Floral Ontogeny in Scirpus, Eriophorum and Dulichium (Cyperaceae),
with Special Reference to the Perianth

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INTRODUCTION

Simpson et al. (2005) made the suggestion, based on molecular phylogenetic analyses, that the Cyperaceae comprises only two subfamilies, the Mapanioideae (with the tribes Hypolytreae and Chrysitricheae) and the Cyperoideae (all the other tribes). Within the Cyperoideae, they recognized a Cariceae–Dulichieae–Scirpeae complex. The present study focuses on the genera Scirpus L., Eriophorum L. and Dulichium L.C.Rich., which all belong to this Cariceae–Dulichieae–Scirpeae complex.

A typical monocot flower can be described as actinomorphic, pentacyclic and trimerous with a superior and syncarpous ovary (e.g. Rudall and Bateman, 2004). Most Scirpus-like flowers, however, are tetracyclic with two alternating whors of three bristles, three stamens opposite the outer bristles and three carpels opposite the inner bristles, surrounding a central ovule. In the other two genera studied, variation on this general floral bauplan was observed. Eriophorum has many hair-like bristles in several perigonal whors, and they are deciduous with the appearance of three adaxial bristle primordia in the zone where an adaxial inner perianth primordium is expected.

Based on molecular phylogenetic analysis, it has been suggested recently that the Cyperoideae comprises only two subfamilies: the Mapanioideae and the Cyperoideae. In most flowers of the Cyperoideae, the whorl of inner stamens is reduced, resulting in tetracyclic flowers. In the more primitive (scirpoid) genera within the Cyperoideae, the perianth consists of two polysymmetric whors, whereas the perianth parts in the more derived genera have been subject to modifications and/or reduction. Comparative studies of the many silky hairs of Eriophorum and of the eight bristles of Dulichium have given rise to much discussion about their homology.

The spikelet and floral ontogeny in freshly collected inflorescences was investigated using scanning electron microscopy.

Key Results Complete floral ontogenies are presented for Scirpus sylvaticus L., Eriophorum latifolium Hoppe and Dulichium arundinaceum (L.) Britton, with special reference to the perianth. The results in S. sylvaticus confirm the trimerous monocot-like organization of the flower. It is used as a model for floral development in Cyperoideae. In the early developmental stages, the androecium of E. latifolium is surrounded by a massive perigonal primordium, from which the many hair-like bristles originate. Consequently, the stamens develop among the hair primordia, more or less simultaneously. The hairs are arranged in whors, which develop centripetally. The development of the perianth in D. arundinaceum starts with the formation of three initial perianth primordia opposite the stamens. Subsequently, two more abaxial bristle primordia, alternating with the stamens, originate simultaneously with the appearance of three adaxial bristle primordia in the zone where an adaxial inner perianth primordium is expected.

Conclusions The floral development in E. latifolium and D. arundinaceum can be considered as variations upon the scirpoid floral ontogenetic theme.

Key words: Dulichium arundinaceum (L.) Britton, Eriophorum latifolium Hoppe, floral ontogeny, perianth, scirpoid flower, Scirpus sylvaticus L., scanning electron microscopy.
perianth parts, is also compared with the floral ontogenetic pattern in *Scirpus sylvaticus*.

### MATERIALS AND METHODS

Young spikelets of three species were collected with prior permission from several botanic gardens (Table 1) and preserved in FAA (70% ethanol, acetic acid, 40% formaldehyde, 90 : 5 : 5). Floral buds were dissected in 70% ethanol under a Wild M3 (Leica Microsystems AG, Wetzlar, Germany) stereo-microscope equipped with a cold-light source (Schott KL1500; Schott-Fostec LLC, Auburn, NY, USA). The material was washed twice with 70% ethanol for 5 min and then placed in a mixture (1 : 1) of 70% ethanol and DMM (dimethoxy methane) for 5 min. Subsequently, the material was transferred to 100% DMM for 20 min, before it was dried using a CPD 030 critical point dryer (BAL-TEC AG, Balzers, Liechtenstein). The dried samples were mounted on aluminium stubs using Leit-C and coated with gold with a SPI-Module™ Sputter Coater (SPI Supplies, West-Chester, PA, USA). Images were obtained using a JEOL JSM-5800 LV (JEOL, Tokyo) scanning electron microscope at the National Botanic Garden of Belgium in Meise and on a Jeol JSM-6360 (JEOL) at the Laboratory of Plant Systematics (K.U. Leuven).

### RESULTS

#### Scirpus sylvaticus L.

The spikelet of *S. sylvaticus* is indeterminate and consists of many spirally arranged glumes, each subtending a bisexual flower (Figs 1A, B and 2D). Under the apex, a new glume becomes apparent as a rim (Fig. 1A and B). Subsequently, a flower primordium originates in its axil (Fig. 1A, B). The flower primordium then develops two lateral primordia (Fig. 1C) and, slightly later, one abaxial stamen primordium (Fig. 1D–F). Subsequently, the gynoecial primordium (Fig. 1G) and the inner as well as the outer tepal primordium (Fig. 1A–E). The gynoecium primordium is formed as a disc-like structure on the top of the flower primordium (Fig. 1F and G), and it differentiates into an annular ovary primordium surrounding a central ovule primordium (Fig. 1H and I). Subsequently, two adaxial and one abaxial stigma primordia (Fig. 1J) become visible on the annular ovary primordium, opposite the three stamens. The two whorls of tepal primordia differentiate more or less simultaneously. Opposite the outer whorl of three tepals are the stamens. The three inner tepals alternate with the stamens (Fig. 1H–J). The tepal primordia develop slowly into long bristles (Figs 1H–K and 2A–C), becoming scabrid in appearance (Fig. 2F) at the end of anthesis, when the achene is ripening (Fig. 2E). The bristles are deciduous with the fruit (Fig. 2E). When the stigma primordia become apparent, the three stamens differentiate into anthers and filaments (Figs 1K and 2A–C). The ovary wall rises forming a single style without thickened or distinct style base (Fig. 2B). Meanwhile, the three stigma primordia differentiate into three stigmas with a papilllose surface (Fig. 2C). After the differentiation of the anthers (Fig. 1K), the stamens grow rapidly and rise above the gynoecium (Fig. 2A–C).

#### Eriophorum latifolium Hoppe

The spikelet of *E. latifolium* is indeterminate and composed of many spirally arranged glumes, each subtending a bisexual flower (Fig. 3A). Immediately below the apex of the spikelet, a rim-like glume primordium is formed (Fig. 3A). Subsequently, a flower primordium appears in its axil (Fig. 3A, B). Two lateral and one abaxial stamen primordia are formed (Fig. 3A, C). Simultaneously with the development of the stamens and the appearance of the gynoecium primordium, a massive, dome-shaped perigonial zone is differentiated (Fig. 3D) at the base of the flower primordium. The development of the third, abaxial stamen primordium is delayed (Fig. 3E, F).

Numerous ‘hair’ primordia originate on the perigonial zone shortly after the appearance of the stamen primordia (Fig. 3G–K). The initial development of the hairs at the adaxial side of the flower is less prominent (Figs 3G, I and 4A). The hair primordia are arranged in several whorls arising centripetally (Fig. 3J, K). The hairs opposite the lateral stamens tend to grow faster than the other ones (Figs 3I, K and 4A). There are no intrastaminal hair primordia (Fig. 3F–J). The growth of the hairs is relatively slow until the stamens are well developed and reaching out above the gynoecium (Fig. 4A, B). Afterwards, the longest hairs reach until the base of the anthers, at the adaxial as well as at the abaxial side (Fig. 4D, E). Only later, after anthesis, the hairs elongate and develop into the well-known typical silky ‘hairs’ (Fig. 4F), which are deciduous with the fruit (Fig. 4C).

The disc-like gynoecium primordium differentiates into an annular primordium, surrounding a central ovule primordium. On the top of it two lateral stigma primordia become apparent (Fig. 3D, E) and, with some delay, a third abaxial one (Fig. 3F, G). The annular gynoecium primordium grows up from the base, forming the ovary wall (Fig. 3F–H), and at a later stage a single style without distinct transition between style and ovary (Figs 3I and 4A). On the top of the rising ovary wall the stigma primordia grow out into long papilllose stigmas (Figs 3I, J and 4B, D). At this stage, the three stamens develop fast, growing out above the gynoecium (Fig. 4D, E).

### Table 1. Species of Cyperaceae studied

<table>
<thead>
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<th>Taxa</th>
<th>Voucher no. (provenance)</th>
</tr>
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<tr>
<td>Dulichium arundinaceum (L.) Britton</td>
<td>PG9914 (Botanical Garden of the University of Gent, Gent, Belgium)</td>
</tr>
<tr>
<td>Eriophorum latifolium Hoppe</td>
<td>AV04 (Botanical Garden of the City of Leuven, Leuven, Belgium)</td>
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<tr>
<td>Scirpus sylvaticus L.</td>
<td>AV03 (Botanical Garden of the City of Leuven, Leuven, Belgium)</td>
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<tr>
<td>Eriophorum latifolium L.</td>
<td>AV02 (Botanical Garden of the ‘Instituut voor Plantkunde en Microbiologie KUL’, Leuven, Belgium)</td>
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Dulichium arundinaceum (L.) Britton

The spikelet of *Dulichium arundinaceum* is indeterminate (Fig. 5A–C) and consists of four to eight distichously placed glumes, which all of them (including the prophyll) subtend a bisexual flower (Fig. 6E, arrowed). The wings of each glume partially envelop the underlying flower (Fig. 5I, L and 6B, D). Under the apex of the spikelet a rim-like
glume primordium appears (Fig. 5A–C). While the glume is increasing in size, its midrib protrudes and a flower primordium appears in its axil (Fig. 5A, B). Subsequently, on the flower primordium, three zones can be recognized; a basal perigonial primordium, a central primordial tissue from which the three staminal primordia originate, and an apical gynoecium primordium (Fig. 5D–F). The perigonial primordium can be distinguished as a separate dome-like mass with two lateral and one abaxial, congenitally fused, perianth part primordia (Fig. 5E, F, arrowed). On the central zone of the flower primordium two lateral, and a third, abaxial stamen primordium appear (Fig. 5E). Subsequently, at both sides of the initial abaxial perianth part primordium, and alternating with the stamens, an extra bristle primordium appears (Fig. 5G). Simultaneously, three adaxial bristle primordium become apparent (Fig. 5H, I). The three abaxial, the two lateral, and the three adaxial bristle primordium develop into eight separate bristles (Fig. 5J–L and 6A–D), which, at maturity, have a scabrid surface (Fig. 6G). They are deciduous with the fruit (Fig. 6G). The apical, disc-like gynoecium primordium (Fig. 5D) differentiates into an annular ovary primordium (Fig. 5E). On the top of the annular ovary primordium two lateral stigma primordia are formed (Fig. 5E, F). The ovary primordium grows up from the base, surrounding the central ovule primordium, and forming an ovary wall (Fig. 5F–H). Meanwhile, the three initial staminal bulges develop into stamens (Fig. 5F–L). The rising ovary wall forms a single style (Fig. 5H) without transition between style and ovary (Fig. 6C). The two stigma primordia elongate and differentiate into two long stigmas (Figs 5K and 6A–C, E), which become papillose (Fig. 6E, F). At maturity, they rise high above the stamens (Fig. 6E).

Scirpoides holoschoenus (L.) Sojak

The spikelet is indeterminate and the glumes are spirally arranged (Fig. 7A). Under the apex, a new glume becomes apparent as a rim (Fig. 7A). Subsequently, a flower primordium is formed in its axil (Fig. 7A). Soon, the flower primordium expands laterally, forming two lateral stamen primordia, more or less simultaneously with the formation of a third, abaxial stamen primordium (Fig. 7A and B).
Fig. 3. Floral ontogeny in *Eriophorum latifolium* Hoppe. Abbreviations: a, stamen (primordium)/anther; FP, flower primordium; G, glume; g, gynoecium (primordium); P, perianth; o, ovule (primordium); sg, stigma (primordium); st, style; *, rachilla apex. (A) Spikelet apex, lateral view, with distichously positioned glumes, each subtending a flower at successive stages of floral development (numbered 1–4). In ‘1’, a glume is being formed. In ‘2’, a flower primordium originates in the axil of the subtending glume. In ‘3’, three stamen primordia are developing. In ‘4’, most of the developing flower is hidden behind the subtending glume. Notice the torsion in the apical part of the spikelet. (B) Apical view of a spikelet apex with two flower primordia at a very early stage of development. The most advanced flower primordium (FP2) is expanding laterally. (C) Apical view of a flower primordium in which two lateral stamen primordia are starting to develop. (D) Differentiation of the gynoecium primordium into an annular ovary wall primordium, with lateral stigma primordia on its top. Notice the massive perigonial primordium at the base of the flower primordium. (E) Lateral–abaxial view of a developing flower. The development of the abaxial stamen primordium is delayed (arrowed). (F) Abaxial view of a developing flower. An abaxial stigma primordium appears. (G) Adaxial view. Same stage as in (F). (H) Centripetal initiation of whorls of hairs (arrowed). Note the delay of the development of the abaxial stamen with respect to the two lateral stamens. (I) Adaxial view of a developing flower. The development of the adaxial hairs is delayed. (J) Apical view of a developing flower. The three stigmas become papillose. (K) Lateral–adaxial view of a developing flower. The adaxial hairs start developing. Note the advanced development of the hairs opposite the lateral stamen.
Meanwhile, a gynoecium primordium appears (Fig. 7B) on the top of the flower primordium. It differentiates into an annular ovary primordium surrounding a central ovule (Fig. 7C). At a later stage, the ovary primordium grows up from the base, forming an ovary wall (Fig. 7D). On the top of the ovary wall, three stigma primordia appear (Fig. 7D). Meanwhile, the stamens start differentiating into filaments and anthers (Fig. 7D). At an intermediary stage, the stamens have grown out above the gynoecium, and the apical part of the connective becomes spiny (Fig. 7E). The stigma primordia develop into three stigmas (Fig. 7F).

**DISCUSSION**

Much of the controversy relating to floral and inflorescence morphology in Cyperaceae arises from the interpretation of a flower according to either the ‘euanthial’ or ‘synanthial’ hypotheses. Scirpoid flowers have been described as conventional flowers with a typical trimerous monocotyledonous arrangement. Alternatively, they have been considered to be composed of floral structures derived from a partial inflorescence with several floral units. According to Sattler (1973), the existing terminology to describe floral organogenesis is often interpretative. For example, based on vasculature patterns, Blaser (1941) named the outer whorl of cyperaceous perianth parts ‘calyx’ and the inner ‘corolla’. Sattler (1973) used the word ‘tepals’ for perianth members in Cyperaceae. Mora-Osejo (1987) considered the inner perianth parts to be ‘petals’. However, perianth parts were also named ‘bracts’ (Mattfeld, 1938; Kern, 1962) or ‘glumellae’, both terms suggesting leaf-like structures that each axillate a stamen (e.g. Meert and Goetghebeur, 1979; Goetghebeur, 1986). Actually, most authors designate the cyperaceous bristle- or scale-like perianth structures as ‘perianth parts’, ‘perianth bristles’, ‘bristles’ or ‘scales’. In an attempt to describe objectively the floral ontogeny in cyperoid flowers, the term ‘tepals’ is used when all perianth parts are similar. If there are morphological differences between the outer and inner perianth parts, the outer perianth parts may be named ‘sepals’ and the inner ones ‘petals’ (e.g. Leins, 2000). In the Cyperoideae morphological differences between the inner and outer whorls of the perianth parts occur in some genera, e.g. *Fuirena* Rottb. (Forbes, 1997; Vrijdaghs et al., 2004), and the number of perianth parts may also be greater than six (e.g. *Dulichium*). In these cases, the general term ‘perianth part’ is used. In *Eriophorum*, with its many hair-like bristles, the word ‘hairs’ is also used to indicate the perianth parts.
Scirpus sylvaticus L.

Payer (1857) described the bristles of *Scirpus palustris* L. as originating from the flower receptacle. According to him, first the stamen primordia protrude as two lateral bulges and an abaxial one, followed by the appearance of the gynoecium, and eventually the bristle primordia. According to Sattler (1973) the development of the flower primordium of *S. validus* Vahl starts with the formation of two lateral...
outer tepal primordia’, followed by the appearance of two lateral stamen primordia. Mora-Osejo (1987) described the floral ontogeny of *S. lacustris* L. in a similar way. The present results show the initial formation of two lateral bulges in *S. sylvaticus*. However, treating them as outer tepal primordia seems to the authors as rather interpretative (Fig. 1C–G). Sattler’s (1973) interpretation needs further explanation regarding the fact that the perianth primordia are not visible between the formation of the lateral bulges and the later stage where they reappear. The perianth members grow slowly, which, according to Sattler (1973), might explain why he observed the abaxial outer tepal only after the initiation of the stamen primordia. However, the floral ontogeny of *S. sylvaticus*, when compared with the floral ontogeny of *Scirpoides holoschoenus*, a species without perianth parts, shows no significant differences in the earliest stages (Figs 1C–G and 7A and B). Therefore, the two lateral bulges that appear first are stamen primordia. The two whorls of tepals develop unambiguously only after the formation of the three stamen primordia (Fig. 1G and H). The outer whorl consists of three tepals opposite the stamens, the inner whorl of three tepals alternating with the stamens. Similar floral ontogenetic patterns were also observed in more distant Cyperoideae taxa such as Fuireneae (Vrijdaghs et al., 2004), and in *Schoenus nigricans* L. (Vrijdaghs et al., 2005).
Fig. 7. Floral ontogenetic stages in *Scirpoides holoschoenus* L. Abbreviations: a, stamen (primordium)/anther; ac, achene; f, filament; G, glume; g, gynoecium (primordium); o, ovule (primordium); ov, ovary (primordium); sg, stigma (primordium); st, style; *, rachilla apex. (A) Apical view of spikelet apex with five successive stages of floral development (numbered 1–5). In ‘1’, a rim-like glume primordium originates. In ‘2’, a flower primordium is being formed in the axil of a glume. In ‘3’ and ‘4’, the flower primordium is expanding laterally. In ‘5’, three stamen primordia are starting to develop. (B) Detail of an early developmental stage of a flower, abaxial view. Three stamen primordia have appeared, and on the top of the flower primordium, a disc-like gynoecium primordium is formed. (C) Abaxial view of a developing flower. The gynoecium primordium is differentiating into an annular ovary wall primordium, surrounding a central ovule primordium. (D) Abaxial view of a developing flower. Stigma primordia opposite the three stamens become apparent. (E) Lateral–abaxial view of a developing flower. One lateral stamen has been removed. The ovary wall grows up from its base. The stamens start differentiating into filament and anthers. Notice the delay in development of the abaxial stamen. (F and G) Abaxial (F) and adaxial (G) view of a nearly mature flower. Note the connective crests on the top of each anther. (H) Mature flower, seen from the adaxial side. (I) Achene with persistent filaments and stigmas.
Eriophorum latifolium Hoppe

Eriophorum, with its many spirally arranged glumes each subtending a bisexual flower, is considered to be very close to Scirpus. The rather artificial separation of both genera is based on the number of perianth parts (Goetghebeur, 1998). Species with six or less perianth parts belong to Scirpus, while species with ten or more perianth parts belong to Eriophorum. However, the perigonal structure of Eriophorum is morphologically different from the trimerous scirpoid perianth. Mora-Osejo (1987) interpreted the ‘perianth parts’ of flowers in Eriophorum as ‘... estructuras sui generis, que se originan “de novo” a partir de la protuberancia meristemática semicircular, resultante del agrandamiento y fusión de los primordios perigonales individuales’ (Mora-Osejo, 1987, p. 23). This seems to agree with Blaser (1941), who stated that the hair-like bristles of E. angustifolium grow faster and appear to be larger where perianth parts could be expected. The present SEM observations in *E. latifolium* confirm that the hairs originate in several whorls, though without any particular relation in number (nor placement) to the staminal or gynoecial primordia. Fields of hairs corresponding to the positions where perianth parts are to be expected (opposite the stamens and opposite the sides of the ovary) were not observed, though the hairs in the zones opposite the lateral stamens tend to grow faster and longer (Figs 3K and 4A). On the other hand, the authors agree with Mora-Osejo’s (1987) interpretation that the perigonial primordium is a structure resulting from congenital fusion of individual bristle primordia. They consider it to be homologous with a scirpoid perianth because (a) its position in the flower and (b) all other flower parts in *E. latifolium* develop according to the the scirpoid pattern. In *E. latifolium* the apical part of the flower primordium expands laterally, before the initiation of the perigonial primordium (Fig. 3A). If the floral development in Eriophorum follows the same sequence as Sattler (1973) observed in Scirpus, the lateral bulges should logically be considered to be perigonial primordia. However, since the early floral ontogeny in Eriophorum does not differ essentially from the early floral ontogeny in Scirpoides holoschoenus (L.) Sojak, the authors consider the initial two lateral bulges, as they did in Scirpus sylvaticus, to be staminal primordia.

Dulichium arundinaceum (L.) Britt.

Mattfeld (1938) used Dulichium as an argument in favour of his synanthium hypothesis. He considered the five bristles at the abaxial side to be fused, and interpreted them to be the remaining veins of one simple bract, which subtended the three stamens. In the same way he interpreted the three remaining adaxial bristles as one intrastaminal bract, subtending the gynoecium, being the female flower. Hence, Mattfeld (1938) concluded that bisexual flowers are derived from the reduction of partial inflorescences consisting of unisexual flowers. However, based on anatomical studies, Blaser (1941) did not agree with Mattfeld’s (1938) interpretation of the bristles of Dulichium as the veins of two different bracts. According to Blaser (1941), sepals can be modified by splitting up along the midvein and the two lateral veins, resulting in three separate bristles. The loss of parts of such tri-partite ‘sepals’ occurs so that one ‘sepal’ can be reduced to two bristles or even one. ‘Petals’ are never increased in number, though they might partially split, or be absent. He considered that the eight bristles in *D. arundinaceum* result from the one bristle-like abaxial ‘sepal’, consisting of the median vein of the ancestral sepal, the two lateral ‘sepals’ each reduced to a bristle consisting of the median vein and a bristle consisting of one lateral vein, and the three reduced, bristle-like ‘petals’.

Mora-Osejo (1987), on the basis of a floral ontogenetic study, stated that all perianth parts in *D. arundinaceum* are positioned extrastaminally. Moreover, he concluded that the floral ontogenies in *D. arundinaceum* and in Scirpus lacustris L. are similar. The present results support this conclusion. During floral ontogeny, three perianth primordia homologous with the perianth parts of the outer whorl are formed first. At a later stage, three bristle primordia appear at the adaxial side of the ovary, in a zone where the adaxial inner perianth part primordium is expected. The authors consider these three adaxial bristles to be homologous with the inner adaxial perianth member as observed in Scirpus sylvaticus L. More or less simultaneously, at both sides of the original abaxial bristle primordium and alternating with the stamens, an extra bristle primordium becomes apparent (Fig. 5F), which the authors consider to be homologous with the inner tepals in Scirpus. Therefore, they conclude that the floral ontogeny of *D. arundinaceum* follows a scirpoid pattern.

**CONCLUSIONS**

Floral structure and development in Scirpus sylvaticus may serve as a model for all scirpoid flowers, even flowers with more than six perianth parts, as found in Dulichium or Eriophorum. A typical scirpoid floral ontogeny starts with the formation of a floral primordium in the axil of a subtending glume. Subsequently, two lateral stamen primordia are formed, usually followed by a third, abaxial stamen primordium. Only then do the perianth primordia appear, more or less simultaneously. Three outer perianth parts are positioned opposite the stamens, and three inner perianth parts alternate with the stamens.

In Eriophorum latifolium, the perianth originates from one circular perigonial primordium. The hair-like bristles develop centripetally, arising in several whorls. No bristles are found intrastaminally. The perigonial primordium of *E. latifolium* is interpreted as resulting from a congenital fusion of individual perianth primordia and it is considered to be homologous with the perianth primordia in Scirpus.

In Dulichium arundinaceum three initial perianth primordia are formed opposite the stamens, forming the outer whorl of perianth parts. Subsequently, three adaxial (homologous with the scirpoid adaxial inner tepal) and two extra abaxial bristle primordia (homologous with the scirpoid abaxial inner tepals), which alternate with the stamens, originate. It is concluded that floral development in *E. latifolium* and *D. arundinaceum* can be considered as variations upon the scirpoid floral ontogenetic theme.
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LITERATURE CITED