

SYSTEMATIC INTERRELATIONSHIPS AMONG SCLERIEAE, LAGENOCARPEAE AND MAPANIEAE (CYPERACEAE)*

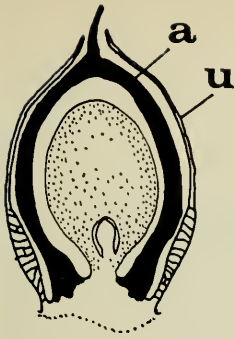
TETSUO KOYAMA

INTRODUCTORY REMARKS

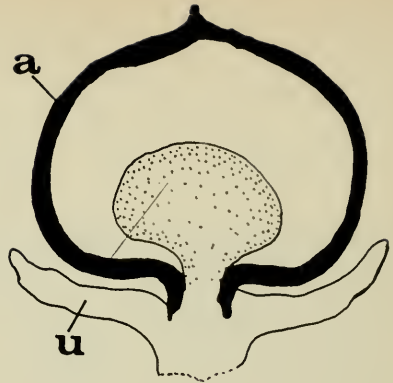
In 1969 I proposed to unite the three tribes — Sclerieae, Lagenocarpeae and Mapanieae — to incorporate a natural group, Mapanioideae. This concept deviates from any previously proposed placement of the three tribes within the Cyperaceae, for up till now the three tribes in discussion have been remotely separated under different subfamilies. In traditional classification systems, normal practices have been to place the tribes Lagenocarpeae and Sclerieae in the neighborhood of Cariceae, while the tribe Mapanieae was included in the Scirpeae. The subfamily Mapanioideae that I recognize is characterized by the peculiar compound fructifications, by which it differs from the other subfamilies of the Cyperaceae possessing the fruits of a true simple achene. The conspicuously cymose partial inflorescences also technically separate Mapanioideae from the remainder subfamilies, in which no cymose structure of partial inflorescences can be discernible due to the extreme reduction in inflorescences. The purpose of the present paper is to discuss the systematic interrelationships among the three tribes of Mapanioideae with a special emphasis on the phylogenetic significance of the characters of cymose partial inflorescences and the compound fructifications.

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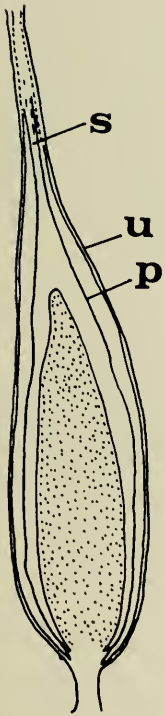
Figs. 1—5. Longitudinal sections of the compound fructifications. 1. *Calyptrocarya bicolor*; 2. *Scleria arundinacea*; 3. *Afrotrilepis pilosa*; 4. *Everardia disticha*; 4. *Lagenocarpus stellatus*. a, Achene; p, Pericarp; s, Style; u, Utricle. Sclerenchymatous portions in solid black. Dotted areas indicate seeds.



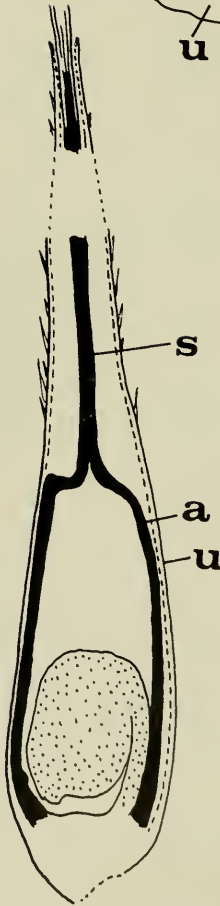
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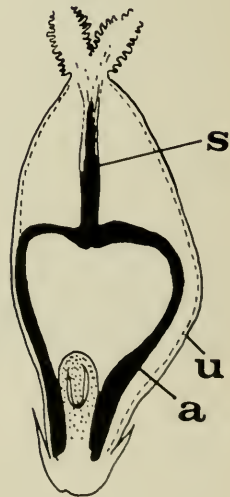
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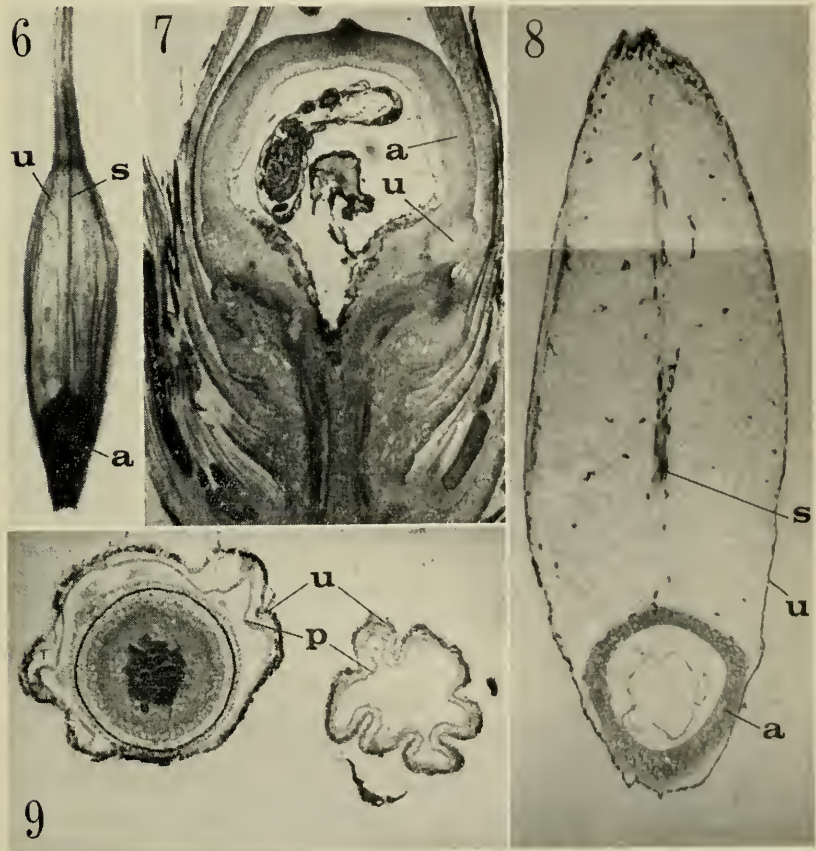
1. MORPHOLOGICAL CHARACTERS THAT DESERVE SPECIAL MENTION

Fruiting structures

The compound fruiting structures of Mapanioideae, described by KOYAMA and MAGUIRE (1965) as fructifications, have a great deal of diagnostic value. The existence of a utricle as a component of such compound fructifications in Lagenocarpeae was first found by NEES VON ESENBECK, who in 1842 described the fructifications in a Brazilian genus, *Trilepis*, as a "perigynium" (utricle). More recently, NELMES (1953) correctly interpreted that the African genus *Coleochloa* has a "Female flower surrounded by a trigonous, sac-like, membranous utricle from the apex of which the 3 stigmas are only just exerted, the style being situated in the upper beak-like portion of the utricle..." Figures 3 and 9 show the corresponding structure of the fructification seen in *Afrotilepis pilosa*, where the utricle (u) is a membranous sac loosely enveloping a true fruit. The space between the utricle and the pericarp (p) is partly filled with a scanty parenchymatous tissue making an imperfect adnation between the two organs. The pericarp of thin membrane is free from the terete seed, and its upper part gradually converges to a very slender style surmounting the beak-like portion of the utricle. The fructification in the African woody genus *Microdracooides* follows the same pattern as in *Coleochloa*. In the South American genus *Trilepis* the fructification shows essentially the same arrangement of organs as in the African genera mentioned above, but the contained fruit is a true achene with a sclerenchymatous pericarp. The striking membranous pericarp is seen in all the African genera of Lagenocarpeae, while in the American genera of the tribe the pericarp is sclerenchymatous. Because of its membranous pericarp *Afrotilepis* is more closely related to *Coleochloa* than to *Trilepis* though *Afrotilepis pilosa* was attributed by GILLY (1943) to *Trilepis*.

In the fructifications of the rest of the Lagenocarpeous genera, which are all South American, the utricles cannot be readily recognizable since the utricles are so completely adnated to the achene pericarp that no superficial distinction can be made between the two organs (Figs. 5 & 8). KOYAMA and MAGUIRE (1965) made a detailed anatomical investigation on the fructifications of this kind. The fructifications of *Cephalocarpus*, *Everardia* and *Lagenocarpus* are divided into two parts, the lower part, body, and the upper part, beak. In the body the wall of the fructification consists of two layers, i. e., the epidermal outer layer (utricle) and the sclerenchymatous inner layer (achene pericarp). In the three genera mentioned above all the specimens so far examined consistently showed that the sclerenchymatous achene pericarp, which occupies the entire space inside the utricle, is abruptly converging at the base of the fructification beak, and in the beak it continues as a surmounted lignified style until its branches are exerted beyond the beak apex as stigmas. In the beak a parenchymatic tissue fills the space between the style and

the wall of the utricle. The *Lagenocarpus* — type pericarp, by itself, is structurally quite similar to those of ordinary cyperaceous achenes such as those mentioned by MAREK (1958). The homology between the sclerenchymatous pericarp in the *Lagenocarpus*-type fructification and the membranous one of the *Coleochloa*-type is obvious because of the apparent position of the pericarp within each organization.



Figs. 6—9. Compound fructifications in Mapanioideae. 6. Young fructification of *Mapania pycnocephala* at low magnification; 7. Longitudinal section of the apical part of a cymose partial inflorescence in *Becquerelia cymosa* showing young fructification and staminate side branches; 8. Longitudinal section of mature fructification in *Hypolytrum nudum*; 9. Transverse sections of fructification in *Afrotrilepis pilosa* at the seed-bearing body (left) and the beak (right). a, Achene; p, Pericarp; s, Style; u, Utricle.

According to my anatomical investigations (KOYAMA 1970), the fruiting structures in the Mapanieae fall under the same morphological category as those of the *Lagenocarpus*-type. The longitudinal section of a fructification of *Hypolytrum nudum* is shown in Fig. 8 as a good example. A broadly ovate achene, marked (a) in the figure, is situated at the bottom of a sac-like utricle (u). A slender lignified style (s) extends through the large utricle and exposes its bi-cleft portion, stigmas, beyond the apex of the utricle. The ample space inside the utricle is filled with a homogeneous parenchymatous tissue. The fructification in Mapanieae does not differ morphologically from that of the *Lagenocarpus*-type, but the parenchymatous filling tissue in the former is generally more intensive than in the latter.

In most genera of the Sclerieae the utricles are easily recognized (KOYAMA 1965). In South American *Calyptrocarya* the utricle is a homogeneous ovate achene, marked (a) in the figure, is situated at the bottom of a sac-like hyaline sac tightly surrounding a bony achene, and is open at the apex part of the utricle forms a white spongy thickening consisting of 1- and in part 2-layered parenchymatous cells. An abscission layer is seen immediately below the point of attachment of the utricle bordering the receptacle from the apex of rhachilla. In *Scleria*, *Diplacrum* and *Becquerelia* the utricles are much reduced in height becoming cup-like and exposing the upper part of the achene above them. Figure 2 shows a longitudinal section of a fructification of *Scleria arundinacea*. Below the achene marked (a) is a cup-like utricle (u), which consists of parenchymatous tissue. The fructification is abscised immediately below the utricle and above the dilated apex of rhachilla, demonstrating that the utricle belongs to the fructification. The fructification in South American *Becquerelia cymosa* (Fig. 7) structurally very well matches with that of *Scleria arundinacea*, but here the spongy utricle (u) is adnated to the achene (a) nearly for its entire length. Again a distinct abscission layer is seen below the utricle. When the *Scleria*-type utricle is reduced a great deal it remains only as the spongy swollen base of the achene as shown in the fructification of South American *Bisboeckelera* as well as in *Diplacrum*.

Partial Inflorescences

Results of a series of anatomical investigations made on the floral parts of the Cyperaceae (KOYAMA 1965, 1967, 1970) demonstrate that in the tribes Mapanieae, Sclerieae and Lagenocarpeae the fruit-bearing partial inflorescences, which have hitherto been termed as spikelets, are determinate forming much reduced cymose inflorescences. Hence it is proposed that the descriptive term, cymelet or cymule, should be applied to the ultimate fruit-bearing units in the inflorescences of the Mapanioideae.

The cymelet in the tribe Mapanieae has a simple short axis, which is terminated by a pistillate flower of a single pistil. At the base of the axis is always a pair of prophylls, each bearing an axillary monandrous staminate

flower. Small glumes (usually termed as "squamellae") of varying number are alternately borne on the axis between the basal prophylls and the terminal pistillate flower. These squamellae as a rule bear an axillary monandrous staminate flower. Variations in the number of the "in-between" staminate flowers and their subtending squamellae show a series of reduction in the cymelets of Mapanieae. Tropical Asian *Scirpodendron* has the cymelets bearing a number of (9 to 12) "in-between" staminate flowers. The cymelets in *Mapania* are composed of 4 to 6 squamellae, the upper few of which may become empty due to the abortion of their staminate flowers. The cymelets in *Hypolytrum* show an ultimate status in the reduction series in the cymelets in Mapanieae, having no squamellae between the pistillate flower and the basal prophylls.

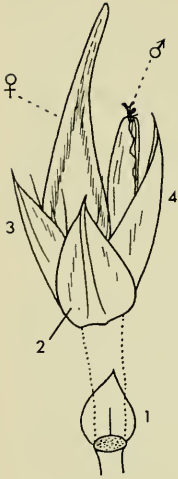
Anatomical investigations on the partial inflorescences in Sclerieae (KOYAMA 1970) substantiated the interpretation of MATTFELD (1935) that "die sogenannten 'androgynen' Ährchen von *Scleria* sind (vielfach in Schraubel übergehende) Fächer aus weiblicher Priman- und männlichen Folgeblüten." In the cymose partial inflorescences of Sclerieae the primary axis is terminated by a single terminal fructification and bears a prophyll at the base. Several glumes are borne on the primary axis between the fructification and the prophyll. When the partial inflorescences are branched, one to few of the glumes bear a small axillary side branch bearing staminate flowers. A much reduced prophyll is present at the base of the staminate branch demonstrating the true lateral position of the branch. Based on which glumes bear the staminate side branch(es), the following two important patterns are recognized in the partial inflorescences of Sclerieae.

(1) A compound bisexual cymose partial inflorescences, of which a few (rather frequently only one) glumes immediately below the fructification bear an axillary staminate branch. The glumes on the lower part of the primary axis are empty. The bisexual cymose partial inflorescences of *Scleria* and *Calyptrocarya* exemplify this type. (2) A compound bisexual partial inflorescences, of which a few glumes on the midway or lower part of the primary axis bear an axillary staminate branch. The glumes borne below the fructification and above the branch-bearing ones are empty. The genera *Diplacrum* and *Becquerelia* possess this type of partial inflorescences.

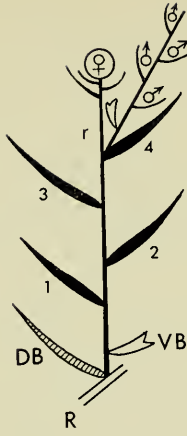
A modification of the latter type of partial inflorescences is seen in the bisexual partial inflorescence of *Bisboeckelera* (*Hoppia*), where the empty glumes between the fructification and the staminate side branches are connate, forming a sac which completely envelopes the fructification (KOYAMA 1965). Therefore, the herbaceous perigynium in *Bisboeckelera* is not homologous with the component utricle of the fructification.

The unisexual simple partial inflorescences such as the pistillate partial inflorescences of many species of *Scleria* may be derived from either type of bisexual ones by the reduction of the staminate side branches. In *Scleria*, however, the pistillate partial inflorescences of a number of species retain a vestigial staminate branch, which usually appears as a minute scale-like organ

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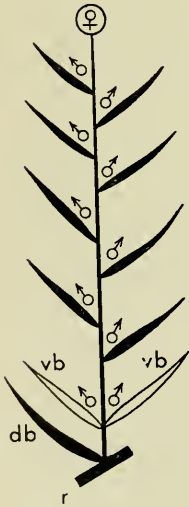
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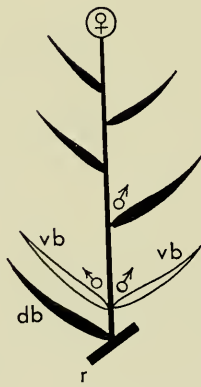
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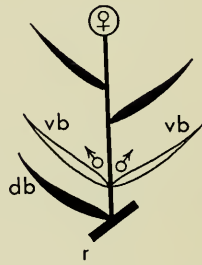
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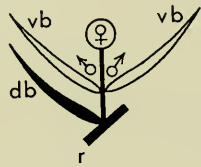
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immediately below the fructification, proving that these unisexual partial inflorescences have descended from the bisexual one of the type (1).

In Lagenocarpeae most of the partial inflorescences are unisexual. The structure of the pistillate partial inflorescences follows exactly the same pattern as those of *Scleria*, i. e., the partial inflorescences have a single axis terminated by a fructification, and several (usually 3 to 5) empty glumes are borne on the axis between the terminal fructification and a prophyll at the base. A bisexual partial inflorescence as illustrated in Fig. 10 is seen in *Afrotrilepis pilosa* as a rare occurrence in the tribe. In this instance a small staminate side branch arises from the axil of the uppermost glume and immediately below the fructification. A small prophyll is found at the base of the side branch confirming its true lateral nature. Consequently the bisexual partial inflorescences in *Afrotrilepis* does not differ in structure from those of *Scleria*. The tribe Lagenocarpeae, therefore, possesses only the *Scleria*-type partial inflorescences.

2. SYSTEMATIC DISCUSSION

Within the Mapanioideae the taxonomic separation among the three tribes involved can be made by using the characters of both partial inflorescences and fructifications. The tribe Mapanieae differs from the other two tribes in its unbranched bisexual cymelets bearing always two prophylls at the base, for in the others the partial inflorescences are either bisexual and branched or unisexual and unbranched, and always bear a single prophyll at the base (compare Figs. 11—13 with Figs. 14—17). The tribe Sclerieae and Lagenocarpeae possess exactly the same type of partial inflorescences, but the fructifications make valid distinction between the two groups. In Sclerieae the utricles of fructifications remain as a cupule surrounding on the basal

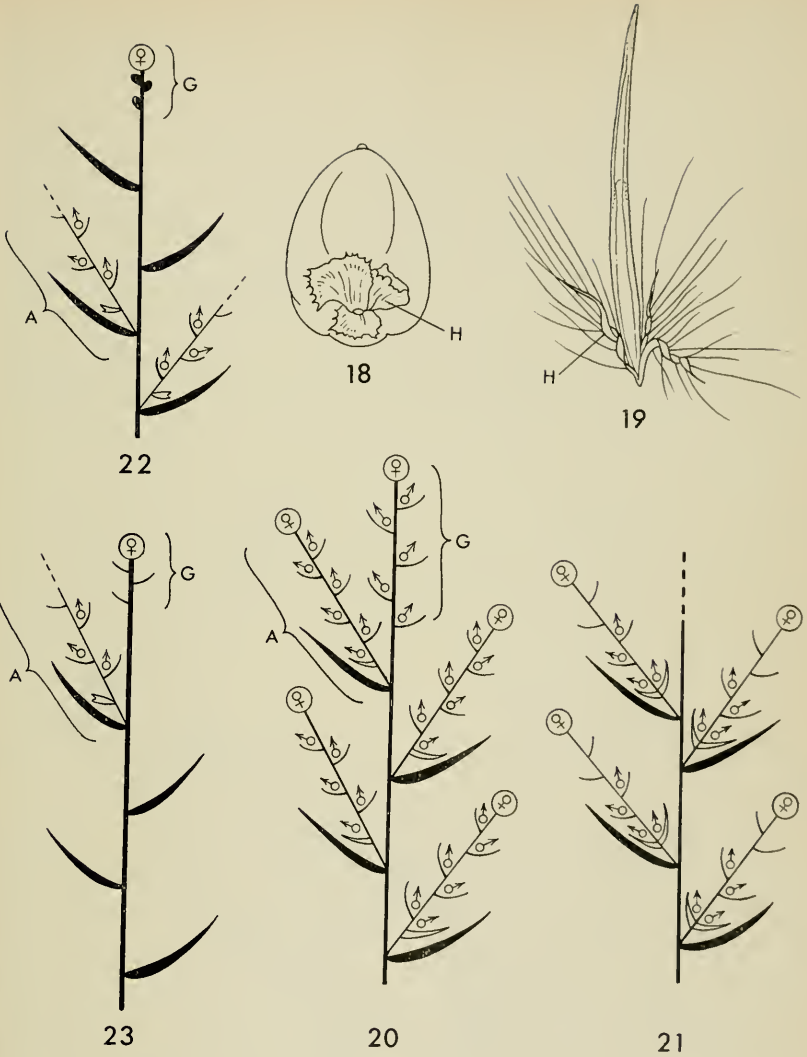
Figs. 10—17. Structure of the cymose partial inflorescences in Mapanioideae. 10. Bisexual partial inflorescence in *Afrotrilepis pilosa*. The glumes 1 to 3 are empty. The fourth glume subtends a staminate side branch (σ). ♀ shows a terminal fructification. 11. Schematic expression of the bisexual partial inflorescence in *Afrotrilepis*. The numbers of glumes correspond to those in Fig. 10. 12. Common pistillate partial inflorescence in *Scleria* and *Lagenocarpeae*. 13. Bisexual partial inflorescence in *Diplacrum*. 14—17. Schemata showing the cymelets in *Scirpodendron* (14), *Mapania* (15 & 16), and *Hypolytrum* (17). DB, bract subtending a partial inflorescence; db, glume subtending a cymelet; VB, prophyll at the base of partial inflorescence; vb, double prophylls at the base of Mapanioid cymelets; R and r show axes of inflorescence at different orders for the details see the text.

part of the achene (Figs. 2 and 7) whereas in Lagenocarpeae the well-developed utricles completely contain the component achene (Figs. 3—6 and 8 & 9). In this relationship a certain similarity in fructifications is seen between the genus *Calyptrocarya* of Sclerieae and the genera *Afrotilepis*, *Coleochloa* and *Trilepis* of Lagenocarpeae, all of which produce a thin-walled bottle-shaped utricle completely enveloping an achene (Figs. 1, 3 and 9). Differences are, however, that in *Calyptrocarya* the utricles of the fructifications do not produce a conspicuous beak, and are completely free from the style of achene, while in the comparable genera of Lagenocarpeae the utricles have a long beak, of which the wall is adnate to the inclosed style. The presence or absence of fructification beak also warrant a valid separation between Lagenocarpeae and Sclerieae.

To discuss the phyletic interrelationships among the three tribes of Mapanioideae the proper morphological coordination between the Mapaniae-type cymelets and the Sclerieae-type partial inflorescence must be made. It is obvious from the morphology of partial inflorescences reviewed in the preceding chapter that there is a great deal of similarity between the cymelets of Mapaniae and the partial inflorescences of Sclerieae and Lagenocarpeae especially concerning the fundamental framework. Nevertheless, there are certain differences between them with respect to the details of composition. (1) In the cymelets of Mapaniae, the staminate flowers are borne on the same axis as that of the terminal gynoeium, whereas in the partial inflorescences of Sclerieae and Lagenocarpeae the staminate flowers always form side branches (Fig. 11 and 13). (2) In the partial inflorescences of Lagenocarpeae three (or rarely five) minute scales are present immediately below the gynoeium (Fig. 18 and 19, H). Such scales are generally called "squameellae hypogynae." In Sclerieae the discoid organ below the gynoeium corresponds to these hypogynous squameellae of Lagenocarpeae. The cymelets in Mapaniae lack any such organ whatsoever at the base of the gynoeium.

In comparing the cymelets of Mapaniae with the partial inflorescences of Sclerieae and Lagenocarpeae two possibilities of coordination exist, i. e., a cymelet in Mapaniae could be equivalent to either (1) a whole cymose partial inflorescence in Sclerieae or (2) its staminate side branch only. I consider that the latter possibility is more realistic than the former in this discussion. If the former possibility be correct, a monandrous flower in a *Mapania* cymelet should be homologous to a whole staminate side branch in a bisexual *Scleria* cymose partial inflorescence. This assumption seems to me to be unrealistic unless the morphology of the Cyperaceae provides an evidence that a branch results in a single stamen through reduction.

The comparison that I follow is illustrated in Figs. 20—23. Figure shows a putative prototype of a cymose partial inflorescence, which consists of a bisexual terminal and lateral cymelets. This arrangement resembles to a considerable extent a portion of a compound spike in Mapaniae, differing therefrom mainly in the existence of terminal cymelet. The lateral cymelets are borne at the axil of bracts, which are arranged in a spicate manner on a

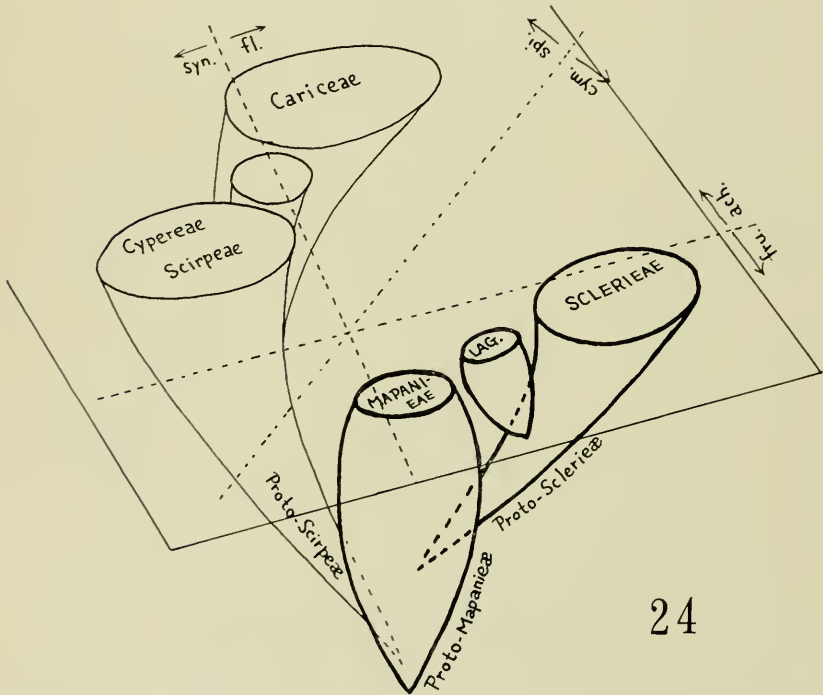


Figs. 18 & 19. Fructifications of *Lagenacarpus adamantinus* (18) and *Microdracoides squamosus* (19) with the hypogynous squamellae (H).

Figs. 20—23. Course of reduction in the cymose partial inflorescences in Mapanioideae. 20. Putative prototype. 21. Mapanieae. 22, 23. Sclerieae and Lagenocarpeae. A, staminate branches, which are homologous to a cymelet marked A in Fig. 20. G, pistillate cymelets, which are homologous to a cymelet marked G in Fig. 20.

downward extension of the axis of the terminal cymelet. If the primary axis of this prototypic panicle loses its terminal cymelet, the inflorescence would then realize such a condition as is exhibited in a compound spiciform panicle in Mapanieae (Fig. 21). On the other hand, the basic pattern of the partial inflorescence in Sclerieae may be derived from the prototypic panicle by the possible reduction in both terminal and lateral cymelets. In this sequence the terminal cymelet dropped off its staminate flowers, while the lateral cymelets lost their gynoecea or in some instance the whole part of the cymelets leaving only the basal prophyll occasionally. In this interpretation the vestigial hypogynous squamellae below the fructification in Lagenocarpeae (Fig. 18 and 19, H) as well as the hypogynous discs in Sclerieae are satisfactorily accounted for as being the remnants of staminate glumes of the lateral cymelets (see Figs. 20 and 23, G).

In the light of this morphological analysis of the partial inflorescences, the tribes Sclerieae and Lagenocarpeae, which possess definitely specialized



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Fig. 24. Schematic expression of the supposed phyletic relationships among the three tribes Sclerieae, Lagenocarpeae and Mapanieae. For the interpretation see the text.

partial inflorescences, would have been evolved from the ancestor of Mapanieae with unspecialized partial inflorescences. Figure 24 illustrates this phyletic consideration in the manner practiced by KIMURA (1956) to better reflect the evolutionary relationships among taxa.

It is appropriate here to refer to other morphological characters that also bear certain evolutionary significance. In the compound fructifications described above, the specialization proceeds with the adnation between the utricle and the contained achene. Therefore, among varying types of compound fructifications, the drupe-like condition as seen in Mapanieae and in the majority of the species of Lagenocarpeae presents the most advanced feature, whereas those of a few remainder genera of Lagenocarpeae in which the utricles are free from the contained achene, show a primitive feature. A more primitive condition of the component utricle is shown by the fructifications in Sclerieae, where the utricles are only poorly developed to surround the basal part of the achene. In this view, PIÉRART (1951) is supported in assuming that an evolutionary tendency in *Scleria* fructifications is from the poorly developed discmargins to the well-developed ones. The tribe Lagenocarpeae would have evolved from the ancestor of Sclerieae by the formation of advanced compound fructifications. An intermediate status in this course of specialization can be seen in *Calyptrocarya* (Sclerieae), and in *Afrotrilepis* and *Trilepis* (Lagenocarpeae). The resemblance in the drupe-like fructifications between Lagenocarpeae and Mapanieae is understood as the result of the parallel evolution since we have no evidence that suggests closer systematic connection between these two tribes than between Lagenocarpeae and Sclerieae.

Besides the fructifications, the tribe Sclerieae retains unspecialized features also in the anatomical characters of leaf blades as compared with Lagenocarpeae and Mapanieae (METCALFE 1963; KOYAMA 1965, 1967; BAAS 1969). The mesophyll in Sclerieae as seen in the transverse sections of leaf blades is often not conspicuously differentiated into the palisade and the spongy assimilatory tissues; or, when a degree of such differentiation is noted, the component assimilatory cells do not show any significant difference in shape and size between the palisade and the spongy portions of chlorenchyma. The development of the surface-to-surface sclerenchymatous tissues, usually described as girders, is the poorest in the leaf-blades in Sclerieae. The vascular bundles in the leaves of Sclerieae are arranged in one row with very few exceptions. In Lagenocarpeae and Mapanieae, the transverse sections of leaf blades show that the mesophyll is clearly differentiated into three portions, i. e., the palisade and the spongy chlorenchyma and the translucent mesophyll, a highly specialized feature of the mesophyll observed in the Cyperaceae. Sclerenchymatous girders connecting both surfaces as well as those between the vascular bundles and the adaxial surface are generally well developed in Lagenocarpeae and Mapanieae. Furthermore, in these two tribes, beneath the adaxial epidermis often exists a one- to three-layered hypodermis, which is absent in Sclerieae. Another specialized feature in the epidermis is the oc-

currence of tetracytic stomata or resembling ones in Lagenocarpeae and Mapaniae in contrast to constantly paracytic stomata in Sclerieae.

In all of the three tribes, the anatomical structure of leaf blades is extremely diversified, hardly permitting the taxonomic delimitation of the tribes on the basis of leaf anatomy. However, the short summary of the leaf anatomy given above seems sufficiently enough to substantiate the phyletic relationships among the three tribes discussed above.

Ecologically, all the species of Mapaniae are forest species, while the species of Lagenocarpeae are confined to the grass-land and the savanna type. The Sclerieae involves both forest and grass-land species. An interesting point in Sclerieae is that the genera with relatively primitive features such as *Becquerelia*, *Calyptracarya* and *Bisbockelera* consist only of forest species. The genera *Diplacrum* and *Scleria* having comparatively advanced characters extend their ranges from forests to savannah grass-lands as well as to the grass-lands on alluvial plains. This evidence also supplements the above phylogenetic assumption that the proto-Sclerieae would have been the connecting tie between Lagenocarpeae and Mapaniae.

Finally, a brief comment on the relationships of the Mapanioideae with other major groups of the Cyperaceae should be made. I am in agreement with MATTFELD (1935, 1938) and SCHULTZE-MOTEL (1959) that the so-called "bisexual flowers" in Scirpeae are synanthia, which have descended from the reduced cymelets of Mapaniae. A synanthium of Scirpeae is, therefore, homologous with a cymelet of Mapaniae. As to the derivation of the spikelets in Cariceae, there are controversial opinions (MORA 1960; KUKKONEN 1967), about which I fully discussed in my previous paper (KOYAMA 1969).

SUMMARY

A natural group Mapanioideae, which is characterized by the peculiar compound fruiting structures and the conspicuously cymose partial inflorescences, can reasonably be subdivided into three tribes, Sclerieae, Lagenocarpeae and Mapaniae. The partial inflorescences in Mapaniae and those of the other two tribes are structurally sufficiently distinctive to suggest two divergent evolutionary trends leading to Mapaniae and Lagenocarpeae respectively. The *Mapania*-type partial inflorescences are definitely more specialized than the *Lagenocarpus*-type to which the partial inflorescences of Sclerieae belong. On the other hand, in both the fruiting structures and the anatomical structure of leaves Sclerieae retains primitive features, while Lagenocarpeae and Mapaniae show advanced features. The tribe Mapaniae would have differentiated from the common ancestor before the Lagenocarpeae evolved from the *Scleria*-type ancestor. Mapaniae, which would have been rather rapidly specialized, possess fruiting structures and leaves comparable to those of Lagenocarpeae. The tribe Sclerieae does not show any significant trace of differentiation except for its *Lagenocarpus*-type partial inflorescences. The morphological similarity in fruiting structures and leaf blades between Mapaniae and Lagenocarpeae is interpreted as the results of parallel evolution.

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