ART. XVII.—*Studies in the Cyperaceæ*; by THEO. HOLM.
 XV. *Carices (Vigneæ) astrostachyæ*. (With five figures in the text.)

IN some previously published papers we have directed attention to the classification of the *Carices* in "*Vigneæ*," "*Vigneastræ*" and "*Carices genuinæ*" as the most natural method under which the species may be arranged in sections or "greges," as suggested by Drejer in his *Symbolæ Caricologicæ*. However, this author only treated some of "*Carices genuinæ*," although he fully recognized the stability of the "*Vigneæ*," while "*Vigneastræ*" did not appear to him as being separable from the paniculate *distigmaticæ*. While maintaining the *Vigneæ*, Drejer did not restrict this section to distigmatic species alone, but he considered, also, certain tristigmatic species, for instance *C. macrocephala*, as belonging to this section; he admitted at the same time a number of distigmatic heterostachyous species among the *Carices genuinæ*, even if he considered this section as consisting of typically tristigmatic species. The number of stigmata was, thus, of minor importance to Drejer in disposing of the species in "greges." We have already touched upon his views concerning the old section "*Psyllophoræ*," but hitherto we have not had an opportunity to discuss his ideas in regard to the arrangement of all the *Psyllophoræ* under *Carices genuinæ*, as "*formæ hebetatæ*" of these. It is, at least, the only way in which we can understand his remark (l. c., p. 8), "*Constituunt ergo Psyllophoræ et Carices genuinæ unam maximeque naturalem sectionem, etc.*," inasmuch as Drejer defined the *Psyllophoræ* as monostachyous, and the *Vigneæ* as possessing decompound spikes (*spica composita præditas*). Moreover, in describing the various forms of perigynium, Drejer points out that, "*omnes fere formæ perigyniorum, exceptis maxime evolutis, quæ apud Carices inveniuntur, inter Psyllophoras quoque occurrunt.*" He compares thus the perigynium of *C. polytrichoides* with that of *C. pallescens*, and of *C. Davalliana* with that of *C. sempervirens*, etc. Whatever his views were in respect to the lesser developed types of *Vigneæ*, Drejer does not seem to have considered any of these to be sought among the monostachyous species, formerly called "*Psyllophoræ*." But his work was left unfinished, and it is more than probable that he would have altered his views, had he prosecuted his studies further.

Tuckermann, whose system of *Carex* was published just one year earlier than Drejer's, adopted *Psyllophoræ* and *Vigneæ*

with the same distinction "spica unica" and "spiculæ plures"; further, he proposed "*Vigneastræ*," "*Leptantheræ*" and "*Legitimæ*," the last mentioned being identical with *Carices genuinæ*. This author, however, seems to have detected some affinity to exist between certain *Psyllophoræ* (*Dioicæ*) and *Vignæ* (*Stellulatæ*), since he makes the following statement about the former (*Dioicæ*), "Stellulatas referentes." In a lately published paper upon South American *Carices* Rev. G. Kükenthal accepts *Vignæ*, *Vigneastræ* and *Eucarex* (*Carices genuinæ*), and he recognizes five sections among the *Vignæ*: *Muricatæ* Fr., *Remotæ* Aschers, *Canescentes* Fr., *Alatæ* Kükenth. and *Capituligeræ* Kükenth. While this author refers certain *Psyllophoræ* (*Nardinæ* Fr.) to *Vignæ*, he does not suggest these to represent lesser developed types of any of the other sections, and the reason may be, that the South American *Capituligeræ*: *C. trichodes* Steud., *C. capitata* L. and *C. caduca* Boott, constitute a small and isolated group of species with no immediate relatives among the higher developed *Vignæ* of that region, the extratropical South America.

The systematic position of a number of monostachyous species of *Carex* thus remains to be decided upon, and it seems as if Tuckermann were the first author who felt warranted in referring some of these to *Vignæ*, the *Dioicæ* to the *Stellulatæ*, while both Drejer and Kükenthal considered several of these as "formæ hebetatæ of *Carices genuinæ*." It may be that the original type of *Carex* was diœcious and that it resembled our monostachyous species, and that both *Vignæ* and *Carices genuinæ* developed from such monostachyous forms as two parallel branches, a theory that has been discussed so excellently by a German author, August Schulz, in a paper upon the morphology of *Carices*. There would in this way hardly be any reason to object to the disposition of some of the monostachyous species among *Vignæ* as "formæ hebetatæ:" lesser developed types of which habit and structure might point towards the earliest fundamental forms of the genus.

In looking over the *Psyllophoræ* as this section is understood by Tuckermann, it is evident that several of these species have no other character in common than that taken from the structure of the inflorescence, being an almost simple spike, androgynous or sometimes diœcious. The purely staminate inflorescence and the staminate portion of the androgynous invariably represent true spikes, while the pistillate, as we have described in previously published papers, are always decomposed, though less so in these species than in others, where several pistillate spikelets may be united so as to form spicate, more or less ramified inflorescences. In the *Psyllo-*

phoræ the sectional character is thus: "spica unica simplicissima androgyna sive dioica," and Tuckermann divided these in nine subsections: *Dioicæ*, *Nardinæ*, *Pulicares*, *Paucifloræ*, *Filifoliæ*, *Scirpinæ*, *Obtusatæ*, *Polytrichoidæ* and *Rupestris*, of which the names readily indicate what species are comprised under these subsections. But on the other hand the characterization of these minor sections is in several cases well comparable with that of several of the *Vigneæ* and *Carices genuinæ*, as defined by Tuckermann, with the only exception of the lesser decompound inflorescence. We find among the *Dioicæ* such species enumerated as *C. dioeca*, etc., *C. exilis* and even *C. capitata* L., the last mentioned being followed by *C. nardina* Fr. (*Nardinæ*), and it seems strange that Tuckermann considered *C. capitata* as being such a close relative of *C. dioeca*, rather than placing it under *Nardinæ*. Elias Fries in enumerating the Scandinavian *Carices** has, also, the *Psyllophoræ* classified as his *Monostachyæ* distinct from his "*Homostachyæ*:" *Hyparrhenæ* and *Acroarrhenæ*, while Kunth only recognized *Vigneæ* and *Careæ*, the former containing all the species with bifid, the latter those with trifid style, thus each of these sections is represented by both mono-, homo- and hetero-stachyous species. The number of stigmata, however, is of little importance in classifying *Carices*, inasmuch as we have already pointed out, the number of stigmata being by no means a constant character in several species of *Vigneæ* and *Carices genuinæ*.

In regard to the distribution of the sexes, diœcious forms are not restricted to the *Psyllophoræ* either, but occur among the *Vigneæ*, e. g., *C. sterilis* Willd., *C. Douglasii* Boott, and occasionally among the *Carices genuinæ*: *C. Parryana* Dew., besides that *C. acuta* L. sometimes occurs with purely staminate spikes, the so-called variety *anomala* Lge., which has been found in Denmark. The very interesting *C. Bouittiana* Benth. is only known as diœcious, but Boott† referred it nevertheless to *Carices genuinæ* on account of its close affinity to *C. Baltzelli* Chapm. However these cases of diœcism may well be considered as exceptional among *Vigneæ* and *Carices genuinæ*, while there are typically diœcious species among the *Psyllophoræ*: *C. dioeca*, *C. parallela*, etc. The character "spica unica" as applied to all the *Psyllophoræ* is, on the other hand, not constant, and we remember for instance that in both *C. scirpoidea* and *C. exilis* additional, lateral spikes may be developed, consisting of several pistillate flowers. Drejer referred *C. scirpoidea* to his *Sphæridiophoræ*, and

* Fries Elias: Summa vegetabilium Scandinaviæ. Sectio prior. Upsala, 1846, p. 73.

† Boott, Francis: Illustrations of the genus Carex, vol. i, London, 1858, p. 16.

Boott* says of *C. exilis*: "The existence of these distinct spiculæ necessarily separate the species from the *Psyllophoræ*. It proves the correctness of the remark of Drejer, that that artificial group is to be considered as "formæ hebetatæ Caricum; monostachyæ incipiunt, evaduntque plioistachyæ. The evident affinity of *C. exilis* is with the *Stellulatæ*;" a similar suggestion was also made by Tuckermann, as mentioned above.

In looking over the *Vigneæ* and *Carices genuinæ* monostachyous specimens are sometimes met with, especially among the latter, but such forms are hardly to be considered as typical, even if they may be quite common, for instance *C. typhina* and *C. squarrosa*, both of which abound in the vicinity of Washington, D. C., with a single gynæcandrous spike, subtended by several leaf-like bracts, indicating the suppression of the lateral spikes; these forms have, also, been found in many other places in the eastern United States, and seem to predominate, the typical plioistachyous forms being much less common in certain regions. It thus appears as if the *Psyllophoræ* in general exhibit some characters by which they may be distinguished from the other *Carices*: "spica unica simplicissima androgyna sive dioica," as indicated by Tuckermann, but beyond this distinction most of the species are readily noticed to be inseparable from *Vigneæ* or *Carices genuinæ*. This becomes the more evident when we consider the structure of utriculus, which furnishes such excellent characters for distinguishing the species and even the "greges," and is of much greater importance than those characters, which are derived from the less decompound inflorescence, the number of stigmata and the separation of the sexes in some of the species. When speaking of utriculus, we must admit, however, that this exhibits a peculiarity which seems characteristic of a number of *Psyllophoræ* in contrast to the *Vigneæ* and *Carices genuinæ* in general; and is evidently a sign of lesser development. This is to be noticed in the orifice of utriculus, which is unequally slit in the *Dioicæ*; thus the upper margin is almost entire on the ventral face, but cut down more or less deeply on the dorsal, the convex face. In the higher developed forms, *Vigneæ* and *Carices genuinæ*, the beak is mostly bidentate or cut down equally on both faces, especially so in the latter. But this character, the unequally slit orifice of utriculus, is not peculiar to all the *Psyllophoræ* and is, moreover, to be observed in some of the *Carices genuinæ*, as pointed out by Drejer. But otherwise the utricle does not show any difference of importance, by which the *Psyllophoræ* may be distinguished from the other *Carices*,

* Ibidem, p. 17.

neither in regard to the mere outline, when considered in transverse section, or as to the minor details of the anatomical structure. The presence of a seta, which, as we have described in previously published papers, depends only upon the prolongation of rhacheola, has by some authors been considered as characteristic of *Psyllophoræ*, being especially well developed in *C. microglochis*, *C. Fraseri* and several others, but is, also, common to many species of *Carices genuinæ*. If we finally compare the position or rather the direction of utriculus in immature and mature specimens of the *Dioicæ*, we notice certain accordances with some of the other *Carices*. In *C. dioeca*, for instance, the utricles are erect during anthesis, but spreading, when the fruit is mature. This change of direction is, also, noticeable in the other species of *Dioicæ* (excluding *C. capitata*), but is, moreover, characteristic of a number of other *Carices* with the spikes squarrose at maturity (*C. echinata*, *C. flava*, *C. Pseudocyperus*, etc.), while in others the utricles maintain their original erect position, being more or less appressed to the rhachis as in *C. vulgaris*, *C. misandra*, *C. pratensis*, etc.

In summarizing these general characters, those that were formerly looked upon as being peculiar to the *Psyllophoræ*, and those which they have in common with the other *Carices*, we cannot consider these monostachyous species as constituting a section or grex distinct from the others, but we feel more inclined to accept them as lesser developed types and referable to the greges of *Vignæ* and *Carices genuinæ*, in the same way as we already outlined the *Stenocarpæ*, including *C. lejocarpa* and *C. circinata* as formæ hebetatæ of these. In the present paper, it is our intention to demonstrate the affinities of the *Dioicæ*, as understood by Tuckermann, although we have felt obliged to exclude *C. capitata* L., which, according to our opinion, is better placed among the *Nardinæ* Fr., as already suggested by Rev. G. Kükenthal. These diœcious species are as follows: *Carex dioeca* L., *C. gynocrates* Wormskj., *C. parallela* Læst., *C. Duvalliana* Sm. and *C. exilis* Dew. However, monœcious forms are known of all these species and are so common in *C. gynocrates* and *C. exilis*, that it is difficult to say whether these two are typically diœcious or monœcious, and in regard to the former this was originally described as a monœcious species with androgynous spike, being the most prevalent form in Greenland. Since then the species has, also, been collected on the North American continent and in Kamtschatka as monœcious and diœcious, the latter being undoubtedly the most frequent form in this country. If Meyer's *C. Redowskyana* be identical with *C. gynocrates*, the plant from Kamtschatka is truly diœcious. To separate

these two forms, the monœcious from the diœcious, as distinct species would not be advisable, inasmuch as we have found no other distinction between these, neither morphological or anatomical, than the varied distribution of the sexes, a character that seems of little import, scarcely even of varietal value, *C. gynocrates* may be considered as being most frequently diœcious, and among the large number of specimens which we have examined from various parts of this country and from Greenland, there were c. 400 diœcious individuals against 76 with androgynous spike. *C. monosperma* Macoun is among these specimens, and we have failed to find any other distinction between this and *C. gynocrates* than the smaller number of pistillate flowers, often only one, at the base of the staminate spike. If we consider the geographical distribution of *C. gynocrates*, it seems as if the monœcious form is the most prevalent in the north, judging from the specimens we have examined, which were collected in Northern Labrador, Alaska and Greenland, where we found this species probably at its most northern limit, "Skarvefjæld," on the island Disco, above 69° N. lat., where it occurred only as monœcious.

In regard to *C. exilis*, this species represents a still more evolute stage, and occurs as diœcious or monœcious, mono- or plio-stachyous. A gynœcandrous spike is frequently met with in this species, besides that the female plant may possess several lateral spikes, from one to six, at the base of the terminal. *Carex Davalliana* exhibits a similar variation, possessing androgynous or gynœcandrous spikes besides purely staminate or pistillate, and, moreover, a few pistillate flowers may be found interspersed with staminate in the middle portion of the spike. Although the male plant is very abundant in Switzerland, Gaudin* states that the female is exceedingly rare. If we now examine the monœcious forms of *C. dioeca* and *C. parallela*, we find these as being much rarer than in the species mentioned above. *Carex dioeca* L. var. *isogyna* and *C. parallela* var. *androgyna* possess only from one to three pistillate flowers at the base of the otherwise staminate spike, but these forms are only known from a very few localities in Northern Europe. We have, thus, in the *Dioicæ* an analogous variation represented by all the species, but merely depending upon distribution of sexes, while in *C. exilis* the variation extends still further, the monostachyous inflorescence passing over into a plio-stachyous. The characterization formerly applied to these species "spica simplicissima androgynosa sive dioica" is actually applicable to each of these, besides that one possesses occasionally a "spica composita" (*C. exilis*).

* Gaudin, I., Flora Helvetica, vol. vi, 1830. p. 27.

In regard to the general habit of these species, *C. Davalliana* and *C. exilis* possess a cespitose rhizome, while in the others the rhizome is stoloniferous; in *C. Davalliana* var. *Sieberiana* Opiz, by Fiegert considered as a hybrid between *C. dioeca* and *C. Davalliana*, the so-called *C. Fiegertii* Vollm.,† the rhizome is not so densely cespitose and often bears short stolons. A very slender and stoloniferous rhizome is observable in both the diœcious and monœcious forms of *C. gynocrates*. The leaves are very narrow in all the species, and the culm is terete and hollow in *C. dioeca*, *C. gynocrates*, *C. Davalliana*, pentagonal in *C. parallela* and obtusely triangular in *C. exilis*. The utricle is usually thickest at the base and tapers gradually into a beak, the orifice of which is cut down on the dorsal face so as to form a slit, but on the ventral side the upper margin is almost entire or slightly emarginate. In *C. exilis*, however, the beak is bidentate with erect teeth. In the last mentioned species, the utricle is, furthermore, a little winged and the margins are very scabrous, especially above, in which character it differs from the other species of the *Dioicæ*. In *C. dioeca* and *C. exilis* the ventral face of utriculus is flat in contrast to the dorsal, which is distinctly convex; in the other species both faces are convex, and the ventral often prominently so in *C. gynocrates*. Nerves are quite distinct on the dorsal face of all the species, less so on the ventral, and are very faint in *C. dioeca* and *C. parallela*. The base of utriculus is thick and spongy, especially after fecundation has taken place.

Another peculiarity common to the *Dioicæ* is the change of direction of the utricle when the achenia are mature. While thus utriculus is erect in these species during anthesis, it gradually bends down later on and occupies a horizontal position in *C. gynocrates*, *C. Davalliana* and *C. exilis*, or it becomes merely spreading (suberect) as in *C. dioeca* and *C. parallela*.

The scale-like bracts (squamæ) which subtend the pistillate spikelets are persistent in these species, while they are deciduous in some of the other *Monostachyæ*, e. g., *C. pulicaris*, *C. nigricans* and *C. pyrenaica*, in which the utricles show a similar change of direction after fecundation has taken place.

By possessing several morphological peculiarities in common, the *Dioicæ* may, thus, be considered as naturally allied species. However, we do not feel satisfied with the arrangement of these species as simply representing a section of their own and separated from *Vigneæ* and *Carices genuinæ* only on account of their lesser decompound inflorescence and their frequent diœcism. It would seem more natural if these *Dioicæ* could

* Vollmann, Fr., Ein Beitrag zur Carex-Flora der Umgebung von Regensburg. (Denkschr. d. k. bot. Gesellsch. Regensburg, vol. vii; new series, vol. i, 1898.)

be arranged with some of the higher developed "greges," and the extreme forms of *C. exilis*, those which possess several lateral spikes at the base of the terminal, suggest some affinity with *C. echinata* Murr., as already observed by Tuckermann and Boott. In *C. echinata* and its allies the direction of utriculus undergoes the same change as we have described as characteristic of the *Dioicæ*, and, moreover, the structure itself of this little organ (utriculus) shows several analogies, which seem to indicate some affinity to exist between these species. We are, thus, more inclined to arrange the *Dioicæ* of Tuckermann (excluding *C. capitata*) under *Vigneæ* rather than under *Carices genuinæ*, and the reason is not so much because they are distigmatic, but on account of the structure of utriculus, which suggests affinities with *Vigneæ*, but not with the other *Carices*.

In regard to *C. echinata* Murr. a number of very diverse species (*C. loliacea*, *C. canescens*, etc.) have been considered as its nearest allies by writers of different periods, who have treated the genus. Nevertheless *C. sterilis* Willd.* is, beyond

* Having studied what Professor L. H. Bailey supposes to be "types" of various species of *Carex*, this author arrived at the conclusion that *C. echinata* Murr. from the Pacific slope appears to be the same as the European plant, but that the type does not occur in the Eastern United States. At that time (1889) Professor Bailey accepted *C. echinata* as an American species with some varieties, among which the var. *microstachys* Boeckl was considered identical with *C. sterilis* Willd and *C. scirpoides* Schk. on the strength of some specimens, preserved in the herbaria of Willdenow and Schkuhr. A few years later (1893) Prof. Bailey made still another disposition of the same species by eliminating *C. echinata* altogether from the North American flora, stating that Francis Boott many years ago "questioned if the American plant is the same as the European *C. echinata*." We are not aware that Boott made this statement in regard to this species in North America, but only so far as concerns specimens from "South of the British provinces" (Ill. genus *Carex*, vol. i, 56, 1858) which he could not satisfactorily refer to the European plant. While thus excluding *C. echinata* from this continent, Prof. Bailey adopts *C. sterilis* Willd. as a species and identical with *C. scirpoides* Schk. of which he claims to have seen the originals. Whether these specimens were the "original" or not, it must be borne in mind that the old botanists did not work with types, and in most cases, it is nothing but a mere guess whether this or that herbarium-sheet contains the specimen, or part of it, from which the original diagnosis was drawn. And it appears to us that this modern investigation of old specimens supposed to be types, arises from inability to faithfully comprehend the descriptions. If, for instance, the old specimens preserved of *C. sterilis* and *C. scirpoides* were "the types," and moreover, identically the same species," one would necessarily expect to find the diagnoses equally uniform; but this is not the case, at least not as these species were understood by Willdenow. Let us, therefore, compare the most salient points in the diagnoses of these three species, *C. sterilis*, *C. scirpoides* and *C. echinata* as described by Willdenow with the one by Prof. Bailey, who has adopted *C. sterilis* as identical with *C. scirpoides*, and formerly even with *C. echinata*.

Willdenow.	Inflorescence.	Utricle.	Squamæ.
<i>C. sterilis</i> .	Spicis dioicis sub- sens alternis ob- longis contiguis.	fruct. ovatis com- presso-triquetris- acuminatis, apice recurvis bicuspi- datis.	ovata acutæ capsulas sub- æquantes.

doubt, a close ally, and *C. elongata* L. and *C. læviculmis* Meins-haus. show so many points in common with *C. echinata*, that they may well be arranged in the same section; to these, we think, may be added *C. remota* L., but only as a “forma desciscens.” The central type of the section seems best illustrated by *C. echinata* Murr., the *C. stellulata* Good., from which we have derived the name “*astrostachyæ*” as being the most appropriate for this new section, while the other species may be classified as follows :

Carices (Vigneæ) astrostachyæ.

hebetatæ	{	<i>C. dioeca</i> L.
		<i>C. parallela</i> Læst.
		<i>C. gynocrates</i> Wormskj.
		<i>C. Davalliana</i> Sm.
centrales	{	<i>C. exilis</i> Dew.
		<i>C. echinata</i> Murr.
		<i>C. sterilis</i> Willd.
		<i>C. elongata</i> L.
desciscens.	{	<i>C. læviculmis</i> Meinshaus.
		<i>C. remota</i> L.

Further research will evidently prove that several other species may be referable to this section, but we have not at present been able to find any others in the very considerable material of the genus which we have studied. It is readily noticed from the above, that we have restricted the number of

Willdenow.	Inflorescence.	Utriculus.	Squamæ.
<i>C. echinata.</i>	Spica androgyna composita, spiculis subquaternis remotiusculis inferne masculis.	ovato-acuminatis bidentatis horizontalibus.	ovatis acutis
<i>C. scirpoides.</i>	Spica andr. comp, spiculis subquat. inferne masculis subapproximatis, ellipticis.	ovatis bidentatis compressis.	ellipticis obtusis.

Prof. Bailey :

<i>C. sterilis</i> Willd. incl. <i>C. scirpoides</i> Schk.	{	3 to 5 contiguous spikes of which the uppermost is usually conspicuously attenuated at base by the presence of staminate flowers.	thin and flat, conspicuously contract-d into a slender beak which is nearly or quite as long as the body.	-----

It is readily seen from the above, that Willdenow had some reason for distinguishing these plants from each other, and that the collective diagnosis, as presented by Prof. Bailey, is too vague to be considered.

allied species in a very considerable degree by omitting *C. canescens*, *C. loliacea*, *C. tenella*, *C. leporina* and several others, which, according to our opinion, do not seem to belong to this section, at least not when we consider the characters, drawn from inflorescence and utriculus. We have enumerated *Carex gynocrates* as a species distinct from *C. dioeca* L., and we have done so after a careful study of a large number of specimens from various regions, besides comparing these with the excellent diagnosis presented by Drejer in his "Revisio critica Caricun borealium." The habit of these two species is the same, but it appears as if the spikes, "squamæ and utriculi," of *C. gynocrates* are generally paler and of a more dull brown color than those of *C. dioeca*. Furthermore the utricles are merely spreading (subarrecti) in *C. dioeca*, but horizontal or sometimes almost reflexed in the other. Utricle is plano-convex and drawn out into a long, flat and scabrous beak in *C. dioeca*, while in *C. gynocrates* this organ is nearly gibbous (biconvex) and the beak is shorter in proportion to the body, terete and a little curved. The scales (squamæ) are obtuse in *C. dioeca*, but more or less acute in the latter species. These morphological characters we consider much more important than those taken from the distribution of the sexes, inasmuch as androgynous spikes are, also, known in *C. dioeca*, as mentioned in the preceding pages. It might seem, however, as if these characters, possessed by *C. gynocrates*, are not sufficient for distinguishing it as a species, and that it simply represents a geographical variety of *C. dioeca*, a suggestion that has been made by both Mr. C. B. Clarke and by Rev. G. Kükenthal "in litteris."

If we examine the central forms, *C. echinata* and *C. sterilis* show a structure of utriculus which reminds us very much of that of *C. exilis*, with the only difference that the base is much broader in the former two species; otherwise the margins are distinctly winged, the beak scabrous and bidentate. In *C. elongata* and *C. læviculmis* the body of utriculus is narrower and tapers more gradually into the beak, which is also bidentate in these species, but less rough or nearly glabrous, besides that the margins are not winged. When the achenes are mature we notice in these species (*formæ centrales*) the same change of direction in the utricule as described as characteristic of the *Dioicæ* (*formæ hebetatæ*), and especially so in *C. echinata*. In regard to *C. remota* this species possesses a utricule of somewhat different structure, since the beak is not pronounced, but bidentate and scabrous; the margins are narrowly but plainly winged, and the base is somewhat thick and spongy as in all the others; at maturity the utricles are spreading, and the species *C. remota* appears to us as inseparable

from the section, even if the structure of utricle leads us to consider it as a "forma desciscens."

In respect to the general habit the central forms and *C. remota* are all cespitose with long, narrow leaves and rather weak culms; the spikes are small and, the uppermost at least, gynæcandrous or purely pistillate; they are mostly contiguous but in *C. læviculmis* they are distant, and especially so in *C. remota*, in which, furthermore, the lower bracts, subtending the spikes, are developed into long leaves, more or less overtopping the inflorescence. The peculiar stellate appearance of the mature spikes is common to all and suggests the affinity with *C. exilis* and its allies among the formerly so-called *Dioicæ*. There are, however, among the other species of *Vignæ* several which possess similarly spreading or even horizontally directed utricles, but the shape of this organ, besides its internal structure, seems very distinct from what we have observed in the *Astrostachyæ*. The diagnosis of the section, derived from the central forms, is as follows:

Carices (Vignæ) astrostachyæ.

Spikes gynæcandrous or the lower ones purely pistillate, sessile. Bracts not sheathing, short and filiform. Utricles horizontally spreading at maturity, broad and spongy at the base, glabrous, nervose, tapering into a distinct beak with scabrous, winged margins and bidentate apex, the teeth erect; stigmas two. Mostly northern species with light-brown or greenish spikes. The lesser developed forms to be sought among the *Dioicæ*, of which *C. exilis*, especially, shows transition to *C. echinata*. *C. remota* may be considered as representing the limit of the section.

When considering the geographical distribution of these species, it appears as if only two are confined to this continent, *C. exilis* and *C. sterilis*, of which the first is a very local plant, only known from some localities in the northeastern section of this country, New Jersey, New Foundland and Eastern Canada; *C. læviculmis* is, also, quite rare, having been recorded from a few places in Kamtschatka, Alaska and Oregon, also from Idaho and Washington Territory, from where Mr. Kükenthal states (in litteris) that he has received some specimens; *C. gynocrates* is known from the west coast of Greenland and from a number of places on this continent especially in the northern and western sections, and also from the Rocky Mountains; it occurs, furthermore, in Alaska and extends from there to Kamtschatka and the Bajkal Mountains; *C. dioeca* and *C. parallela* are inhabitants of the northern countries of Europe and Asia, and the latter species is not infre-

quent in the Arctic region and the higher mountains of Norway; *C. Davalliana* is a more southern type distributed over Middle Europe and some parts of Asia, Altai for instance; *C. elongata* shows a corresponding distribution, but extends a little farther north, at least in Europe; *C. remota* accompanies *C. elongata*, but seems to be more frequent and is, moreover, known from Sikkim Himalaya, where it reaches an elevation of 12,000 feet;* it is, also, known from Japan. The widest geographical range is, however, exhibited by *C. echinata*, which is very abundant in Europe and Asia; besides it is, also, known from North America and New Zealand; *C. sterilis* has been reported only from this continent, from Canada to Carolina (fide Boott). While thus the dioecious *C. parallela* and *C. dioeca* appear to have their center of distribution farther north than any of the others, the monœcious *C. gynocrates*, although being much less frequent, exhibits a similar range in contrast to its dioecious form, which is more southern. *C. exilis* represents the most evolute stage of the "hebetatæ" and may be considered as a good illustration of the development of the section in this country with its herd of *C. echinata* and *C. sterilis* in a number of varieties, of which only the typical *C. echinata* is distributed in the old world. The nearest allies of *C. echinata* are, thus, to be sought in this country, where, moreover, *C. gynocrates* and *C. læviculmis* have their geographical center. *C. dioeca* and *C. parallela* are, no doubt, the oldest remnants of the section as this is preserved in recent time, and actually demonstrate a closer affinity to *C. exilis* than to *C. gynocrates* and *C. Davalliana*, even if *C. exilis* may be considered as younger than any of these. *C. elongata* and *C. remota* possess certain points in common with the others, and may represent the farthest developed types in the section. While thus, considered from a geographical viewpoint, the earlier types belong to the northern parts of the old world, the more modern forms are represented farther south, not only in Europe and Asia, but also in New Zealand and in this country. It might seem strange that the "formæ hebetatæ" of the section are so remote from each other as they really are: *C. dioeca* and *C. parallela* in Europe and Asia, *C. gynocrates* in this country, without being connected with each other by some circumpolar type; yet we must bear in mind that the development of the section and the migration of the species is not by any means to be fully explained by the present geographical range of a few old types, that are still in existence.

We have in the preceding pages given a brief account of the morphological characters of the *Astrostachyæ*, and we

* Clarke, C. B., *Cyperaceæ* in Hooker's Flora of British India, vol. vi, London, 1894, p. 699.

might append to these some observations upon the internal structure of the species in order to illustrate the section as completely as possible.

The root.

Having examined roots of a number of specimens from widely separated localities and of different age and development, we have, nevertheless, failed to detect any anatomical character of importance by which the "*formæ hebetatæ*" might be distinguished from each other or from their allies among the "*centrales*" and "*desciscentes*." Like most of the other *Carices* examined, the root possesses a hypoderm of a single layer inside the epidermis, and this tissue is thinwalled in all the species of *Astrostachyæ*. The cortex is differentiated into two zones, an outer and an inner, of which the former is distinctly thickwalled in contrast to the inner, which shows the usual tangential collapsing. The endodermis is more or less thickened, but as it seems constantly as an U-endodermis; it is very heavily thickened in *C. echinata*, less so in the other species. In *C. gynocrates* the endodermis showed only a very slight thickening of the inner cell-wall in specimens from arctic Greenland, while others from Canada, Alaska and Wyoming showed a very pronounced thickening of both the inner and radial cell-walls. The pericambium is usually thinwalled or moderately thickened as in *C. exilis*, *C. echinata*, *C. sterilis* and *C. laviculmis*; it was found to be interrupted by all the proto-hadrome vessels, without exception, in all the species of the *Astrostachyæ*. The leptome and hadrome is well developed, and the central portion of the root is occupied by conjunctive tissue, which is quite thickwalled in all the species, especially in *C. exilis*, *C. echinata* and *C. sterilis*.

In considering the development of the outer cortex, the endodermis and the conjunctive tissue, the roots of these species seem well supported in mechanical respect, and equally well in species from bogs or woodlands.

The rhizome.

The rhizome of the "*formæ hebetatæ*" is stoloniferous in *C. dioeca*, *C. gynocrates* and *C. parallela*, but cespitose in the other species. Epidermis is mostly thickwalled, and a hypoderm of a single stratum is noticeable inside the epidermis. The cortical parenchyma is, also here, differentiated into two zones, of which the outer is quite thickwalled. The endodermis shows the same manner of thickening as observed in the roots, and is especially thickwalled in *C. parallela* and *C. Davalliana*. The stereome occurs in *C. parallela* as a peripheral band of small isolated groups near epidermis, but is in the

other species only observable inside endodermis, where it forms a few strata around the mestome-bundles. The arrangement of the mestome-bundles is somewhat variable in these species; in *C. dioeca* and *C. gynocrates*, for instance, they form one very regular band, while two in *C. exilis*, three in *C. Davalliana*, and in *C. parallela* they seem scattered without order inside the endodermis; they occur mostly as collateral and bicollateral, perihadromatic, together, but in *C. gynocrates* we noticed only the collateral type in specimens from Greenland, Alaska and Canada, while in some rhizomes from Wyoming the mestome-bundles showed a tendency to become perihadromatic. Most of the mestome-bundles in *C. Davalliana* were observed to be bicollateral, while only a very few showed this structure in *C. exilis*. The pith occupies a very small portion of the central-cylinder in *C. parallela* and *C. Davalliana* and is solid in these species; in the others, on the contrary, the pith is larger and broken in the middle so as to form a wide central cavity.

The stem.

A triangular and solid stem is generally attributed to the *Cyperaceæ* in contrast to a cylindric and hollow culm in the *Gramineæ*. There are, however, many exceptions to this rule, and in both orders; we have, already, called attention to the outline of this organ in the "formæ hebetatæ" of *Astrostachyæ* being mostly cylindric and hollow inside. *Carex exilis* is the only species of these in which the stem is triangular, though merely obtusely; but if we examine the higher developed types we find the stem to be triangular in all the species with the exception of *C. echinata*, in which it is almost regularly hexagonal; the pith seems invariably broken down in these species, as we, also, observed in the lesser developed types. The epidermis is quite thickwalled in all the species and nearly glabrous, the development of prickly-like projections being very scant except in *C. elongata*. The cortical parenchyma consists of short palisades radiating towards the center of the stem in the "hebetatæ," also in *C. echinata*, *C. sterilis* and *C. elongata*, while in *C. læviculmis* and *C. remota* the bark is composed of polyedric cells and no distinct palisades; intercellular spaces are very distinct in all the species, and lacunes are present, one between each two mestome-bundles; thus the cortical parenchyma does not represent any very firm or solid tissue in these species, and is especially open in *C. elongata*. Stereome occurs as hypodermal on the leptome-side of the larger mestome-bundles, besides that it is, also, developed on the hadrome-side of these, where it borders on the pith; at the smaller mestome-bundles there is less stere-

ome, and, with the exception of *C. læviculmis* (fig. 1), this is here separated from the epidermis by strata of cortical parenchyma on the leptome-side. It may be said about the stereome in these species, that it is generally well developed and seems to be especially thickwalled in *C. læviculmis* and *C. remota*. In regard to the mestome-bundles, these are arranged in one peripheral band and represent larger, in transverse section oval, and smaller, which are nearly orbicular in outline; the parenchyma-sheath is thinwalled and the mestome-

FIG. 1. Transverse section of the stem of *Carex læviculmis* Meinshaus.

The cortex is painted black in the figure, lacunes are to be seen between the mestome-bundles, and the central portion of the pith is broken down into a wide cavity. $\times 75$.

sheath shows a distinct thickening of the inner cell-wall in all the species, and to the same extent. The mestome-bundles are thus of the same development as is usually observed in the genus, and we might state besides, that we found no trace of the inner chlorophyll-bearing sheath, which Haberlandt and Rikli detected in some of the other genera of the order.

The leaf.

This organ exhibits a much greater variation in these species than observed in the root, the rhizome and the stem. It is mostly hemicylindric in the "hebetatæ," at least in *C. dioeca*, *C. gynocrates* (fig. 2) and *C. exilis*, where this leaf-shape is characteristic of both the male and female plant, besides in monœcious specimens of *C. gynocrates*; in *C. parallela*, on the other hand, we noticed the leaf to be broader in the male than in the female plant, and in *C. Davalliana* the leaf is still broader and almost carinate. In the central forms as well as

in *C. remota* we find the leaves to be almost flat with a distinct keel as is characteristic of the majority of the higher developed *Vigneæ* and *Carices genuinæ*. In the "hebetatæ" the leaves are smooth and mostly glabrous, with the exception of *C. Davalliana*; in the others, "centrales and desciscentes," we find prickle-like projections to be quite abundant along the margins and the midrib, rendering the leaves more or less scabrous. Very characteristic in this respect is the leaf of

FIG. 2. *Carex gynocrates* Wormskj.; monoecious specimen from Wyoming; transverse section of leaf; mesophyll painted black; M.=midrib; E.=epidermis of upper face. $\times 120$.

C. læviculmis (fig. 4), of which both surfaces show the development of a number of obtuse papillæ. The cuticle is very distinct and smooth in all the species, and the epidermis shows relatively the same modifications as seen in most of the other *Carices*: the cells being generally larger on the upper face outside the mesophyll than on the lower. Bulliform cells are well developed as a single group above the midrib in all the central forms and in *C. remota*, besides that an additional group of these may be seen in *C. remota* (fig. 3) above one of the lateral mestome-bundles. The "hebetatæ" are mostly destitute of these bulliform cells, and it is only in the broader leaves of *C. parallela* (male specimens) and of *C. Davalliana* that some of the epidermal cells have attained such development, although in a much smaller degree than in the "formæ centrales." If we consider epidermis of the lower surface and outside the stereome, we notice the cells to be of a somewhat different size and shape than in the surrounding stomatiferous strata; the radial walls are less undulate and the cells often shorter and narrower than those adjoining. In *C. parallela* and in *C. exilis*, for instance, these epidermal cells outside the stereome are shorter than the others; in *C. Davalliana*, *C. sterilis*, *C. remota* and *C. læviculmis* they are much narrower.

but not shorter, while in *C. echinata* and *C. elongata* the same cells are not only much narrower, but also shorter than the others. The stomata are restricted to the lower surface of the leaf-blade outside the mesophyll; they are free in all species, even in *C. læviculmis* with its numerous papillæ, and the guard-cells are level epidermis in most of the species, with the exception of *C. parallela*, *C. sterilis*, *C. elongata* and *C. læviculmis*, in which they are slightly projecting.

FIG. 3. *Carex remota* L.; fig. 4, *C. læviculmis* Meinshaus.; fig. 5, *C. echinata* Murr. Transverse sections of leaves; M.=midrib; E.=epidermis of upper face, developed in bulliform cells above the midrib; mesophyll painted black. $\times 120$.

The mesophyll consists mostly of a homogeneous tissue of short palisades vertical on the leaf-blade or radiating towards the center of the mestome-bundles as we observed in *C. Davalliana*; in *C. echinata*, *C. sterilis* and *C. læviculmis* the palisades are very short and often too irregular in shape to be called "palisades." In *C. remota* the mesophyll is differentiated into a ventral palisade- and dorsal pneumatic-tissue, this species being, thus, the only one of the section that possesses a typical bifacial leaf-blade. The cells of the mesophyll are

only occasionally closely packed in these species, and intercellular spaces are often not only numerous, but also quite wide; moreover, lacunes are observable in this tissue and are very broad in all the species, in the "hebetatæ," the "centrales" and in *C. remota* (fig. 3).

The stereome is thickwalled and occurs as hypodermal groups accompanying the mestome-bundles, or separated from the epidermis by the mesophyll, or as isolated groups in the leaf-margins. In the "hebetatæ" there is only hypodermal stereome on the leptome-side of the midrib, and also in the margins of the blade, while the smaller mestome-bundles are so deeply imbedded in the mesophyll that the stereome which supports these does not extend to epidermis. In the higher developed types ("centrales," etc.) there is usually hypodermal stereome above and below the larger mestome-bundles, especially well developed in *C. læviculmis* (fig. 4), where it is hypodermal on the lower surface at all the mestome-bundles, even at the smallest ones. Considering the mestome-bundles, these constitute only a single band in all the species, and are surrounded by a thinwalled parenchyma-sheath and a mestome-sheath, of which the inner wall is moderately thickened; the leptome and the hadrome exhibit the usual structure, and the bundles occur as oval (in transverse section) or as nearly orbicular.

The leaves of the *Astrostachyæ* exhibit certain modifications not only in respect to the outline of the leaf, but also in the development of epidermis as bulliform cells or as papillæ (*C. læviculmis*); moreover, the bifacial leaf of *C. remota* seems very exceptional, when we compare it with the nearly isolateral leaves of the other species. The structure of *C. exilis*, although this seems to represent the highest developed type of the "hebetatæ," at least morphologically, is actually identical with that of the lower forms: *C. dioeca* and *C. gynocrates*, while in both *C. Davalliana* and certain specimens of *C. parallela* the leaf shows some resemblance to that of the "centrales." A small leaf-surface is characteristic of the "hebetatæ" in contrast to the other types, in spite of the fact that several of these occupy the same kind of soil and live under the same climatological conditions; even in *C. gynocrates* and *C. parallela* from high northern latitudes the structure of such specimens agree very well with that of others from more southern latitudes or from subalpine regions.

When we finally compare the "hebetatæ" of *Astrostachyæ* with those of some other sections, we do not observe the leaf-blade uniformly narrow in all of these. We have described the relatively broad leaf of *C. lejocarpa* C. A. Mey. in contrast to that of *C. circinata*, both of the *Stenocarpæ*; further-

more in *C. pulicaris* the leaf is very narrow as in *C. pyrenaica*, but broad in *C. nigricans*, their nearest ally; a relatively broad blade is noticeable in the "hebetatæ" of *Sphæridiophoræ*, e. g., *C. scirpoidea* and *C. oreocharis*, and in *Lamprochilænæ*: *C. rupestris* and *C. obtusata*.

Utriculus.

If it were not that this organ possesses such excellent morphological characters, by which our species of *Astrostachyæ* may be readily distinguished from each other, one would naturally suppose that the number of species were much smaller by examining the anatomical structure. The fact is, that when we examine the structure of utricle, we do not find any points of importance by which these species may be distinguished anatomically. The differences are so slight and seem merely to depend upon a relative broader or narrower mesophyll and a larger or smaller number of isolated stereome-bundles, that none of these may be considered as being neither constant or of sufficient importance to be used as anatomical characters. Common to all is the broad mesophyll at the base of utricle, and the presence of only two mestome-bundles; furthermore, the stereome is equally well developed in these species, not only as accompanying the mestome-bundles, but also by occurring as isolated, hypodermal groups between these. The number of these isolated stereome-bundles varies from 15 to 36, the strongest mechanical structure being possessed by *C. elongata*, *C. dioeca* and *C. gynocrates*. The outer epidermis is thickwalled in most of the species excepting *C. remota* and *C. læviculmis*.

When we finally compare the morphological and anatomical characters with each other, it seems as if our species may be naturally classified as representing a section of *Vignæ*. The transition from the "hebetatæ" to the "centrales" seems very gradual and as we have shown in the preceding, none of these species possess characters that stand as isolated among the others, neither in morphological or anatomical respects. If our disposition of these species, classified as "*Astrostachyæ*," may prove to be correct or at least quite natural, our observations have simply confirmed a suggestion, already proposed by both Tuckermann and Boott, whose remarks upon the affinities have been presented in the introduction to this paper.

Brookland, D. C., July, 1900.