

INTERPRETATIVE FLORAL MORPHOLOGY OF THE CYPERACEAE ON THE BASIS OF THE ANTHOID CONCEPT

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SUMMARY

A re-consideration of the phylogenetic origin of the functional reproductive units of the Cyperaceae on the basis of the anthoid concept reveals that at one time or another a macroblastic preanthoid of the *Scirpodendron* type originated from some (perhaps pro-pandanoid?) progenitorial taxon. Brachyblasty and oligomerisation, frequently followed by a sometimes complete depauperisation of the sterile meromonandrial members of the floral region, resulted in the modification of this archetype into the predominantly ambisexual anthoids of the scirpoid type (in the subfamily of the Scirpoideae = Cyperoideae), and into the almost invariably unisexual and (especially in the female sex) often extremely oligomerised anthoids of the Caricoideae (= Kobresioideae). Previous neological interpretations by Holttum, Kern and others, although sometimes essentially correct in many respects, were very much confused owing to connotations and notions emanating from the classical floral doctrines such as the postulation of a pseudanthial (synanthial) nature of some manifestly pluriaxial structures conventionally regarded as "flowers". The ensuing inconsistencies in nomenclature render the anthomorphological relations rather obscure; what is called a "flower" in one genus is referred to by the name of "inflorescence" ("spikelet") in another one, although the two are in fact homologous entities.

The scirpoid assembly differs from the caricoid taxa in the more or less imperfect radial symmetry of the anthoids if tepals (or vestigial tepals in the form of scales or bristles) were retained, whereas the unisexual anthoids of the latter group do not show such a tendency. The fundamental equivalence of the bisexual scirpoid anthoid and the unisexual (and often depauperated) caricoid anthoid permits the evaluation of the nature of the florescences. The ultimate ramifications of the reproductive region (if not the whole inflorescence) must be indeterminate (although sometimes considered determinate on account of a pseudo-terminal pistil passing by the name of "female flower"), so that the incidence of both "cymose" and "racemose" part-inflorescences in the Scirpoideae as reported by some workers is, therefore, highly improbable.

The possible phylogenetic significance of the archetypic procyperaceous reproductive region is discussed.

1. INTRODUCTION

The "classical" interpretation of the cyperaceous reproductive units, based on the concept of the generalised, ambisexual, pentacyclic and trimerous, basic floral pattern in the Monocotyledons (BLASER 1941, 1944) has repeatedly been challenged (compare SCHULTZE-MOTEL 1959, KERN 1962, and MEEUSE 1965, for details). The alternative interpretations were, previous to the ideas expressed

by the present author, largely based upon the most confusing, supposedly pseudanthial (synanthial) nature of what is commonly called the cyperaceous "flower". This idea has been severely criticised (see MEEUSE 1972b) because "to make a flower out of flowers" is methodologically unsound (the same approach to the floral morphology of the Hamamelididae was shown to lead to inconsistencies and controversies: MEEUSE, in the press). The problems encountered in such attempts to explain the cyperaceous "flowers" are partly caused by the occurrence of unisexual and ambisexual reproductive units (blossoms) in different taxa of this family (the sex distribution is sometimes rather curious indeed: compare, for instance, the Sclerieae and the genera *Carex* and *Kobresia/Elyna*), and partly by the difficulty which structural pattern (floral groundplan) to select as a suitable starting point. KERN (1962, p. 145) has pointed out some of the problems one runs into when the change-over from unisexual blossoms to ambisexual ones (or vice versa) must be accounted for. The prototypic architecture was believed to be best approximated by the recent genus *Dulichium* by MATTFELD (1938) who, accordingly, "explained" the bisexual cyperaceous "flower" as a secondary aggregate (i.e., pseudanthial complex) of a number of unisexual "flowers". HOLTUM (1948) and Kern regarded *Scirpodendron* as the living genus with the most basic floral morphology, but they disagreed as far as the explanation of the sex distribution is concerned.

The present author also accepts the primitive status of *Scirpodendron*, but for different reasons. The confounding concept of the "pseudanthial" nature of the reproductive units of such forms as *Scirpodendron* and the other Mapanieae, of *Scirpus*, etc. (i.e., of the supposed equivalence of the so-called "flower" with an inflorescence) must be rejected in favour of the postulation of the primarity of a pluriaxial archetype of the reproductive region called an *anthocorm*. The question whether the conventional, more or less actinomorphic, "flowers" of the Mapanieae and other Scirpoid forms represent modified holanthocorms or units of a lower order (anthoids) can now be answered by applying the criteria mentioned elsewhere (MEEUSE 1975). The compound inflorescences, the rather constant occurrence of perianth lobe (tepals)/stamen units with a single stamen (see, e.g., the diagrams in KERN 1962, p. 143, figs. 2-4, 11), the incidence of monoclony and of monosexuality in related taxa, and the isomorphy of the meromonandrial tepals, are more compatible with an anthoidal nature of these conventional "flowers" than with their equivalence with an anthocorm. The identity of the traditional "flowers" in other groups, more particularly in the Caricoideae, will be assessed later on. An additional consideration is the simple fact that so many monocotyledonous blossoms are apparently conformable to the same, traditionally "pentacyclic trimerous" floral unit, that they are most probably all homologous (and, accordingly, anthoidal rather than holanthocormoid). This simplifies the interpretation appreciably as far as the sex distribution is concerned: gonoclads, and consequently anthoids, can be unisexual or ambisexual, in the latter case with the monandrial elements more proximally, and the monogyna more distally, inserted on the cladic part of the gonoclad

(= future anthoid axis) as a rule. Generally speaking, the anthoids are brachyblastic and tend to be cyclic in monocotyledonous forms, but the situation in the Commelinidae requires a closer re-examination as we shall see.

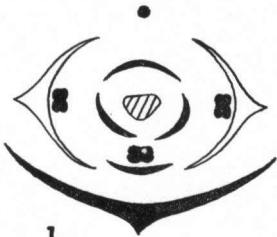
The comparative floral morphology of the Cyperaceae will be treated on the basis of the anthoidal nature of some of its scirpoid subordinate taxa (and subsequently "extended" to Caricoideae, etc.). The classification is that of SCHULTZE-MOTEL (1964). For the terminology the reader is referred to previous publications of the present author. The following abbreviations will be used: FRU = functional reproductive unit (often agreeing with the conventional "flower"); AC = anthocormoid; AD = anthoid; GB = gonoclad bract (= anthoid bract); SPU = stamen-perianth (tepal) unit (derived from the same holomonandron and in the Cyperaceae apparently often unistaminate); and MG = monogynon (MGa = monogyna).

2. SCIRPOIDEAE (CYPEROIDEAE)

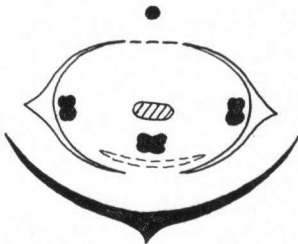
It seems logical to assume that, generally speaking, a plurality and an indefinite number of floral parts is a more primitive condition than a smaller and fixed number of such parts. *Scirpodendron* thus qualifies as a primitive taxon as far as its FRU is concerned, and this monotypic genus already drew the attention of Holttum and Kern as we have seen. The interpretation of its FRU as an AD is simple (see *fig. 1*): the bract (GB) subtends an axis bearing a number of SPUs in a helical to subcyclic anthotaxis (the lowermost, opposite two excepted), followed by a few scaly appendages manifestly representing sterile, exstaminate derivatives of SPUs, and one MG (or occasionally 2–3 MGa). The upper, void properianth members and sometimes also the MG(a) may be lacking, and if this is the case the FRU is male (obviously by reduction); the variation in sex distribution is usually observed in the same florescence (an AC or compound AC): the most reduced (and all-male) ADs are found in the uppermost glumes (= GBs), and the most pleiomerous (and ambisexual) ones in the axils of the lower glumes of the AC (KERN 1962). Such a "degeneration" of FRUs (and of floral members) towards the apex of the inflorescence is a wide-spread phenomenon among angiospermous forms (it is also manifest in the Sclerieae) and pleads in favour of the primitive nature of the pleiomerous (and ambisexual) ADs in *Scirpodendron*. KERN (p. 143) has shown how a number of plausible oligomerisations and reductions and the (partial) concrescence of the outer (opposite) paired properianth scales, concomitant with a tendency towards the cyclisation of the other floral parts, transformed an archaic type of anthoidal FRU, apparently still rather closely approximated in *Scirpodendron*, into the seemingly diverse ADs of the Mapanieae. This is also essentially the gist of HOLTTUM's earlier paper, but KERN's diagrams render the deductions much better surveyable (see also *fig. 1*). For details the reader is referred to their papers and to SCHULTZE-MOTEL (1959). One must be well aware of confusing connotations, however. KERN (p. 142) says "that it is impossible to distinguish between the partial inflorescences of *Hypolytrum* and *Diplasia*, and the flower



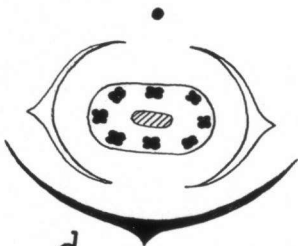
a



b



c



d



e



f



g

of *Scirpus*", meaning: between the diagrams shown in his figures 5, 6, and 9 (on p. 143); see also *fig. 1*. This is one of the reasons why an interpretation of all these FRUs as ADs is to be preferred; for one thing, what would, if the erroneous train of thought is carried through to its ultimate consequences, the so-called "partial inflorescences" (in the sense of KERN, SCHULTZE-MOTEL (1900) and others) of the precursors of *Scirpodendron* with, as the classical doctrines prescribe, "complete", i.e., polymeric and bisexual, flowers have looked like?

HOLTUM and KERN both assumed that the FRU of *Scirpus* and related genera can thus be derived from a (proto-)mapanioid type with the FRU of *Scirpodendron* or a very similar structure as the ultimate archetype, but "*Scirpus*" is taxonomically not sharply defined. Forms with a floral (= anthoid) morphology corresponding with, say, KERN's figure 6 (and with my *fig. 1e*), and sometimes provided with scales or bristles (obviously representing depauperated properianth lobes of monandrial derivation) have been referred to this genus, but also to some segregates of *Scirpus* such as *Fuirena*. The question whether *Scirpus* must be split up into a number of smaller genera, or united with *Fuirena*, etc., is, therefore, a moot point. However, the above-mentioned derivation of anthoids of the *Scirpus* type from those of *Hypolytrum*- or *Diplasia*-like progenitors suggests various alternative pathways of floral evolution which may account for the great diversity of floral patterns in the large *Scirpus* aggregate by both parallel and convergent specialisations. Supposing that a trend towards a trimeric cyclisation and oligomerisation prevailed which resulted in a FRU resembling that of some representatives of the genus *Paramapania*, but with a "double whorl" of SPUs, a condition arises which is rather close to the diagram no 11 (of *Fuirena*) of KERN's publication (see *fig. 1e*) if the inner whorl of stamens is reduced (only the inner scales remaining). This yields a neatly actinomorphic AD, whereas a direct derivation from a *Mapania*-*Paramapania*-*Hypolytrum*-type results in a bilaterally symmetrical arrangement: the stamens of the opposite lateral bracts are transversely oriented, and the third is median-anticous. The bilateral arrangement is important in connection with the inter-

Fig. 1. (adapted from KERN 1962 and other sources) Floral diagrams of (a:) *Scirpodendron*, (b:) *Mapania*, (c:) *Paramapania*, (d:) *Diplasia*, (e:) *Fuirena* (Kern's interpretation, (f:) *Fuirena*, (Clarke's interpretation), (g:) *Scirpus* p.p., *Cyperus*, etc.

It is clear that the reduction of perianth members and of sterile scales surrounding the pistil (present in a and in b) ultimately leads to the condition in g, but also the situations: d (by the reduction of the fused perianth members and of some of the stamens), e, and f (by the reduction of the fused perianth members and/or inner scales) may lead to g. Kern has, therefore, accepted a pleiophyletic origin of the FRU of the *Scirpus* s.l. aggregate and possibly of *Cyperus* and related genera.

The difference in interpretation between Clarke and others (such as Kern) is the relative position of the stamens in respect of the inner whorl of perianth members; it does not necessarily follow that the condition in *Fuirena* agrees with e or with f, but may agree with Clarke's diagram (f) as far as the position of the stamens is concerned and with Kern's (e) in the position of the inner perianth lobes. Anthoid bract drawn in black, lateral elements, sometimes connate at the dorsal (posticous) side, outlined, perianth lobes (and scales replacing them) and stamens drawn in black, gynoecium hatched.

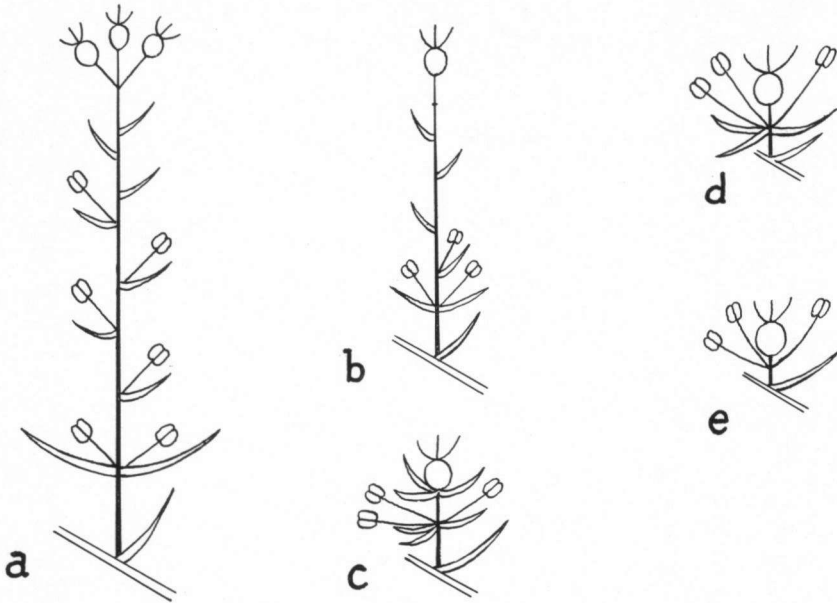


Fig. 2. Diagrams of anthoids corresponding with the diagrams in fig. 1: *a* agrees with fig. 1, *a*; *b* with fig. 1, *b* and *f*; *c* with fig. 1, *e*; *d* with fig. 1, *c*; *e* with fig. 1, *g*.

pretation of the floral morphology of the Commelinidae (and the Orchidales?), and the actinomorphic pattern with the floral architecture of other monocotyledonous groups (liliids, arecids, alismatids): it is clear that both kinds of androecial structure can be derived from a common prototype resembling *Scirpodendron* (see also fig. 2, *b*, *c*). These two alternative arrangements, combined with 0, 3(2), or 6(4) perianth lobes, in a bisexual AD, explain the floral architecture in the other genera of the Scirpoideae.

KERN is rather sceptical about the separate status of the Rhynchosporioideae in the sense of Kükenthal as a separate subfamily. The anthoidal morphology is not essentially different from that of the *Scirpus*-type and need not be discussed in detail here (SCHULTZE-MOTEL 1964, places this taxon in the subfamily Scirpoideae as the tribe Rhynchosporae). The construction of the structure usually called an inflorescence or pseudo-spike will be discussed in one of the following chapters.

3. CARICOIDEAE

In this group a consistent form of unisexuality prevails. One must be well versed in the kind of terminology that is used by SCHULTZE-MOTEL (1900) in his treatment of the Cyperaceae in the *Syllabus*: "*Blüten... meist zwittrblütige Synanthien durch Reduktion von Partialinfloreszenzen... entstanden*" (Scirpoideae) as against: "*Blüten stets ♂♀. Partialinfloreszenzen nie zu zwittrblütigen*

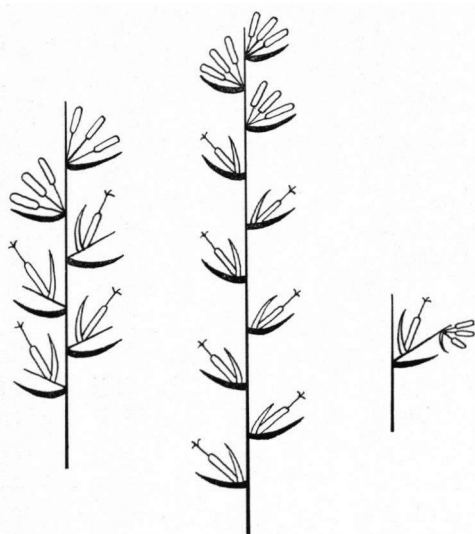


Fig. 3. Diagrams of caricoid reproductive structures (after Kern, partly modified). Left: *Kobresia* (typical). Centre: *Carex*, Right: *Kobresia* (*Elyna*) part-florescence. In *Kobresia* and *Carex* the gynoclads are normally reduced to a single bracteate (utricled) gynoecium or a group of stamens, but in the *Elyna* type (and in some species of *Carex*) the plurality (polymery) of the gonoclads is still manifest. The *Elyna* type suggests the equivalence of a so-called female flower (a utricled axis bearing one remaining monogynon) and the so-called male flower (presumably an anthoidal entity that lost its perianth as in *Cyperus*, etc.).

Synanthien vereinigt" (Caricoideae). One does not know where the "inflorescence" ends and the flower is supposed to begin. That is why this terminology must be condemned, and the limits of anthocorms and gonoclads (anthoids or pre-anthoids) provide a better and unambiguous yardstick of the relations between all cyperaceous FRUs.

It may be taken for granted that the caricoid utricule is a modified bract-like organ subtending an often much reduced axis on which the pistil is inserted. The interpretation of the caricoid pistil is not important in this connection, because it is ebracteate and pseudoterminal; in other words: the utricule represents the bract of a depauperated and oligomerised gynoclad of which only a single gynoecial unit remains. The utricule and its contents are coaxial with male FRUs consisting of a glumaceous element and, normally, 3 stamens in such genera as *Kobresia* (*Elyna*) but also in some species of *Carex* (see fig. 3). We know that in the primitive *Scirpodendron* each monandrial complex was already reduced to a properianth member with a single stamen, so that the occurrence of three stamens associated with a glume is probably not a monandrial complex but, like the coaxial utricles, of an anthoidal nature and comparable with the atepalous anthoidal FRUs of many scirpoid taxa. In *Kobresia*, aggregates of coaxial reproductive units sometimes consist of one proximal utricule and 2–3 more distally inserted androcladial FRUs (as in several species of *Carex*), see fig. 3. The "spikelets" are manifestly modified anthocorms bearing the derivatives of coaxial male and female gonoclads, whereas the gonoclads in the Scirpoideae are fundamentally ambisexual. This points to a basic difference between the two groups most probably attributable to an early divergence in the evolution of the sedge family.

The Sclerieae are apparently also monoecious (or mostly so), but the con-

struction of their florescences differs from that of the Cariceae. In the *Scleria*-group of taxa the staminate FRUs consist of a subtending glume and 3 (or fewer) stamens, and are usually borne in a frequently distichous arrangement (at least in a large portion of the compound inflorescence). Their interpretation as anthoids is rather obvious, but the ovuliferous FRUs are single and seemingly terminal pistils associated with a number of "bracts" or "glumes". The arrangement suggests that these "bracts" must be "sterile" gynoclad bracts, the associated (and already reduced) gynoclad having disappeared. Such a female complex seemingly coaxial with several bracts can only represent a depauperated anthocorm. The oligomerised and depauperated anthocorms are variously united into complex inflorescences (see MORA 1959, p. 324, Abb. 46, figs. 2, 3, p. 325, Abb. 47, figs. 2-5, etc.). The problem morphologists had to face is the seemingly terminal position of the pistil (= convential "female flower" of most workers, in fact a monogynon). This has resulted in the interpretation of what is usually called inflorescences (or part-inflorescences) as "cymose" in structure in the *Sclerieae* (and *Rhynchosporae*) and as "racemose" in the *Cariceae* (and in the *Scirpoideae*, the *Rhynchosporae* excepted). This is rather incongruous because there is a consensus of opinion as regards the greater taxonomic affinity between *Sclerieae*, *Cryptangieae* (= *Lagenocarpeae*), and *Cariceae* than between these groups of the *Caricoideae* and the *Scirpoideae*. The question of a terminal versus a lateral (appendicular) position of certain organs is a very old bone of contention which is rendered even more complicated in interpretative floral morphology if an additional distinction is being made between a holanthocormous flower and an anthoid, because the central axis of the two kinds of FRUs is of a different order, viz., represents an anthocorm axis and a subordinate (= gonoclad) axis, respectively, so that there are two different and uncomparable situations. The extreme depauperisation of a whole AC, only a single pistil (MG) remaining, may also obscure the situation.

The incidence of two fundamentally different types of inflorescences in the same caricaceous subfamily is less probable than a consistent architecture of the floral region. It follows that the acceptance of a division of the *Cyperaceae* into groups with "cymose" and groups with "racemose" inflorescences (compare, e.g., the classification of SCHULTZE-MOTEL 1964: *Sclerieae* and *Lagenocarpeae* – "♀ Blüten terminal", against *Cariceae* – "♀ Blüten seitlich...") is to be rejected.

4. TERMINAL OR LATERAL POSITION OF THE PISTILS?

The first point to be decided is the identity of the pistils. The present author believes that the one-chambered and uni-ovulate female organs of the *Cyperaceae* represent monogyna, but for several reasons (such as the presence of 3 stigmas in most cases) the idea has become accepted that the pistils are tri-carpellate and "pseudomonomerous". If we assume that the pistil is indeed a trimerous aggregate it cannot possibly be anything else but a modified and brachyblastic gynoclad bearing a terminal trimerous "whorl" of laterally connate (and variously modified) MGa, so that the relative position of this

supposedly "terminal" pistil can be used as a basis of comparison. If the ovuliferous FRU is equivalent to a single MG, however, it is terminal if it has its own stalk, but the actual condition (especially in the Cariceae) does not suggest the presence of a "stalk" under the pistil. The cladic element on which the pistil is borne in a truly or spuriously terminal position is at least of the order of magnitude of a gonoclad axis.

KERN (1962) has shown the way to clear up some of the controversies: in the cryptangiid *Bisboeckeleria* the pistils are surrounded by an urn-shaped structure which he does not identify as a homologue of the caricoid utricle (which is a modified gynoclad bract: the *Carex*-pistil is a depauperated anthoid!) but as a fusion of coaxial bracteoid elements as found below the pistil(s) in *Becquerelia* and in *Scirpodendron* (and some other Mapanieae) and, in the present author's opinion, of meromonandrial nature. Similar bracteoid floral members occur in *Scleria* and sometimes also form a kind of involucre. KERN clearly states that in his opinion the so-called female flower (= monogynon in my terminology, a solitary pistil) is terminal in the so-called spikelets of *Scleria* (p. 145: "*The bract of the whole spikelet is pertinent to the female flower*"), but also in the Mapanieae and Cryptangieae. MORA shows a terminal position of the pistil in his diagrams (see, e.g., his Abb. 47, on p. 325) of Cryptangieae (e.g., *Becquerelia*) and Sclerieae (supposed to have cymose inflorescences), but his diagrams of scirpoid inflorescences which are said to be racemose are also shown with a terminal "flower" (see, e.g., his figures on p. 266 and 267: Abb. 6 and 7). What is called a "flower" of Scirpoideae-Mapanieae, -Scirpeae, and -Cypereae by KERN and many other workers (or a "synanthium", "pseudanthium", or "pseudanthial flower" by SCHULTZE-MOTEL 1959) apparently seems to bear a terminal pistil, and the same holds for the so-called "spikelet" or partial inflorescence of the Rhynchosporae, *Scleria*, and the Cryptangieae. This all points to a similar morphology, which, I believe, can be explained by assuming that the pistils are not terminal but consistently pseudoterminal. There must be a topological correspondence between monogyna and monandrial units, and between gynoclads and androclads. In the Cariceae this is manifest: the gynanthoid (= everything contained in a utricle) is often coaxial with the male anthoids (bract + three stamens): diagrams, e.g., in KERN (p. 146, figs. 16-20).

The archaic *Scirpodendron* is provided with laterally inserted complex monandra (consisting of a properianth glume or "bract" plus a stamen), so that the sterile elements below the pistil are also of meromonandrial derivation. The occasional presence of several pistils distally of these sterile properianth glumes (instead of only one) clearly points to the initially lateral attachment of the former; if there is only a single pistil, it must consequently also be lateral and pseudoterminal. This renders a reconstruction of an archetype possible. At some early stage of floral evolution a divergent trend of specialisation must have resulted in the development of procyperaceous forms with ambisexual (androgynous) gonoclads and of other ones with unisexual anthocorms (progenitors of some Cariceae), and a third group with anthocorms bearing coaxial

gynoclads and androclads (in Cariceae with this condition: *Kobresia*, some sections of *Carex*, the gynoclads are proximally inserted and the androclads distally; in Sclerieae and Cryptangieae the order is usually reversed). One only has to assume that (1) the androclads (primarily bearing coaxial aggregates of a stamen plus its associated properianth member) often became modified into a bract subtending three stamens (in other words, such a FRU represents a modified, viz., brachyblastic and atepalous androclad); (2) the gynoclads are almost always extremely oligomerised and have become monomeric; in some cases (but not in Scirpoideae) a single pseudoterminal pistil and the "bracts" or "scales" ("hypogynous scales", etc.) below it presumably represent an extremely oligomerised and brachyblastic aggregate of coaxial gynoclads (compare, e.g., some Cryptangieae with a single pistil "terminating" an axis bearing lateral androclads such as *Becquerelia* and *Bisboeckeleria*: for reasons of homotopy the same axis must originally have borne some gynoclads coaxial with the androclads; in the "spikelet" of *Scleria* the single pistil and a few scales may be derived from an anthocorm); (3) in the Scirpoideae the androgynous gonoclads have a proximal pair of opposite fertile "bracts" which with a third (and most probably, immediately adjacent) "bract" and the pseudoterminal pistil form the scirpoid anthoid, secondarily often depauperated (by the loss of the tepals) into three stamens and a pistil subtended by the bract, and in the Cryptangieae the androclads remain macroblastic, whereas they are brachyblastic and anthoidal in the Sclerieae and Cariceae; and finally, as we have seen, (4) in the Cariceae the gynoclads bear a single pistil which is manifestly lateral. The reconstruction of the archetype anthocorms and polyanthocorms is easy enough and points to a consistent basic architecture (see fig. 4). It appears that there is no common basic archetype because the sex distribution found among the recent cyperaceous taxa (see above) requires at least three different ones, viz., unisexual anthocorms only (in diclinous Cariceae), an ambisexual type with coaxial gynoclads and androclads, and one with coaxial androclads and gynoclads (inserted in the reverse order), and one with androgynoclads (the latter occurring in most Scirpoideae). The explanation is that an original dicliny became replaced by one of the forms of ambisexuality of the anthocorm, to be retained only in the monoecious and dioecious Cariceae.

5. SOME PHYLOGENETIC SPECULATIONS

In current systems of classification of the Monocotyledons the most primitive taxa are supposed to be either the Alismatidae (Helobiae) or the Liliidae (Liliiflorae). Either assumption suggests the primarity of a strictly actinomorphic floral architecture with a "double whorl" of stamens. The prevalence of an asymmetrical androecium in the Commelinidae sensu TAKHTAJAN (1969) (and in the Orchidales!) is explained by assuming the retention of the median (anticous) stamen of the outer, and of the lateral stamens of the inner androecial whorl. The interpretation of the scirpoid FRU by such authors as Clarke (see KERN 1962, fig. 9,10) is also along these lines and starts from the supposedly

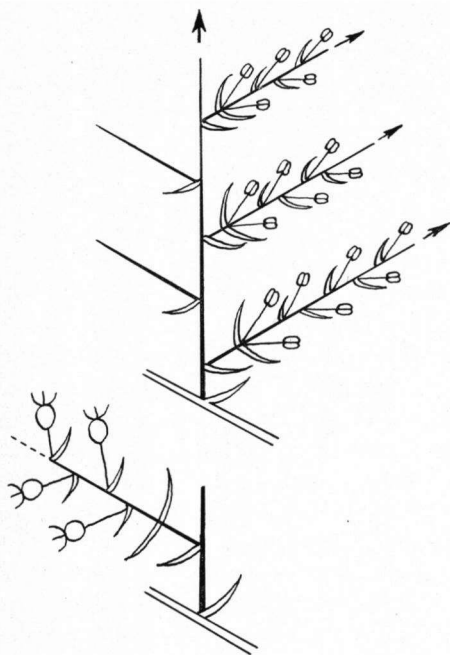


Fig. 4. General diagram of cyperaceous reproductive regions, all-male anthocorm (above) and part of female one (below) shown. The general build-up is that of a group of coaxial, bracteated gonoclasts (male, female, or ambisexual) bearing monandra or monogyna (or both); the male and ambisexual ones originally provided with a pair of opposite glumes (which may or may not have something to do with the prophyll and are shown in the female version below) and a number of PSUs in helical arrangement. The female version is rather similar but bears ebracteated monogyna (compare also fig. 3). The ambisexual version of an antheid is shown in fig. 3a, and the corresponding male and female ones can also be deduced from this diagram by omitting either the PSUs or the monogyna. The occurrence of three stamens associated with a glume in Caricoideae (see fig. 3) is most probably to be interpreted as an antheid structure.

basic, "trimerous and pentacyclic" floral diagram (see fig. 17). KERN and SCHULTZE-MOTEL (1959) do not agree with this view (their concept of a pseud-anthial or synanthial character of the cyperaceous FRUs of at least the scirpoid assembly already precludes its acceptance), and they demonstrated the primarity of two lateral SPUs more proximally inserted than the third (median and anticus) stamen (see fig. 1). Conceivably, a trimerous, asymmetrical androecium is primitive in all Commelinidae exhibiting this type of floral morphology, which implies that they are derived from a more or less protocyperalean group of progenitors rather than from an actinomorphic liliid archetype which biseriate tepals and stamens. The origin of the Orchidales from a liliid precursor also becomes doubtful. One must bear in mind that the gynoeceium of the Cyperaceae is secondarily monomerous, but was pleiomerous in their progenitors, each single monogynon of the polymerous pistil (sometimes) originally containing more than one ovule.

The liliid assembly may have originated from the same ancestral group by a divergent trend of specialisation, more of the helically arranged SPUs being retained, but the basal pair of opposite bracts becoming sterile and dorsally connate (as in the series *Hypolytrum*→*Lipocarpa*→ and *Hemicarpa*, see KERN 1962). The connate bracts may have given rise to the so-called "prophyll" characteristic of the Liliidae (but absent in most of the Commelinidae); this

“prophyll” may, according to the interpretation of the diagrams by Kern, therefore well be a fusion product of *two* elements. These bracts are not void in the majority of the Cyperaceae of the scirpoid type and account for the asymmetrical androecium as we have seen; if they do not subtend a stamen, however, the more distal stamens of the anthoid (which were helically inserted, compare *Scirpodendron*) may have become cyclic. One thus can only link the floral morphology of liliid forms with that of early commelinid forms by accepting a more or less macroblastic, common prototype resembling *Scirpodendron*, but cannot directly derive a glumiflorous floral structure (anthoid) from a typically liliid FRU.

The suggested alternative derivation of liliid forms from a ranunculid progenitorial group may well have to be abandoned in favour of a proto-commelinaceous origin. The connections between the liliid assembly and the ranalean assembly are doubtful: Magnoliales and Nymphaeales have holomonandrial stamens and holanthocormous flowers and do not qualify as taxa ancestral to monocotyledonous forms with meromonandrial androecia and anthoid FRUs. The Ranunculidae do not exhibit manifest monocotyledonous affinities either, some phytochemical features excepted.

The question whether the monocotyledons are monophyletic is a moot point (compare METCALFE 1971, MEEUSE, in preparation), but the morphology of the early cyperaceous type of plant suggests some relationship with the Pandanales (HOLTTUM 1948, KERN 1962, MEEUSE 1965). Whether the Pandanaceae are primitive is a matter of opinion, but the present author accepts this view. The next question is whether the floral morphology of the family can be adequately described in terms of the Anthocorm Theory. STONE (1969) has given a survey of the conditions in the genus *Pandanus*, but his chosen starting point is an ambisexual structure, which is unacceptable (MEEUSE 1972a, 1973). *Sararanga*, the most primitive genus, does not show any indication of ambisexuality (STONE 1961), and functionally unisexual FRUs (“flowers”) containing pistillodes (or staminodes) are of very rare occurrence in the genus *Pandanus*. I can follow most of Stone’s deductions regarding the evolution of the reproductive region in *Pandanus*, provided a unisexual archetype is selected. It is highly probably that reductions of “bracts” took place, as assumed by Stone, but these are most probably meromonandrial elements (properianth members, i.e., potential tepals), so that their absence in ovuliferous structures is explained (there *never were* any). Stone’s archetype must be replaced by a female structure resembling his fig. 2A but without the stamens and without the “bracteoles” borne on the “tertiary axes”, and by a separate male one in which these so-called bracteoles are present (but the ovuliferous elements are missing). The genus *Freycinetia* is different in that the pistils are compounded of units each containing numerous ovules. This is biologically significant in connection with the wide-spread (or perhaps universal?) ornithophily and chiropterophily of the genus (in contrast to anemophilous FRUs, which often have pauci- to uniovulate pistils – as in *Pandanus* and *Sararanga*, but also in Amentiferae, Urticales, etc. – zoophilous FRUs are more efficient if their pistils are plurio-

vulate). A secondary multiplication of the ovules is not altogether inconceivable, but a primarity of pluriovuly seems more acceptable. The incidence of pauciovulate and pluriovulate FRUs in one taxon (Pandanaeae; Juncaceae-Cyperaceae) is certainly a most intriguing problem.

The possible phylogeny of the Monocots will be discussed in a separate paper by the present author.

6. DISCUSSION

The interpretation of the scirpoid FRU and some comparable structures as pseudanthial (synanthial) complexes must be rejected, and replaced by the assumption that a primitive gonocladial structure (almost always ambisexual in scirpoid forms and unisexual in caricoid taxa) gave rise to the various and diverse floral regions of the Cyperaceae. The question whether the florescences of some groups are "racemose" and other ones "cymose" can be answered by accepting that a pistil can be pseudo-terminal or lateral: initially several ovuliferous (gynoeclial) units occurred coaxially in a lateral position, but as a rule only one of them remained after oligomerisation and assumed a terminal position. The nature of this pistil is most probably that of a primarily one-ovuled, single (monomerous) organ; all attempts to interpret it as a basically "tricarpellate" structure are unconvincing (compare also BARNARD 1957).

The reproductive region of the ancestral taxon must have been a polymonogynous and/or polymonandrous anthocormoid which was either unisexual (and basic to that of some caricoid taxa) or ambisexual; in the latter case the gonoclads (pre-anthoids) may have been unisexual (and archetypic in respect of other Cariceae and Sclerieae, polliniferous and ovuliferous gonoclads being borne coaxially in the same anthocorm), or androgynous (androgynoclads being present: Scirpoideae).

A consistent trait is the early oligomerisation of the meromonandrial stamens to a single one. In this respect the Cyperaceae are not more primitive, nor more advanced than the other groups of monocots, the few taxa with pleiomerous phalanges of meromonandrial stamens excepted. Such taxa include some Helobiae (Alismatales, Alismatidae), whose taxonomic affinities are decidedly obscure, the Pandanales, and a few scattered groups. A relation between Cyperaceae and Pandanales has repeatedly been suggested, so that a comparative analyses of the reproductive regions is indicated. The most primitive pandanaeous genus is definitely *Sararanga* (compare STONE 1961). The male plants bear complex anthocormoids whose terminal members (androclads) appear as fascicles of stamens surrounded at the base by a shallow, lobed structure (sometimes passing by the name of "perianth", which interpretation almost certainly hits the nail on the head) and borne on a common, bracteated stalk. The "perianth" may well represent a whorl of cyclicised meromonandrial pro-perianth lobes each associated with some stamens; the cladic part of the androclad is obsolete beyond the whorl of monandrial elements. In *Pandanus*, also primarily dioecious in spite of repeated suggestions that it was originally

monoclinous (compare STONE 1969), the male plants bear staminate structures (currently called "male flowers") in more or less complex and compound inflorescences. These staminate structures are presumably androclads which, in contrast to those of *Sararanga*, are not cyclic or fasciculate but bear the monandra in a more or less helical arrangement; the monandrial aggregates are most frequently depauperated and only represented by a stamen or a small fascicle of stamens, much more rarely the meromonandrial properigone lobes being retained. The Cyperales and the Pandanales (and Typhales) most probably had a common group of progenitors, and this conclusion forms a basis for speculations concerning the ancestry of other monocotyledonous taxa.

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