Mitt. Bot. Staatssamml. München | 10 | 577—585 | 1. 12. 1971

SOME RELATIONSHIPS IN SCIRPEAE BEARING ON THE DELINEATION OF GENERA

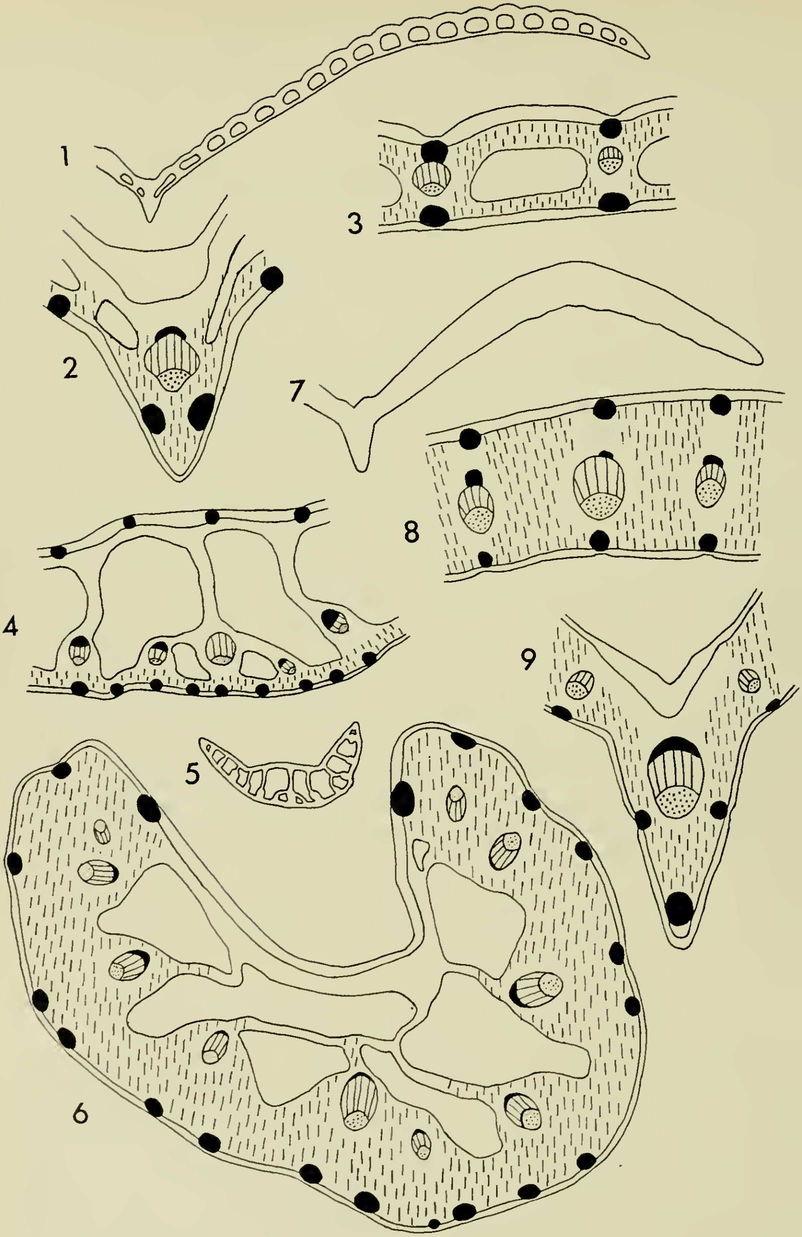
ALFRED E. SCHUYLER

When one considers the Cyperaceae on a world-wide scale, particularly with regard to Africa and South America, it is apparent that much taxonomic research is ahead of us. Because of the botanically unexplored nature of these two continents, as well as their environmental diversity, I suspect there may be hundreds of species yet undescribed by botanists. Even with this challenge of discovery, the Cyperaceae have other offerings for the systematic botanist, namely: what are the characteristics of these plants? The reduced structure of flowers has caused us to rely on inflorescence structure to a large extent for important characteristics. In many cases, such structure is very useful, but, for all practical purposes, we have barely begun the search for taxonomically significant characteristics in this large, and somewhat neglected, family.

My work in the Cyperaceae has dealt with a portion of the genus *Scirpus.* More than one taxonomist has pointed out that this genus is an assemblage of unrelated plants, and this is something I take for granted. We now need to find characteristics which demonstrate the discontinuity and relationships that exist among groups of species in *Scirpus.* In the following discussion I hope to contribute some preliminary bases for taxonomically delineating some of the diverse groups of species in *Scirpus.* For the present, however, I urge some restraint on the part of taxonomists at the genus level until a thorough systematic analysis of microscopic characteristics has been conducted.

SCIRPUS SYLVATICUS AND RELATED SPECIES

This group of about 32 species has its largest concentration in eastern North America and eastern Asia. The plants grow primarily in swamps and marshes which are wet in the spring but gradually become drier during the summer. Plants with flowering culms may grow in wet substrates, but the culms are not submerged or partially submerged in water. In this respect they are not true aquatics. Culm leaves are well-developed and have keeled, broadly V-shaped, blades in transverse section (as in *S. georgianus,* fig. 1). Chlorenchyma is more developed on the adaxial side than on the abaxial side


1
3
2
7
8
4
9
5
6

of the blade (fig. 3), and stomates are mostly restricted to the abaxial epidermis. Inflorescences usually are much-branched and contain numerous spikelets. The styles are delicate and have rounded protrusions around them (as in *S. lineatus,* fig. 17). Achenes are mostly less than 1,5 mm long and have comparatively thin, delicate pericarps. Achene epidermal cells usually have wavy inner cell walls, a convex or conical internal body with one nodular peak, and ridge-like buttresses between the lateral cell walls and the body (as in *S. microcarpus,* figs. 20 & 21). These latter characteristics, recently observed with a scanning electron microscope (SCHUYLER, 1971), help confirm that these species compose a natural group.

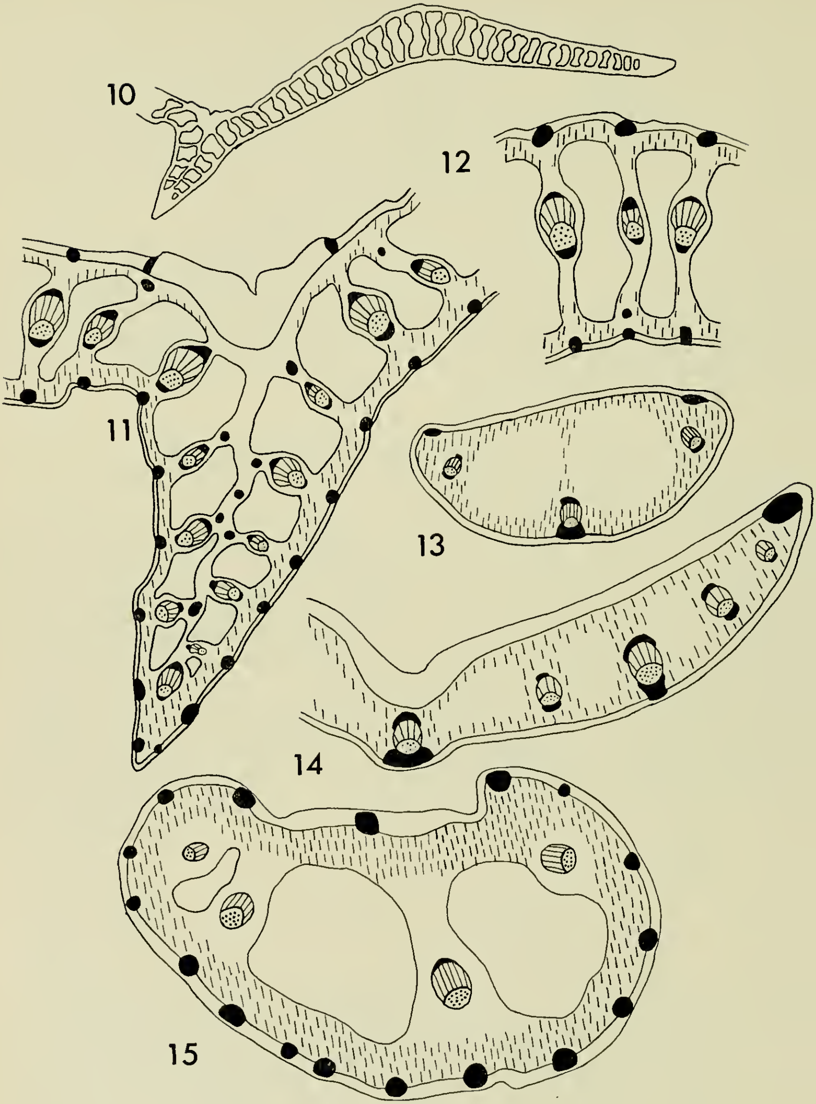
The above characteristics, and others, separate this group of species from most other species in *Scirpus.* Some species of *Eriophorum,* particularly *E. crinigerum* and *E. japonicum,* bear a close resemblance to species in the *Scirpus sylvaticus* group. However, these two species are separable from the *S. sylvaticus* group on the basis of their coarser styles (as in *E. crinigerum,* fig. 18) and larger achenes.

SCIRPUS LACUSTRIS AND RELATED SPECIES

This group is widely distributed around the world, and numerous species, many undescribed, grow in Africa. The plants differ from those of the previous group by often growing in water. Flowering culms can be initiated under water and often protrude above the water surface at maturity. Often the leaves are confined to basal portions of the culm, and the blades are only short projections from the sheaths. Leaf blades are variable in transverse section, but, most often, they are crescentform in outline and have chlorenchyma only below the air cavities (as in *S. heterochaetus,* figs, 4, 5, and *S. rhodesicus* fig. 6). Thin diaphragms, as described for *S. validus* by SNOW (1914), frequently develop across air cavities and possibly have an important role with respect to adaptation to an aquatic environment. Generally, the

---

Figures 1—9. Transverse sections of leaf blades showing epidermis, chlorenchyma (short vertical lines), sclerenchyma (solid black), vascular bundles with xylem (lined) and phloem (stippled), and air cavities (empty space separated from other tissue). 1. Portion of blade including midrib and one margin of *S. georgianus.* 2. Midrib of *S. georgianus.* 3. Portion outside midrib of *S. georgianus.* 4. Mid-portion of blade of *S. heterochaetus.* 5. Entire blade of *S. heterochaetus.* 6. Entire blade of *S. rhodesicus.* 7. Portion of blade including midrib and one margin of *S. robustus.* 8. Portion outside midrib of *S. robustus.* 9. Midrib of *S. robustus.*


10
11
12
13
14
15

inflorescences are relatively compact and subtended by involucral bracts which appear to be continuations of the culms. The styles are strap-like (as in *S. heterochaetus*, fig. 19) and lack the pronounced protrusions which occur on styles of species in the previous group. Achenes have comparatively hard walls and are dark brown to black at maturity. Some species have vertically elongate achene epidermal cells with little internal differentiation of structure (as in *S. smithii*, fig. 22) while others have much shorter cells and much more internal differentiation (as in *S. tabernaemontanii*, fig. 23). Whether or not such characteristics will be useful in delineating groups of species (i. e., sections, subgenera, or genera) remains to be demonstrated.

Chromosome numbers are particularly interesting in the Cyperaceae because they vary so much among species, and, occasionally, within species. This variation gives botanists more taxonomic information as long as there is a correlation between chromosome number and other characteristics. Chromosome numbers help verify relationships and determine polyploid trends among species, and thus contribute to overall knowledge bearing on the delineation of genera. Among one group of aquatic species with comparatively open inflorescences — *S. acutus, S. heterochaetus, S. lacustris, S. tabernaemontanii, S. triqueter*, and *S. validus* — haploid numbers of 18—21 have been determined by various authors (Hicks, 1928; Otzen, 1962; and Smith, 1969). A large unit, possibly resulting from fusion of chromosomes, has been observed in *S. heterochaetus* (fig. 24), *S. acutus* (Smith, 1969), and plants from Japan resembling *S. lacustris* (Tanaka, 1938). The taxonomic implications of this large unit remain to be clarified but it certainly is evidence of a close relationship among these species. In closely related species with comparatively compact inflorescences — *S. americanus, S. deltarum*, and *S. olneyi* — haploid numbers of 38 and 39 have been determined (Hicks, 1928; Otzen, 1962; and Schuyler, 1970). Whether or not polyploidy is involved here is something that may be known after more cytological investigation.

Some plants with well-developed leaves, occasionally treated generically as *Bulboschoenus* (Komarov, 1935), are closely related to other aquatic

---

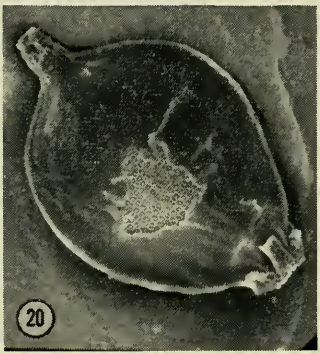
Figures 10—15. Transverse sections of leaf blades showing epidermis, chlorenchyma (short vertical lines), sclerenchyma (solid black), vascular bundles with xylem (lined) and phloem (stippled), and air cavities (empty space separated from other tissue). 10. Portion of blade including midrib and one margin of *S. grossus*. 11. Midrib of *S. grossus*. 12. Portion outside midrib of *S. grossus*. 13. Entire blade of *S. cespitosus*. 14. Portion of blade including midrib and one margin of *E. alpinum*. 15. Entire blade of *S. cernuus*.

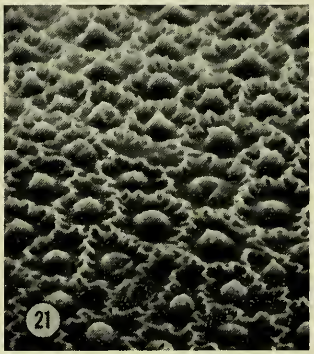

⑯

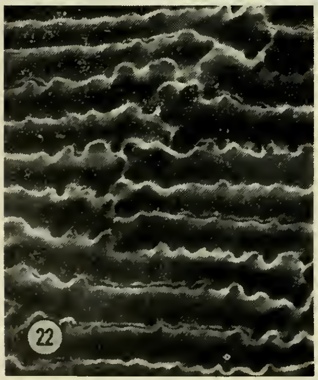

⑰


⑱

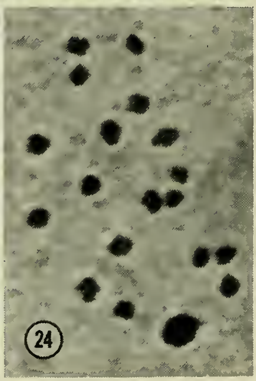

⑲


⑳


㉑


㉒


㉓


㉔

species of *Scirpus* such as *S. lacustris* on the basis of inflorescence and floral morphology. The leaves of plants referred to *Bulboschoenus* are distinctive because the chlorenchyma is about equally developed on the adaxial and abaxial side of the leaf blade (as in *S. robustus*, fig. 8). Furthermore, stomates are present in about equal abundance in the adaxial and abaxial epidermis. This type of leaf structure is also found in *S. grossus* (fig. 12), a distinctive Asiatic species whose relationship with other species of *Scirpus* needs study. Evidence of homology between these well-developed leaf blades and the more reduced leaf blades of other aquatic species of *Scirpus* is provided by the somewhat intermediate leaf blade of *S. americanus* (fig. 16). Near the margin of the blade of this species, the chlorenchyma is equally developed adaxially and abaxially, and stomates are present in the adaxial and abaxial epidermis. One possibility this suggests is that the well-developed leaf blades of species such as *S. robustus* may represent an elaboration of the margin of blades similar to those of *S. americanus*. If such is the case, the broad leaf blades of species referred to *Bulboschoenus* are not as distinctive as they first appear, but, instead, are modifications of the reduced leaf blades characteristic of most other aquatic species of *Scirpus*.

SCIRPUS SECT. BAEOTHRYON

Plants referred to this section (KOYAMA, 1958, excluding ser. *Anthelophorum*) have an inflorescence consisting of a single spikelet subtended by a short erect involucral bract. This group does not appear to be closely related to the aquatic species previously discussed on the basis of floral and leaf morphology. Styles are not strap-like and the leaf blades have sclerenchyma girders associated with at least some of the vascular bundles.

Of interest here are the plants originally described as *Eriophorum alpinum* L. In recent works (FERNALD, 1950), these plants are usually associated

---

Fig. 16. Transverse section of leaf blade margin of *S. americanus*.
Fig. 17. Style tip of *S. lineatus*.
Fig. 18. Style tip of *E. crinigerum*.
Fig. 19. Style tip of *S. heterochaetus*.
Fig. 20. Achene of *S. microcarpus* showing outer walls of epidermal cells partially removed.
Fig. 21. Achene epidermal cells of *S. microcarpus* with outer walls removed.
Fig. 22. Achene epidermal cells of *S. smithii* with outer walls removed.
Fig. 23. Achene epidermal cells of *S. tabernaemontanii* with outer walls removed.
Fig. 24. Meiotic chromosomes, metaphase I, of *S. heterochaetus* (New York: Washington Co., SCHYLER 3988, Ph).

with species of *Scirpus* in sect. *Baeothryon*, such as *S. cespitosus*, and given the name *Scirpus hudsonianus*. However, there are important differences between *E. alpinum* and species of sect. *Baeothryon*. Achene epidermal cells of *E. alpinum* have broad internal platforms with more than one body and resemble some species of *Eriophorum* in this respect (Schuyler, 1971). The structure of such cells in species of sect. *Baeothryon* varies remarkably among species but does not resemble that of *E. alpinum*. The chromosome number reported for *E. alpinum* also indicates a closer relationship to species of *Eriophorum*. Many species of *Eriophorum* have 58 somatic chromosomes which is also the number reported for *E. alpinum* (Löve & Ritchie, 1966). In sect. *Baeothryon*, 104 somatic chromosomes have been reported for *S. cespitosus* (Löve & Löve, 1966; Scheerer, 1940) and I have observed 42 meiotic units in *S. clintonii* (New York: Warren Co., Howard, PH) and about 46 in *S. verecundus* (Pennsylvania: Berks Co., Schuyler 3835, PH).

Leaf blade anatomy indicates that *Scirpus* sect. *Baeothryon* is an unnatural group. Crescentform blades with abaxial girders and lacking bulliform cells have been observed in *S. cespitosus* (fig. 13), *S. clementis*, and *S. rollandii*. In contrast, the V-shaped blades of *S. clintonii* and *S. verecundus* have adaxial and abaxial girders and bulliform cells. The blade of *E. alpinum* (fig. 14) bears a close resemblance to these latter species except that it has only abaxial girders.

SCIRPUS SECT. ISOLEPIS

These small plants have reduced structural features and it is difficult to make statements about their relationships within sect. *Isolepis* (as delineated by Koyama, 1958) and to other groups (such as sect. *Eleogiton*) at the present time. Embryo structure clearly distinguishes them from groups previously discussed here (van der Veken, 1965) and also indicates a close relationship among species within sect. *Isolepis*. Leaf blades have been examined in *S. cernuus* (fig. 15), *S. inundatus*, *S. koilolepis*, and *S. setaceus*, and have the same basic structure. In contrast to embryo and leaf blade structure, however, that of achene epidermal cells is remarkably diverse among species in this group (Schuyler, 1971). The horizontally elongated cells of *S. setaceus*, which lack apparent internal structure, are strikingly different from those of *S. koilolepis* which have more equal dimensions and pronounced internal conical bodies with nodular peaks. Further study of African species in this group should determine if other characteristics are correlated with such diversity.

CONCLUDING REMARKS

In conclusion, it seems to me that we have much to do before generic boundaries can be properly made among species of *Scirpus* and related genera. Not only do we have to deal with undescribed or poorly known taxa from Africa, but also we need to systematically evaluate microscopic characteristics of all taxa, including those described by LINNAEUS. As far as the African flora is concerned, I think it is best to follow an established treatment of genera until we know more about characteristics of groups on a world-wide scale.

Acknowledgements. Harold Howard, Stanley Smith, and Hans Wilkens were helpful in obtaining specimens in the field; John Braxton prepared leaf blade sections for microscopic examination; Joan Apfelbaum, Florence Givens, and Stan Luszcz helped with the use of the scanning electron microscope; Barbara Jones typed the manuscript; and Mary A. Garback did library reference work. Grant number 5435 of the Penrose Fund of the American Philosophical Society provided funds for renting use of the scanning electron microscope at the Franklin Institute, Philadelphia.

LITERATURE CITED

FERNALD, M. L. Gray's Manual of Botany. 8th ed. American Book Co., New York. lxiv + 1632 pp. (1950).

HICKS, G. C. Chromosome Studies in the Cyperaceae, with Special Reference to *Scirpus*. Bot. Gaz. 86: 295—317 (1928).

KOMAROV, V. L. (ed.). Flora of the U.S.S.R., Vol. III. Israel Program for Scientific Translations Ltd., Jerusalem. xxiv + 512 pp. (1964).

KOYAMA, T. Taxonomic Study of the Genus *Scirpus* LINNÉ. Jour. Fac. Sci. Tok. Bot. 7: 271—366 (1958).

LÖVE, A. & D. Cytotaxonomy of the Alpine Vascular Plants of Mount Washington. Univ. Col. Stud. Biol. No. 24: 1—74 (1966).

LÖVE, A. & J. C. RITCHIE. Chromosome Numbers from Central Northern Canada. Canad. Jour. Bot. 44: 429—439 (1966).

OTZEN, D. Chromosome Studies in the Genus *Scirpus* L., Section *Schoenoplectus* BENTH. et HOOK., in the Netherlands. Acta Bot. Neerl. 11: 37—46 (1962).

SCHEERER, H. Chromosomenzahlen aus der schleswig-holsteinischen Flora, II. Planta 30: 716—725 (1940).

SCHUYLER, A. E. A New North American Aquatic Bulrush (Cyperaceae: *Scirpus*). Not. Nat. No. 427: 1—4 (1970).

— — Scanning Electron Microscopy of Achene Epidermis in Species of *Scirpus* (Cyperaceae) and Related Genera. Proc. Acad. Nat. Sci. Phila. 123: 29—52 (1971).

SMITH, S. G. Natural Hybridization in the *Scirpus lacustris* Complex in the North Central United States *in* Current Topics in Plant Science (J. E. GUNCKEL, ed.) 175—200. Academic Press, New York (1969).

SNOW, L. M. Contributions to the Knowledge of the Diaphragms of Water Plants, I. *Scirpus validus*. Bot. Gaz. 58: 495—517 (1914).

TANAKA, N. Chromosome Studies in the Cyperaceae, II. *Scirpus lacustris* L. Cytologia 8: 515—520 (1938).

VAN DER VEKEN, P. Contribution à l'embryographie systématique des Cyperaceae — Cyperoideae. Bull. Jard. Bot. Bruxelles 35: 285—354 (1965).

ZOBODAT - www.zobodat.at

Zeitschrift/Journal: Mitteilungen der Botanischen Staatssammlung München

Jahr/Year: 1971

Band/Volume: 10

Autor(en)/Author(s): Schuyler Alfred E.

Artikel/Article: Some relationships in scirpeae bearing on the delineation of genera 577-585