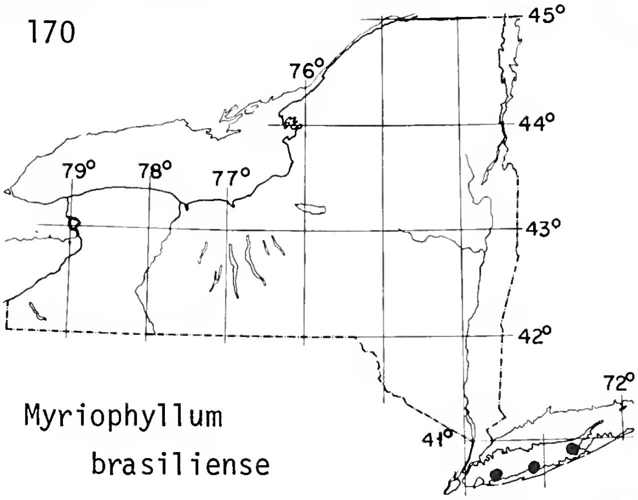
Trapa natans

169



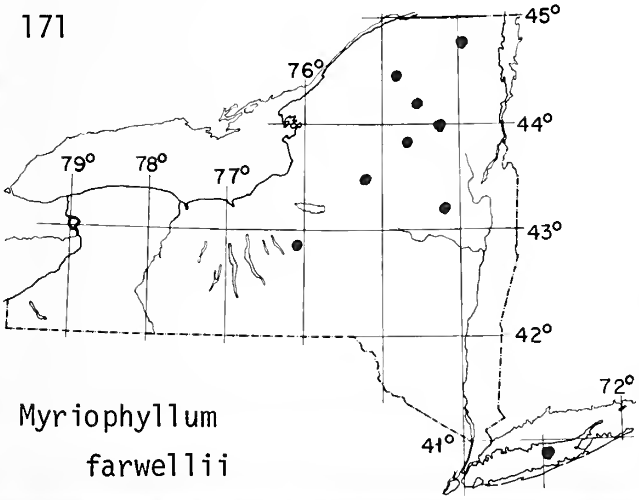
Myriophyllum alterniflorum

170



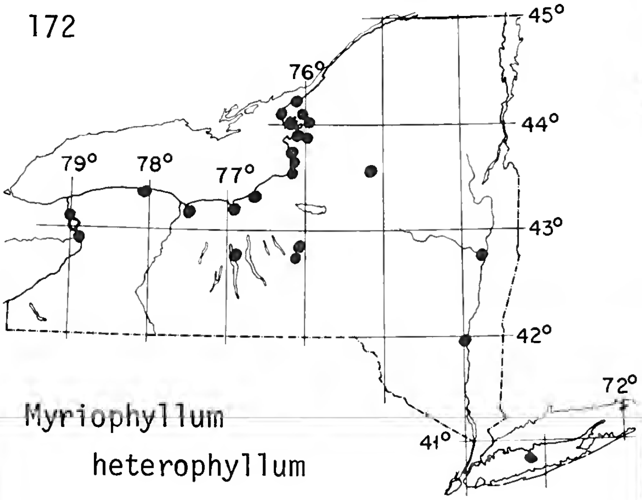
Myriophyllum brasiliense

171



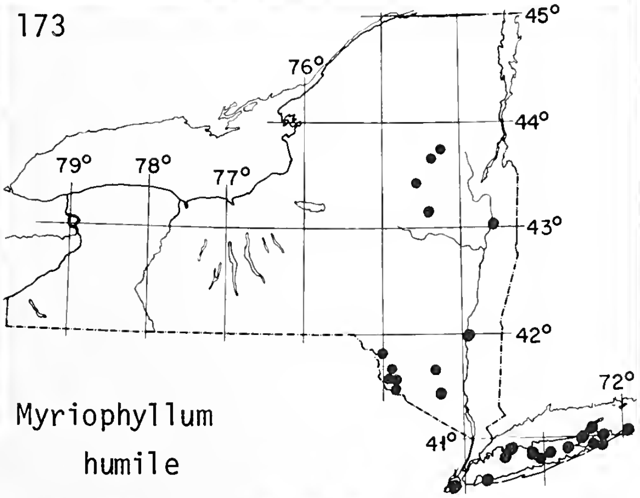
Myriophyllum farwellii

172



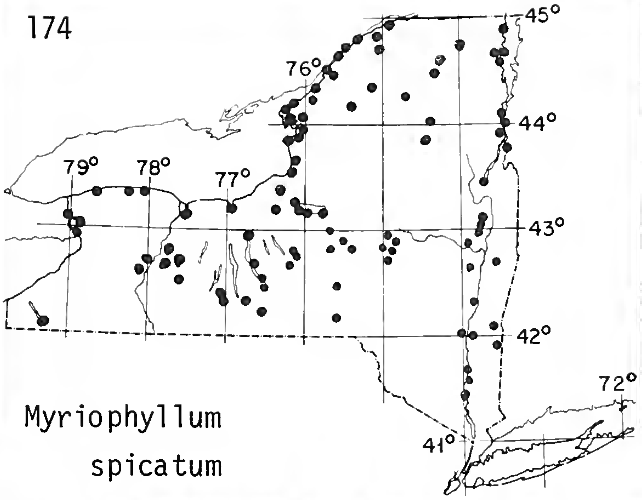
Myriophyllum heterophyllum

173



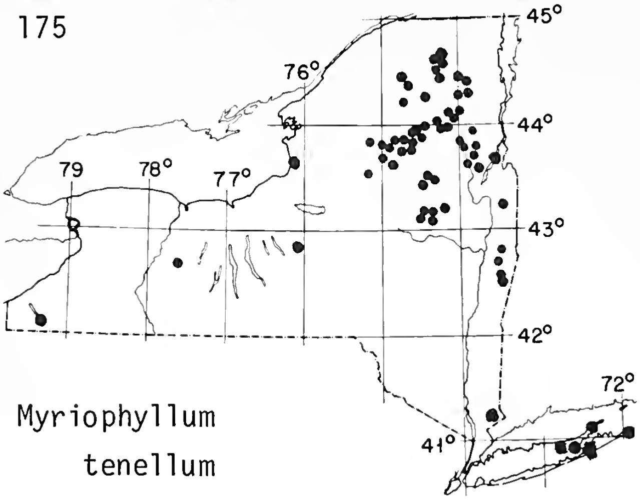
Myriophyllum humile

174



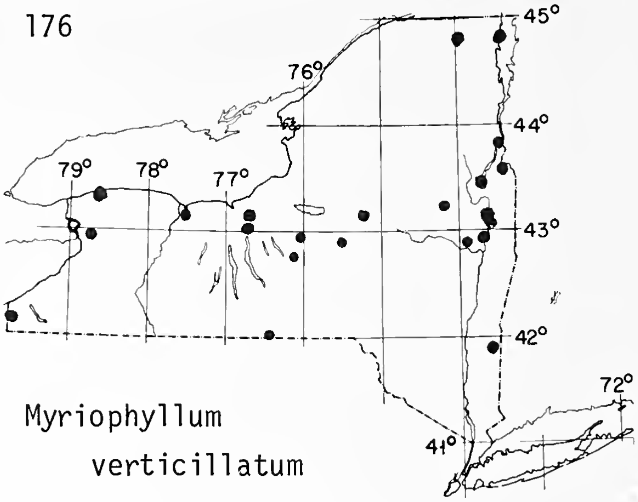
Myriophyllum spicatum

175



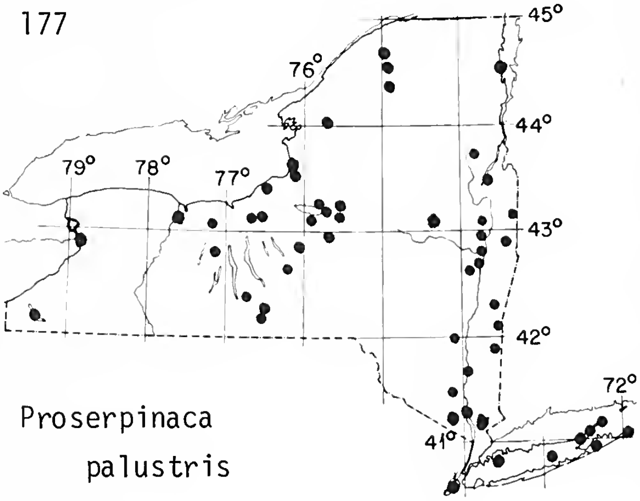
Myriophyllum tenellum

176



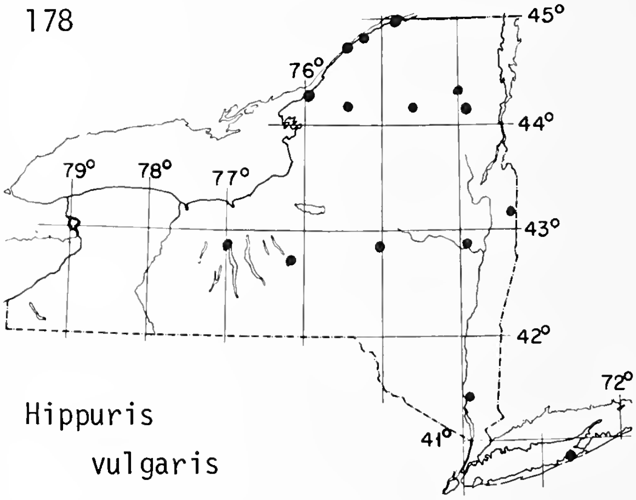
Myriophyllum verticillatum

177



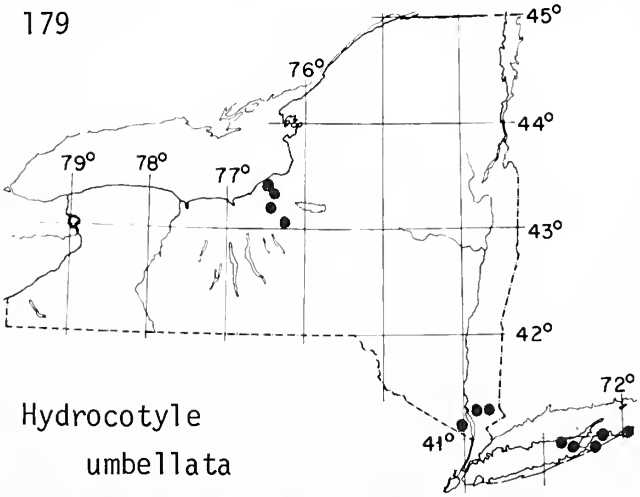
Proserpinaca palustris

178



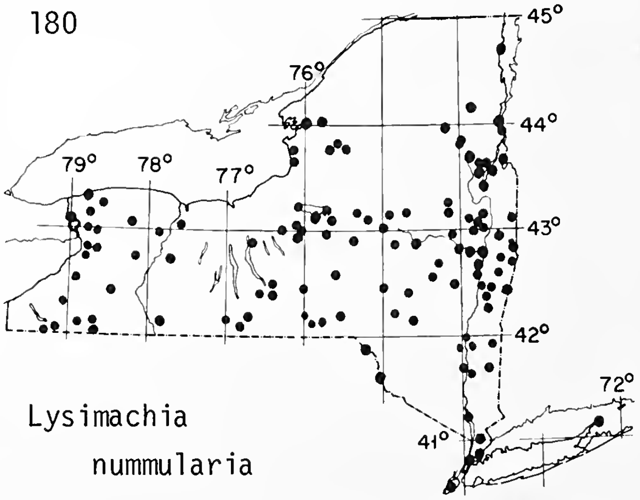
Hippuris vulgaris

179



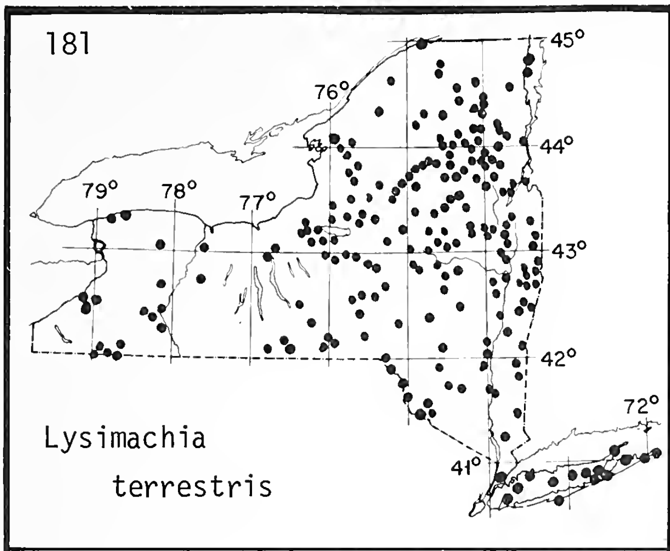
Hydrocotyle umbellata

180



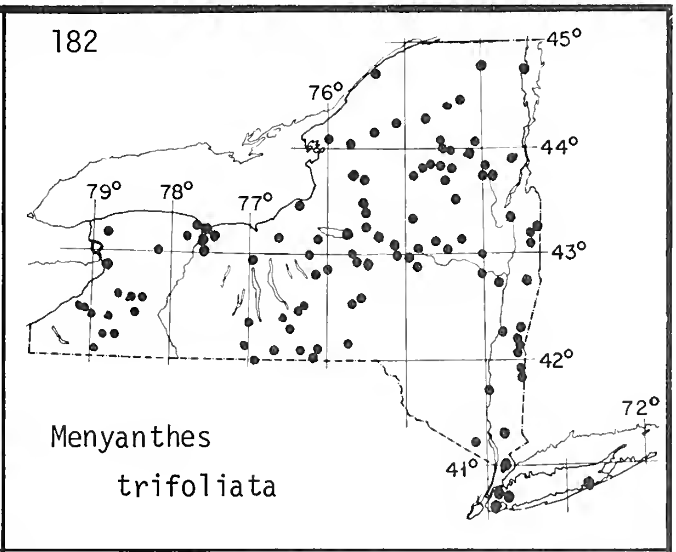
Lysimachia nummularia

181



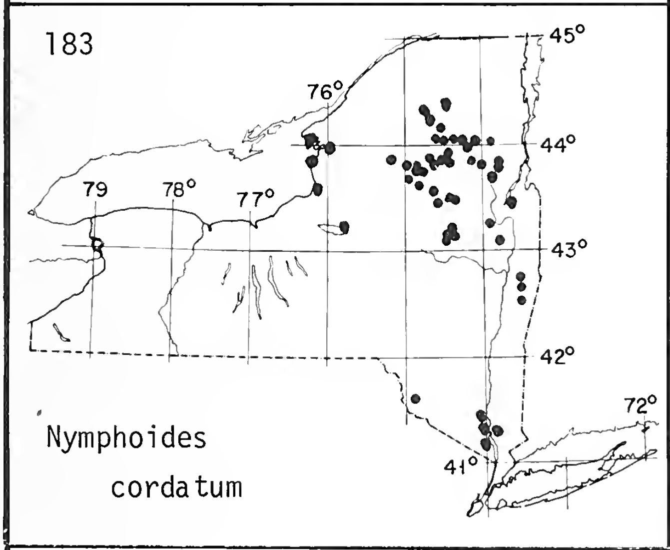
Lysimachia terrestris

182



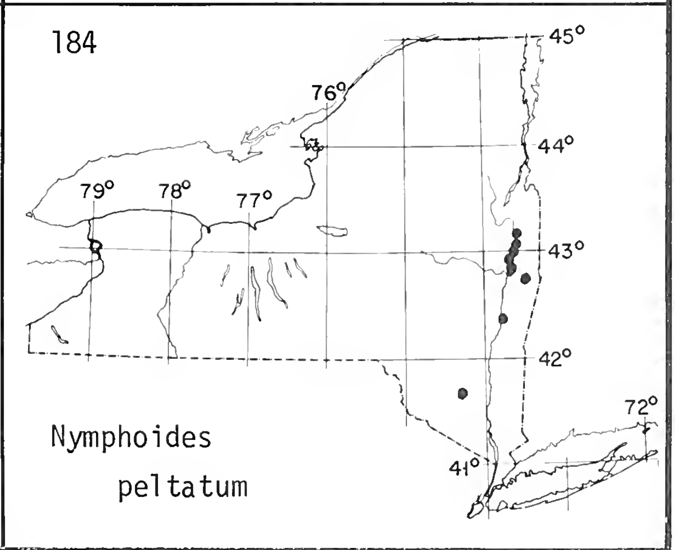
Menyanthes trifoliata

183



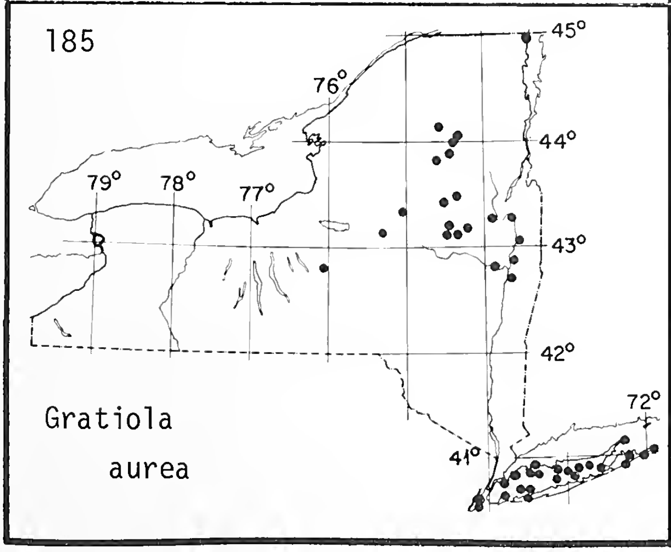
Nymphoides cordatum

184



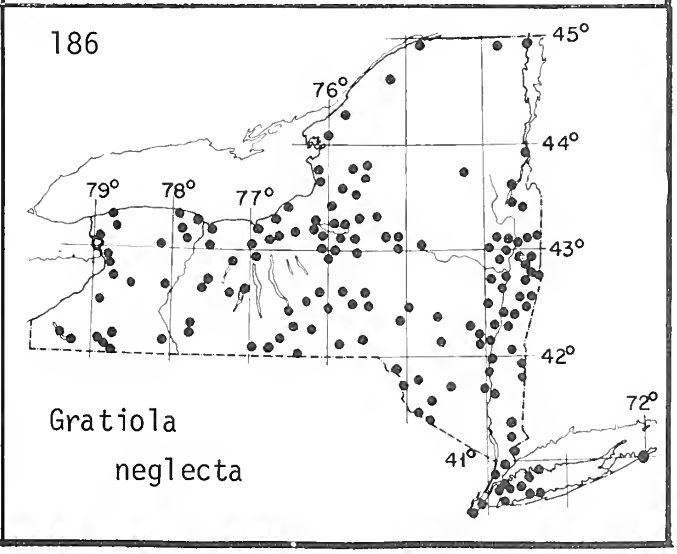
Nymphoides peltatum

185



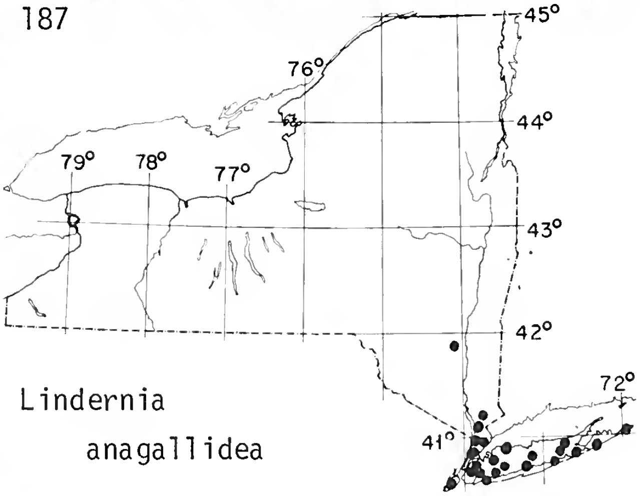
Gratiola aurea

186



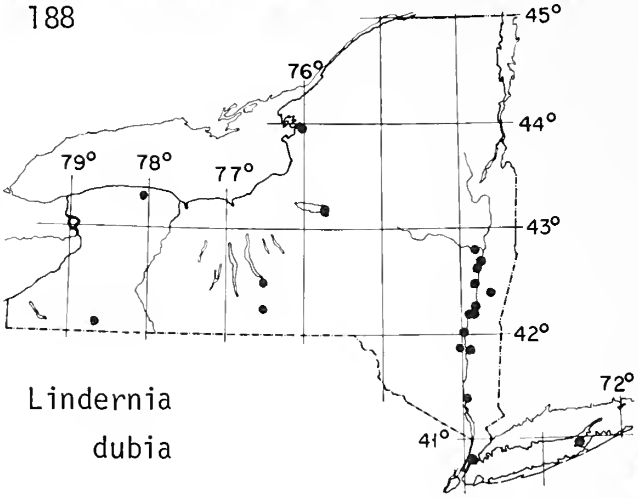
Gratiola neglecta

187



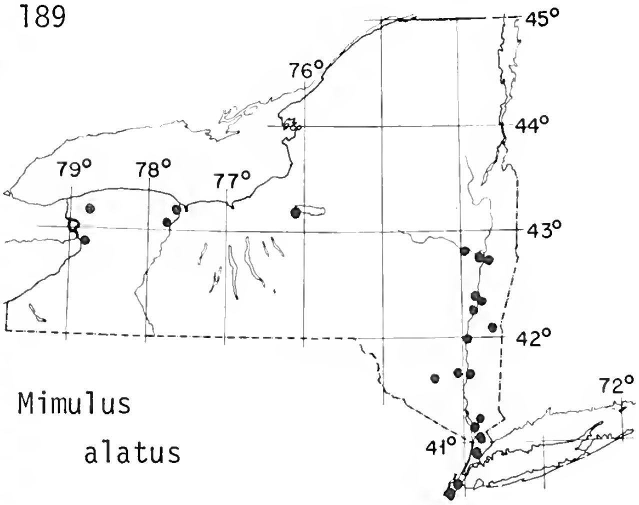
Lindernia anagallidea

188



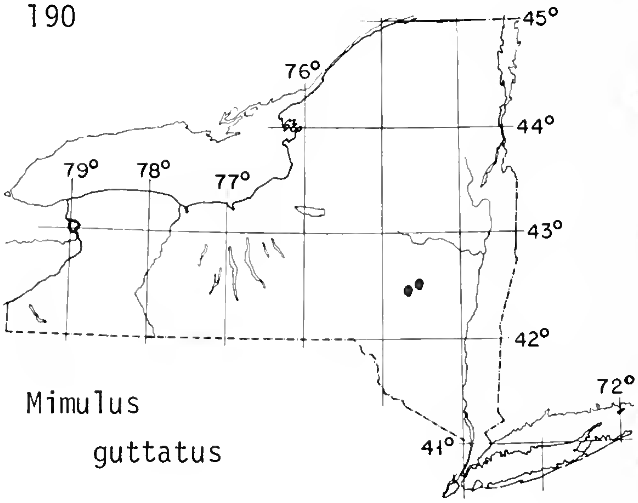
Lindernia dubia

189



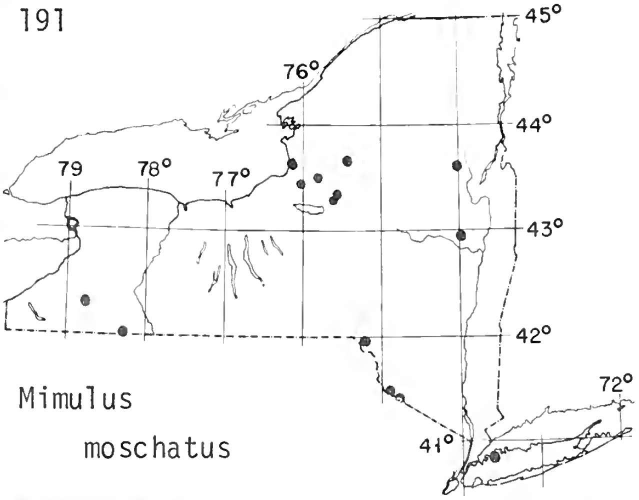
Mimulus alatus

190



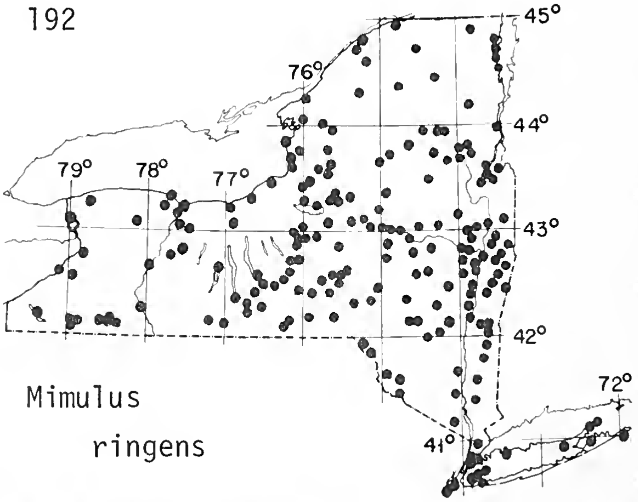
Mimulus guttatus

191



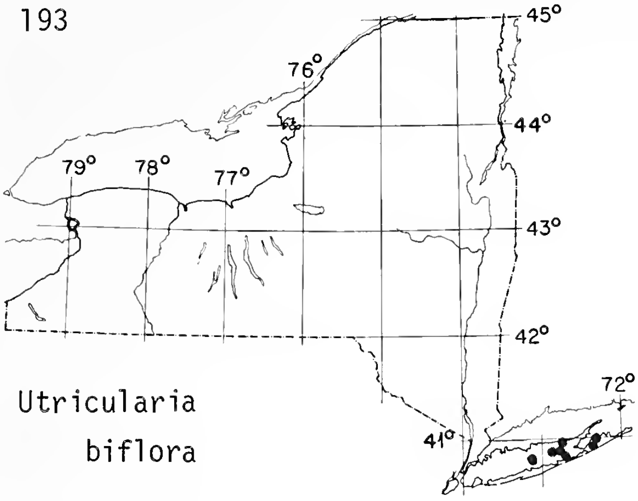
Mimulus moschatus

192



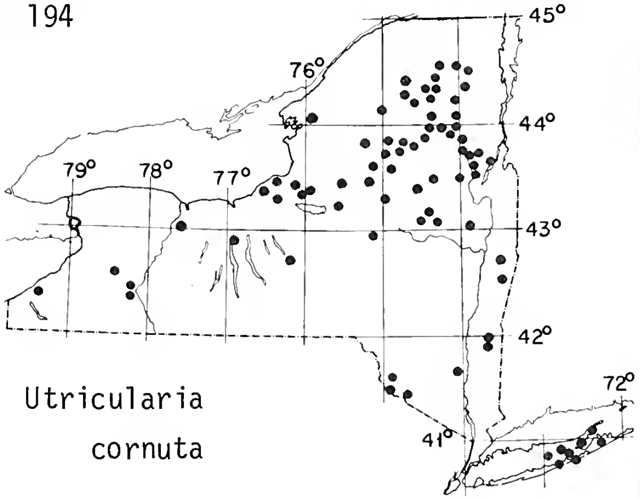
Mimulus ringens

193



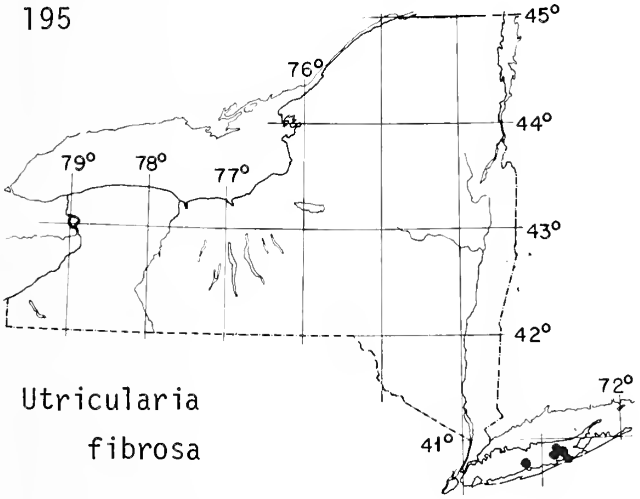
Utricularia biflora

194



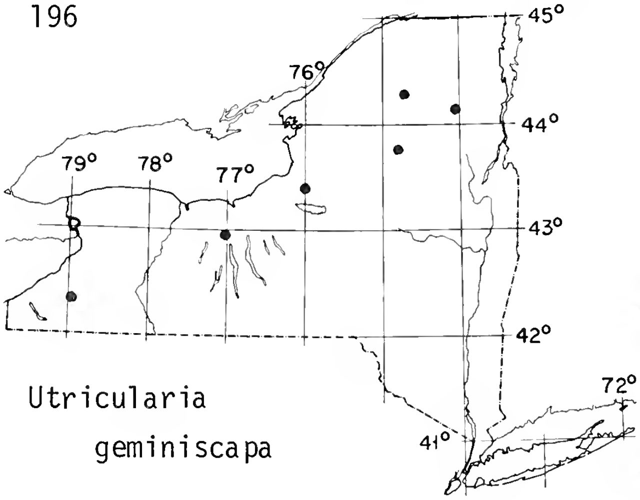
Utricularia cornuta

195



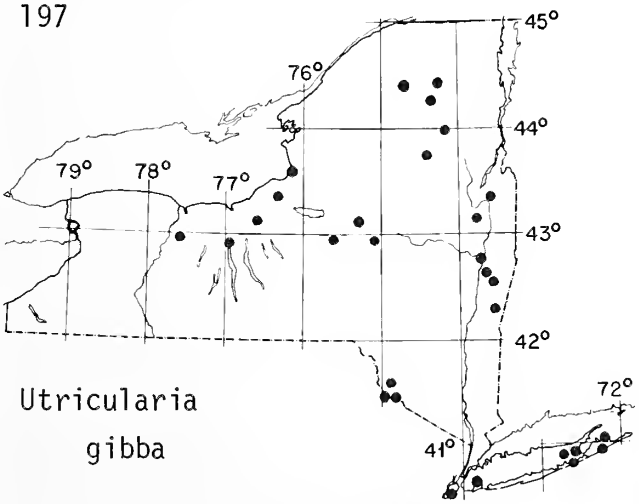
Utricularia fibrosa

196



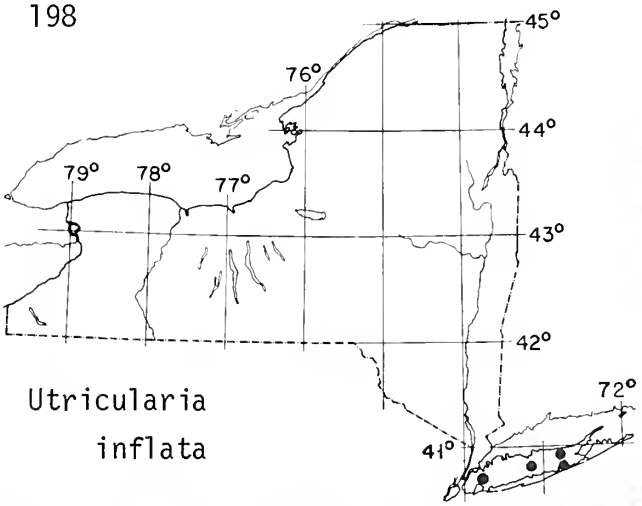
Utricularia geminiscapa

197



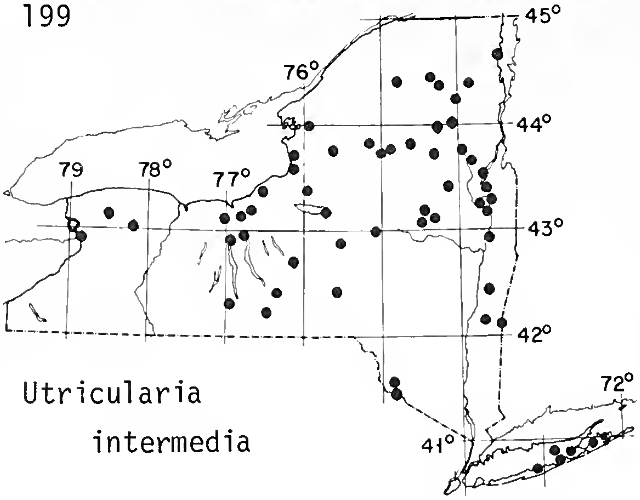
Utricularia gibba

198



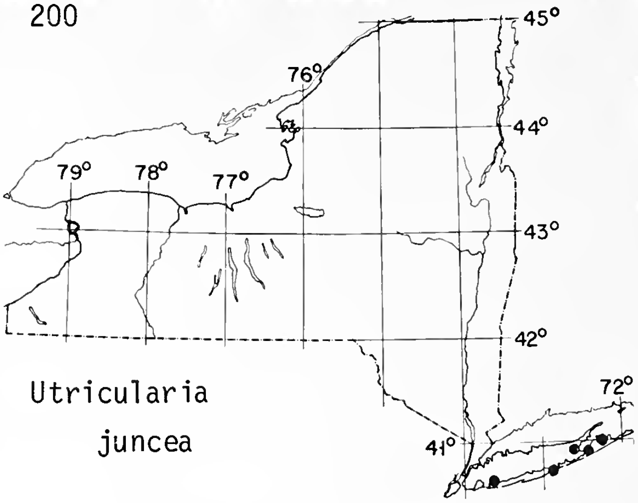
Utricularia inflata

199



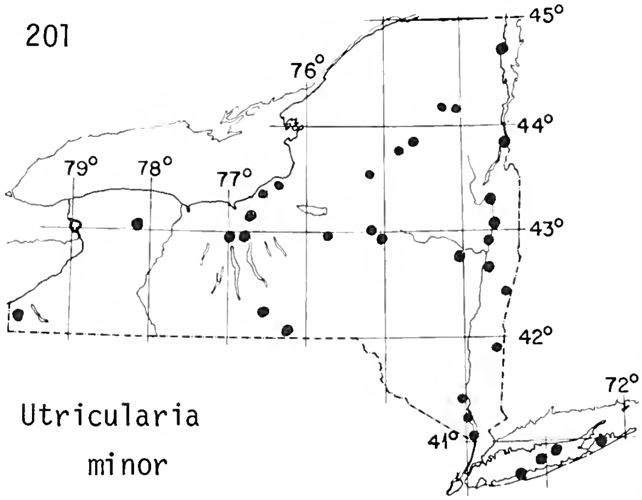
Utricularia intermedia

200



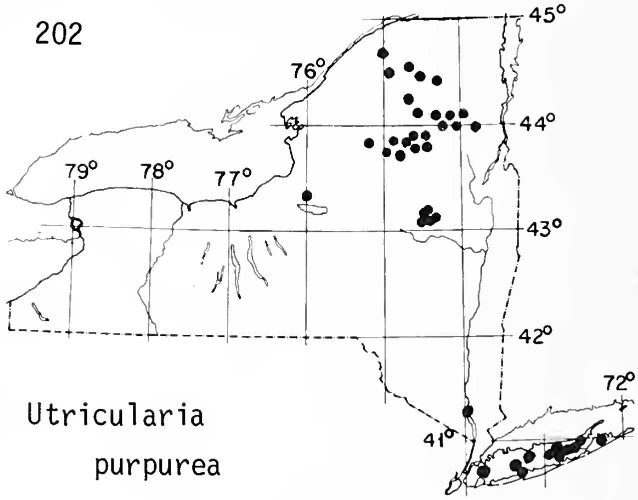
Utricularia juncea

201



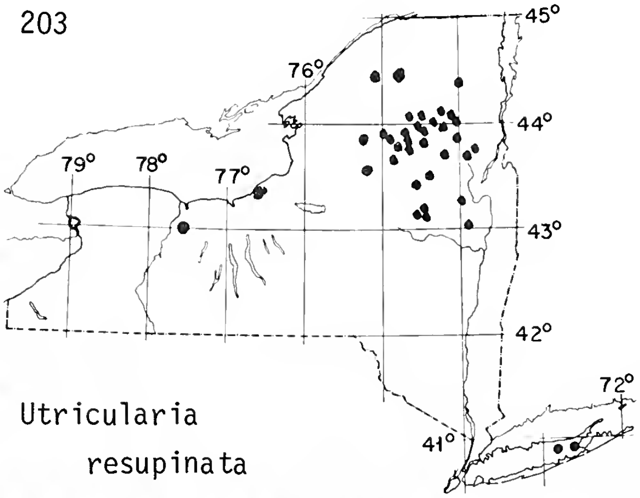
Utricularia minor

202



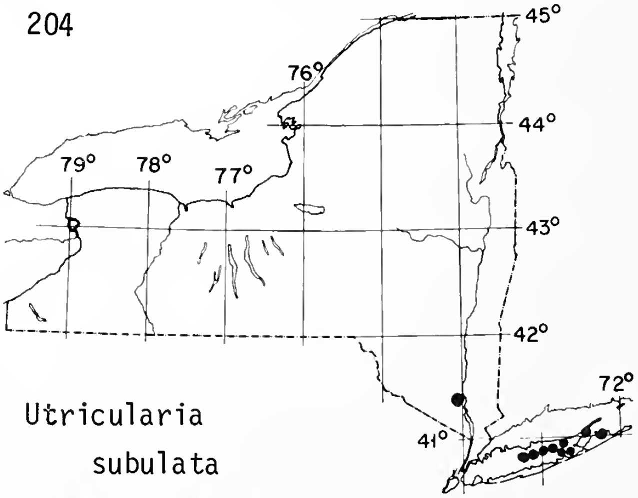
Utricularia purpurea

203



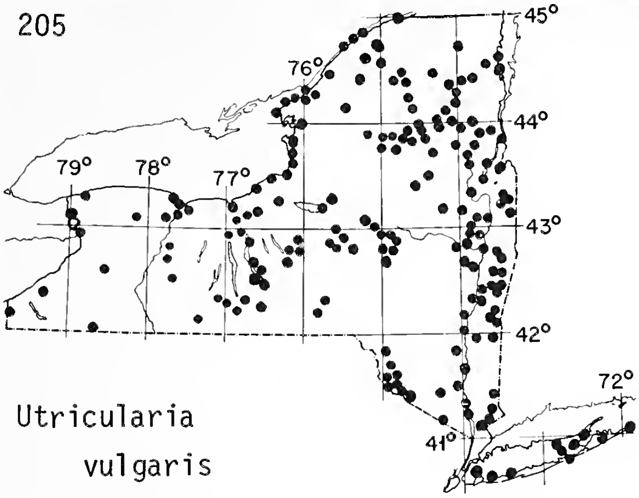
Utricularia resupinata

204



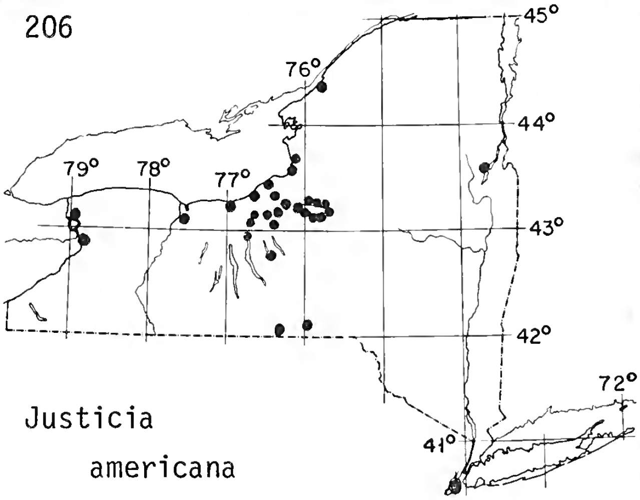
Utricularia subulata

205



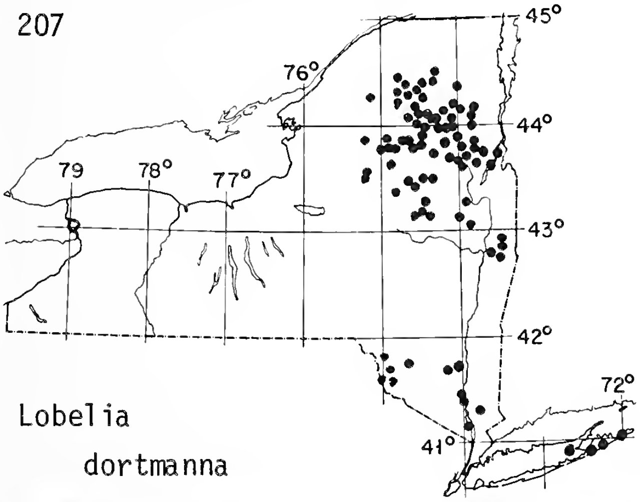
Utricularia vulgaris

206



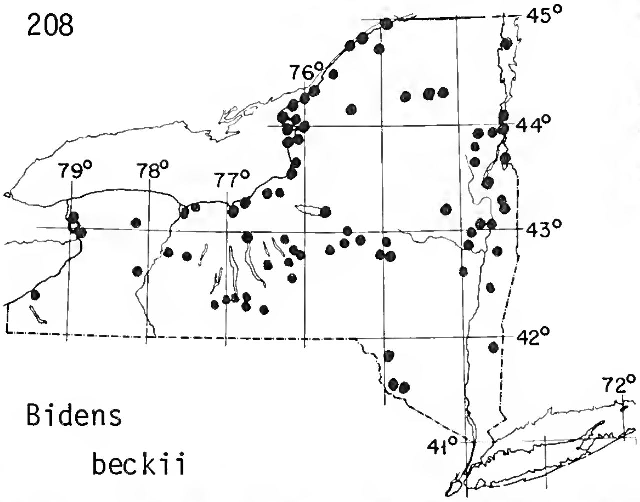
Justicia americana

207



Lobelia dortmanna

208

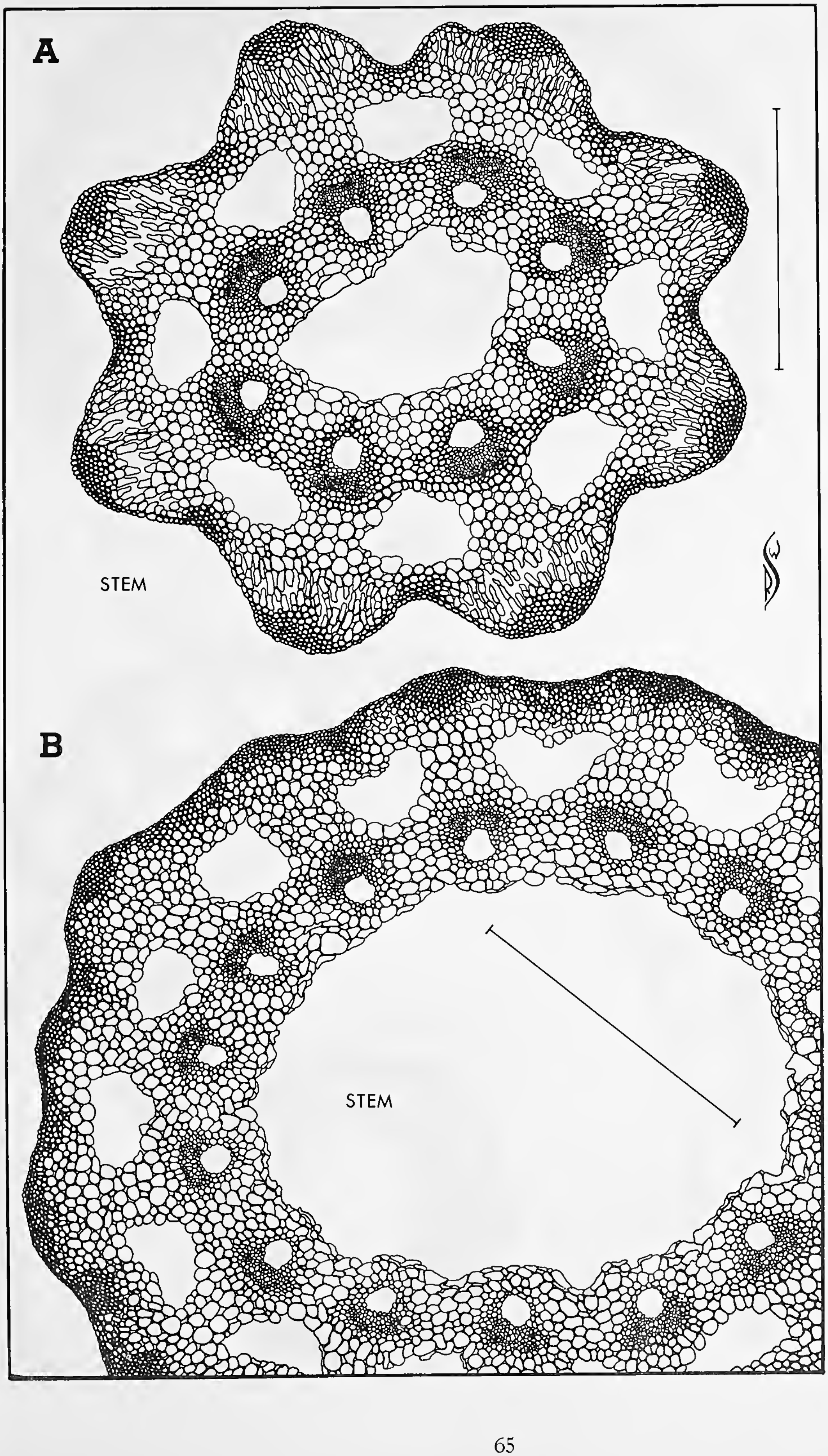


Bidens beckii

Plates of Drawings

1. Equisetum arvense
   Equisetum sylvaticum
2. Equisetum fluviatile
   Equisetum hyemale
3. Equisetum variegatum
   Equisetum scirpoides
4. Isoetes echinospora
5. Marsilea quadrifolia
6. Sparganium americanum
7. Sparganium angustifolium
8. Potamogeton crispus
   Potamogeton foliosus
9. Potamogeton gramineus
10. Potamogeton natans
11. Potamogeton pectinatus
12. Potamogeton perfoliatus
13. Potamogeton pulcher
14. Potamogeton zosteriformis
15. Ruppia maritima
16. Zannichellia palustris
17. Najas flexilis
18. Scheuchzeria palustris
19. Alisma plantago-aquatica
20. Sagittaria latifolia
21. Sagittaria latifolia
22. Butomus umbellatus
23. Butomus umbellatus
24. Elodea canadensis
25. Vallisneria americana
26. Carex comosa
   Fuirena squarosa
27. Cladium mariscoides
28. Dulichium arundinaceum
29. Eleocharis palustris
30. Eriophorum vaginatum
31. Rhynchospora alba
32. Scirpus americanus
33. Scirpus validus
34. Acorus calamus
35. Calla palustris
36. Peltandra virginica
37. Eriocaulon septangulare
38. Heteranthera dubia
39. Pontederia cordata
40. Juncus articulatus
41. Juncus effusus
42. Brasenia schreberi
43. Cabomba caroliniana
44. Nuphar luteum
45. Nymphaea odorata
46. Ceratophyllum demersum
47. Caltha palustris
48. Armoracia aquatica
49. Nasturtium officinale
50. Hypericum ellipticum
   Triadenum virginicum
51. Ludwigia palustris
52. Trapa natans
53. Trapa natans
54. Myriophyllum brasiliense
55. Myriophyllum spicatum
56. Hippuris vulgaris
   Proserpinaca palustris
57. Hydrocotyle umbellata
58. Lysimachia terrestris
59. Menyanthes trifoliata
60. Nymphoides cordatum
   Nymphoides peltatum
61. Gratiola aurea
62. Lindernia dubia
63. Mimulus ringens
64. Utricularia vulgaris
65. Justicia americana
66. Lobelia dortmanna
67. Bidens beckii

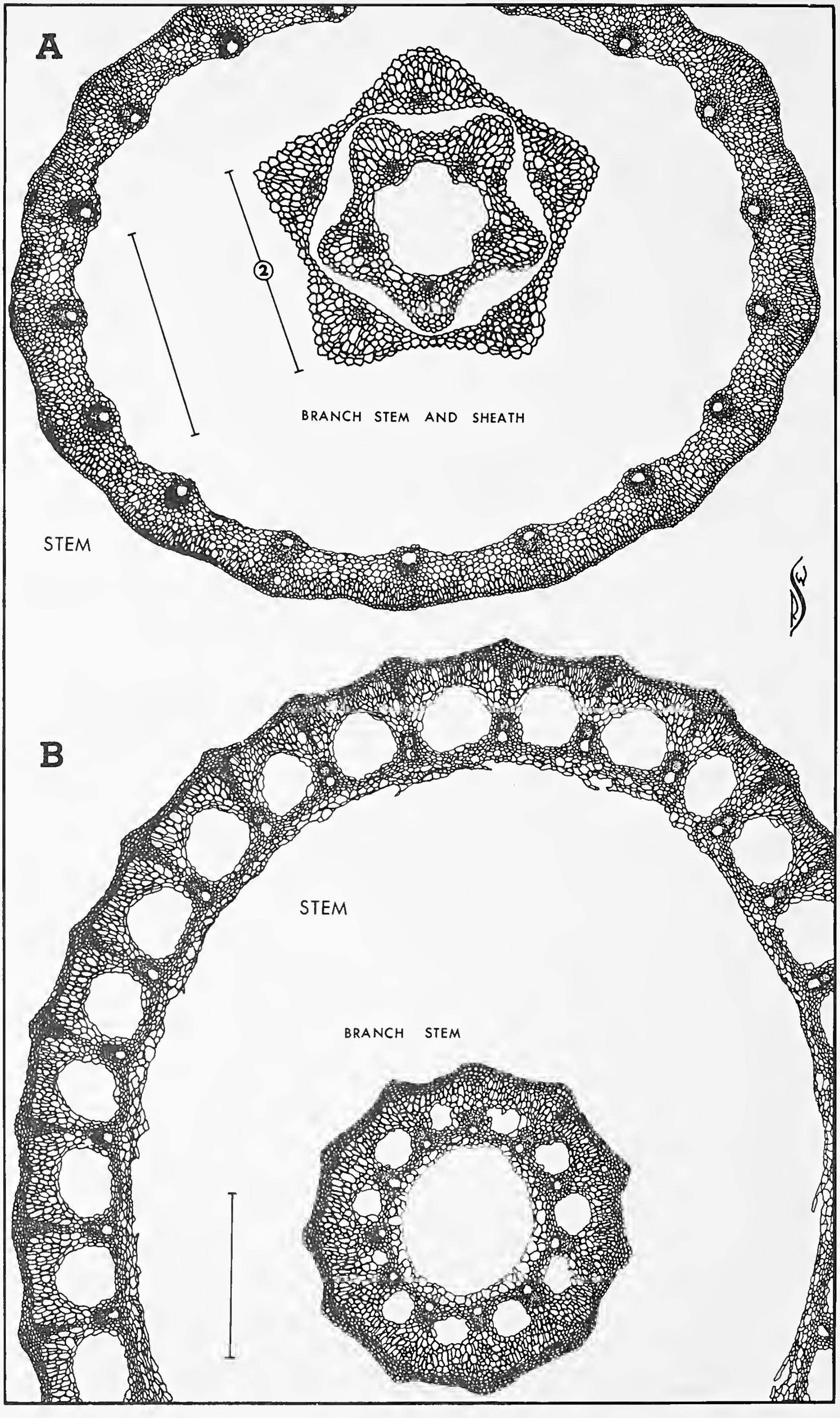
Plate 1



EQUISETUM

E. arvense (A)
E. sylvaticum (B)

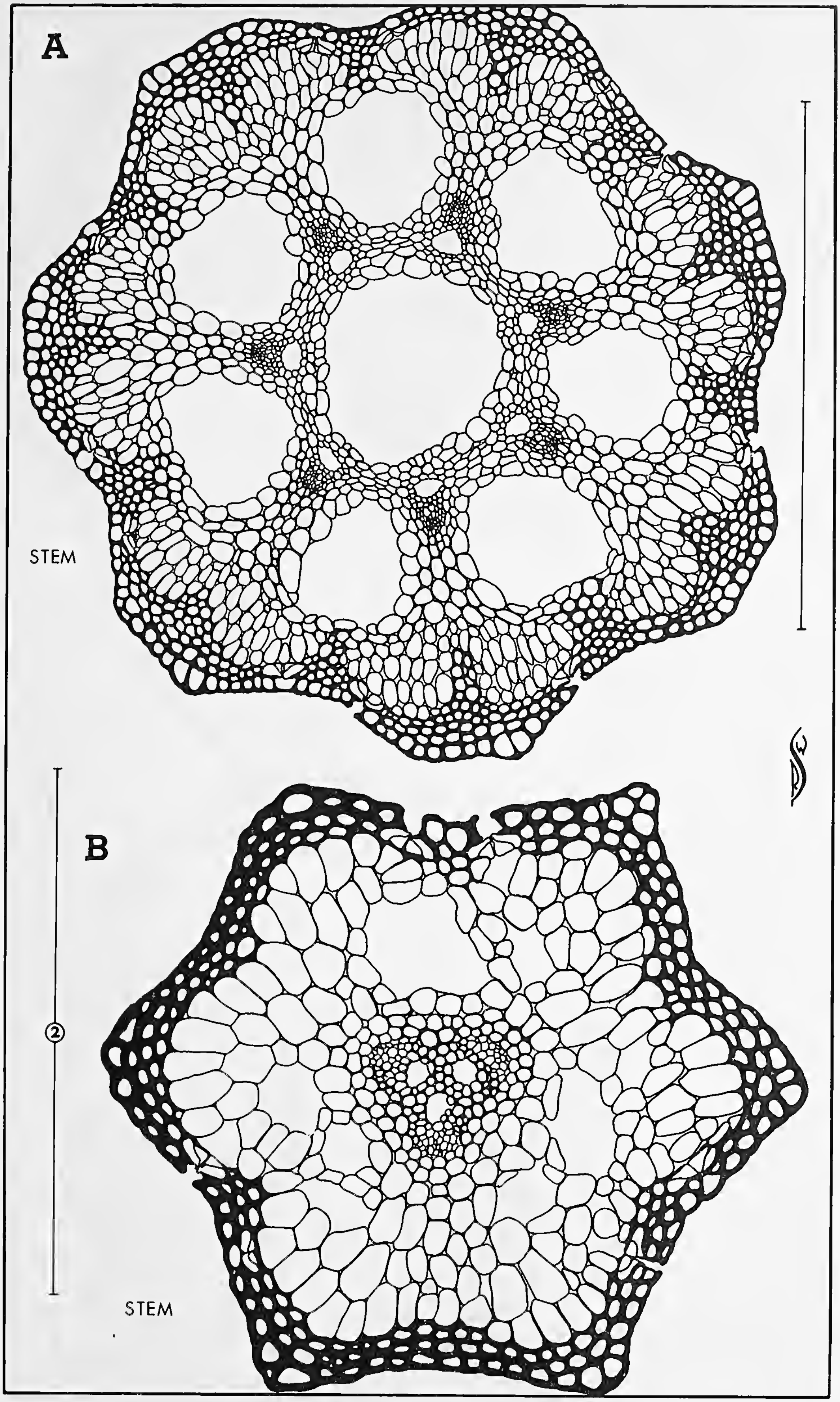
Plate 2



EQUISETUM

E. fluviatile (A)
E. hyemale (B)

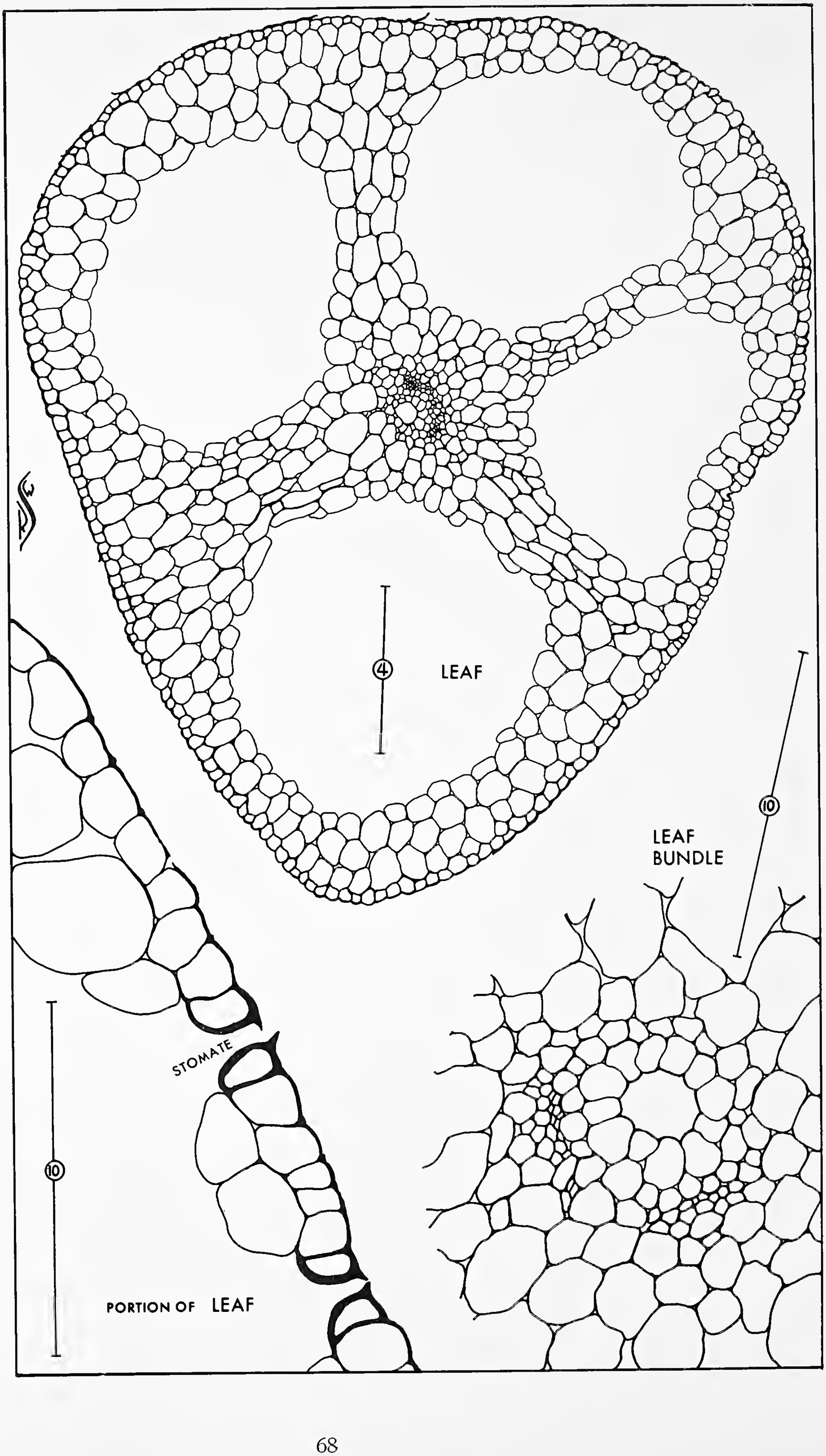
Plate 3



EQUISETUM

E. variegatum (A)
E. scirpoides (B)

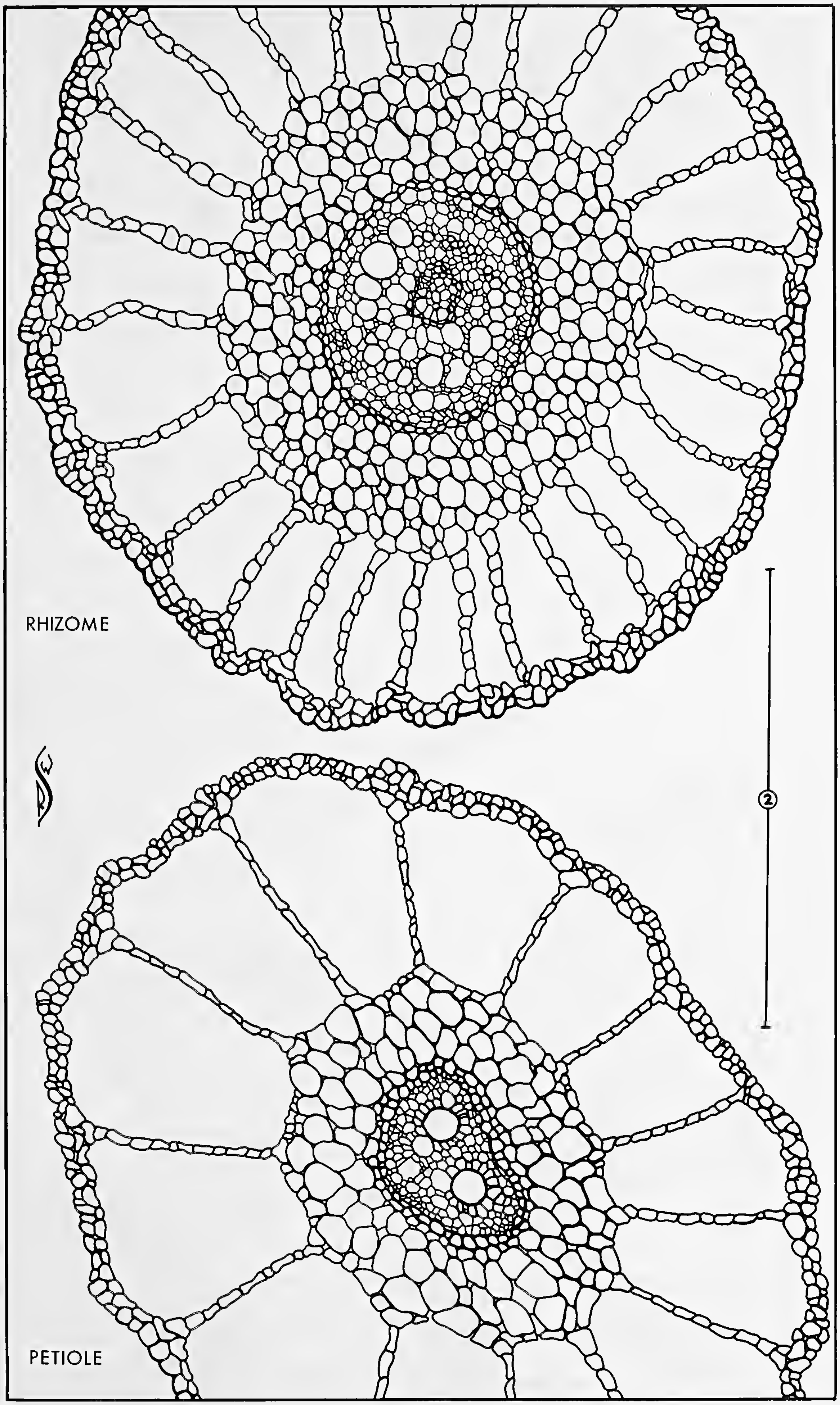
Plate 4



ISOETES

I. echinospora

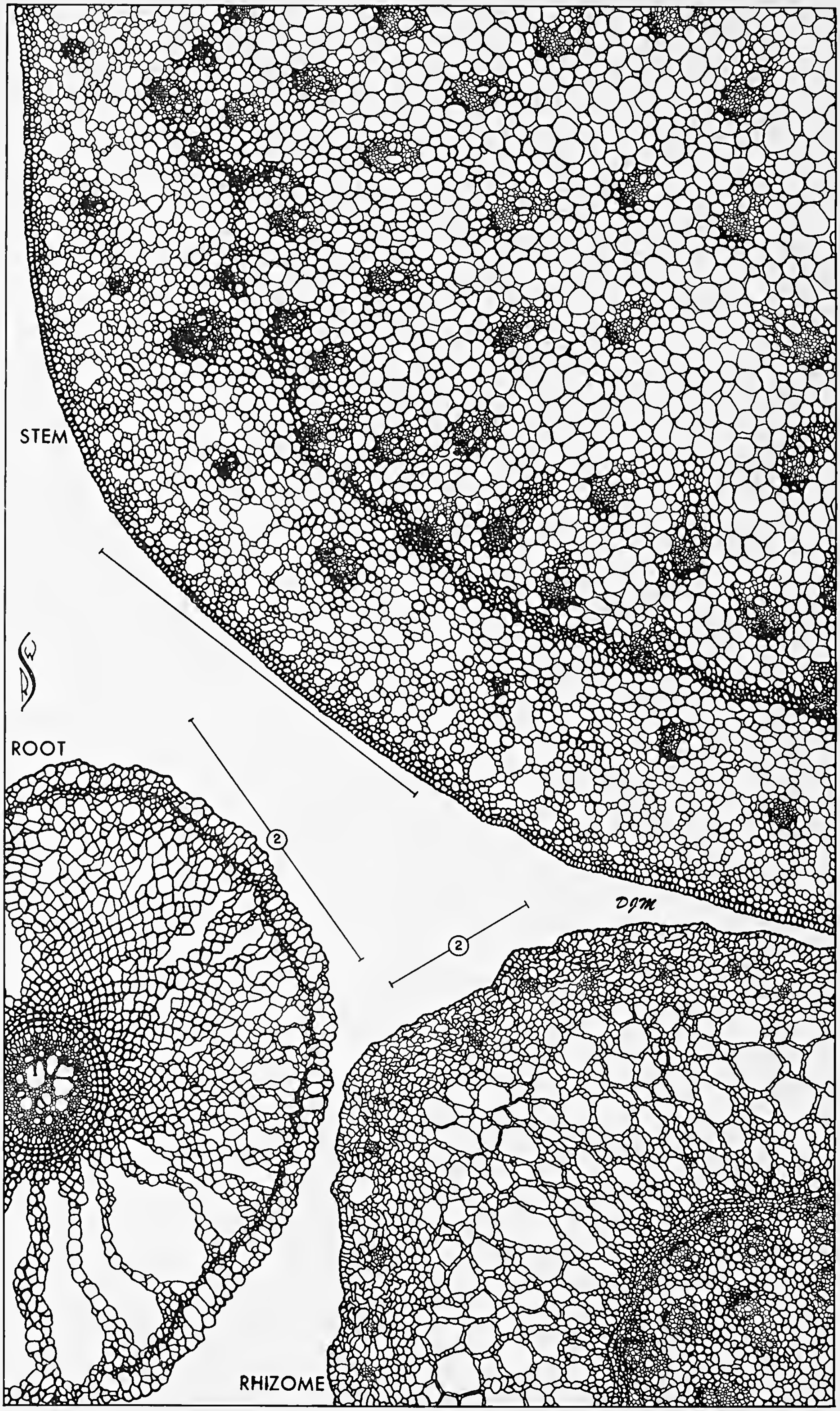
Plate 5



MARSILEA

M. quadrifolia

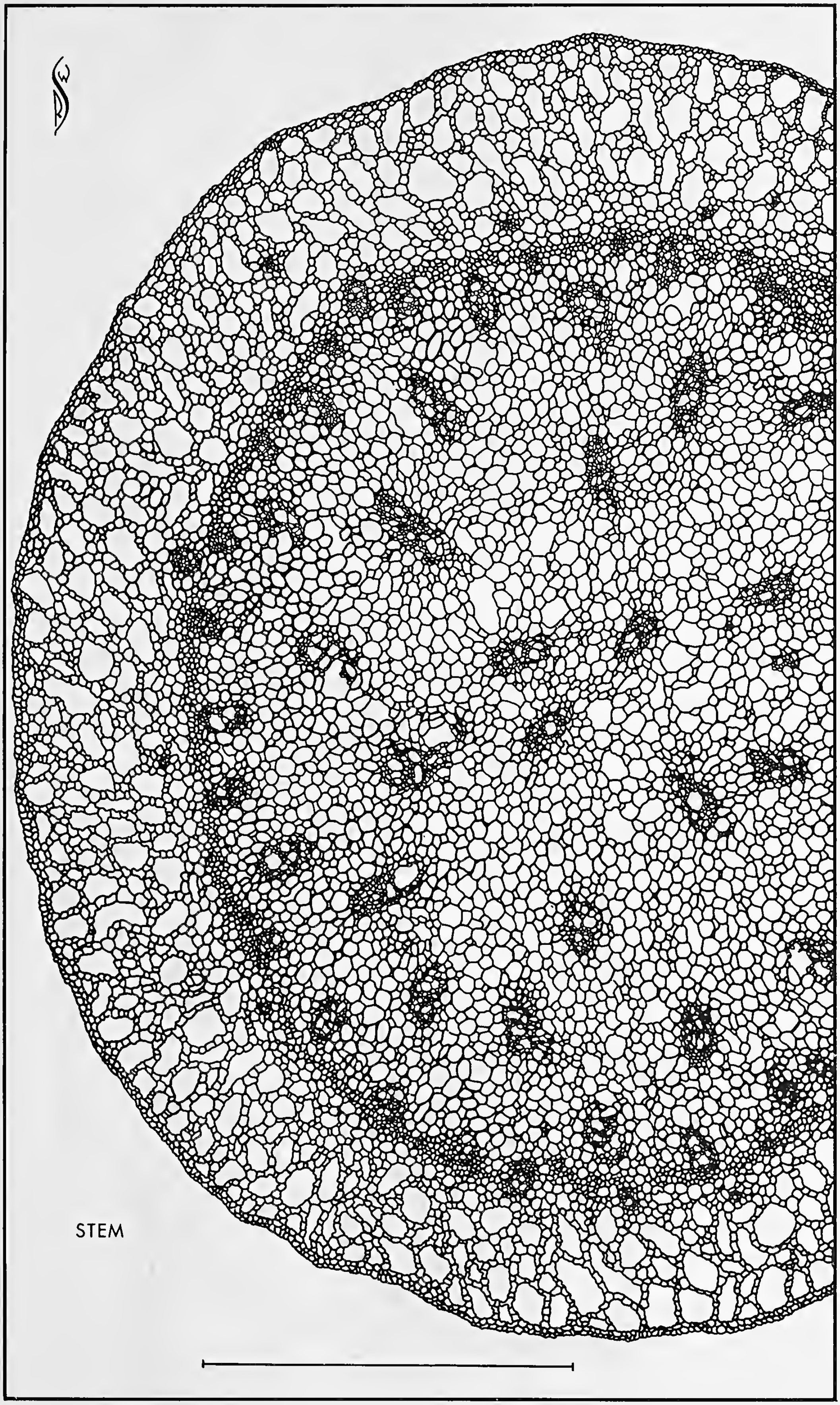
Plate 6



SPARGANIUM

S. americanum

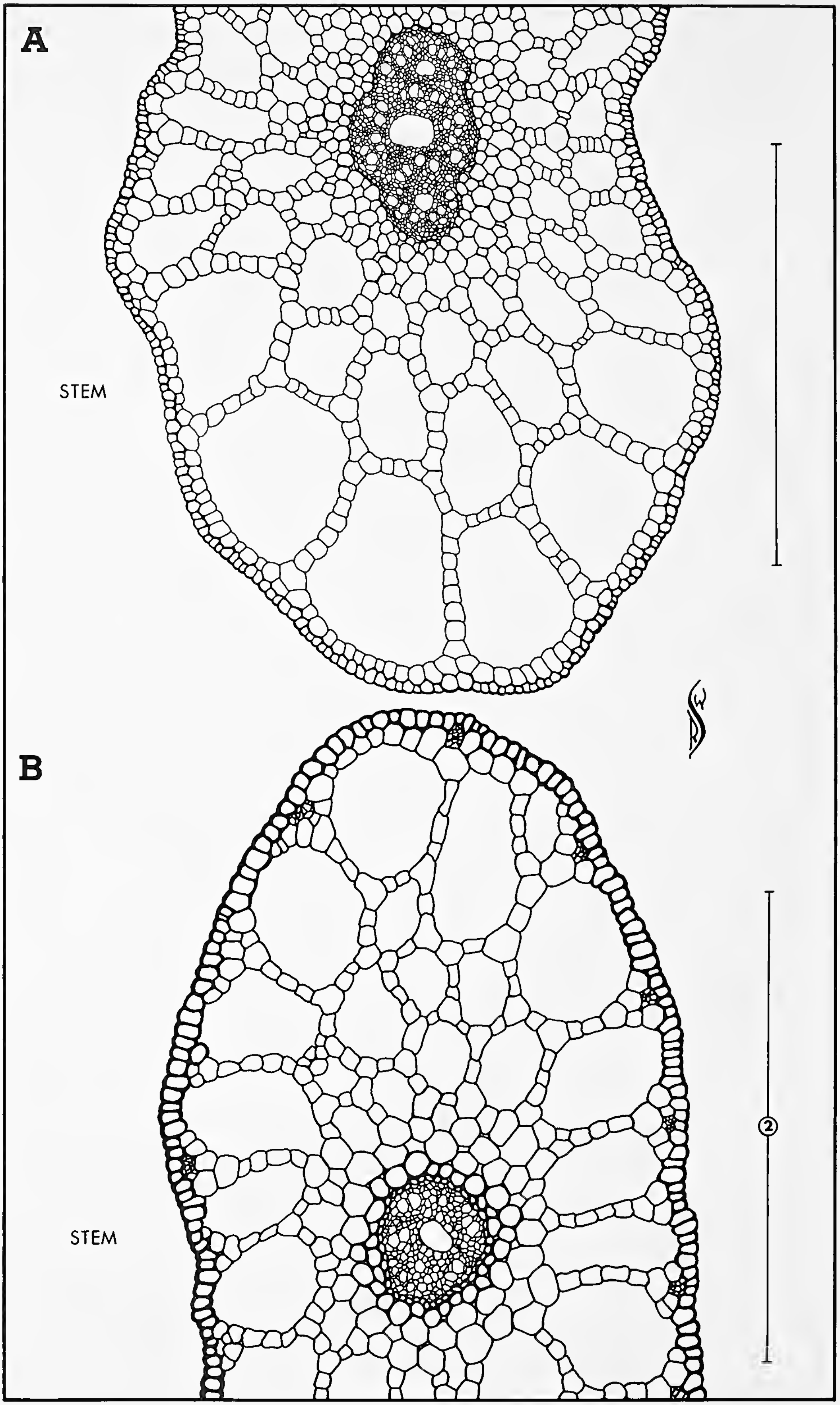
Plate 7



SPARGANIUM

S. angustifolium

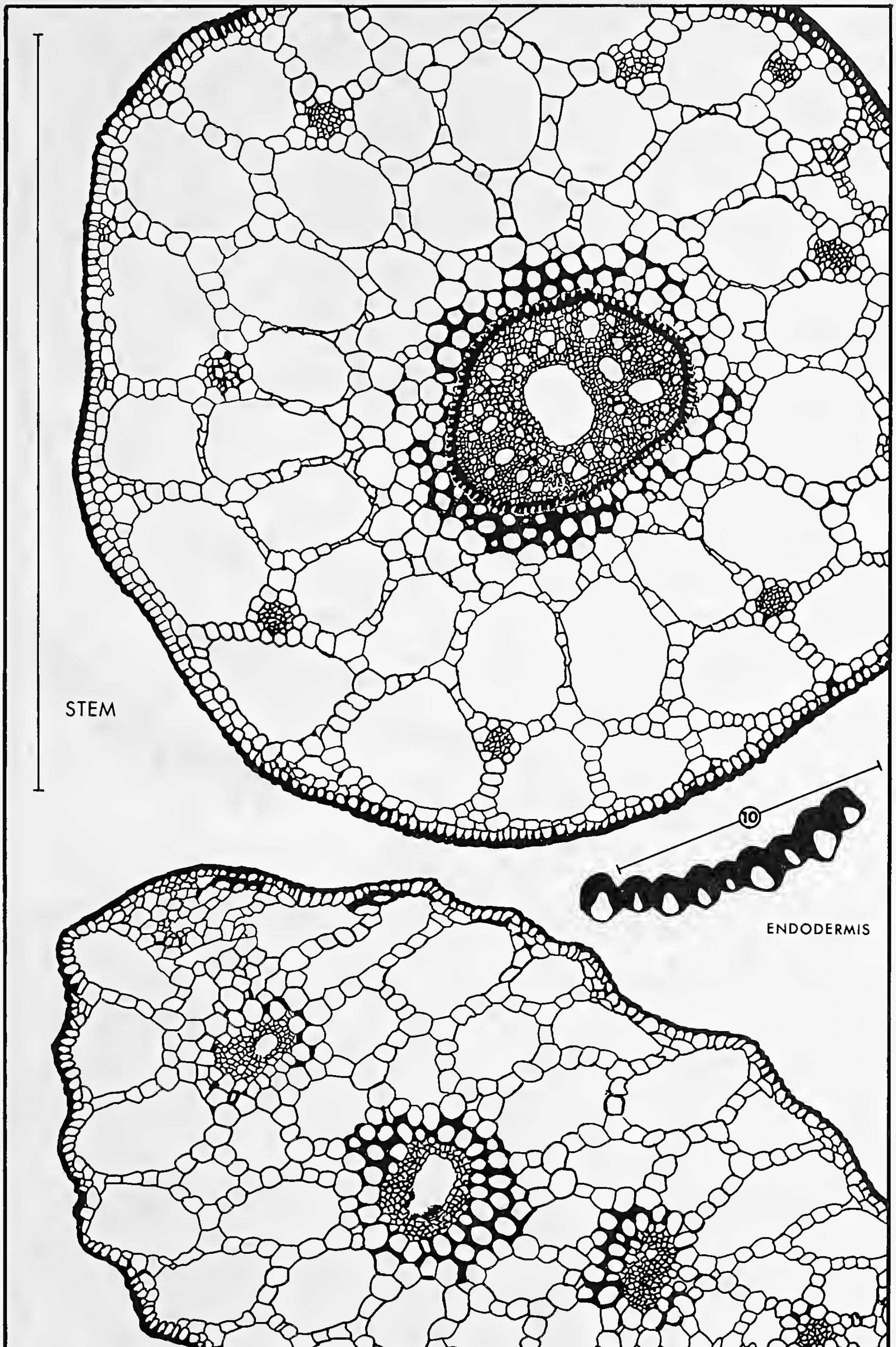
Plate 8



POTAMOGETON

P. crispus (A)
P. foliosus (B)

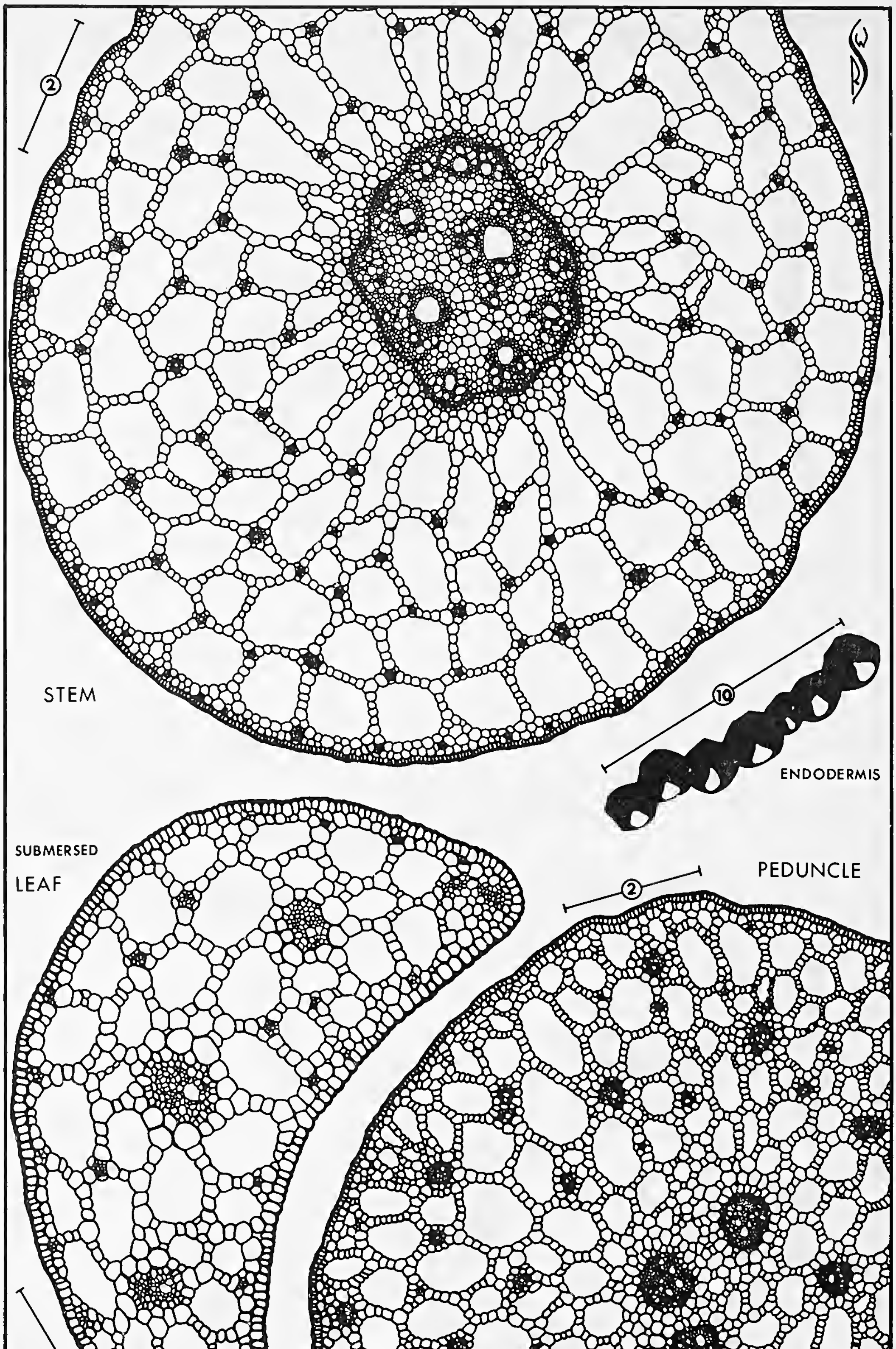
Plate 9



POTAMOGETON

P. gramineus

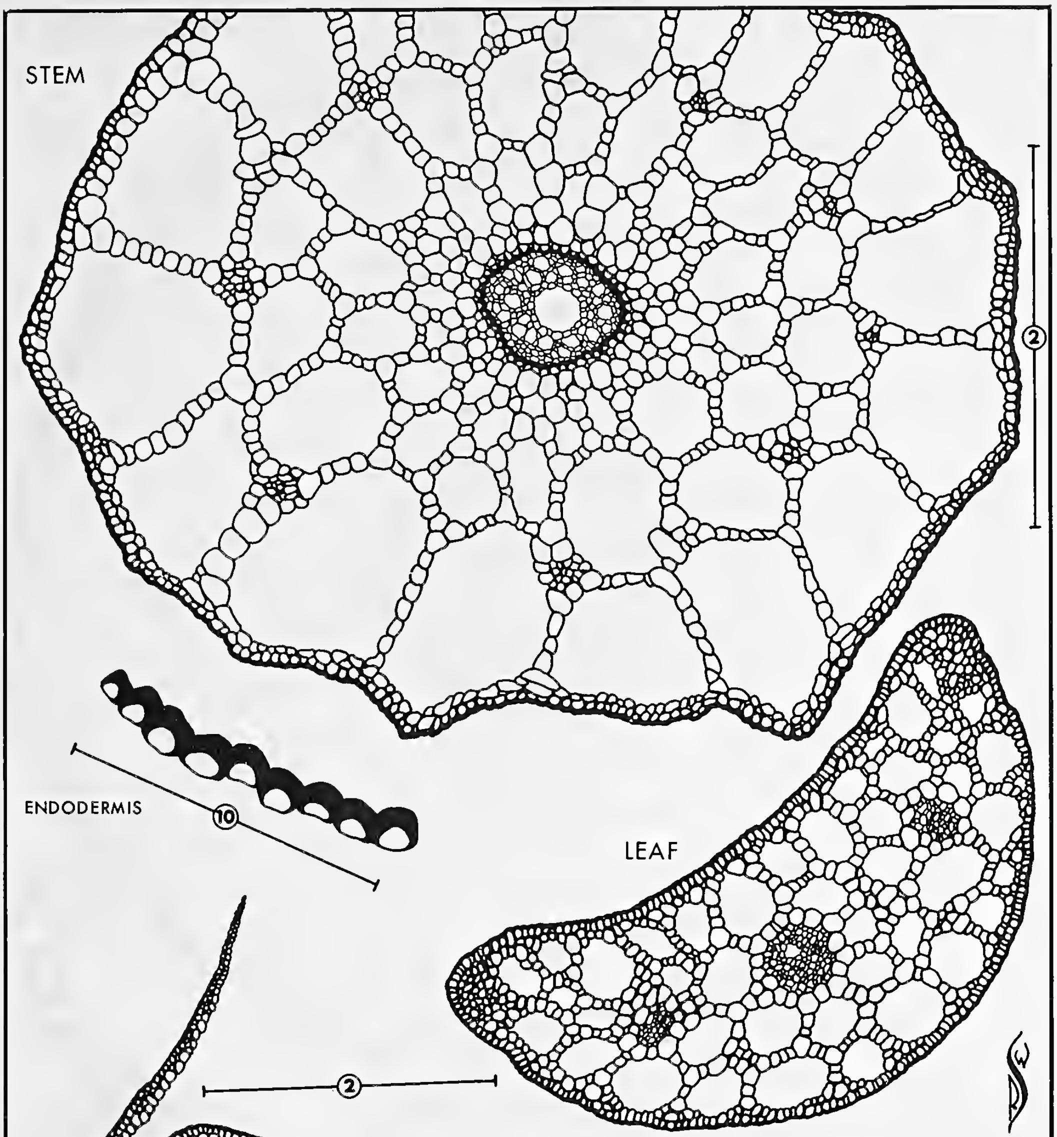
Plate 10



POTAMOGETON

P. natans

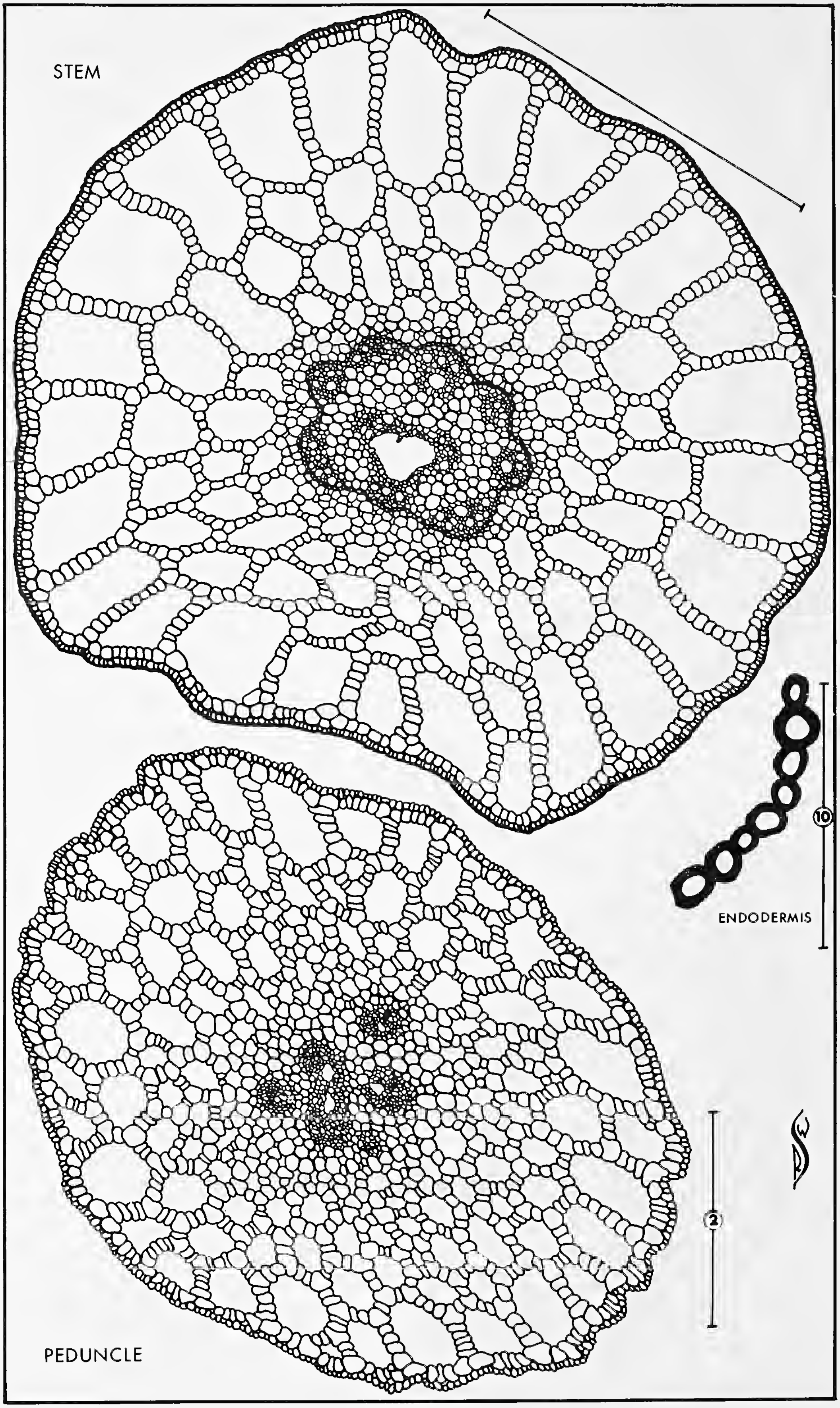
Plate 11



POTAMOGETON

P. pectinatus

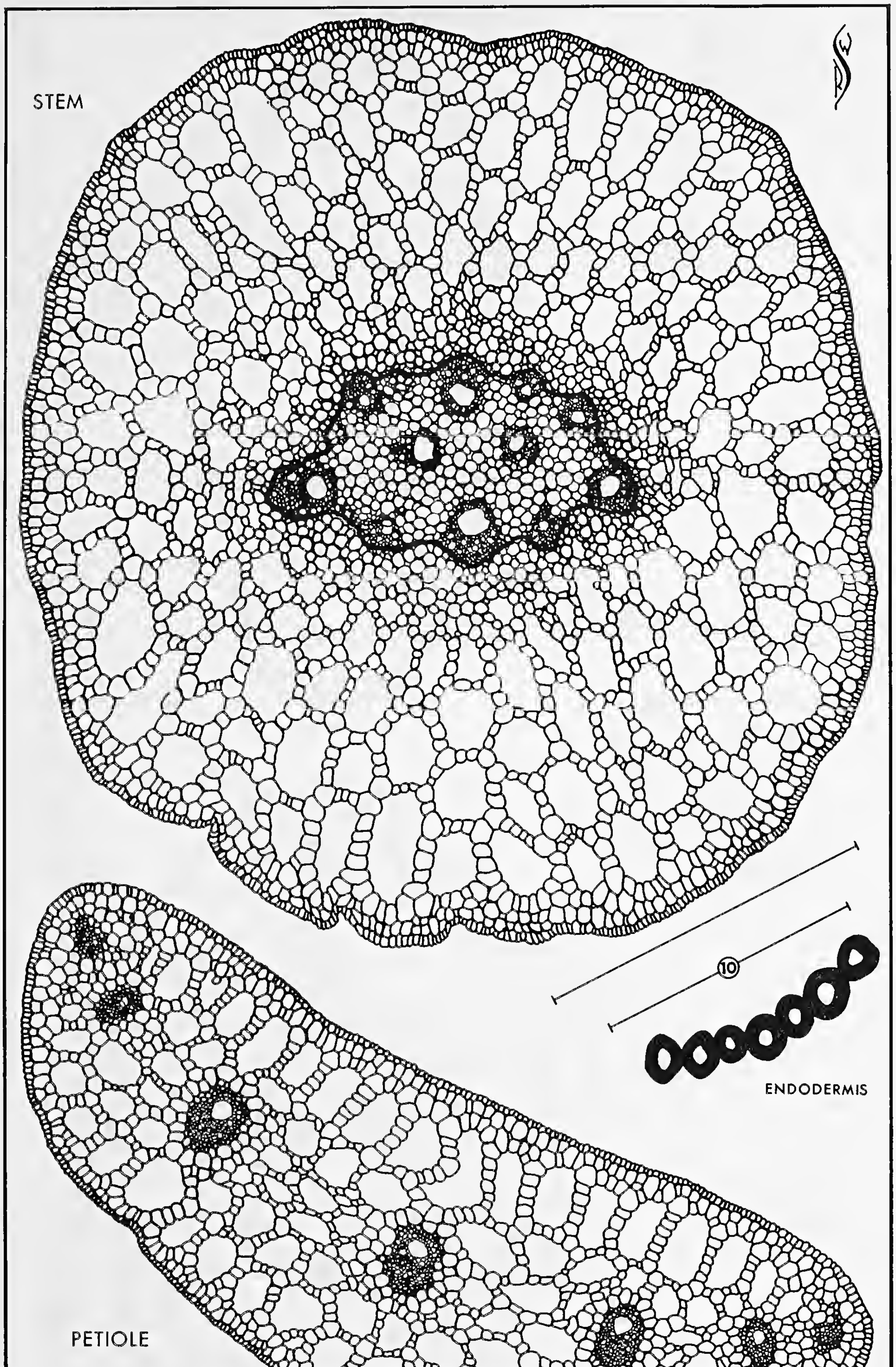
Plate 12



POTAMOGETON

P. perfoliatus

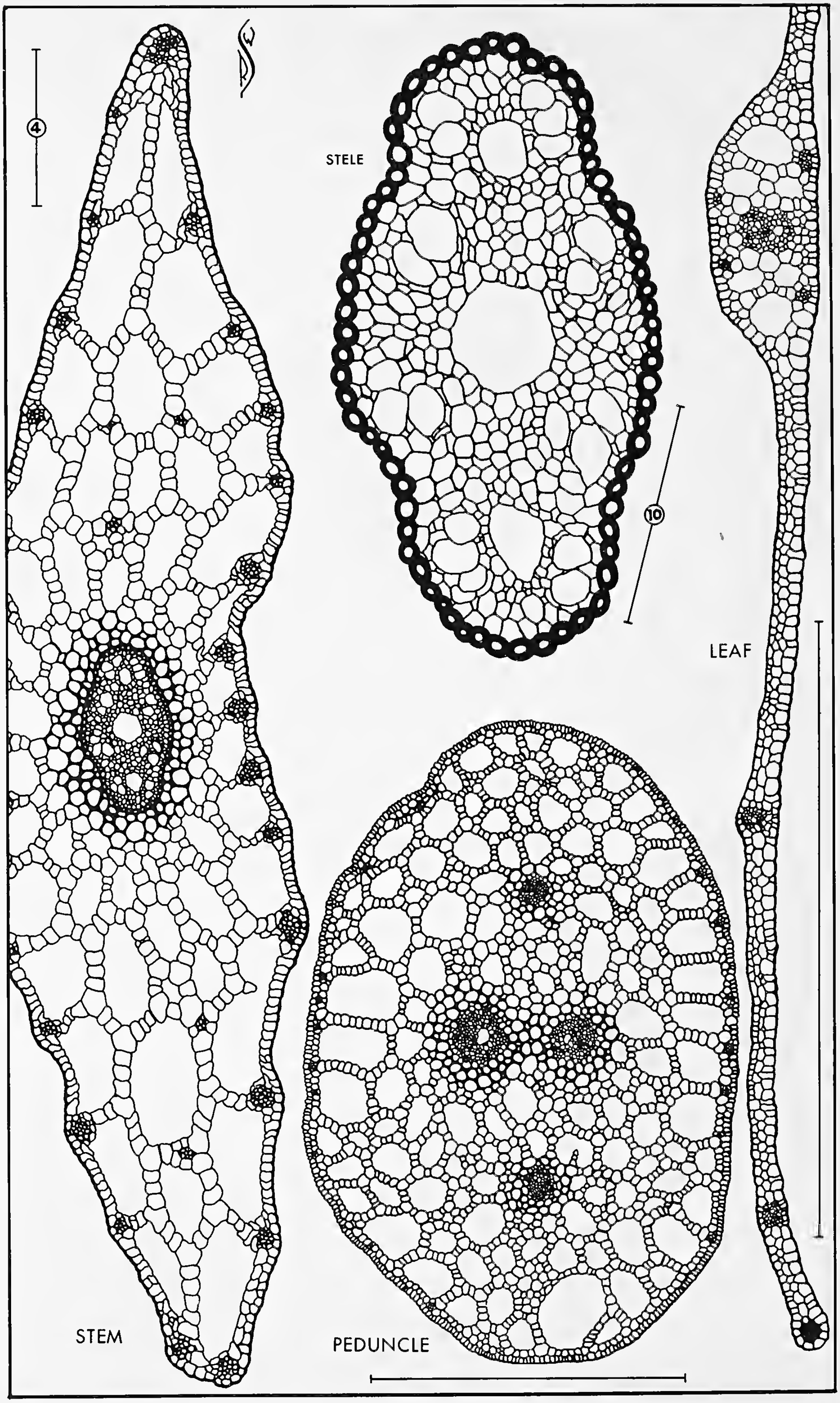
Plate 13



POTAMOGETON

P. pulcher

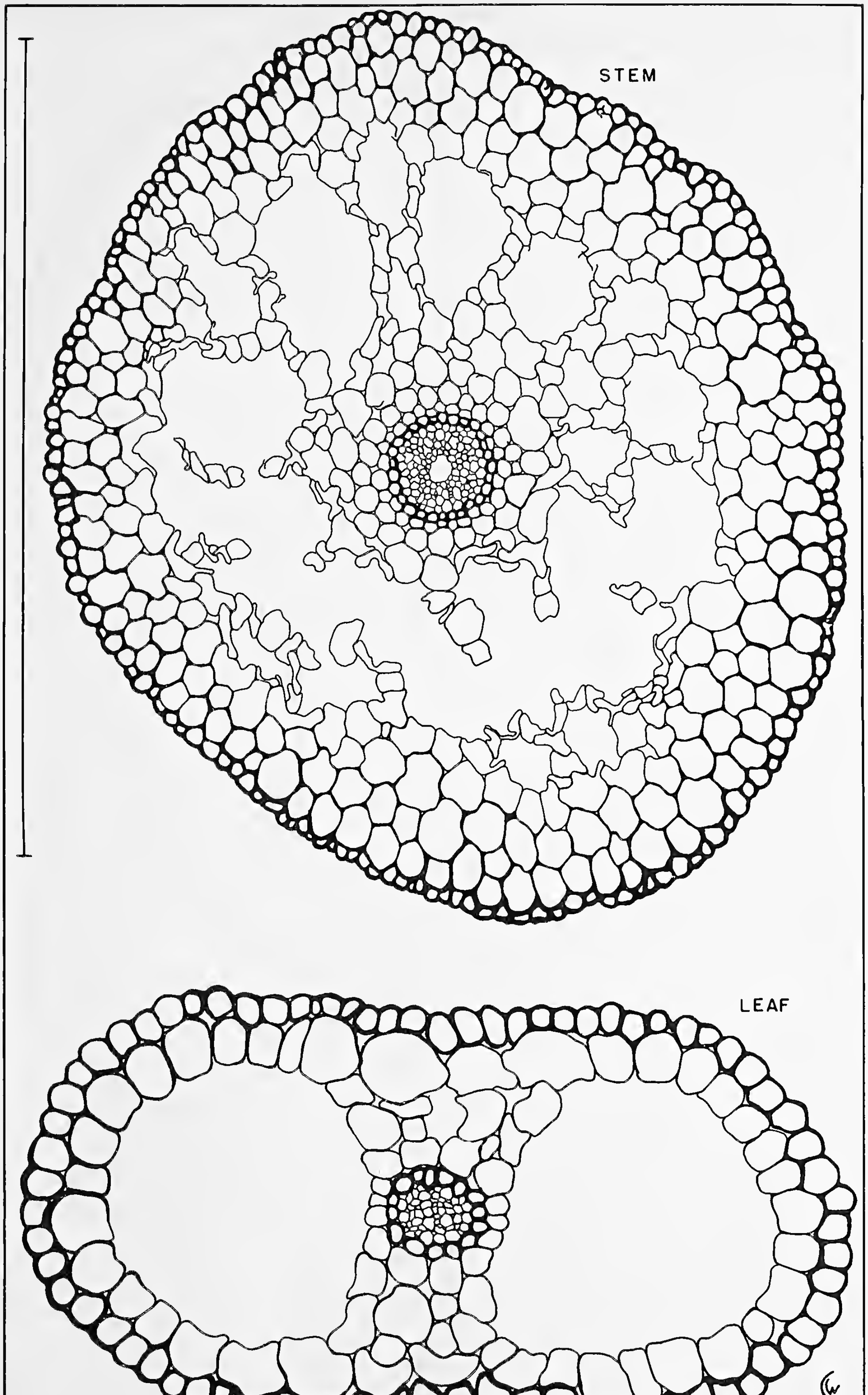
Plate 14



POTAMOGETON

P. zosteriformis

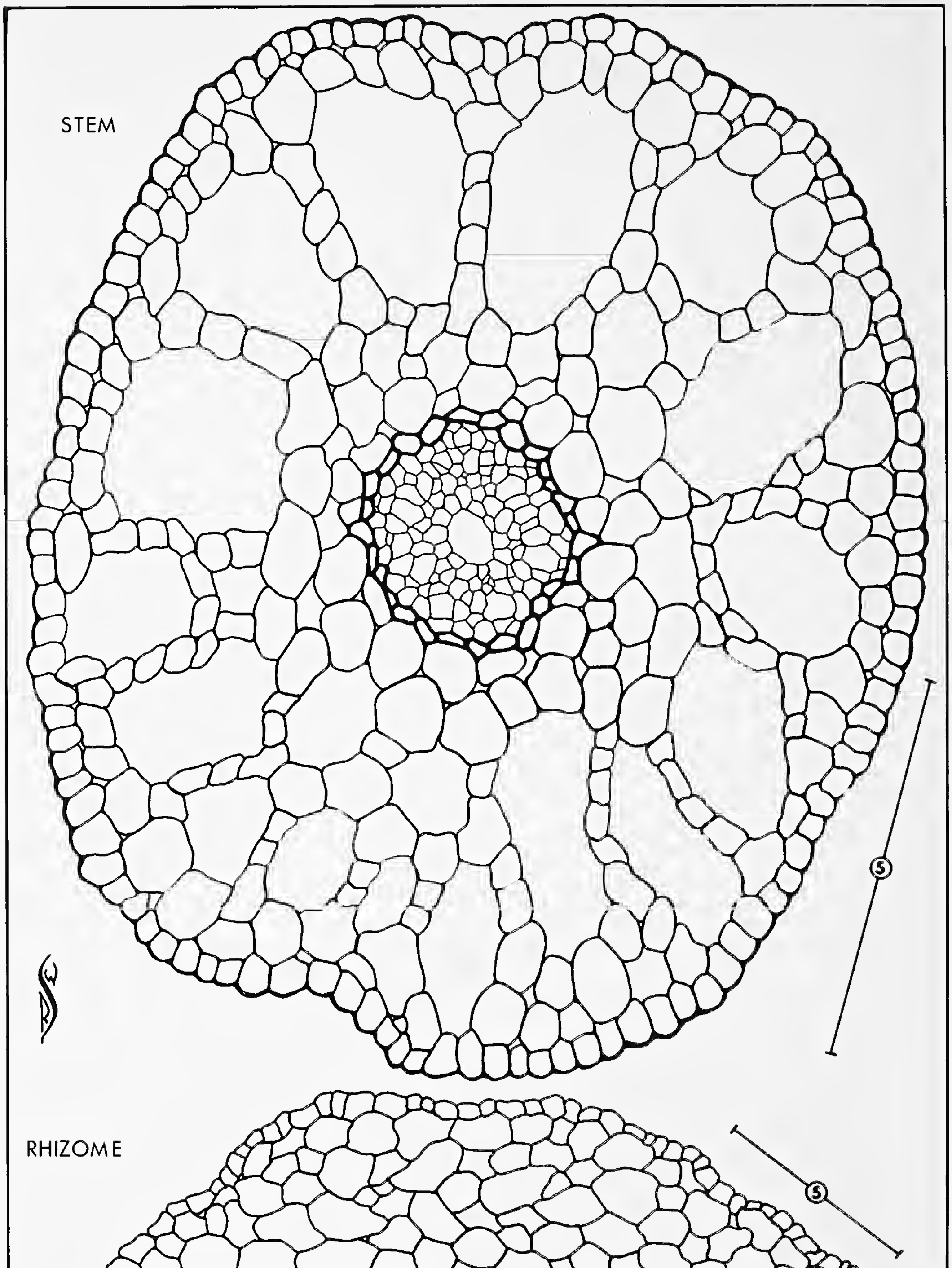
Plate 15



RUPPIA

R. maritima

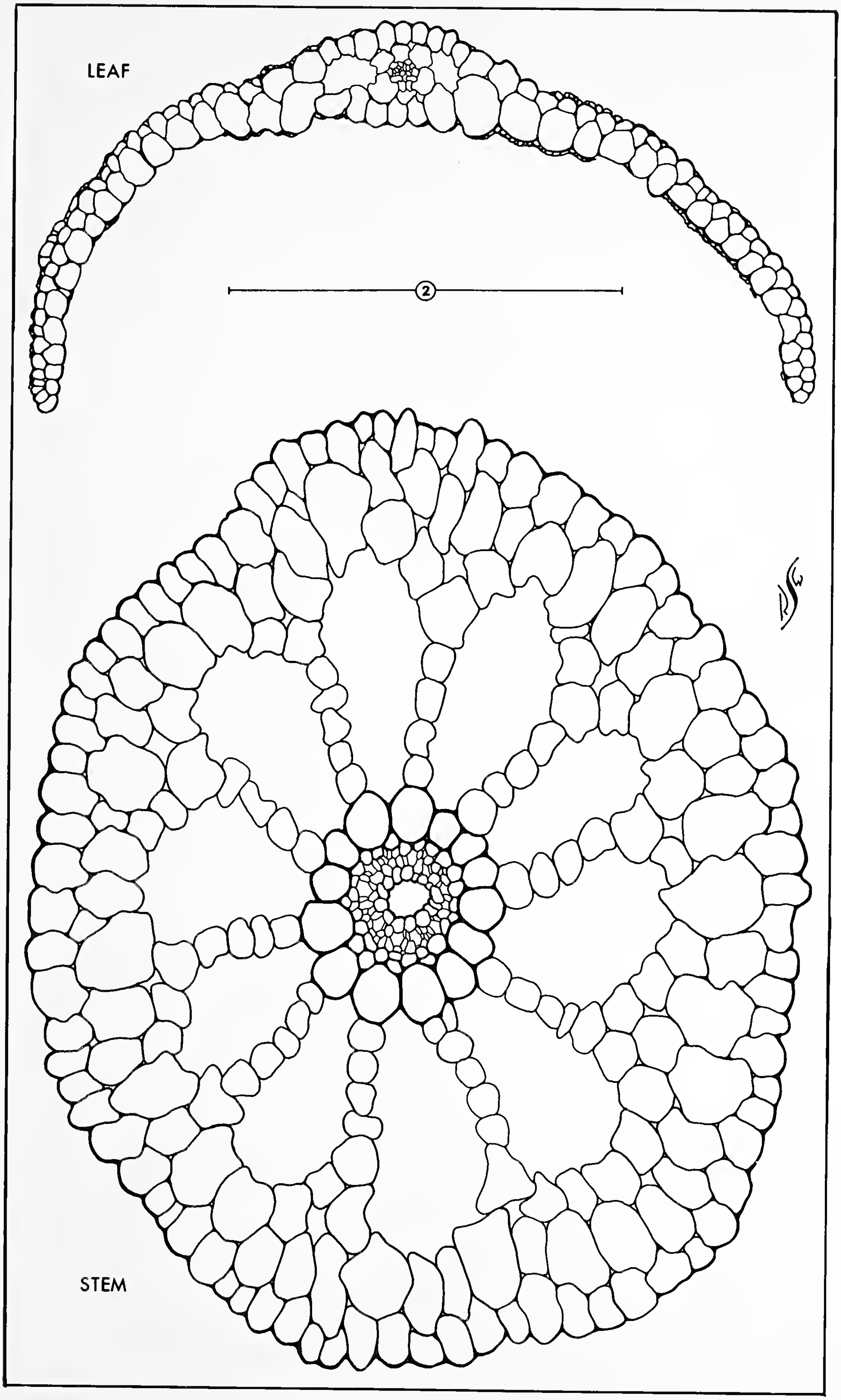
Plate 16



ZANNICHELLIA

Z. palustris

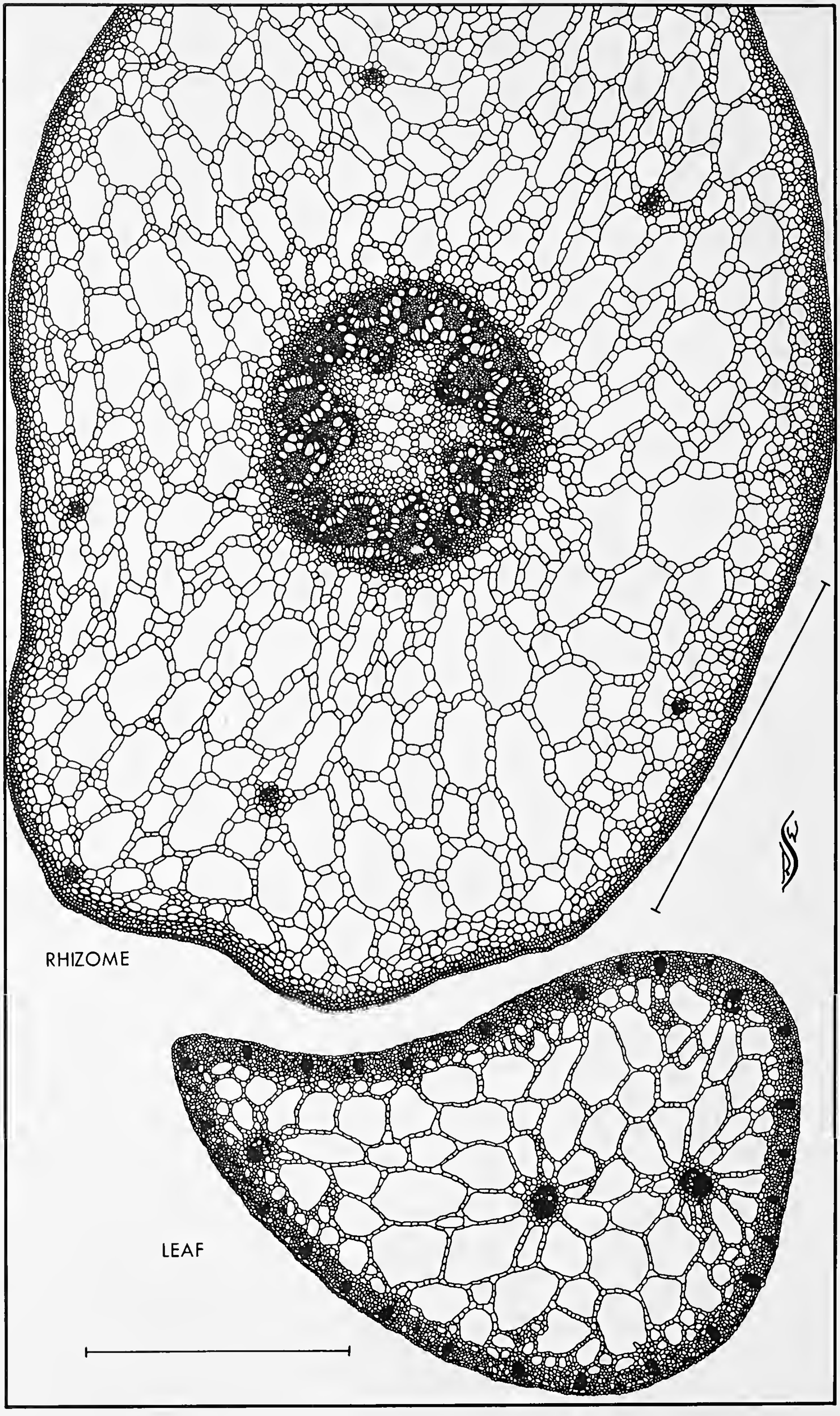
Plate 17



NAJAS

N. flexilis

Plate 18



SCHEUCHZERIA

S. palustris

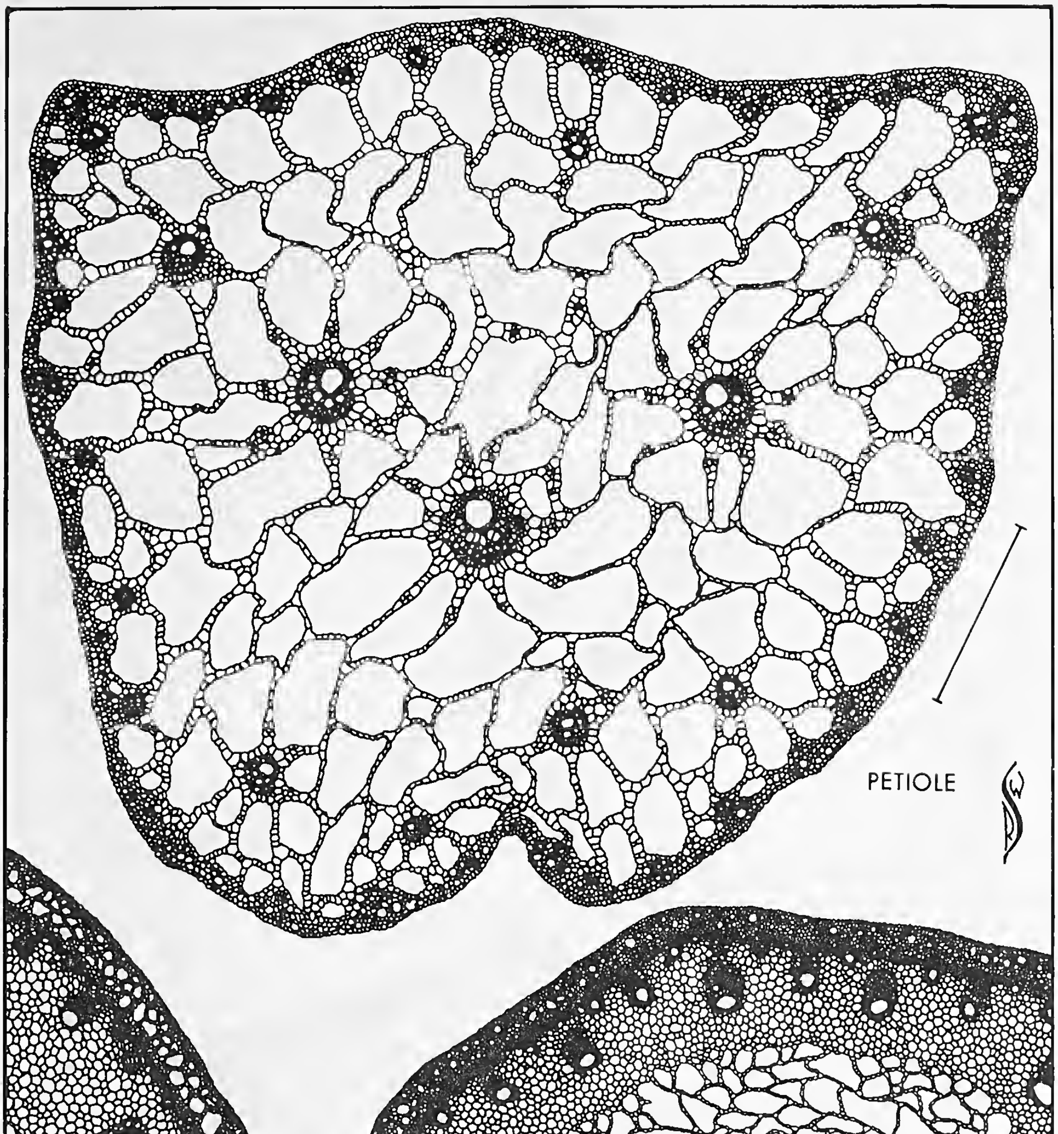
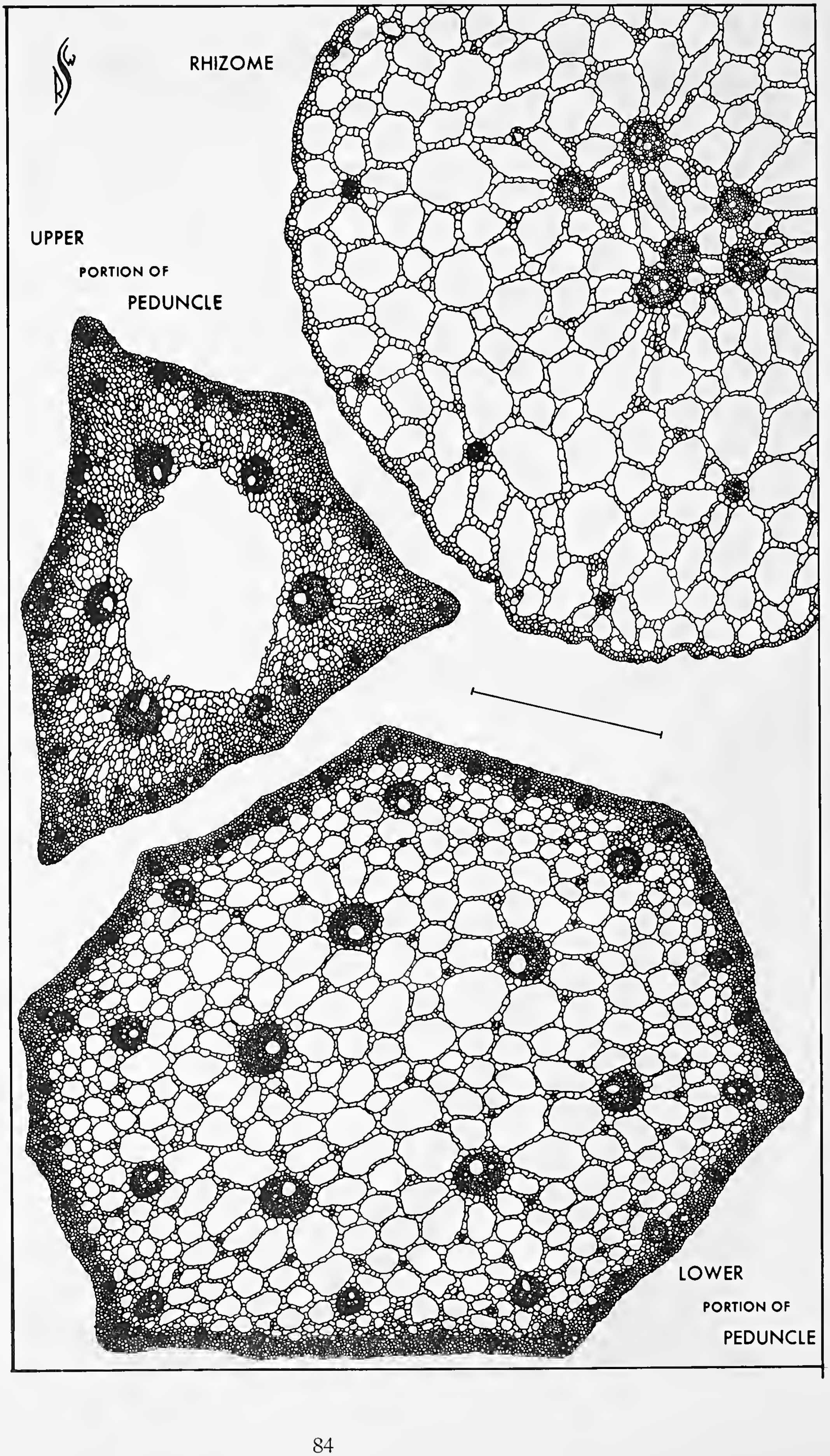


Plate 19

ALISMA

A. plantago-aquatica

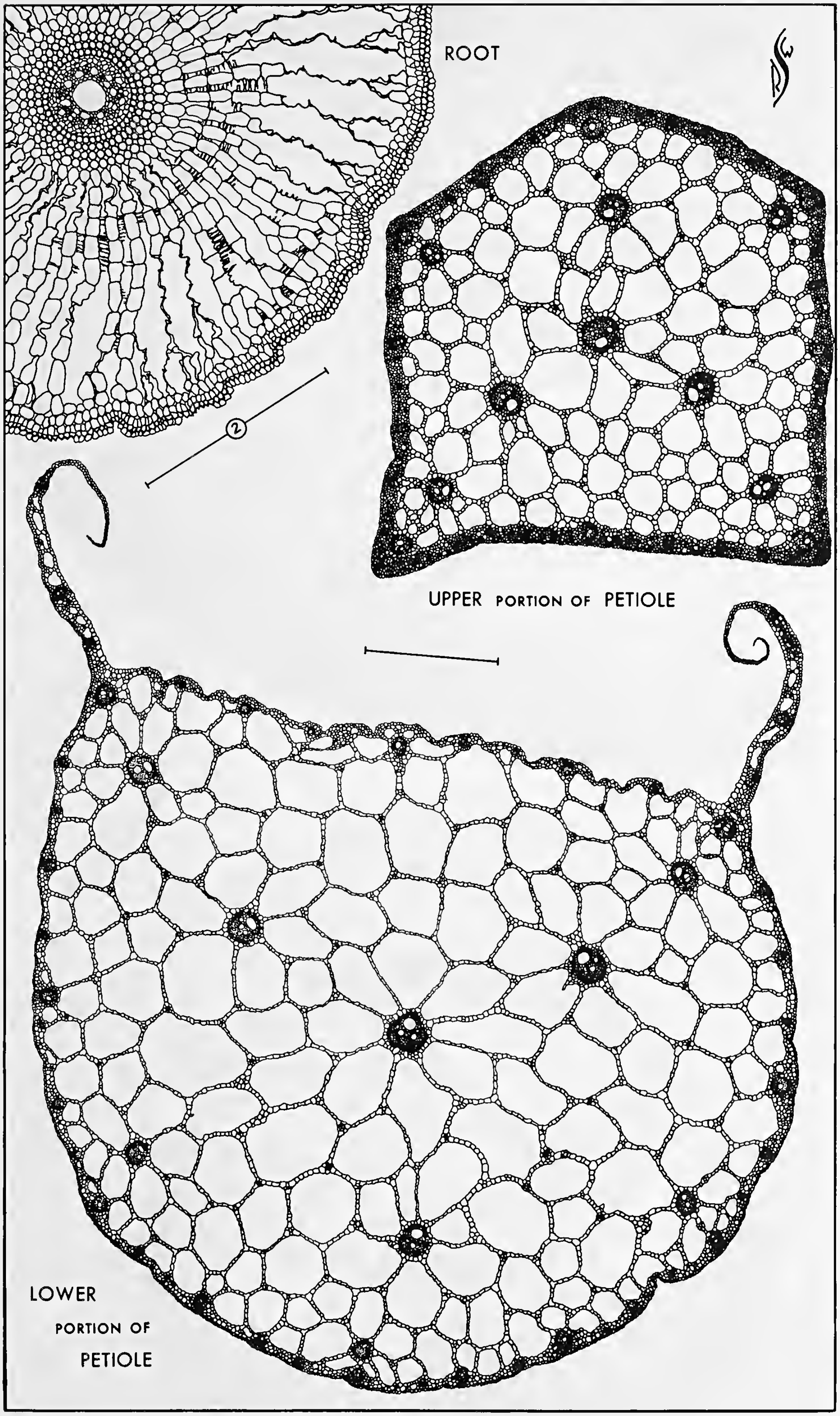
Plate 20



SAGITTARIA

S. latifolia

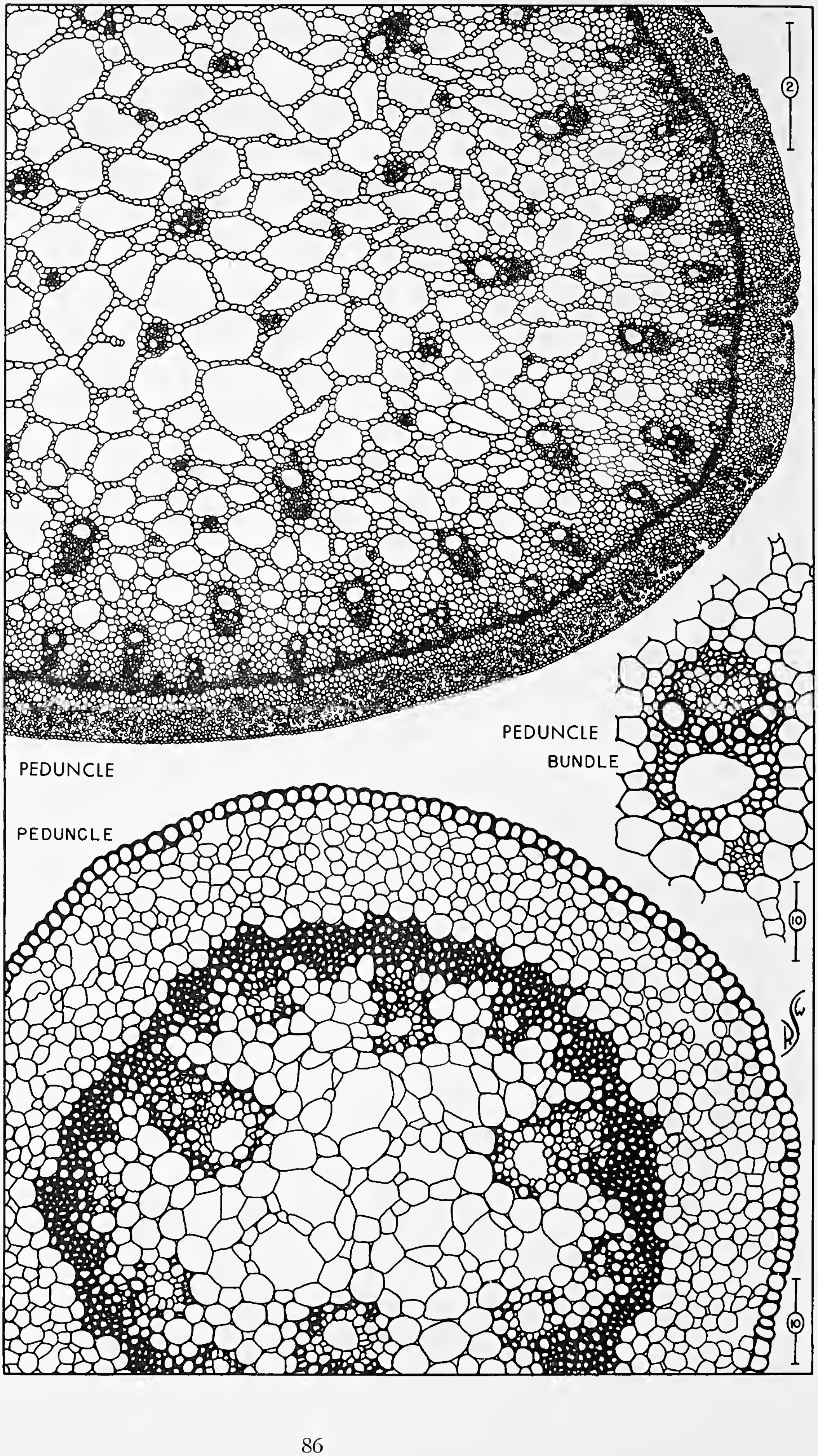
Plate 21



SAGITTARIA

S. latifolia

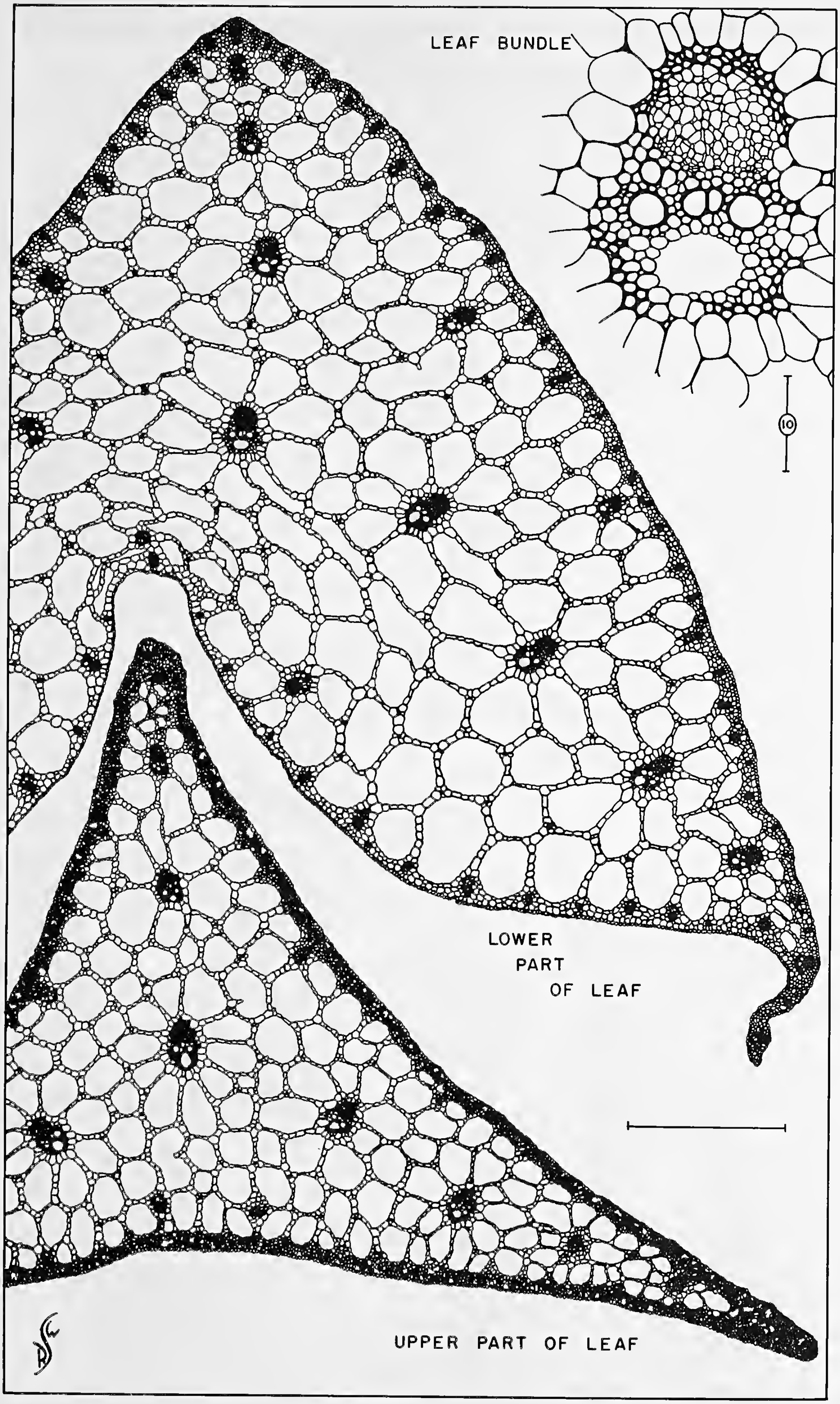
Plate 22



BUTOMUS

B. umbellatus

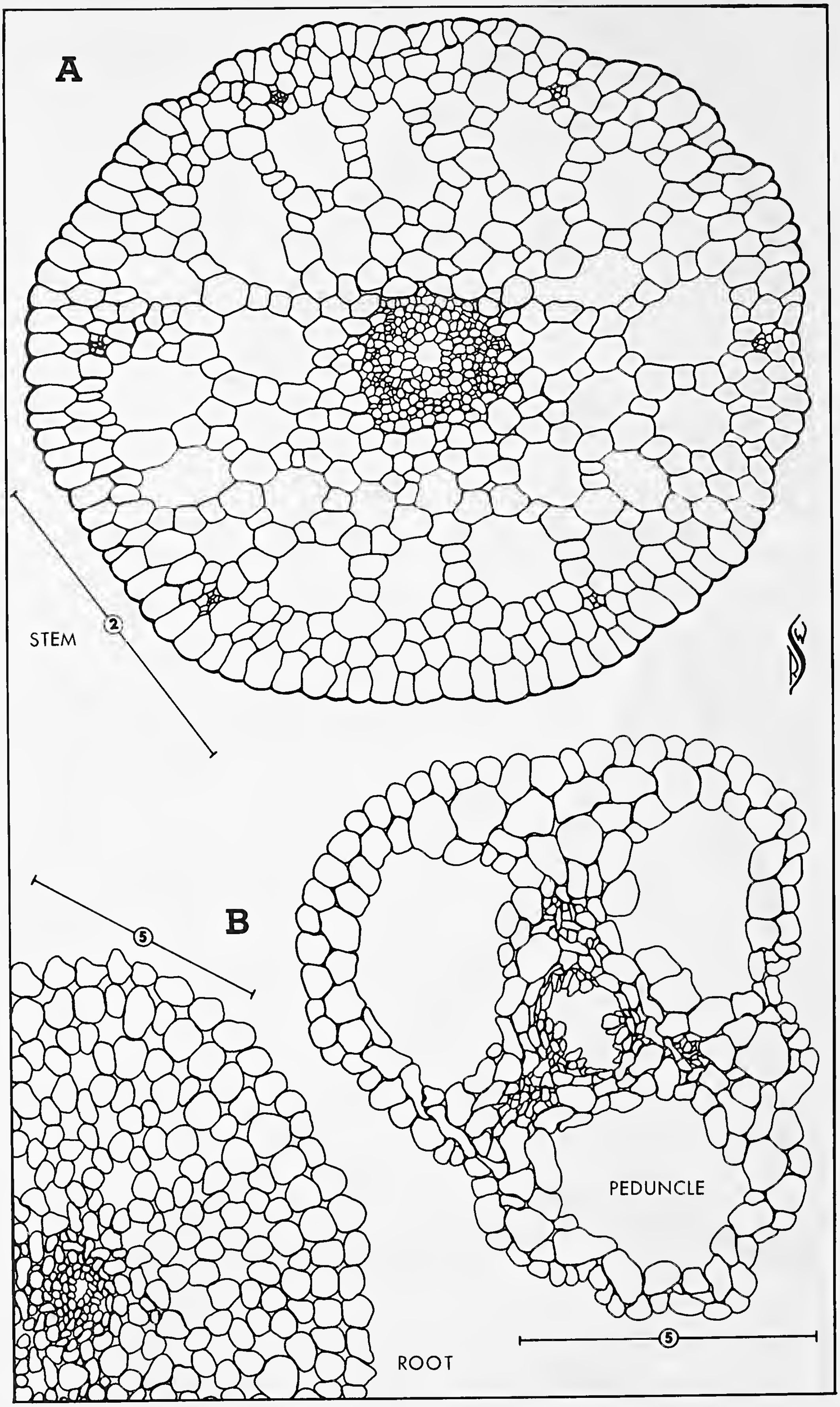
Plate 23



BUTOMUS

B. umbellatus

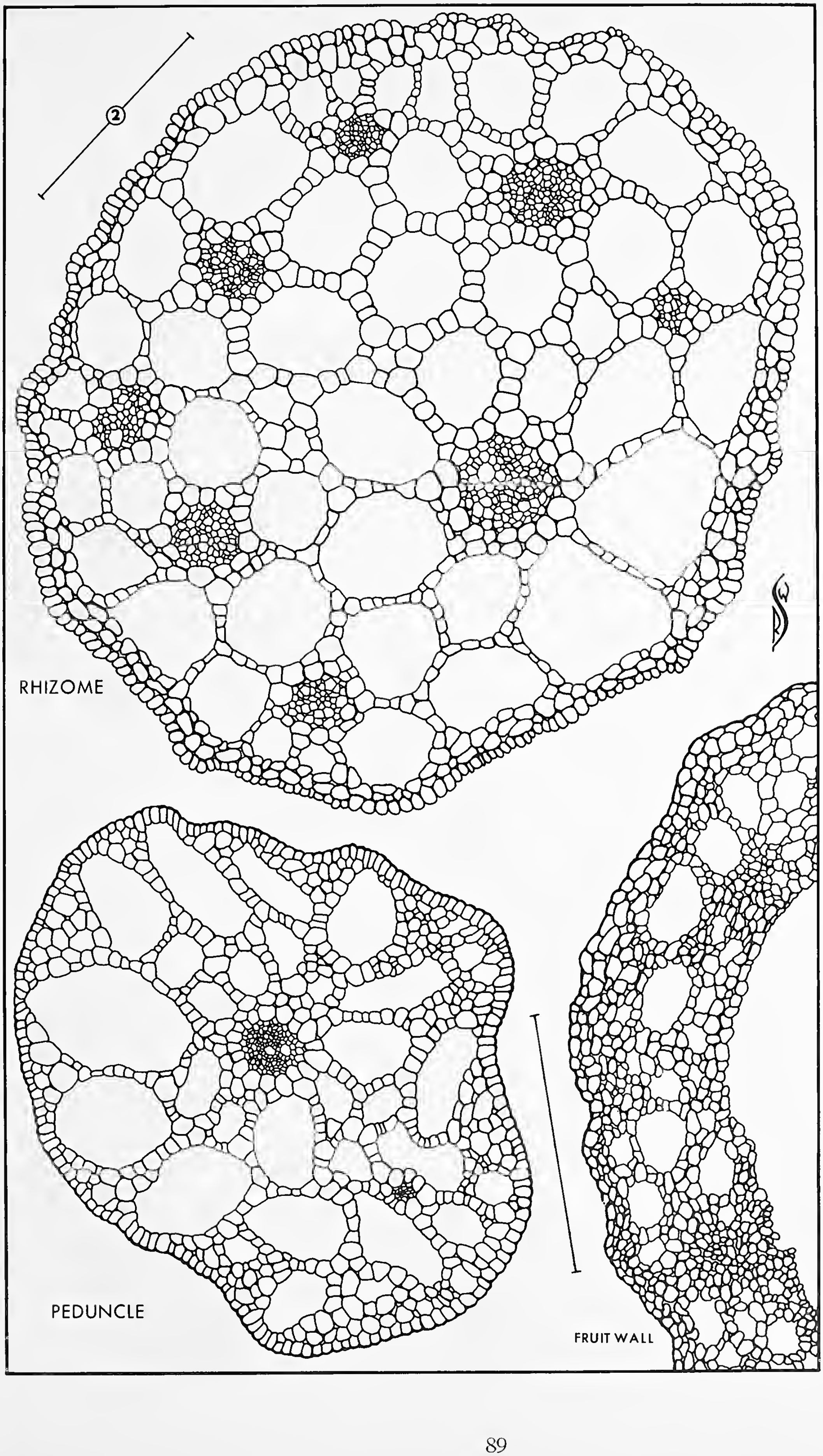
Plate 24



ELODEA

E. canadensis (A)
E. nuttallii (B)

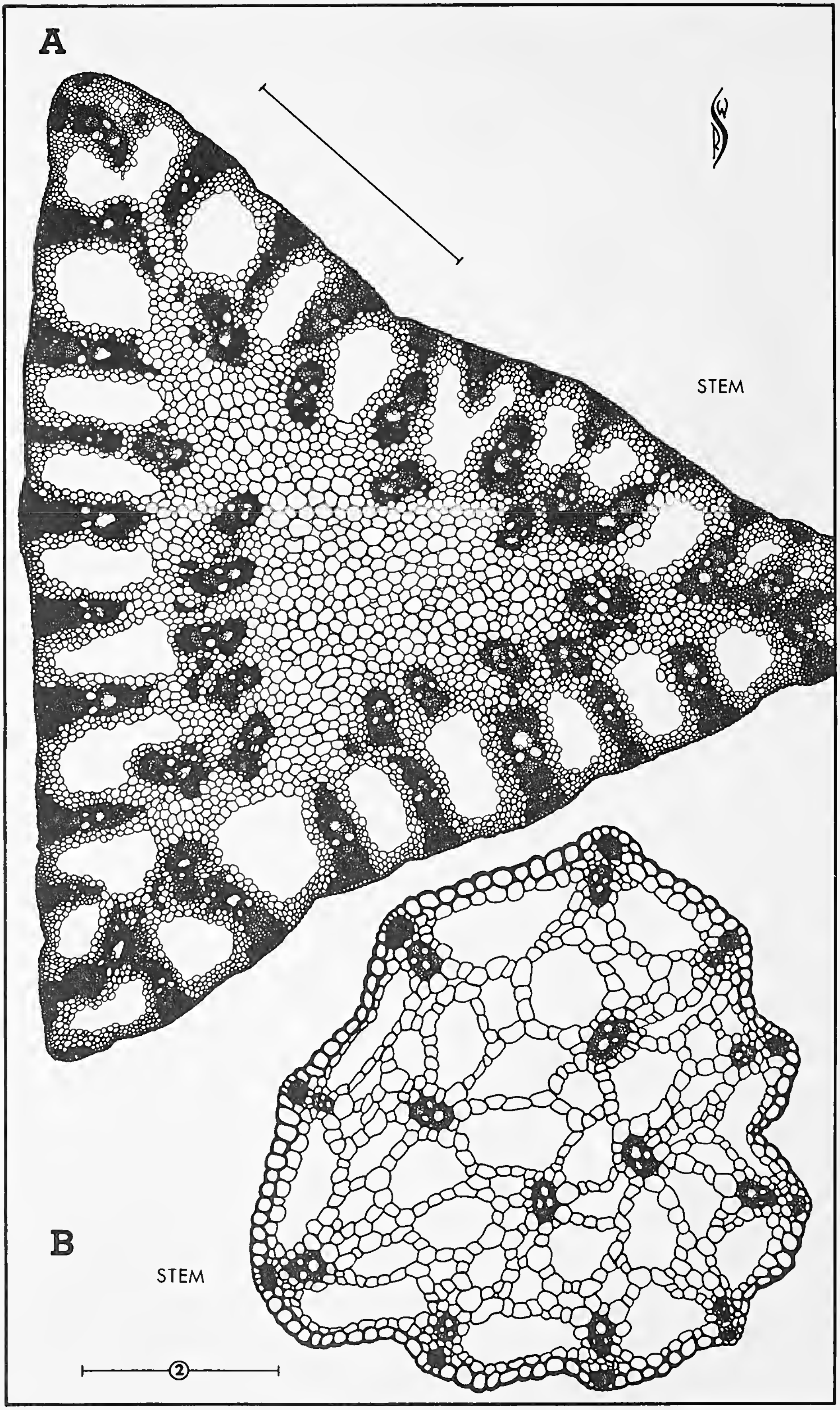
Plate 25



VALLISNERIA

V. americana

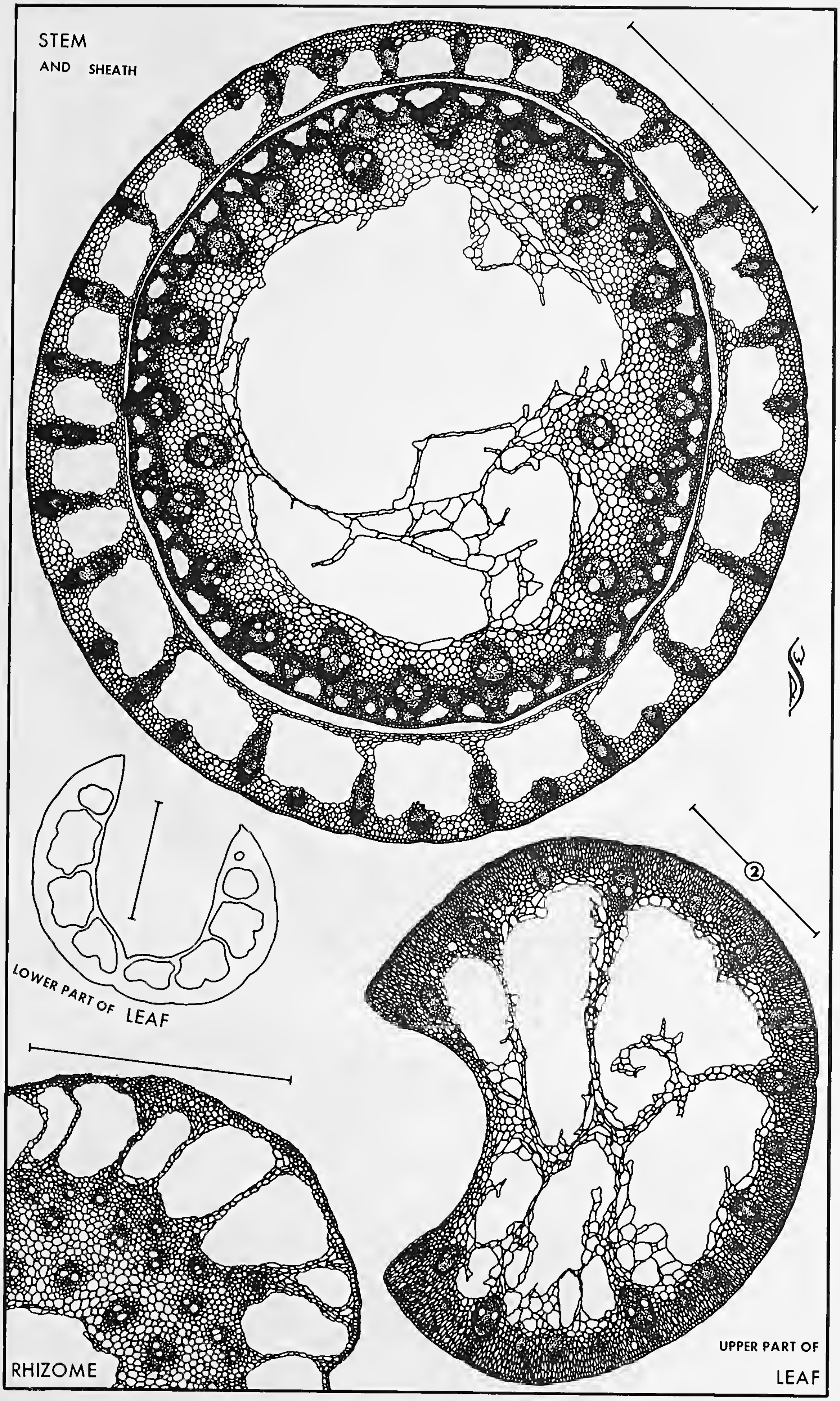
Plate 26



CAREX
FUIRENA

C. comosa (A)
F. squarosa (B)

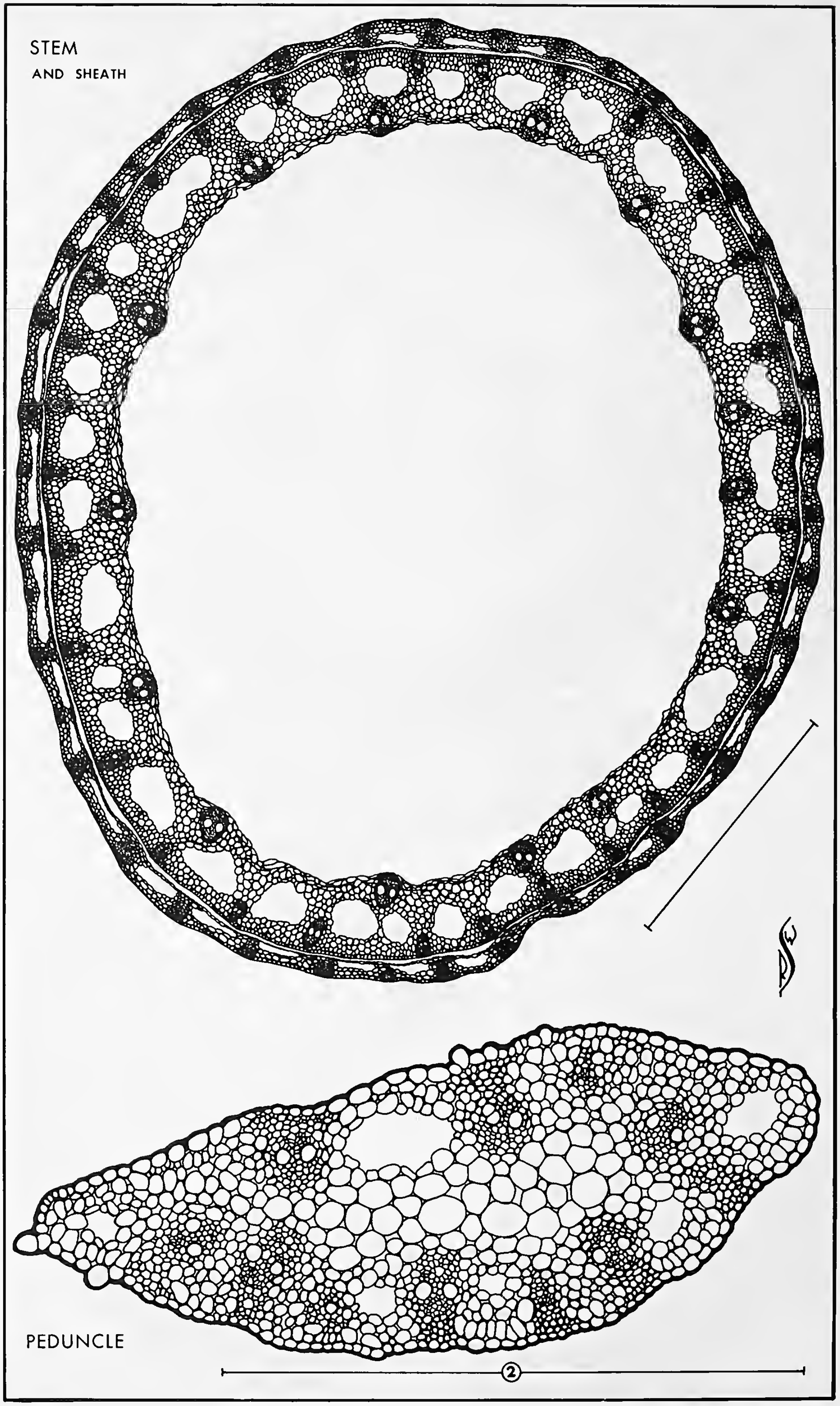
Plate 27



CLADIUM

C. mariscoides

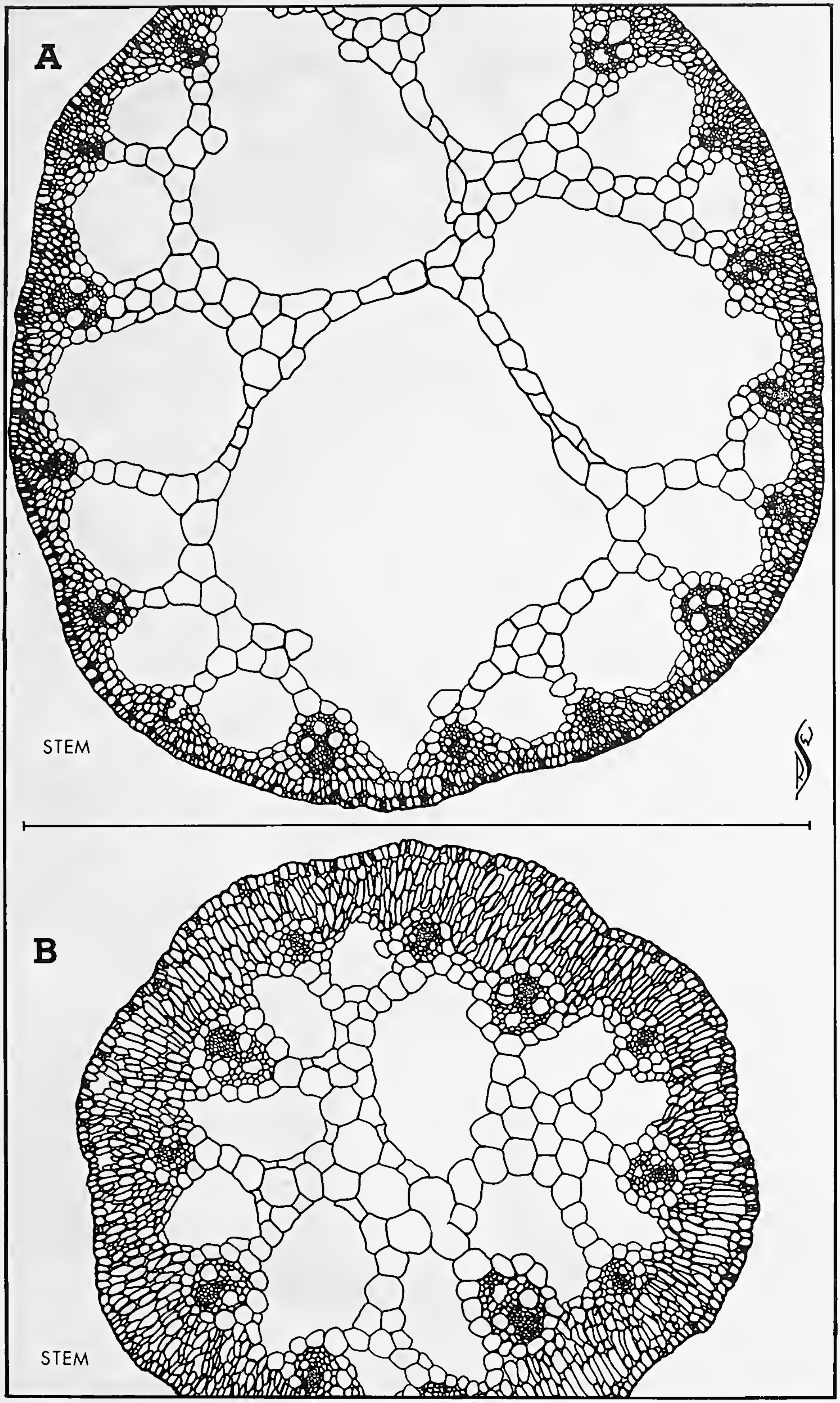
Plate 28



DULICHIUM

D. arundinaceum

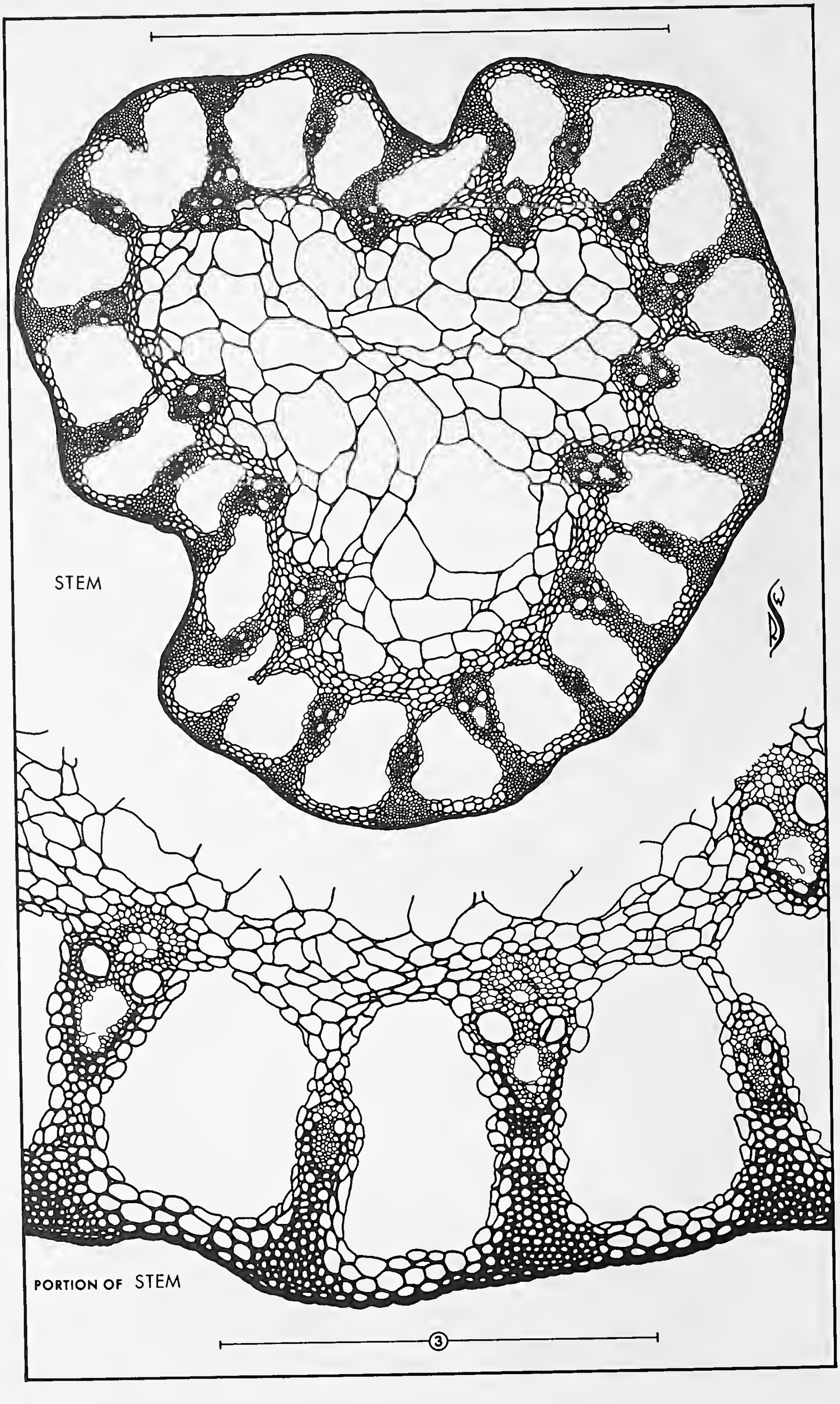
Plate 29



ELEOCHARIS

E. obtusa (A)
E. palustris (B)

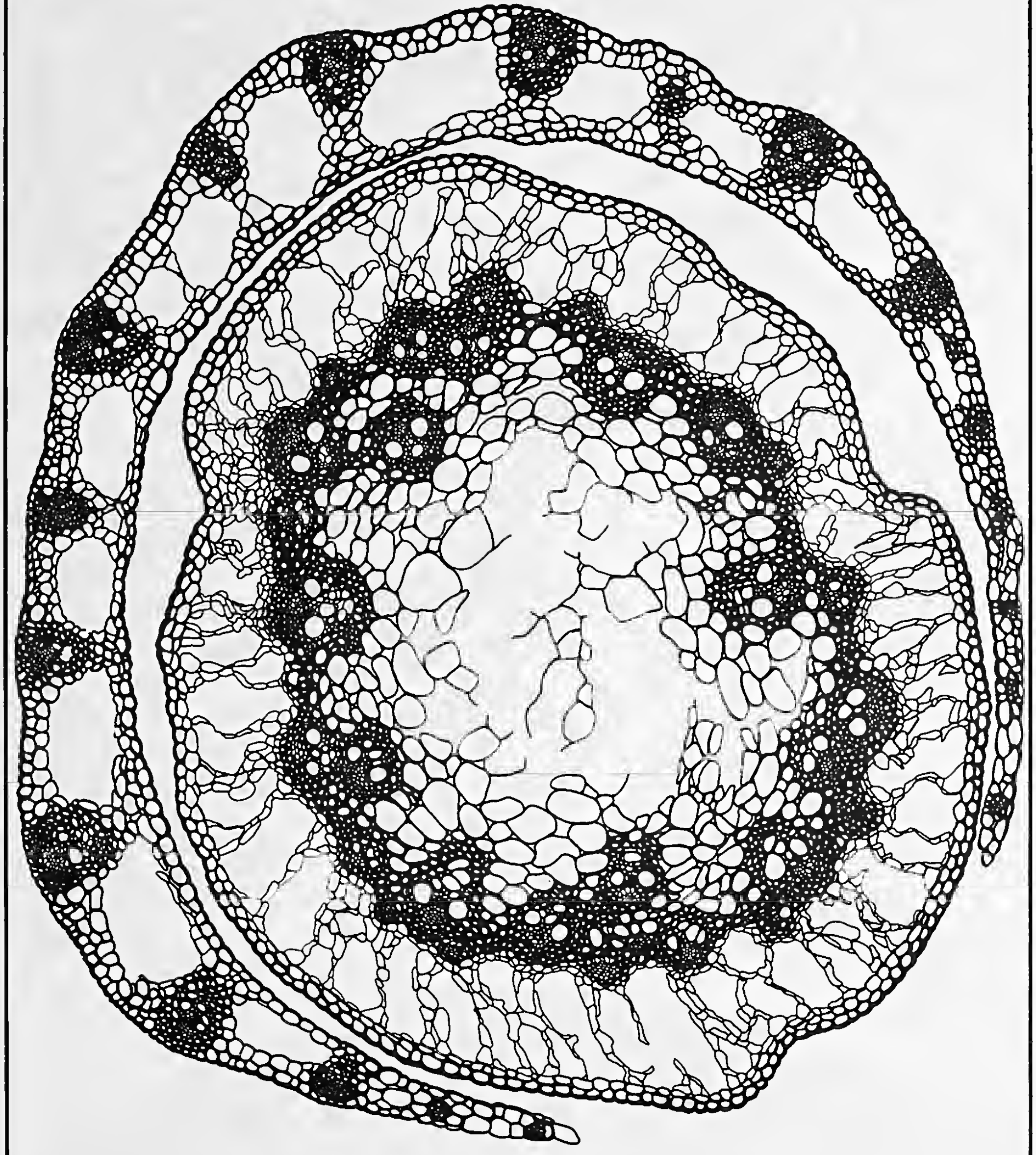
Plate 30



ERIOPHORUM

E. vaginatum

Plate 31

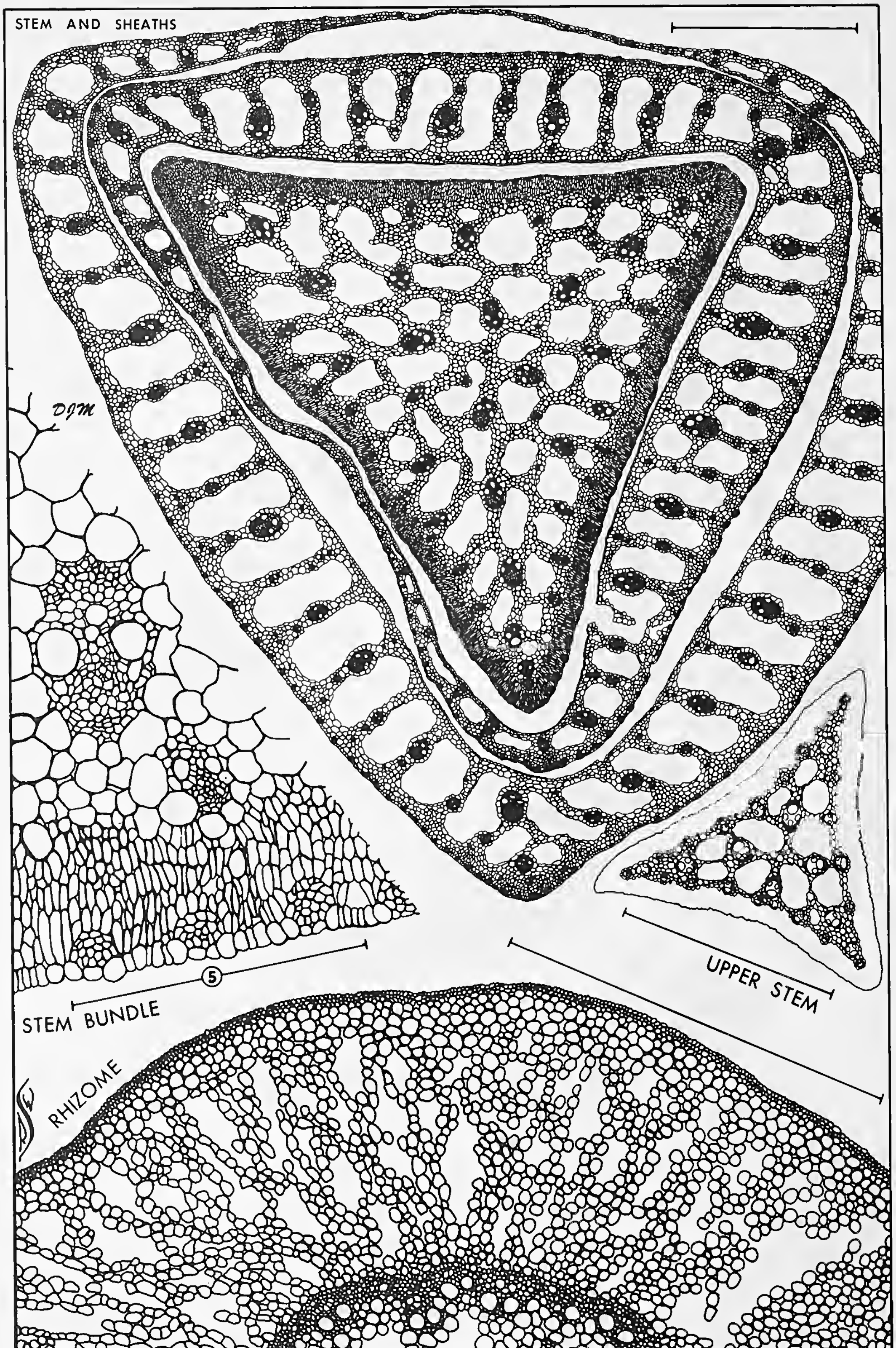


STEM AND SHEATH

RHYNCHOSPORA

R. alba

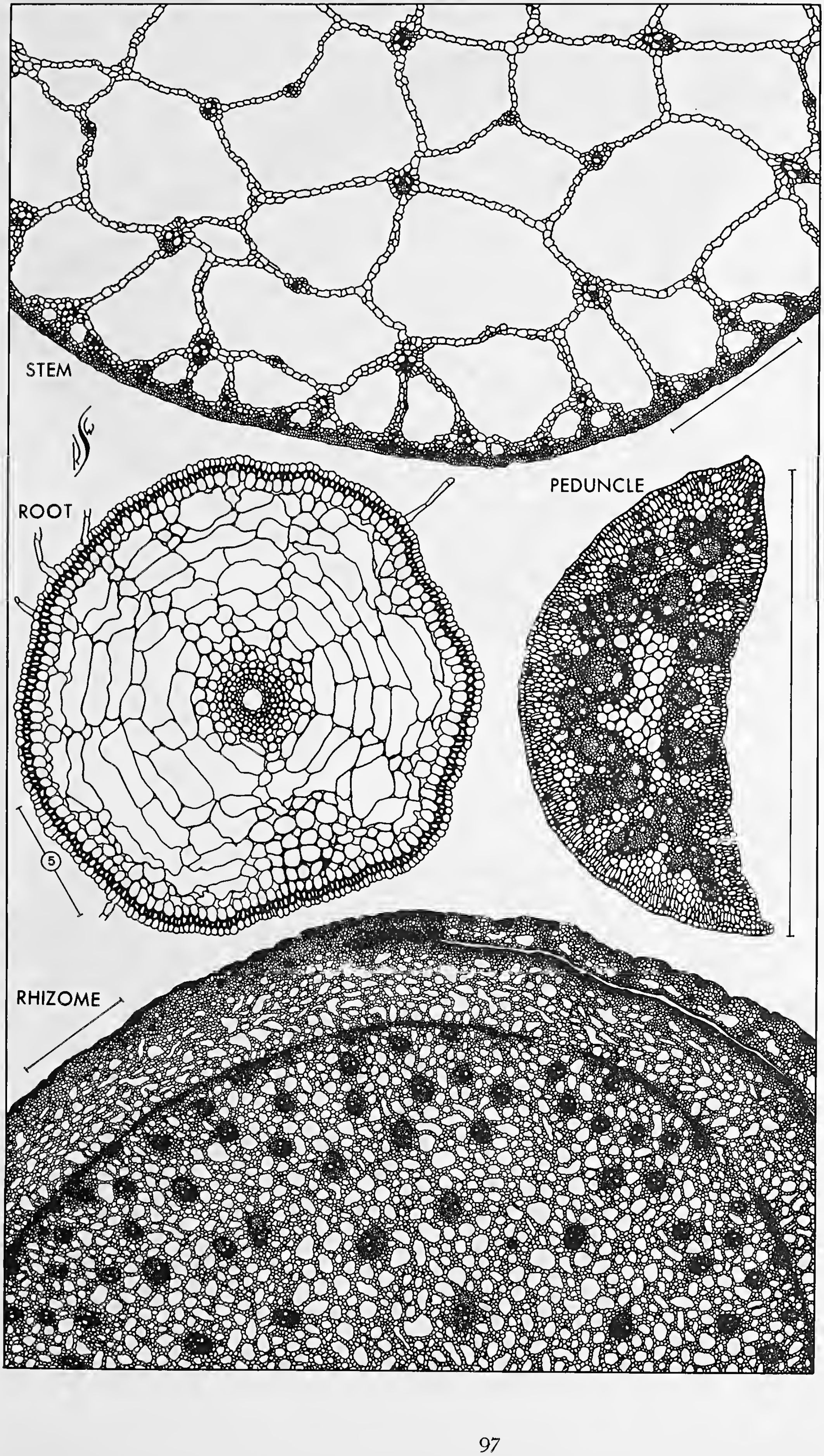
Plate 32



SCIRPUS

S. americanus

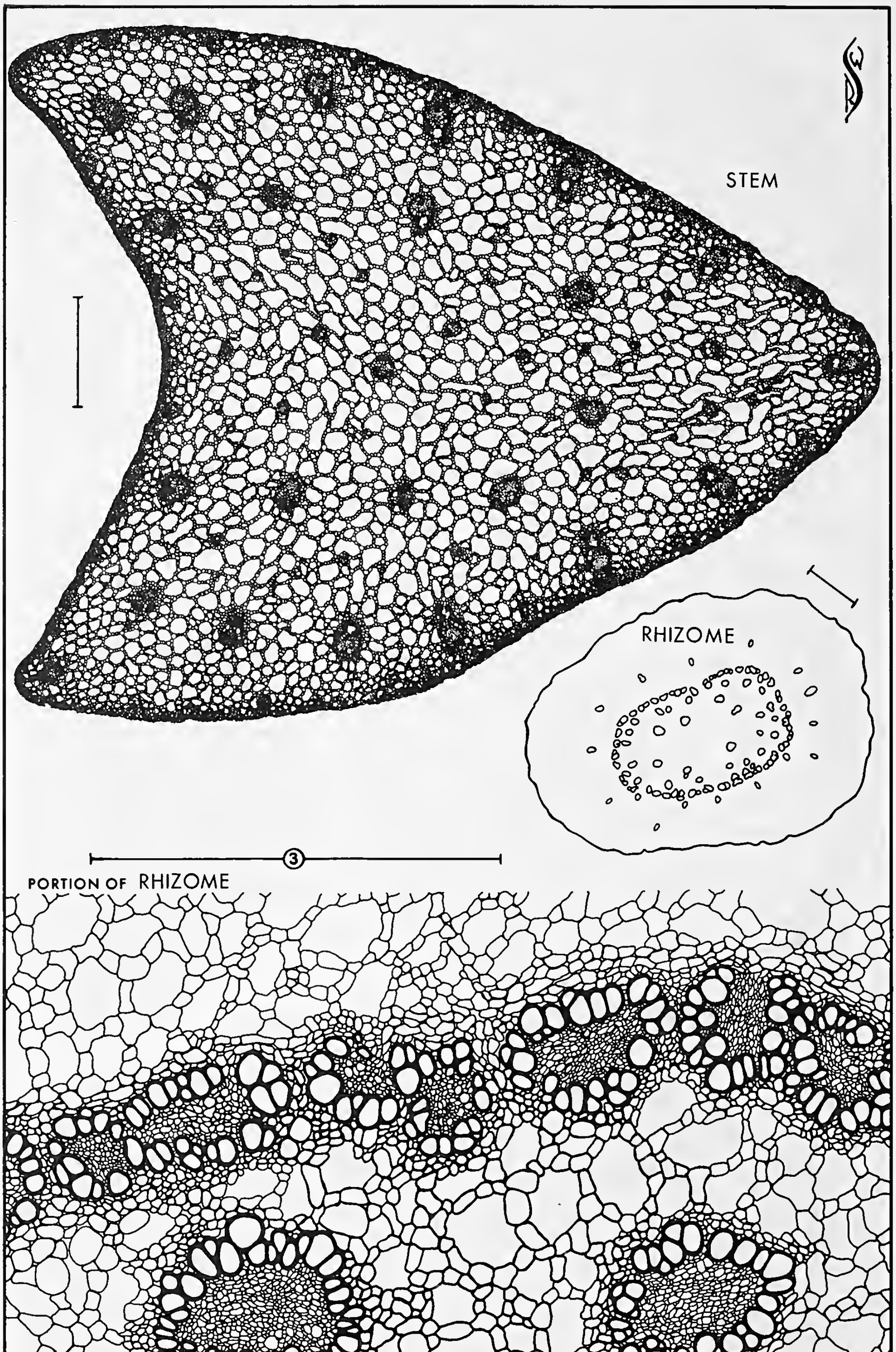
Plate 33



SCIRPUS

S. validus

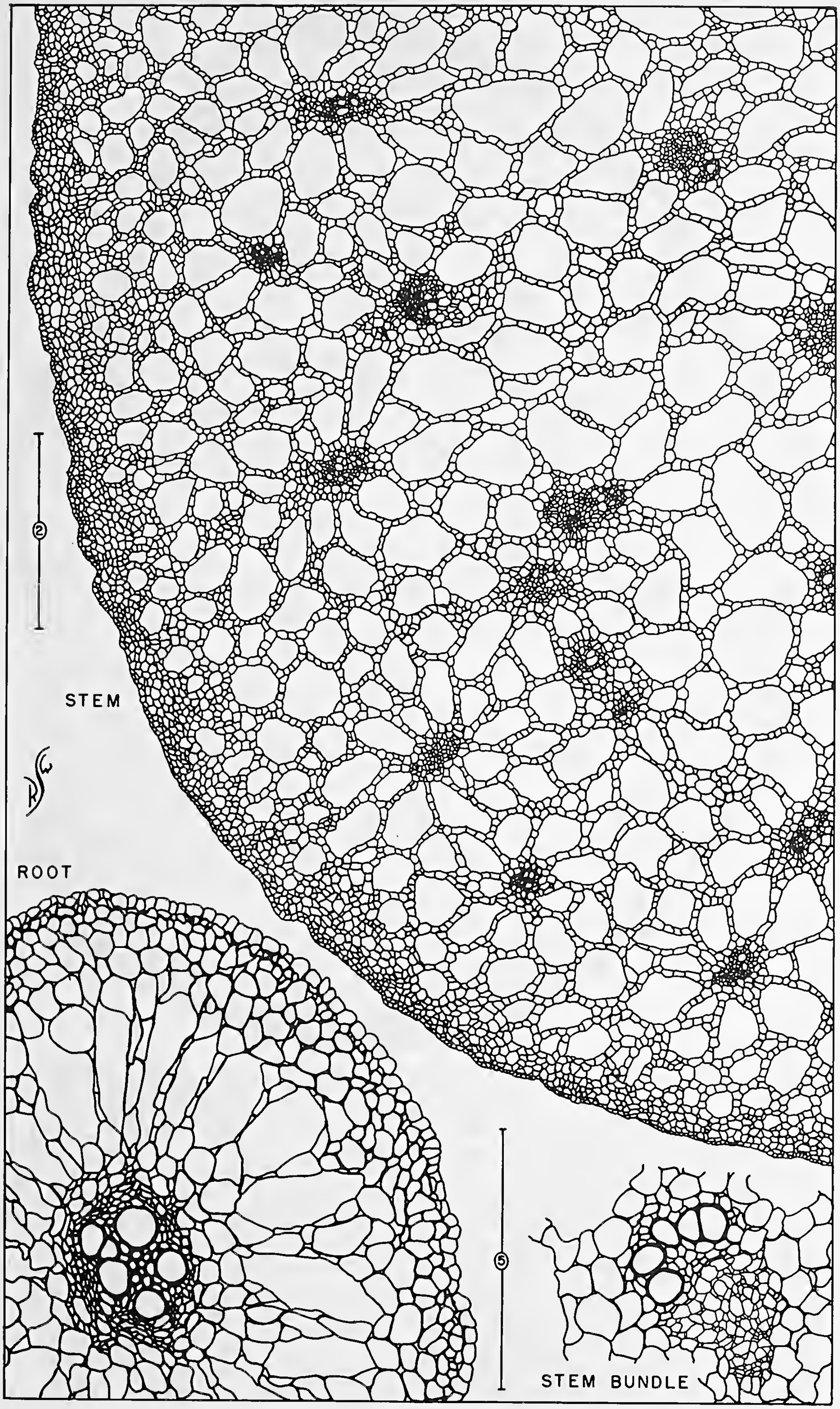
Plate 34



ACORUS

A. calamus

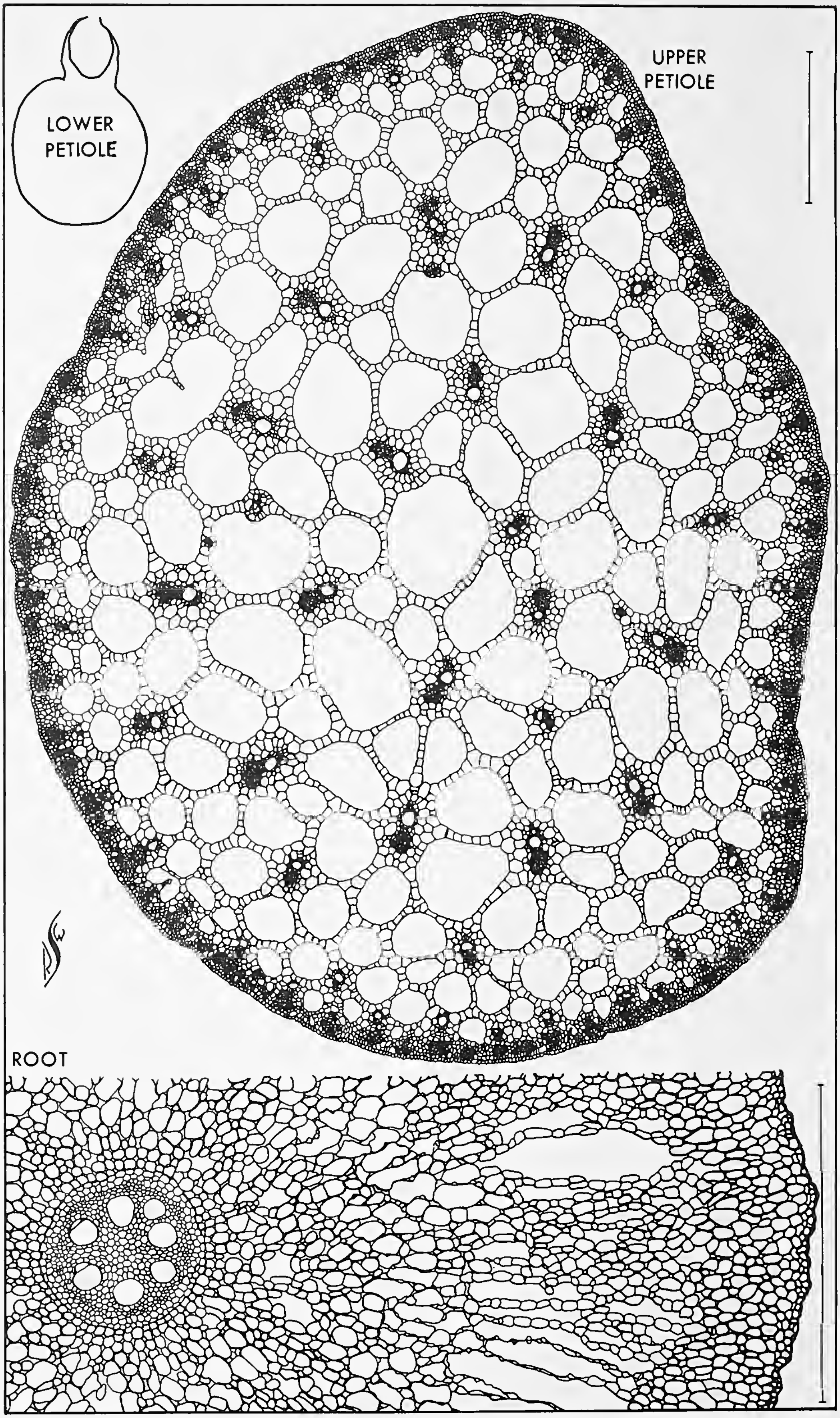
Plate 35



CALLA

C. palustris

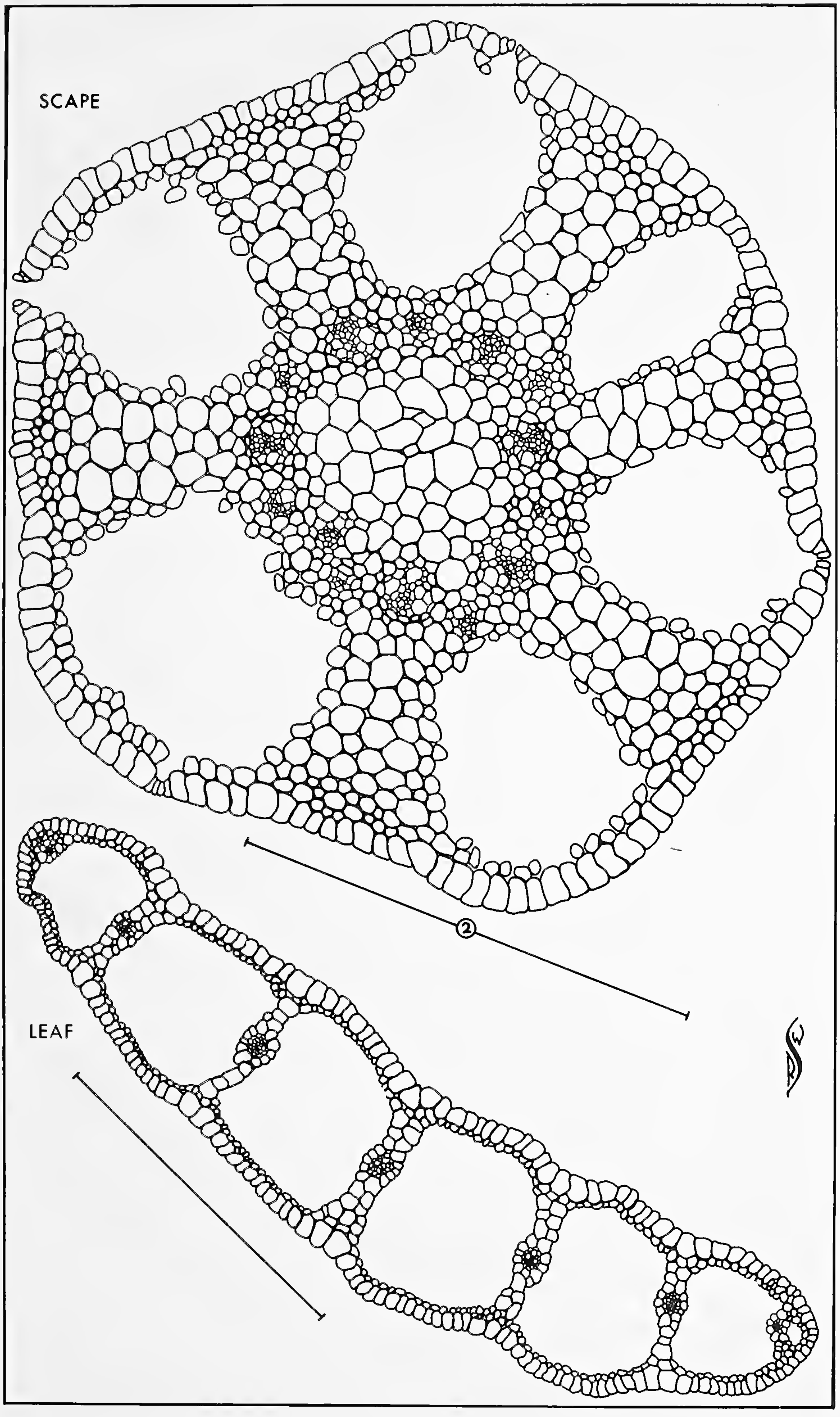
Plate 36



PELTANDRA

P. virginica

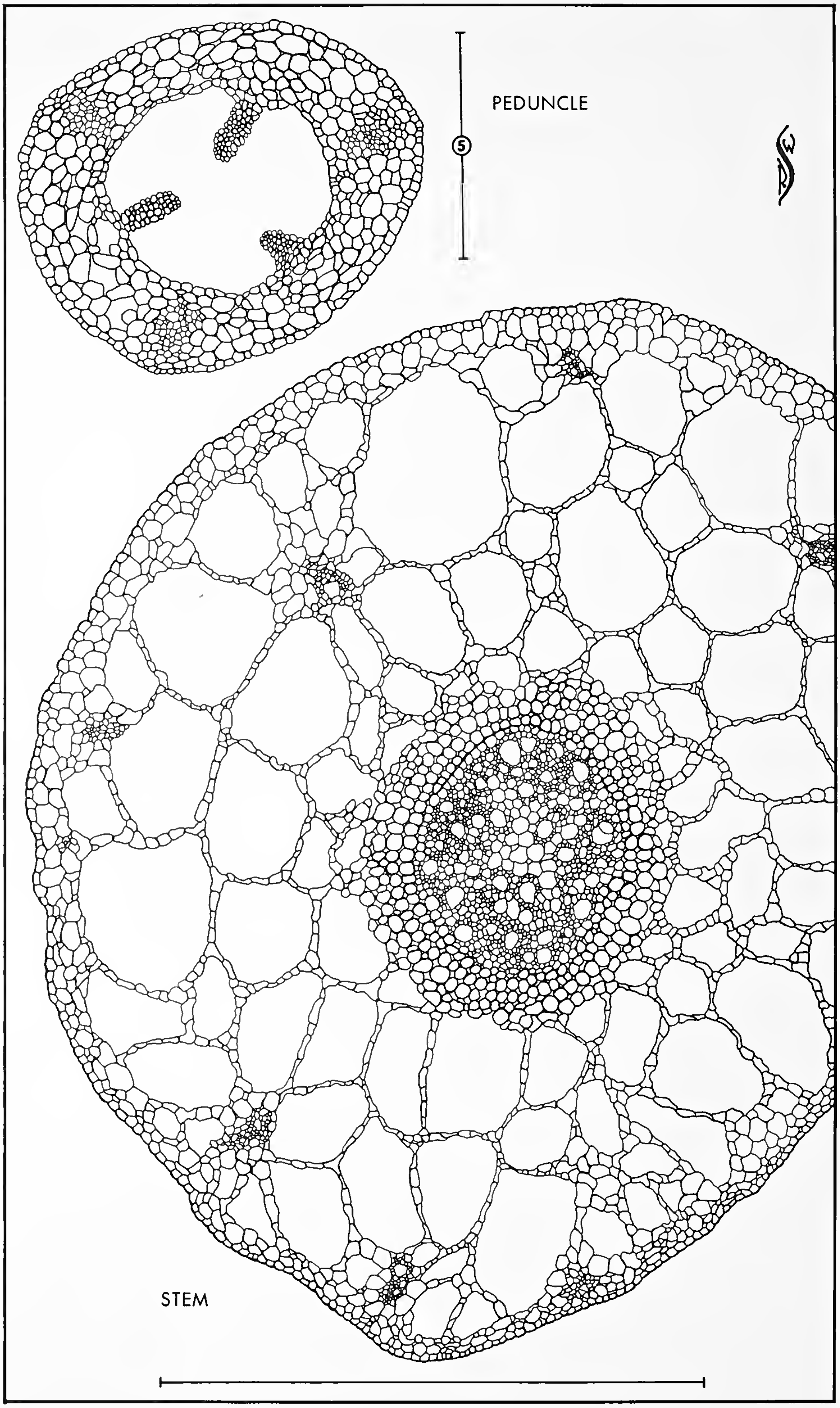
Plate 37



ERIOCAULON

E. septangulare

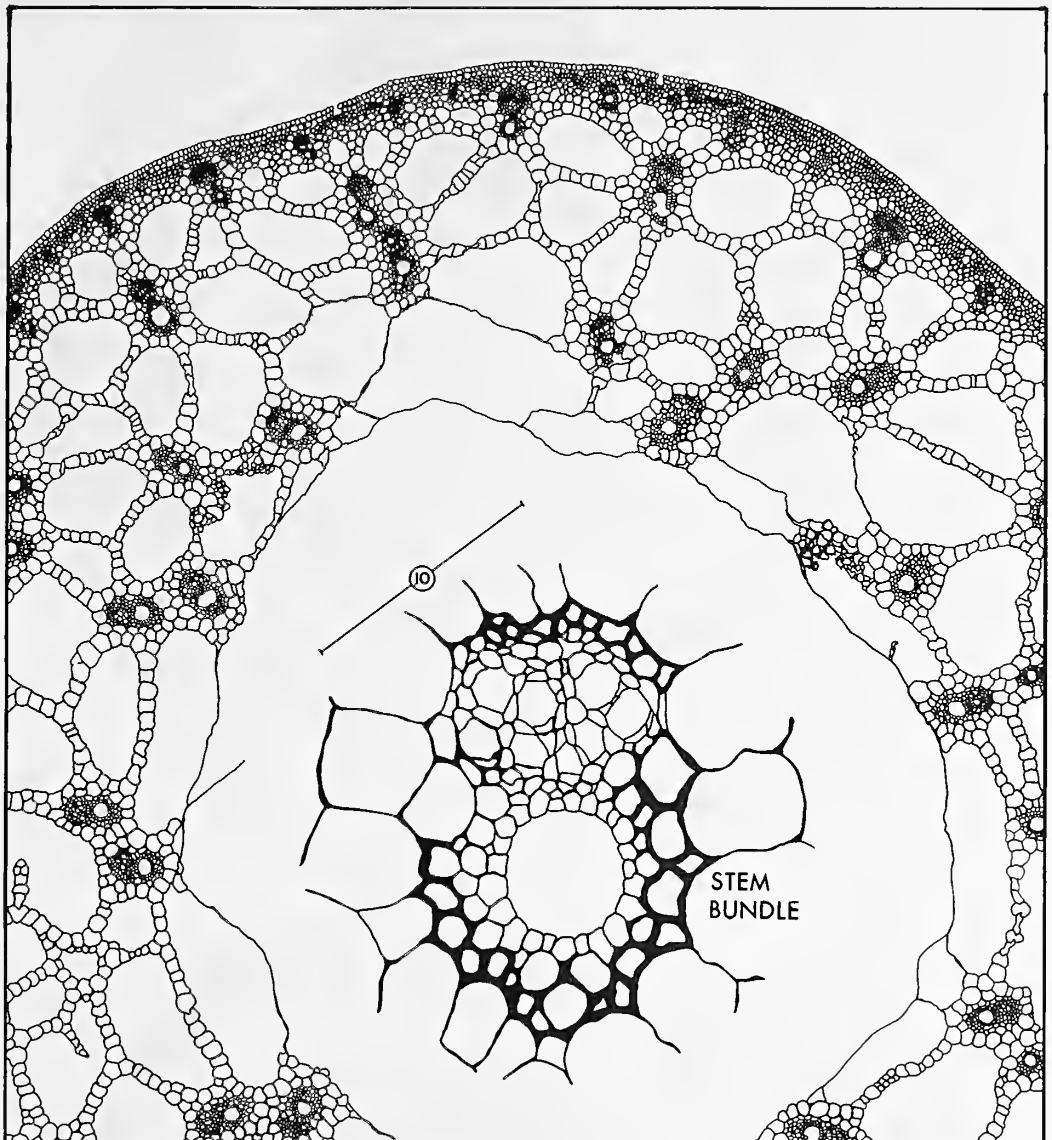
Plate 38



HETERANTHERA

H. dubia

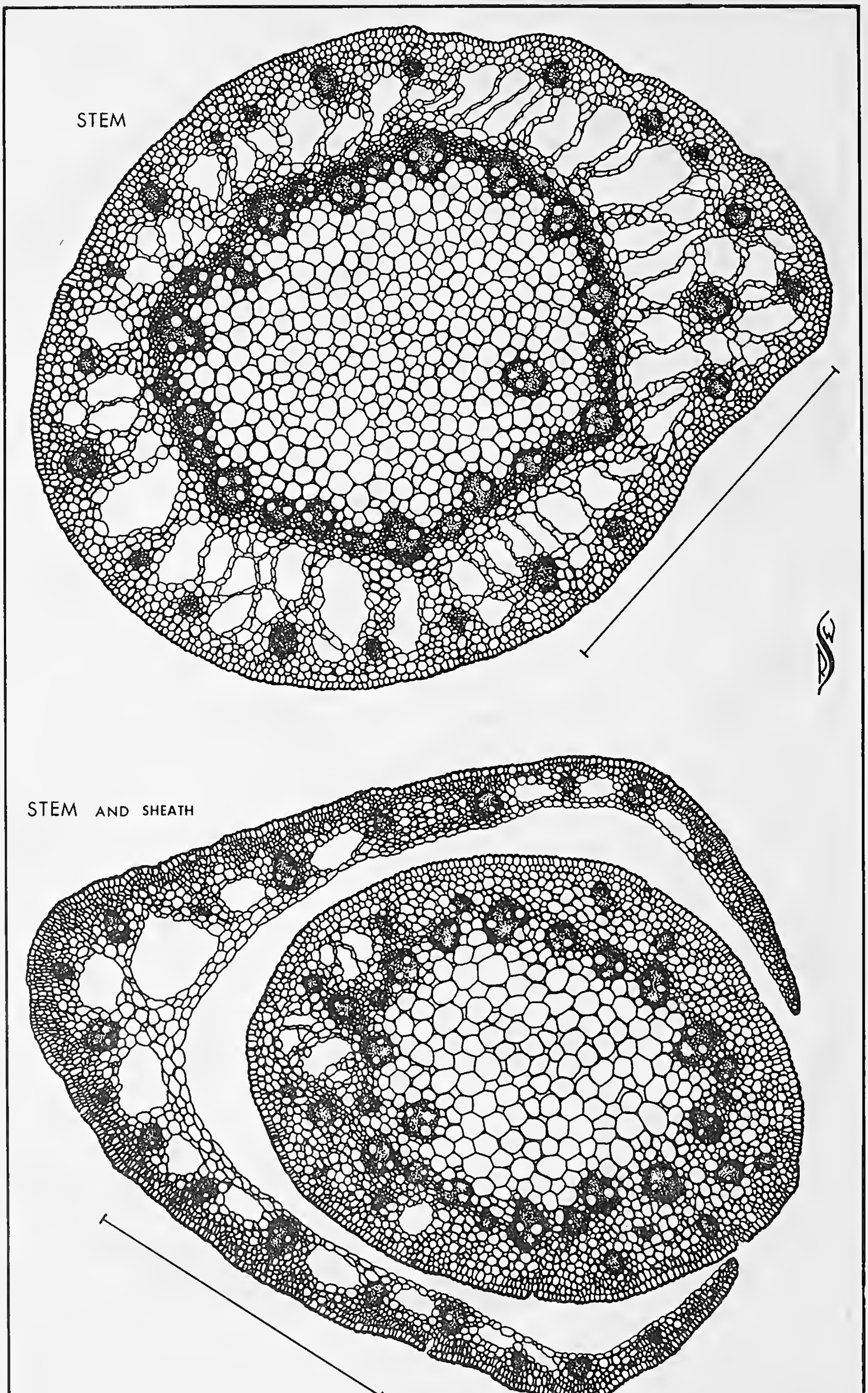
Plate 39



PONTEDERIA

P. cordata

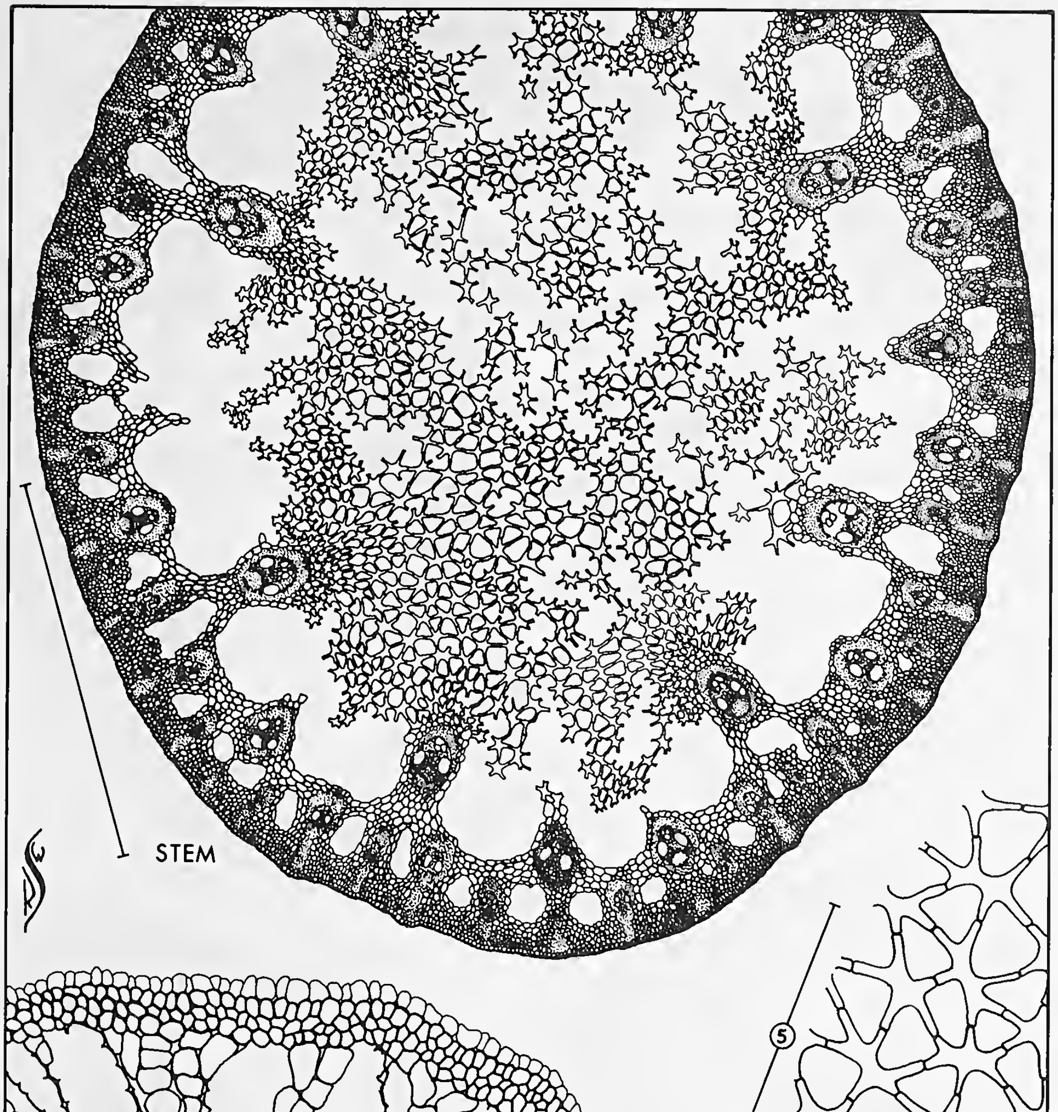
Plate 40



JUNCUS

J. articulatus

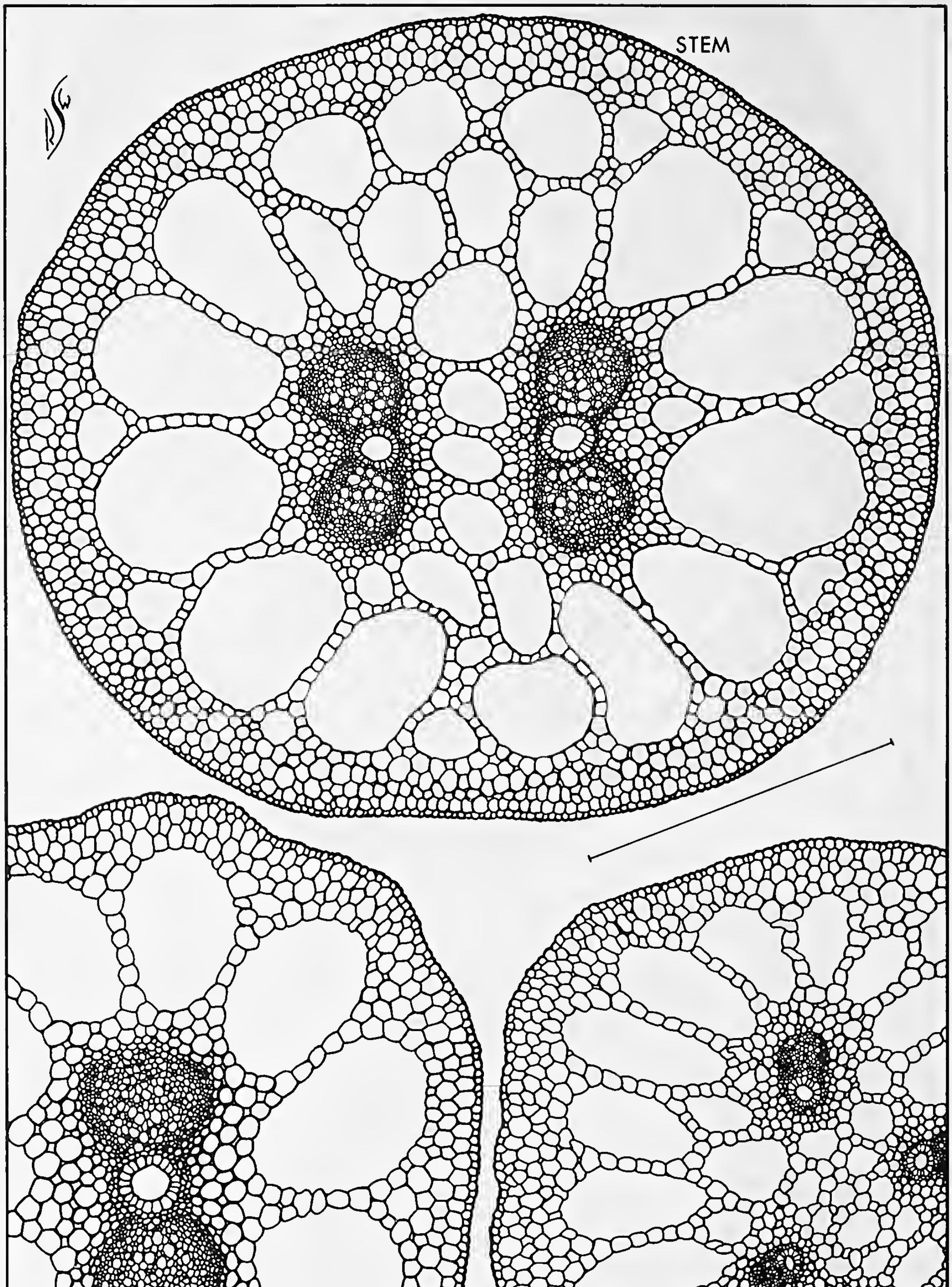
Plate 41



JUNCUS

J. effusus

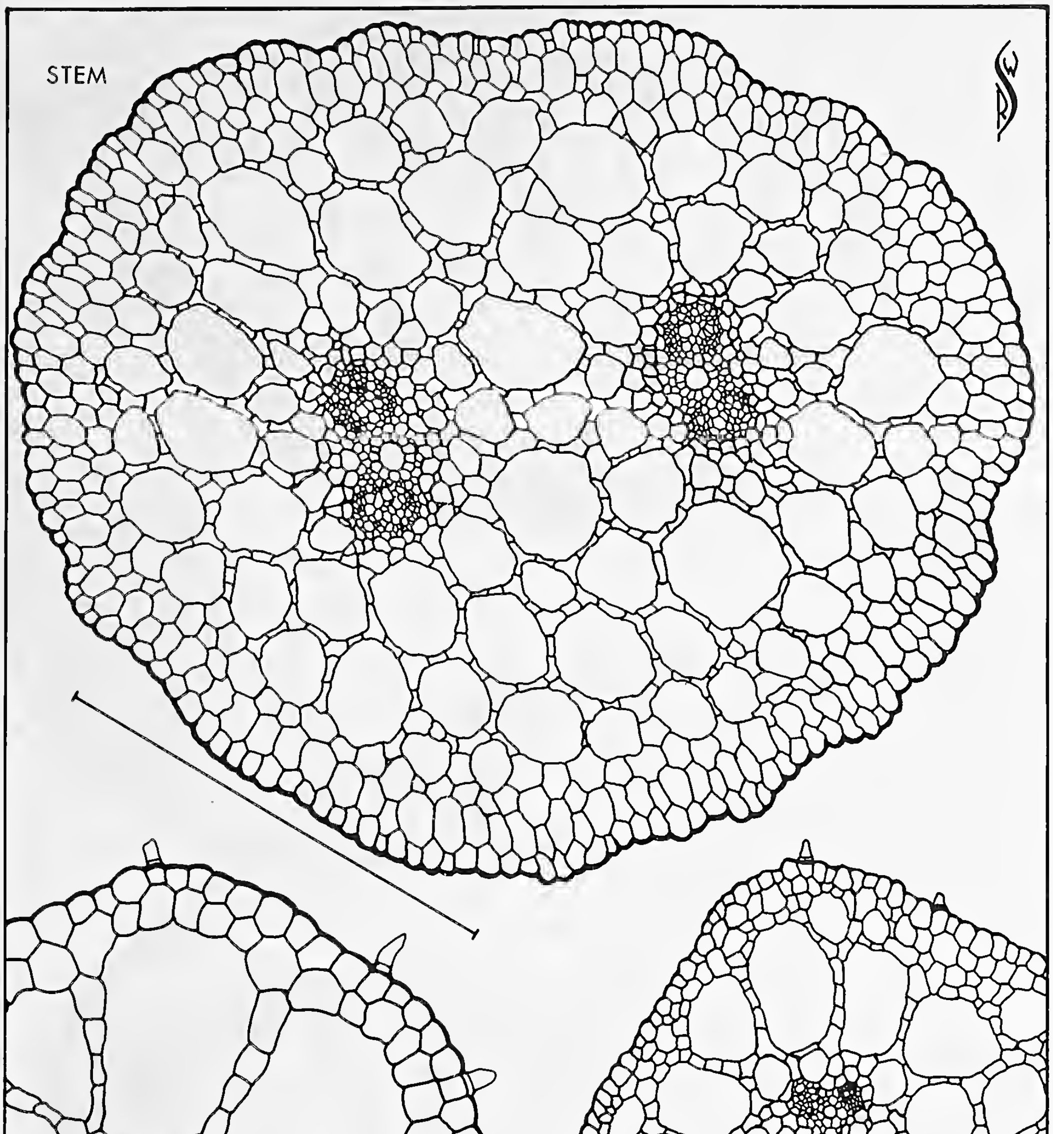
Plate 42



BRASENIA

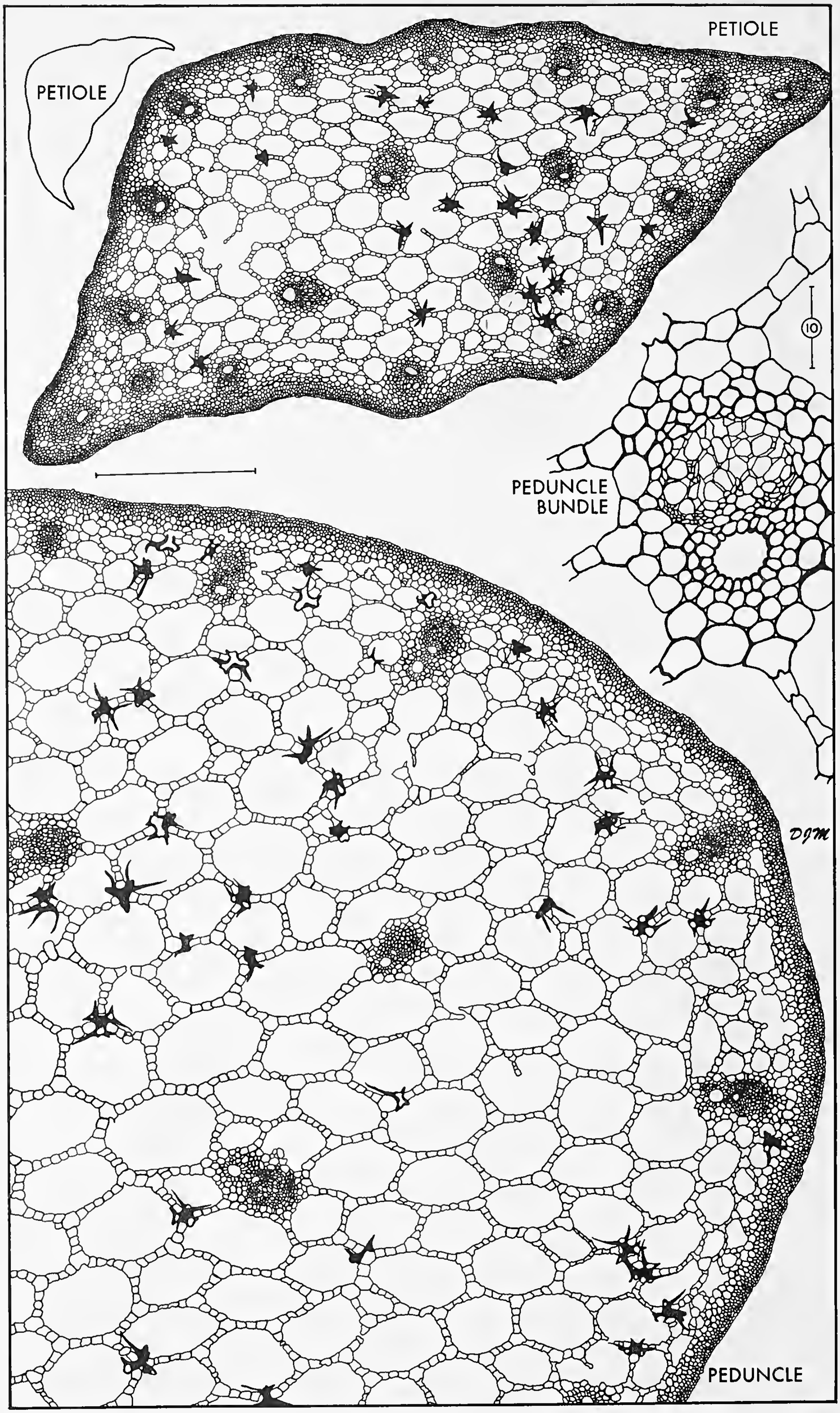
B. schreberi

Plate 43



CABOMBA

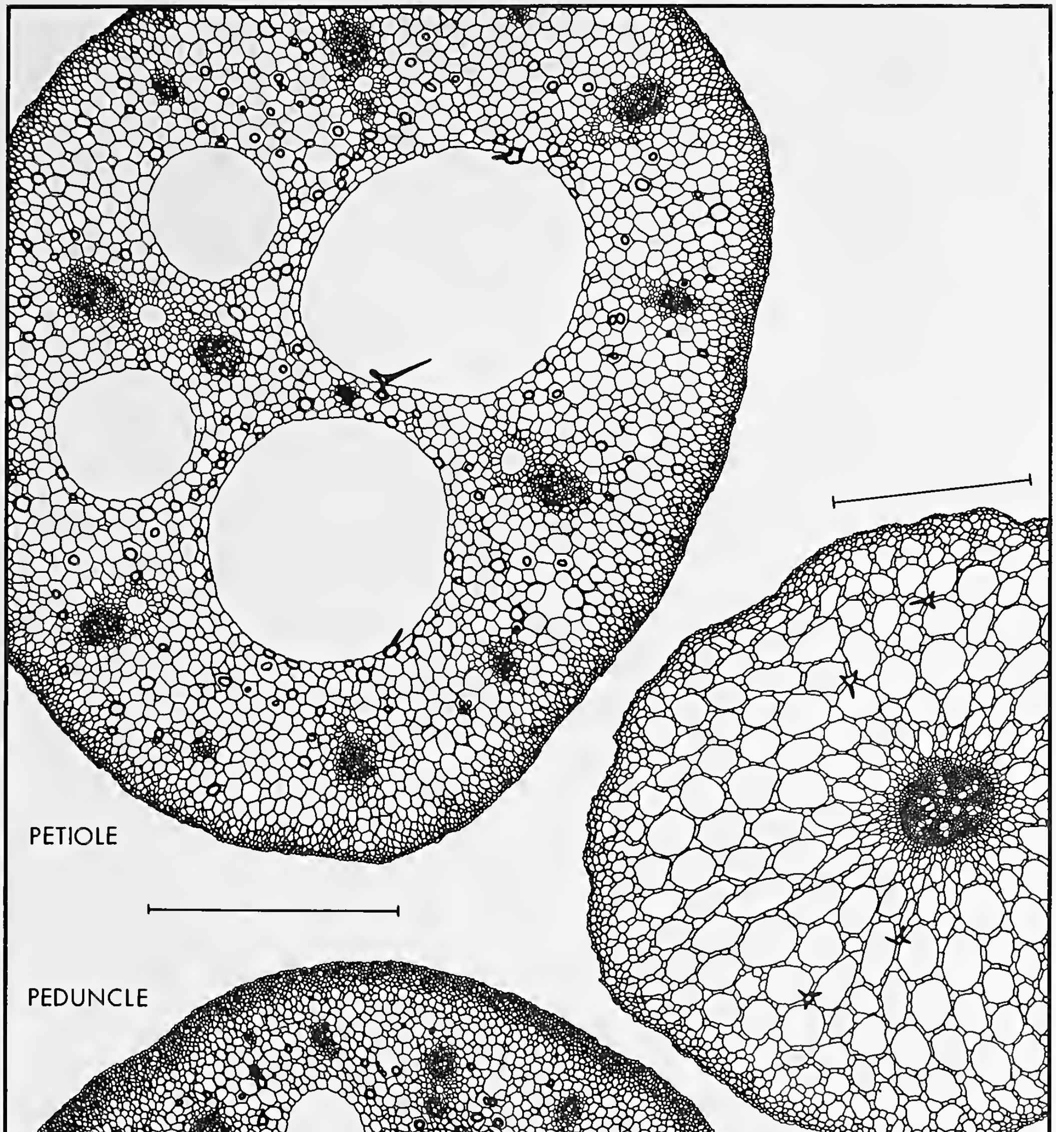
C. caroliniana



NUPHAR

N. luteum

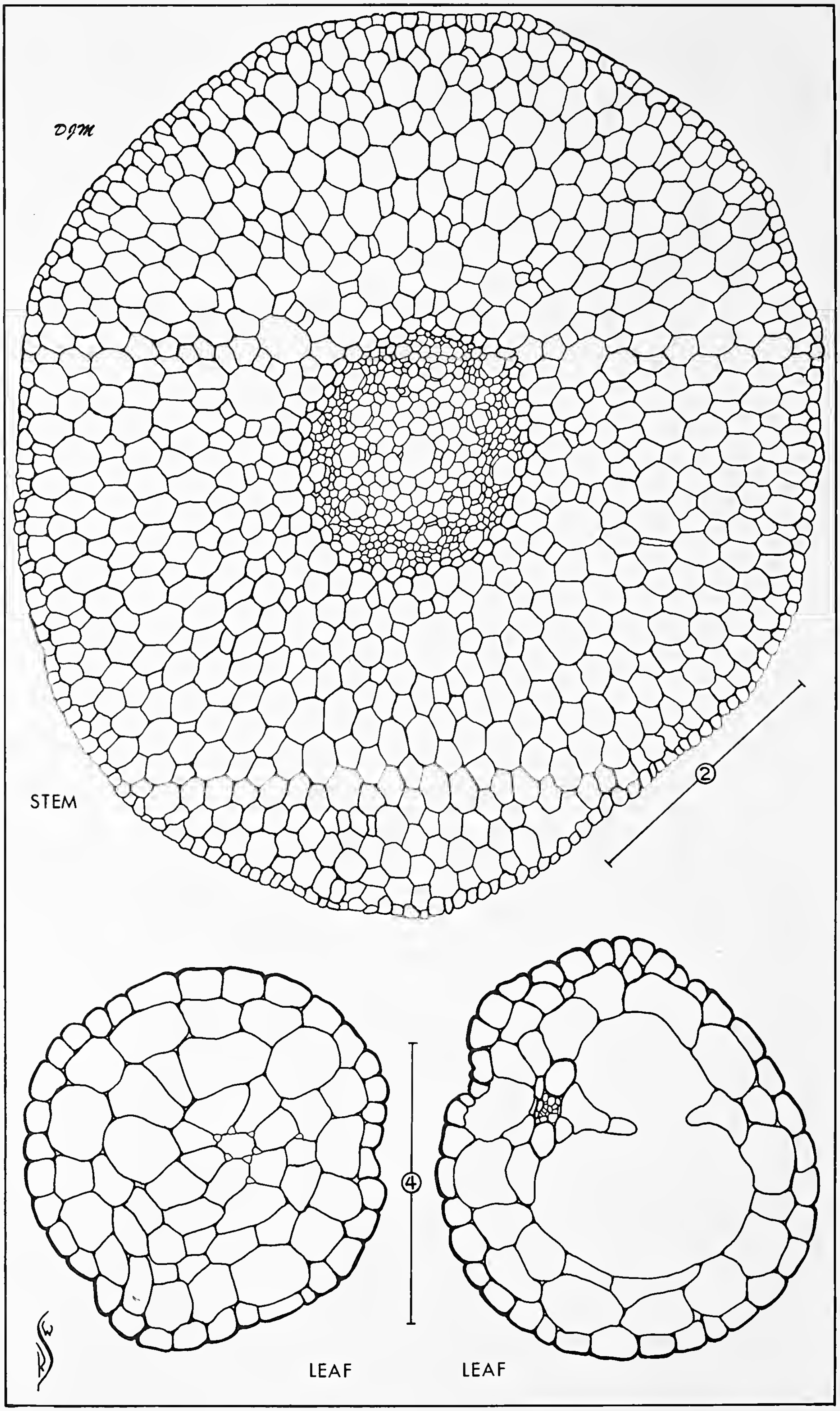
Plate 45



NYMPHAEA

N. odorata

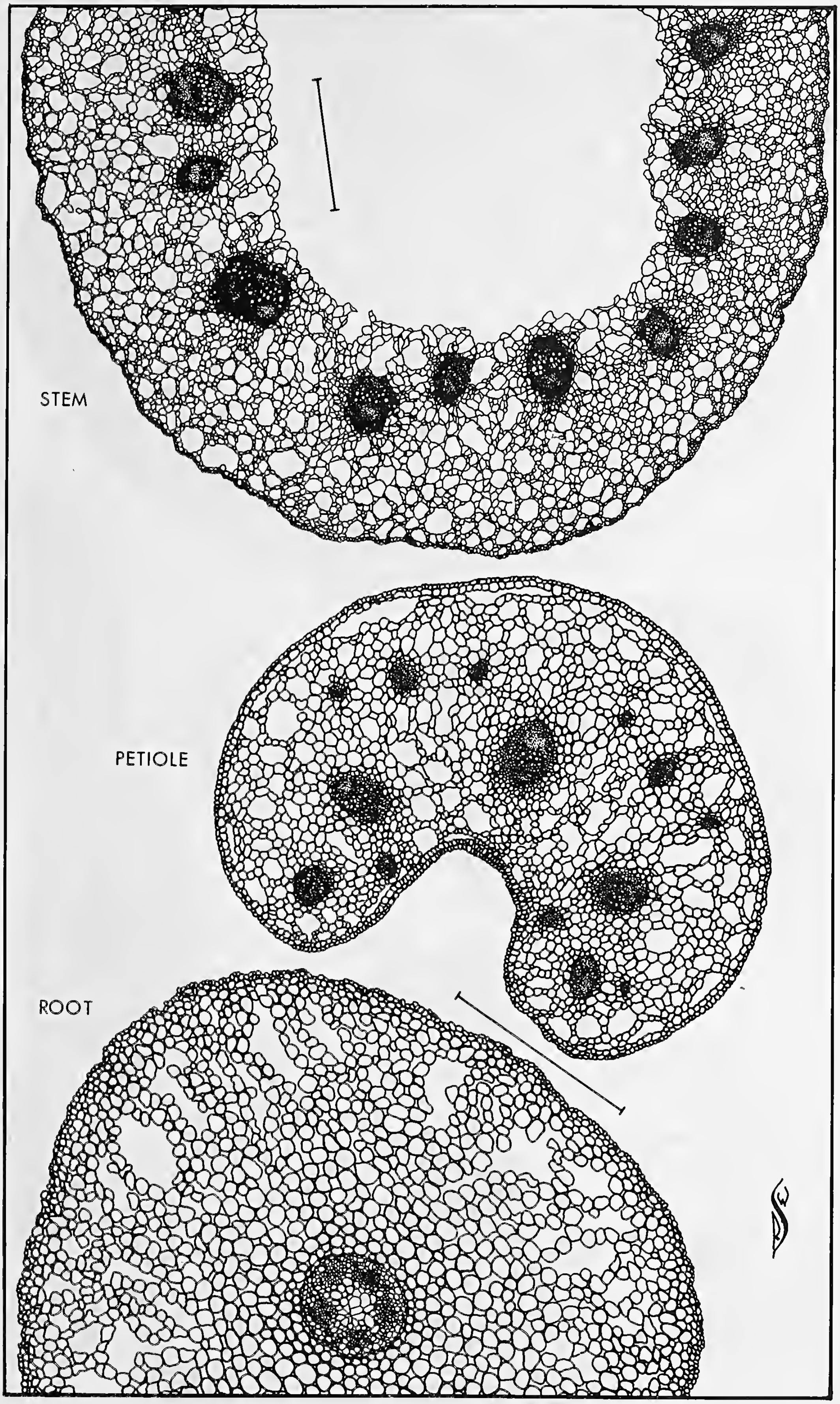
Plate 46



CERATOPHYLLUM

C. demersum

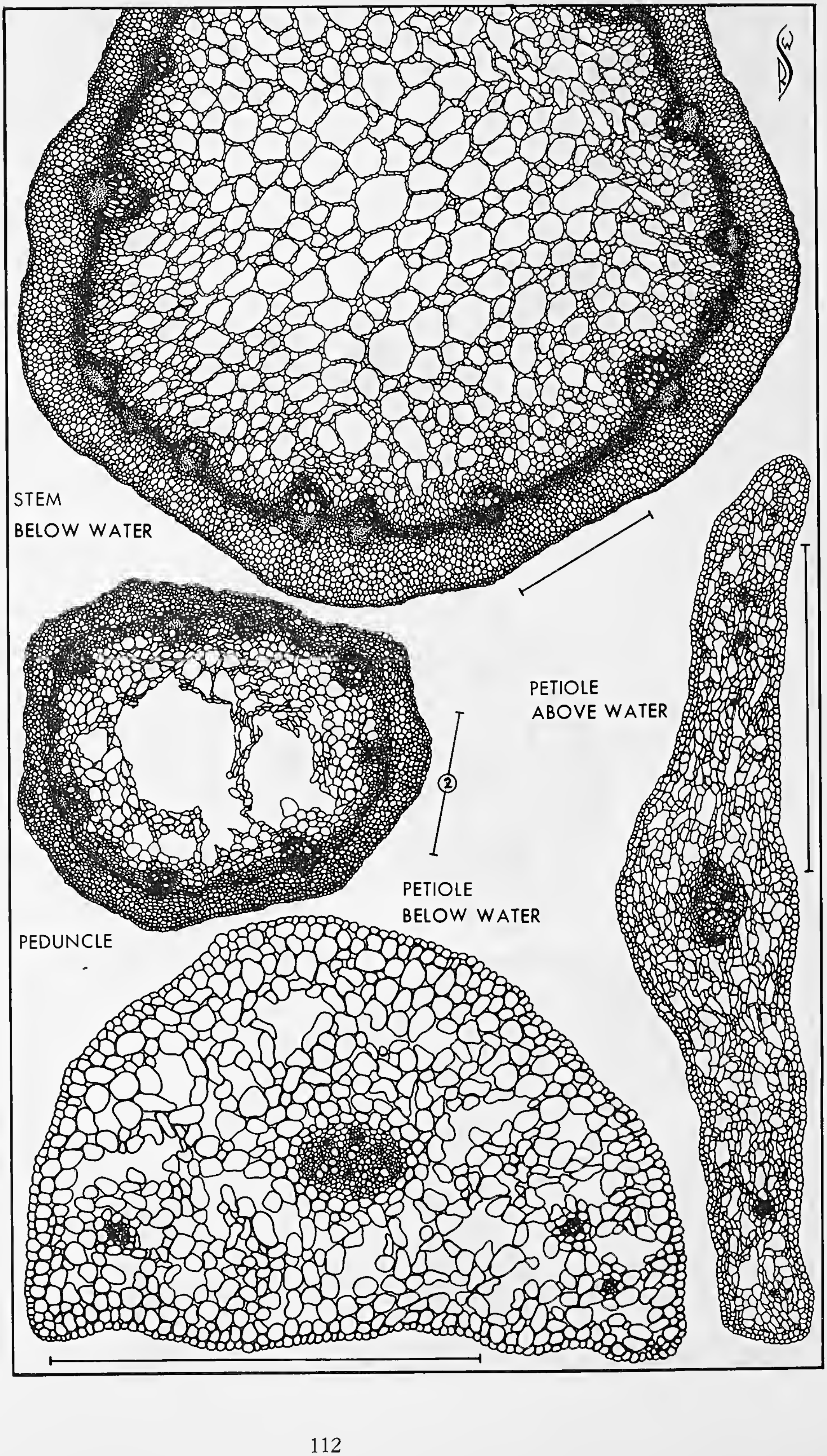
Plate 47



CALTHA

C. palustris

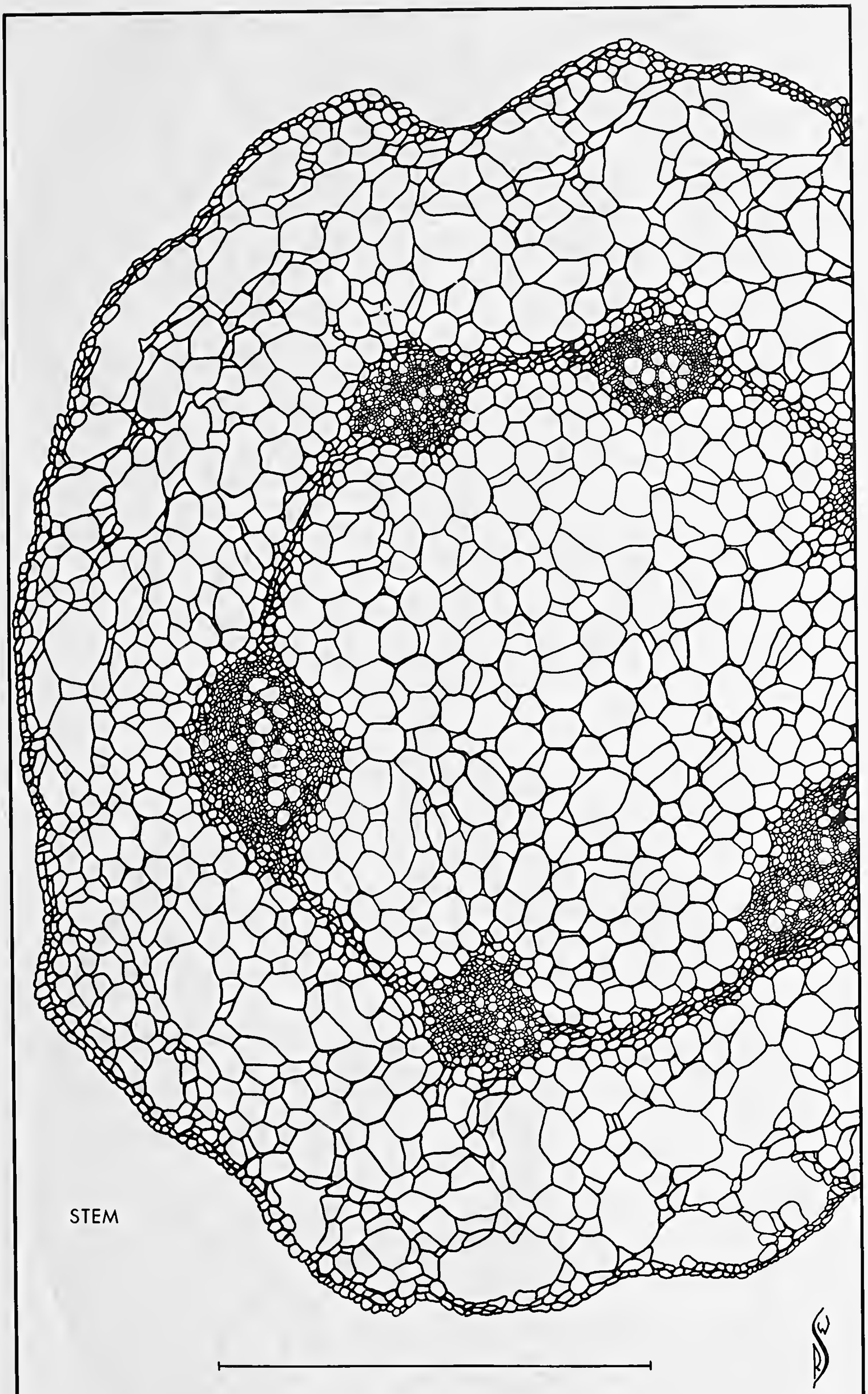
Plate 48



ARMORACIA

A. aquatica

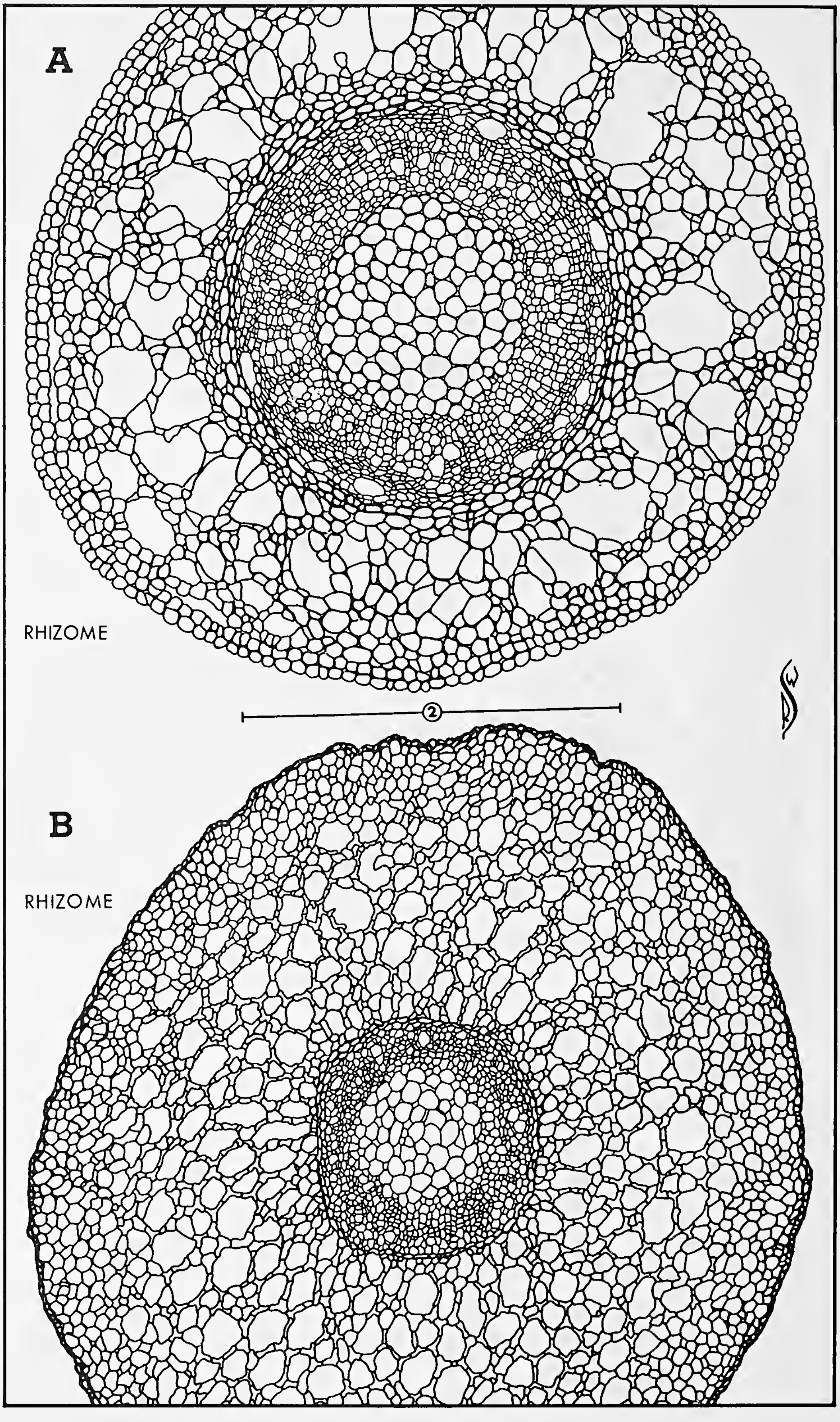
Plate 49



NASTURTIUM

N. officinale

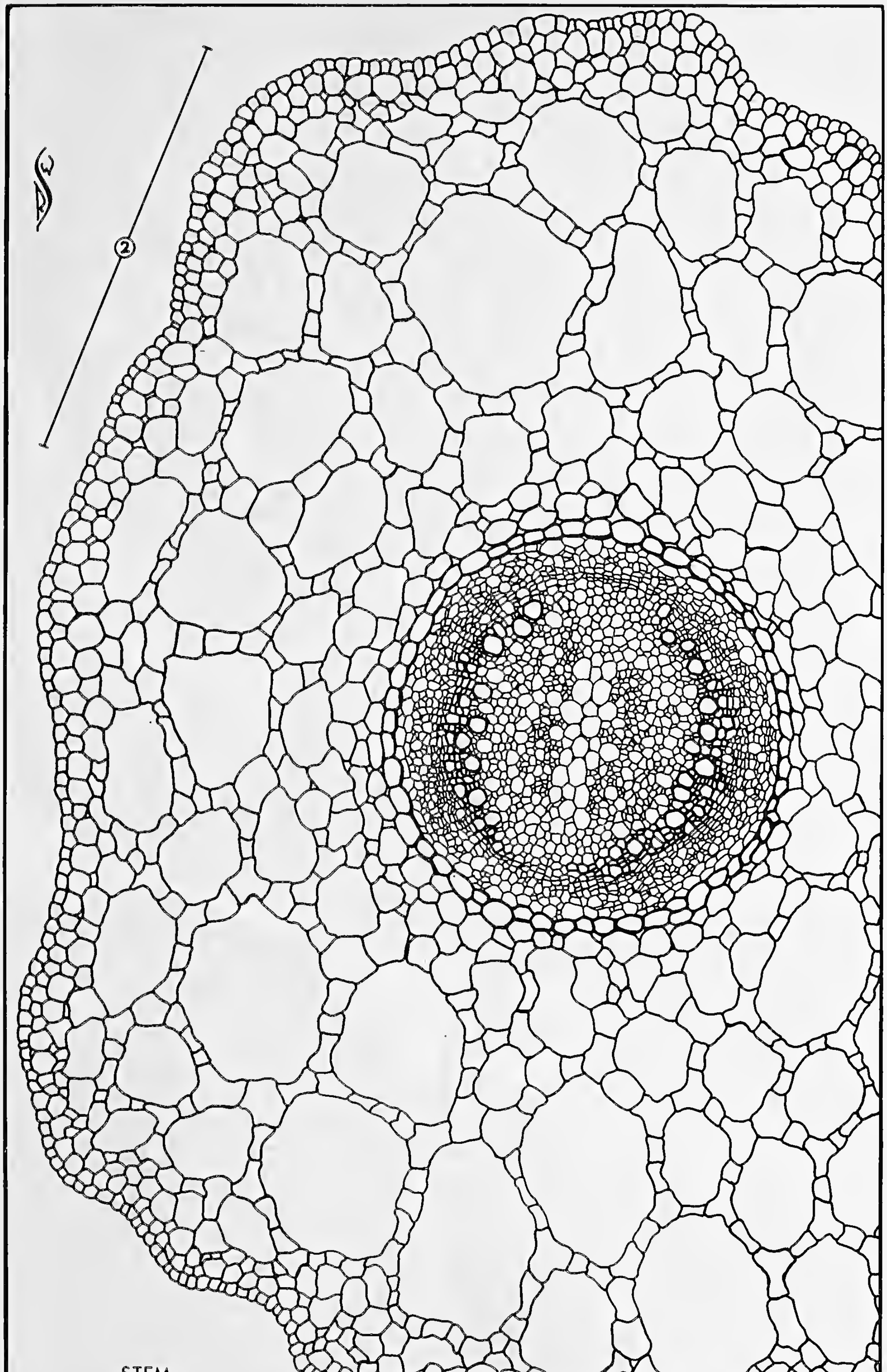
Plate 50



HYPERICUM
TRIADENUM

H. ellipticum (A)
T. fraseri (B)

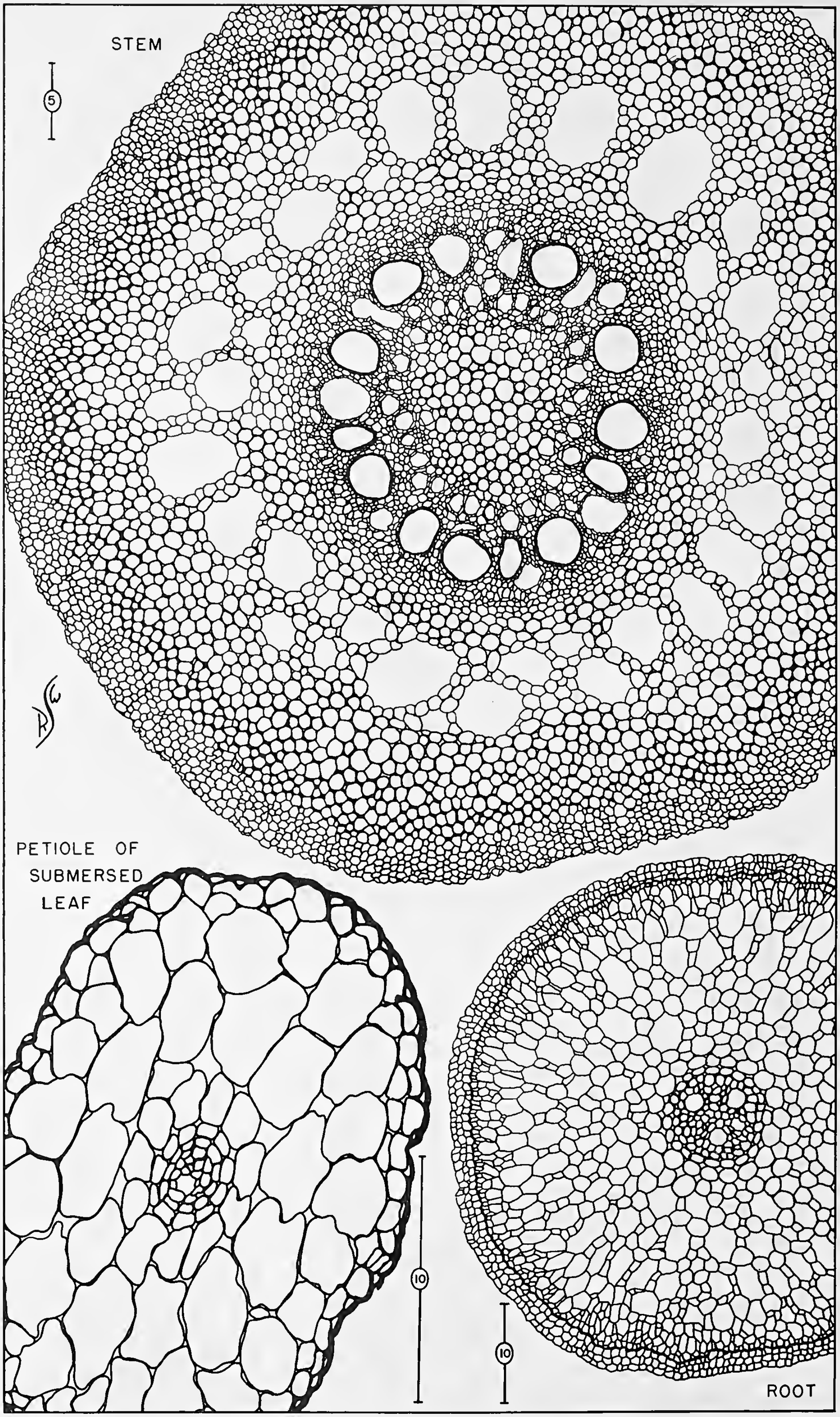
Plate 51



LUDWIGIA

L. palustris

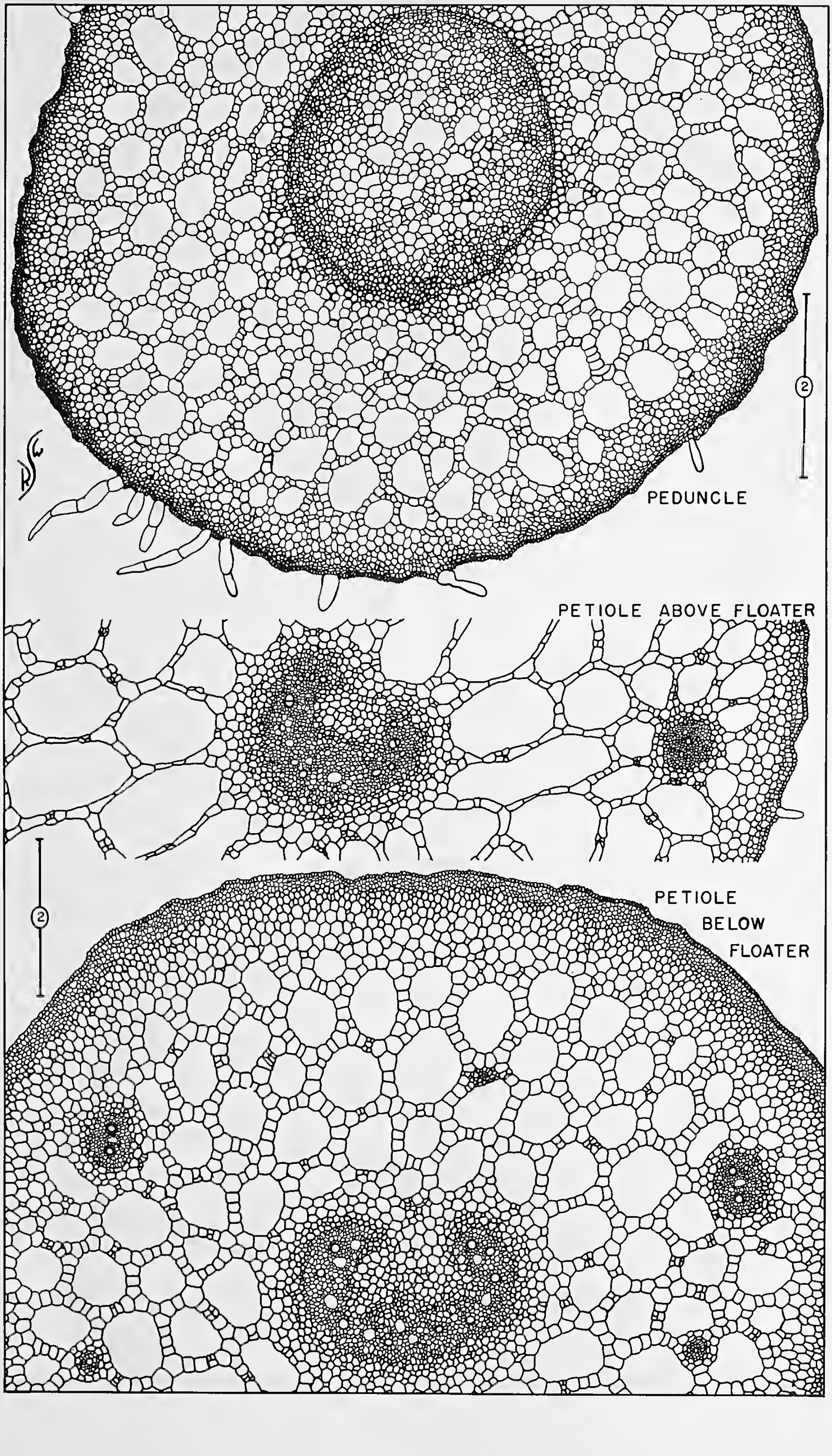
Plate 52



TRAPA

T. natans

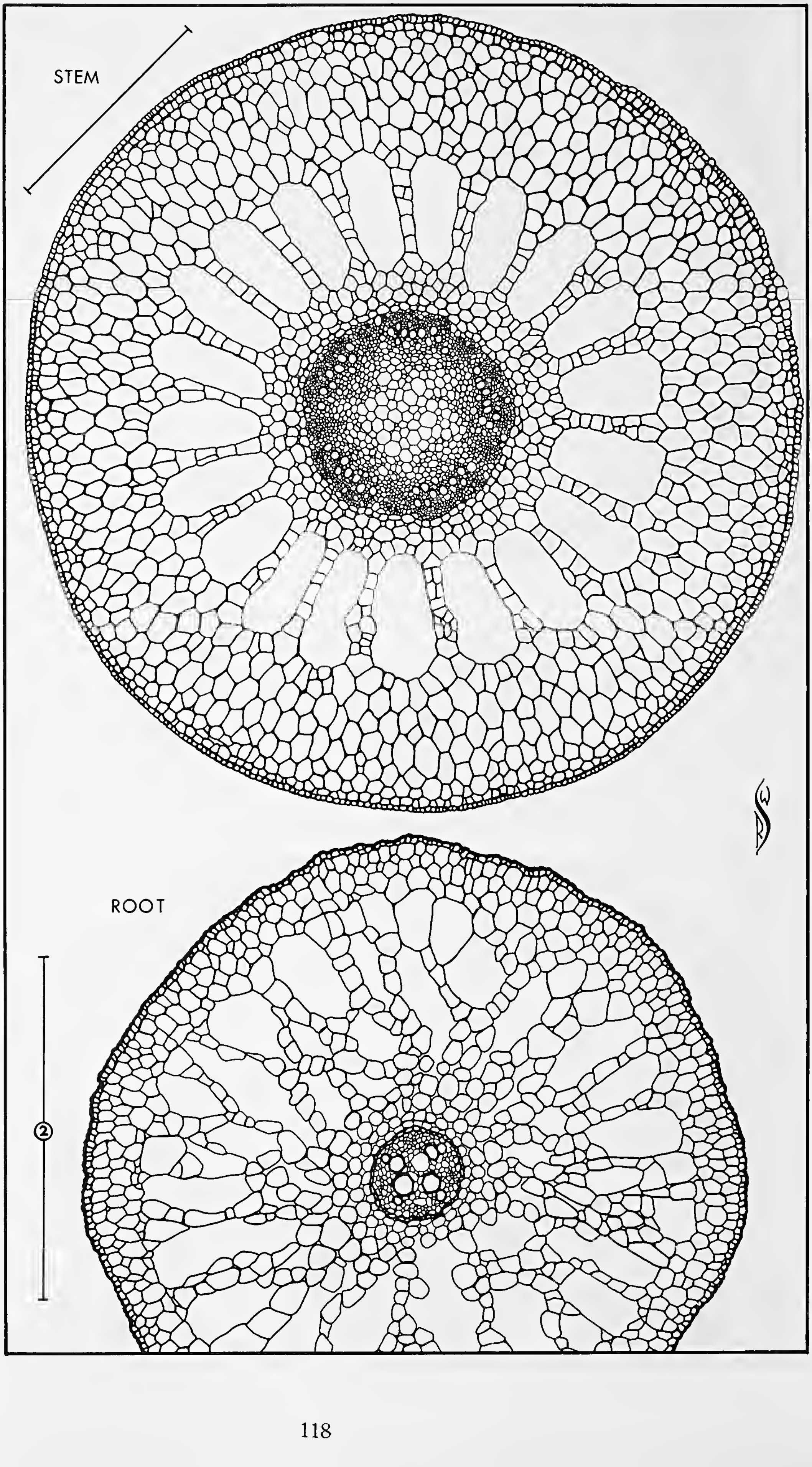
Plate 53



TRAPA

T. natans

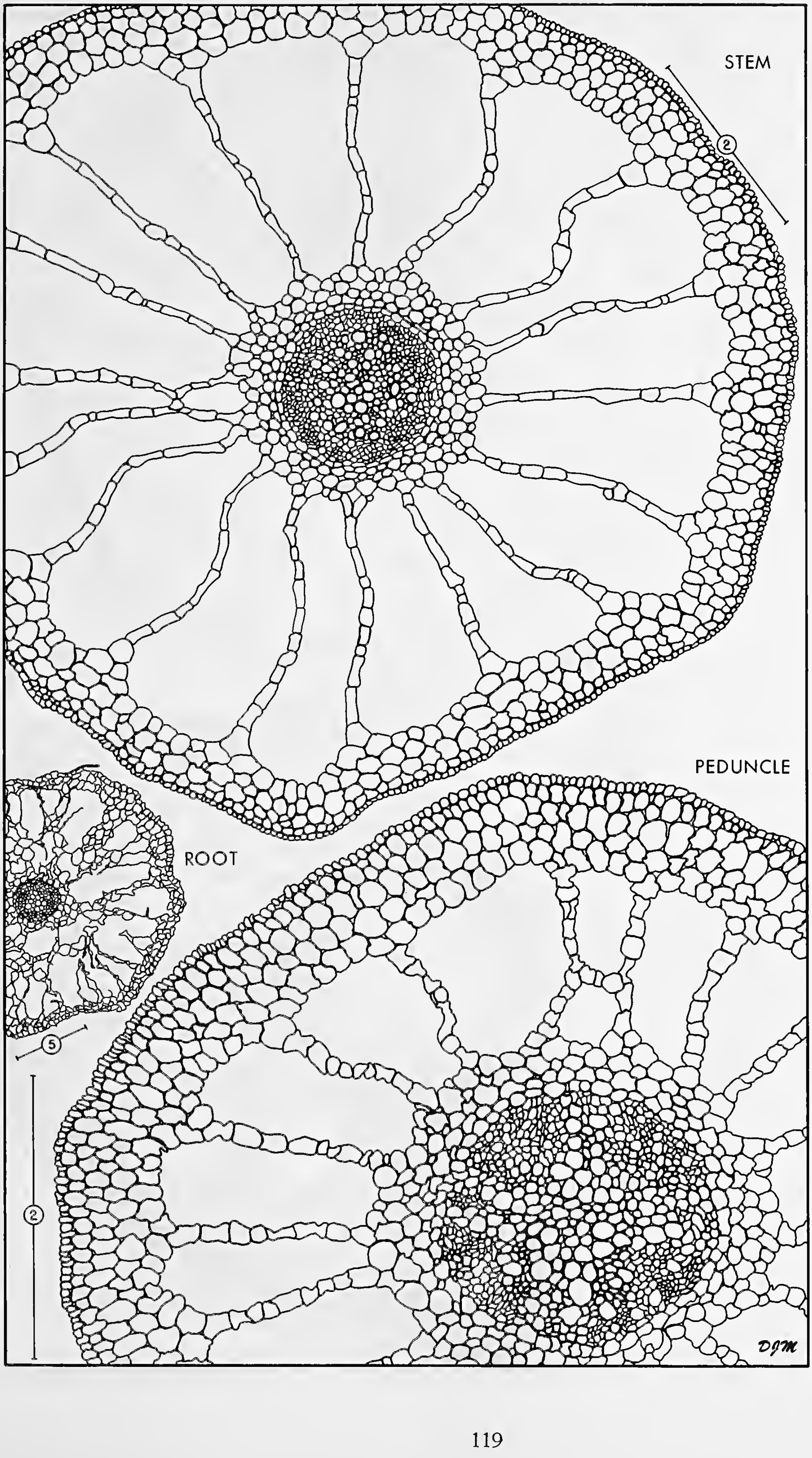
Plate 54



MYRIOPHYLLUM

M. brasiliense

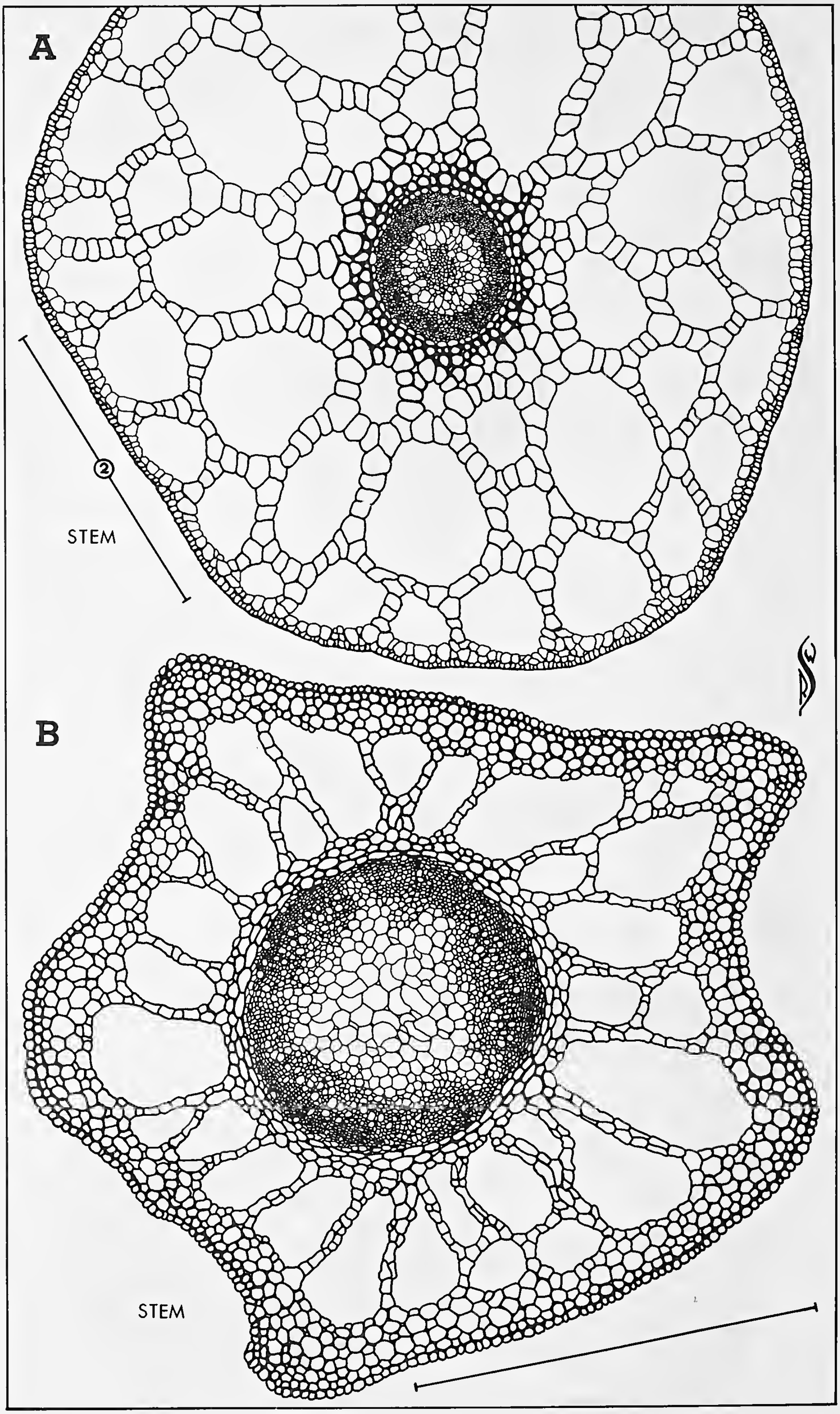
Plate 55



MYRIOPHYLLUM

M. spicatum

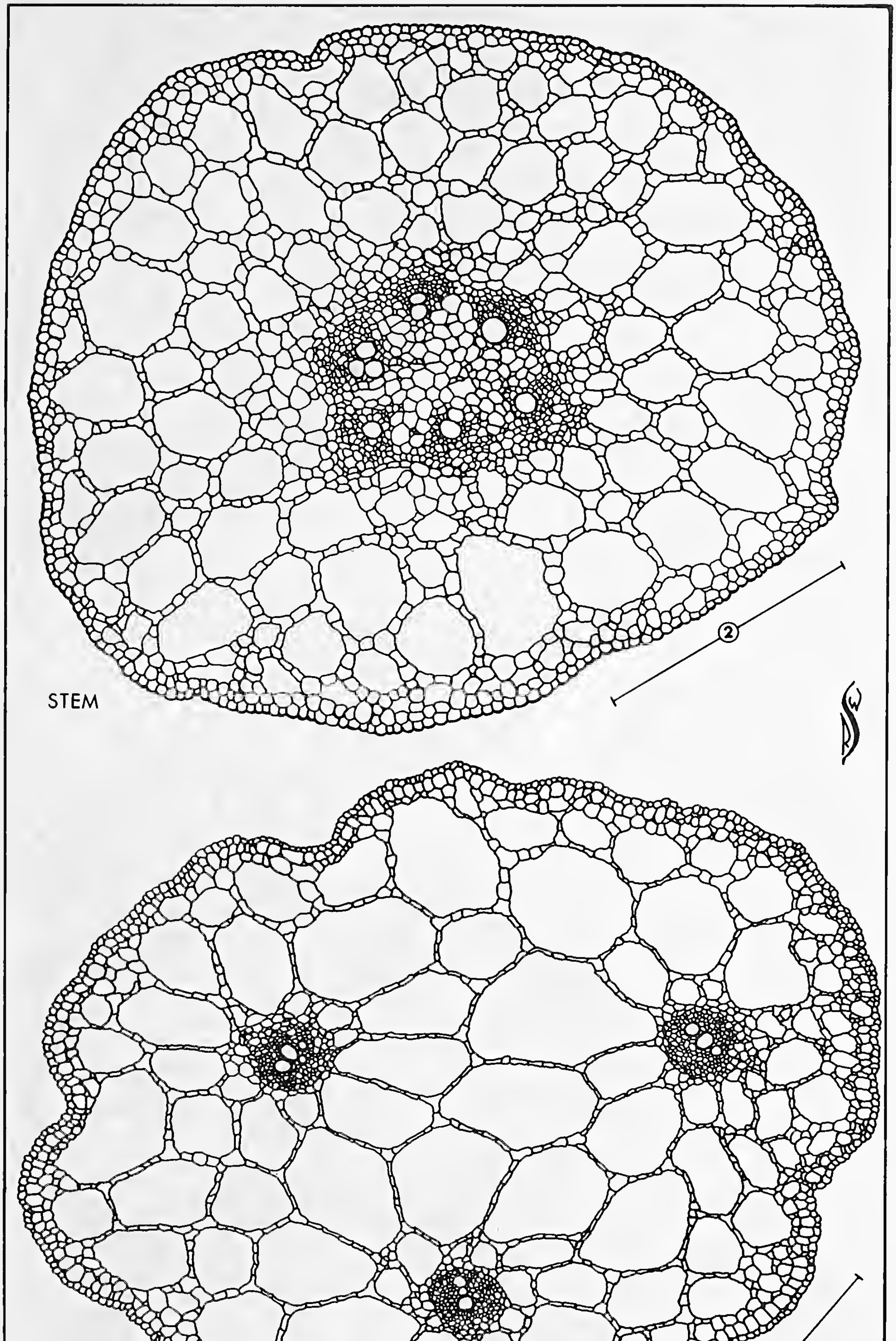
Plate 56



HIPPURIS
PROSERPINACA

H. vulgaris (A)
P. palustris (B)

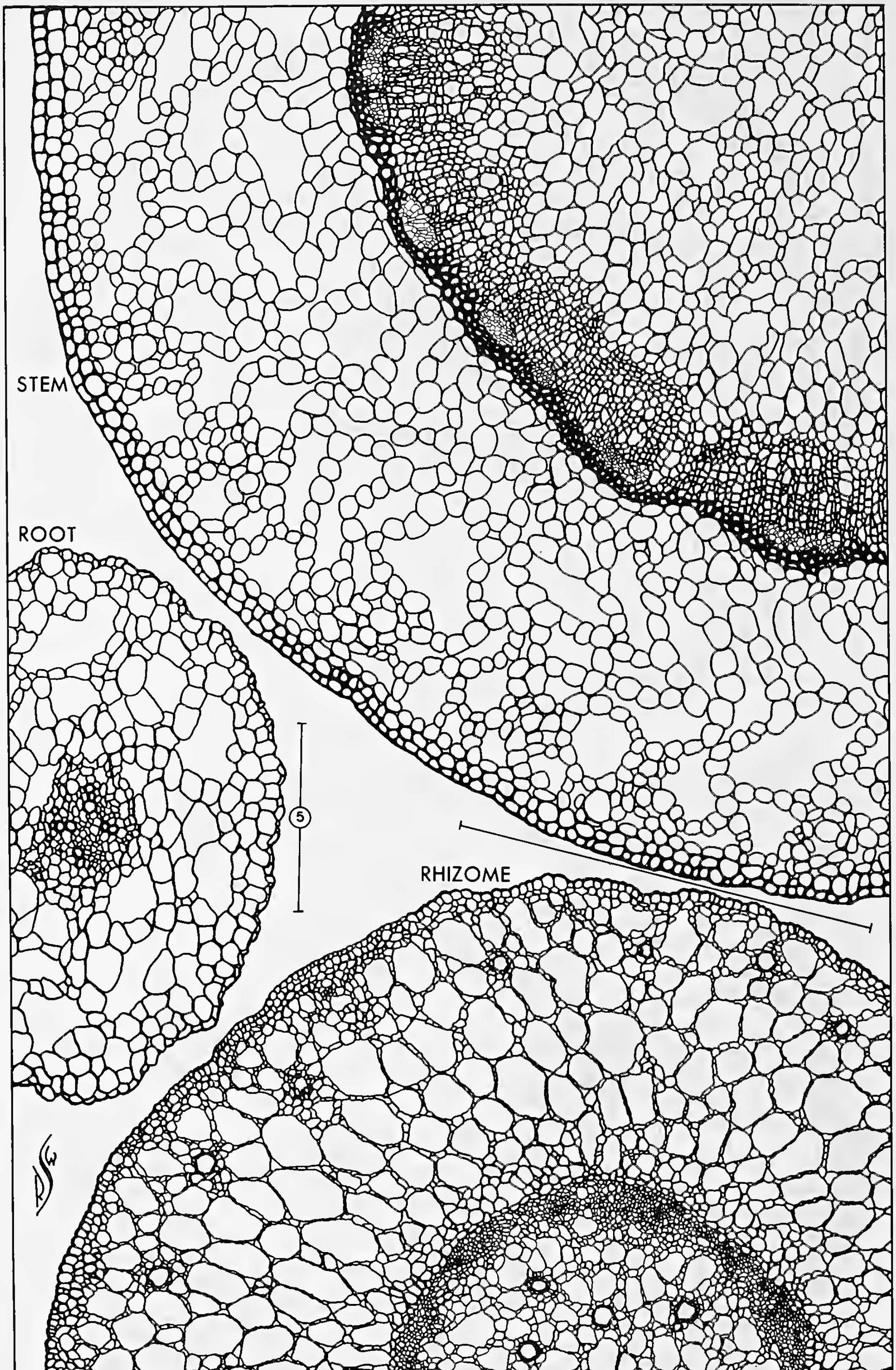
Plate 57



HYDROCOTYLE

H. umbellata

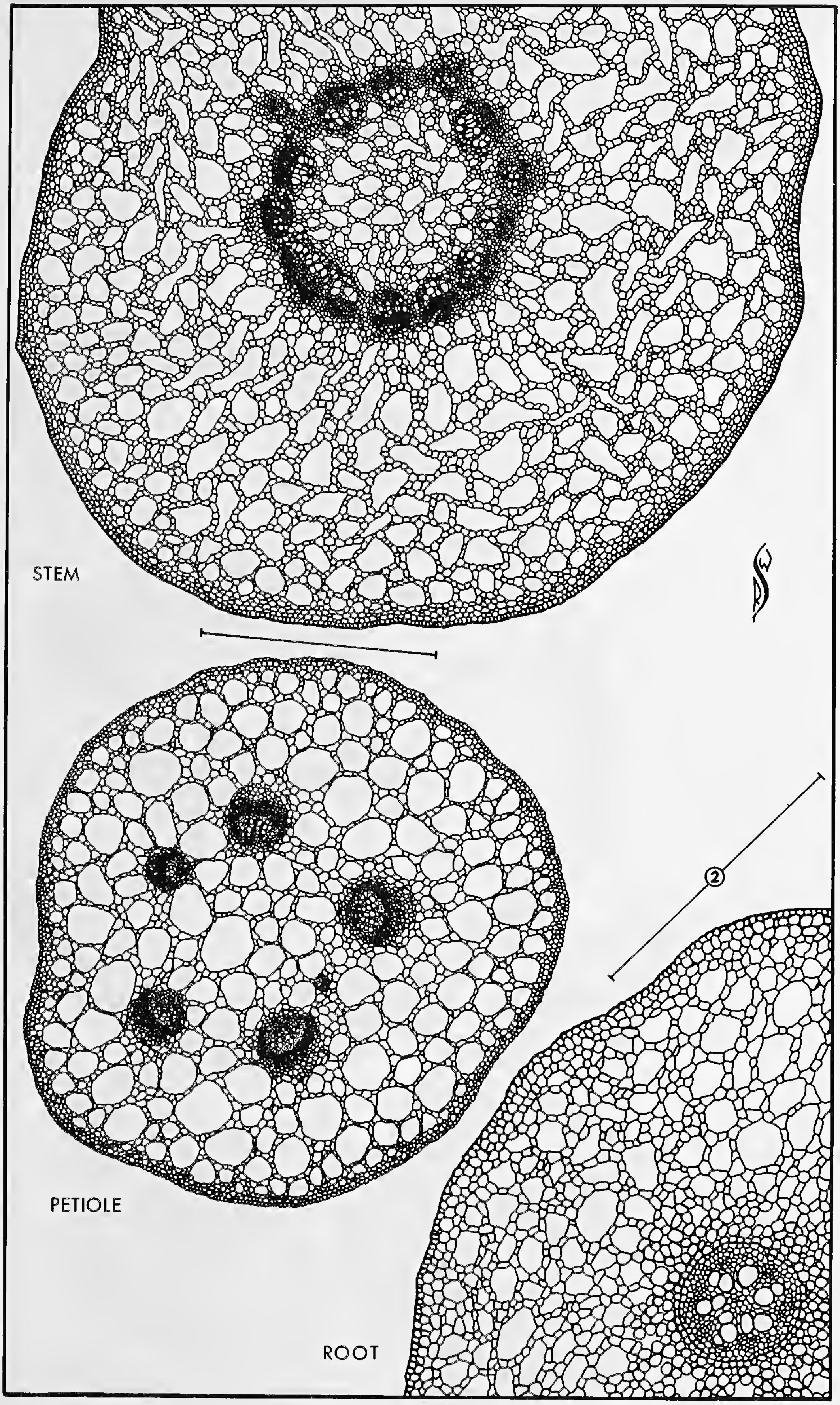
Plate 58



LYSMACHIA

L. terrestris

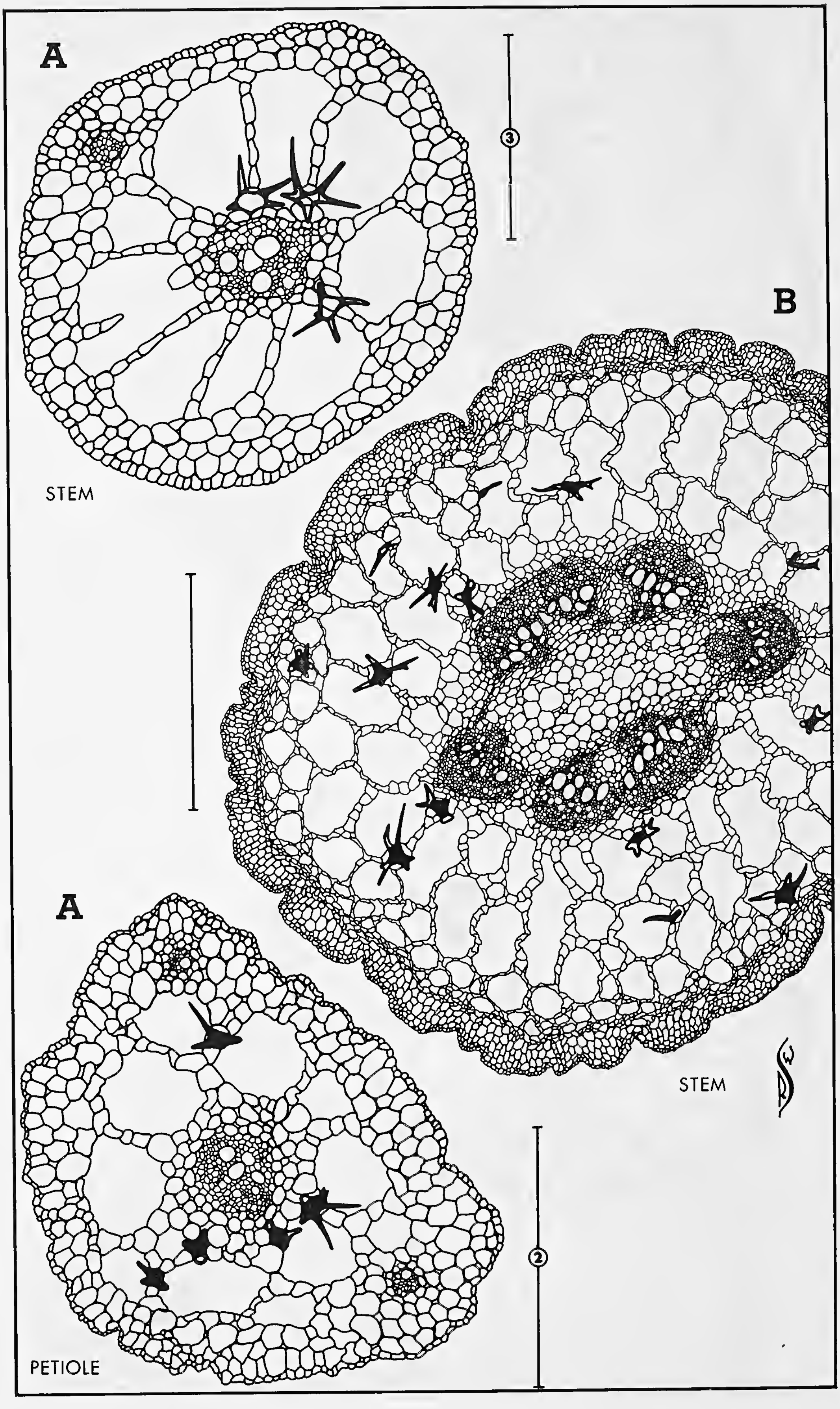
Plate 59



MENYANTHES

M. trifoliata

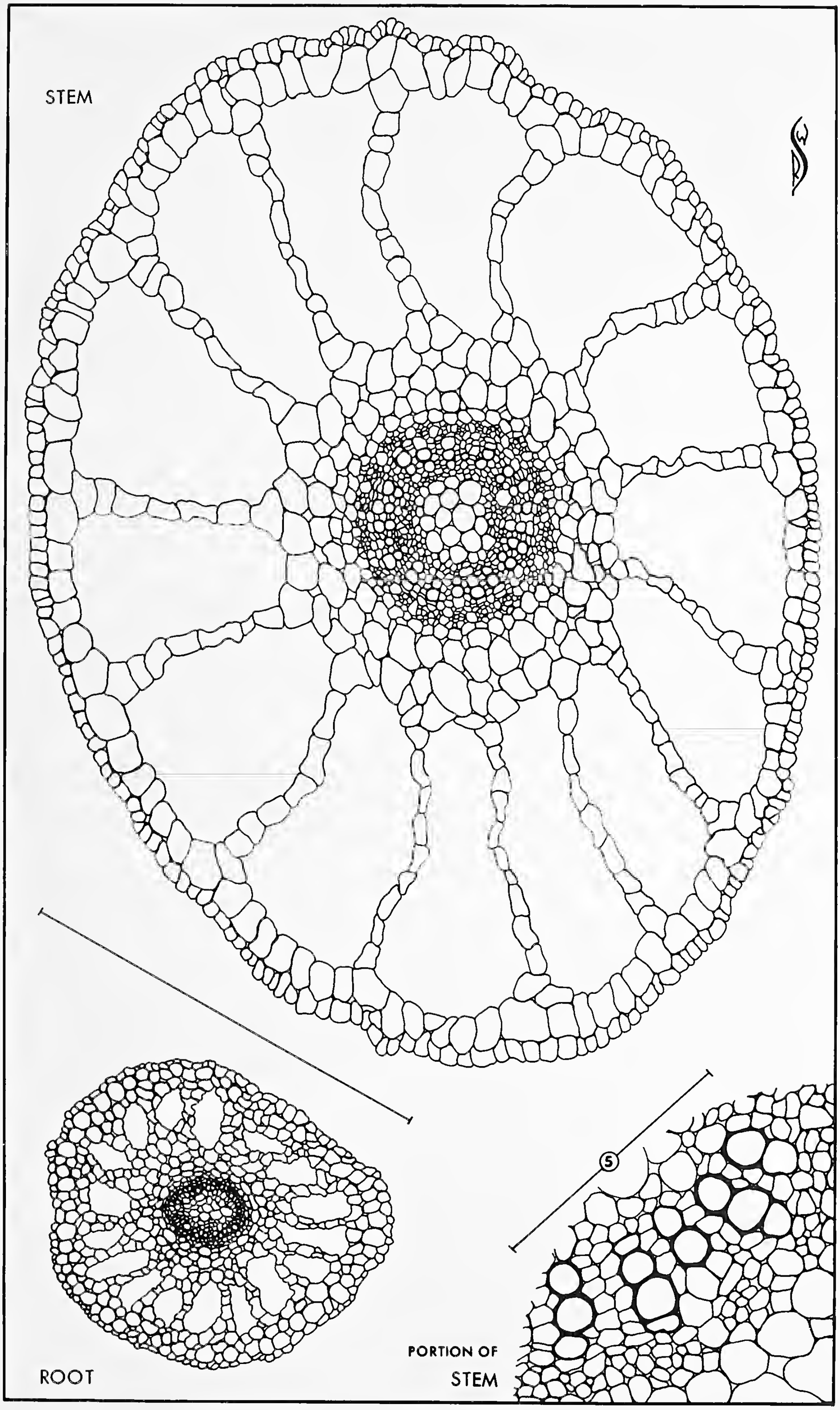
Plate 60



NYMPHOIDES

N. cordatum (A)
N. peltatum (B)

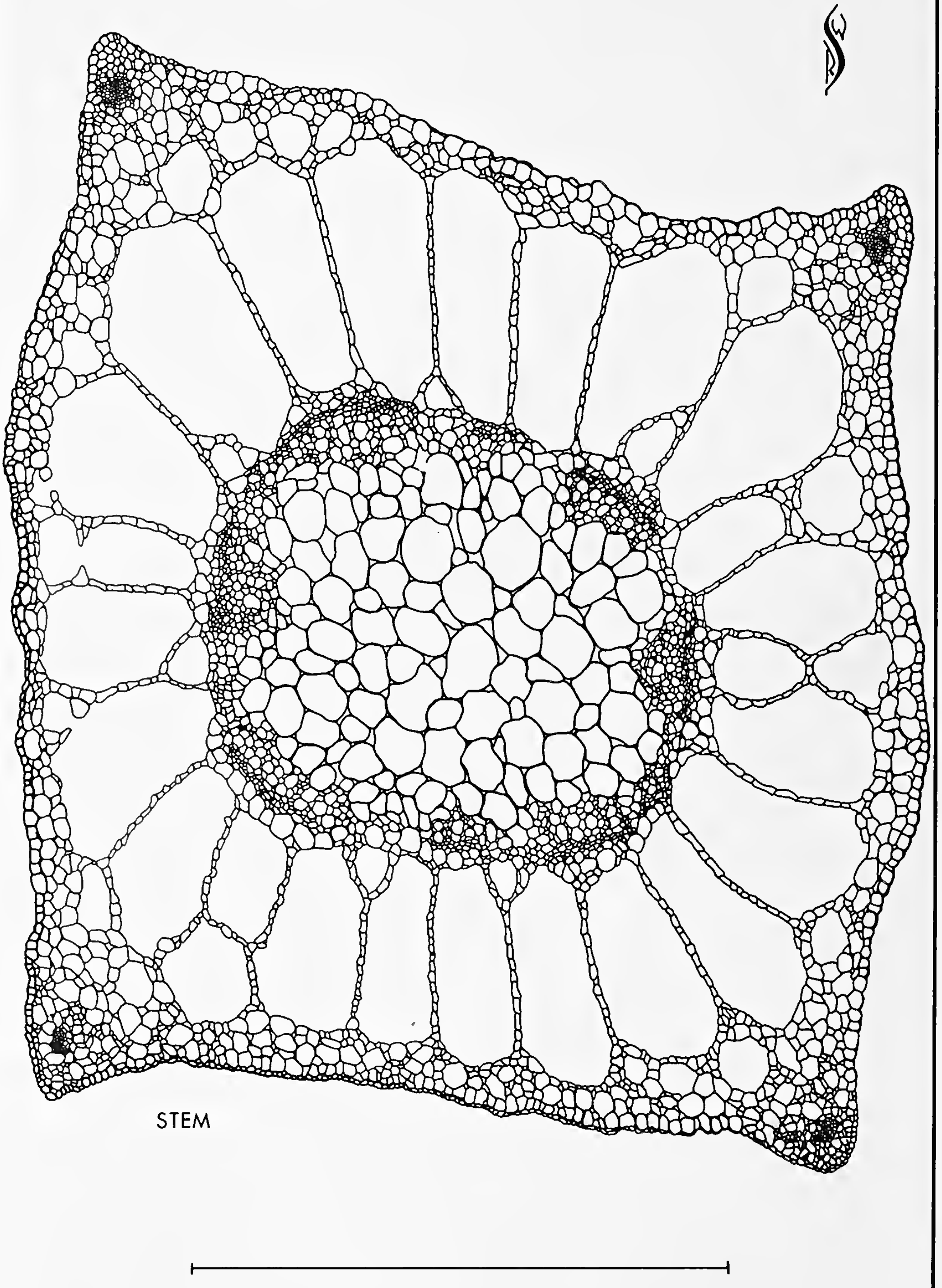
Plate 61



GRATIOLA

G. aurea

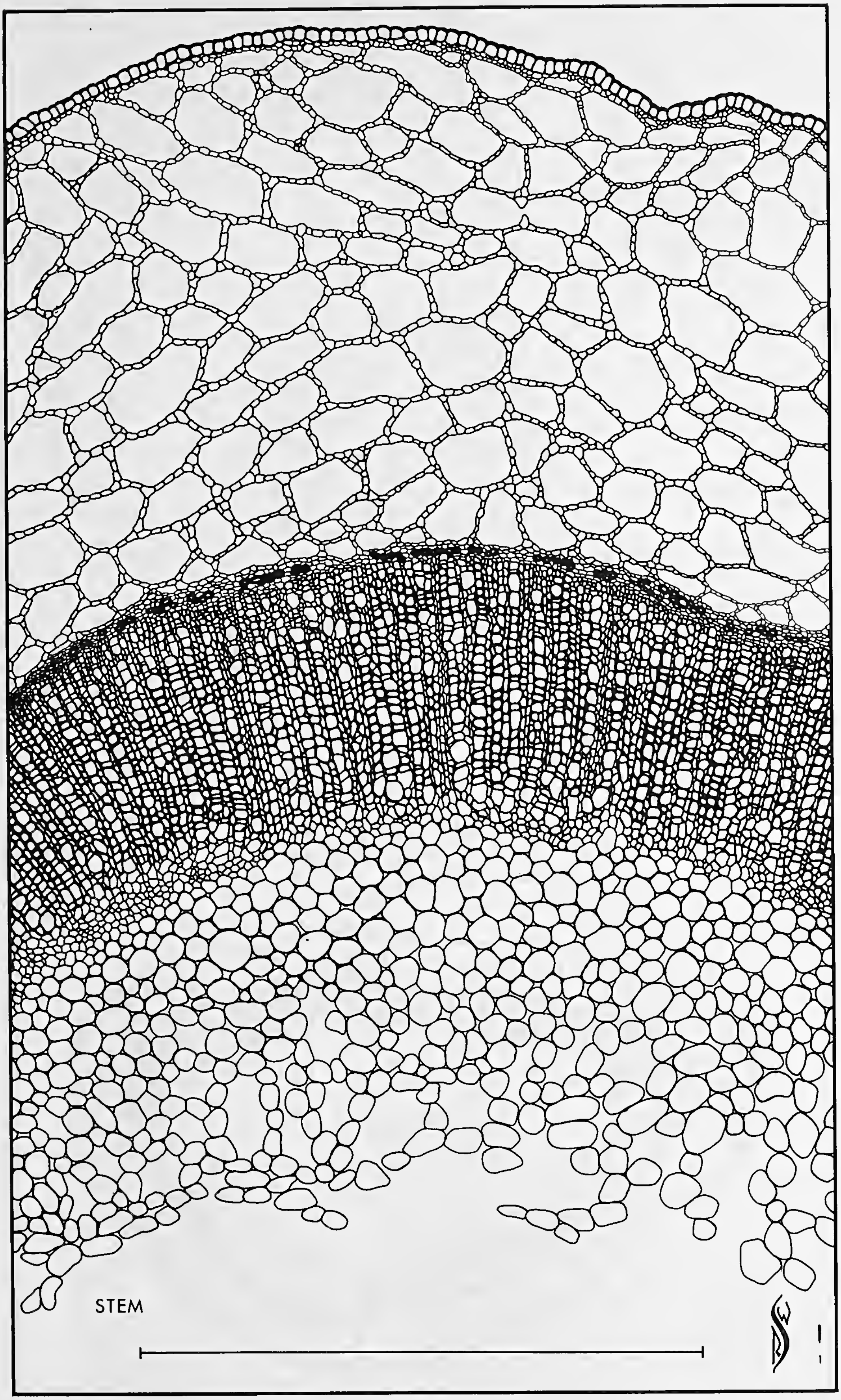
Plate 62



LINDERNIA

L. dubia

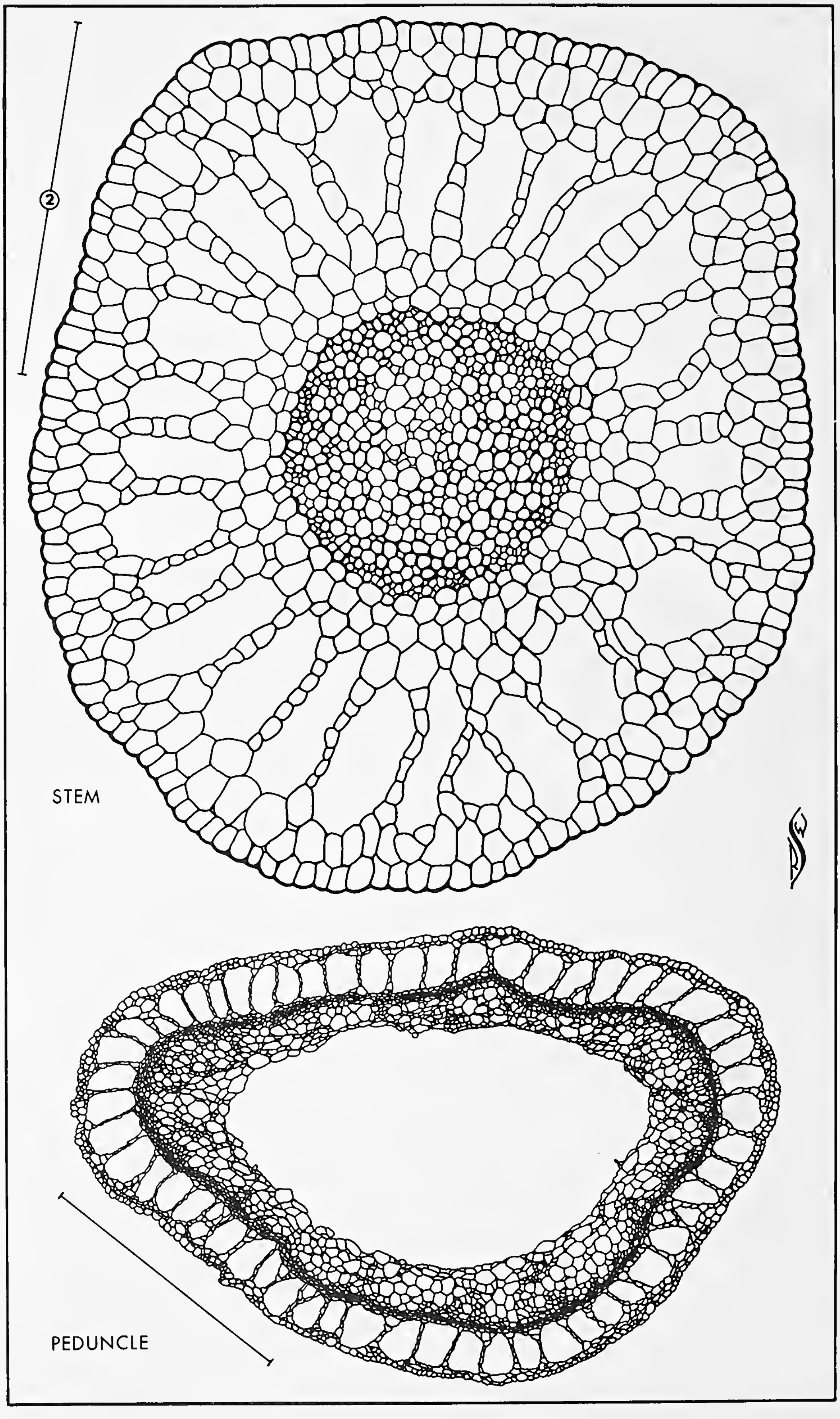
Plate 63



MIMULUS

M. ringens

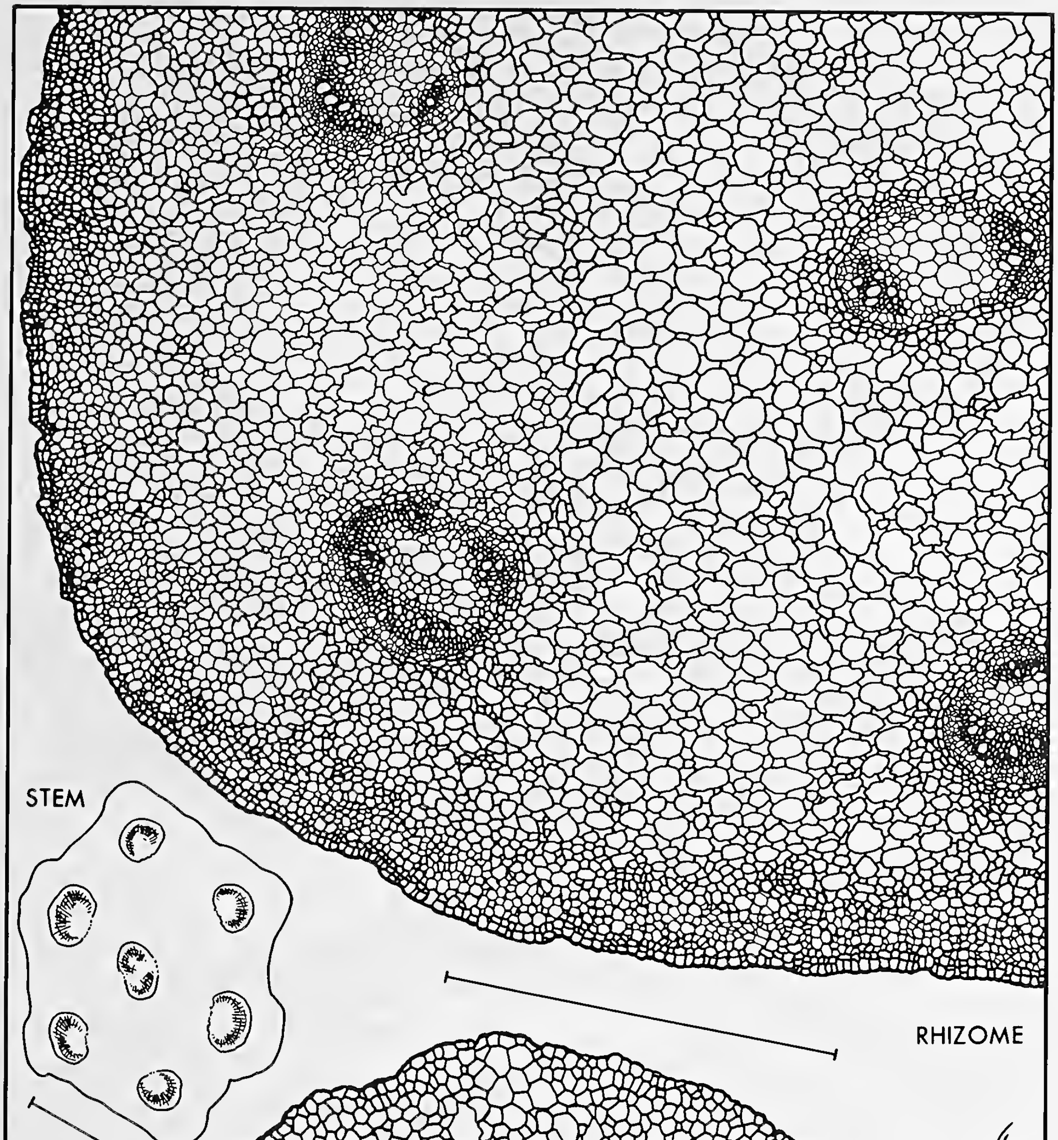
Plate 64



UTRICULARIA

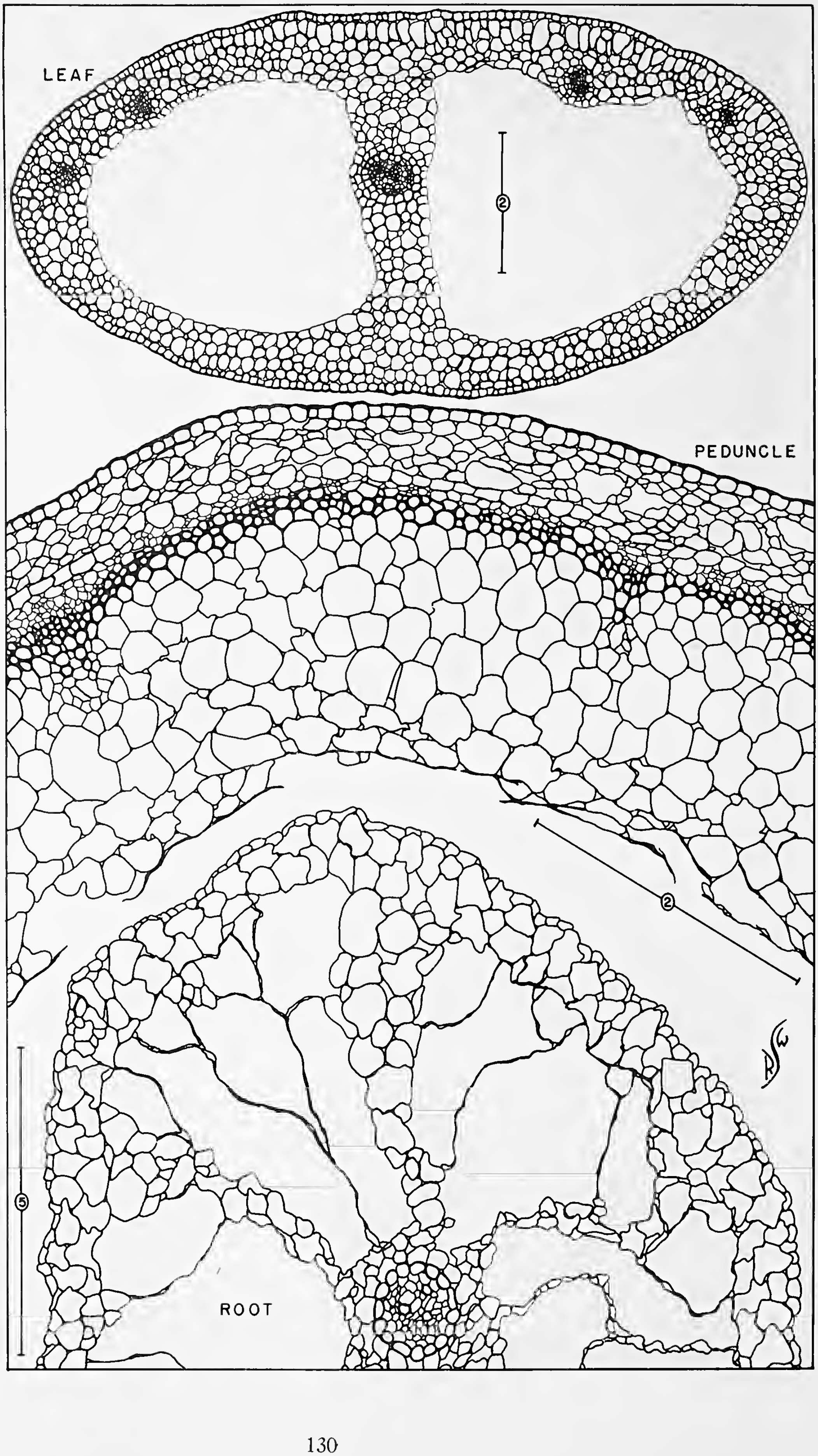
U. vulgaris

Plate 65



JUSTICIA

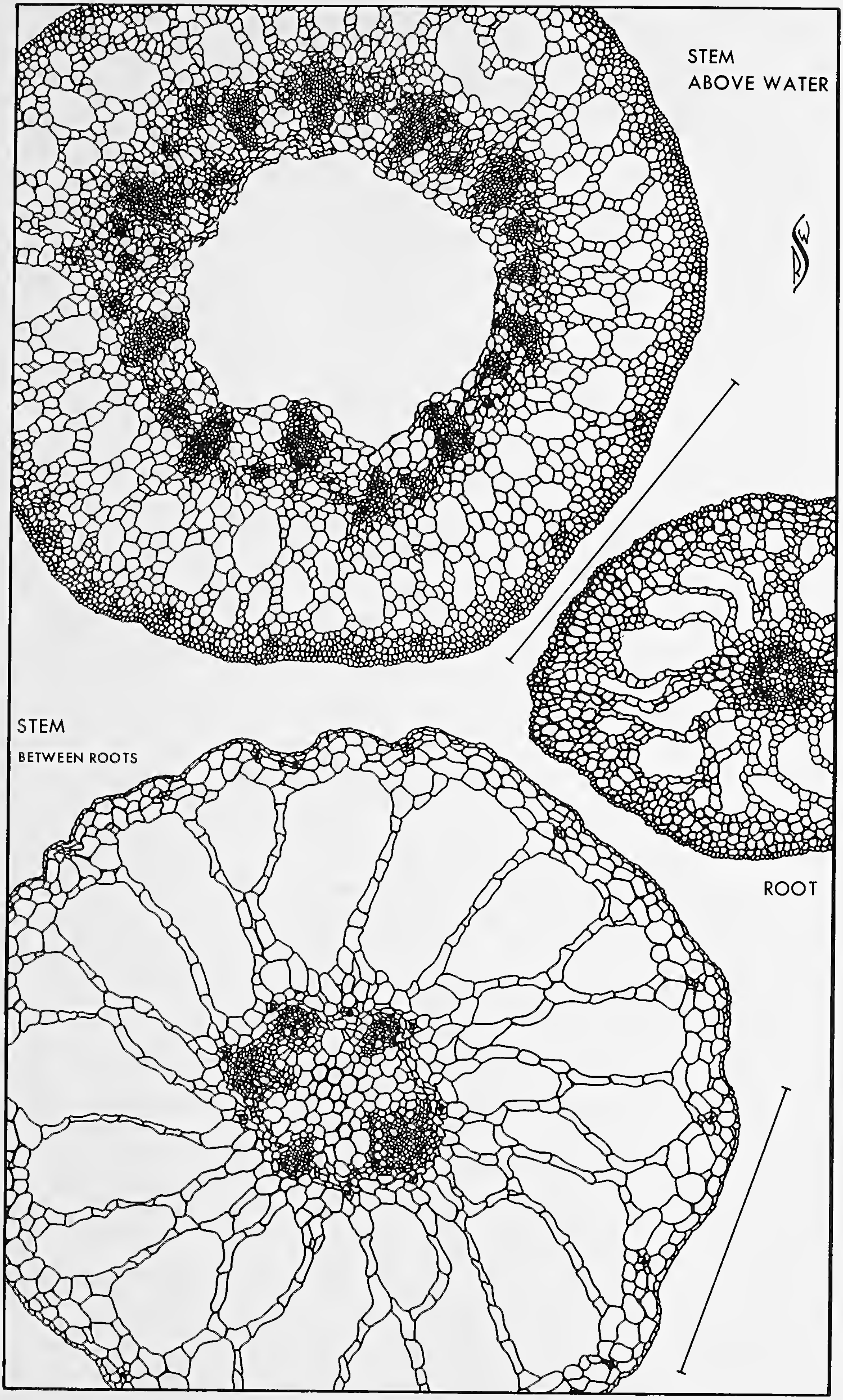
J. americana



LOBELIA

L. dortmanna

Plate 67



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Devonian Ophiuroids from New York State: Reclassification of *Klasmura*, *Antiquaster*, and *Stenaster* into the Suborder Scalarina nov., order Stenurida

by Frederick H. C. Hotchkiss
Peabody Museum of Natural History
Yale University

BULLETIN NUMBER 425

New York State Museum

The University of the State of New York
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Devonian Ophiuroids from New York State: Reclassification of *Klasmura, Antiquaster,* and *Stenaster* into the Suborder Scalarina nov., order Stenurida

by Frederick H. C. Hotchkiss[1]

ABSTRACT

The morphology of *Klasmura* Ruedemann, 1916, (Klasmuridae Spencer, 1925), has been misunderstood. Ossicles called spines are lateral plates. Ossicles called laterals are sublateral plates. The genus and family are therefore transferred from the order Oegophiurida to the order Stenurida. The recently described stenuridan *Antiquaster magrumi* Kesling, 1971, (Antiquasteridae Kesling, 1971), type of its genus, belongs in the Klasmuridae, and the genus *Protasteracanthion* Stuertz, 1886, may also belong there. The family is placed near the Stenasteridae in the suborder Scalarina nov. established for stenuridans with opposite ambulacrals. The new data make it clear that *Stenaster* is an ophiuroid.

All the figured syntypes of *Klasmura mirabilis* Ruedemann, 1916, and the holotype and paratype of *K. clavigera* Ruedemann, 1916, are reillustrated with photographs. A lectotype is designated for *K. mirabilis.* Two species are in the remaining original type material of *K. mirabilis: K. mirabilis* proper with short (about two arm segments long) spine-like side processes on the laterals, and ?*K. macropleura* n. sp. with long (about four arm segments long) side processes. New records extend (1) the range of *Antiquaster magrumi* to include the Devonian of New York State and the Silurian of Herefordshire, England, and (2) the range of *Stenaster* to include the Ordovician of California. A unique specimen of *Stenaster obtusus* is hexamerous.

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[1] Present address: Department of Geology and Paleontology, The Academy of Natural Sciences, Nineteenth and the Parkway, Philadelphia, Pa. 19103.

Introduction

It came as a great surprise to find that *Klasmura* belongs to the order Stenurida. Its true affinities were deduced after lengthy study of a fossil belonging to Cornell University and now identified as *Antiquaster magrumi* Kesling, 1971, an acknowledged stenurid.

Ruedemann placed *Klasmura* in the family Eoluidiidae Gregory, 1897, itself placed (following Schuchert, 1915) in the order Streptophiurae Bell, 1892, subclass Auluroidea Schöndorf, 1910. Ruedemann's impression that *Klasmura* had ventral arm-plates and had ambulacrals fused to form vertebral ossicles placed it for him among "the most advanced of the Devonian Auluroidea" (Ruedemann, 1916, p. 62). It fell to Spencer (1925, p. 258) to find that none of the Eoluidiidae, not even *Klasmura*, have ventral arm-plates; previous observers had been mistaken on this point. Spencer (1925, pp. 241–242) divided the Eoluidiidae among his Hallasteridae, Furcasteridae, and Klasmuridae, only to reunite them (Spencer, 1951) under his superfamily Zeugophiuricae, suborder Oegophiurina. Except for resurrecting the older family name Lapworthuridae Gregory, 1897, to replace the younger Hallasteridae Spencer, 1925, these families have been maintained in the *Treatise on Invertebrate Paleontology* (Spencer and Wright, 1966). These families plus the extant monotypic Ophiocanopidae constitute the suborder Zeugophiurina, order Oegophiurida, of the *Treatise* classification. The present reclassification of the Klasmuridae in the order Stenurida and earlier reclassification of the Ophiocanopidae in the order Phrynophiurida (Hotchkiss, in press) reduces the suborder Zeugophiurina to two families, the Lapworthuridae and the Furcasteridae.

Kesling (1971) reported that neither of his two specimens of *Antiquaster magrumi* had ventral arm-plates, and that the nearly complete holotype has deeply incised interradii at the arm bases, typical of somasteroid petaloid arms. He also reported what might be inner and outer rows of virgalia, another somasteroid character. At the same time, however, Kesling observed that the bordering plates of the arm bear spines as do the laterals of ophiuroids, and that the inner row of plates could be compared with stenuridan sublaterals. It was the grade of development of the mouth frame that convinced him that this was an ophiuroid rather than a somasteroid. He classified it in its own family Antiquasteridae in the order Stenurida.

The major differences between the accounts of Ruedemann and Spencer on *Klasmura* and that of Kesling on *Antiquaster* stem from the former authors' mistaking laterals for spines and sublaterals for laterals. This explains why *Klasmura* was classified in the Oegophiurida and *Antiquaster* in the Stenurida. The structure of *Klasmura mirabilis* Ruedemann, 1916 (the type-species), *K. clavigera*, and ?*K. macropleura* n. sp. substantiate Kesling's analysis of the structures present in *Antiquaster magrumi*.

Notes on terminology: The term **ventral** designates the side or surface that faces the substrate in life; conversely for the term **dorsal.** **Ventral** and **dorsal** do not always correspond with **oral** and **aboral.** The extant phrynophiurids *Euryale aspera* Lamarck, *Astrogymnotes catastica* H. L. Clark and *Astrotoma agassizii* Lyman face away from the substrate (Clark, 1946, p. 172; Mortensen, 1932, pp. 10–11; Fell, 1961, p. 27). The terms **oral** and **aboral** are therefore preferable in morphological descriptions.

The terms **proximal** and **distal** mean close to or far from an imaginary axis passing through the center of the mouth at one pole and the aboral disk at the other.

Spine refers to an articulated spine, and **process** refers to an outgrowth from a parent body.

In the solid designates that the specimen exists as original or replaced mineral matter, in contrast to preservation as an impression left in the rock after dissolution of original or replaced mineral matter.

Systematic Paleontology

Class Stelleroidea Lamarck, 1816
Subclass Ophiuroidea Gray, 1840
Order Stenurida Spencer, 1951
Suborder Scalarina nov.

Diagnosis: Stenurida with ambulacrals in opposite pairs.

Content: (1) Klasmuridae Spencer, 1925, emended herein to include Antiquasteridae Kesling, 1971; (2) Stenasteridae Schuchert, 1914.

Remarks: The Scalarina (Stenurida), Zeugophiurina (Oegophiurida), Phrynophiurida, and Ophiurida represent successive grades of development of the stock of ophiuroids with opposite ambulacrals. The Proturina, Parophiurina (both Stenurida), and Lysophiurina (Oegophiurida) represent the same for the stock with alternating ambulacrals.

Classification into Stenurida and Oegophiurida is "horizontal" according to grade rather than a phylogenetically more correct "vertical" classification (Mayr, 1963, p. 609) and should eventually be abandoned (for a contrasting view see Fell, 1963, pp. 414–415). Recognition of the Scalarina is a first step in that direction.

Close similarity of ambulacral structure in the Klasmuridae and Stenasteridae make the Scalarina a compact group (see below). Adambulacral differences and lack of sublaterals in *Stenaster* distinguish the two families.

Etymology: The subordinal name refers to the ladder-like appearance (Latin: *scalaris*) of the ambulacrum created by partitions between successive cups for tube feet.

Klasmuridae Spencer, 1925, emended herein (incorporating Antiquasteridae Kesling, 1971)

Diagnosis: Scalarina with arms flat, without distinct oral ambulacral grooves, relatively long, hence ribbon-like. Ambulacrals in unfused opposite pairs simulating vertebrae: aborally, prominent aboral radial sulcus confluent from vertebra to vertebra; orally, a low radial ridge transforms distally into a characteristic bulbous swelling which overlaps the next distal vertebra; bulbous swelling longitudinally creased by a carinal cleft. Sublaterals transversely elongate and forming walls between successive podial basins. Laterals a characteristic saddle-shape, interlocking, with distal obliquely projecting spine-like side process bearing a tuft of minute needle-like spines at tip. No interbrachial disk. No madreporite. Aboral integument does not cover side processes of laterals. Buccal slit reduced to small notch; a single ambulacral enters the mouth frame.

Content: (1) *Klasmura* Ruedemann, 1916; (2) *Antiquaster* Kesling, 1971; and perhaps also (3) *Protasteracanthion* Stuertz, 1886 (objective synonym: *Palasteracanthion* Stuertz, 1886b).

Remarks: The family Klasmuridae Spencer, 1925, has been maintained by Spencer (1927, p. 326), Cuénot (1948, p. 237), Spencer (1951, p. 121), Ubaghs (1953, p. 821), Fell (1963, p. 407), and Spencer and Wright (1966, p. U89). Spencer (1925, pp. 242, 282) founded the family on the long spine-like side process to each lateral, which, however, he mistook for a spine. Later (1927, p. 326) he added as "subsidiary characters": "the very small disc, the long arms capable of considerable enrollment, and a mouth-frame with the outer angles of the first ambulacralia produced backwards to form inter-radial V's." Cuénot (1948, p. 237) emphasized resemblances between *Klasmura* and *Onychaster*, but enrollment of arms (see plate III, figure 1) is less prevalent, and the association with crinoids is less intimate than the comparison suggests. The mouth frame of *Antiquaster* (also *Protasteracanthion*) is quite different from that of any *Onychaster*. Fell (1963, p. 407) concluded that the madreporite is "ventral," and this has been accepted by Spencer and Wright (1966, p. U89). In fact, the madreporite has yet to be observed in either *Klasmura* or *Antiquaster* (or in *Protasteracanthion*). Ruedemann (1916, p. 63) pointed to one of the cardinal distinguishing marks of the Klasmuridae: "We believe that the lateral series of long wedge-shaped, hollow spines with their saddle-shaped interlocking bases will, in time, be found to constitute a character distinguishing *Klasmura* from the other genera of the Eoluidiidae." (Note, however, that his "spines" are actually processes of the laterals.) Because Kesling more fully understood the structure of *Antiquaster*, his tabular comparison of his Antiquasteridae with the Eophiuridae, Palaeuridae and Stenasteridae continues to apply.

Specimens have not been available with which to test the hypothesis that *Protasteracanthion* Stuertz may also belong here. The hypothesis assumes that *P. primus* Stuertz, the only species, has been somewhat misunderstood, particularly in regard to detecting the junction between ambulacrals and sublaterals. The median row of paired structures on the oral surface of its arms are probably the most elevated portions of the distal bulbous swellings of successive vertebrae, separated left and right by the carinal cleft. Lehmann (1957, pp. 147–151) removed *Protasteracanthion* from synonymy with the starfish genus *Urasterella* M'Coy, 1851, but found the structure so puzzling that he left it *incertae sedis*. This advance was regrettably ignored by Spencer and Wright (1966, p. U71) who left it in synonymy with *Urasterella*.

Klasmura Ruedemann, 1916

Klasmura Ruedemann, 1916, p. 62 (type-species *K. mirabilis* Ruedemann by original designation). Spencer, 1925, pp. 258 (open ambulacral groove), 282 (key to genera), 289, 300 (mentions only). Spencer, 1927, pp. 326–331, text-figs. 213–215 (redescribed). Spencer, 1940, p. 525 (mention only). Cuénot, 1948, p. 237 (diagnosis). Ubaghs, 1953, p. 821 (diagnosis). Kilfoyle, 1954, pp. 202–203 (types catalogued). Fell, 1963, p. 407 (Klasmuridae diagnosed). Owen, 1965, p. 557 (curatorial notes). Spencer and Wright, 1966, p. U89 (diagnosed).

Diagnosis: Klasmuridae with arm width 0.6 to 0.8 of diameter of mouth frame. Mouth frame with outer angles of first ambulacrals produced outwards to form interradial V's. First ambulacrals and mouth angle plates unusually large in the oral-aboral dimension.

Content: (1) *K. mirabilis* Ruedemann, 1916, type-species by original designation; (2) *K. clavigera* Ruedemann, 1916; and (3) ?*K. macropleura* n. sp.

[Plate and figure references for specimens mentioned in the following pages are given in the "Remarks" column of Table I.]

DISK AND MOUTH FRAME

[Five specimens show the mouth frame: NYSM Nos. 7771, 7772, and 7773 of *K. mirabilis*, NYSM 13217 of *K.* sp. indet., and NYSM 13221 of *K. clavigera*. Ruedemann stated he had only two disks and figured each (his pl. 22, figs. 1, 2). Kilfoyle (1954, p. 202) catalogued three disks saying that NYSM 7773 was used to complete the illustration of NYSM 7772 (Ruedemann's pl. 22, fig. 2); NYSM 7771 is the original for Ruedemann's pl. 22, fig. 1. NYSM 7771 was also the subject of Spencer's text-figure 215A of the mouth frame in oral view; his text-figure 215B of the mouth frame in aboral view was "from a specimen not hitherto figured," but of which Owen (1965, p. 557) says "original not recognized." The two other mouth frames were among previously uncatalogued material.]

There are no interbrachial areas and so there is no disk in the conventional sense. In the lectotype of *K. mirabilis* (pl. I, fig. 4; pl. II, figs. 1, 2) the distance from the center of the mouth to the tip of "backwardly directed interradial wedges formed from the outer ends of the first ambulacralia" is 2.9 mm. Spencer (1927, p. 331) correctly noted that these pairs of interradial wedges are reminiscent of the *Onychaster* mouth frame, recently redescribed by Bjork, Goldberg, and Kesling (1968).

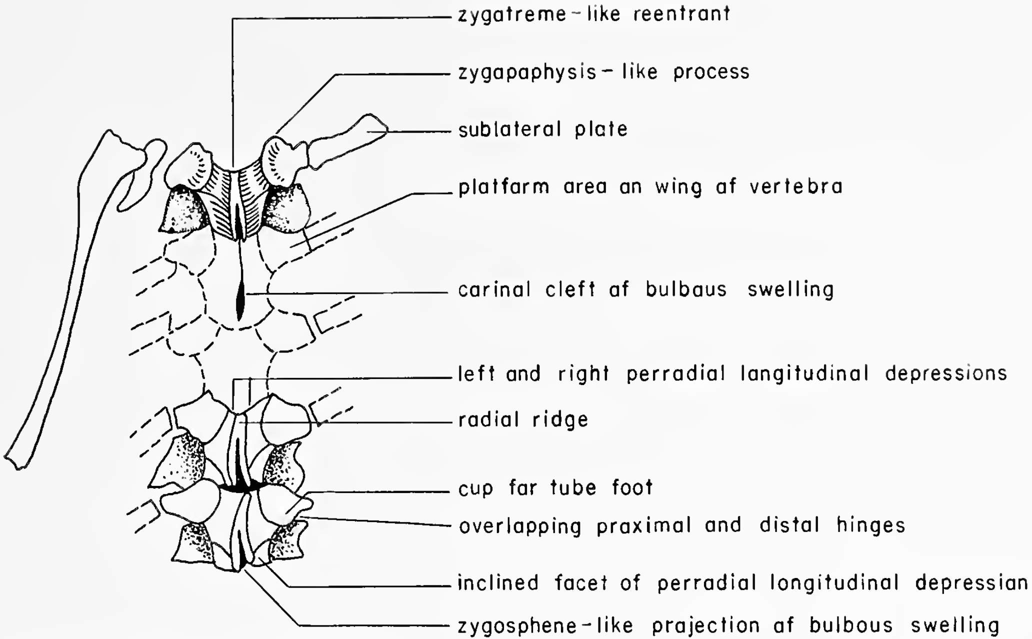
The mouth frame of NYSM 13217 (pl. I, fig. 2) is 6 mm in diameter and 2.5 mm in thickness. This is an extraordinary thickness making it look more like an Aristotle's lantern or an acorn than an ophiuroid mouth frame. The mouth frames of NYSM 7772 and 7773 (pl. I, figs. 1 and 3) are 5.8 mm and 6.4 mm in diameter, respectively. Their full thickness is hidden in the rock, but the appearance of unusual thickness is nevertheless unmistakable.

ARMS

[Except as noted, this section was first written from study of the holotype of ?*K. macropleura* n. sp. (pl. IV, figs. 1-3) because of its excellent detail. It was then verified against the holotype of *K. mirabilis* (pl. II, figs. 1, 2) plus other specimens.]

Ambulacrals: The ambulacrals form vertebrae. Although displaced ambulacrals often appear to retain left and right correspondence, slight dislocations relative to one another show that the halves of vertebrae are not actually fused together. As noted by Spencer (1927, p. 328), the details of the oral surfaces of the ambulacrals are controlled by whether or not the partition forming the oral wall of the closed ambulacral channel is in place. This description applies to those which have it in place.

Oral view (text fig. 1): The wings of the vertebrae, to which the sublaterals articulate, are proximal. Left and right perradial longitudinal depressions are separated by a radial ridge. This ridge becomes swollen distally and overhangs the next distal vertebra, recalling the zygosphene (Clark, 1914, p. 101) of recent ophiuroids. The compound origin of this ridge from left and right perradial ridges is evident from the carinal cleft which longitudinally creases the bulbous swelling. The left and right perradial longitudinal depressions mark off platform areas on the two wings of a vertebra. Cups for the tube feet are located left and right on the distal two-thirds of each vertebra, distal to each wing. Two-thirds of a cup's ambulacral side walls are provided by its "parent" ambulacral, the remaining one-third by the next distal ambulacral. The roof of each cup is formed by a shelf-like expansion of the "parent" ambulacral. These left and right shelf-like expansions continue distally as processes which pass from view aboral to the platform areas of the next distal

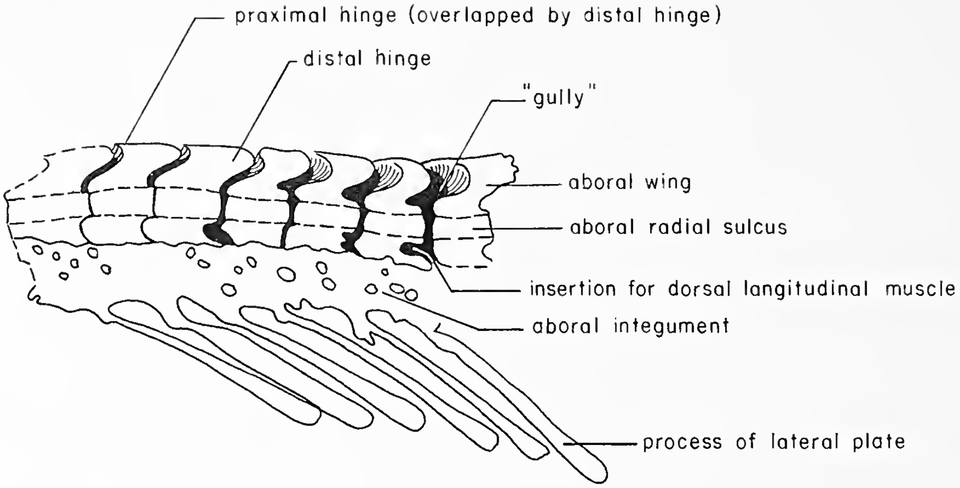


Text-figure 1. ?*K. macropleura* n. sp. Oral view of arm of holotype; highly diagrammatic; sketched from plate IV, figure 3.

vertebra. These overlapping parts correspond to the "adoral" and "aboral," or proximal and distal "hinges," also called "articulating pegs," of authors. The platform area of each ambulacral half vertebra has a prominent proximal rounded corner. The two such rounded corners form proximally directed processes between which the zygosphene-like process of the next proximal vertebra inserts. These processes therefore recall the zygapophyses, and the space between them recalls the zygotreme of recent ophiuroids (cf. Clark, 1914, p. 101). The distal part of the perradial longitudinal depressions in the region on either side of the distal bulbous swelling of the radial ridge is an inclined facet and may be the proximal insertion for the appropriate, left or right, intervertebral ventral longitudinal muscle. Because the zygapophysis-like processes somewhat overlap (in oral view) the facets in question, the distal insertion would appear to be hidden apical to these processes. There is only a miniscule space for the ventral longitudinal muscle.

Aboral view (text fig. 2): [NYSM 7774 (pl. VII, fig. 1) and 7775 (pl. IV, fig. 4) of ?*K. macropleura* n. sp. provide aboral views of vertebrae; this surface is hidden from view in specimens of *K. mirabilis* and *K. clavigera* by preserved aboral integument.]

A wide and deep aboral radial sulcus, about as wide as deep, runs continuously from vertebra to vertebra (pl. VII, fig. 1). Its width occupies about one-fourth the width of each vertebra. There is no overlapping between vertebrae within the sulcus. The line of junction of the vertebral halves marks the midline of the sulcus, and demonstrates in places (pl. III, fig. 2) a slight displacement of the vertebral halves, evidence that they were not fused together. Left and right perradial crests wall the sulcus (pl. VII, fig. 1). These crests are the perradial and most elevated portions of the aboral vertebral wings. Each crest appears to form a proximal process which appears capable of fitting an excavation on the distal end of the appropriate crest of the next proximal vertebra. The crest does not, however, overlap the next proximal vertebra. The excavation on the distal end of each perradial crest appears to be for the insertion of the dorsal longitudinal muscle. Each such excavation is confluent with a space that extends distally and obliquely away from the center-line of the arm. These obliquely directed gullies on each side of a row of vertebrae are separated one from the next by the appropriate left or right aboral wing of the intervening vertebra. The aboral wings are therefore likewise directed distally and obliquely away from the center-line of the arm. Their perradial and most elevated portions are the perradial crests already described. Distally and obliquely outward from the center-line, each wing is confluent with a shelf-like process which is the "aboral" or distal hinge of authors. The distal hinge overlaps the "adoral" or proximal hinge of the next distal vertebra. The apical surface of the proximal hinge is confluent with the floor of the space (gully) which housed the dorsal longitudinal



Text-figure 2. ?*K. macropleura* n. sp. Aboral view of arm; highly diagrammatic; sketched from plate VII, figure 1.

muscle. These two shelf-like processes of a vertebra, the distal hinge and the proximal hinge, repeated left and right, are separated from each other only by their elevation, and their surfaces are confluent at their outward periphery which is the lateral margin of the vertebra.

Sublaterals: The sublaterals (pl. IV, figs. 2, 3; pl. V, fig. 2) are straight pieces, about three times as long as wide. Except when displaced, the flat oral surface of each is coplanar with, and an outward extension of, the platform area of the oral wing of the vertebra to which it articulates. Not uncommonly, the line of juncture between ambulacral and sublateral is difficult to observe, and the two appear to be but a single plate. This contributes substantially to the exceptionally flat oral aspect of the arms. The sublaterals form walls between successive podial basins. Rotation of sublaterals about their ambulacral fittings is never oral (? ventral) and so they form no oral groove to the arm. Rotation about the ambulacral fitting leaves the sublaterals directed obliquely outward from the arm axis and may be directed either proximally or distally. In the extreme, the sublaterals are subparallel to the arm axis and present the appearance of being laterals, outside of which are, of course, the true laterals. Because this rotation diminishes the size and alters the shape of the cups for tube feet, it probably occurs post mortem.

Laterals: The laterals have a complicated shape (plates II-VIII). Most prominent is a distally pointing spine-like process or shaft directed obliquely outward from the axis of the arm. The succession of shafts on the two sides of each arm is in echelon, forming a chevron (pl. II, fig. 3). From base to tip the shaft is about two arm segments long in *K. mirabilis* and *K. clavigera*, about 4 arm segments long in ?*K. macropleura* n. sp. Their length in ?*K. macropleura* n. sp. brings about a fanciful resemblance to sets of oars (pl. V, figs. 1, 2). These shafts carried a tuft of exceedingly fine needle-like spines at their tip (pl. VII, fig. 3). The shafts are not round but are rather squared off, much like a board of wood, the length, width, and thickness of which would correspond respectively to the length (base to tip), height (oral to aboral) and width (of the oral face) of the shaft. The shafts gradually increase in dimensions from their bases to their tips, but the increase is so slight that edges remain nearly parallel. The "base" is in fact the "main body" of the lateral despite its minor dimension compared with the spine-like process or shaft which it bears. The bases have been aptly characterized as saddle-shaped and interlocking (Ruedemann, 1916, p. 63). The distally directed spine-like process projects obliquely from the pommel of the saddle at about 45 degrees from the arm axis. The oral edges of the laterals are all in nearly the same horizontal plane; there is no oral or ambulacral groove (pl. IV, fig. 1). The distal end of each saddle-shaped base overlaps the proximal end of the next distal lateral. It appears as though one is issuing from the next, much like an exploded view of cone-in-cone structure (pl. V, fig. 2). The distal one-third of the saddle resembles a ridge and has granulose tubercles. This ridge is confluent with the shaft of the spine-like process and in ?*K. macropleura* n. sp. appears to give the shaft a club-shaped base. In photographs, where the three-dimensional saddle-shape cannot be observed, the "main body" of the lateral looks triangular (pl. V, fig. 2; pl. VIII, figs. 2, 3). One vertex is confluent with the spine-like process. The proximal of the other two vertices of this triangle articulates with the sublateral and is overridden by the distal edge of the next proximal triangular "main body." The remaining vertex is closest to the center-line of the arm, and is closer than is the abradial end of a sublateral.

Remarks: *Klasmura* can be distinguished from *Antiquaster* only by the mouth frame. The one syntype which preserves both mouth frame and arm structure (NYSM 7771) is chosen as the lectotype of the type-species of *Klasmura*.

Klasmura mirabilis Ruedemann, 1916

Plate I, figures 1, 3, 4; Plate II, figures 1–3; Plate III, figure 2

Klasmura mirabilis Ruedemann, 1916, pp. 64–65 (the originals of pl. 22, figs. 1, 2, and no others). Spencer, 1925, pp. 241, 242 (mention only). Spencer, 1927, pp. 326–331 (text-fig. 215A only). Kilfoyle, 1954, pp. 202–203, 682 (types catalogued; specimens NYSM 7771–7773 only). Owen, 1965, p. 557 (curatorial notes; specimen NYSM 7771 only).

Diagnosis: *Klasmura* with side processes of laterals about two arm segments long. About 13 arm segments in the space of 10 mm.

MATERIAL

Ruedemann described this species from "five drawers" of material containing "hundreds of rays and fragments of rays" and two disks, "one with no rays left and the other with but two fragmentary rays remaining." This last, the most complete specimen, is here selected as the lectotype (NYSM 7771). Kilfoyle (1954) catalogued as "cotypes" only the 13 specimens figured by Ruedemann (NYSM Nos. 7770–7782).

Spencer studied "impressions of most of the material figured" by Ruedemann. He refigured certain ones (NYSM Nos. 7771, 7774, 7779, 7782), and published two illustrations based on specimens "not hitherto figured" (Spencer, 1927, text-figs. 213A, 215B), the originals for which have not yet been relocated (Owen, 1965).

Two kinds of individuals are present: ones with short (about two arm segments long) spine-like side processes to the laterals, and ones with long (about four arm segments long) processes (pl. III, fig. 2). The lectotype of this species is of the former type. The latter, none of which preserve the disk, are ?*K. macropleura* n. sp. In particular: specimens NYSM 7771 (the lectotype), 7772, and 7773 have short side processes and are *K. mirabilis*.

Specimens NYSM 7770, 7774, and 7776–7782 have long side processes and are ?*K. macropleura* n. sp. Specimen NYSM 7775 is unidentifiable because laterals (and disk) are not preserved. All are reillustrated with photographs (pls. I–VII).

In the uncatalogued portion of the collection (NYSM accessions 3629, 3634, and 4046), are two more specimens of *K. mirabilis sensu stricto:* one on the same slab with NYSM 7771 is now catalogued NYSM 13218; the other on a different slab is now catalogued NYSM 13219.

MEASUREMENTS

See Table I.

FORMATION AND LOCALITY

NYSM 7773 is part of NYSM accession No. 4046. NYSM 13219 is part of NYSM accession No. 3629. The other specimens are from one or the other (unspecified) of these accessions. The catalogue entries read (Robert Conrad, personal communication):

3629—Portage (West Hill flags). Large gully at head of Italy Hollow, Yates County, New York. D. D. Luther coll., 1908.

4046—West Hill flags and shales. Italy Hollow, Yates County, New York. D. D. Luther coll., 1910.

Klasmura clavigera Ruedemann, 1916

Plate VIII, figures 1–3

Klasmura clavigera Ruedemann, 1916, p. 66, text-fig. 30, pl. 23, figs. 8, 9. Spencer, 1925, Pt. VI, pp. 241, 242 (mention only). Spencer, 1927, pp. 326, 331 (suggests *K. clavigera* is young *K. mirabilis*). Kilfoyle, 1954, pp. 202, 682 (types catalogued).

Diagnosis: A *Klasmura* with side processes of laterals about two arm segments long. Twenty-five to thirty arm segments in the space of 10 mm.

MATERIAL

Ruedemann founded this species on "a ray and a fragment of another that exhibit so striking characters that it is safe to describe their species from them." The caption to his plate 23, fig. 9, designates the more complete specimen as the holotype, and that of plate 23, fig. 8, names the other as paratype. Kilfoyle (1954, p. 202) catalogued the holotype as NYSM 7768 and the paratype as NYSM 7769. Each is an impression of the oral surface of an arm, the original calcite having dissolved away.

NYSM 13221: This specimen was evidently overlooked by Ruedemann, for it is part of accession No. 3629 which furnished him certain of his figured types of *Klasmura mirabilis*. The fossil is a cast of the aboral aspect of one arm and of the mouth frame.

MEASUREMENTS

See Table I.

REMARKS

The side processes of the laterals project past the aboral integument and therefore fringe the arm in NYSM 13221 (plate VIII, fig. 1).

Specimens of *K. mirabilis* are uniformly larger than those of *K. clavigera*, and it may be (Spencer, 1927, p. 331) that *K. clavigera* are young *K. mirabilis*.

FORMATION AND LOCALITY

NYSM 13221 is part of accession No. 3629 from the head of Italy Hollow (see *K. mirabilis*). The two types of *K. clavigera* are from accession No. 3634, for which the catalogue entry reads (Robert Conrad, personal communication):

3634—West Hill flags. Gardeau-Ingleside at Deyo Basin two miles south of Naples, Ontario County, New York. D. D. Luther coll., 1908.

?*Klasmura macropleura* n. sp.

Plate III, figure 1; Plate IV, figures 1–3; Plate V, figures 1–3; Plate VI, figures 1, 2; Plate VII, figures 1–3

Klasmura mirabilis Ruedemann, 1916, pp. 64–65 (the originals of: text-fig. 29; pl. 20, fig. 3; pl. 21 (restoration); pl. 22, figs. 3–8; pl. 23, figs. 1–7, 7a; and no others). Spencer, 1927, pp. 326–331 (the originals of text-figs. 213, 214, and no others). Kilfoyle, 1954, pp. 202–203 (types catalogued; specimens NYSM 7770, 7774, 7776–7782 only). Owen, 1965, p. 557 (curatorial notes; specimens NYSM 7774, 7779, 7782 only).

Diagnosis: A *Klasmura* with side processes of laterals about four arm segments long.

MATERIAL

Holotype: NYSM 7770. Paratypes: NYSM 7774, NYSM 7776–7782, NYSM 13220. For comments see *K. mirabilis*.

MEASUREMENTS

See Table I.

REMARKS

No specimen preserves the mouth frame, and therefore the generic assignment is queried. This species differs from *K. mirabilis* only in the length of the process of its laterals, and from the diminutive *K. clavigera* and *Antiquaster magrumi* in size as well. The specific epithet translates as "having long sides," and is a reference to the length of the side processes of the laterals.

Specimens such as NYSM 13220 (plate III, fig. 1) illustrate Ruedemann's remark (1916, p. 65) that: "Many of the broken rays are rolled up into circles." The fact, however, that these rolled up arms are detached from the disk makes it dubious that this is a normal pose. Comparison with the rolled up arm posture of *Onychaster* spp. made by Spencer (1927, pp. 326–327) is therefore highly speculative. Neither should the purely incidental association of *Klasmura* spp. fragments with crinoid remains (pl. III, fig. 1) be compared to the intimate associations between *Onychaster* spp. and crinoids.

FORMATION AND LOCALITY

Same as for *K. mirabilis*. NYSM 7770 is from accession No. 3629; NYSM 7774 from accession No. 4046.

Antiquaster Kesling, 1971

Plate VIII, figure 4; Plate IX, figure 1

Antiquaster Kesling, 1971, pp. 181–191 (formal description p. 184), text-fig. 1, pls. 1–4.

Bdellacoma Salter, 1857. Spencer, 1940, p. 529 (the specimen 40296b only). Owen, 1965, p. 548 (the specimen 40296b only).

Diagnosis: Klasmuridae with width of proximal stretch of arm 1.1 to 1.2 times the diameter of the mouth frame. Hence with petaloid arm bases and incised interradii. Outer angles of first ambulacrals not produced outwards. First ambulacrals and mouth angle plates of normal oral-aboral dimension.

Content: *A. magrumi* Kesling, 1971, type-species by original designation.

Remarks: *Antiquaster* can be distinguished from *Klasmura* only on characters of the mouth frame. The chance that *Antiquaster* is merely an ontogenetic stage of *Klasmura* is reduced by the fact that specimen NYSM 13221 of *K. clavigera*, while of comparable arm segment repetition rate (32.3 per 10 mm), already has the unusually thick mouth frame. Measurements are in Table II.

New records: Specimen NYSM 13227 (plate VIII, fig. 4), formerly in the Paleontological Museum, Cornell University, is identified as *A. magrumi*. Casts of the oral aspect of the major portion of one arm and a minor portion of an adjacent arm are freshly exposed and well preserved, but the rest of the animal is weathered and faint. It is without counterpart. The faintly visible mouth frame is of normal, rather than excessive, oral-aboral dimension. Labels state that the specimen is out of a boulder of Ludlowville Formation shale (Hamilton Group; Middle Devonian) found near Danby, south of Ithaca, Tompkins County, New York.

Specimen No. 40296b in the British Museum (Natural History) (plate IX, fig. 1) is also an *A. magrumi*. Spencer (1940, p. 529; also Owen, 1965, p. 548) identified this specimen as *Bdellacoma vermiformis* (Salter, 1857). The specimen is of a nearly entire animal and is preserved in crisp detail. Labels state (David Lewis, personal communication) that the specimen is from the Lower Ludlow Shales (Silurian) at Church Hill, Leintwardine, Herefordshire, England, and was collected and presented to the Museum by A. Marston in 1862.

The types, until now the only known specimens of *A. magrumi*, are housed in the University of Michigan Museum of Paleontology. The holotype, UMMP 57863a, is a nearly complete specimen. The one paratype, UMMP 57863b, has only the proximal parts of three arms preserved. Both specimens are in the solid with some pyritization. Both show just the oral surface, except at the tip of an arm of the holotype, and are on the same small piece of shale (Kesling, 1971, p. 187). They come from the Silica Formation (Middle Devonian) at Silica, near Sylvania, Lucas County, Ohio (Kesling, 1971, p. 181).

Stenasteridae Schuchert, 1914

Diagnosis: Scalarina with stocky arms composed of about 15 ossicles in series. Arm skeleton of ambulacrals, laterals, and an aboral integument of minute rod-shaped spicules. Ambulacrals in unfused opposite pairs; aboral radial sulcus present; oral perradial ridge caps T of T-shaped ridge, and the upright separates successive podial basins; no distal swelling to radial ridge. Laterals with broad oral surface, superficially rectangular, arranged somewhat in chevron, and assymetrically scalloped at their perradial edges (slightly proximally, deeply distally) by the podial basins. Interbrachial disk areas web-shaped, confluent with arms, composed of rod-shaped spicules. No madreporite. Buccal slit a small notch; single or two ambulacrals in mouth frame; first one to several laterals of each half-arm pressed closely against corresponding laterals of the adjacent half-arm of same interradius.

Content: *Stenaster* Billings, 1858, is the only genus. *Tetraster* Etheridge and Nicholson, 1880, is a subjective synonym. *Stenaster* Lambert, 1905, is an echinoid genus now bearing the substitute name *Parmulechinus* Lambert, 1906. The type-species of *Stenaster* is *S. salteri* Billings, 1858, by subsequent designation of Miller (1889, p. 283). Latest revisions refer *Stenaster pulchellus* Billings to *Urasterella* M'Coy; *S. grandis* Meek and *S. huxleyi* Billings to *Salteraster* Stuertz; *S. coronella* (Salter) to *Phillipsaster* Spencer; and *S. confluens* Trautschold to *incertae sedis*. *Stenaster* sp. of Newton (1878, p. 36) is the holotype of *Platanaster ordovicus* Spencer (A. W. A. Rushton, personal communication). *S. salteri* Billings, 1858, is a subjective junior synonym of *S. obtusus* (Forbes, 1848), the only species in the genus:

Stenaster obtusus (Forbes, 1848)

Plate IX, figure 2; Plate X, figures 1–3

Uraster obtusus Forbes, 1848, p. 463. Forbes, 1849, p. 2, pl. i fig. 3. Murchison, 1854, p. 182, fig. 17.

Palaeaster obtusus (Forbes). Salter, 1857, p. 326. Dujardin & Hupé, 1862, p. 435. Wright, 1863, p. 24. Baily, 1865, pp. 21, 30. Salter, 1866, pp. 262, 289, pl. 33 figs. 1a-c. Bigsby, 1868, p. 28. Woodward, 1869, p. 244. Salter, 1873, p. 4. Salter & Etheridge, 1881, pp. 394, 407, 418, 479, 480, pl. 23 fig. 1. Etheridge, 1888, p. 30. Reed, 1897, pp. 506, 510. Groom & Lake, 1908, p. 572.

Stenaster salteri Billings, 1858, p. 78, pl. 10 figs. 1a-b. Lyon & Casseday, 1859, p. 303. Bronn, 1860, p. 288. Chapman, 1861, p. 517. Billings, 1863, p. 941. Wright, 1863, p. 28, fig. 15(2) on p. 24. Chapman, 1864, p. 14. Shumard, 1868, p. 396. Bigsby, 1868, p. 28. Woodward, 1869, p. 245. Meek, 1872, p. 259. Meek, 1873, p. 67. Miller, 1877, p. 92. Ami, 1884, p. 58. Stürtz, 1886, p. 152. Miller, 1889, p. 282. James, 1896, pp. 126, 135 (in part). Gregory, 1899, p. 352. Ami, 1901, p. 61G. Grabau & Shimer, 1910, p. 572, fig. 1910. Springer, 1911, p. 45. [Johnston, 1911, p. 189.] Raymond in Johnston, 1912, p. 258. Schuchert, 1914, p. 40. Schuchert, 1915, pp. 164–165, pl. 32 fig. 1. Bassler, 1915, p. 1185. Ruedemann, 1916, pp. 52–54, pl. 2 figs. 1–2. [Foerste, 1922, p. 85.] Shimer & Shrock, 1944, p. 211, pl. 81 fig. 1. Wilson, 1946, pp. 5, 44, pl. 6 fig. 9. Sinclair, 1954, p. 36. Kilfoyle, 1954, p. 199. Bolton, 1960, p. 92. Mensah, 1962, pl. 11 fig. 4, pl. 12 figs. 1, 2. Shrock, 1972, p. 456. Bergstrom, Riva & Kay, 1974, p. 1629.

Stenaster obtusus (Forbes). Stürtz, 1886, p. 153. Spencer, 1914, pp. 22, 31, 49, text-figs. 21, 28, pl. 1 figs. 6–7. Schuchert, 1914, pp. 12, 29, 39, 44. Schuchert, 1915, pp. 165, 167. Ruedemann, 1916, p. 52. Spencer, 1918, p. 157. Spencer, 1919, p. 173. Spencer, 1927, pp. 329, 343–359, 372, text-figs. 221–226, 227A, 228A, 229–231, pl. 23 figs. 1–9, pl. 24 fig. 10. [Iakovlev, 1929, p. 63.] Spencer, 1930, p. 416. Spencer, 1934, pp. 452, 453, 470, text-fig. 294A. Fedotov, 1936, pp. 3, 10–17, 28, 30, text-figs. 2–3, pl. 1 figs. 3–6. Iakovlev, 1941, p. 180. Cuénot, 1948, p. 236. Spencer, 1950, pp. 398, 401. Spencer, 1951, p. 111. Ubaghs, 1953, pp. 816, 818, figs. 20, 34. [R. J. Ross, 1964, p. C39.] Owen, 1965, pp. 545, 546, 552, 570. Spencer & Wright, 1966, p. U82, figs. 70.2a-d. Kesling, 1971, p. 184.

Tetraster wyvillethomsoni Etheridge & Nicholson in Nicholson & Etheridge, 1880, p. 324, pl. 21 figs. 1–8. Salter & Etheridge, 1881, p. 407. Etheridge, 1899, p. 129. Peach & Horne, 1899, pp. 526, 687. Gregory, 1899, p. 345. Schuchert, 1914, pp. 5, 7, 42. Schuchert, 1915, p. 168, pl. 33 fig. 4. Bather, 1915, p. 426. Anderson, 1949, p. 31.

Tetraster obtusus (Forbes). Nicholson & Etheridge, 1880, p. 325.

Palaeaster wyvillethomsoni (Etheridge & Nicholson). Lapworth, 1882, p. 619 [not p. 618 (=crinoid stems according to Lamont, 1934, p. 174)].

Urasterella salteri (Billings). Hall, 1868, p. 9 (by implication). Stürtz, 1890, pp. 219, 220. Stürtz, 1893, pp. 41, 56.

Urasterella obtusus (Forbes). Stürtz, 1893, pp. 41, 56.

Hudsonaster batheri Schuchert, 1915, pp. 55, 65, 167, pl. 3 fig. 3.

Material examined: From Girvan, Scotland: USNM 60601, USNM 60614, USNM 97002, and BM(NH) E52410a,b (hexamerous, see plate IX, fig. 2). From Kirkfield, Ontario: USNM S3865 (plate X, fig. 3), USNM S3896, NYSM 7744, NYSM 7745, NYSM Powell Collection No. 57927. From Ottawa, Ontario: USNM 92633. From Curdsville, Kentucky: USNM 60628. From Panton, Vermont: MCZ 486. From California: USNM 165255–165258 (plate X, figs. 1, 2).

DISTRIBUTION OF *Stenaster obtusus*

Although there is but a single species in the family, it has been found in Central Asia, the British Isles, and eastern and western North America. For general accounts of the distribution of Paleozoic Asterozoa, see Foerste (1922) and Spencer (1950).

Mistaken records: Ruddy's (1885, p. 118) Welsh specimens of "*Palaeaster obtusus* Forbes" are Nos. E13530–E13532 in the British Museum (Natural History) (David Lewis, personal communication). Spencer (1916, pp. 74–75, and pp. 83–84) reidentified No. E13532 as *Belaster ordovicus* Spencer, and No. E13531 as *Caractacaster caractaci* (Gregory). The BM(NH) label to No. E13530 reads "Indet. asteroid."

Lapworth's (1882, pp. 618, 621) "*Palaeaster wyvillethomsoni*" from Quarrel Hill, Girvan, Scotland, is probably based instead on stellate casts of crinoid parts from the Crinoid Bed of the Lower Drummuck Group (J. L. Begg, in Lamont, 1934, pp. 174–175).

Shimer and Shrock (1944, p. 211) listed New York as a locality for *S. salteri*, but this appears to be a *lapsus calami* for Kentucky: "N.Y." for "Ky." (cf. Shrock, 1972).

Valid Records:

Kazakhstan, S.S.R.: 1) Lower part of the Anderkenyn Horizon (the beds containing *Isotelus romanovski* Weber and considered probable Late Llandeilo by Keller, 1962, p. 1192), Anderkenyn-Akchoku tract, Chu-Iliyskiye Mountains (Iakovlev, 1941, p. 180); 2) Chagyrly Mountains, Chetsky region, at a presumably comparable horizon (Fedotov, 1936).

Ireland: Tramore Limestones (Caradoc), townland of Pickardstown, County Waterford (Reed, 1897, pp. 505, 510; 1899, p. 740).

Scotland: Starfish Bed of the Upper Drummuck Group (Ashgill), Girvan district, Ayershire (Anderson, 1949, p. 29) (plate IX, fig. 2).

Wales: 1) Lower Bala Group (Caradoc), Moel-y-Garnedd, Bala district, Merionethshire (Forbes, 1848). Prof. H. B. Whittington informs me *in litt.* that the locality suggests the lower part of the Glyn Gower Siltstones. 2) Dolhir Beds (Ashgill Series) of Glyn Ceiriog, Denbighshire (Groom & Lake, 1908).

Kentucky: Curdsville Limestone Member of the Lexington Limestone (Trenton) at 1) Curdsville, Wilmore Quadrangle, Mercer County (Schuchert, 1915), and 2) USGS locality 5101-CO, Nicholasville Quadrangle, Jessamine County (J. W. Branstrattor, personal communication).

Vermont: "Trenton," Panton, Addison County (Schuchert, 1915). Prof. C. W. Welby suggests *in litt.* that a possible source of the specimen is the Glens Falls Limestone along the lake shore north of Arnold's Bay in Panton. The specimen is in the Museum of Comparative Zoology, Harvard University (MCZ 486).

Ontario and Quebec: 1) "Dalmanella beds" and perhaps also the "Crinoid beds," within the upper member of the Bobcaygeon Formation (enclosing the Kirkfield fauna of Trenton age), near Kirkfield, Carden township, Victoria County, Lake Simcoe district, Ontario (Johnston, 1912, pp. 257–259) (plate X, fig. 3); 2) Belleville (Billings, 1858), Thurlow township, Hastings County, Ontario, perhaps along the Moira River where the Verulam Formation is exposed: here and eastward to the Kingston area the lowest Verulam strata enclose the Kirkfield fauna (Prof. B. A. Liberty, *in litt.*); 3) "Cystid beds," near the top of the Couberg beds of the Ottawa Formation, vicinity of Ottawa, Ontario, including Philemon Island, Hull, Quebec (Wilson, 1946, p. 44).

Newfoundland: Lourdes Limestone, Long Point Group (Porterfieldian), Long Point, Newfoundland (Bergstrom, Riva & Kay, 1974). The specimen is in the American Museum of Natural History, AMNH No. 29022 (Dr. Miles Eldridge, personal communication).

New record: The unidentified "asteroid" of R. J. Ross, Jr., (1964, p. C39) from the Middle Ordovician Johnson Spring Formation in the Inyo Mountains of California is identifiable as *Stenaster* cf. *S. obtusus*. The four incomplete ?silicified arm fragments are very poorly preserved but show most of the characters listed above as diagnostic (plate X, figs. 1, 2). Similarly but better preserved arm fragments from Curdsville, Kentucky, helped in the identification. The California specimens are Nos. USNM 165255–165258 in the National Museum of Natural History, Smithsonian Institution. They measured 6.7 mm, 9.2 mm, 10.2 mm, and 10.3 mm in length prior to some crumbling.

The following locality data (verified by R. J. Ross, Jr., *in litt.*) accompany the specimens: USGS Collection D1023C0. Measured section JS-11 of D. C. Ross (1966, p. 52 and pl. I), unit 2, basal 1 foot of limestone = Johnson Spring Formation, approximately 10–15 feet above base in a limestone lens. Mazourka Canyon, Independence Quadrangle, Inyo County, California. Altitude 7860 ft. California coordinate system, zone 4: E. 2, 271,000 ft., N. 584,700 ft. (not E. 2,281,000 ft.).

Stenasteridae and Klasmuridae Compared

There has been some question as to whether *Stenaster* is an ophiuroid (Spencer, 1927, p. 343) or an asteroid (Schuchert, 1915, p. 163). The structure of *Klasmura* and *Antiquaster* show that *Stenaster* is an ophiuroid. The evidence is in the ambulacrals. Similarity of the ambulacrals of *Klasmura* with those of *Stenaster* was noticed by Spencer (1927, pp. 327, 329); similarity of the ambulacrals of *Antiquaster* with those of *Stenaster* was noticed by Kesling (1971, p. 184).

The similarities in ambulacral structure between *Stenaster* and *Klasmura* are very detailed: In common is the aboral radial sulcus. Left and right aboral perradial crests wall the sulcus and form proximal processes for insertion of dorsal longitudinal muscles. There is little space for ventral longitudinal muscles. Shelf-like processes form proximal and distal hinges suited to vertical arm flexure. Left and right oral perradial ridges wall off the radial canal. Also, left and right perradial longitudinal depressions separate the perradial ridges from the transverse oral ridges, but this is difficult to demonstrate in *Stenaster*.

My conclusion is that although there are ample differences that validate the families Stenasteridae and Klasmuridae, these similarities of ambulacral structure make the Scalarina a homogeneous group.

Synopsis of New York State Paleozoic Ophiuroids

The State of New York is perhaps the most prolific area in North America for collecting Devonian brittle stars. The following list based on the published record will swell considerably when specimens already in the collections of the New York State Museum and other repositories are duly accounted for.

ORDER STENURIDA

Family Helianthasteridae
  Helianthaster gyalinus Clarke, 1908 (syn.: *Lepidasterella babcocki* Schuchert, 1915; consult Kesling, 1964). Tompkins, Seneca, and Steuben Counties.
Family Rhopalocomidae
  Ptilonaster princeps Hall, 1868 (consult Wells, 1952). Cortland County, Tompkins County.
Family Klasmuridae (reclassified and emend. Hotchkiss, herein)
  Klasmura mirabilis Ruedemann, 1916. Yates County.

Klasmura clavigera Ruedemann, 1916. Yates and Ontario Counties.
?*Klasmura macropleura* n. sp. Yates County.
Antiquaster magrumi Kesling, 1971. Tompkins County (new record).

ORDER OEGOPHIURIDA

Family Encrinasteridae
Encrinaster pusillus Ruedemann, 1916. Chemung County.
Encrinaster sp. Cooper, 1932. Madison County.
Encrinaster n. sp. McIver and McIver, 1955. Otsego County.
Family Protasteridae
Eugasterella logani (Hall, 1868). Madison County.
Eugasterella bicatenulata Ruedemann, 1916. Ontario County, Tompkins County.
Mastigactis aranea (Ruedemann, 1916) (thin oral edges to the laterals place the monotypic genus in the family). Chemung County.
Stratuster n. sp. Hotchkiss, in prep. (the n. gen., n. sp. of McIver and McIver, 1955). Otsego County.
Family Lapworthuridae
Hallaster forbesi (Hall, 1859). Herkimer County.

UNIDENTIFIED

Ophiuroids of R. B. Johnson, 1949. Cortland County.

Ophiuroids also occur in the Ordovician and Silurian rocks of the State. Published records concern four species of Oegophiurida:

Family Protasteridae
Taeniaster spinosus (Billings, 1857) (Ruedemann, 1912, as *T. schohariae;* consult Hotchkiss, 1970, p. 74). Ordovician, Schoharie County.
Protaster? *stellifer* Ringueberg, 1886. Silurian, Niagara County.
Eugasterella? *concinna* (Ringueberg, 1886). Silurian, Niagara County.
Family Furcasteridae
Furcaster leptosoma (Salter, 1857) (Ringueberg, 1886, as *Squamaster echinatus;* consult Spencer, 1925, p. 319). Silurian, Niagara County.

The family-level diversity (seven families recorded) of brittle stars recovered from the rocks of the State affords material for the investigation of questions at the higher levels of classification. The results of such a study have been the subject of this paper.

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EXPLANATION OF COLUMNS, TABLES I, II

L	length of arm piece, from center of mouth frame if such is present (mm).
W	width of arm piece (mm).
D	diameter of mouth frame (mm).
W:D	indicated ratio.
J	number of arm 'joints' in 10 mm.
B	breadth of lateral from edge of cup for tube foot to tip of side process (mm).
JB	breadth of lateral measured in arm 'joints.'
V	width of vertebra (mm).
CTF	width of cup for tube foot (mm).
I	width covered by aboral integument of arm (mm).
SL	length of sublateral (mm).
ARS	width of aboral radial sulcus (mm).

TABLE I

K. clavigera

NYSM	L	W	D	W:D	J	B	JB	V	CTF	I	SL	ARS	Remarks
7768	10.0	2.3	—	—	26.0	0.7	1.86	0.6	0.4	—	—	—	Holotype; Lot 3634; pl. VIII, fig. 3
7769	3.2	2.3	—	—	25.3	0.7	1.77	0.5	0.4	—	—	—	Lot 3634; pl. VIII, fig. 2
13221	16.1	2.2	2.7	0.8	32.3	—	—	—	—	1.4	—	—	Lot 3629; pl. VIII, fig. 1

K. mirabilis

7771	14.3	3.3	5.6	0.6	14.3	1.2	1.76	1.3	—	—	0.3	—	Lectotype; pl. I, fig. 4; pl. II, figs. 1, 2
7772	11.6	3.3	5.8	0.6	12.0	2.1	2.48	—	—	—	—	—	In the solid; pl. I, fig. 1
7773	—	—	6.4	—	—	1.7	—	—	—	—	—	—	Lot 4046; pl. I, fig. 3
13218	9.0	4.0	—	—	14.4	1.5	2.17	1.4	—	—	0.3	—	Pl. II, fig. 3
13219	10.0	—	—	—	14.3	1.0	1.43	—	—	—	—	—	Lot 3629; pl. III, fig. 2

?*K. macropleura*

NYSM	L	W	D	W:D	J	B	JB	V	CTF	I	SL	ARS	Remarks
7770	37.1	5.9	—	—	11.4	3.6	4.08	1.3	0.8	—	0.7	—	Holotype; Lot 3629; pl. IV, figs. 1–3
7774	6.5	5.1	—	—	15.3	2.8	4.33	1.2	—	1.8	—	0.3	Lot 4046; pl. VII, fig. 1
7776	8.0	5.1	—	—	15.0	2.2	3.35	—	—	—	—	—	Pl. VI, fig. 2
7777	14.3	—	—	—	16.0	2.0	3.2	0.9	0.6	—	0.5	—	Pl. V, fig. 2
7778	11.3	7.1	—	—	12.0	4.0	4.8	1.5	—	—	—	—	In the solid; pl. VI, fig. 1
7779	11.4	3.8	—	—	17.1	2.0	3.41	1.0	0.6	—	—	—	Pl. V, fig. 3
7780	25.0	4.7	—	—	12.6	3.2	3.99	—	—	2.0	—	—	Pl. VII, fig. 3
7781	10.8	5.3	—	—	19.6	2.2	4.4	—	—	2.5	—	0.3	Pl. VII, fig. 2
7782	11.4	4.7	—	—	13.5	2.7	3.6	1.2	0.3	—	0.5	—	Pl. V, fig. 1
13220	—	—	—	—	—	—	—	—	—	—	—	—	Rolled into a circle; pl. III, fig. 1; measurements not taken

?*Klasmura* sp.

7775	—	—	—	—	—	—	—	—	—	—	—	—	Pl. IV, fig. 4; measurements not taken

Klasmura sp.

13217	—	—	6.1	—	—	—	—	—	—	—	—	—	Pl. I, fig. 2

TABLE II. *Antiquaster magrumi*

	L	W	D	W:D	J	B	JB	V	CTF	I	SL	ARS	Remarks
UMMP 57863a	17	3	2.6	1.2	32	0.6	1.92	0.7	0.7	—	0.6	—	Holotype
UMMP 57863b	10+	3	—	—	30	—	—	—	—	—	—	—	Paratype
NYSM 13227	16.7	3.2	2.9	1.1	30.0	0.6	1.90	0.6	0.7	—	0.5	—	Pl. VIII, fig. 4
BM(NH) 40296b	4.8	1.9	1.5	1.3	38.6	0.4	1.42	0.5	0.3	—	0.2	—	Pl. IX, fig. 1

Literature Cited

Ami, H. M. 1884. List of fossils from Ottawa and vicinity. Ottawa Field-Naturalists' Club, Trans. No. 5, 2:54–62.

Ami, H. M. 1901. Preliminary lists of the organic remains occurring in the various geological formations comprised in the map of the Ottawa district, including formations in the provinces of Quebec and Ontario, along the Ottawa River. Geol. Surv. Can. Ann. Rep. (new ser.) 12:49G–77G.

Anderson, F. W. 1949. Ordovician and Silurian. *In* Eyles, V. A., J. B. Simpson, and A. G. MacGregor, Geology of central Ayrshire (Explanation of one-inch Sheet 14), second edition (including explanation of limited portions of one-inch Sheets 8, 13, 15, 22). Dept. Sci. & Ind. Res., Mem. Geol. Surv. Scot., p. 21–32.

Baily, W. H. 1865. Palaeontological notes. *In* G. V. Du Noyer, Explanation to accompany Sheets 167, 168, 178, and 179 of the Maps, and Sheet 18 of the Longitudinal Sections of the Geological Survey of Ireland, illustrating parts of the Counties of Waterford, Wexford, Kilkenny, and Tipperary. Mem. Geol. Surv. Ireland, p. 18–30.

Bassler, R. S. 1915. Bibliographic index of American Ordovician and Silurian fossils. Smithsonian Inst., U.S. Nat. Mus. Bull. 92.

Bather, F. A. 1915. (Review of) C. Schuchert. Revision of Paleozoic Stelleroidea, with special reference to North American Asteroidea. Geol. Mag., dec. 6, 2(615):425–426.

Bell, F. J. 1892. A contribution to the classification of ophiuroids, with descriptions of some new and little-known forms. Proc. Zool. Soc. London 1891:175–183.

Bergstrom, Stig, J. Riva and M. Kay. 1974. Significance of conodonts, graptolites, and shelly faunas from the Ordovician of western and north-central Newfoundland. Can. J. Earth Sci. 11(12): 1625–1660.

Bigsby, J. J. 1868. Thesaurus Siluricus. The flora and fauna of the Silurian period, with addenda (from recent acquisitions). John Van Voorst, Paternoster Row.

Billings, Elkanah 1857. New species of fossils from the Silurian rocks of Canada. Geol. Surv. Can., Rep. Prog. 1853–54–55–56:256–345.

Billings, Elkanah 1858. On the Asteriadae of the Lower Silurian rocks of Canada. Geol. Surv. Can., Figs. and Descriptions of Canadian Organic Remains, dec. 3:75–85.

Billings, Elkanah 1863. A catalogue of the Lower Silurian fossils of Canada. Geol. Surv. Can., Rep. Prog. 1863:936–956.

Bjork, P. R., P. S. Goldberg, and R. V. Kesling 1968. Mouth frame of the ophiuroid *Onychaster*. Contrib. Mus. Paleontol. Univ. Mich. 22(4):45–60.

Bolton, T. E. 1960. Catalogue of type invertebrate fossils of the Geological Survey of Canada, vol. I. Dept. Mines and Tech. Surv. Can., Geol. Surv. Can.

Bronn, H. G. 1860. Die Klassen und Ordnungen des Thierreichs. vol. 2, Leipsig und Heidelberg.

Chapman, E. J. 1861. A popular exposition of the minerals and geology of Canada. Part IV. Some remarks on organic remains, with special reference to Canadian forms. Can. J. Ind., Sci., and Art 6(36):500–518.

Chapman, E. J. 1864. A popular and practical exposition of the minerals and geology of Canada. W. C. Chewett & Co., Toronto.

Clark, H. L. 1946. The echinoderm fauna of Australia, its composition and its origin. Carnegie Inst. Wash. Publ. no. 566.

Clarke, J. M. 1908. A Devonic brittlestar. N.Y. State Mus. Bull. 121:61–64.

Cooper, G. A. 1932. Dry-dredging in eastern central New York. Explorations and Field-Work of the Smithsonian Institution in 1931. Smithsonian Publ. 3134:19–22.

Cuénot, L. 1948. Anatomie, éthologie et systématique des Échinodermes. *In* Traité de Zoologie (Pierre-P. Grassé, ed.), 11:3–272. Masson et Cie., Paris.

Dujardin, M. F. and M. H. Hupé 1862. Histoire Naturelle des Zoophytes Échinodermes comprenant la description des Crinoïdes, des Ophiurides, des Astérides, des Échinides et des Holothurides. Librairie Encyclopédique de Roret, Paris.

Etheridge, Robert 1888. Fossils of the British Islands stratigraphically and zoologically arranged. Vol. I. Palaeozoic comprising the Cambrian, Silurian, Devonian, Carboniferous, and Permian species with supplementary appendix brought down to the end of 1886. Clarendon Press, Oxford.

Etheridge, Robert Jr. 1899. On the occurrence of a starfish in the Upper Silurian series of Bowning, New South Wales. Rec. Australian Mus. 3(5):128–129.

Fedotov, D. M. 1936. Zur Morphologie und Evolution der Seestern und Ophiuren des unteren Silur. Travaux Inst. Paléozool. Acad. Sci. URSS 5:3–33.

Fell, H. B. 1961. The fauna of the Ross Sea, Part I, Ophiuroidea. New Zealand Dept. Sci. Ind. Res. Bull. 142.

Fell, H. B. 1963. The phylogeny of sea-stars. Phil. Trans. Roy. Soc. London, ser. B, 246(735):381–435.

Foerste, A. F. 1922. The distribution of the Ottawa Trenton echinoderm faunas. Can. Field-Natur. 36(5):84–86.

Forbes, Edward 1848. On the Asteriadae found fossil in British strata. Mem. Geol. Surv. Great Britain and Mus. Pract. Geol. London, 2(2):457–482.

Forbes, Edward 1849. Silurian species of *Uraster*. Mem. Geol. Surv. U.K., Figures and Descriptions illustrative of British Organic Remains, dec. I.

Grabau, A. W. and H. W. Shimer 1909–1910. North American Index Fossils. A. G. Seiler & Co., New York.

Gregory, J. W. 1897. On the classification of the Palaeozoic echinoderms of the group Ophiuroidea. Proc. Zool. Soc. London 1896:1028–1044.

Gregory, J. W. 1899. On *Lindstromaster* and the classification of the Palaeasterids. Geol. Mag., new ser., dec. 4, 6:341–354.

Groom, Theodore and Philip Lake 1908. The Bala and Llandovery rocks of Glyn Ceirog (North Wales). Quart. J. Geol. Soc. London 64:546–595.

Hall, James 1859. Descriptions and figures of the organic remains of the Lower Helderberg group and the Oriskany sandstone. N.Y. Geol. Surv., Palaeontol. 3.

Hall, James 1868. Note on the genus *Palaeaster* and other fossil starfishes. Twentieth Report N.Y. State Cabinet Nat. Hist., pp. 324–345.

Hotchkiss, F. H. C. 1970. North American Ordovician Ophiuroidea. The genus *Taeniaster* Billings, 1858 (Protasteridae). Proc. Biol. Soc. Wash., 83(5):59–76.

Hotchkiss, F. H. C. 1974. Studies on Paleozoie ophiuroids and the ancestry of the Asterozoa. Ph.D. dissertation, Yale University. [Diss. Abstr. Int. 35(6):2922B.]

Hotchkiss, F. H. C. in press. Ophiuroid *Ophiocanops* (Echinodermata) not a living fossil. J. Nat. Hist.

Iakovlev, D. I. 1929. Vostochnaya chasti Chu-Iliyskikh gor (Eastern part of the Chu-Iliyskiye Mountains). Izv. Glavn. geol.-razved. upr. 5:55–81.

Iakovlev, D. I. 1941. Siluriyskiye otlozheniya yuzhnykh rayonov Vostochnogo Kazakhstana. Chu-Iliyskiye vodorazdely (Silurian deposits in southern regions of eastern Kazakhstan: Chu-Iliyskiye watersheds). Geologiya SSSR (Cosgeolizdat, Leningrad) 20:178–183.

James, J. F. 1896. Manual of the paleontology of the Cincinnati Group, Part VII. Monticuliporidea (concluded)—Echinodermata. J. Cincinnati Soc. Natur. Hist. 18(3&4):115–140.

Johnson, R. B. 1949. Upper Devonian ophiurans in central New York (abs.). Geol. Soc. Amer. Bull. 60:1971.

Johnston, W. A. 1911. Simcoe District, Ontario. Can. Dept. Mines, Geol. Surv. Br. Sum. Rept. 1910:188–192.

Johnston, W. A. 1912. Geology of Lake Simcoe area, Ontario, Brechin and Kirkfield Sheets. Can. Dept. Mines, Geol. Surv. Br. Sum. Rept. 1911:253–261.

Keller, B. M. 1962. General outline of the Ordovician stratigraphy of the Chu-Iliyskiye Mountains. Int. Geol. Rev. 4(11):1175–1205.

Kesling, R. V. 1964. A drastic reappraisal of "*Lepidasterella babcocki* Schuchert" as *Helianthaster gyalinus* Clarke a streptophiuran auluroid. Contrib. Mus. Paleontol. Univ. Mich. 19(9):115–133.

Kesling, R. V. 1971. *Antiquaster magrumi*, a new unusual brittle-star from the Middle Devonian Silica Formation of Northwestern Ohio. Contrib. Mus. Paleontol. Univ. Mich. 23(10):181–191.

Kilfoyle, C. F. 1954. Catalog of type specimens of fossils in the New York State Museum, supplement 4. N.Y. State Mus. Bull. 348.

Lambert, Jules 1905. Notes sur quelques échinides éoceniques de l'Aude et de l'Hérault. Ann. Univ. Lyon, new ser. 17:131–164.

Lambert, Jules 1906. (Review of) Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault, par L. Doncieux. Rev. Critique de Paléozool. 10:62–64.

Lamont, Archie 1934. Lower Paleozoic brachiopods of the Girvan district: suggestions on morphology in relation to environment. Ann. Mag. Natur. Hist., ser. 10, 14:161–184.

Lapworth, Charles 1882. The Girvan succession. Quart. J. Geol. Soc. London 38:537–666.

Lehman, W. M. 1957. Die Asterozoen in den Dachschiefern des rheinischen Unterdevons. Abhandl. hess. Landesamt. Bodenforsch 21.

Lyon, S. S. and S. A. Casseday 1859. A synonymic list of the Echinodermata of the Paleozoic rocks of North America. Amer. Acad. Arts, Proc. 4:282–304.

Mayr, Ernst 1963. Animal Species and Evolution. The Belknap Press of Harvard University Press.

McIver, M. A. and E. P. McIver 1955. 300-million-year-old starfishes. Natur. Hist. 64(3):159.

Meek, F. B. 1872. Description of two new star-fishes, and a crinoid from the Cincinnati Group of Ohio and Indiana. Amer. J. Sci., 3d ser., 3:257–262.

Meek, F. B. 1873. Descriptions of the invertebrate fossils of the Silurian and Devonian systems. Rept. Geol. Surv. Ohio, 1(2):1–243.

Mensah, K. M. 1962. Lithology, palaeontology, and palaeoecology of the Upper Kirkfield Member (Middle Ordovician) in the type area at Kirkfield, Ontario. Master's thesis, University of Toronto.

Miller, S. A. 1877. The American Palaeozoic Fossils: A catalogue of the genera and species, with names of authors, dates, places of publication, groups of rocks in which found, and the etymology and signification of the words, and an introduction devoted to the stratigraphical geology of the palaeozoic rocks. xv+245 pp., published by the author, Cincinnati, Ohio. (The second edition published January 1883 is the 1st edition with a supplement of pp. 246–334.)

Miller, S. A. 1889. North American Geology and Palaeontology for the use of amateurs, students, and scientists. 664 pp., published by the author, Cincinnati, Ohio.

Mortensen, Th. 1932. On an extraordinary Ophiurid, *Ophiocanops fugiens* Koehler, with remarks on *Astrogymnotes*, *Ophiopteron*, and on an albino *Ophiocoma*. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København 93:1–21.

Murchison, R. I. 1854. Silurica. The history of the oldest known rocks containing organic remains, with a brief sketch of the distribution of gold over the earth. John Murray, London.

Newton, E. T. 1878. A catalogue of the Cambrian and Silurian fossils in the Museum of Practical Geology. H.M.S.O., London.

Nicholson, H. A. and Robert Etheridge, Jr. 1880. A monograph of the Silurian fossils of the Girvan district in Ayrshire with special reference to those contained in the "Gray Collection," fasc. III (The Annelida and Echinodermata, with supplements on the Protozoa, Coelenterata, and Crustacea). William Blackwood & Sons, Edinburgh & London.

Owen, H. G. 1965. The British Palaeozoic Asterozoa, table of contents, supplement and index. Palaeontographical Soc., London.

Peach, B. N. and John Horne 1899. The Silurian rocks of Britain, Vol. I. Scot. Mem. Geol. Surv. U.K.

Reed, F. R. C. 1897. Notes on the geology of County Waterford. 1. The fauna of the Ordovician beds near Tramore. Geol. Mag., new ser., dec. 4, 4:502–512.

Reed, F. R. C. 1899. The lower Palaeozoic bedded rocks of County Waterford. Quart. J. Geol. Soc. London 55:718–772.

Ringueberg, E. N. S. 1886. New genera and species of fossils from the Niagara shales. Bull. Buffalo Soc. Natur. Sci. 5:5–22.

Ross, D. C. 1966. Stratigraphy of some Paleozoic formations in the Independence Quadrangle, Inyo County, California. U.S. Geol. Surv. Prof. Pap. 396.

Ross, R. J., Jr. 1964. Middle and Lower Ordovician formations in southernmost Nevada and adjacent California, with a section on paleotectonic significance of Ordovician sections south of the Las Vegas shear zone. U.S. Geol. Surv. Bull. 1180–C.

Ruddy, Thomas 1885. List of Caradoc or Bala fossils found in the neighborhood of Bala, Corwen, and Glyn Ceirog. Proc. Chester Soc. Natur. Sci. 3:113–124.

Ruedemann, Rudolf 1912. The Lower Siluric shales of the Mohawk Valley. N.Y. State Mus. Bull. 162.

Ruedemann, Rudolf 1916. Paleontologic contributions from the New York State Museum. I. Account of some new or little-known species of fossils. N.Y. State Mus. Bull. 189.

Salter, J. W. 1857. On some new Palaeozoic starfishes. Ann. Mag. Natur. Hist., ser. 2, 20:321–334.

Salter, J. W. 1866. On the fossils of North Wales. *In* A. C. Ramsay, ed., The geology of North Wales, with map and sections and an appendix on the fossils, with plates. Mem. Geol. Surv. Great Britain and Mus. Pract. Geol. 3:240–381.

Salter, J. W. 1873. A catalogue of the collection of Cambrian and Silurian fossils contained in the Geological Museum of the University of Cambridge, with a preface by Adam Sedgwick and a table of genera and index added by Prof. Morris. Cambridge University.

Salter, J. W. and Robert Etheridge Jr. 1881. On the fossils of North Wales. *In* A. C. Ramsay, ed., The geology of North Wales, with an appendix on the fossils by J. W. Salter revised and added to by Robert Etheridge. Mem. Geol. Surv. Great Britain and Mus. Pract. Geol. 3 (2nd edition).

Schöndorf, Friedrich 1910. Ueber einige "Ophiuriden und Asteriden" des englischen Silur und ihre Bedentung fur die Systematik paläozoischen Seesterne. Jahrb. nassau. Ver. Naturk., Wiesbaden 63:206–256.

Schöndorf, Friedrich 1910. Paläozoische Seesterne Deutschlands. II. Die Aspidosomatiden des deutschen Unterdevon. Palaeontogr. 57:1–63.

Schuchert, Charles 1914. Stelleroidea palaeozoica. Fossilium Catalogus I: Animalia, F. Frech, ed., pars 3. W. Junk, Berlin.

Schuchert, Charles 1915. Revision of Paleozoic Stelleroidea with special reference to North American Asteroidea. U.S. Nat. Mus. Bull. 88.

Shimer, H. W. and R. R. Shrock 1944. Index Fossils of North America. Technology Press, Massachusetts Institute of Technology. John Wiley & Sons, Inc., New York.

Shrock, R. R. 1972. Corrigenda II for "Index Fossils of North America." J. Paleontol. 46:455–459.

Shumard, B. F. 1868. A catalogue of the Palaeozoic fossils of North America. Trans. Acad. Sci. St. Louis, 2:334–407.

Sinclair, G. W. 1954. The age of the Ordovician Kirkfield Formation in Ontario. Ohio J. Sci. 54(1):31–41.

Spencer, W. K. 1914–1940. A Monograph of the British Palaeozoic Asterozoa. Palaeontographical Society (London). Ten parts. Published as follows: 1914, Part I. 1916, Part II. 1918, Part III. 1919, Part IV. 1922, Part V. 1925, Part VI. 1927, Part VII. 1930, Part VIII. 1934, Part IX. 1940, Part X.

Spencer, W. K. 1950. Asterozoa and the study of Palaeozoic faunas. Geol. Mag. 87(6):393–408.

Spencer, W. K. 1951. Early Palaeozoic starfish. Phil. Trans. Roy. Soc. London, ser. B, 253(623): 87–129.

Spencer, W. K. and C. W. Wright 1966. Asterozoans. *In* Treatise on Invertebrate Paleontology, R. C. Moore, ed., Part U, Echinodermata 3:4–107. Univ. Kansas Press and Geol. Soc. Amer., Lawrence, Kansas.

Springer, Frank 1911. On a Trenton echinoderm fauna at Kirkfield, Ontario. Can. Dept. Mines, Geol. Surv. Br. Mem. 15–P.

Stürtz, Bernhard 1886a. Beitrag zur Kenntnis paläozoischer Seesterne. Palaeontogr. 32:75–98.

Stürtz, Bernhard 1886b. Ueber paläozoische Seesterne. Neues Jahrb. Mineral., Geol. und Paläontol. 2:142–154.

Stürtz, Bernhard 1890. Neuer Beitrag zur Kenntniss paläozoischer Seesterne. Palaeontogr. 36:203–247.

Stürtz, Bernhard 1893. Ueber versteinerte und lebende Seesterne. Verh. naturhist. Ver. preuss. Rheinl. u. Westf. usw., 50:1–92.

Ubaghs, Georges 1953. Class des Stelléroides (Stelleroidea). *In* Traité de Paléontologie, J. Piveteau, ed., 3:774–842.

Wells, J. W. 1952. A specimen of the starfish *Ptilonaster* from the Upper Devonian of central New York. J. Paleontol. 26:120–122.

Wilson, A. E. 1946. Echinodermata of the Ottawa Formation of the Ottawa-St. Lawrence Lowland. Can. Dept. Mines, Geol. Surv. Br., Bull. 4.

Woodward, Henry 1869. On *Eucladia*, a new genus of Ophiuridae, from the Upper Silurian, Dudley. Geol. Mag. 6:241–245.

Wright, Thomas 1863. Monograph on the British fossil Echinodermata of the Oolitic Formations. Vol. II. The Asteroidea. Palaeontogr. Soc. 1861.

Explanation of Plates

PLATE I

Figure 1. *Klasmura mirabilis.* Mouth frame in aboral view. NYSM 7772. Original for Ruedemann's pl. 22, fig. 2. In the solid. Bar represents 2 mm.

Figure 2. *Klasmura* sp. Mouth frame in oral view. NYSM 13217. Not previously figured. Latex pull. Bar represents 2 mm.

Figure 3. *Klasmura mirabilis.* Mouth frame in aboral view. NYSM 7773. Used to complete Ruedemann's pl. 22, fig. 2. Latex pull. Bar represents 2 mm.

Figure 4. *Klasmura mirabilis.* Mouth frame in oral view. NYSM 7771. Lectotype. Original for Ruedemann's pl. 22, fig. 1. Original for Spencer's text-fig. 215A. Latex pull. Bar represents 2 mm.

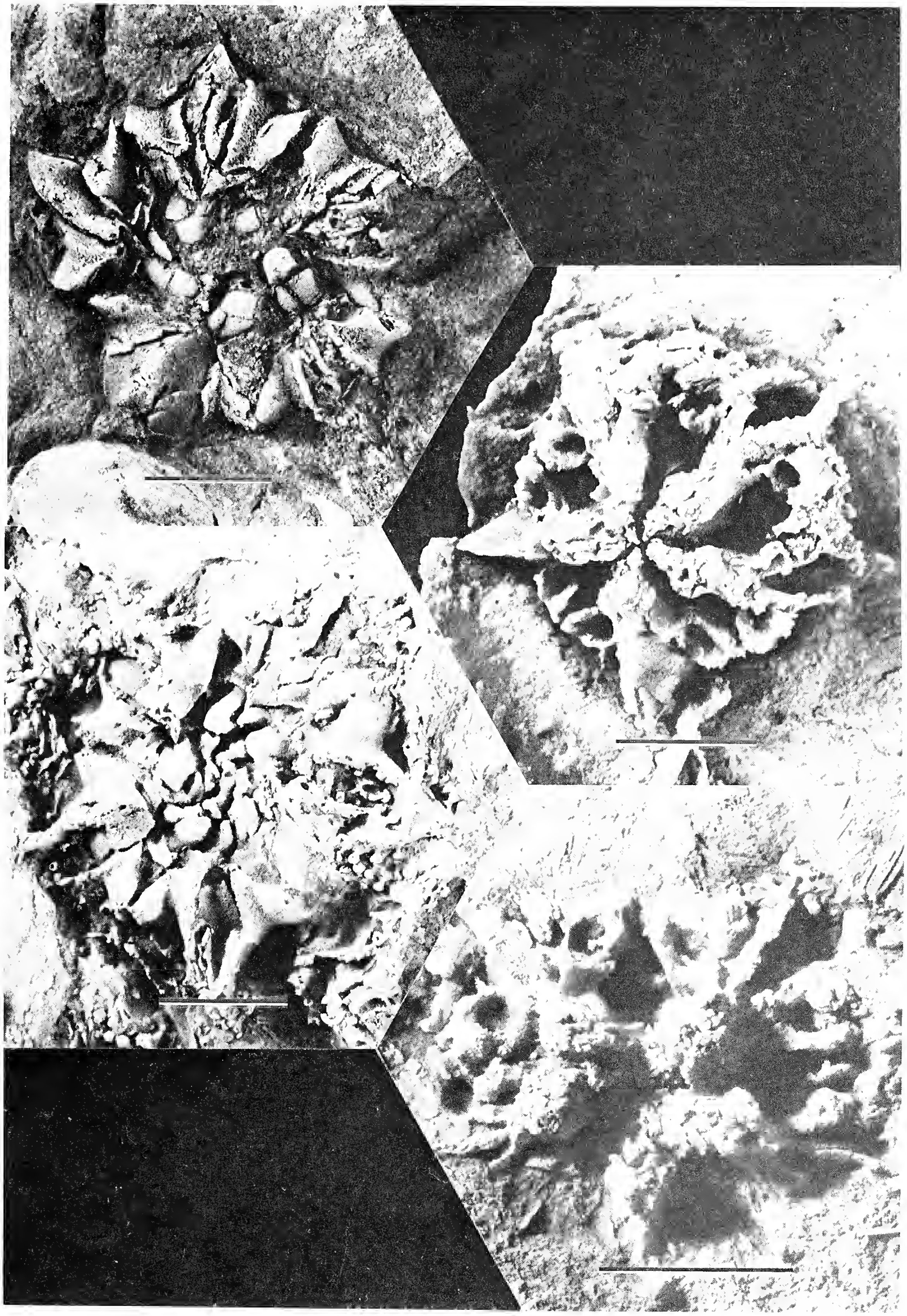
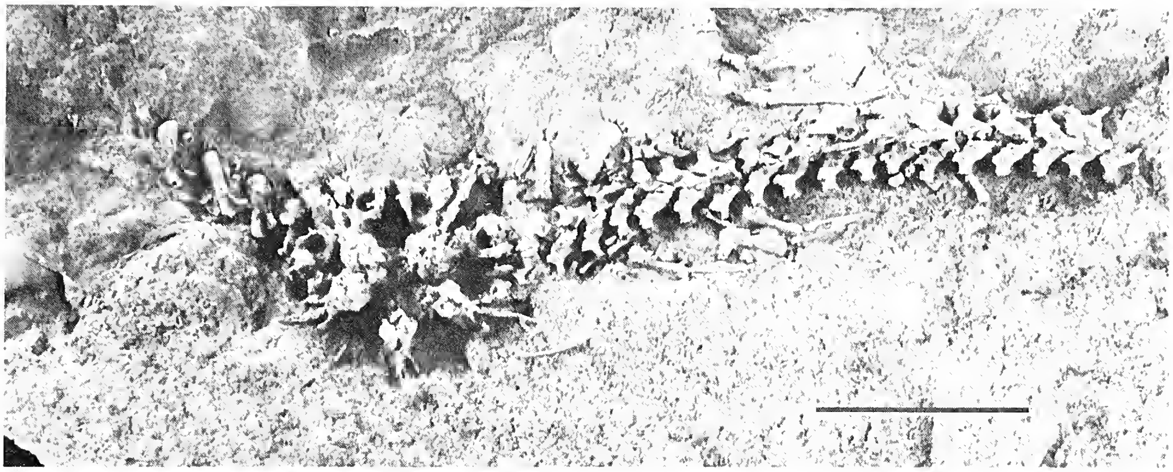


PLATE II

Figures 1, 2. *Klasmura mirabilis.* Oral view. NYSM 7771. Lectotype. Original for Ruedemann's pl. 22, fig. 1. Original for Spencer's text-fig. 215A. Latex pull. Bar in figure 1 represents 4 mm. Bar in figure 2 represents 2 mm. For greater detail of mouth frame see plate I, figure 4.

Figure 3. *Klasmura mirabilis.* Oral view. Note spines at base of shaft of spine-like process of some laterals. Floor of radial canal missing in places, exposing pores for passage of branches to tube feet. NYSM 13218. Not previously figured. Same slab with NYSM 7771 and others. Latex pull. Bar represents 2 mm.



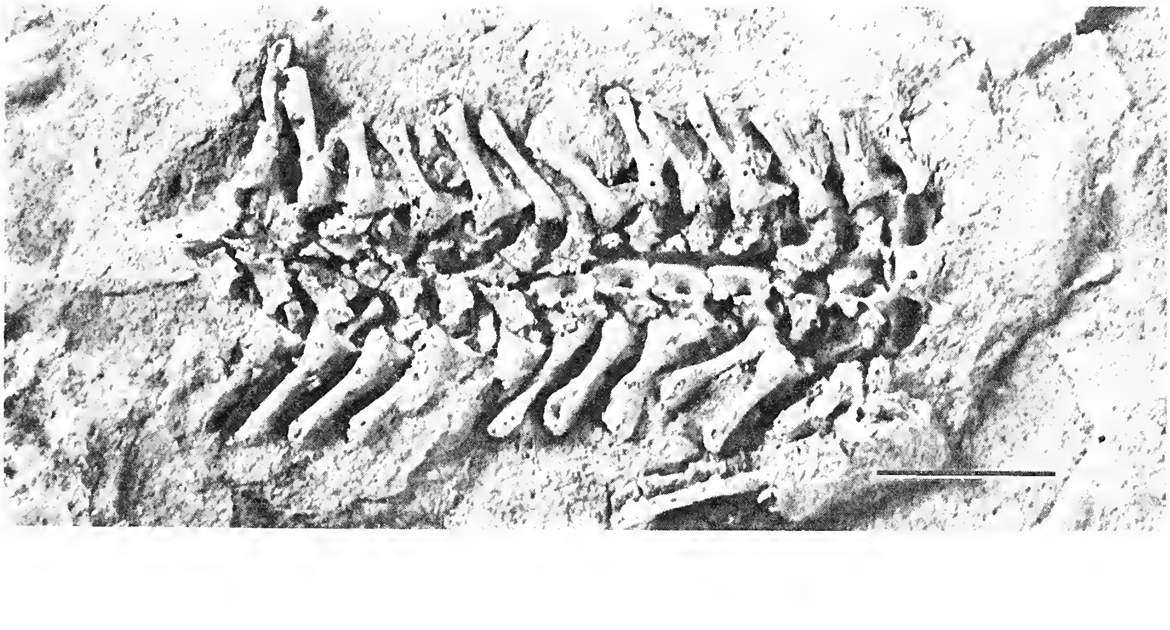
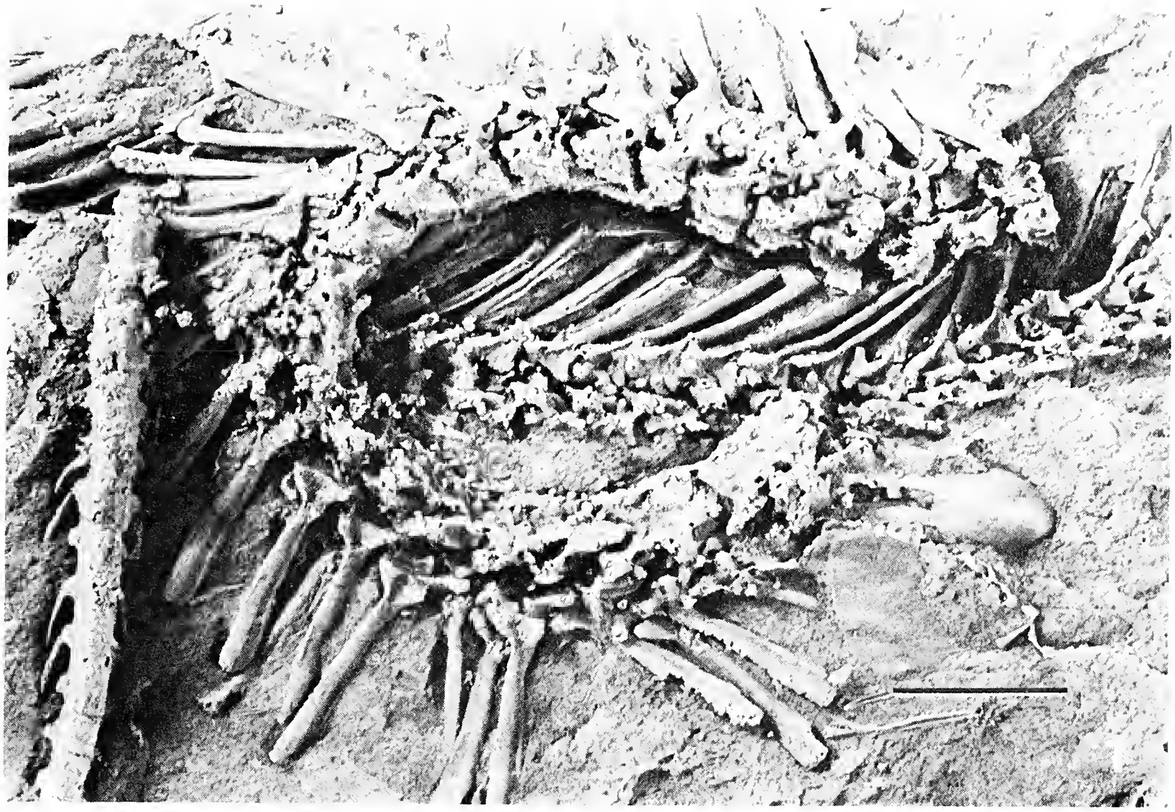


PLATE III

Figure 1. ?*Klasmura macropleura* n. sp. Lateral view. Arm fragment rolled into a circle; aboral surface forms inside of circle; laterals fringe the oral surface outside of circle. Crinoid fragment at left. Ethological comparison with *Onychaster* spp. by authors founded on this sort of data; the present paper finds the comparison unconvincing. NYSM 13220. Not previously figured. Same slab as NYSM 7771 and others. Latex pull. Bar represents 2 mm.

Figure 2. *Klasmura mirabilis* (upper specimen). Oral view of laterals (the rest is confused) showing interlocking saddle-shaped laterals. Beneath is a specimen (unregistered) of ?*Klasmura macropleura* n. sp. showing slight displacement of vertebral halves and allowing side by side comparison of the two species: processes to laterals short in *K. mirabilis*, long in ?*K. macropleura*. NYSM 13219. Not previously figured. Same slab with NYSM 13221.



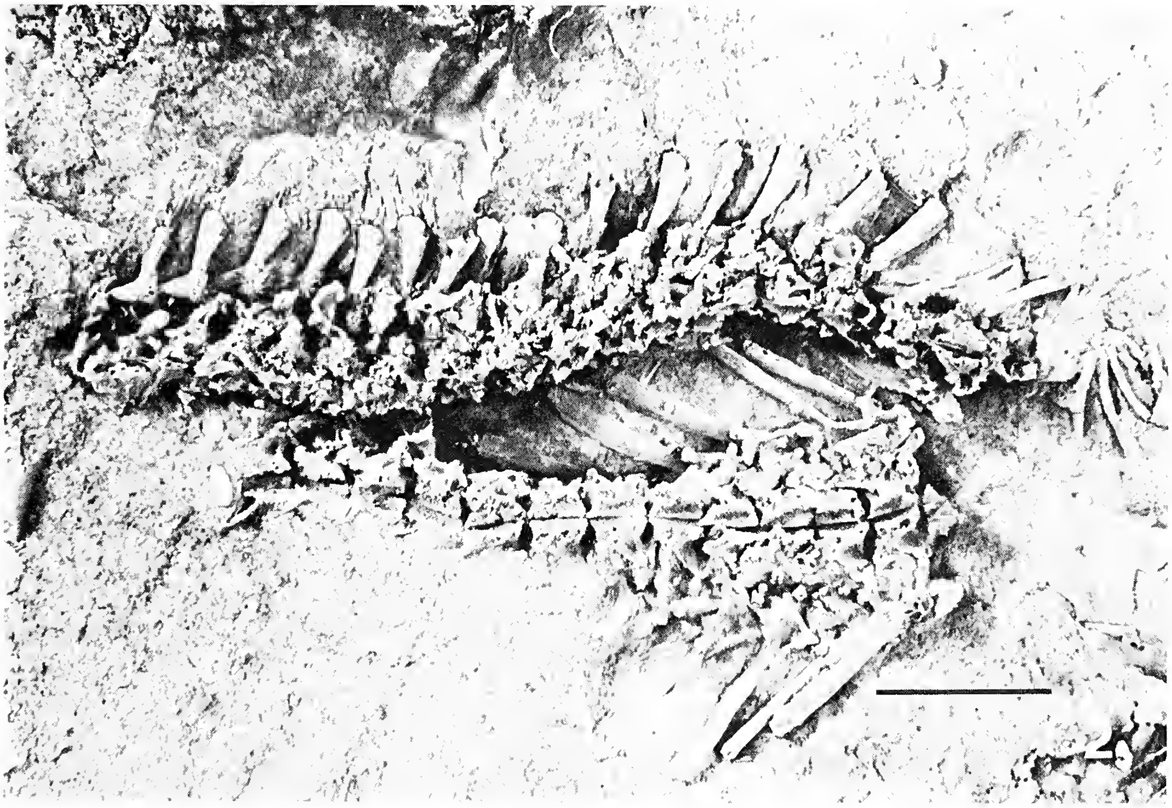


Plate IV

Figures 1, 2, 3. ?*Klasmura macropleura* n. sp. Oral view. NYSM 7770. Holotype. Original for Ruedemann's pl. 20, fig. 3 and pl. 23, fig. 4. Latex pull. Bar in figure 1 represents 5 mm. Bars in figures 2, 3 represent 2 mm.

Figure 4. ?*Klasmura* sp. Aboral view. NYSM 7775. Original for Ruedemann's pl. 22, fig. 4. Latex pull. Bar represents 2 mm.

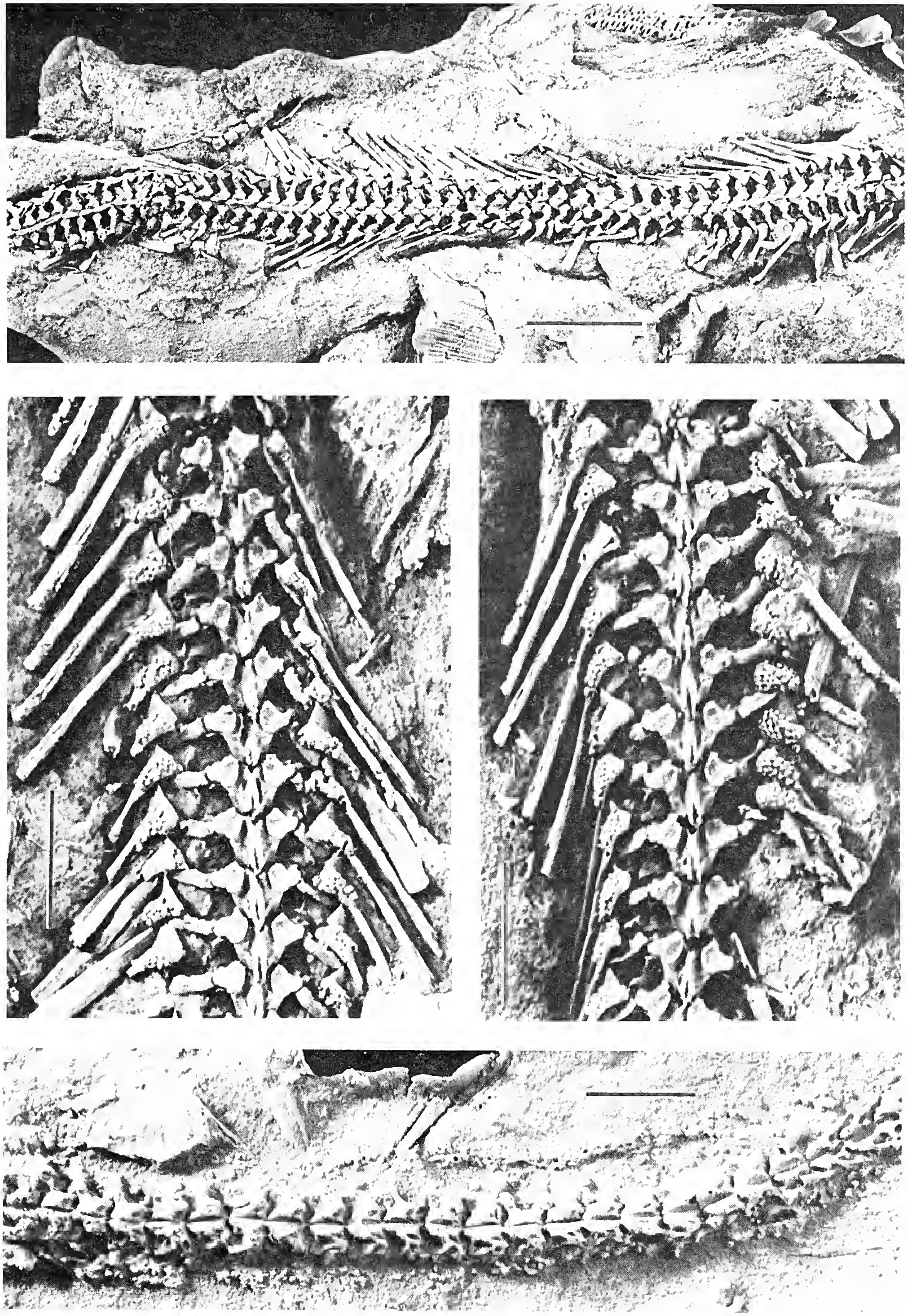
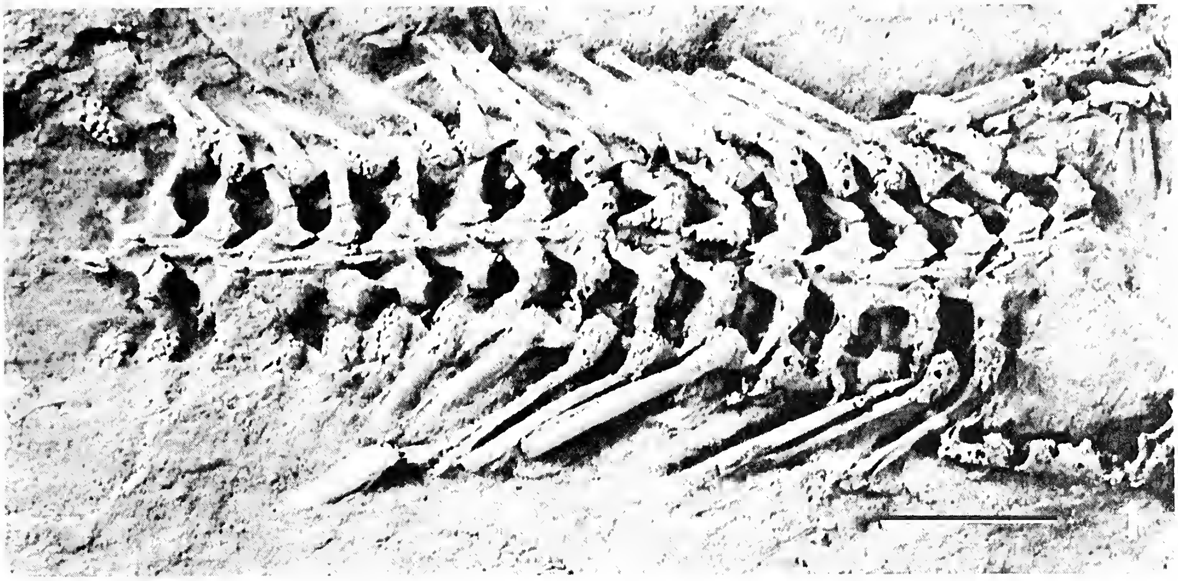


PLATE V

Figure 1. ?*Klasmura macropleura* n. sp. Oral view. NYSM 7782. Original for Ruedemann's pl. 23, fig. 3. Original for Spencer's text-fig. 213B. Latex pull. Same slab as NYSM 7771 and others. Bar represents 2 mm.

Figure 2. ?*Klasmura macropleura* n. sp. Oral view. NYSM 7777. Original for Ruedemann's pl. 22, fig. 6. Latex pull. Bar represents 2 mm.

Figure 3. ?*Klasmura macropleura* n. sp. Oral view except at left where bent over itself giving aboral view. Detail weathered away at right. NYSM 7779. Original for Ruedemann's pl. 22, fig. 8. Latex pull. Bar represents 2 mm.



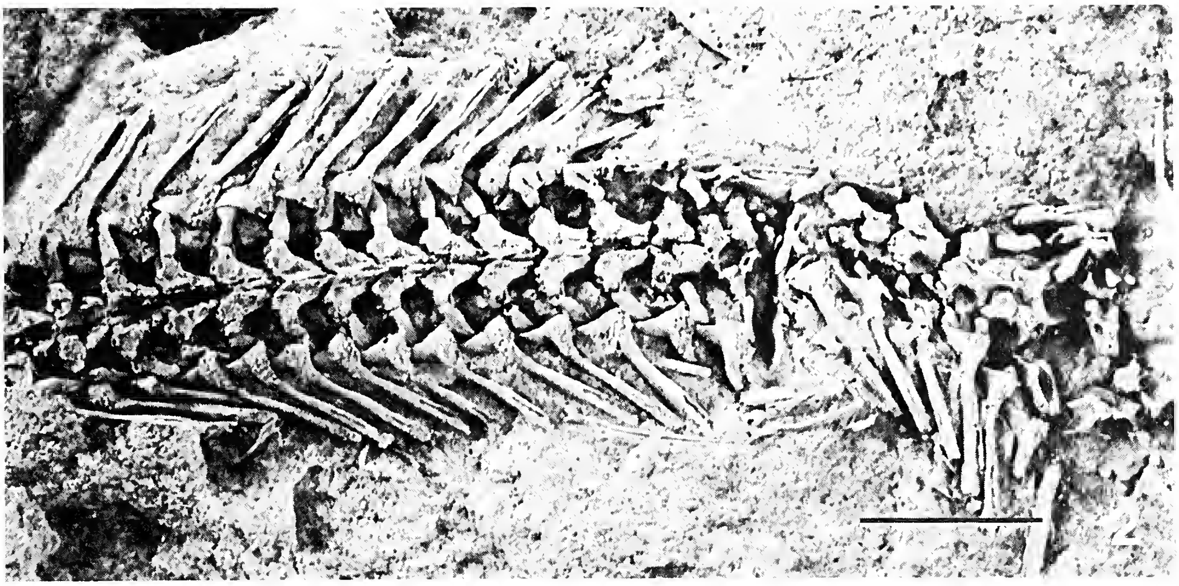

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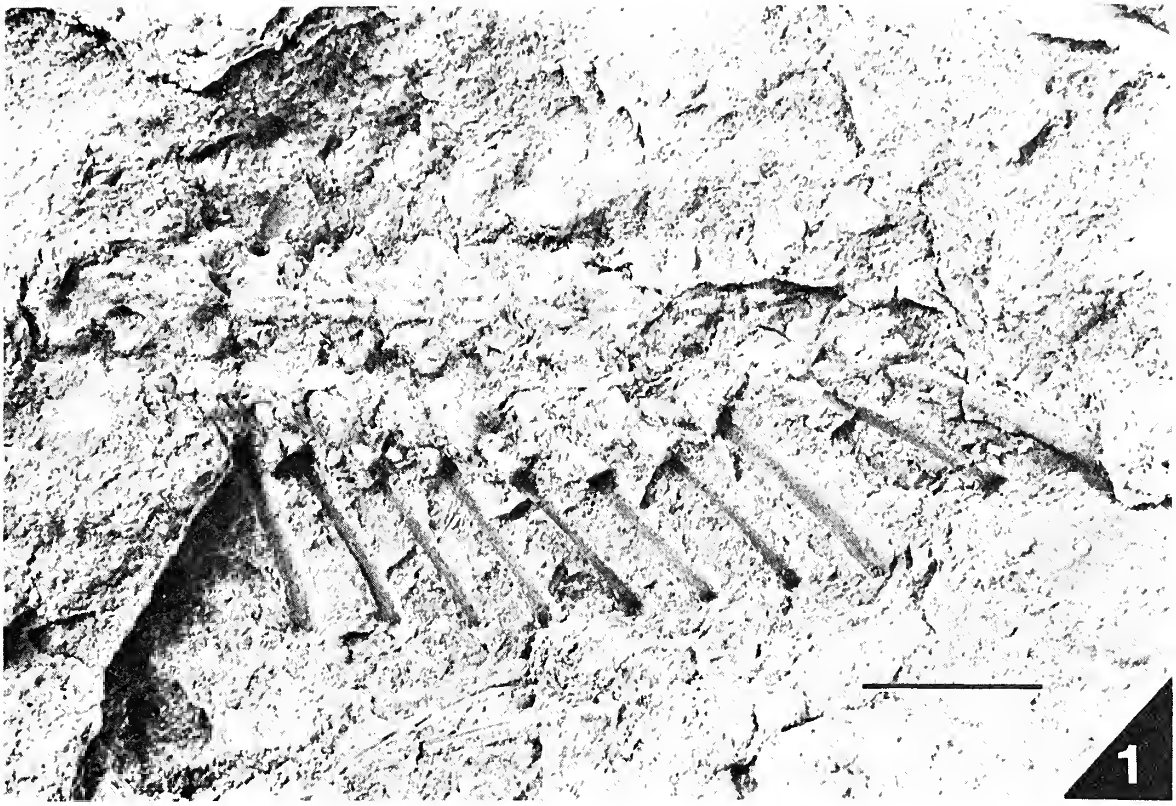
PLATE VI

Figure 1. ?*Klasmura macropleura* n. sp. Oral view. Mostly obscured by matrix, but carinal cleft of vertebrae shows through. In lower half of figure, side processes of laterals have broken out of matrix and are lost. NYSM 7778. Original for Ruedemann's pl. 22, fig. 7. In the solid. Bar represents 2 mm.

Figure 2. ?*Klasmura macropleura* n. sp. Oral view. Much weathered. NYSM 7776. Original for Ruedemann's pl. 22, fig. 5. Latex pull. Same slab as NYSM 7780. Bar represents 2 mm.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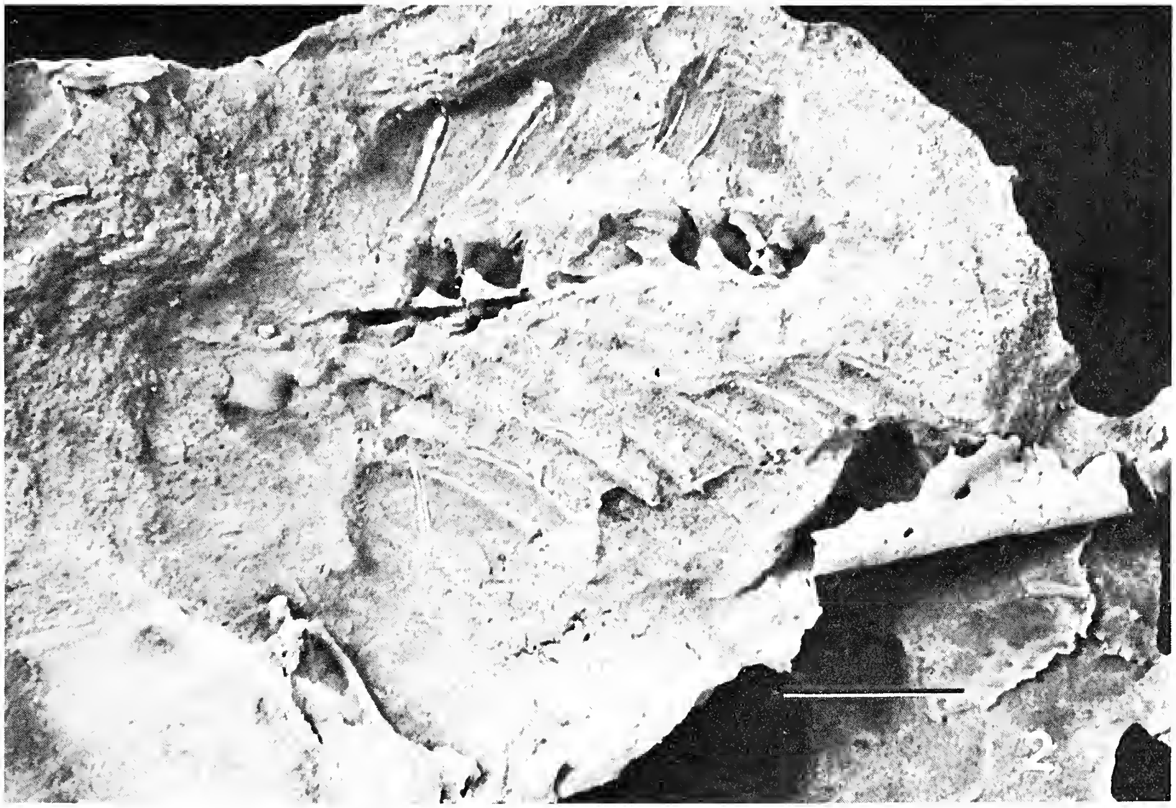
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PLATE VII

Figure 1. ?*Klasmura macropleura* n. sp. Aboral view. Note aboral radial sulcus. NYSM 7774. Original for Ruedemann's pl. 22, fig. 3. Original for Spencer's text-fig. 214. Latex pull. Bar represents 2 mm.

Figure 2. ?*Klasmura macropleura* n. sp. Aboral view. Note aboral radial sulcus. NYSM 7781. Original for Ruedemann's pl. 23, fig. 2. Latex pull. Bar represents 2 mm.

Figure 3. ?*Klasmura macropleura* n. sp. Aboral view. Aboral radial sulcus visible at left, obscured by integument at right. Note tufts of spines at tips of some processes to laterals. NYSM 7780. Original for Ruedemann's pl. 23, fig. 1. Latex pull. Same slab as NYSM 7776. Bar represents 3 mm.

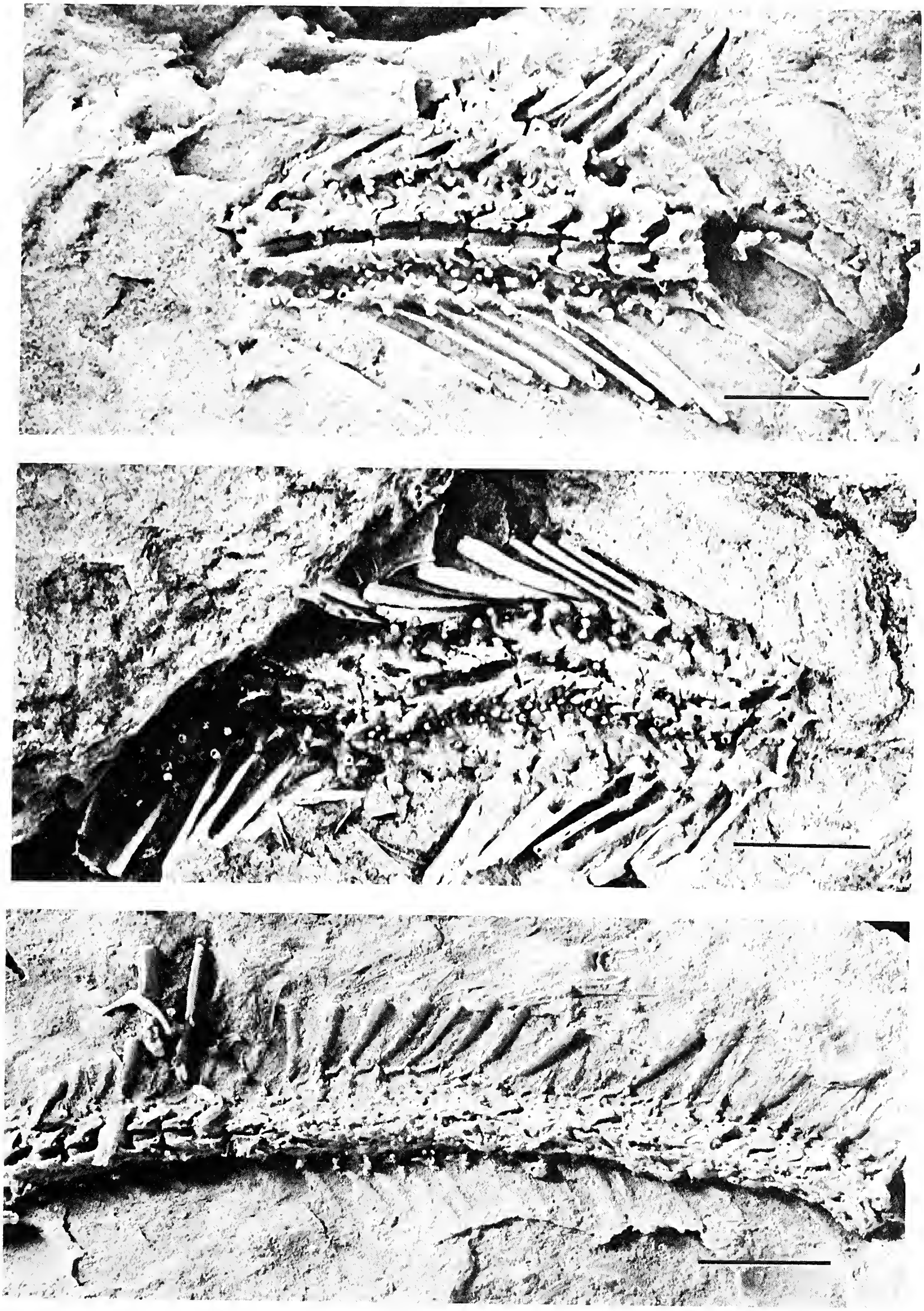

PLATE VIII

Figure 1. *Klasmura clavigera.* Aboral view. Mouth frame at right shows excessive oral-aboral dimension. NYSM 13221. Not previously figured. Same slab as NYSM 13219. Latex pull. Scale of figure 4 applies.

Figure 2. *Klasmura clavigera.* Oral view. NYSM 7769. Paratype. Original for Ruedemann's pl. 23, fig. 8. Latex pull. Scale of figure 4 applies.

Figure 3. *Klasmura clavigera.* Oral view. NYSM 7768. Holotype. Original for Ruedemann's pl. 23, fig. 9. Latex pull. Scale of figure 4 applies.

Figure 4. *Antiquaster magrumi.* Oral view. The faintly visible mouth frame (not shown in photograph) is of normal, rather than excessive oral-aboral dimension. NYSM 13227. Latex pull. Out of a boulder of Ludlowville Formation shale (Middle Devonian) found near Danby, south of Ithaca, Tompkins County, New York. New record. Bar represents 2 mm.

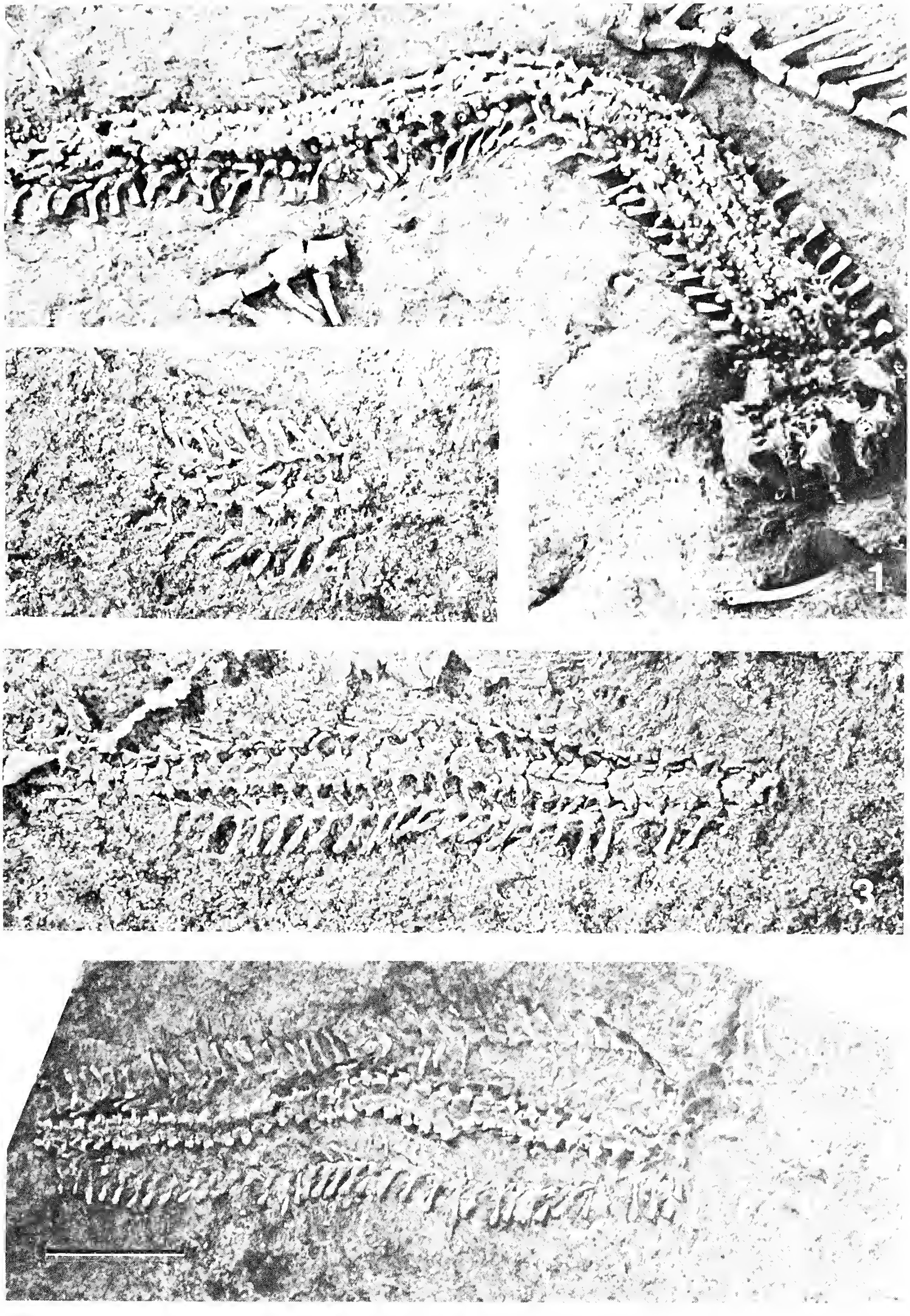
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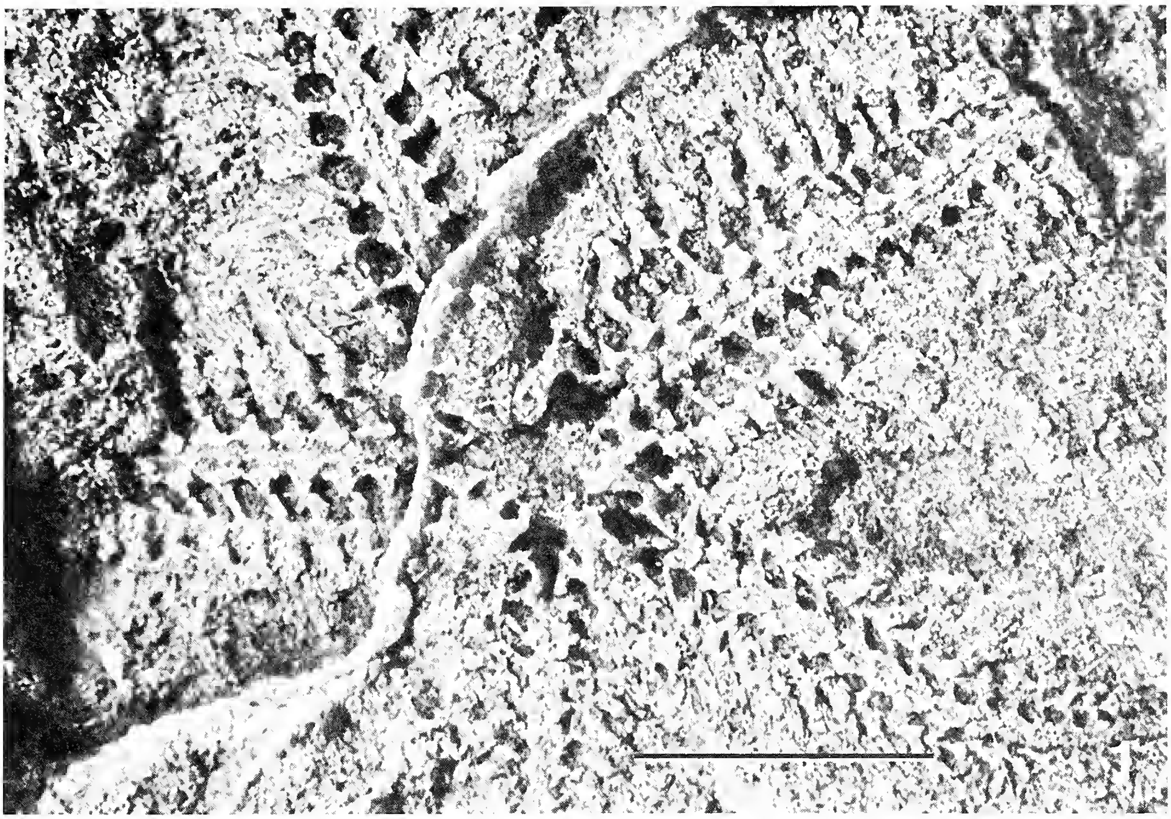
PLATE IX

Figure 1. *Antiquaster magrumi.* Oral view. BM(NH) 40296b. Identified by Spencer as *Bdellacoma vermiformis* but not figured or described. Latex pull. Lower Ludlow Shales (Silurian) at Church Hill, Leintwardine, Herefordshire, England. New record. Bar represents 2 mm.

Figure 2. *Stenaster obtusus.* Aboral surface of unique hexamerous specimen. BM(NH) E52410b. The spicular integument is preserved on the central disk but not on the arms, which therefore show the ambulacrals and laterals in aboral view. Latex pull. Girvan district, Scotland. Bar represents 7 mm.



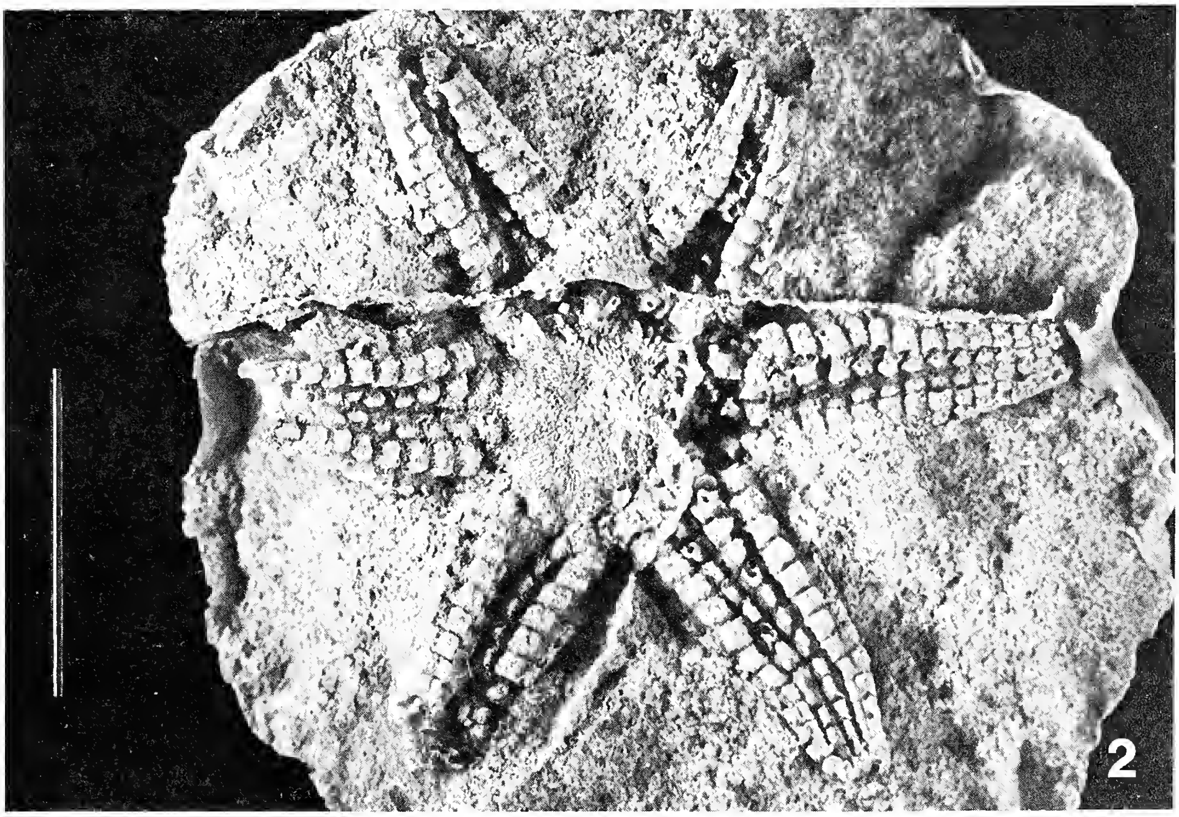

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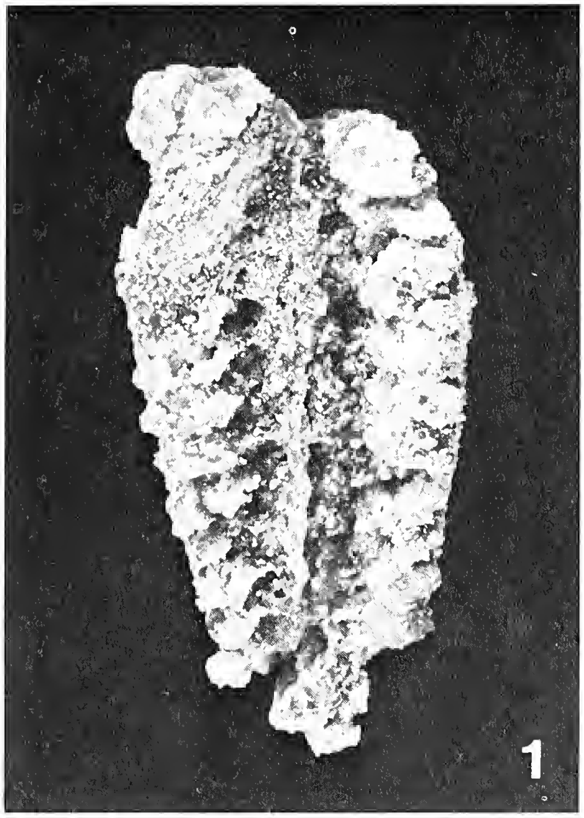
PLATE X

Figures 1, 2. *Stenaster* cf. *S. obtusus.* Oral surface (figure 1) shows broad laterals scalloped at their perradial edges. Aboral surface (figure 2) is the crusty remains of a spicular integument. USNM 165257. In the solid. Johnson Spring Formation (Middle Ordovician), Mazourka Canyon, Independence Quadrangle, Inyo County, California. New record. Bar represents 3 mm.

Figure 3. *Stenaster obtusus.* Oral surface for comparison with figure 1. USNM S3865. In the solid. Kirkfield, Ontario. Bar represents 7 mm.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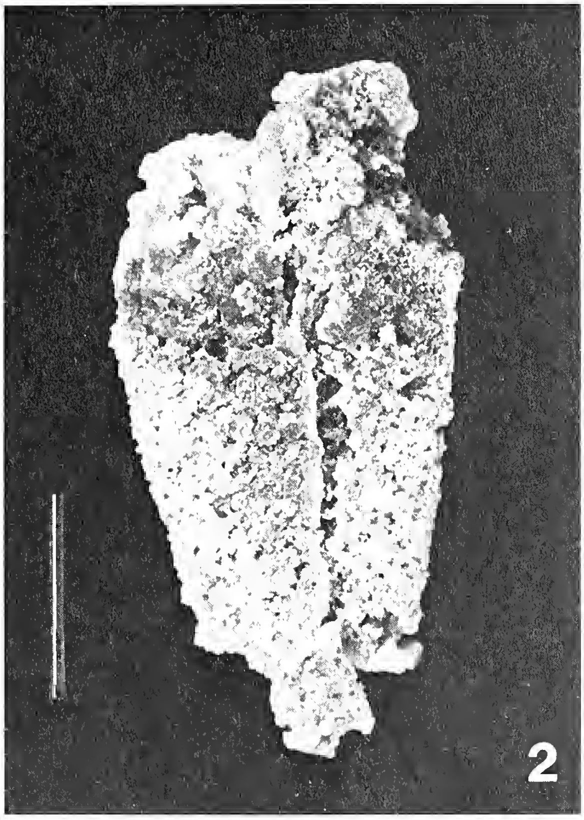
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