The Comparative Anatomy and Phylogeny of the Cyperaceae[1].

BY

AMON B. PLOWMAN.

With Plates I and II and two Figures.

SYNOPSIS.

---

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 2.

[Annals of Botany, Vol. XX. No. LXXVII. January, 1906.]

INTRODUCTION.

SINCE the publication of De Bary's (12) great work on Comparative Anatomy, and Van Tieghem's (57) subsequent 'stelar theories,' there has accumulated a considerable body of literature devoted to this phase of botanical study. The work of De Bary marked the culmination of that earlier mode of treatment which considered the axis of vascular plants to be made up of more or less numerous, wholly independent fibro-vascular bundles, embedded in a common matrix of fundamental tissue. Van Tieghem (57) later introduced the idea of a fundamental stelar unity of the fibro-vascular system, and showed that this unity held essentially true of all the Vasculares. The elaboration of this view lent new interest and broader possibilities to the anatomical study of plants; and while many of the details and assumptions of Van Tieghem's theory have been disproved or modified by the later investigations of Gwynne-Vaughan (20), Jeffrey (27), Boodle (4), Faull (18), Worsdell (61), Schoute (45), Chrysler (9), and others (5, 17, 21), yet the important fact still remains that in the fibro-vascular system of higher plants we find an essential unity of plan which is fairly comparable to that found in the skeletal system of vertebrate animals, and which is apparently of hardly less importance from the phylogenetic point of view.

In the hope of gaining some new light upon the vexed question of the relationships of the Monocotyledons, the writer has undertaken the present study of the Cyperaceae, a group which is especially interesting on account of its apparently somewhat isolated position and its clearly-marked characters.

Upon making a general survey of the problem before us, the following questions, among others, present themselves for careful consideration, if not, indeed, for solution :—

1. Anatomically considered, do the Cyperaceae constitute a clearly-defined group?
2. What subdivisions of the Cyperaceae may be made upon the basis of anatomical characters?
3. Of what importance are oecological factors in determining the anatomical features of the group?
4. What is the nature, origin, distribution, and significance of the amphivasal bundles found in this group?
5. What is the course of the fibro-vascular bundles through the stem?
6. Of what importance are leaves as factors in stelar development?
7. What structural characters of the Cyperaceae are ancestral, and what are more recently acquired?
8. What are the probable phylogenetic inter-relationships of the Cyperaceae?

9. What is the position of the Cyperaceae among the Monocotyledons?

10. What bearing have the observed facts upon the phylogeny of the Monocotyledons as a whole?

Before entering upon a discussion of these problems it will be necessary to consider in more or less detail some of the structural characteristics of representative genera and species of the Order.

THE ROOT.

The internal structure of the root in the Cyperaceae presents a striking degree of uniformity. The central cylinder is compact and relatively small, surrounded by a well-marked endodermal sheath, the cells of which commonly have the inner wall much thickened. The medulla is composed of round, more or less sclerotic cells of relatively small size, with sharply-defined intercellular spaces. The xylem masses are radially disposed within the bundle-sheath, alternating with the phloem masses. Their number is variable, but rather smaller than that found in the majority of Monocotyledons, ranging from six to eight in species of *Eleocharis* to fifteen to eighteen in certain Carices, while, according to Kny (32), these numbers may approach or even exceed 100 in the roots of some Palmales. Each xylem-mass consists of a few short, small, thin-walled tracheids arranged in a radial plate terminated centrally in a single relatively large vessel. It frequently happens that there are not as many large vessels as there are xylem-masses, in which case growth pressure may cause a vessel to lie at the point of a V of which the arms are two distinct xylem-masses, which are brought in this way to subtend the intervening phloem-mass, in a manner remotely suggestive of the collateral arrangement of the elements found in the stem. It is worthy of note that, as shown by Klinge (31), the elements of the protoxylem are as a rule neither spiral nor annular, but scalariform, reticulate or pitted.

The phloem is less conspicuously developed, the masses being quite small and often but slightly differentiated. In mature roots the elements are either partially lignified or considerably crushed by growth pressure. It has been shown by Chauvaud (8) that the sieve-tubes are derived in each case from a 'pericambial' cell lying next to the endodermis. The phloem is separated from the xylem by a few or sometimes numerous rows of usually somewhat sclerotic parenchyma-cells.

The cortex of the young root consists of many layers of thin-walled cells arranged with great regularity in radial rows. In mature roots this regularity of structure is usually wanting, owing to the presence of large air-chambers in the cortex, separated by very thin radial plates of cells. This feature is especially conspicuous in sedges of aquatic or limicolous habit. The piliferous layer is not specially modified, and is usually strengthened by a narrow hypodermal zone of more or less sclerotic mechanical tissue. Tannin-sacs are of quite common occurrence in all parts of the root.

The primary root arises from the micropylar end of the protocaulome. It is of relatively short duration and little importance. Secondary roots arise endogenously from the rhizome. Rootlets are derived from the rhizogenous pericambium situated just within the endodermal sheath. It is a well-known fact that in the Gramineae this pericambial sheath is interrupted at the xylem plates, which lie in actual contact with the endodermis. The earlier investigators believed the grasses to be altogether unique in this respect, all other Monocotyledons as far as studied showing a continuous rhizogenous zone. An uninterrupted pericambium has been demonstrated by Van Tieghem (54) in species of *Carex* and *Cyperus*, and more recently by Holm (25) in *Carex Fraseri.* However, later studies by Van Tieghem and Douliot (58), De Bary (12), and Klinge (31), reveal the interesting fact that the majority of the Cyperaceae resemble the Gramineae in the possession of an interrupted rhizogenous pericambium, while a few species have a uniform, continuous pericambial sheath, and still other species show various stages intermediate between these two conditions. Consequently there are two types of origin of rootlets. In the majority of cases, where the rhizogenous zone is interrupted by the smaller xylem-elements, the rootlet is inserted opposite a phloem-strand, and the xylem-elements are derived from the two adjacent xylem-strands, so that the oval base of origin of the rootlet has its longer axis transverse to the main axis of the parent root. On the other hand, in those cases in which the pericambium is continuous the rootlets are inserted directly upon the xylem-strands, each rootlet connected with but a single strand, and having the longer axis of its oval base of attachment parallel to the main axis of the parent root.

These facts have a certain interest from their bearing upon the relationships of grasses and sedges as expressed by Van Tieghem (56) and others, and to be considered more fully on a subsequent page. In its apical development the root presents no features uncommon to the great majority of the Monocotyledons. As shown by De Bary (12), Van Tieghem (56), Treub (53), and others, the root-cap is developed from a distinct calyptrogenic initial meristem, outside and independent of the dermatogen, so that the piliferous layer presents a smooth contour, traceable under the root-cap quite to the initial region.

THE RHIZOME.

The great majority of the Cyperaceae grow by a perennial root-stock, which is in some cases long and slender, in other cases extremely short and compact, while other members of the Order present all intermediate conditions. Even the annual species commonly preserve the rhizomatous habit, the first few internodes of the stem being very short and usually growing more or less obliquely in the soil. Indeed, where the rhizomatous character of the stem-base is not apparent externally, it is always demonstrable from internal structure.

Frequently the rhizome bears hard, brown leaves of considerable size at the nodes, but more generally the leaves are reduced to mere scales. After a period of horizontal or oblique growth the rhizome bifurcates to give rise to an aerial stem or culm which is commonly leafy, at least at the base, and which ultimately bears the inflorescence. Not infrequently several aerial axes are given off from the rhizome in a single season's growth, some of them being only vegetative, while others bear both leaves and flowers. But it more often happens that the number of aerial shoots is very small in each season's growth, and all of them ultimately develop flowers. Fibrous roots are produced in large numbers from the nodes of the rhizome. In most cases the elongated rhizomes are not of uniform size throughout their length, but consist of swollen nodes and slender internodes, as in *Scirpus americanus*; or the rhizome may be made up of swollen tuberous portions connected by slender internodes, as in *Cyperus esculentus*, and to a less marked degree in *Scirpus cyperinus*, *S. atrovirens*, *S. lineatus*, &c.; only rarely does one find the rhizome of uniform size for a considerable part or the whole of its length, as in *Scirpus robustus* and a few of the Carices.

Internally the rhizome consists of a central cylinder which is very rarely hollow in the mature condition, as in *Carex scoparia*, *Cladium mariscoides*, *Dulichium arundinaceum*, &c., but which as a rule is solid or only slightly aerenchymatous, and composed of several to very many fibrovascular bundles embedded in fundamental tissue and surrounded by a well-defined endodermal sheath (except in *Scirpus microcarpus* and *Cladium mariscoides*), which is either simple or variously reinforced by circular fibres or a sclerotic zone. Outside the endodermis is the very variable cortex, bounded externally by the epiderm. The cortex may be sclerotic in whole or in part, unmodified parenchyma, aerenchymatous in varying degree, or even cavernous as in the upper side of the rhizome of *Dulichium*. Bordet (6), Palla (35), and others have attempted to utilize the characters of the cortex as diagnostic features of the Cyperaceae, but with very doubtful success, owing to the fact that these features are extremely variable under change of environment. The peripheral portion of the cortex is very generally modified to form a sclerotic hypodermal zone, or at least a series of hypodermal ribs, of which the function is clearly mechanical. The epidermis is not infrequently sclerotic, and rarely covered with a thick cuticle. Tannin-sacs are of common occurrence throughout most rhizomes. With a few rare exceptions among the Carices, starch is everywhere present in the rhizome of the Cyperaceae. It is found in especially great quantities in *Scirpus robustus* and *S. americanus*, and in the tuberous rhizomes of many species of *Cyperus*.

It has been found that outside the central cylinder all of the characters are more or less highly susceptible to the influence of environment, often presenting a considerable range of variation within the same species, and consequently possessing comparatively little value from a phylogenetic point of view. Accordingly our attention will be directed more specifically toward the characters of the central cylinder itself.

In the seedlings of *Scirpus microcarpus* the central cylinder presents a condition of affairs strikingly similar to that described and figured by Chrysler (9) for *Smilacina*, the only difference being found in the somewhat more numerous leaf-gaps and in the earlier appearance of numerous medullary strands, which, however, are almost without exception of the collateral type. Young plants of other species indicate a similar tubular condition of the central cylinder in its earlier stages, followed in later development by the appearance of medullary strands, which in the majority of the Cyperaceae are of the concentric type. Thus it appears from a cursory glance at the seedling of the Cyperaceae that the central cylinder in its earliest stages is a simple siphonostele of the phyllosiphonic type, similar in every essential particular to that of the Dicotyledons. Only in later stages of growth does one find a highly complicated arrangement of stelar structure. It seems very desirable that the developmental history of the Cyperaceae should be more thoroughly studied.

The central cylinder of the mature rhizome may be described under two fairly well-marked general types, which are characterized by the disposition of the xylem-elements of the fibro-vascular bundles. In the first of these types, which is by far the more common among the Cyperaceae, all or most of the bundles are of the concentric sort, with the xylem distributed more or less uniformly all around the phloem. To such bundles the term ‘amphivasal’ has been very generally applied, and those Cyperaceae which present this type of rhizome bundle may, for purposes of description, be grouped together as the Amphivasae. Here belong most species of *Scirpus*, *Cyperus*, *Eleocharis*, *Eriophorum*, *Rhynchospora*, and *Carex*. In certain other forms, notably *Dulichium*, *Cladium*, *Scirpus microcarpus*, *S. americanus*, *S. robustus*, &c., the bundles are of the simple collateral type, with the relatively few xylem-elements disposed on the centripetal side of the bundle. Those forms which present this arrangement may be termed the Centrivasae.

Scirpus cyperinus will serve as an example of the Amphivasae. A part of the central cylinder of this species is shown in Pl. I, Fig. 3, and a part more highly magnified in Fig. 4. It will be observed that the bundles are very numerous and almost exclusively of the amphivasal type. The majority of them are grouped near the peripheral portion of the central cylinder, while each of those lying nearer the centre is characterized by the possession of a large centripetal mass of sclerenchymatous tissue. This is the greatly exaggerated peridesm of the bundle, which in the peripheral bundles is either more uniformly distributed or even wholly undifferentiated.

The phloem-mass is composed of very numerous, small, thin-walled elements of fairly uniform size, not readily distinguishable as sieve-tubes and companion-cells. However, in closely related species of less compact habit of growth, such as *S. atrovirens* and *S. sylvaticus*, it is often possible to make out these different elements of the phloem quite definitely. The xylem-elements are rather small but of various sizes, crowded in a dense ring around the phloem. Often there may be more than a single ring of xylem, or an irregular massing on one side. In some of the bundles, particularly those lying centrally, there is a small but unmistakable protoxylem-lacuna on the central margin. This is an indication of the original collateral nature of these bundles. As Chrysler (9) and other observers have shown from developmental studies, amphivasal bundles are derived from collateral bundles by excessive development of the xylem elements, so that the original broad V-shaped cross-section of the xylem takes on a U-shape, and finally closes completely into an O-shape. The same result is often to be observed in the fusion of collateral bundles in the nodal anastomoses of the aerial stems. A fuller consideration of the origin and phylogenetic significance of the amphivasal bundles is reserved for a later page.

Very commonly in rhizomes of this type there is a dense plexus of transverse and oblique fibro-vascular strands in the surface of the central cylinder, just inside the endodermis. Fig. 10 represents a radial section through this region. This superficial plexus in many cases undoubtedly affords the chief mechanical support to the central cylinder, while to it are attached all of the root-strands and many of the smaller leaf-trace bundles. The larger leaf-trace bundles, on the other hand, like the ramular bundles, pass inward to the medulla and then outward to the superficial plexus, following a course very similar to that figured by De Bary for the Palm-stem (B, Fig. 1). It should be noted in passing that fully 90 per cent. of the branching and anastomosing of bundles in the rhizome takes place in the superficial plexus.

As an example of the Centrivasae we may examine more in detail the root-stock of *Scirpus americanus*, Pers. (*S. pungens*, Vahl), a form in which the internodes are long and the leaves reduced to the merest brown scales. Here the central cylinder (Fig. 16) is less compact; the bundles are much less numerous, and collateral throughout; the peridesm is only slightly developed, as is also true of the endodermal sheath; there is no dense superficial plexus of fibro-vascular strands. The phloem-mass of each bundle is made up of a few rather large, very thin-walled sieve-tubes, with undoubted companion-cells lying in the angles between them. The xylem consists of usually two large vessels and a few small tracheids arranged in the conventional broad V-shaped section, at the point of which the protoxylem-lacuna is often conspicuously developed. At the nodes root-strands are attached directly to the superficial bundles of the cylinder, while the inconspicuous leaf-trace bundles pass inward to fuse with the medullary strands. The course of these bundles may be represented quite satisfactorily by Mohl's original diagram of the bundles of the Palm-stem (A, Fig. 1).

The fusion takes place by the strands becoming approximated laterally, phloem upon phloem, and xylem upon xylem. The union of the phloem elements is accomplished much more promptly than is that of the xylem-elements, as a result of which the xylem occasionally forms a semicircular zone about the inner side of the phloem. In no instance, however, has a true amphivasal bundle been found in the rhizome of this species, either at an ordinary node or at the origin of a branch.

Although the Amphivasae include a vast majority of the Cyperaceae, yet there are no great variations from the type in any essential feature of the structure of the central cylinder. The most striking irregularity appears in the development of the peridesm, which may be almost wholly undifferentiated in *Eleocharis*, uniformly two- or three-layered in *Scleria* and some Carices, or restricted to a few relatively enormous masses in certain species of *Eriophorum*. The endodermis is always well defined, and projected some distance upon outgoing strands, except at the origin of aerial shoots, where the cortex and medulla are in free communication. The bundles are always relatively numerous, and there is always more or less evidence of a superficial plexus, though this is less marked in *Eleocharis*.

The Centrivasae, though very few, present a range of variability quite as wide as the larger group. The medulla varies from cavernous in *Dulichium* and *Cladium* to densely sclerotic in *Scirpus robustus*; the peridesm may be centripetally massed in *S. rivularis* and *Dulichium*, or wholly undifferentiated in *S. microcarpus*; the endodermis may be reinforced to an unusual and unique degree as in *S. fluviatilis*, of a quite normal type as in *Dulichium* and *S. robustus*, or apparently quite wanting in *S. microcarpus*; finally, there may be a well-developed superficial fibro-vascular plexus, as in *S. fluviatilis*, or there may be nothing of the kind, as in *Cladium*. There is free communication between cortex and medulla through all foliar and ramular gaps in this group except in *S. fluviatilis*, in which the peculiar sclerotic jacket mentioned above closely encases the central cylinder of the rhizome in every part, even cutting directly across the base of the aerial stem and closely investing the outgoing bundles for some distance. This jacket consists of about three layers of somewhat elongated, pointed or irregular, thick-walled, profusely pitted cells, of a more or less tracheidal appearance, with the longer axis radially disposed, and arranged in a dense zone bordering directly upon the outside of a little-differentiated endodermis. This peculiar sheath is apparently unique, and duplicated in no other species in the entire Order.

The accompanying Table I presents in concise form the more salient features of the rhizome in the more interesting species studied. Besides the species named in the table, some twenty other Carices have been examined, together with a few additional species of *Scirpus*, *Eleocharis*, and *Fimbristylis*. For purposes of confirmation and comparison, a study has been made of species of *Juncus*, *Streptopus*, *Pontederia*, various grasses, &c.

The more striking features of the rhizome of the Cyperaceae may be summarized briefly in the following key, based chiefly upon the generic characters of the central cylinder.

Generic Key to the Cyperaceae.

I. Centrivasae. Bundles of the rhizome collateral, or rarely amphivasal at the periphery.
1. Medulla cavernous.
a. Endodermis and peridesm conspicuously sclerotic . . *Dulichium.*
b. Endodermis and peridesm not sclerified . . . . *Cladium.*
2. Medulla not cavernous.
a. Endodermis not apparent . . . . . *Scirpus microcarpus.*
b. Endodermis distinct.
aa. Simple, medulla thin-walled . . . . . *Scirpus americanus.*
bb. With sclerotic medulla . . . . . . *Scirpus robustus.*
cc. With external sclerotic zone continuous across base of culm . . . . *Scirpus fluviatilis.*
II. Amphivasae. Bundles of the rhizome all amphivasal.
1. Peridesm only slightly developed, or undifferentiated.
a. Medulla aerenchymatous . . . . *Stenophyllus.*
b. Medulla compact.
aa. Rhizome tuberous . . . . *Lipocarpha.*
bb. Rhizome not tuberous.
aaa. Small, bundles few . . . . . . *Eleocharis.*
bbb. Small, bundles many . . . . . . *Scleria.*
ccc. Large, bundles very many . . . . *Cyperus Papyrus.*
2. Peridesm uniformly well developed.
a. Rhizome tuberous . . . . *Kyllinga.*
b. Rhizome not tuberous.
aa. Internodes long, xylem elements large . . . . . *Carex.*
bb. Internodes short, xylem elements small, few . . *Hemicarpha.*

- 3. Peridesm more or less massed centripetally.
  - *a.* Rhizome tuberous, or the internodes very short.
    - *aa.* Endodermis not reinforced.
      - *aaa.* Cortex very aerenchymatous . . . . . . *Psilocarya.*
      - *bbb.* Cortex compact or sclerotic . . . . . . *Cyperus.*
    - *bb.* Endodermis reinforced by sclerotic zone . . . *Fuirena.*
  - *b.* Rhizome elongated, not tuberous.
    - *aa.* Medulla sclerotic . . . . *Rhynchospora.*
    - *bb.* Medulla not sclerotic.
      - *aaa.* Xylem elements few.
        - *aaaa.* Peridesm slightly developed . . *Eriophorum* (in part).
        - *bbbb.* Peridesm very strongly developed in four or five central bundles . . . *E. Scheuchzeri, E. alpinum.*
        - *cccc.* Peridesm well developed in all of the central bundles . . . . *Dichromena.*
      - *bbb.* Xylem elements many.
        - *aaaa.* Peridesm slightly developed . . . . . *Fimbristylis.*
        - *bbbb.* Peridesm very largely developed in all central bundles . . . . *Scirpus* (chiefly).

TABLE I. RHIZOME CHARACTERS. (EXPLANATION.)

The symbols + and –, when standing alone or before another descriptive symbol, have a numerical significance, as 'many' or 'few.' When they follow another symbol they have a purely qualifying meaning, signifying that the preceding character is either well developed or the contrary. The qualifying symbol is doubled for emphasis.

1. Class: A, Amphivasae; or C, Centrivasae.
2. Form: t, tuberous; s, with short internodes; or l, with long internodes.
3. Central cylinder: c, compact or small; l, loose or large.
4. Endodermis: +, reinforced; –, simple; or 0, undifferentiated.
5. Medulla: a, aerenchymatous; c, compact; or s, sclerotic.
6. Bundles: s, scattered; or c, crowded.
7. Xylem elements: l, large; s, small; +, many; or –, few.
8. Peridesm: =, uniform; c, centripetal; or 0, undifferentiated.
9. Cortex: a, aerenchymatous; c, compact; or s, sclerotic.
10. Hypoderm: s, complete sheath; or r, ribs.
11. Tannin: +, much; –, little; or 0, absent.
12. Starch: +, much; –, little; or 0, absent.

THE AERIAL STEM.

The aerial stem or culm of the Cyperaceae presents a considerable variety of forms. In *Cyperus* and *Eleocharis* it assumes practically a scapose habit, with a few small or moderately large leaves clustered at its base, and terminated above by the simple or compound inflorescence, which is naked in *Eleocharis*, and provided with large leafy bracts in *Cyperus*. The great majority of the Cyperaceae, however, possess a jointed culm with a few or many rather long internodes. The lower node commonly bears only a reduced or sometimes even scale-like leaf, while the larger leaves occur higher up the stem. The leaf-base always forms a closed sheath for some distance above its node of attachment.

The culm of *Dulichium* is cylindrical. The same is true of some species of *Eleocharis* in the young stages, but most of these are more or less flattened in the mature condition. *E. mutata* is unique in that its culm is sharply quadrangular with concave surfaces. With these few exceptions the culm of the Cyperaceae is triangular in cross-section; sometimes more or less obscurely so, owing to the convexity of the surfaces, as in *Scirpus lacustris*, *S. Californicus*, *S. caespitosus*, &c.; or with very sharp angles, as in *S. robustus*, *S. americanus*, some Carices, &c.

As previously stated, and as described by Pax (36), the aerial stem is commonly derived from the rhizome by a bifurcation of the growing point of the latter organ. In some cases numerous aerial stems arise from the root-stock by small lateral buds, as in *Eriophorum alpinum*. In still other cases the culm is terminal upon the short rhizome, as in short tuberous and annual species of *Cyperus*, *Psilocarya*, *Stenophyllus*, &c. At the point of origin of the aerial stem there is an extensive gap in the endodermal sheath of the rhizome, and through this gap the cortex and medulla are in free communication. The one unique exception to this rule is found in *Scirpus fluviatilis*, which has been described on a previous page. The bundles of the first leaf-sheath are derived from the superficial plexus of the central cylinder of the rhizome, while the cauline bundles are continuous with the deep-seated medullary strands. As these latter bundles begin to turn upward they branch more or less profusely, so that the number of bundles in the base of the culm is usually considerably greater than the number of rhizome strands to which they are directly traceable. Moreover, it is to be noted that these bundles of the culm-base are always collateral, whatever the nature of the rhizome strands from which they are derived.

The apical development of the culm has been studied by Miss Anderssohn (1), Guillaud (19), and Van Tieghem (56). It presents no features of special interest in the present investigation beyond the fact that here, as in some other Monocotyledons, cambial activity continues for some time after complete differentiation of the fibro-vascular bundles. We shall have occasion to refer to this fact again presently.

Dulichium is the only hollow-stemmed form among the Cyperaceae. *Eleocharis*, a few aquatic species of *Scirpus*, and *Cyperus Papyrus* possess very large medullary air-spaces, separated by delicate plates of parenchyma; and many other species present this feature in a much less conspicuous

TABLE I.

Rhizome.	Class.	Form.	Central Cylinder.	Endoderm.	Medulla.	Bundles.	Xylem Elements.	Peridesm.	Cortex.	Hypoderm.	Tannin.	Starch.
Cyperus flavescens, L.	A —	t	l	—	c	—	— s	0 —	c	r —	+	—
,, *rivularis*, Kunth	A —	t	l	— —	c —	— —	— l	0c	c —	r —	—	— —
,, *Nuttallii*, Eddy	A —	t	l	— 0	c	— s	— s	c —	c	r	+	—
,, *dentatus*, Torr.	A —	t	l	—	c	—	— l	0c —	a —	r —	—	—
,, *strigosus*, L.	A —	t	l	0 —	c	+	+ s	0	c	r —	+ +	—
,, *filiculmis*, Vahl	A	st	c	—	s —	—	+	= 0	s —	r —	+	+
,, *Grayi*, Torr.	A —	st	c —	— +	c +	—	—	= c	s —	r —	—	— —
,, *alternifolius*, L.	A	s	c —	— +	c —	c	— l	0c	c —	r +	+	+
,, *Papyrus*, L.	A —	s	l	+	c	+ +	— l	0 —	c	r	+	+
Kyllinga pumila, Michx.	A —	st —	l	—	c —	+	— l	=	c	r —	—	— —
Dulichium arundinaceum (L.), Brit.	C —	l	c —	—	c	c —	— l	c +	c	0	+	—
Eleocharis mutata (L.), R. and S.	A	s	l —	—	c	sl	—	= 0	a +	r — —	—	0
,, *ovata*, R. and S.	A	st —	l	—	c	— s	— l	0	a	r —	—	0
,, *palustris*, R. and S.	A +	s —	l	+	s —	— s	— l	0	a +	r +	+	0
,, *acicularis*, R. and S.	A —	s	c	—	c	— —	— s	0	c	r —	— —	0
,, *tuberculosa*, R. and S.	A	s	l	—	c —	+	— s	0c —	c —	r	+	—
,, *rostellata*, Torr.	A	s	l	+	c	— s	— l	0	c	r +	—	—
Dichromena latifolia, Baldw.	A	l —	l	+	c —	s —	—	c +	c	r — —	+	—
Psilocarya scirpoides, Torr.	A —	st	l	—	c	+ l	— s	c —	a —	r	—	0
Stenophyllus capillaris, Britton	A — —	st	c	+ —	a —	— l	— s	0	c —	0	— —	— —
Fimbristylis castanea (Michx.), Vahl	A —	st —	c	—	c	c +	+	c +	c	sr +	+	—
,, *laxa*, Vahl	A	s	c	+ —	c	c	+	= c —	c	0	+	— —
,, *autumnalis* (L.), R. and S.	A	s	c —	—	c —	c —	+ —	= 0	c	0	— —	0
,, *Warei*	A —	st	c —	—	c	+	—	c —	c —	0	—	0

Scirpus debilis, Pursh	A—	t	l	—	c	s	—	c—	c—	r—	—	—
,, *americanus*, Pers. . . .	C+	l+	l	—	c—	s+	—l	c—	a—	s	— —	+ +
,, *robustus*, Pursh . . .	C	l—	c+	+	s—	s—	— —	c—	c	s	—	+ +
,, *fluviatilis*, Gray . . .	C—	l	l+	+ +	a—	s	— —	c—	a—	r—	—	— —
,, *sylvaticus*, L.	A	l—	c	— +	a—	c—	l	c+	c—	r	—	—
,, *atrovirens*, Muhl. . . .	A	l—	l	—	c—	c—	+s	c	a—	r+	— —	—
,, *microcarpus*, Presl . . .	C—	l	l+	0	a—	s+	— —	c—	a	sr	+	—
,, *polyphyllus*, Vahl . . .	A	l	c—	— +	c—	c	+s	c—	c—	r—	—	— —
,, *lineatus*, Michx. . . .	A	s—	l	+ —	c	+c	+s	c	c	r—	—	—
,, *cyperinus* (L.), Kunth . .	A	s	c	—	c	c+	+	c+	a—	r	—	—
Eriophorum alpinum, L. . . .	A	l—	l	+ —	c—	—s	—	0	c—	0	—	0
,, *vaginatum*, L. . . .	A—	s—	l	—	a—	—	—	c—	a	0	+	—
,, *Scheuchzeri*, Hoppe . .	A	s	c—	+	c	—	—	+ ▬ c	a	r—	—	0
,, *polystachyon*, L. . .	A	s—	l—	+	c	s—	+s	c	a	0	+	—
,, *gracile*, Koch . . .	A—	s	l+	—	a	s+	+	0—	a	r—	+	—
,, *Virginicum*, L. . . .	A	l—	l	+	c—	—s	+s	c+	a—	0	+	—
Fuirena squarrosa, Michx. . . .	A—	st	l	+ +	c	+s	—	c+	c	r	+	+
Hemicarpha micrantha (Vahl), Brit. .	A—	s—	c	—	c	—	—s	▬ c	c	r—	—	—
Lipocarpha maculata (Michx.), Torr. .	A—	st	c	—	c	s—	—l	0	c	r—	+	—
Rhynchospora alba (L.), Vahl . .	A—	s	c	+ —	s—	—	—s	0c—	c—	0	+	—0
,, *glomerata* (L.), Vahl .	A	s	c	+ —	s+	+	l—	—c—	s	0	+	0
Cladium mariscoides, Torr. . . .	C+	l	l	0	a+	s—	— —	▬ c—	a+ +	s—	—	— —
Scleria Baldwinii	A—	l	l+	—	c	+s	+s	0	c	r	—	—
,, *gracilis*, Ell.	A—	s	l—	—	c	s	s	0c—	c—	0	+	—
Carex folliculata, L.	A	l	c—	—	c	+c	—l	▬ —	a+	0	0	— —
,, *intumescens*, Rudg. . . .	A	l	c—	+ —	c	—c	l	▭ —	c—	0	— —	—
,, *lupulina*, Muhl.	A	l	c—	+ —	c—	+	—l	▭	a+	r—	0	—
,, *Baileyi*, Britton	A	l	c—	+ —	s	+	—l	▬ +	c	r+	— —	—
,, *Pseudo-Cyperus*, L. . . .	A	l	c	—	c	+	+l	▬	c	r—	—	—
,, *comosa*, Boott	A	l	c	—	c+	+c	—l	▬	a ▭	0	0	—
,, *prasina*, Wahl.	A	l	c	—	c+	—c	+	▭	c	r—	— —	—
,, *aestivalis*, Curtis	A—	l	c	+	c	+	—	▭ —	a—	s—	— —	—
,, *vulpinoidea*, Michx. . . .	A	l	c—	—	c	+ —	+	▭	c	r—	0	—
,, *xanthocarpa*, Bicknell . . .	A	l	c	—	s—	+	—l	▬	c	r—	—	—
,, *siccata*, Dewey	A	l	c	+	c+	+c—	—l	▬	c+	r—	—	—
,, *scoparia*, Schk.	A	l	c	—	c	+	—l	═	c	r	—	—
,, *straminea*, Willd. . . .	A	l	c—	+	sc+	—l	—l	▭	c—	r—	— —	—
,, *stenolepis*, Torr.	A—	l	c	+	c+	—l	—s	▬ —	a—	r—	— —	—

degree. A form of aerenchyma is found in the medulla of several species of *Scirpus*, notably *S. fluviatilis*, *S. atrovirens*, and *S. microcarpus*, and in *Fuirena* and *Stenophyllus*. Elsewhere the medulla is usually more or less compact. Sclerosis is conspicuously developed in the nodal diaphragms of *Dulichium* and in the nodal regions of *Scirpus robustus*, *Fuirena*, and certain species of *Eriophorum* and *Carex*.

The sclerotic tissue of the cortical region presents a number of types of adaptation to mechanical purposes, as described by Schwendener (47). In some cases there is a dense hypodermal zone of sclerenchyma, while in other forms the mechanical tissue may be confined to numerous or few, large or small hypodermal ribs, or these may even give place entirely to a zone of assimilatory tissue which is not infrequently in the form of typical palisade cells. Following in part the suggestion of Rickli (40), we may divide the Cyperaceae into two classes, based upon the relative prominence of mechanical and assimilatory tissue in the cortex. Those forms which possess but little mechanical sclerenchyma in the cortex, but which show well-developed assimilatory tissue and numerous stomata, may be termed the Chlorocyperaceae. To this group naturally belong those species which are scapose in habit, or of which the leaves are much reduced in size or number. On the other hand, those forms in which the assimilatory mechanism gives place wholly or in large measure to sclerenchymatous elements may properly be called the Sclerocyperaceae.

As typical of the first class we may consider the culm of *Scirpus robustus*, a cross-section of which is shown in Fig. 11. It will be observed that the fibro-vascular bundles are collateral, not numerous, and scattered irregularly throughout the section. The medulla contains very large schizogenous air-spaces separated by plates of parenchyma only one cell thick. The medullary bundles lie at the intersections of these plates. It should be noted in passing that these large air-chambers are divided into compartments by occasional transverse partitions or 'bulkheads.' De Bary (12) has shown that these partitions are made up of dense tissue in species growing in dry situations, while in aquatic species the partitions are composed of thin-walled, stellate cells similar to those found in the medullary plates of certain Juncaceae. Frequently the fibro-vascular bundles anastomose in their course, in which case the transverse strands lie in these 'bulkheads.'

The epidermis is covered by a thin cuticle, which in some small amphibious species is distinctly papillate. Numerous somewhat depressed stomata open into the thick assimilatory zone, which is made up of two or three layers of typical palisade cells. The mechanical tissue of the stem is reduced to a few very small hypodermal ribs and a few sclerenchyma strands embedded in the inner margin of the palisade zone. The figure of *Eleocharis* (Fig. 12) represents another type of this class, in which the medullary tissue is still further reduced, and the assimilatory zone is quite undifferentiated.

We may now examine the culm of *Scirpus cyperinus* as a fair type of the Sclerocyperaceae, though it is by no means an extreme example of the sclerotic habit. As shown in Fig. 5, the bundles of the internode are fairly numerous, collateral, and with centripetally massed peridesm. The bundles of the outermost series alternate with rather large irregular air-spaces. It should be observed in passing that these air-spaces differ from those occurring in the medulla of the Chlorocyperaceae in that they are lysigenous, or rhexigenous, according to De Bary (12). The medulla consists of thin-walled parenchyma, which in this species shows a tendency to break down in mature stems. The epidermis is covered by a thin, smooth cuticle. In species which show conspicuous hypodermal ribs, as in *S. robustus*, the epidermal cells are very much smaller over these ribs than elsewhere. In *S. cyperinus* the epidermis shows no stomata, and is subtended by a continuous zone of sclerenchyma which in very many cases is produced into strong ribs which connect internally with the peridesm of the interlacunar bundles. The more general anatomical features of the aerial stems of the Cyperaceae studied in the present investigation are briefly set forth in Table II.

TABLE II. AERIAL STEM CHARACTERS. (EXPLANATION.)

The symbols + and − are used here with the same variations in significance as already indicated in Table I.

1. Class: S, Sclerocyperaceae; or C, Chlorocyperaceae.
2. Form: t, triangular; q, quadrangular; r, round; s, scapose; or j, jointed.
3. Medulla: a, aerenchymatous; c, compact; s, sclerotic; or 0, a large lacuna.
4. Cortical Air-spaces: +, numerous; −, few; or 0, none.
5. Cauline Bundles: s, scattered, few; or c, crowded, many.
6. Peridesm: =, uniform; c, centripetal; 0, undifferentiated; or ×, joined in a continuous mechanical zone.
7. Cortical Bundles: +, many; −, few; or 0, none.
8. Hypodermal Sheath: +, strongly developed; −, slightly developed; or 0, wanting.
9. Hypodermal Ribs: +, numerous; −, small or few; or 0, none.
10. Palisade and Stomata: +, well developed; −, poorly developed; or 0, absent.
11. Tannin-sacs: +, many; −, few; or 0, none.
12. Bundles of Leaf-trace: average number, where observed.

TABLE II.

Aerial Stem.	Class.	Form.	Medulla.	Cortical Air-spaces.	Cauline Bundles.	Peridesm.	Cortical Bundles.	Hypodermal Sheath.	Hypodermal Ribs.	Palisade and Stomata.	Tannin Sacs.	Bundles of Leaf-sheath.
Cyperus flavescens, L.	C –	sr –	c	+	–	= –	–?	0	–	–	–	?
,, *rivularis*, Kunth	C –	st –	c –	–	– –	= c	0	0	– –	–	– –	?
,, *Nuttallii*, Eddy	C –	st –	c	+	–	– c –	+ ?	0	+	–	–	30 ?
,, *dentatus*, Torr.	C	sr	c	+	–	0	0	0	– – –	–	– –	?
,, *strigosus*, L.	C –	st	a –	0	c –	= c	0	0	+	–	–	25
,, *filiculmis*, Vahl	C –	st	c +	0	–	=	0	0	+	– –	–	?
,, *Grayi*, Torr	C –	st	c	0	–	= c	0	0	+	–	–	?
,, *alternifolius*, L.	C –	st	c	–	s	= c –	0	0	+	– 0	–	?
,, *Papyrus*, L.	C	st –	a +	0	s +	0	?	0	+	+	–	?
Kyllinga pumila, Michx.	C –	jt –	c	– –	– s	=	–	0	– –	–	0	?
Dulichium arundinaceum (L.), R. and S.	C –	jr	0	+	–	c +	+	0	– –	–	–	50
Eleocharis mutata (L.), R. and S.	C +	sq +	a + +	0	– s	– c	0	0	+	+ +	+	?
,, *ovata*, R. and S.	C +	sr	a + +	0	– s	=	0	0	+	+ +	+	?
,, *palustris*, R. and S.	C	sh –	a + +	0	– – s	– c –	0	0	+	–	–	?
,, *acicularis*, R. and S.	C	sr –	a + +	0	–	=	0	0	–	+	–	?
,, *tuberculosa*, R. and S.	C +	sr –	a + +	0	– –	=	0	0	+	+ +	– –	?
,, *rostellata*, Torr.	C	sr	a + +	0	–	= –	0	0	+ –	+	– –	?
Dichromena latifolia, Baldw.	C –	jr –	c	–	–	c –	–	0	– –	–	– –	?
Psilocarya scirpoides, Torr.	S –	jt –	a –	+ + +	– c	xc –	0	0	0	0	– –	30
Stenophyllus capillaris, Britton	C –	jr –	a +	–	– –	= –	0	0	– –	–	– –	?
Fimbristylis castanea (Michx.), Vahl	C –	jt –	a	0	– s	– c –	0	0	–	–	–	?
,, *laxa*, Vahl	C	jr –	a +	–	– –	= c	–	0	– –	–	– –	?
,, *autumnalis* (L.), R. and S.	C –	jr –	a –	–	–	=	– –	0	+	–	–	?
,, *Warei*	S –	jr –	c	–	–	=	– –	0	+ +	– –	–	25

Scirpus debilis, Pursh	C	sr	a + +	0	– s	c – –	0	0	+	+	– –	?
,, *americanus*, Pers.	C +	st +	a +	0	s +	c – –	0	0	–	+ +	– –	25
,, *robustus*, Pursh	S –	jt +	c –	+	s +	c –	+	0	+	– 0	–	36
,, *fluviatilis*, Gray	S –	jt	a +	+	+	c	+	–	+	–	–	50
,, *sylvaticus*, L.	S	jt –	a –	+	s	c +	+	+	+	0	–	40
,, *atrovirens*, Muhl.	S	jt –	a +	+	s +	c +	+	+	+ +	0	–	55
,, *microcarpus*, Presl	S	jt	a +	+ +	– s	c –	+	+	+ +	– –	+	60
,, *polyphyllus*, Vahl	S –	jt –	a	+	s	c	+	–	–	– 0	–	50
,, *lineatus*, Michx.	S	jt –	c	–	s –	c	+	+	0	0	+	55
,, *cyperinus* (L.), Kunth	S	jt –	a –	+	c –	+ c	+	+	–	0	+	40
Eriophorum alpinum, L.	S	jt	a0	+ +	–	+	– –	–	+	0	–	?
,, *vaginatum*, L.	S	jt	a0	+ +	– c	+ –	– –	–	+	0	–	?
,, *Scheuchzeri*, Hoppe	S	jr –	a0	+	–	c	–	0	+	0	–	?
,, *polystackyon*, L.	S	jt –	a	+	c +	c	+	–	+ +	0	+	30
,, *gracile*, Koch	S	jt –	a0	+ +	s +	=	–	–	+ +	– 0	–	24
,, *Virginicum*, L.	S	jt –	a +	+	+	c –	+ –	–	+	0	–	?
Fuirena squarrosa, Michx.	S –	jt –	a +	–	– s	x +	–	– –	+ +	0	+	25
Hemicarpha micrantha (Vahl), Brit.	C	jr –	c	0	– –	0	0	–	+	– –	–	15
Lipocarpha maculata (Michx.), Torr.	C	jr –	c –	0	– s	= c	0	0	+	–	– –	25
Rhynchospora alba (L.), Vahl	S –	jr –	a	+ +	– c	x +	– –	–	0	0	–	?
,, *glomerata* (L.), Vahl	S –	jr –	c –	+ +	–	x +	– –	–	0 –	0	–	20
Cladium mariscoides, Torr.	C –	jt –	c +	0	–	x +	0	0	– –	+	–	15
Scleria Baldwinii	S	jt +	c	–	c –	= +	+	+	+	0	–	36
,, *gracilis*, Ell.	S	jt	c –	– –	–	c –	– –	–	–	0	–	?
Carex folliculata, L.	?S –	jt	c	–	–	=	–	+ –	+	0	–	?
,, *intumescens*, Rudg.	S	jt	c –	–	+ –	=	–	–	+	0	–	30
,, *lupulina*, Muhl.	S	jt	c –	+	–	=	+	+	+	0	0	25
,, *Baileyi*, Britton	C –	jt	a +	0	– c	x +	0	0	–	+	0	?
,, *Pseudo-Cyperus*, L.	S –	jt +	a –	+ +	– s	=	+	0	+ +	0	0	30
,, *comosa*, Boott	S –	jt +	c	+	–	=	+	+	+	0	–	38
,, *prasina*, Wahl.	S +	jt	c	–	–	=	+	+	+	0	– –	25
,, *aestivalis*, Curtis	S	jt	c –	–	– –	=	–	+	+	0	0	25
,, *vulpinoidea*, Michx.	S	jr –	a0	+	+	c –	+	+	0	0	– –	36
,, *xanthocarpa*, Bicknell	S	jt –	c –	–	–	=	+	+ +	+	0	0	30
,, *siccata*, Dewey	C –	jt –	a –	0	–	x +	– –	0	–	+	–	?
,, *scoparia*, Schk.	S	jr –	a0	+	–	= –	+	+	+	0	– –	36
,, *straminea*, Willd.	S	jr –	a0	+	+ c	= c	+	+	+	0	0	?
,, *stenolepis*, Torr.	S	jt –	a –	–	+	= –	+	0	+ +	– –	– –	30

At this point it is proper to call attention to the fact that evidence of cambial activity has been observed in the internodal bundles of practically all the examples of the Cyperaceae which have been studied. Fig. 6 is taken from a section near the base of an internode of *S. cyperinus.* The cambial nature of the zone between xylem and phloem in this instance can scarcely be questioned, as it comes well within the definition of 'cambium,' as originally laid down by De Bary (12). We certainly do not have here a 'closed' collateral bundle such as is commonly represented as being the exclusive type among the Monocotyledons. Queva (38) has demonstrated a similar cambium in *Gloriosa,* Guillaud (19) observed a persistent cambiform tissue in *Canna,* and Miss Sargant (43) cites still other examples. Through the kindness of Dr. Chrysler, the writer has been able to examine sections of several grasses, some of which show a far more typically developed cambium than has hitherto been described in the Monocotyledons. It should be said, however, that it happens in certain instances that the xylem and phloem are completely separated in the mature bundle by a plate of sclerotic tissue, as shown in Fig. 13 of *Dulichium,* and as described by De Bary (12) for species of *Rhapis* and *Calamus.* More or less complete lignification of the phloem, such as that observed in *Helianthus* by Boodle (3), occurs in *Fuirena* and species of *Eriophorum.*

We have now to consider the structure of the nodes, and the course of the bundles through the stem. A study of the nodal structures represented in Figs. 7, 8, 9 from *Scirpus cyperinus* will make it evident that the arrangement of the fibro-vascular elements of the stem is profoundly disturbed at this point. Moreover, other parts of the structure are often specially modified in this region. The medulla is usually more compact, if not, indeed, sclerotic; and it is of less breadth, owing to the encroachment of the anastomosing fibro-vascular strands. There are no cortical air-spaces, and in the jointed Chlorocyperaceae the assimilatory zone is either much reduced at the nodes or is even entirely wanting. The longitudinal extent of the nodal plexus varies from less than half a millimetre in *Dulichium* and the slender Carices to over half a centimetre in *Scirpus sylvaticus* and large plants of *Carex comosa.*

Approaching the node from below, the first indication of a departure from the simple internodal condition is seen in the interlacunar bundles of the cortex. Here the xylem-elements rapidly increase in number, spreading around the phloem in a broad U-shaped mass. The arms of the U next become involuted in such a manner as to include a portion of phloem on either side of the original phloem, after which the small lateral amphivasal strands separate off from the main central narrow V-shaped strand thus: oVo. This stage is represented, though in a somewhat complicated form, in Fig. 7. Passing to a slightly higher level, the small lateral amphivasal strands are seen to pass divergently obliquely inward and upward, where they anastomose with similar strands from adjacent cortical bundles, forming a dense circular plexus of amphivasal strands, to which are added strands from the peripheral zone of proper cauline bundles, which here bend more or less sharply inward to pass into the base of the next internode. A little higher up (Fig. 8) we find the general anastomosis extending to the remainder of the bundles, practically all of which assume the amphivasal character for at least a short distance at some part of their course through the nodal complex. The latest evidence of nodal irregularity, as we pass upward into the internode, is to be seen in the deeper-seated medullary bundles. The central strand from the original cortical bundle passes upward and sometimes slightly outward into the leaf-sheath. In other words, it is a bundle of the leaf-trace. From the circular plexus already described are developed new peripheral strands which pass upward as the cortical bundles of the next internode.

It appears that there is a remarkable constancy in the number of cortical bundles in the several internodes of a given plant, and, indeed, of a species. However, the number of cauline bundles usually decreases considerably from the base upward. Thus, in an average specimen of *S. cyperinus*, the cortical bundles numbered about forty in each internode; the cauline bundles in the first internode were eighty-seven, in the second eighty-two, in the third seventy-six, in the fourth seventy, in the fifth sixty-six, and in the sixth (just below the inflorescence) sixty-eight. In the first branch of the inflorescence there were twenty bundles, and in its subtending bract thirty, while in the main axis above this branch there were thirty-five bundles.

In *Dulichium* we find the fibro-vascular system of the Cyperaceae occurring in its simplest form, and a study of the course of the bundles in this group may lead to a clearer conception of the state of things in the highly complicated *Scirpus cyperinus.* Here the bundles of the internode are arranged in two circles only. The outer bundles alternate with the large air-spaces, and are clearly cortical bundles. The inner circle constitutes the cauline system. At the nodes there is formed a circular plexus uniting all of these bundles by amphivasal strands. These strands are given off from the bundles almost at right angles, and consequently there is little or no evidence of amphivasal bundles in the transverse section. A section through the upper part of the node shows three series of bundles—the outer series continuous below with the cortical series, but now passing off into the leaf-sheath; the inner series continuous below with the cauline series, and itself the cauline series of the next higher internode; the middle series, newly derived from the circular plexus, and constituting the cortical series of the next higher internode. The diagrams of Fig. 2 and the photographic Figs. 13, 14, will serve to make this point quite clear. And in the light of these facts the diagram G, Fig. 1, will convey a more or less correct idea of the course of the bundles in the stem of *Scirpus cyperinus*, which is in this respect typical of the greater part of the Cyperaceae.

It appears evident, then, that the bundles of the leaf-trace in most Cyperaceae do not enter the cauline system of the stem at the point of insertion of the leaf, either in the manner described by Mohl (33), De Bary (12), and Kny (32), for the Palms, or in that found by Falkenberg (16), Queva (39), and Chrysler (9), among the Liliales. The arrangement more nearly resembles that observed by Guillaud (19) in the cortical bundles of the rhizome of *Acorus calamus* (D, Fig. 1), with this important difference—that in the Cyperaceae *all* of the bundles of the leaf-trace pass down through one internode as cortical bundles. Consequently we find in the bundle arrangement of the aerial stem of most Cyperaceae nothing in common with Mohl's Palm type; and the 'reparatory bundles' described by Queva (38), as occurring in *Gloriosa*, and observed by the writer in a confirmatory study of *Streptopus*, are here to be found, if at all, in the peripheral cauline bundles rather than in the medullary ones.

Cortical bundles are of quite general occurrence in many widely separated groups of plants. Wossidlo (62) has described a dense anastomosing cortical system in the *Cocos* type of Palm. Wittmack (59) showed that the cortical strands in *Musa ensete* are connected by re-entrant anastomoses at the nodes with the cauline system, and De Bary (12) describes a similar re-entrant connexion of the amphivasal bundles in the secondary thickening of *Dracaena*. Sanio (41) considered the so-called sieve-tube strands in the cortex of *Elodea* to be greatly reduced cortical fibro-vascular bundles. More recently Hartog (22) has found typical cortical bundles in the Lecythideae (Myrtales) and in the Barringtoneae, while Boodle and Worsdell (5) have found less typical cortical strands in *Casuarina*. Col (10) describes cortical bundles in several Dicotyledonous plants, and gives an admirable summary of the literature upon the subject of bundle-distribution.

De Bary (12) indicates four general modes of arrangement of cortical bundles, as follows:—Firstly, all bundles of the leaf-trace enter the cauline system at the same node, after passing as cortical bundles through one or more internodes below the insertion of the leaf. Here De Bary places *Casuarina* and *Osmunda*, with single leaf-trace bundles; species of *Begonia*, *Aspidium*, *Pteris*, *Cyathea*, &c., with several leaf-trace bundles; and Rhipsalidaceae, with peculiar winged stems. Evidently we may now add to these the majority of the Cyperaceae with jointed culms. Secondly, the central leaf-trace bundle enters the central cylinder directly, while the lateral bundles pass down through the cortex to the next node.

Here are certain Calycanthaceae and Melastomaceae, in the first of which the cortical bundles show a reversed orientation of xylem and phloem. Thirdly, the central and larger lateral leaf-bundles enter directly, while the marginal bundles become cortical, as in certain Aroideae, Palmae, Bromeliaceae, and most of the Scitamineae. Fourthly, it rarely happens that the middle leaf-trace bundle passes down through the cortex to a lower node, while the lateral strands join directly with the cauline system, as in *Arceuthobium*.

Van Tieghem (56) has suggested a possible explanation of the cortical course of the leaf-trace upon the hypothesis that the leaf-sheath has fused with the stem for one or more internodes above its actual origin. Some weight is lent to this view by the mode of leaf-insertion observed by the writer in *Streptopus*. Here, especially in *S. amplexifolius*, the margins of the leaf-base are frequently fused with the stem for two centimetres or more above the nodal complex.

In the scapose Cyperaceae the bundles of the involucral bracts enter the stem in a broad curve and unite with the medullary bundles at the basal part of the nodal complex, in a manner very like that prevailing among the Liliales. A similar mode of leaf-insertion is found in the nodes of *Scirpus robustus*. Accordingly, these forms show no cortical fibro-vascular bundles, though the deep-seated cortical sclerenchyma strands may be vestigial indications of a cortical system of bundles.

The culm of the Cyperaceae does not normally branch except in giving rise to the axes of the inflorescence. However, abortive axillary buds are of very common occurrence. The fibro-vascular strands supplying these buds are always collateral, and may be traced downward to their insertion upon the cauline bundles just below the nodal plexus. They have no direct connexion with the leaf-trace, differing in this respect from the axillary buds of certain Liliales described by Queva (38), and also from those of *Alchemilla* described by De Candolle (13), as well as from the Palm type of Mohl (33). It is important to note that in the Cyperaceae the ramular bundles have nothing to do with the nodal amphivasal plexus, contrary to the principles laid down by Queva (38), in connexion with his study of *Gloriosa*. This point will be referred to again in considering the floral axis.

THE LEAF.

The narrow linear leaves of the Cyperaceae, without exception, present a strongly xerophytic type of structure. In all cases they surround the stem for a considerable distance by a closed sheathing base. The free lamina is usually deeply grooved, presenting a V-shaped cross-section in the narrower forms, while the broader ones show a horizontal portion extending outward from the end of each arm of the V, as in *Carex lupulina*.

The amount of mechanical tissue is relatively very large, and the mesophyll is sometimes almost wholly lacking in the mature condition, owing to the development of large air-cavities in the body of the leaf. The parallel fibro-vascular bundles or 'veins' are very numerous, there being as many as sixty in some species. The middle one is considerably larger than the average, and in the broader leaves the bundle at the top of each arm of the V is also larger, so that in this case there are three principal veins. The bundles are always collateral, with well-developed peridesm, which is produced from each pole into a strong hypodermal rib. The assimilatory zone is rarely differentiated into a true palisade layer. The upper epidermis is covered by a strong cuticle, and is frequently developed into short, sharp, sclerotic spines, especially along the margins of the leaf. Over the hypodermal ribs the epidermal cells are smaller and thinner-walled, as already seen in the stem, and as described by De Bary (12) and Spinner (50). The epidermis of the under surface is thinner-walled, and commonly bears more or less conspicuous cuticular 'pegs' or papillae, at least in all aquatic and limicolous species. The stomata are relatively few and usually somewhat depressed. In their essential structural features the leaves of the Cyperaceae show little, if any, more variation than do the roots. Eichler (15) and Trécul (52) have shown that the leaf of the Cyperaceae is basipetal in its growth, and that the fibro-vascular strands are projected inward to their insertion upon the cauline system.

Both Guillaud (19) and Gwynne-Vaughan (20) have emphasized the great importance of the leaf in the Monocotyledons as a determining factor in the development of the central cylinder of the stem. The latter observer points out the fact that in the apical growth of the young stem the terminal cone is altogether insignificant in comparison with the latest-formed leaf, and the procambial strands of the young leaf are more numerous and larger than those of the cauline ring where first differentiated.

We have already alluded to the fact, established by the investigations of Chrysler (9) and others, that in an early stage of its growth the stem of a monocotyledonous plant has its fibro-vascular elements disposed in a single circle of collateral strands, and that it is only at a later stage that medullary strands, collateral or amphivasal, make their appearance. That is to say, it is only after the introduction of a number of leaf-traces into the cauline system that we find the characteristic Monocotyledonous type and arrangement of bundles making their appearance. It is a well-known fact that the leaf-trace of the Monocotyledons is made up of a far greater number of bundles than is that of any other group, and, as Jeffrey (30) points out, it is probably the accommodation of this large number of incurrent bundles that accounts for the dense nodal complexes which are so common a feature of this group. These bundles do not end blindly in the medulla, according to the ancient doctrine of Desfontaines, but each of them, from its very nature, must find attachment on the cauline system in order to be of any service in the economy of the plant. Accordingly the leaf-trace strands invest the cauline strands with a network of vascular elements, giving them an amphivasal character, which may be lost again in the internode by reorientation, or subdivision, as in the culms of the Glumales, or which may persist throughout, as in the rhizomes of the Cyperaceae and in the subterranean stems of many Arales and Liliales. The whole matter may be summed up in the statement that among the Monocotyledons the leaf is the dominant organ in determining the characteristic stelar development.

THE FLORAL AXIS.

The inflorescence of the Cyperaceae, with a few exceptions such as *Dulichium* and some Carices, is terminal upon the culm. It occurs in the form of a head, a spike, or a single or compound umbel. Caruel's (7) observations upon the structure and development of the floral organs indicate that there is in this subject a wide and interesting field for investigation. However, this matter is worthy of separate and special treatment, and we shall not attempt to consider it here.

The particular fact to which we would direct present attention is the reduction in number and characteristic arrangement of the bundles in the floral axis. This axis arises from the terminal node of the culm, except in the cases mentioned above, where it is axillary. In case the leaves of the involucre are large, this node shows amphivasal bundles, which may even be continuous through the short internodes of the involucroid region, as in *Cyperus strigosus*; but if the involucral scales are small or absent the bundles in the node are not amphivasal, as in *Eleocharis*. The bundles of the axis are seen to be continuous with the cauline system below the node. Passing upward in the axis these bundles quickly arrange themselves in a single circle, from which strands are given off to the individual florets. Each floral trace arises from two adjacent strands of the cylinder, leaving the gap between them considerably wider as it passes off. On the way obliquely outward through the cortex the trace separates into two parts—an outer, slender strand, which is the trace of the subtending scale or glume; and an inner, larger, double mass, which later breaks up into a circle of extremely delicate strands which pass to the floral organs proper. Fig. 20 will serve to make these facts quite clear, so far as the structure of the central cylinder is concerned. It is to be observed that the bundles are here arranged in a single circle, and that there is no indication whatever of the amphivasal condition. There is a very remarkable uniformity in this respect throughout the entire Order. The structure prevailing in this region cannot fail to remind one of the arrangement already described as occurring in the young seedling of the Monocotyledons, and, in turn, of that present in the mature axis of the Dicotyledons. If we bear in mind the fact that in the floral axis of the Cyperaceae there are no large and numerous incurrent leaf-trace bundles, we should not be surprised to find here retained the primitive siphonostelic central cylinder. And, conversely, if we find that this primitive arrangement of the stelar elements is disturbed only where there are large and numerous incurrent leaf-trace bundles, we are certainly justified in the statement previously made regarding the dominance of the Monocotyledonous leaf in determining characteristic stelar development. The significance of these facts will be considered more at length presently.

FOSSIL CYPERACEAE.

According to Seward (49) there were probably no Monocotyledons earlier than the Cretaceous period. Owing to the soft structure of primitive plants of this group, their preservation is rendered most unlikely. At any rate, it has been shown conclusively by the investigations of Scott (48) and others that the supposed Monocotyledons of remotest antiquity were in reality primitive Gymnosperms. Certainly no Cyperaceae have been described as from earlier than the Tertiary period. Heer (24) mentions a somewhat doubtful *Cyperacites Dallensis* from the early part of that epoch. By the close of the Tertiary the grasses and sedges were fully established. Schimper (44) describes for that period eleven Carices, eight species of *Cyperus*, thirty-three *Cyperacites*, and a number of more or less doubtful Cyperaceous forms. Hartz (23) has recently described typical spikes of *Dulichium* as occurring in the interglacial beds of Southern Jutland, Denmark.

PHYLOGENETIC CONSIDERATIONS.

The primitive ancestral Cyperaceous type is necessarily more or less a matter of conjecture. Among the earliest known fossils of this Order we find the two widely divergent genera *Carex* and *Cyperus*, occurring in about the middle of the Tertiary epoch. Apparently we must look to a considerably more remote period for the common ancestor of these forms. That is to say, the primitive Cyperaceous stock probably extended back well into the beginnings of the Monocotyledons as a whole, and consequently we should expect to find in this Order some indication of the original characters of the division. Miss Sargant (43) has expressed a tentative view that the ancestral Monocotyledons were geophilous in habit. However, this habit usually implies a more or less xerophytic type of structure; certainly, at least, a well-developed mechanical system in some part of the plant. But we have seen that the geological record of the Cyperaceae is blank prior to the appearance of species of *Carex* and *Cyperus*, which would indicate that their ancestors must have been of a less enduring type of structure.

In view of these facts, we are inclined to adopt the hypothesis suggested by Jeffrey (30) and others, to the effect that the Monocotyledonous prototype was aquatic in habit, of soft, loose texture, and provided with large leaves. Moreover, these primitive Monocotyledons were in all probability fresh-water forms, for otherwise they must have taken on a xerophytic structure, as a result of which they no doubt would have been preserved somewhere in the geological record. Indeed, we may venture the opinion that this is precisely what did happen in the course of time to the primitive Cyperaceae. Driven by torrential currents or the drying-up of streams, these ancestral sedges became adapted to the dry banks, or were carried into humus bogs and salt marshes. By the first course we might very readily derive the tuberous *Cyperus*; by the second, the long rhizome of *Carex*. By either course we should expect the plant rapidly to lose its hydrophytic character, with reduction of fundamental tissue and consequent decrease in size of members. At the same time, the more conservative fibro-vascular system would respond much less quickly to this reduction process, and the stelar structure would grow more and more compact, with all the attendant phenomena of nodal complexes, amphivasal bundles, medullary strands, and cortical leaf-traces.

Apparently such an extreme degree of specialization and comparative isolation as that shown by the genus *Carex* could have been reached only through a very long period of adaptation. Hence we may consider *Carex* to be a highly-developed, relatively modern genus, derived from a successful early variant from the primitive Cyperaceous stock. *Cyperus*, with few exceptions, presents the tuberous, scapose habit and a high degree of uniformity in structural details. While *Carex* and *Cyperus* are thus seen to be very clearly defined and somewhat divergent genera, each presenting a fairly striking degree of structural unity, it appears that *Scirpus* presents the opposite extreme of great variability. It alone of the entire Order refuses to fit as a whole into any scheme of morphological or anatomical classification. In *Scirpus* we find both Chlorocyperaceae and Sclerocyperaceae; both Amphivasae and Centrivasae; both scapose and jointed culms. Altogether the genus appears to be anatomically in the 'experimental stage'; the focus of evolutionary activity in the Order; the terminal bud, so to speak, of this particular phylogenetic branch. These facts, however, do not necessarily indicate that the genus is a recently established one, but that it may be a somewhat ancient and generalized type.

As for the more intimate phylogenetic relations of the various genera of the Cyperaceae, it must be conceded that the whole matter is at best highly problematic, and we shall venture to add only the most general statements in regard to it. On anatomical grounds it seems reasonable to place *Kyllinga*, *Dichromena*, *Fuirena*, *Hemicarpha*, and *Lipocarpha* on the side of *Cyperus*, though probably of more recent derivation; *Rhynchospora*, *Cladium*, and *Scleria* tend strongly toward *Carex*; while *Psilocarya*, *Stenophyllus*, *Fimbristylis*, and *Eriophorum* seem to lie more directly in the line of descent of *Scirpus*. *Eleocharis* is apparently a long-established and much reduced limicolous genus from near the common origin of the Order. *Dulichium* is probably a highly specialized but less successful early variant from the central line of descent.

From what has already been said it will appear that the Cyperaceae are a relatively primitive group among the Monocotyledons, and that they have suffered a considerable morphological reduction and specialization in acquiring their present amphibious to xerophytic mode of life. Their closest affinities appear to be with the Juncaceae on the one hand, and with the Gramineae on the other. Upon embryological evidence Van Tieghem (56) concludes that the Cyperaceae serve as the connecting link between the true Monocotyledons and the so-called anisocotyledonous Gramineae. This view, however, is not supported by the facts observed by Miss Sargant (43) in her extensive studies of the cotyledon of the Monocotyledons. At all events, anatomical evidence points to a somewhat intimate relationship between the two groups. Nevertheless, they are clearly marked off from each other by morphological differences in the structure of the culm, the arrangement and insertion of leaves, the character of floral parts, and in the pronounced difference in character and occurrence of amphivasal bundles.

In the work on cotyledonary development already cited, Miss Sargant (43) ably supports the view that the Monocotyledons are derived from the Dicotyledons, or that both spring from a common Angiospermous ancestry. The evidence afforded by the developmental and morphological data accumulated by recent investigators renders the correctness of this view highly probable. We may now add to this evidence the facts learned from our study of the Cyperaceae. (1) It is to be recalled that in the young condition of the seedling of this group the central cylinder is typically tubular as in the Dicotyledons. (2) The same tubular type of central cylinder is of universal occurrence in the floral axis of the Cyperaceae. (3) It is only where large and numerous leaf-trace bundles enter the central cylinder that we find the typical Monocotyledonous type and arrangement of stelar elements. Hence we may conclude that the type of central cylinder found in the conservative seedling and floral axis is ancestral or palingenetic, while the medullary and amphivasal bundles occurring elsewhere are more recently acquired or caenogenetic features. But those stelar characters which we find to be palingenetic in the Monocotyledonous axis are precisely those which are observed to be characteristic of the stelar system of the Dicotyledons. In so far, then, as the anatomical characters of the Cyperaceae are of importance, they point somewhat strongly to a common ancestry of the two grand divisions of Angiospermous plants.

SUMMARY AND CONCLUSIONS.

In the course of the present investigation a somewhat careful study has been made of the structural characters of some eighty species of Cyperaceae, representing seventeen North American genera. In addition to these, representatives of several other Monocotyledonous groups have been examined by way of confirmation and comparison. The following conclusions, based upon the results of this study, may be offered in answer to the questions propounded in the introductory paragraphs:—

1. Amphivasal fibro-vascular bundles are continuous throughout all Cyperaceous rhizomes which bear conspicuous leaves at all of the nodes, and in which the internodes are relatively short (Amphivasae). Such bundles are absent from the rhizome only where the leaves are very small and widely scattered (Centrivasae).

2. In the culms of the Cyperaceae amphivasal fibro-vascular bundles commonly occur only in the nodal complexes; rarely such bundles are continuous through the very short internodes of the involucroid region of certain species. Elsewhere the bundles of the culm are strictly collateral.

3. Amphivasal bundles are derived from collateral bundles by the multiplication of xylem-elements, resulting from the introduction of large and numerous leaf-traces into the central cylinder. In the Cyperaceae the amphivasal condition is not in any way related to the phenomenon of branching.

4. A study of the Cyperaceae shows that the leaf is the dominant factor in the development of the stelar characteristics of the Monocotyledons. Branching of the axis does not affect the nature of the fibro-vascular bundles.

5. The foliar fibro-vascular bundles pass downward through the culm as cortical bundles to the next lower node, where they fuse with the cauline bundles and with the subtending leaf-trace, through a ring-like amphivasal plexus. The cauline bundles pass continuously, but with nodal anastomoses, from the base of the culm to their termination in axillary buds or floral axes, or, less frequently, in nodal complexes. In the rhizome the course of the bundles more nearly resembles that which is typical of the Palm-stem. Fusions and anastomoses of the bundles of the rhizome take place chiefly in the superficial reticulum of the central cylinder.

6. The simple tubular central cylinder which has been found in the seedling and the floral axis proper of all the Cyperaceae which have been examined is to be considered ancestral or palingenetic; while medullary strands and the amphivasal bundles characteristic of most rhizomes and of the nodal complexes of aerial stems apparently must be regarded as more recently acquired or caenogenetic features.

7. On anatomical grounds the Cyperaceae appear to be one of the more primitive groups among the Monocotyledons, considerably specialized and reduced from the common megaphyllous, possibly hygrophilous ancestor. They present a high degree of anatomical unity, not only in floral and foliar characters, but also in their internal structure, and especially in the mode of occurrence, number, and development of their amphivasal bundles.

8. The anatomy of the Cyperaceae seems to point strongly to the derivation of the Monocotyledons and Dicotyledons from a common ancestry which presented characters essentially Dicotyledonous in the arrangement and structure of fibro-vascular bundles, and in the presence of cambial growth.

In conclusion, I desire to express my obligations to Professor L. L. Hudson, of Delaware, Ohio; to Professor S. F. Poole, of Wichita, Kan.; to Miss Helen Plowman, of Greenville, Ohio; and to Mr. A. H. Moore, Mr. J. G. Hall, and Mr. M. L. Fernald, of Cambridge, Mass., for material; and, above all, to Professor E. C. Jeffrey, for material and for the many suggestions and criticisms offered throughout the course of this investigation.

PHANEROGAMIC LABORATORIES, HARVARD UNIVERSITY:
April, 1905.

LITERATURE.

Comparatively little has been written which bears directly upon the subject under consideration, but a great many authors refer to it in a more general and incidental way. In the following list no attempt has been made to include any but the more interesting and suggestive of the works which have been consulted.

1. ANDERSSOHN, MISS S.: Ueber d. Entwickel. d. primären Gefässbündelstränge d. Monokotylen. Bihang till K. Sv. Vet. Akad. Handl., xii, 1889, p. 188.
2. BARANETZKY, I.: Sur le développement des points végétatifs des tiges chez les Monocotylédones. Ann. Sci. Nat. Bot., 8e sér., tome 3, 1897.
3. BOODLE, L. A.: On lignification of phloem in *Helianthus*. Annals of Bot., xvi, 61 : 3[1], 1902.
4. ————: Comparative Anatomy of the Hymenophyllaceae, Schizaeaceae, and Gleicheniaceae. Annals of Bot., xiv, 1900, p. 455; and xv, 1901, pp. 359, 703.
5. ———— AND WORSDELL, W. C.: On the Comparative Anatomy of the Casuarinae. Annals of Bot., x, 31 : 9, 1894.
6. BORDET, M.: Recherches anatomiques sur le genre Carex. Revue gén. de Bot., tome 3, 1891.
7. CARUEL, F.: Observations sur la fleur femelle du Carex. Ann. Sci. Nat. Bot., 5e sér., tome 7, 1867.
8. CHAUVAUD, G.: Sur la mode de formation des faisceaux libériens de la racine des Cypéracées. Bull. de la Soc. bot. de France, 1895, p. 450.
9. CHRYSLER, M. A.: The development of the central cylinder of Araceae and Liliaceae. Bot. Gaz., 38 : 9, 1904.
10. COL, A.: Recherches sur la disposition des faisceaux dans la tige et les feuilles de quelques Dicotylédones. Ann. Sci. Nat. Bot., 8e sér., tome 20, 1904.
11. CORMACK, B. G.: On Cambial Development in *Equisetum*. Annals of Bot., vii, 25 : 3, 1903.

---

[1] For month of publication—so elsewhere.

12. DE BARY, A.: Comparative Anatomy of Phanerogams and Ferns. Eng. transl. by Bower and Scott, 1884.
13. DE CANDOLLE, M. CASIMIR: L'Anatomie des Alchemillae. Bull. de l'Herbier Boissier, tome 1, No. 10.
14. DUVAL-JOUVE: Étude histo-taxique des Cyperus, 1874.
15. EICHLER: Zur Entwickelungsgeschichte des Blattes. Marburg, 1861.
16. FALKENBERG, P.: Vergl. Untersuch. u. den Bau d. Vegetations-Organe der Monocot. Stuttg., 1876.
17. FARMER, J. B., AND HILL, T. G.: On the Arrangement and Structure of the Vascular Strands in *Angiopteris evecta* and some other Marattiaceae. Ann. of Bot., xvi, 1902, p. 371.
18. FAULL, J. H.: Anatomy of the Osmundaceae. Bot. Gaz., 32: 12, 1901.
19. GUILLAUD, A.: Anatomie de la tige des Monocotylédones. Ann. Sci. Nat. Bot., 6^e^ sér., tome 5, 1878.
20. GWYNNE-VAUGHAN, D. T.: On Polystely in the genus Primula. Annals of Bot., xi, 1897, p. 317.
21. ——————: Observations on the Anatomy of Solenostelic Ferns. Annals of Bot., xv, 1901, p. 71.
22. HARTOG, M. M.: On Cortical Bundles in Lecythideae and Barringtoneae. Annals of Bot., iv, 14: 5, 1890.
23. HARTZ, N.: On a Fossil Dulichium from Denmark. Meddel. Dansk. Geol. Foren., 10: pp. 13-22, 1904.
24. HEER: Flora fossilis Helvetiae, p. 170.
25. HOLM, TH.: Studies in the Cyperaceae. A series of papers appearing in the Am. Jour. of Sci. since 1896.
26. JEFFREY, E. C.: A Theory of the Morphology of Stelar Structures. Proc. R. S. Can., 1896.
27. ——————: Morphology of the Central Cylinder in Vascular Plants. Rep. B. A. A. S., 1897.
28. ——————: Morphology of the Central Cylinder in the Angiosperms. Trans. Can. Inst., 6: 1900.
29. ——————: Structure and Development of the Stem in Pteridophyta and Gymnosperms. Phil. Trans. R. Soc. London, cxcv, 1902, p. 119.
30. ——————: In Coulter and Chamberlain's Morphology of Angiosperms. 1903.
31. KLINGE: Vergl.-histol. Unters. der Gramineen- und Cyperaceen-Wurzeln. Mém. de l'Acad. des Sci. de St.-Pétersbourg, 1879.
32. KNY, L.: Bot. Wandtafeln. Texte, vi. Abt., 1884, and vii. Abt., 1886.
33. MOHL, H. VON: Structure of the Palm-stem. Eng. transl. by Henfrey, in Reports and Papers of the Ray Society, 1849.
34. NÄGELI, C.: On Arrangement of Bundles in Stems. Beitr. zur wiss. Botanik, i. Heft, p. 10.
35. PALLA, E.: Zur Systematik der Gattung Eriophorum. Bot. Zeit., Heft 8, 1896, p. 141.
36. PAX, F.: Cyperaceae, in Engler und Prantl, Natürl. Pflanzenfamilien, ii. Teil, 1889, p. 98.
37. ———: Beiträge zur Morph. u. Systematik d. Cyperaceae. Engler's Jahrb., vii, p. 287.
38. QUEVA, C.: Contributions à l'anatomie des Monocotylédonées. I. Trav. et Mém. de l'Univ. de Lille, vii, No. 22: 1899.
39. ————: Recherches sur l'anatomie de l'appareil végétatif des Taccacées et des Dioscorées. Lille, 1904.
40. RICKLI, MARTIN: Beiträge zur vergl. Anatomie der Cyperaceen mit besonderer Berüchsichtigung der inneren Parenchymscheide. Pringsh. Jahrb. f. wiss. Bot., Bd. xxvii, Heft 4, 1895.
41. SANIO: Botan. Zeit., 1865, p. 196.
42. SARGANT, MISS E.: The Evolution of Monocotyledons. Bot. Gaz., 37: 5, 1904, p. 325.
43. ——————: A Theory of the Origin of Monocotyledons, founded on the Structure of their Seedlings. Annals of Bot., 17: 1, 1903.
44. SCHIMPER: Traité de Paléont., II, p. 408.
45. SCHOUTE, J. C.: Die Stelär-Theorie. Groningen, 1902.
46. ——————: Die Stammesbildung der Monocotylen. Flora, 1903.
47. SCHWENDENER, S.: Das mechanische Prinzip der Monocotylen. 1874.
48. SCOTT, D. H.: Studies in Fossil Botany. 1900.
49. SEWARD, A. C.: On Fossil Monocotyledons. Annals of Bot., x, 38: 6, 1896.

50. SPINNER, HENRI: L'Anatomie foliaire de Carex suisses. 1903.

51. STRASBURGER, E.: Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Histologische Beiträge, iii, 1891.

52. TRÉCUL: Mémoire sur la formation des feuilles. Ann. Sci. Nat. Bot., 4e sér., tome 20, 1853.

53. TREUB, M.: Le méristème primitif de la racine dans les Monocotylédones. Musée Botan. de Leyde, tome 2, Leiden, 1876.

54. VAN TIEGHEM, PH.: Symmétrie de structure des plantes. Ann. Sci. Nat. Bot., 5e sér., No. 13, 1870-71.

55. ——————: Traité de botanique. 1884.

56. ——————: Morphologie de l'embryon et de la plantule chez les Graminées et les Cypéracées. Ann. Sci. Nat. Bot., 8e sér., 3, p. 259.

57. —————— ET DOULIOT: Sur la polystélie. Ann. Sci. Nat. Bot., vii, 8: 1886.

58. ——————: Recherches comp. sur l'origine des membres endogènes. Ann. Sci. Nat. Bot., 7e sér., tome 8, 1888.

59. WITTMACK: Anatomy of Monocotyledons. Linnaea, Halle, 1867.

60. WORSDELL, W. C.: The Evolution of the Vascular Tissue of Plants. Bot. Gaz., xxxiv, 1902, p. 216.

61. ——————: The Stelar Theory. The New Phytologist, 1903, p. 140.

62. WOSSIDLO: Quaedam additamenta ad Palmarum anatomiam. Diss. Vratisl., 1860.

EXPLANATION OF THE FIGURES

Illustrating Mr. Plowman's paper on Cyperaceae.

Fig. 1. Diagrams illustrating the course of the fibro-vascular bundles in various Monocotyledonous stems. The broken lines represent the imaginary inner boundaries of the cortical zone, while the nodes are indicated by the horizontal lines. *A*, Mohl's plan of the Palm type. *B*, De Bary's plan of the distichous Palm type. *C*, plan of bundles in the rhizome of *Convallaria majalis*. *D*, plan of bundles in the rhizome of *Acorus Calamus*. *E*, plan of bundles in the stem of *Tradescantia virginica*. *F*, plan of bundles in the rhizome of *Luzula campestris*. *G*, plan of bundles in the aerial stem of *Scirpus cyperinus*. (*C*, *D*, *E*, and *F* adapted from Guillaud.)

Fig. 2. Diagrammatic representation of the course of the fibro-vascular bundles in the aerial stem of *Dulichium arundinaceum*. *A*, transverse section of part of stem just above a node, including the leaf-sheath. *B*, section passing through the nodal complex. *C*, section some distance below the node. *D*, projection of fibro-vascular elements from tangential section. *E*, radial longitudinal section of the stem. *a.c.l.*, air-cavity in leaf; *a.c.s.*, cortical air-space; *c.b.*, cortical bundles; *l.b.*, leaf-bundle; *l.t.*, leaf-trace bundle; *n.a.*, nodal anastomosis; *n.d.*, nodal diaphragm; *n.p.*, nodal plexus; *s.b.*, cauline bundle; *l.*, leaf.

PLATE I.

Fig. 3. Part of a transverse section of the rhizome of *Scirpus cyperinus*, showing typical amphivasal bundles in the central cylinder, and centripetal massing of the peridesm in part of the bundles. A type of the Amphivasae. × 50.

Fig. 4. High-power detail of the same, showing endodermal cells thickened on the inner wall, and peripheral amphivasal bundles with but slightly differentiated peridesm. × 175.

Fig. 5. Part of a cross-section of an internode in the culm of *Scirpus cyperinus*, showing cortical and cauline fibro-vascular bundles, cortical air-spaces, and hypodermal sclerotic zone. A type of the Sclerocyperaceae. × 40.

Fig. 6. Collateral fibro-vascular bundle from a transverse section near the base of an internode of the culm of *Scirpus cyperinus*, showing the type of cambial development commonly occurring in this region of Cyperaceous culms. × 350.

Fig. 7. Part of a transverse section of the culm of *Scirpus cyperinus*, taken just at the base of the nodal region, showing the beginning of division in the cortical bundles to form the annular anastomosis. × 75.

Fig. 8. Part of a transverse section through the middle of a node of an aerial stem of *Scirpus cyperinus*. Most of the fibro-vascular bundles show the amphivasal condition; a few are collateral, while certain ones show intermediate conditions. × 50.

Fig. 9. Part of a radial longitudinal section through a node of the culm of *Scirpus cyperinus*, showing the annular amphivasal bundles of the nodal complex in cross-section. The base of the leaf-sheath appears above at the right. × 40.

Fig. 10. Part of a radial longitudinal section of a rhizome of *Scirpus cyperinus*. The endodermis is just to the right of the centre. On the right is the cortex, showing a leaf-trace on the extreme margin. To the left is the outer portion of the central cylinder, with the circular amphivasal strands of the superficial reticulum appearing in cross-section. × 40.

Fig. 11. Part of a transverse section through an internode of the culm of *Scirpus robustus*. A type of the Chlorocyperaceae, with large medullary air-spaces, well-developed palisade layer, and numerous stomata. × 75.

Fig. 12. Part of a transverse section through the culm of *Eleocharis palustris*, showing extreme reduction of the tissues. A few stellate 'bulkhead' cells are shown on the left. × 75.

Fig. 13. Part of a transverse section of the culm of *Dulichium arundinaceum*, just above a node, showing a section of the leaf-sheath externally, and the two circles of bundles in the stem, the inner of which is the proper cauline series, and the outer or cortical series, alternating with large air-spaces. × 30.

Fig. 14. Part of a slightly oblique transverse section through a node of the culm of *Dulichium*. The portion at the right is the lower, showing two series of bundles. At the left the section passes into the upper part of the node, where there are three series of bundles: the inner, or cauline; the outer, or leaf-trace; and the middle, or cortical series of the next higher internode. The central part of the figure shows the nodal anastomosis, with part of the nodal diaphragm below. × 20.

PLATE II.

Fig. 15. Part of a transverse section of the rhizome of *Scirpus fluviatilis*, showing the peculiar sclerotic zone outside the endodermis. × 50.

Fig. 16. Part of a transverse section of the rhizome of *Scirpus americanus*. A type of the Centrivasae. × 60.

Fig. 17. Transverse section of the central cylinder of the rhizome of *Carex lupulina*. A type of the Amphivasae. × 20.

Fig. 18. Part of a transverse section of the central cylinder of the rhizome of *Cladium mariscoides*. Cavernous medulla and cortex, and endodermis hardly distinguishable. × 50.

Fig. 19. Part of a transverse section of the rhizome of *Eleocharis palustris*. × 40.

Fig. 20. Transverse section of the axis of the inflorescence of *Eleocharis palustris*, showing the simple tubular central cylinder which is characteristic of the floral axis proper throughout the Cyperaceae. × 25.

Note.—The nomenclature embodied in this paper is based chiefly upon that found in Gray's Manual, sixth edition, and in the Flora of Britton and Brown, edition of 1896. Upon more critical study, and after a comparison with the results of recent investigations in this field, it appears that the following corrections are desirable:—

For *Scirpus microcarpus*, Presl, read *Scirpus rubrotinctus*, Fernald.
For *Eleocharis ovata*, R. & S., read *Eleocharis obtusa*, Schultes.
For *Eriophorum gracile*, Koch, read *Eriophorum tenellum*, Nutt.
For *Eriophorum vaginatum*, L., read *Eriophorum callitrix*, Cham.

On these matters see Rhodora, ii, 1900, p. 20, and vii, 1905, pp. 85–87. Also Proc. Am. Acad. Sci., xxxiv, 1899, p. 492.

The writer is indebted to Mr. M. L. Fernald, of the Gray Herbarium, for these facts.

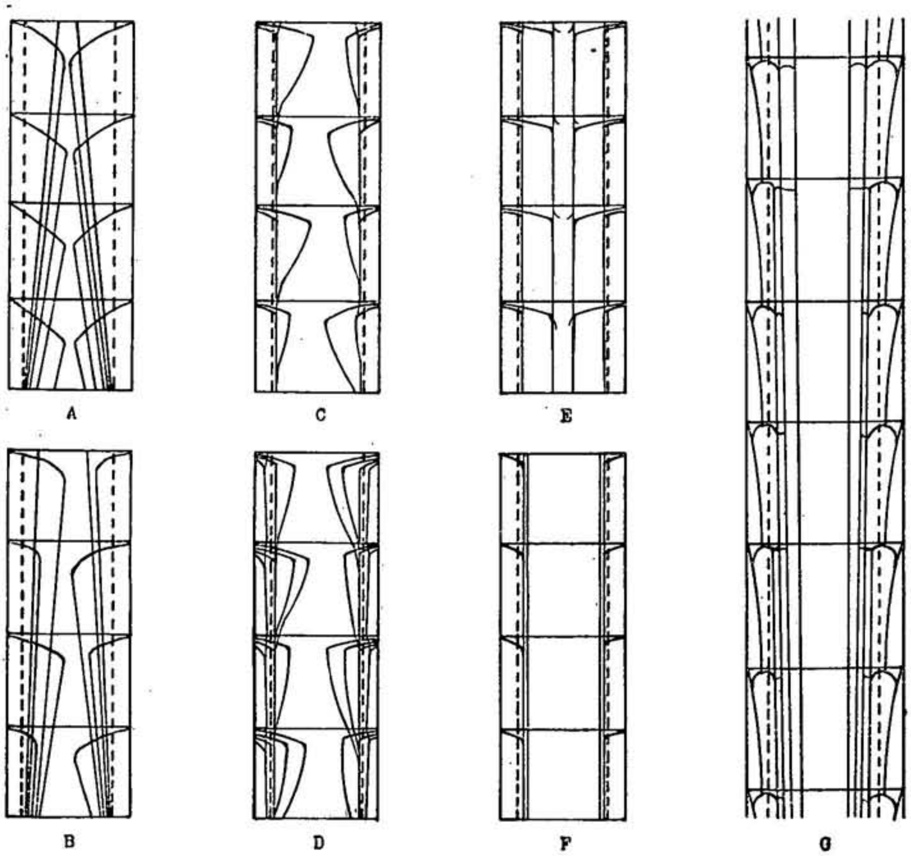


FIG. 1.

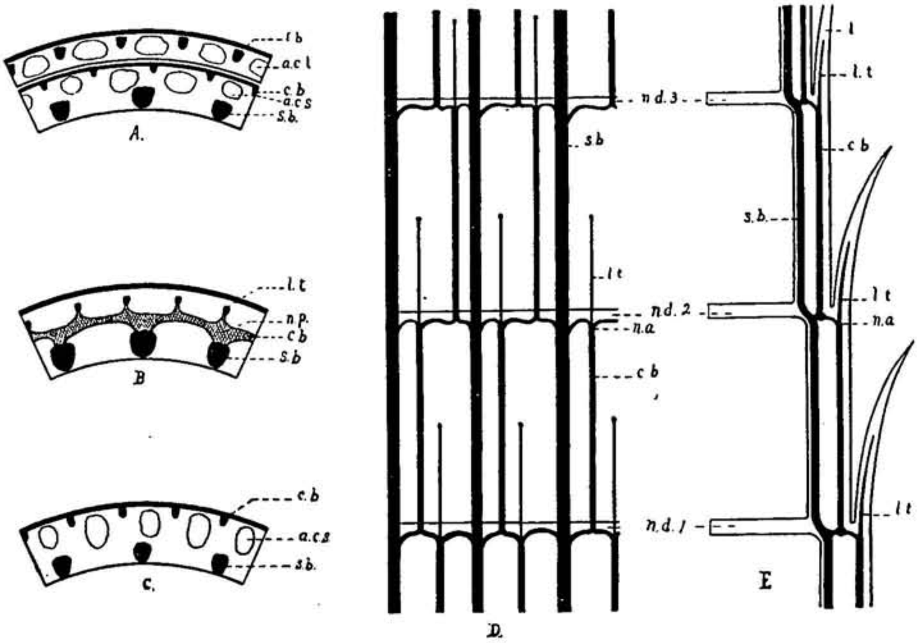
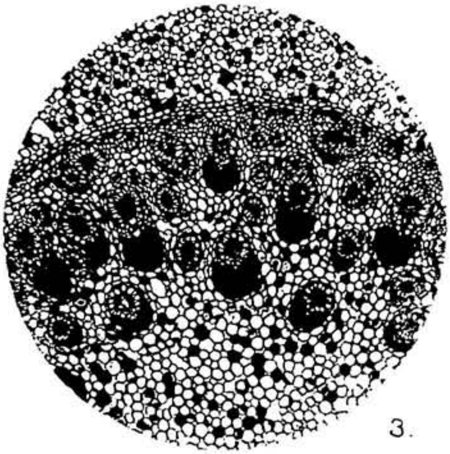
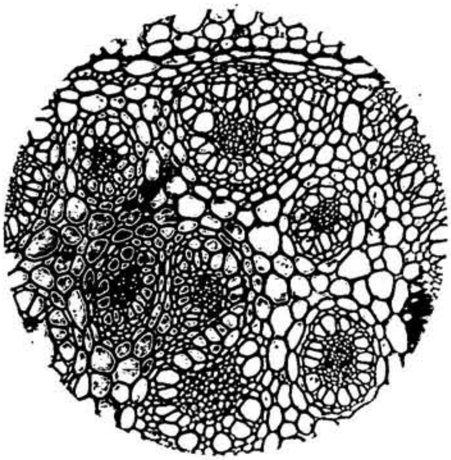
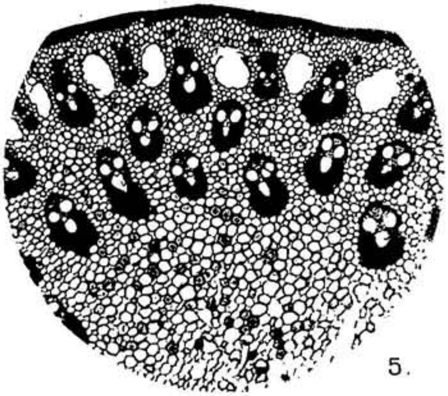

l b
a.c l
c b
a.c s
s.b.
A.
l.t
n p.
c b
s b
B
c.b
a.c.s
s.b.
C.
n d.3
s b
l t
n d. 2
n.a
c b
n.d. 1
D.
l
l. t
c b
s. b.
l t
n.a
l t
E

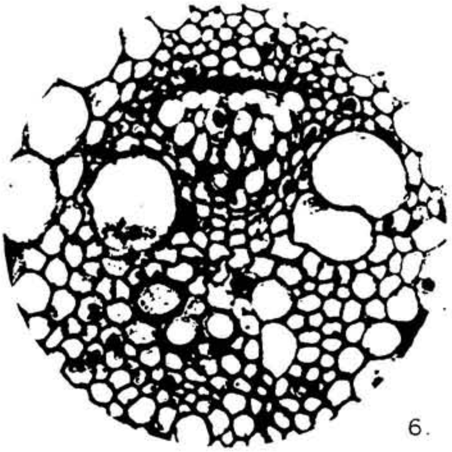
FIG. 2.

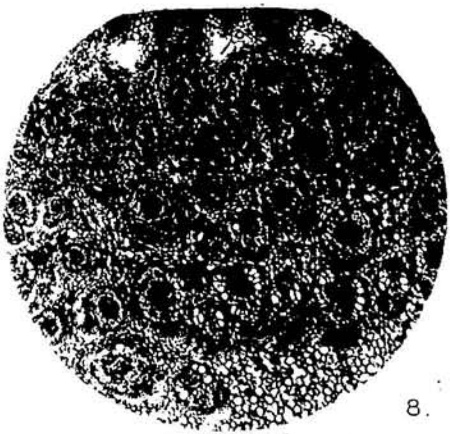
Annals of Botany.


3.




5.

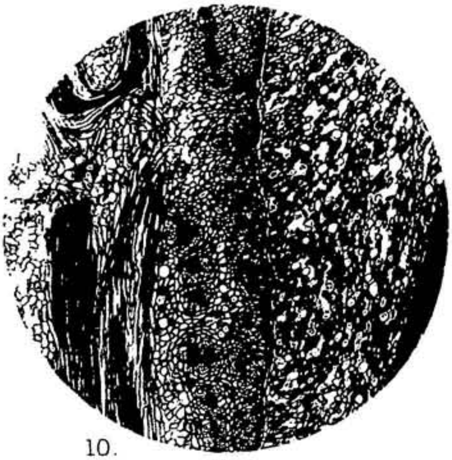

6.


8.

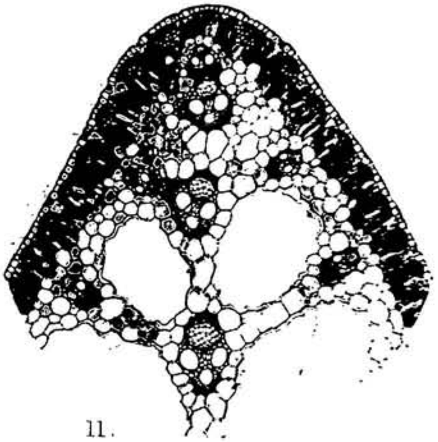
A.B.P photo

PLOWMAN.—ANATOMY OF CYPERACEAE.

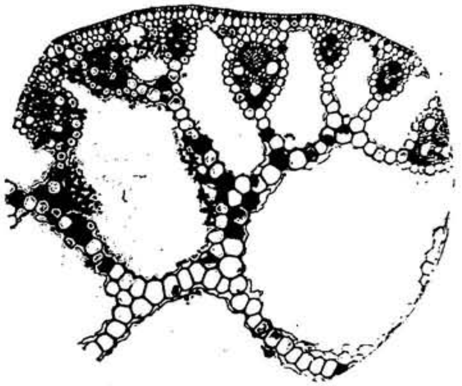
9



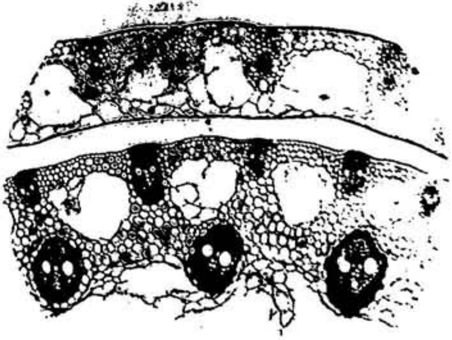
10.



11.



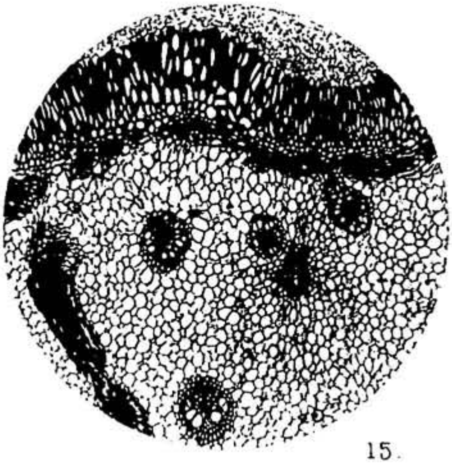
12.



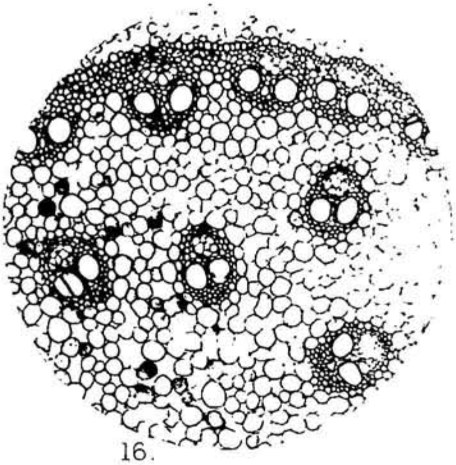
13

14.

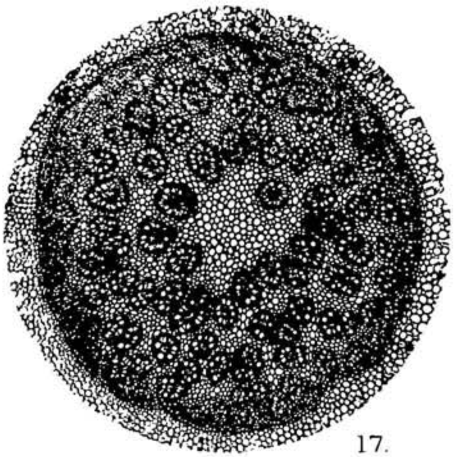
Huth, London.



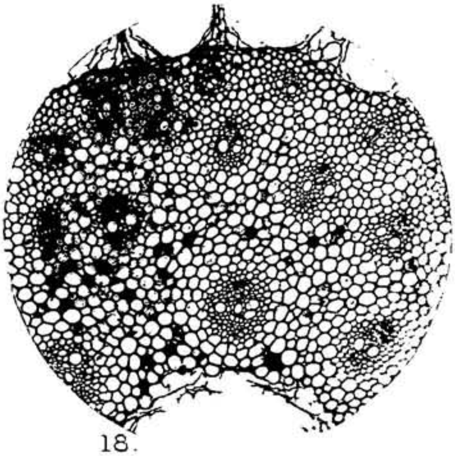
15.



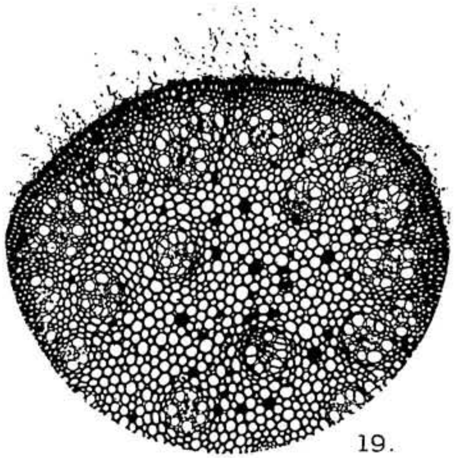
16.



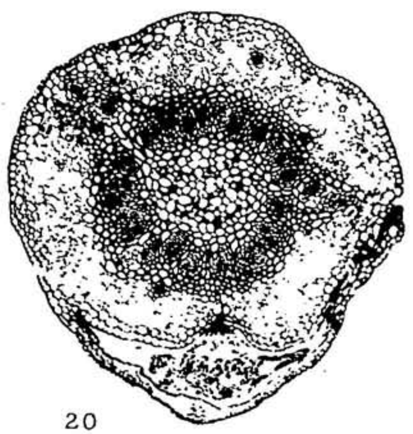
17.



18.



19.



20

A.B.P. photo. Huth, London.

PLOWMAN.—ANATOMY OF CYPERACEAE