

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

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• **Background and Aims** Based on molecular phylogenetic analysis, it has been suggested recently that the Cyperaceae 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 whorls, 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.

• **Methods** 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 perigonial 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 whorls, 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.

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 whorls 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 perigonial whorls, and they are deciduous with the fruit (Mora-Osejo, 1987; Goetghebeur, 1998). *Dulichium*, which is traditionally placed in the Dulichieae together with *Blysmus* Panzer ex Schultes and *Sumatrosirpus*

Oteng-Yeb. (e.g. Goetghebeur, 1998), possesses bisexual flowers with mostly eight bristles.

As Bruhl (1991, 1995) stated earlier, there are still many questions about the interpretation of partial inflorescences and flowers in the Cyperaceae. Some authors have considered cyperaceous flowers to be synanthia, resulting from the reduction of partial inflorescences with a terminal female flower and numerous male flowers. According to the synanthium (Mattfeld, 1938) and the anthocorm (Meeuse, 1975a, b) hypotheses, tepals (bristles) were defined in the past as bracts or as ‘glumellae’ (e.g. Meert and Goetghebeur, 1979). The perianth in *Dulichium*, with its eight bristles, has been used to argue in favour of both views (e.g. Mattfeld, 1938; Blaser, 1941; Kern, 1962).

In this study, the floral ontogenies of *Scirpus sylvaticus* L., *Eriophorum latifolium* Hoppe and *Dulichium arundinaceum* (L.) Britton are presented. The organization and floral ontogeny of the flowers in *S. sylvaticus* as a model for Cyperoideae flowers is used. *Eriophorum* has traditionally been considered to be a scirpoid genus (e.g. Goetghebeur, 1998), though its flowers have a very unusual perianth. *Dulichium* was selected for this study because of its perianth with eight bristles. The floral ontogeny of *Scirpoides holoschoenus* (L.) Soják, a genus without

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TABLE 1. *Species of Cyperaceae studied*

Taxa	Voucher no. (provenance)
<i>Dulichium arundinaceum</i> (L.) Britton	PG9914 (Botanical Garden of the University of Gent, Gent, Belgium)
<i>Eriophorum latifolium</i> Hoppe	AV04 (Botanical Garden of the City of Leuven, Leuven, Belgium)
<i>Scirpoides holoschoenus</i> (L.) Soják	AV03 (Botanical Garden of the City of Leuven, Leuven, Belgium)
<i>Scirpus sylvaticus</i> L.	AV02 (Botanical Garden of the 'Instituut voor Plantkunde en Microbiologie KUL', Leuven, Belgium)

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 (dimethoxymethane) 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-ModuleTM 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 gynoeceal primordium (Fig. 1G) and the inner as well as the outer tepal primordia (Fig. 1H, arrowed) appear. Meanwhile, the subtending glume increases in size and protrudes along its midrib (Fig. 1A–E). The gynoeceum 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 papillose surface (Fig. 2C). After the differentiation of the anthers (Fig. 1K), the stamens grow rapidly and rise above the gynoeceum (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). Simultaneous with the development of the stamens and the appearance of the gynoeceum primordium, a massive, dome-shaped perigonal 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 perigonal 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 gynoeceum (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 gynoeceum 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 gynoeceum 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 papillose stigmas (Figs 3I, J and 4B, D). At this stage, the three stamens develop fast, growing out above the gynoeceum (Fig. 4D, E).

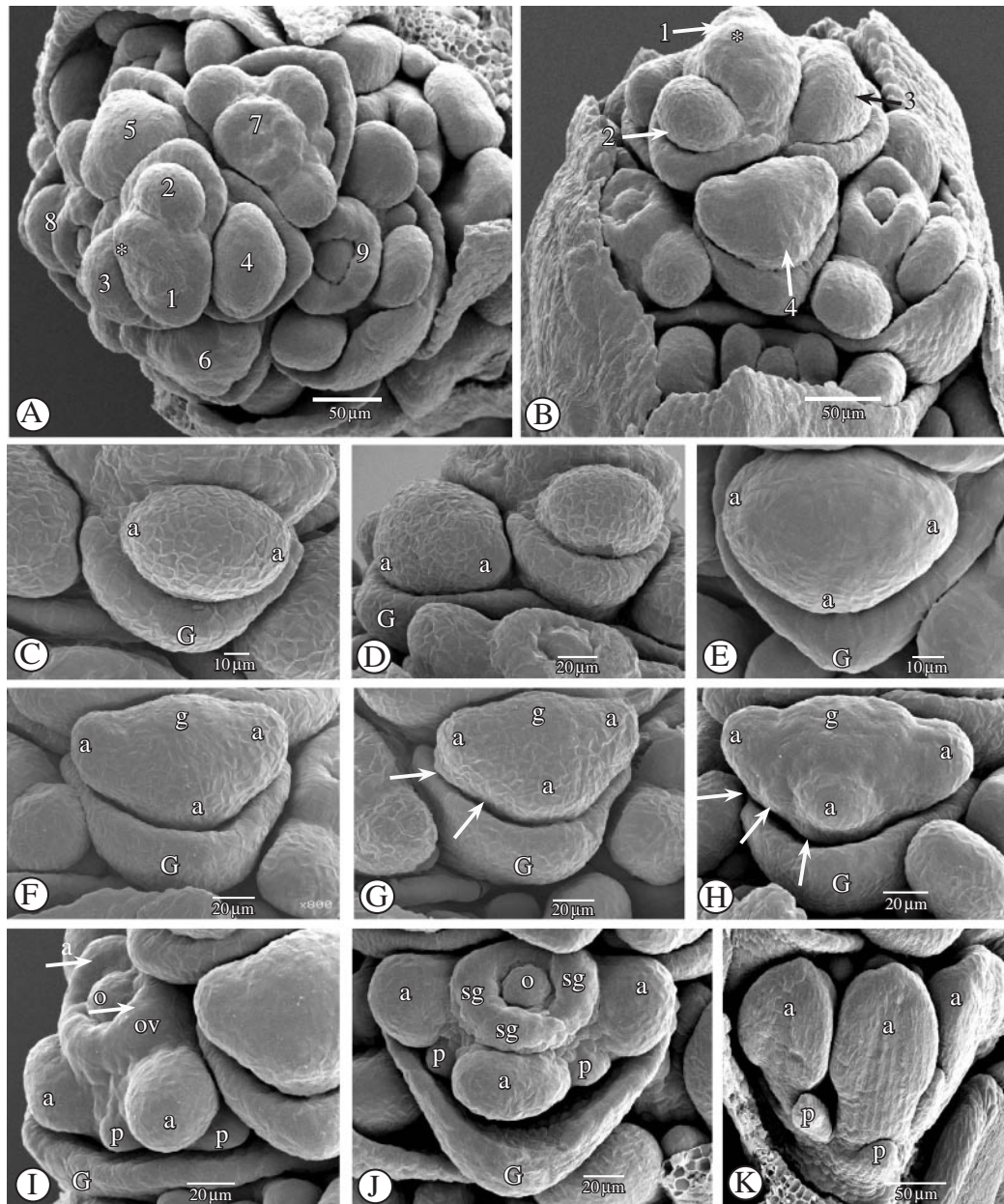


FIG. 1. Floral ontogeny in *Scirpus sylvaticus* L. Abbreviations: a, stamen (primordium)/anther; G, glume; g, gynoecium (primordium); p, tepal (primordium); o, ovule (primordium); ov, ovary; sg, stigma (primordium); *, rachilla apex. (A) Apical view of the apex of a spikelet with spirally arranged glumes and several successive stages of floral development, numbered 1–9. (B) Lateral view of the apex of a spikelet with successive stages of the development of flowers and flower subtending glumes, numbered 1–4. In '1', a rim-like glume primordium is being formed. In '2', a flower primordium is apparent in the axil of the subtending glume. In '3', the flower primordium expands laterally. In '4', three stamen primordia are starting to develop. (C) Flower primordium in the axil of a glume, apical–abaxial view. At the lateral sides stamen primordia start bulging out. (D) Detail of early successive stages of developing flowers under the spikelet apex. In the most advanced flower (left-hand side), the abaxial stamen primordium is being formed. No perianth primordia can be observed at this stage. (E) Apical view of a flower with the three stamen primordia starting to develop. (F) Abaxial view of a developing flower with stamen initiation. Notice the appearance of the gynoecium primordium on the top of the flower primordium. (G) Abaxial view of a developing flower. The perianth primordia become visible (arrowed). (H) Abaxial view of a developing flower. The gynoecium primordium becomes a disc-like structure. Note the inner and outer perianth primordia (arrowed). (I) Lateral view of a developing flower. Primordia of all flower parts are present. The gynoecium primordium has differentiated into an annular ovary wall primordium, surrounding the central ovule. On the top of it two lateral stigma primordia appear (arrowed). (J) Apical view of a developing flower. The stamens start differentiating into a filament and anthers. The abaxial stigma primordium becomes apparent. (K) Abaxial view of a developing flower with differentiation of the stamens into filament and anthers.

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

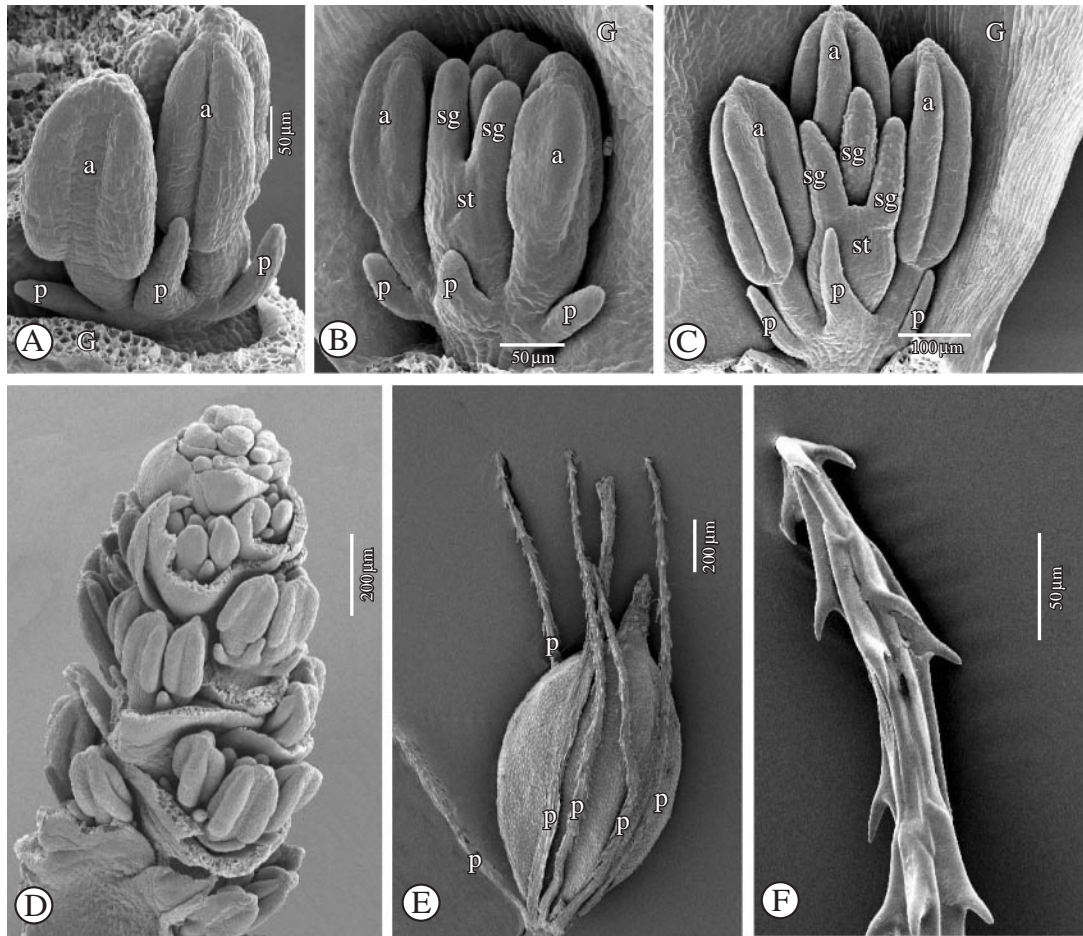


FIG. 2. Floral ontogeny in *Scirpus sylvaticus* L. Abbreviations: a, stamen (primordium)/anther; G, glume; p, tepal; sg, stigma (primordium); st, style. (A) Lateral-abaxial view of a developing flower. The bristles are growing out. (B) Adaxial view. Same stage of development as in (A). The ovary wall has formed a single style and the three stigmas are growing. (C) Adaxial view of a developing flower. The surface of the stigmas becomes papillose, and simultaneously on the top of the anthers connective crests are formed. (D) Lateral view of a complete spikelet as a typical example of a racemose partial inflorescence with acropetally developing flowers. (E) Achene with persistent bristles. Note the beak at the top of the nutlet. (F) Detail of a mature bristle.

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 primordia become apparent (Fig. 5H, I). The three abaxial, the two lateral, and the three adaxial bristle primordia develop into eight separate bristles (Fig. 5J–L and 6A–D), which, at maturity, have a scabrid surface (Fig. 6G) and are longer than the nutlet. 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.) Soják

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).

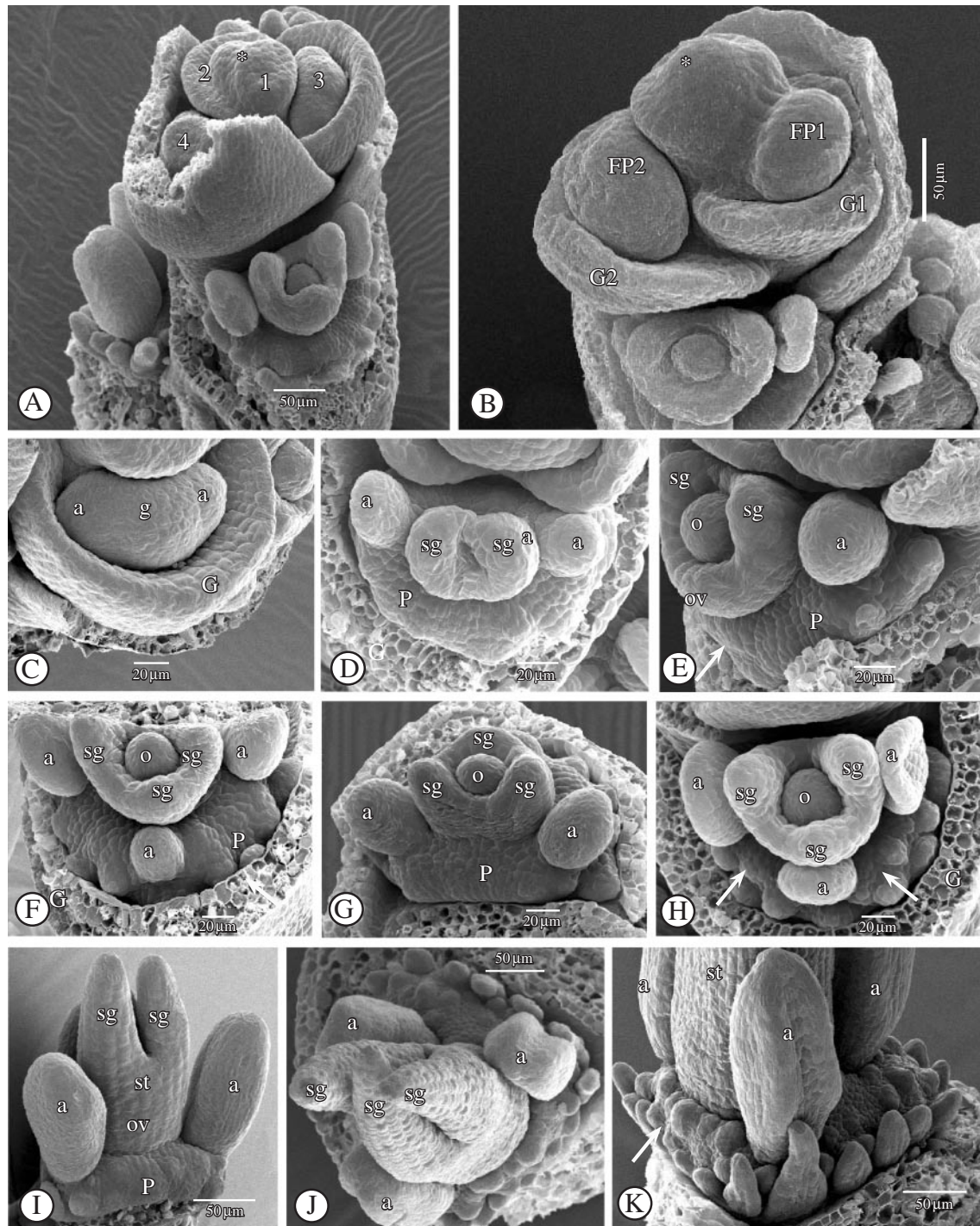


FIG. 3. Floral ontogeny in *Eriophorum latifolium* Hoppe. Abbreviations: a, stamen (primordium)/anther; FP, flower primordium; G, glume; g, gynoecium (primordium); P, perianth; o, ovule (primordium); sg, stigma (primordium); st, style; *, rachilla apex. (A) Spikelet apex, lateral view, with distichously 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.

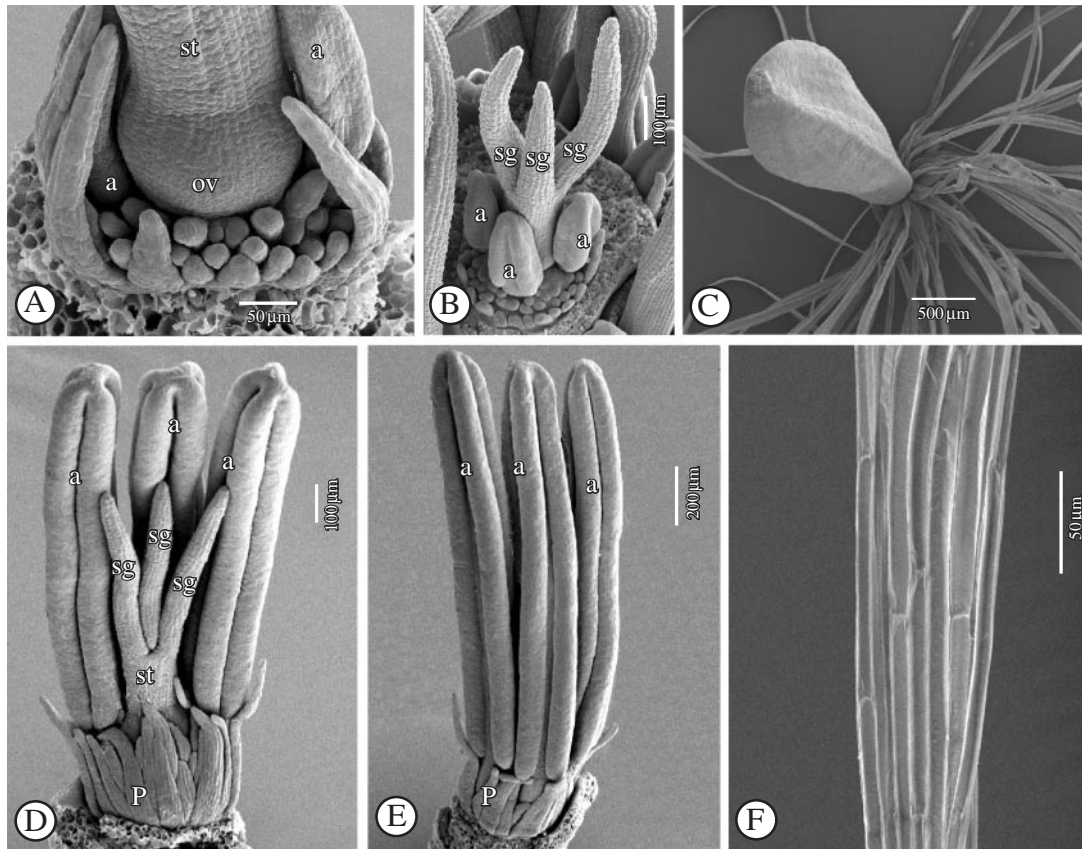


FIG. 4. Floral ontogeny in *Eriophorum latifolium* Hoppe. Abbreviations: a, stamen/anther; P, perianth; ov, ovary; sg, stigma; st, style. (A) Adaxial view of a developing flower. Notice the centripetal development of the perigonium, and the advanced development of the bristles opposite the lateral stamens. (B) Apical–abaxial view of a developing flower. The surface of the three stigmas is becoming papillose. (C) Achene with persistent hairs. (D–E) Adaxial (D) and abaxial (E) view of the same flower at nearly mature stage. The stamens are growing up above the gynoecium, and the hairs are developing rapidly. Note the advancement of the hairs opposite the lateral stamens. (F) Detail of a hair.

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 Cyperoidae 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.

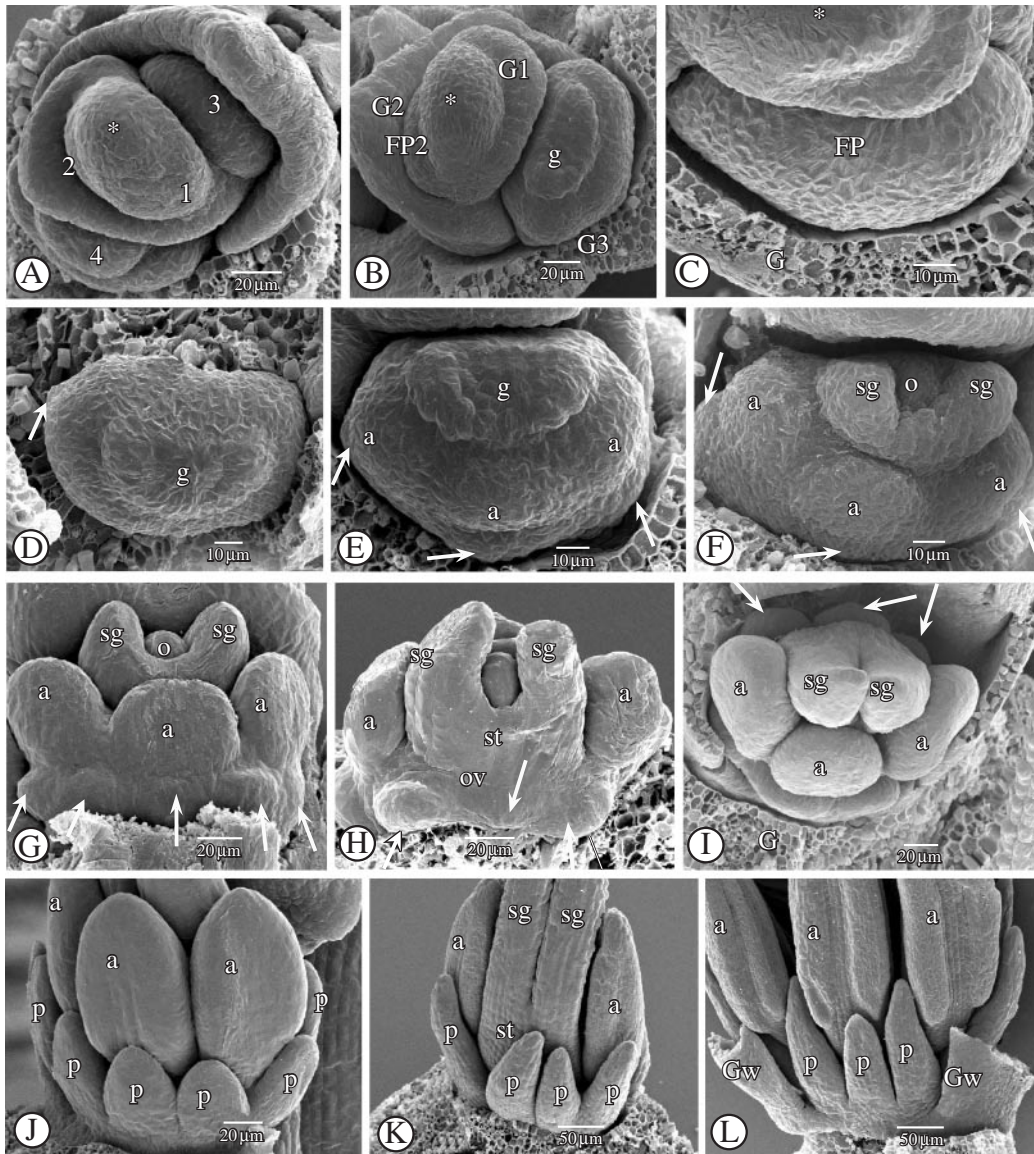


FIG. 5. Floral ontogeny in *Dulichium arundinaceum* (L.) Britton. Abbreviations: a, stamen (primordium)/anther; FP, flower primordium; G, glume; g, gynoecium (primordium); Gw, wing of the next glume; p, bristle (primordium); o, ovule (primordium); sg, stigma (primordium); st, style; *, rachilla apex. (A) Apical view of the apex of a spikelet with four very early stages of floral development, numbered 1–4. In '1', a glume primordium is originating. In '2', the glume is protruding along its midrib and a flower primordium is originating in its axil. In '3', the flower primordium is expanding laterally. In '4', a disc-like gynoecium primordium can be seen on the top of the flower primordium. (B) Apical view of a spikelet apex. Below the apex, a glume is differentiating (G1). Opposite and more proximal, glume G2, subtending the yet undifferentiated flower primordium FP2, can be seen. Under G1, there is a developing flower primordium, subtended by glume G3, on which a disc-like gynoecium primordium becomes apparent. (C) Abaxial view of a very early flower primordium. The subtending glume has been removed. (D) Apical view of a flower primordium with three primordial zones: basally the perigonal zone (arrowed), a central zone, and apically the gynoecium primordium. (E) Abaxial view of a flower primordium, in which the differentiation of two lateral and one abaxial stamen primordia becomes apparent, as well as the initiation of an annular ovary primordium with two lateral stigma primordia on its top. Basally, three perianth part primordia (arrowed) appear. (F) Abaxial view of a developing flower. The stamen primordia are now visible and the ovary wall grows up from the base, surrounding the central ovule. Note the three perianth part primordia (arrowed). (G) Abaxial view of a developing flower. The stamens are developing and the ovary wall is rising. Notice the appearance of two bristle primordia, alternating with the stamens, at both sides of the initial abaxial perianth primordium (all bristle primordia arrowed). (H) Adaxial view of a flower at the same stage as in (G). Note the three adaxial bristle primordia. The central one is arrowed. (I) Apical view of a developing flower with two stigmas. Note the three bristle primordia at the adaxial side (arrowed). (J) Abaxial view of a flower with six developing bristles. The stamens are differentiating into anthers and filaments. (K) Adaxial view of a developing flower, with the three growing adaxial bristles and a lateral one (left). (L) Abaxial view of a developing flower, with the remains of the wings of the next glume. The lateral bristles are growing faster.

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

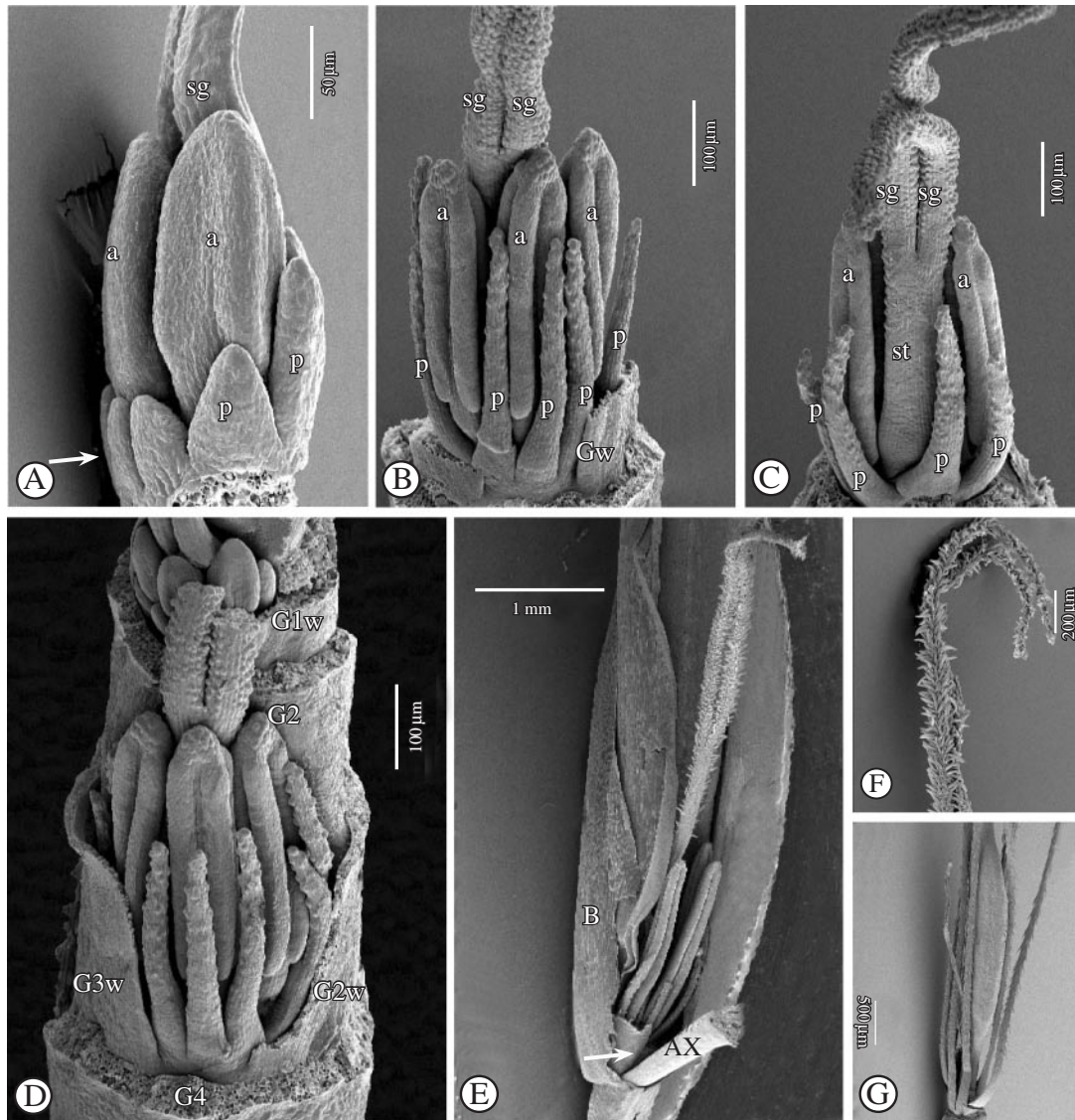


FIG. 6. Floral ontogeny in *Dulichium arundinaceum* (L.) Britton. Abbreviations: a, stamen/anther; AX, relative main axis; B, bract; G, glume; Gw, glume wings; p, bristle; sg, stigma; st, style. (A) Lateral view of a developing flower, with five developing bristles. (B) Abaxial view of a nearly mature flower. The surface of the bristles becomes scabrid. Connective crests appear on the top of each anther. The stigmas become papillose. (C) Same stage as in (B) adaxial view. Note the single style without distinctive style base. (D) Detail of a proximal part of a spikelet. Note how the wings of the next glume partially envelop the underlying flower. Four flowers at different stages of development are visible (numbered 1–4). (E) Lateral view of an entire spikelet. The prophyll has partially been removed (arrowed) and the relative main axis is folded aside, in order to visualize the flower subtended by the prophyll. (F) Mature stigmas. (G) Nutlet with persistent bristles.

‘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 Cyperoidae taxa such as Fuireneae (Vrijdaghs *et al.*, 2004), and in *Schoenus nigricans* L. (Vrijdaghs *et al.*, 2005).

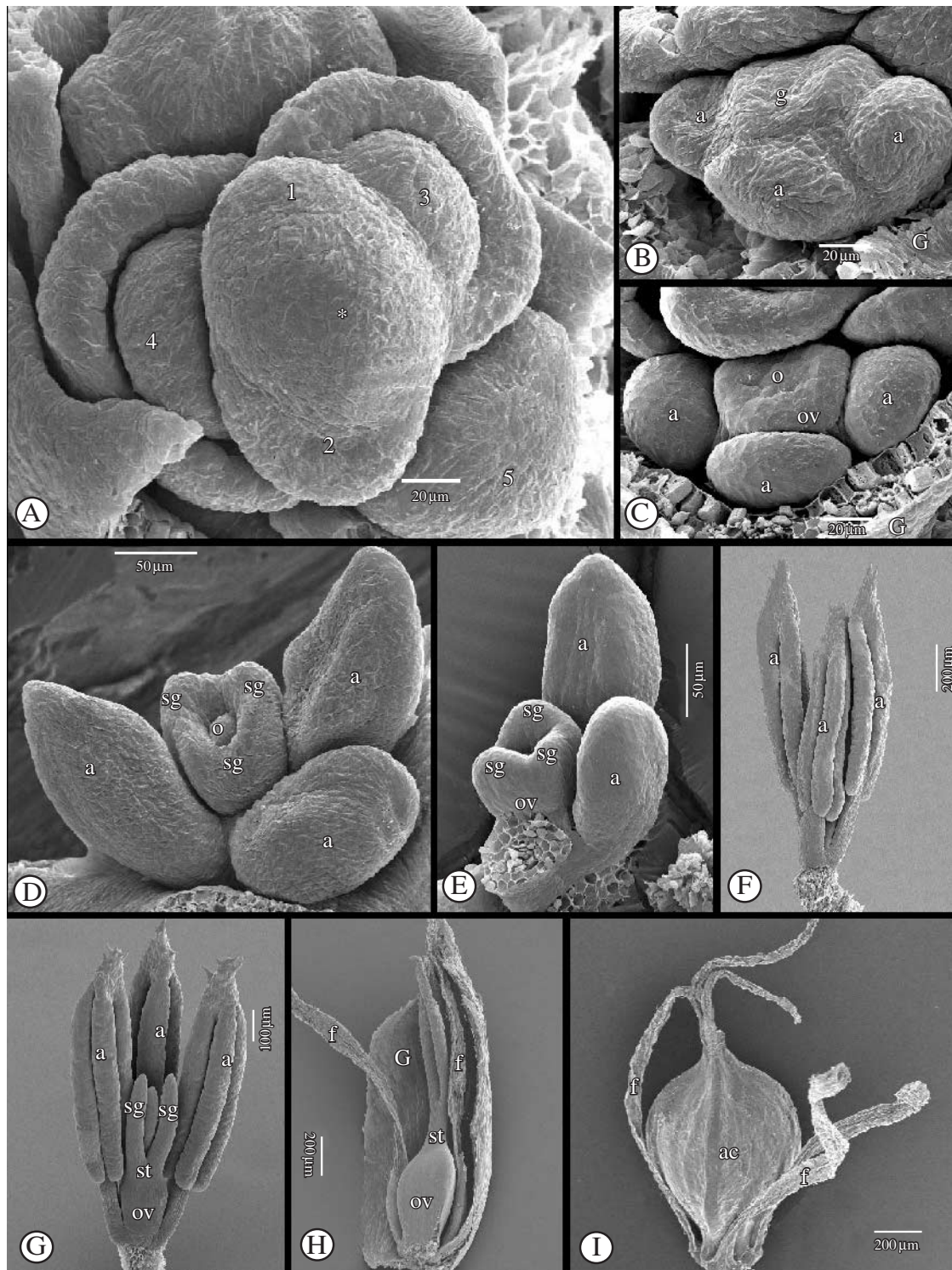


FIG. 7. Floral ontogenetic stages in *Scirpoides holoschoenus* L. Abbreviations: a, stamen (primordium)/anther; ac, achene; f, filament; G, glume; g, gynoecium (primordium); o, ovule (primordium); ov, ovary (primordium); sg, stigma (primordium); st, style; *, rachilla apex. (A) Apical view of spikelet 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 stamens. (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 géneris, que se originan "de novo" a partir de la protuberancia meristemática semicircular, resultante del agradamiento 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 perigonal primordium is a structure resulting from congenital fusion of individual bristle primordia. They consider it to be homologous with a scirpoid perianth because (a) of its position in the flower and (b) all other flower parts in *E. latifolium* develop according to the scirpoid pattern. In *E. latifolium* the apical part of the flower primordium expands laterally, before the initiation of the perigonal 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 perigonal primordia. However, since the early floral ontogeny in *Eriophorum* does not differ essentially from the early floral ontogeny in *Scirpoides holoschoenus* (L.) Soják, 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 perigonal primordium. The hair-like bristles develop centripetally, arising in several whorls. No bristles are found intrastaminally. The perigonal 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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