

Ontogeny and evolution of the flowers of South African Restionaceae with special emphasis on the gynoecium

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Abstract. The South African Restionaceae make up a highly diverse group of genera displaying several reductive trends in the configuration of the flower, especially in the gynoecium. In this paper the floral ontogeny of fourteen species representing nine of the 11 genera of the *Restio* clade is studied with the SEM. Although flowers are basically simple, the variability in both mature and developmental stages is striking. Differences between species are the result of changes in growth rate, coupled with differential pressures of organs. Trends in the elaboration of bracts, perianth, androecium and gynoecium are compared. Together with data that have been presented elsewhere about the other clade of African Restionaceae, viz. the *Willdenowia*-clade, a scheme with potential developmental pathways is proposed and the most evident routes are selected based on ontogenetic evidence. Nine possible reductions are presented arising through three main routes.

Key words: Restionaceae, *Restio* clade, *Willdenowia* clade, Floral ontogeny, gynoecium, reductions, scanning electron microscopy, staminodes.

Introduction

There has been considerable progress in the understanding of the phylogenetic patterns in

the African Restionaceae since the earlier taxonomic treatments of Masters (1869, 1878), Pillans (1928) and Gilg-Benedict (1930). While Masters and Pillans based the generic delimitation and grouping entirely on the spikelet and flower morphology, Gilg-Benedict also incorporated anatomical data, and Linder (e.g. 1984, 1991) used, in addition, palynological and phytochemical data. More recently DNA sequence data were also incorporated (Eldenäs and Linder 2000, Linder 2000). These diverse data sets lead to a phylogenetic framework within which the morphological evolution in the family can be studied. Phylogenetic investigations using molecular (Eldenäs and Linder 2000), as well as morphological data (Linder et al. 1998, 2000), or a combination of both (Eldenäs and Linder 2000, Linder 2000) have provided a strong signal for the existence of two major clades within the South African Restionaceae which also represent a clade separate from the Australian Restionaceae: a *Willdenowia*-clade, comprising eight genera and ca. 55 species, and a *Restio*-clade comprising ten genera and ca. 280 species. The Restionaceae confined to the Cape Kingdom also have the greatest incidence of reductive trends for the family.

As discussed in Linder (1992a, b) and Ronse Decraene et al. (2001) the Restionaceae show a tremendous variation in the reduction of flowers, especially in the gynoecium. The gynoecia of the Restionaceae range from three fully fertile carpels, each with a separate style, to fertile and sterile carpels with variable number and position, to a single carpel. A single reduction event in carpel number is incongruent with the culm anatomy, pollen morphology, spikelet morphology, chemotaxonomy, and *trnL-trnF* sequence data (Linder 1984, 2000; Linder et al. 2000; Eldenäs and Linder 2000). Instead, the reductions appear to have followed several routes, so manifesting much parallelism in evolution. When mapped on the most parsimonious cladogram for the south African Restionaceae, reductions appear at least seven times. To unravel such parallelisms it is necessary to study the ontogeny of flowers and gynoecia in detail.

There are two ways of investigating gynoecial reduction: one based on the comparison of mature carpels, including anatomical observations, the other on investigating the ontogenetic sequence of carpel initiation. While the comparison of the mature carpels is easy, since it is based on anthetic flowers which can be readily collected, and on anatomical and morphological studies, it may have less resolution than the ontogenetic methodology. However, the latter is more difficult, needing the right developmental stages of flowers, and requiring electron microscopic investigations. A comparative anatomical study was conducted by Linder (1992a, b), and found evidence for what carpel relative to the floral axis is retained or lost. However, this study lacks evidence on the ontogeny of carpel reduction, and details describing the reductional pathway and degree of sterilisation. Sterile carpels may be similar to fertile carpels except that they bear ovule rudiments or no ovules at all; the development may be truncated at an early ontogenetic stage, or they may be lost entirely. Indeed, mature gynoecia may look similar but can have arisen in highly different ways. By comparing ontogenies of the gynoecia of

representative species it is possible to reconstruct the character phylogeny of carpel losses in the Restionaceae. Early floral ontogeny has great potential in understanding mature structures, as well as testing hypotheses concerning systematic relationships within the Restionaceae (see also Ronse Decraene et al. 2001). Therefore, the study of the ontogeny of flowers is important to back the results obtained by the molecular data; on the other hand the use of the phylogenetic framework obtained by molecular characters makes it possible to map the evolution of morphological characters more accurately. This ontogenetic information gathered from both studies can be set up in valuable characters and character states that we want to plot on available cladograms planned as a forthcoming contribution (Linder and Ronse Decraene, unpubl. data).

In a previous contribution we studied the floral development of a representative number of genera of the *Willdenowia*-clade of South African Restionaceae (Ronse Decraene et al. 2001). In that paper we demonstrated that floral ontogeny provides good synapomorphies in support of the monophyly of the clade: all studied species are characterised by a concordant reductive trend involving the one-time loss of the abaxial carpel and a displacement of the remaining carpels. We demonstrated how reduction series affect the carpel number and the configuration of the flower. Perianth and staminode reduction were shown to be independent of changes in the gynoecium.

In the present paper we analyse the floral development of the other major clade of African Restionaceae, viz. the *Restio* clade, comprising several large genera, in order to understand patterns of perianth, staminode, and gynoecial reduction, and to set up a semophyletic scheme comprising the data available for the *Willdenowia* clade. The following genera make up the *Restio* clade (Linder 1984, 1992a, b, 2000, 2001): *Elegia* (35 species), *Chondropetalum* (ten species), *Askidiosperma* (ten species), *Dovea* (one species), *Thamnochortus* (34 species), *Staberoha* (nine

species), *Rhodocoma* (eight species), *Calopsis* (23 species), *Ischyrolepis* (48 species), *Restio* (90 species), and *Platycaulos* (eight species). We studied at least one representative of each genus, except for *Platycaulos* and *Calopsis*. The delimitations of some genera, viz. *Calopsis* and *Restio*, are not well defined, and they may be polyphyletic (cf. Eldenäs and Linder 2000).

Material and methods

Collections of the species studied were made from wild populations or from plants grown in the Botanic Garden of Kirstenbosch. Origin and voucher information are listed in Table 1.

Species selection was constrained by three criteria. Firstly, we wanted to represent all possible reduction series proposed by Linder (1992a, b), rather than all genera. Secondly, species with many-flowered spikelets were chosen for ease of study. Thirdly, we were limited by which species we found at a suitable stage. Material was collected in the field and fixed in F.A.A. Later spikelets were dissected in 70% alcohol under a Wild M3 stereomicroscope. Material was prepared for SEM using customary methods (see also Ronse

Decraene et al. 2001). First the spikelets were dehydrated in increasing alcohol series before critical-point drying, or alternatively they were left for 5 minutes in a 1:1 mixture of alcohol and dimethoxymethane, and finally in pure dimethoxymethane for 20 minutes. Critical-point drying was carried out using liquid CO₂ in the CPD 030 (Balzers). The dried material was mounted on aluminium stubs using Leit-C (after Göcke), double tape, or a 1:1 mixture of tapestry glue and colloidal graphite (Agar Scientific Ltd.). Coating with about 180 nm of gold was carried out with the spi-coater^{TR} of Spi-Supplies before observations with the SEM at about 20 KV. Observations were carried out at the Electron Microscope Unit of the University of Cape Town (UCT) using a Leica Cambridge Stereoscan 2000 and 440 scanning electron microscopes and at the Katholieke Universiteit Leuven (KUL) using a Jeol 6400 SEM.

Results

As for our investigation of taxa of the *Willdenowia* clade most flowers studied were pistillate. Staminate spikes may have striking differences in morphology, but were seldom

Table 1. Species investigated with source of the material studied

Species	Voucher	Location and date of collection
<i>Askidiosperma paniculatum</i> (Mast.) H.P. Linder	Linder 6827	Kirstenbosch 4/11/97; Bainskloof 31/1/98; Baviaanskloof 1/2/98
<i>Chondropetalum ebracteatum</i> (Kunth) Pillans	Linder s.n.	Kirstenbosch 23/10/97
<i>Dovea macrocarpa</i> Kunth	Linder 6832	Citrusdal, near Allandale, 7/2/98
<i>Elegia capensis</i> (Burm. f.) Schelpe	127/78	Kirstenbosch 23/10/97
<i>E. grandispicata</i> H.P. Linder	Linder s.n.	Kirstenbosch 23/10/97–20/11/97
<i>E. cuspidata</i> Mast.	168/78	Kirstenbosch 23/10/97
<i>E. racemosa</i> (Poir.) Pers.	Linder 6836	Caledon, Perdeberg Trail, 11/2/98
<i>Ischyrolepis ocreata</i> (Kunth) H.P. Linder	Linder 6998	Cederberg, between Heuningvlei and Boontjieskloof, 14/12/99
<i>Restio multiflorus</i> Spreng.	Linder 6824	Table Mountain, common on slopes N of Skeleton George, 27/1/98
<i>R. dispar</i> Mast.	Linder 6834	Caledon, Perdeberg Hiking Trail, common in wetter places, 11/2/98
<i>Rhodocoma capensis</i> Steud.	Linder 6828	Ceres, Agterwittenberg Pass, 7/2/98
<i>Staberoha cernua</i> (L.f.) T. Durand & Schinz	20/91	Kirstenbosch, 23/10/97
<i>S. vaginata</i> (Thunb.) Pillans	Linder 6823	Table Mountain, along Window Stream, 24/1/98
<i>Thamnochortus lucens</i> Poir.	Linder s.n.	Kirstenbosch, 12/9/97

included in this study due to difficulties in obtaining the right material. Although the two perianth whorls were on the whole largely similar, and should therefore be referred to as the outer and inner tepals, for brevity sake we refer to them as sepals and petals. The position of the carpels is given by numbers as done by Linder (1992a, b): the carpel situated in an adaxial (posterior) position on the left (when the spikelet is viewed from the abaxial side) is carpel one; carpel two is situated in an adaxial position on the right, carpel three is abaxial (anterior).

***Elegia capensis* (Burm. f.) Schelpe (Figs. 1–9).** Only pistillate spikes were investigated. Spikelets are highly complex, consisting of several clusters of smaller partial spikelets, enclosed by a common bract (Fig. 1). These clusters are inserted in a semi-circle at each node of a large conical inflorescence (spike) and are enclosed by a larger bract. Several nodes bear flowers that become progressively younger towards the top of the spike. For details of mature spikelets we refer to Kircher (1986). Within each spikelet flowers arise spirally and acropetally (Fig. 2). The apex of each spikelet remains uncovered and has a globular shape (Figs. 2, 3). This is so because the bract growth rate is initially slow. Bract primordia arise as a broad flat rim below the top; they grow slowly and just hide half of the flower when the tepals are being initiated (Fig. 2); they only cover the flower completely at petal initiation. Bracts retain a truncate shape with no indication of a *Vorläuferspitze* or awn. The two latero-adaxial sepal primordia arise simultaneously; they precede the median sepal, which is usually hidden by the bract (Fig. 2). After initiation the lateral sepals grow unequally with the one situated opposite the fertile carpel preceding the other (Figs. 5, 6). In later stages unequalities disappear. Growth is not rapid and the sepals only cover the whole flower at the differentiation of the styles. The sepals have a rounded shape and are never laterally compressed. Basally the sepal lobes are fused by common zonal growth (Figs. 5, 6). Petal initiation is sequential,

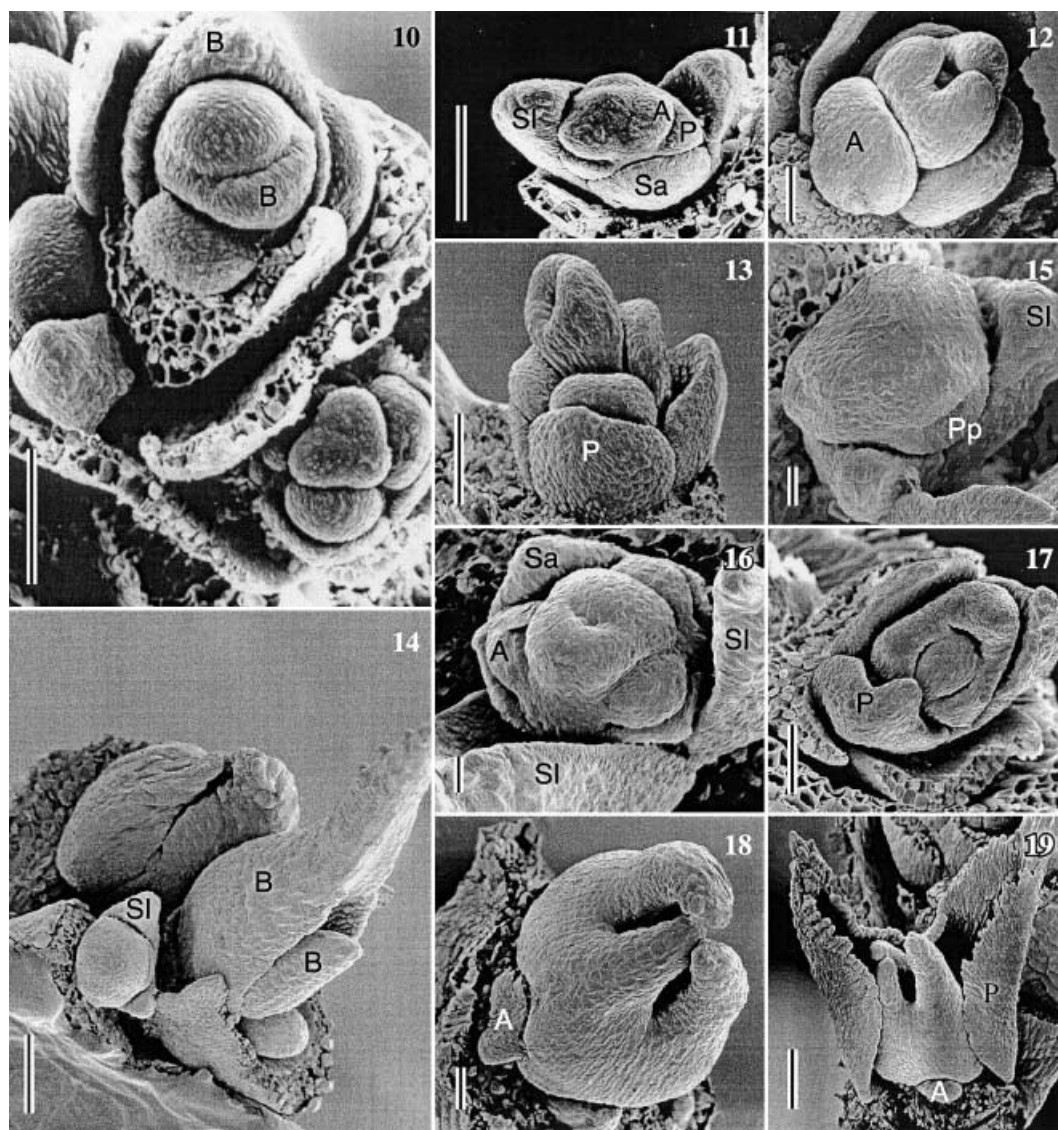
starting with the adaxial petal (Fig. 3); the anterior petals follow in a rapid sequence (Fig. 4). The stamen primordia emerge in the same sequence above the petal primordia, which are nested in the interstices of the sepals (Fig. 4). Staminodes are large in early stages relative to the petals. However, their growth is soon truncated before further differentiation and they are rapidly concealed by the petals (Figs. 6, 8). At anthesis the staminodes are not visible. The apical meristem of the flower becomes irregular (Fig. 4) as one peripheral girdling primordium is differentiated opposite the first-formed (and still largest sepal), concomitant with the development of a transverse furrow (Fig. 5). Two other shallow furrows arise on each side of the larger one (Fig. 6). As a result the peripheral parts become a continuous girdle connected with the central meristem at three points. This girdle extends in height as a saccate structure and three styles become differentiated, the largest being the fertile carpel (Fig. 7). The position of the fertile carpel is always adaxial and lateral, but can be either left or right. Styles are erect and spread in later stages (Figs. 8, 9). Along the dorsal part of each carpel a future dehiscence slit is formed (Fig. 9, arrow). At anthesis the fertile style is much longer than the sterile ones and its ventral slit is bordered with papillae (Fig. 9). In some cases, only a single carpel is initiated; there is no trace of the sterile lobes, or their development is much retarded. Later stages of development of flowers were not observed.

***Elegia grandispicata* H.P. Linder (Figs. 10–22).** Staminate and pistillate spikes were investigated. Male and female flowers are very similar up to the initiation of the carpel primordia.

Spikelets are multibranched and are enclosed by larger bracts or spathellae. Flowers arise acropetally in a spiral sequence (Figs. 10, 14). The apical meristem is rounded and bract primordia emerge as crescent-shaped structures at the periphery of the apex (Fig. 14). The bract primordia bear a *Vorläuferspitze* and grow initially fast into ovate structures slightly



Figs. 1–9. *Elegia capensis*. Development of pistillate spikelet and flowers. **Fig. 1.** Lateral view of group of spikelets at different stages of development. **Fig. 2.** Detail of young spikelet with flowers initiated acropetally. The flower in the upper part of the figure shows the initiation of two lateral sepals. **Fig. 3.** Detail of flower at petal initiation. The adaxial petal (arrow) precedes the others; the abaxial sepal is hidden by the bract. **Fig. 4.** Initiation of staminodes. **Fig. 5.** Initiation of fertile carpel; the sepals start covering the flower. **Fig. 6.** Initiation of the sterile carpels. **Fig. 7.** The gynoecium wall grows up as a continuous rim. **Fig. 8.** Formation of the styles. Note the small staminodes at the base. **Fig. 9.** Preanthetic gynoecium with development of stigmatic papillae. Note the formation of a dehiscence slit (arrow). Abbreviations: A, staminode primordium; B, bract; P, petal primordium; SL, lateral sepal; SA, abaxial (median) sepal. Bars: 100 µm; Fig. 4: 10 µm



Figs. 10–19. *Elegia grandispicata*. Development of staminate (Figs. 10–13) and pistillate flowers (Figs. 14–19). **Fig. 10.** Apical part of spikelet with initiation of flower buds and subtending bracts. **Fig. 11.** Initiation of androecium. **Fig. 12.** Nearly mature bud with development of carpelloids. **Fig. 13.** Abnormal flower with tubular pistillodium. **Fig. 14.** Uppermost part of spikelet. Note early sepal initiation on a flower bud. **Fig. 15.** Detail of same bud. Early initiation of the adaxial petal (Pp). The abaxial sepal is not present. **Fig. 16.** Adaxial view of flower at initiation of the carpels. **Fig. 17.** Slightly older stage; the petal lobes hide the staminodes at this stage. **Fig. 18.** Gynoecium at the formation of the styles. **Fig. 19.** Adaxial view of flower, one petal removed. Note the large winglike petals and small staminodes. A, stamen or staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bars: Figs. 10–14, 19 = 100 μm ; Figs. 15, 16 = 20 μm ; Figs. 17, 18 = 50 μm

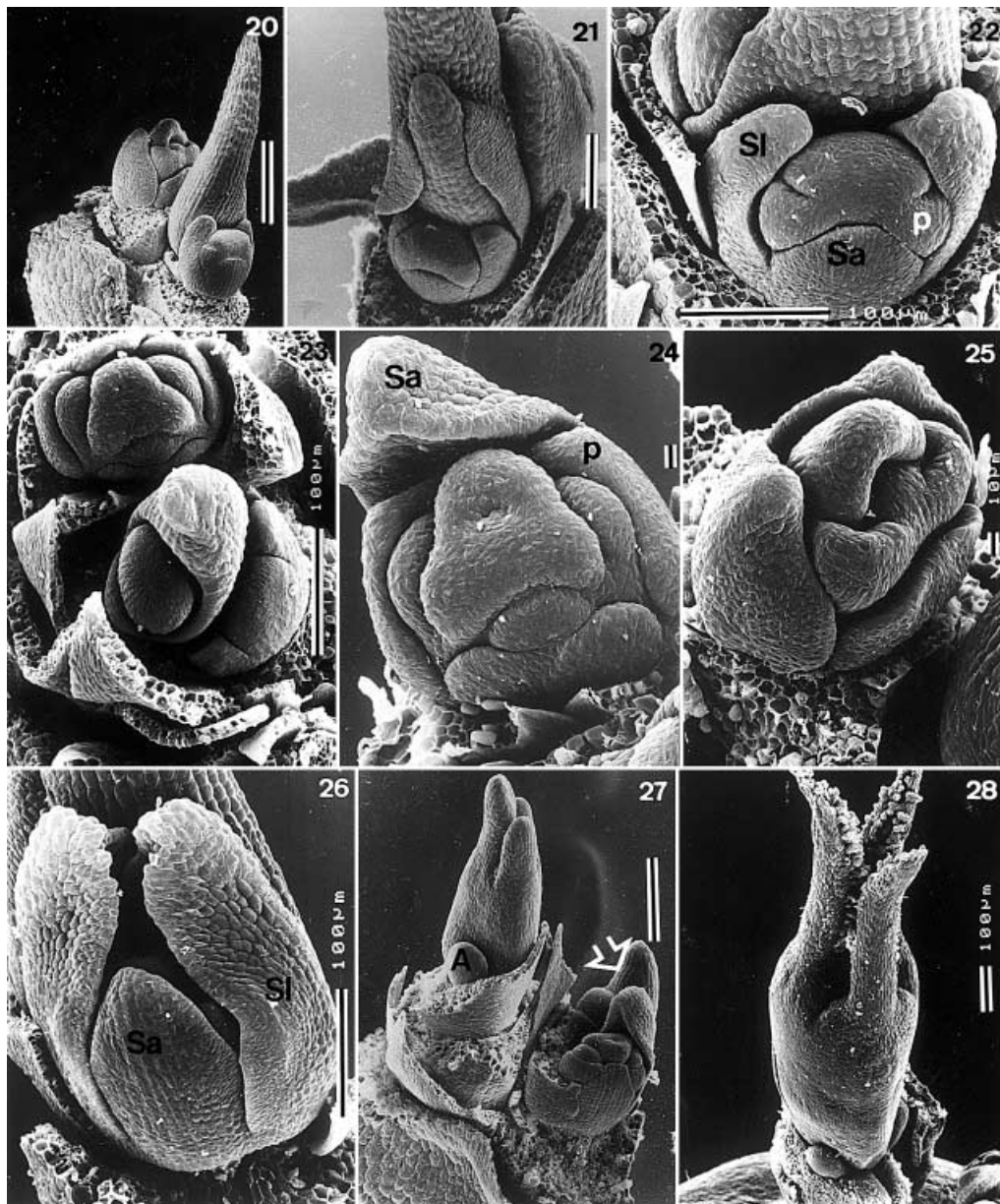
incurved at the top. Later, they become more scarious and dentate along the edges. Floral primordia emerge as hemispherical entities, as the bracts cover the apical meristem of the spikelet (Figs. 10, 14). The latero-adaxial sepal

primordia arise sequentially before the median abaxial primordium which is much retarded (Figs. 14, 15). The lateral sepals are strongly laterally compressed and bear a dorsal crest; they remain unequal in size during the whole

development (Figs. 15, 16). The median sepal remains flattened and is only clearly visible after petal initiation (Figs. 11, 16). The three petal primordia arise in a rapid sequence, first the adaxial petal, followed by the abaxial pair (Fig. 15). The stamen primordia are rapidly initiated opposite the petals (Fig. 11). In pistillate spikelets, staminode growth stops early and they remain hidden as small humps behind the petals (Figs. 18, 19). Before anthesis the margins of petals and sepals alike become sinuate (Fig. 19). After stamen initiation the triangular floral apex develops in different ways; either it forms one larger latero-adaxial and two smaller carpellary lobes, or only one adaxial lobe between the adaxial stamen and one latero-abaxial stamen. In pistillate spikelets the first trace of gynoecium initiation is the unilateral development of a lobe against a central slit-like depression (Fig. 16). The lobe grows upwards and two additional lobes are formed with corresponding slits (Fig. 17). Centrally a concave apical residue is delimited by the slits lying in a girdle. As the first primordium grows more strongly than the two others, the gynoecium becomes strongly monosymmetric, and this remains visible until style formation (Figs. 17–19). Basal growth lifts the three carpel lobes into three more or less equal styles. The abaxial carpel is always sterile while it is either the left or the right adaxial that is fertile (Figs. 16–19). In the staminate spikelets the three carpel primordia develop equally (Fig. 12) and growth is arrested after formation of short stylar primordia. In some cases only one carpel occupies the whole apical meristem by circumplastic growth. As a result a stalked structure with lateral aperture is formed (Fig. 13). As we only found this condition in staminate flowers it can be a derived condition linked with an increased sterility.

***E. cuspidata* Mast. (Figs. 20–28).** Only pistillate spikelets were studied. Spikelets bear few flowers on a main stalk or branch moderately (Figs. 20, 23, 27). Mature bracts subtending individual flowers are stout with a main vein extended into an awn. Bracts grow

rapidly and bear a *Vorläuferspitze* (Figs. 20, 21). The bracts emerge in spiral sequence and each encloses the subsequent one arising at about 90° from the first with basal lateral flaps (Fig. 21). Each bract arises as a hemispherical bulge extending laterally around the spikelet apex (Fig. 23). Very early the bract apex starts growing in a cap-like structure, while the margins grow around a next primordium that has been formed. This process continues until about four to five flowers are formed. A flower primordium initiates in the axil of the bract as a flattened protuberance following the curving of the stem (Fig. 23). The two latero-adaxial sepals appear first and (almost) simultaneously, each taking up about 1/4 of the flower bud (Fig. 23). Then an abaxial sepal is formed and becomes continuous with the other sepals by basal growth (Figs. 21, 22). The lateral sepals tend to grow as angular, erect flaps, while the abaxial sepal remains smaller and more rounded (Fig. 26). Two latero-abaxial petals appear simultaneously in the interstices of the sepals; they are more or less hemispherical, becoming inverted-triangular and nested in the slits between the sepals (Figs. 20–22). The adaxial petal is only visible at the time of staminode initiation; it appears as a flattened, bilobed rim compressed between flower and receptacle, as equal growth is apparently obstructed by the adaxial staminode (Figs. 23, 24). The adaxial petal remains smaller compared to the lateral petals and only picks up growth later (Fig. 25). The two latero-abaxial staminodes arise simultaneously, followed by an adaxial staminode (Figs. 22, 23). Staminode growth becomes arrested shortly after initiation, and they are soon hidden by the petals (Figs. 25–28). They persist up to anthesis. The staminodes delimit a triangular area on the floral apex, with the abaxial side higher than the adaxial ones (Figs. 23, 24). The fertile carpel is situated on the abaxial side and is initiated as a rim around a shallow depression (Fig. 24). The two adaxial, sterile carpels arise as two mounds. The abaxial side of each carpel differentiates as the carpel wall delimiting three continuous depressions while the lateral flanks of the fertile



Figs. 20–28. *Elegia cuspidata*. Development of pistillate spikelet and flowers. **Fig. 20.** Lateral view of young spikelet. **Fig. 21.** Upper part of spikelet. Note the imbricate arrangement of the bracts. **Fig. 22.** Detail of flower at the initiation of the petals. **Fig. 23.** Apical view with two flowers at different stages of development. The flower in the upper part of the figure shows the initiation of the carpels; the flower on the right shows the initiation of the lateral sepals. **Fig. 24.** Adaxial view of flower with the initiation of the carpels. **Fig. 25.** Lateral view at a slightly older stage. **Fig. 26.** Abaxial view of preanthetic flowers with arrangement of sepals. **Fig. 27.** Partial view of spikelet. Note that the most advanced flower overtops the spikelet apex (arrow). Development of styles on the flower on the left of the figure. **Fig. 28.** View of preanthetic flower. Note the subequal papillate styles and small staminodes. A, staminode; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bar: Figs. 22, 23, 26, 28 = 100 µm; Figs. 20, 21, 27 = 50 µm; Figs. 24, 25 = 10 µm

carpel tend to grow within the sterile carpels (Fig. 25). On the flanks between the two sterile carpels a protuberance is produced that curves within the space left by the fertile carpel; it grows as a median pendent ovule (Fig. 25). In later stages the upper part of the carpels becomes lifted by basal circumzonal growth and three subequal styles with a ventral vertical slit are formed (Figs. 27, 28). A saccate ovary is formed in which the ovule becomes nestled. Papillae start to develop on the inner margins of the slits formed by the styler lobes; they grow into long hairs (Fig. 28). Styles are erect with the extremities bent outwards; they are unequal in length. The sepals and petals are bract-like and not angular, with a strong main vein. At anthesis the sepals and petals are erect, with the stigmatic lobes inserted between the slightly longer petal lobes. Fusion at the base of the sepals is limited, while the petals remain free.

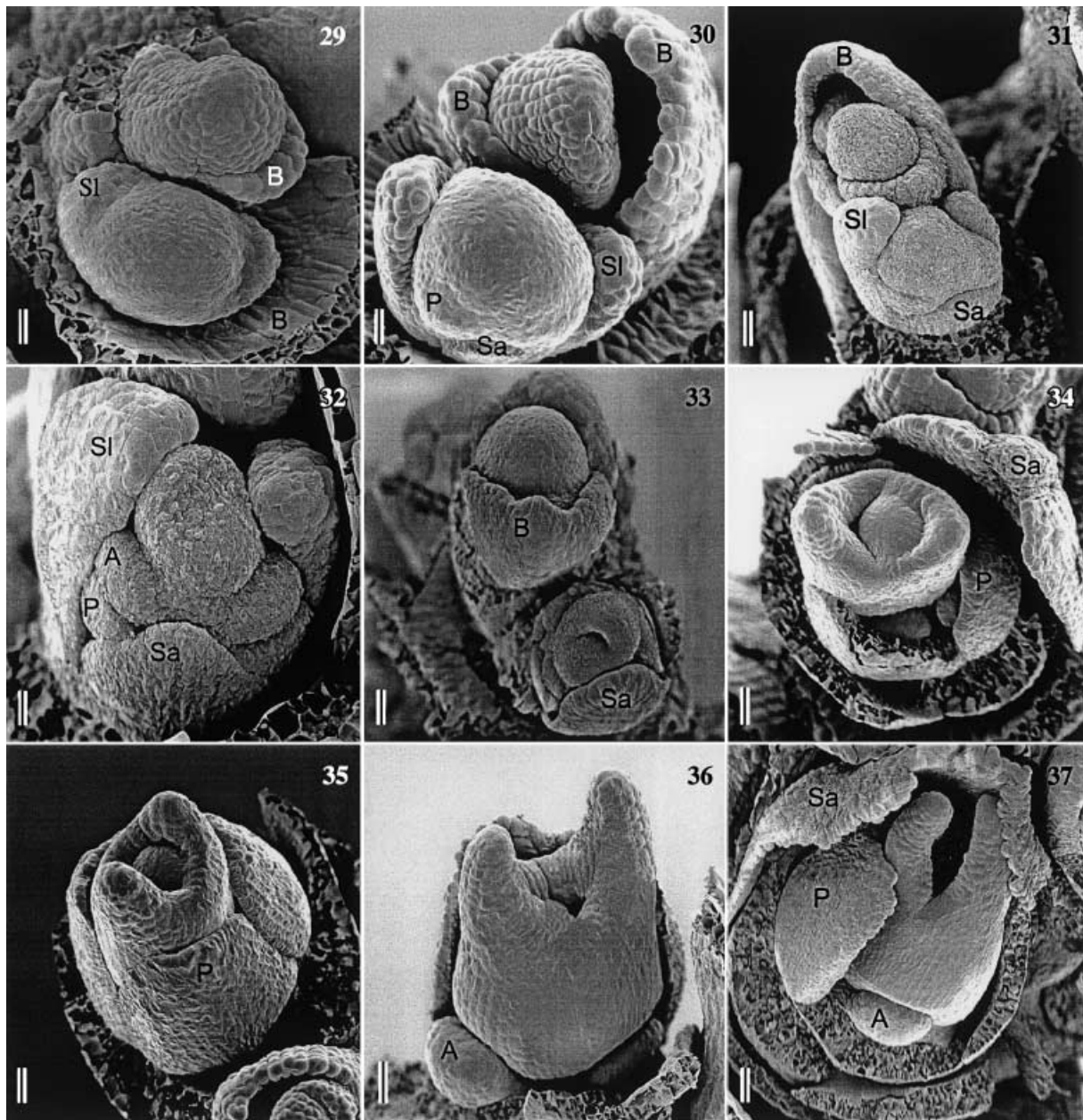
***Elegia racemosa* (Poir.) Pers. (Figs. 29–37).** Flowers arise in few-flowered spikelets. Bracts have a weakly developed *Vorläuferspitze* (Fig. 30). Bract growth is initially slow and they do not cover the convex spikelet apex. They arise in a decussate sequence with the margins of opposite bracts not overlapping (Figs. 29–31).

Sepal initiation is sequential and starts with the lateral sepals (Fig. 29). Initiation and growth of the abaxial sepal is retarded and it only increases in size at a much later stage (Figs. 30–33, 37). The lateral sepals appear slightly laterally compressed in young stages, while the abaxial sepal is flat (Figs. 31, 32). Growth of the sepals is slow at first; they only cover the apex of the flower after gynoecium initiation (Figs. 32, 33). Lateral petal initiation appears to be sequential and slightly earlier than the adaxial petal (Figs. 30, 31). As for the sepals growth of the petals is relatively slow and they only become slightly longer than the sepals before anthesis (Figs. 35, 37). Petals are rapidly followed by the antepetalous stamens, first the abaxial ones. They stop growing soon after their initiation (Figs. 31, 32, 34, 36, 37) but are still visible at anthesis. The

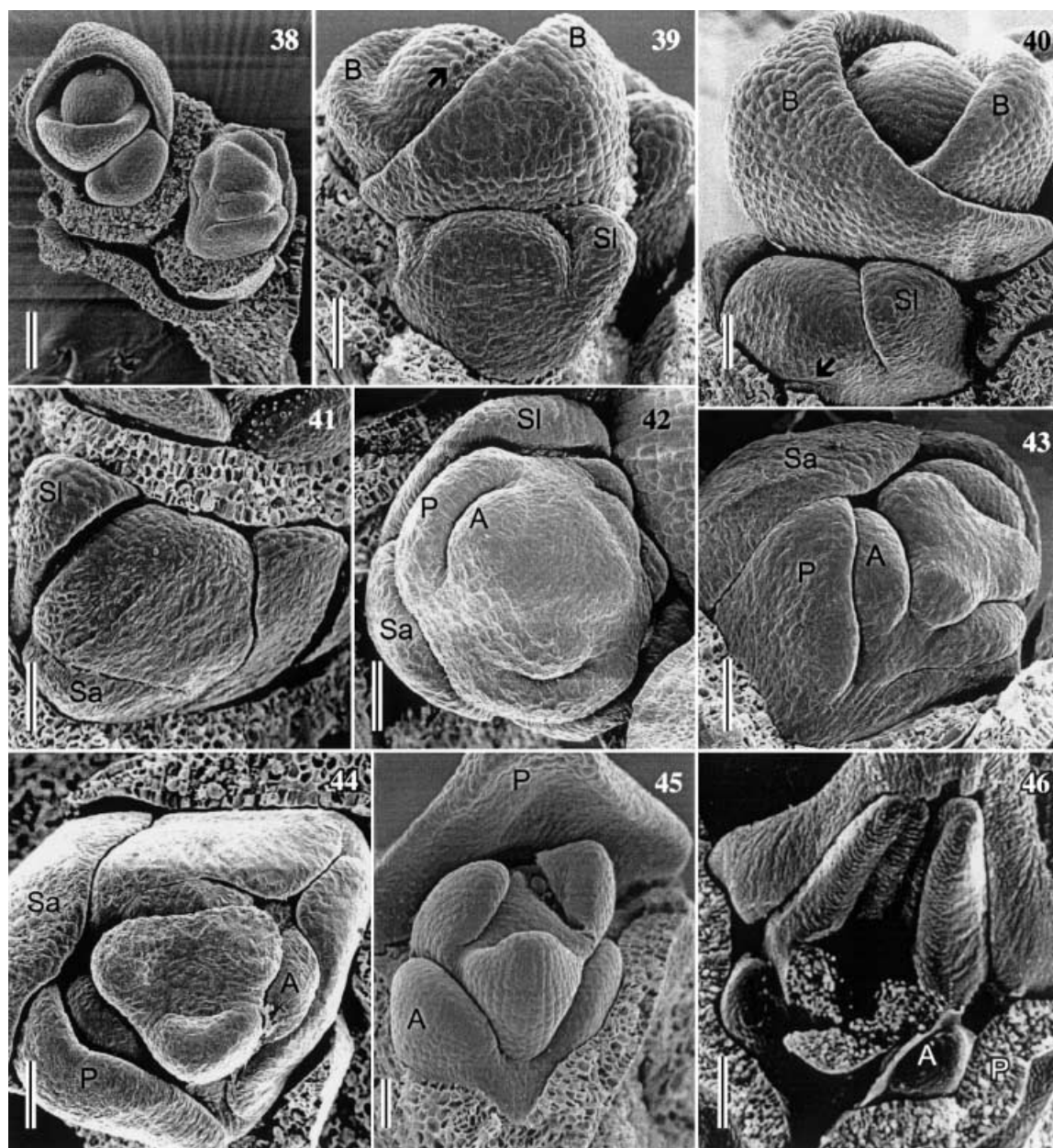
remaining floral apex forms a circular gynoecium primordium that is higher towards the larger lateral sepal (Figs. 32, 33). A peripheral rim is formed opposite the first (and still largest) sepal, concomitant with the appearance of a transversal slit. A smaller lobe with fainter slit arises on the opposite side of the gynoecium (Fig. 34). By circumzonal growth the peripheral rims extend into a continuous girdle connected with the central meristem at two points. This girdle develops into a saccate structure and two subequal, erect styles are formed, the largest being the fertile carpel (Figs. 35–37). The position of the fertile carpel is always adaxial and lateral, but either situated left or right. There is no indication of a third abaxial carpel.

***Dovea macrocarpa* Kunth (Figs. 38–46).** Pistillate as well as staminate flowers were studied. Pistillate spikes consist of about three terminal spikelets enclosed by a bract. There are about seven sterile bracts at the base of each spikelet. Each bract embraces the whole stem. There are about seven flowers per spikelet, with the lowermost sterile. All flowers of the staminate spikelet are fertile; there are no sterile bracts at the base.

Bract primordia arise as circular rims at the periphery of the hemispherical spikelet apex (Fig. 39). The bracts lack a *Vorläuferspitze* and cover about half the circumference of the axis; seen from the inner side the upper rim of the bract appears as an arch. As older bracts cover the spikelet apex, new primordia arise spirally (Figs. 38–40). On the spikelet apex we observed drops of an exudate which might have a function of preventing dehydration (Figs. 39, arrow, 40). Flower primordia are compressed by the bract primordium but soon attain a more polysymmetric outline. Two angular latero-adaxial sepal primordia arise in rapid sequence (Figs. 38–40), followed by a flattened abaxial primordium (Fig. 41). The abaxial sepal has a rounded apex with lateral flaps; it remains much smaller than the lateral ones, which develop a dorsal crest at anthesis (Figs. 41, 42, 44). Three petal primordia arise at the periphery of the flattened bud. The



Figs. 29–37. *Elegia racemosa*. Development of pistillate spikelet and flowers. **Fig. 29.** Spikelet apex with initiation of lateral sepals on flower bud. **Fig. 30.** Lateral view of spikelet apex with older flower showing initiation of abaxial sepal and petals. **Fig. 31.** Slightly older stage. **Fig. 32.** Flower with initiation of staminodes and gynoecium. **Fig. 33.** View of spikelet apex; in the flower at the bottom the gynoecium is slightly older. **Fig. 34.** Gynoecium with both carpels having formed concave areas; petals partly removed to show staminodes. **Fig. 35.** Apical view of gynoecium with beginning styler development. **Fig. 36.** Lateral view of gynoecium with development of saccate gynoecium with overtopping styles. **Fig. 37.** Lateral view of partly dissected flower. A, staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bar: Figs. 29, 30, 32, 36 = 20 μm ; Figs. 34, 35, 37 = 50 μm



Figs. 38–46. *Dovea macrocarpa*. Development of pistillate spikelet and flowers. **Fig. 38.** Partial view of young spikelet top with two flowers. **Fig. 39.** Detail of upper part of spikelet with initiation of bracts and young flower. Arrow points to droplets of exudate. **Fig. 40.** Lateral view with slightly older flower. The abaxial sepal is just visible below the remains of the bract (arrow). **Fig. 41.** Development of the abaxial sepal. **Fig. 42.** Initiation of staminodes and triangular gynoeceium. Note the two-parted shape of the adaxial petal. **Fig. 43.** Lateral view of flowers at slightly older stage. **Fig. 44.** Apical view of slightly older stage. **Fig. 45.** View of slightly older stage. **Fig. 46.** Frontal view of nearly mature bud; abaxial carpel removed. A, staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bars: Figs. 39–45 = 50 μm ; Figs. 38, 46 = 100 μm

abaxial petal pair arises simultaneously before the adaxial petal (Fig. 42). The adaxial petal is squeezed between the staminode and spikelet

apex and can just extend as a bilobed structure before surpassing the staminode in a later stage of development (Figs. 42–44). The petals grow

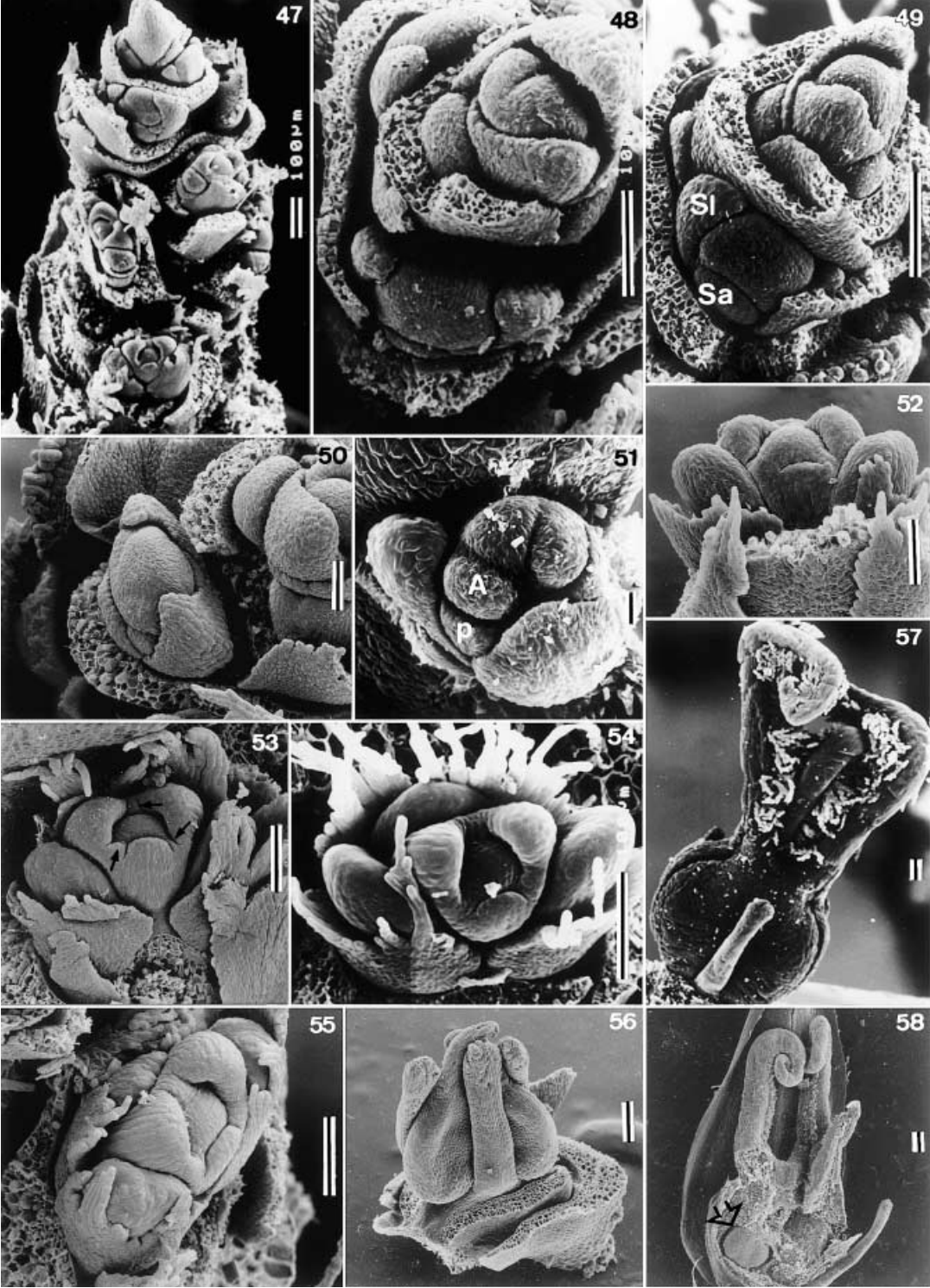
rapidly and attain a considerable size at anthesis (Figs. 43–46). As the petals elongate, three antepetalous staminode primordia are delimited, leaving a triangular apex in the centre of the flower (Figs. 42, 43). Staminode growth soon ceases and they can only be seen as small humps in older flowers (Figs. 45, 46). Three carpels are formed in the angles of the remaining floral apex, apparently in a rapid sequence (Figs. 43–45). The three carpels extend in size and grow up as folded emergences which are basally continuous. The upper parts differentiate as three more or less equal and erect styles (Fig. 46). The development of staminate flowers concurs up to this stage. Later, the gynoecium does not develop any further and the stamens extend in size.

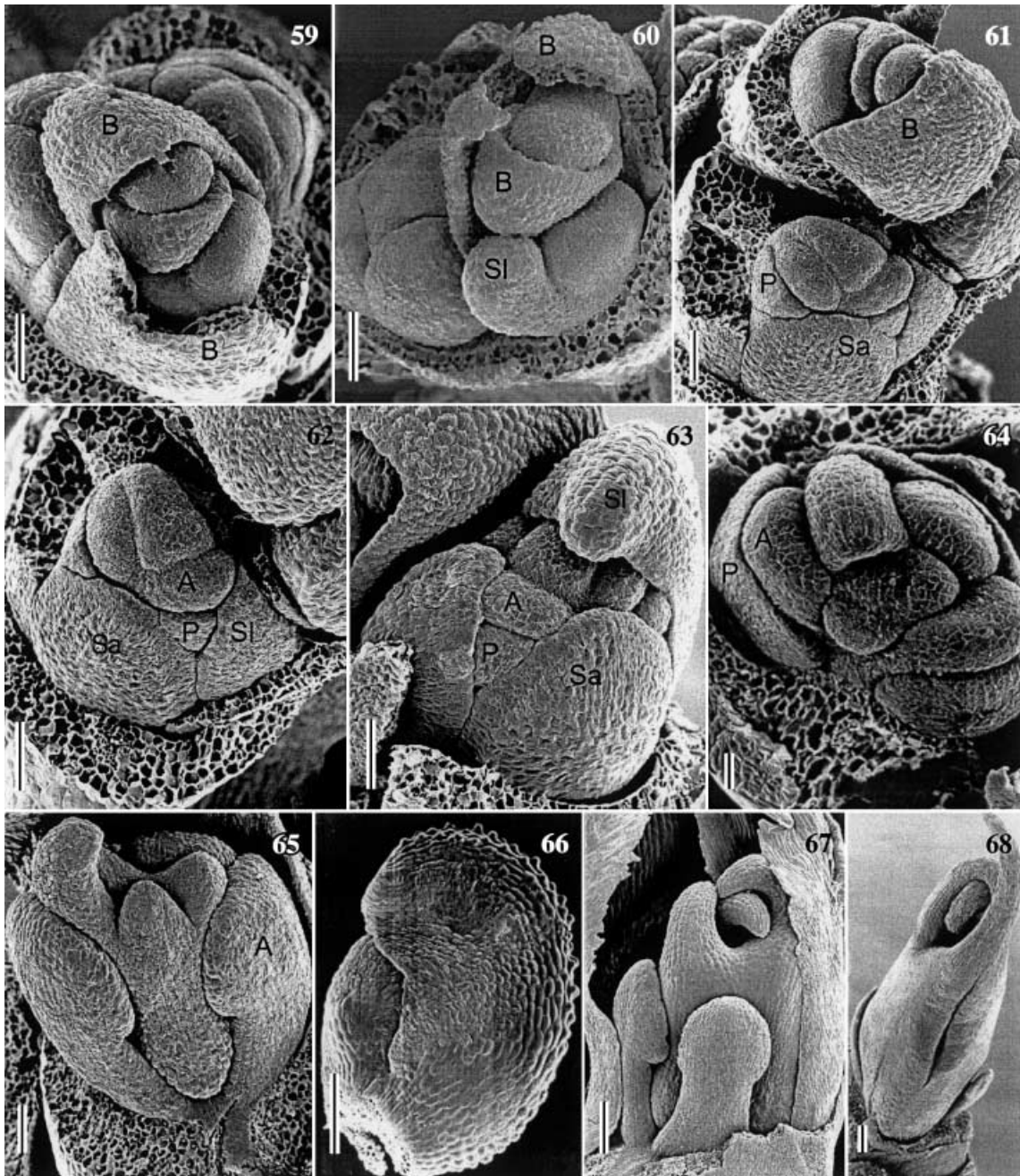
***Restio multiflorus* Spreng. (Figs. 47–58).** Pistillate as well as staminate spikes were studied. Staminate spikes contain many spikelets with lacerate bracts and numerous flowers (Fig. 47). The differentiation between male and female flowers occurs late in ontogeny. Pistillate spikelets have fewer flowers (about five) with a number of sterile bracts. Some partial spikelets are necrotic or reduced to a single flower. The gynoecia have three circinate styles and staminodes are filament-like (Figs. 56, 57, 58). The two outer lateral sepals bear a fringe of tightly packed hairs on the back. The petals are papery at anthesis; they have the same size as the sepals and have their upper margin irregularly dissected with numerous hairs (Figs. 53–55). The fertile carpels have a well developed dehiscence slit (Fig. 57).

Flowers arise in a spiral sequence. The *Vorläuferspitze* on the bract is almost not

developed (Fig. 48). The median part grows into a cap-like apex, while the margins extend around the axis enveloping younger bracts (Fig. 48). Floral primordia are elliptic-hemispherical in shape. Two rounded lateral sepal primordia emerge in a rapid sequence, followed by a flattened median sepal (Figs. 48–49). Sepals are basally continuous and grow initially slowly. The lateral sepals become abaxially angular. Between the sepals three petal primordia are initiated simultaneously (Fig. 50). Petals are rapidly followed by superposed staminode or stamen primordia (Figs. 47, 51). The staminodes grow rapidly and they remain visible for a long time as the petals develop a truncate apex bordered with numerous branching papillar trichomes (Figs. 52–55). The staminodes extend as a long filament tipped by papillate cells (Figs. 56–58). No anther tissue is formed. The apical gynoecial primordium is triangular at first, and three carpel primordia emerge in the angles (Fig. 52). The latero-adaxial carpel primordia are equal in size and become much larger than the median-abaxial primordium, which represents a sterile carpel (Figs. 53–55). A transverse slit is formed adaxially of each carpel. The carpels increase in size and extend as cap-like structures around the convex centre of the gynoecium before extending as three almost equal styles (Fig. 57). The abaxial style is always shorter. By differential growth the upper portion of the styles becomes coiled, while numerous papillae develop on the adaxial side (Figs. 57, 58). The ovary is flattened as only two carpels form an ovule (Fig. 58).

Figs. 47–58. *Restio multiflorus*. Development of pistillate spikelets and flowers. **Fig. 47.** Lateral view of young spikelet showing successive flower formation. **Fig. 48.** Detail of top of spikelet with early sepal formation on lower flower. **Fig. 49.** Similar view with slightly older floral bud. **Fig. 50.** Lateral view at petal initiation. **Fig. 51.** Frontal view at staminode initiation. **Fig. 52.** Frontal view with three carpels formed. **Fig. 53.** Slightly older flower with gynoecium with intercarpellary bulges (arrows). **Fig. 54.** Flower at similar stage with sterile abaxial carpel clearly retarded. **Fig. 55.** Lateral view of similar stage. **Fig. 56.** Adaxial view of older bud with fully developed staminodes at style formation. **Fig. 57.** Preanthetic gynoecium with circinate styles and two dehiscence slits. **Fig. 58.** Dissected preanthetic gynoecium showing one of the apical ovules (arrow). A, staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bars: 100 µm; except Fig. 52 = 60 µm





Figs. 59–68. *Restio dispar*. Development of pistillate spikelet and flowers. **Fig. 59.** Apical view of young spikelet with initiation of bracts and three flowers. **Fig. 60.** Lateral view of similar spikelet. Note the unequal development of the lateral sepals on the flower in front. **Fig. 61.** Partial view of spikelet with flower below at staminode initiation. **Fig. 62.** Detail of flower of Fig. 61. **Fig. 63.** Lateral view of flower at gynoecium initiation. Note the unequal size of the lateral sepals overtopping the flower. **Fig. 64.** Apical view of flower after carpel initiation. **Fig. 65.** Lateral view of older flower with fully developed staminodes. **Fig. 66.** Lateral view of the lateral sepals on preanthetic flower. **Fig. 67.** View of flower bud at style formation. **Fig. 68.** Detail of preanthetic gynoecium. Note the dehiscence slit on the back of the carpel. A, staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bars: Figs. 59–63 = 50 μ m; Fig. 64 = 10 μ m; Figs. 65–68 = 100 μ m

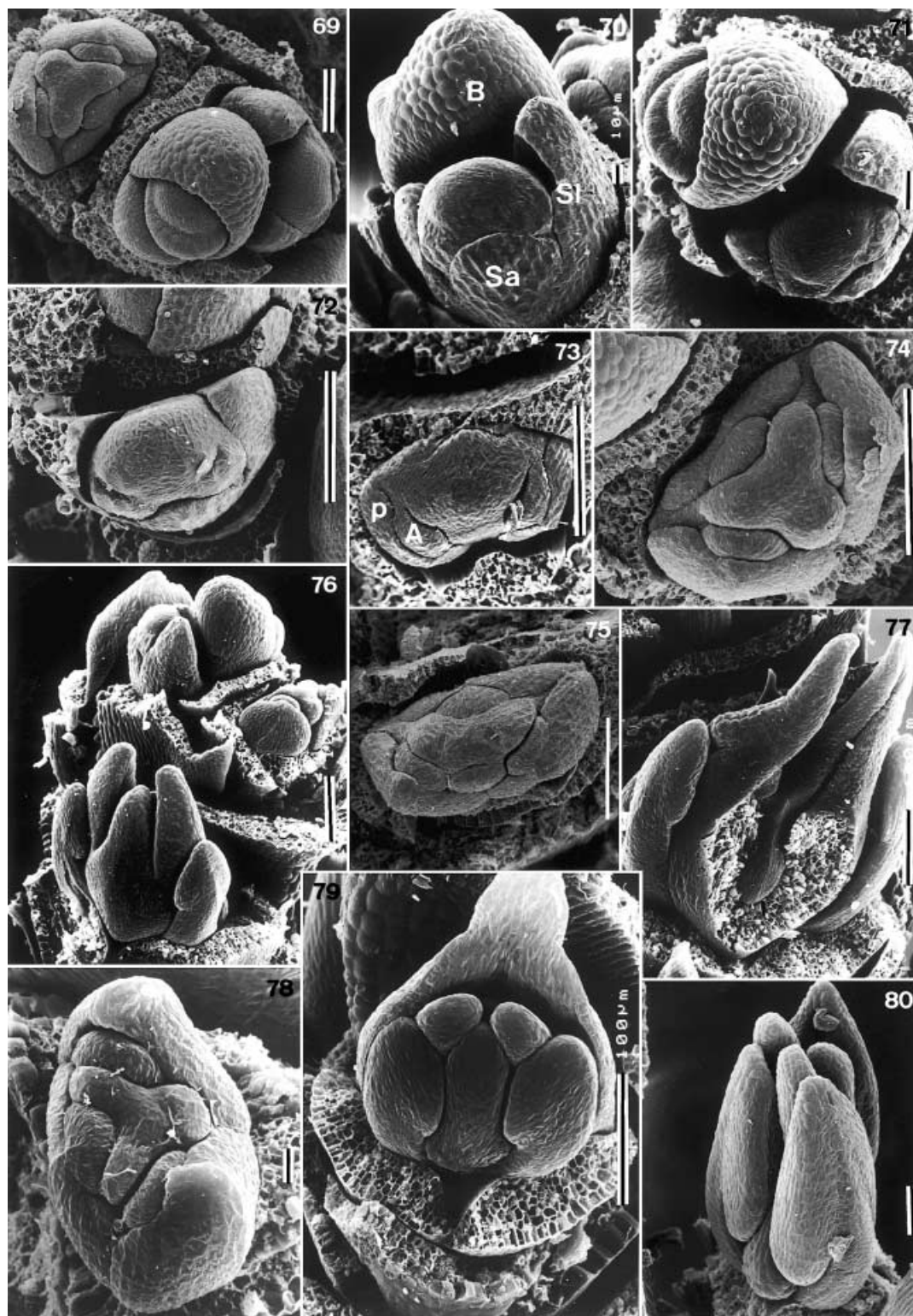
***Restio dispar* Mast. (Figs. 59–68).** Both pistillate and staminate flowers were studied. Spikes consist of clusters of four-five spikelets. Pistillate spikelets are few-flowered while staminate spikelets bear eight-nine flowers in the axil of long acute bracts. Upper flowers are not developed. The outer lateral sepals are highly unequal in size and have a papillate dorsal crest (Fig. 66); the median sepal is flattened. Petals are equal in size and membranous with a single vein. Pistillodes and staminodes are well developed.

Bract initiation is rapid in a spiral sequence. A *Vorläuferspitze* is not formed except for the elongate tip of the bract (Figs. 59–61). Bract margins overlap. Sepal initiation is sequential with one of the lateral sepals arising first (Fig. 60). This difference in size persists up to anthesis (Figs. 61, 63, 66). The largest sepal grows rapidly and overtops the floral apex, while the other sepals remain of a moderate and comparable size (Figs. 62, 63). Petal initiation is sequential with the lateral petal towards the largest sepal preceding the two others (Figs. 61, 62). Petals are rapidly followed by staminodes taking up considerable space on the floral apex (Figs. 61–64). Petal growth is initially retarded until well after gynoecium initiation. The staminodes develop to a considerable size and form anther tissue before aborting (Fig. 65). After staminode initiation the triangular floral apex develops three carpel primordia in succession. The largest, fertile carpel is formed on the side towards the largest sepal, while the two other carpels are sterile (Figs. 65, 67, 68). The fertile carpel pushes the staminodes aside on its dorsal side and overtops the sterile carpels. By circumzonal growth the three styles are lifted up with their ends curved inwards (Figs. 65, 67). Finally all three carpels become equal in size. Styles are coiled at anthesis (Fig. 68). A dorsal dehiscence line is clearly developed.

***Chondropetalum ebracteatum* (Kunth) Pillans (Figs. 69–80).** Staminate and pistillate spikes were available for study; in both sexes the shortly stalked spikelets are clustered

together. The flower buds are flattened-angular and the lateral sepals become strongly keeled at anthesis with short trichomes arising on the dorsal ridge; the differentiation of genders occurs late in ontogeny. Staminodes bear rudimentary anthers (Fig. 77) while carpellodes have erect styles (Figs. 79–80). Young bracts are coiled; they become brittle and hard at anthesis. The bracts arise spirally as a flattened rim extending for half of the stem; they are laterally enclosed by the margins of an older bract (Figs. 69, 71). A *Vorläuferspitze* is not formed except for the elongate tip of the bract (Figs. 69–71). Each flower is initiated as a transversally elongate primordium in the axil of a bract (Fig. 69). The lateral sepals arise sequentially, followed by the abaxial sepal (Figs. 69–72). The lateral sepals are clearly angular from early on and soon become equal in size; their flanks extend and meet adaxially while they enclose the third flattened sepal abaxially (Figs. 71, 72). Sepals grow rapidly and enclose the bud completely. Dorsiventral petal primordia are initiated in a rapid sequence between the sepals, the lateral ones simultaneously and before the adaxial one (Figs. 70–72). Lateral petals are slightly angular, while the adaxial one is flattened and becomes two-lobed (Figs. 74, 75, 78). Staminode initiation follows in the same sequence as the petals (Fig. 73). Growth is continuous until after anther formation (Figs. 76, 77, compare with Figs. 79, 80). The gynoecium arises as a triangular structure, delimiting three carpel primordia (Figs. 74, 75). By the stronger development of the abaxial side of each carpel three erect styles with a ventral slit are initiated (Figs. 76–77). The abaxial style may occasionally be shorter (Figs. 76, 79).

***Thamnochortus lucens* Poir. (Figs. 81–89).** Only female spikelets were examined. There is only one fertile carpel situated in a latero-abaxial position. The spike is terminal with several flowers arising spirally and acropetally in the axil of a bract (Fig. 81). Bracts arise as broadly extended primordia (Figs. 81, 82). As they grow in size they sheath younger bracts by extending basally and

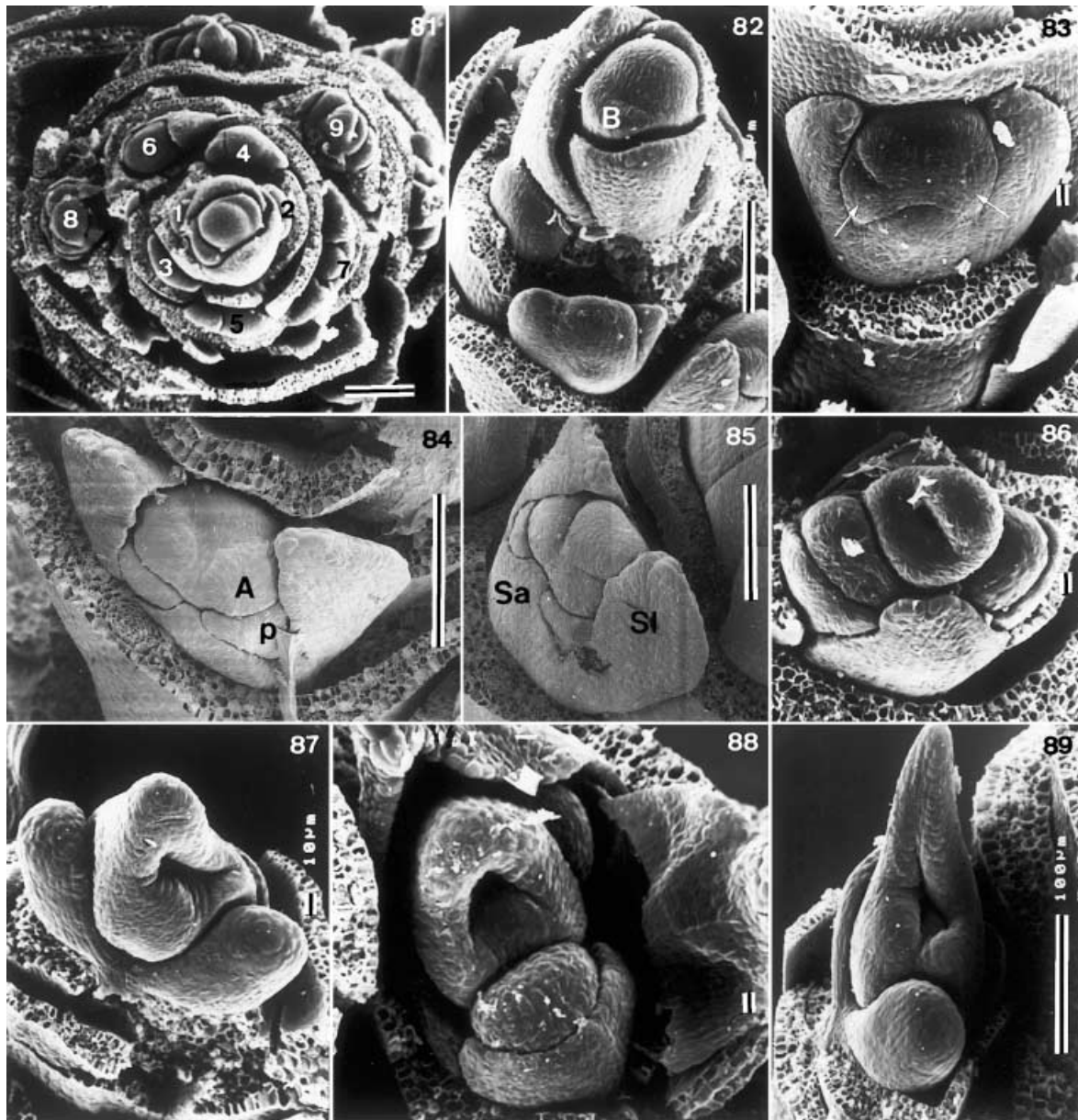


enwrapping the spikelet axis. A *Vorläuferspitze* is not formed except for the elongate tip of the bract (Fig. 82). Two lateral sepals arise in rapid sequence (Fig. 82); they are followed by a much smaller abaxial sepal that is pressed between flower and bract (Figs. 82, 83); it only extends slightly upwards between the petals and staminodes (Figs. 84, 85). The laterally compressed lateral sepals become rapidly keeled and of equal size (Figs. 83–85). At anthesis the lateral sepals are winged. Lateral petals apparently arise almost simultaneously and in very rapid sequence; we did not observe the initiation of the adaxial petal but suspect that it is retarded (Figs. 83, 84). The sequential initiation of the staminodes could be observed more clearly; first the two abaxial ones simultaneously and taking up a big section of the flower, and later the adaxial (Figs. 84, 85). The residual floral apex is relatively small and triangular, with the broader side adaxially (Fig. 85). A carpel is initiated in a latero-adaxial position, either left or right (Figs. 86–89). While this carpel elongates the two remaining angles of the triangle develop as inconspicuous carpel primordia that abort consecutively (Figs. 87, 89). In some instances there is no evidence of these smaller primordia and only one carpel is distinct (Fig. 88). The asymmetrically growing carpel rapidly extends into an erect, plumose style with adaxial slit (Fig. 89). Staminodes become relatively large and are basally confluent; the adaxial staminode is markedly smaller and sometimes not developed (Figs. 87, 89). We did not see any development of anther tissue.

***Staberoha vaginata* (Thunb.) Pillans (Figs. 90–100).** Pistillate as well as staminate spikes were available for study. Staminate spikelets contain a large number of flowers (Figs. 90, 91) in comparison with pistillate spikelets (Fig. 93). In staminate spikelets there are about 50 flowers arising in a spiral sequence. The fast growing bracts have a strong dorsal ridge and a *Vorläuferspitze* (Fig. 91). Sepal initiation is similar for the staminate and pistillate flowers, although the pressure on the flower primordia is less obvious in the staminate spikelets; there is more space for the lateral sepals to arise transversally and more regularly. The lateral sepals arise simultaneously and are laterally compressed; they are followed by the smaller abaxial sepal (Fig. 90, arrow). Stamens arise simultaneously (Figs. 90, 91, arrows). It was not clear whether the petal primordia preceded the stamens or the opposite, but petals were small and inconspicuous and were rapidly overtopped by the stamens at least in young stages (Fig. 90). Stamens rapidly extend in size and grow from hemispherical structures into two-lobed organs (Fig. 92). A long anther is finally formed by the development of a ventral groove and the tip extends as a protuberance. Filaments extend only at anthesis. The petal primordia grow continuously but slowly and they finally overtop the stamens as long tapering appendages. The central area of the floral apex grows in a filament-like undifferentiated organ representing the pistillode which is not visible at anthesis (Fig. 92). Pistillate flowers differ in several respects from the

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Figs. 69–80. *Chondropetalum ebracteatum*. Development of pistillate (Figs. 69–77) and staminate (Figs. 78–80) spikelet and flowers. **Fig. 69.** Apical view of spikelet with three flowers. **Fig. 70.** Lateral view of flower at early petal initiation. **Fig. 71.** Apical view of older spikelet. **Fig. 72.** Detail of flower at early petal initiation. **Fig. 73.** Sequential formation of the staminodes. **Fig. 74.** Flower after gynoeceium initiation. **Fig. 75.** Slightly older stage. **Fig. 76.** Lateral view of older spikelet with flower at style formation. Note the shorter anterior style. **Fig. 77.** Dissected preanthetic bud showing one of the ovules. **Fig. 78.** Development of staminate flower at the same stage as Fig. 74. **Fig. 79.** Abaxial view of preanthetic staminate flower. Note the three short stylodes. **Fig. 80.** Lateral view of anthers alternating with stylodes. A, stamen or staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. All bars = 100 µm, except Figs. 70, 71, 78 = 10 µm; Fig. 75 = 75 µm



Figs. 81–89. *Thamnochortus lucens*. Development of pistillate spikelet and flowers. **Fig. 81.** Apical view of spikelet apex with large number of flower primordia; the numbers give the inverse sequence of initiation. **Fig. 82.** Lateral view of spikelet apex with sequential sepal formation on lower flower. **Fig. 83.** Flower with petal initiation (arrows). **Fig. 84.** Flower with staminode initiation. **Fig. 85.** Lateral view of slightly older flower. **Fig. 86.** Flower after carpel initiation. **Fig. 87.** Flower with style formation and limited upward growth of the staminodes. **Fig. 88.** Apical view of gynoecium without distinct sterile carpels. **Fig. 89.** Lateral view of preanthetic flower with single style; note the smaller adaxial staminode. A, staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bars: Figs. 81, 82, 84, 85, 89 = 100 μm ; Figs. 83, 86–88 = 10 μm

staminate flowers. They arise on few-flowered spikes and are tightly enclosed by the cochlear bracts. In the pistillate spikes the bracts tightly

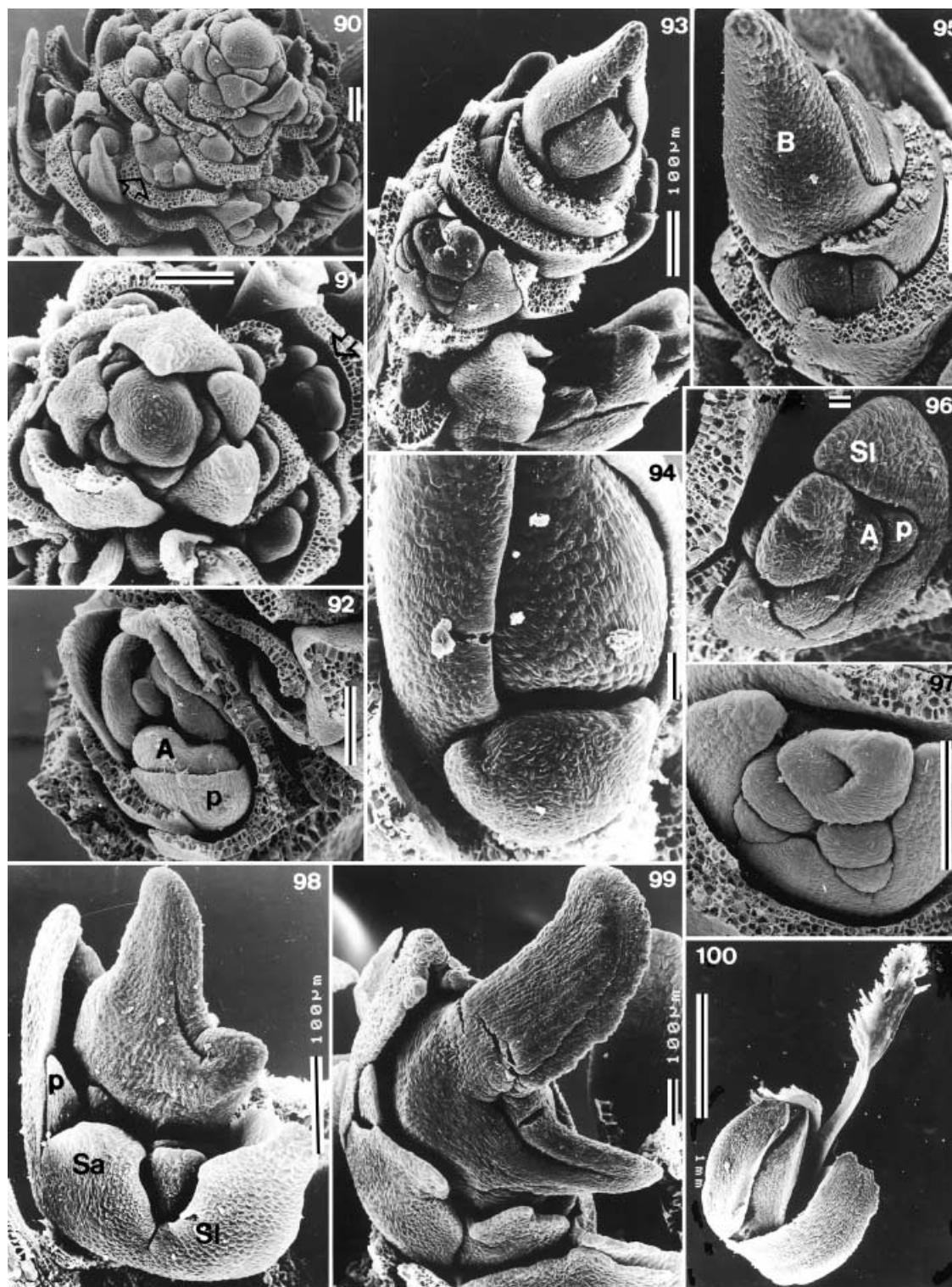
embrace the flowers and following bracts with extended margins. They bear a strongly developed *Vorläuferspitze* (Figs. 93, 95). The lateral

sepals arise sequentially in a more adaxial position and are followed by the abaxial sepal (Figs. 94, 95). The lateral sepals are compressed and produce a crest at anthesis; size differences persist during the whole development (Figs. 96–100). The abaxial sepal has its tip squeezed between staminodes and petals. All sepals are lifted by common zonal growth at the base (Figs. 96–98). Then petals are initiated and are rapidly followed by the staminodes. The lateral petals and staminodes arise simultaneously (Figs. 96, 97). It was not possible to determine the sequence of initiation of the adaxial petal and staminode. Staminode growth rapidly ceases and the staminodes ultimately become enclosed by the petal primordium (Figs. 98, 99). Petals grow slowly at first but ultimately grow slightly longer than the sepals (Fig. 100). The lateral sepals are keeled or occasionally compressed, while the abaxial sepal and petals are flat. The pistil primordium emerges uncovered above the sepals as an irregular elliptical structure. There is no abaxial carpel present. Two lateral carpels emerge sequentially and only one locule is differentiated first as a v-shaped slit (Figs. 96, 97). After the second carpel has been initiated the tissue abaxial of the slits extends upwards but not equally. As a result the gynoecium becomes highly asymmetric and the originally separate slits coalesce into a narrow locular slit (Figs. 98, 99). The fertile carpel has a laterally flattened massive style with ventral slit. The style is lifted and the slit becomes flanked by long stigmatic hairs. The sterile carpel grows more or less horizontally and has a much shorter style with stigmatic hairs (Figs. 99, 100). At anthesis the much shorter sterile style is horizontally curved, while the fertile one is erect.

***Staberoha cernua* (L.F.) T. Durand & Schinz (Figs. 101–104).** Only staminate flowers were available for study and no stages of gynoecium initiation could be observed. Flowers arise in compressed spikelets tightly enclosed by the bract bearing a *Vorläuferspitze* (Fig. 101). The lateral sepals emerge more or less simultaneously and rapidly increase in size.

They become only angular at stamen initiation (Fig. 104). The abaxial sepal is strongly retarded at first, emerging as a shallow ridge slightly before the petals arise (Fig. 101). Growth of the abaxial sepal is retarded until after stamen initiation (Figs. 102, 103), and it appears as a narrow lobe (Fig. 104). Petals emerge nearly simultaneously and grow slowly relative to the stamen primordia (Figs. 101–104).

***Askidiosperma paniculatum* (Mast.) H.P. Linder (Figs. 105–112).** Only pistillate flowers were examined. There are about eight equally fertile spikelets per spike. At anthesis the bracts are lacinate almost to the base and therefore appear awnlike with fibrelike lateral trichomes. At anthesis the petals are longer than the sepals and staminodes are filament-like (Fig. 112). There are three equally fertile carpels. The three styles are erect and are covered with papillae on their inner side (Fig. 112). On each spikelet, flowers arise spirally in the axil of narrow bracts bearing a *Vorläuferspitze* (Fig. 105). There is little compression between bract and axis so that the flowers appear triangular. Two narrow lateral sepals emerge simultaneously and rapidly overtop the floral apex, while the abaxial sepal only arises after petal initiation (Figs. 105, 106). The lateral sepals become rapidly erect and pressed with their adaxial sides against each other (Figs. 106, 107, 109). Growth of the abaxial sepal is retarded until carpel initiation and it has an acute triangular shape. The lateral petals arise simultaneously slightly ahead of the adaxial one (Figs. 107, 108). They are rapidly followed by the simultaneously arising staminodes (Fig. 110). Growth of the staminodes and petals is continuous and retardation of the stamens only occurs at anther differentiation. At anthesis the filaments are well developed, but the anthers appear shriveled (Fig. 112). The gynoecium initiates as a triangular primordium with three equal carpels (Fig. 111). Stages of gynoecial development were not observed. After anthesis the carpels dehisce by a dorsal slit exposing the seeds between the stiff erect perianth lobes (Fig. 112).



***Ischyrolepis ocreata*. (Kunth) H.P. Linder (Figs. 113–124).** Pistillate and staminate spikelets were available for study. Pistillate spikelets bear three to four basal bracts with sterile flowers. Mature flowers are flattened; the lateral sepals are compressed and have trichomes on the back; the abaxial sepal and petals are flattened and without hairs on the dorsal vein (Fig. 124). The two lateral carpels are fertile and have long expanding styles fused at the base. The ovary is flattened and bears two dorsal slits. Neither staminodes nor pistillodes are visible at anthesis.

Pistillate spikelets are few-flowered (Figs. 113, 114, 116). Bract primordia have a *Vorläuferspitze* and their margins partly enwrap younger bracts. Flower primordia are compressed against the spikelet (Fig. 114). The two latero-adaxial sepals emerge first and in a rapid sequence (Figs. 113, 115); they become soon equal in size and attain a flattened hood-like shape (Figs. 114, 116). The abaxial sepal emerges at the same time as the abaxial petals (Figs. 116, 117). Growth is retarded relative to the lateral sepals and remains so during the whole development (Figs. 118, 121). All sepals are lifted by common zonal growth. The abaxial petals arise simultaneously, slightly ahead of the adaxial (Figs. 117, 119). Growth is slow and the petals are still small at late ontogeny, not reaching beyond the top of the ovary (Figs. 120, 121). The petals have a rounded shape with their margins compressed and with some basal zonal growth. There is no trace of staminode initiation (Figs. 117, 118).

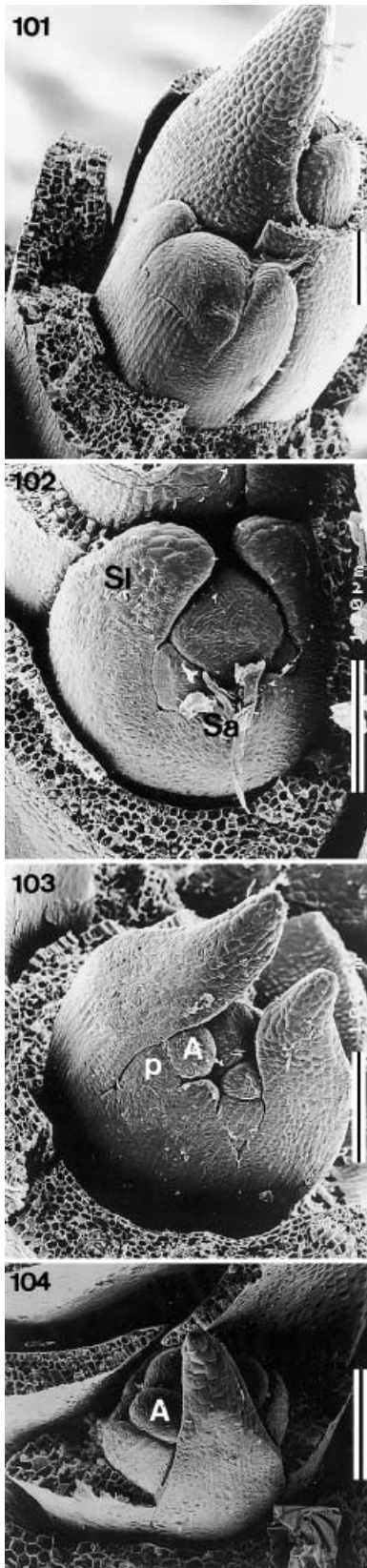
Gynoecium initiation starts as a broad elliptical primordium. Two carpel primordia are initiated laterally, slightly towards the adaxial side (Figs. 113, 118). There is no trace of a third carpel primordium although the abaxial side of the gynoecial dome is broader than the adaxial side (Fig. 118). Carpels grow upwards and converge with their margins and become laterally united (Figs. 119, 120). Two erect styles soon develop and are sometimes pressed against the top of the spikelet. One of the carpels has a slightly shorter style, although both are fertile. Styles are very long relative to the ovary.

Staminate flowers resemble the pistillate ones up to stamen initiation (Fig. 122). Stamen primordia grow into large structures overtopping the slow growing petals. There is no trace of a gynoecium primordium.

***Rhodocoma capensis* Steud. (Figs. 125–131).** Few-flowered terminal spikelets are grouped on long stalks with elongate bracts of which the lower ones are sterile. The bract primordia have a clear *Vorläuferspitze* which grows upwards (Figs. 126, 127); the tissue abaxially of the *Vorläuferspitze* extends in size as to cover the spikelet apex as well as the sides of the flower and younger bracts (Figs. 125–128). The result is a cap-like organ or a hood as the *Vorläuferspitze* is moved to the abaxial side (Fig. 125). Flower primordia have a sequential sepal initiation with the first sepal arising either left or right (Figs. 126, 127). Sepal growth is slow relative to the flower and the adaxial sepal emerges after the

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Figs. 90–100. *Staberoha vaginata*. Development of staminate (Figs. 90–92) and pistillate (Figs. 93–100) spikelet and flowers. **Figs. 90–91.** Two views of staminate spikelets showing the abundance of flowers and loosely arranged bracts. Different stages of floral development can be seen (arrows). **Fig. 92.** Preanthetic staminate flower. Note the filament-like pistillode. **Fig. 93.** Lateral view of pistillate spikelet with low number of flowers pressed against the axis by the bracts. **Fig. 94.** Detail of upper part of spikelet with early sepal initiation. **Fig. 95.** Detail of slightly older flower below the spikelet apex. **Fig. 96.** Flower with early gynoecium formation. **Fig. 97.** Asymmetric development of the fertile carpel primordium. **Fig. 98.** Preanthetic flower with asymmetric gynoecium. Note that the staminodes are hidden by the petals. **Fig. 99.** Slightly older flower showing horizontal direction of the sterile carpel. **Fig. 100.** Lateral view of mature flower with one erect and one recurved style. Note the compressed lateral sepals. A, stamen or staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. All bars = 100 µm, except Fig. 100 = 1 mm; Figs. 94, 96 = 10 µm



initiation of the abaxial petals (Fig. 128). The adaxial sepal emerges as a shallow curved ridge and is strongly retarded. At this stage the flower has become triangular; petals arise simultaneously as inversed triangular primordia. They are promptly followed by three equal staminode primordia (Figs. 129, 130). Growth of the staminodes and petals ceases early while the gynoecium initiates as a triangular primordium (Fig. 132). No stages of carpel development were observed. At anthesis the three carpels are fertile and staminodes are visible.

Discussion

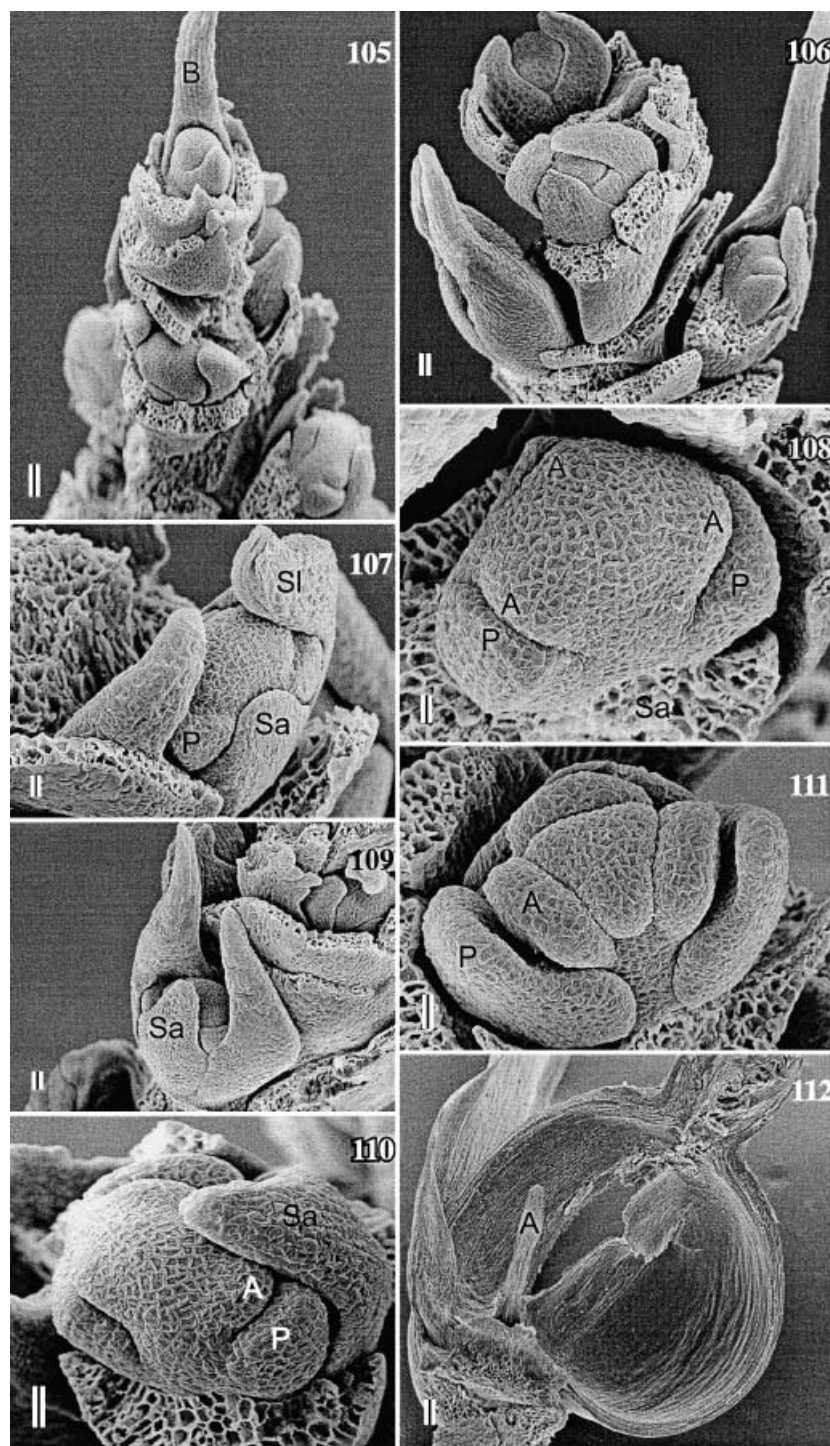
In addition to the data obtained for the *Willdenowia*-clade (Ronse Decraene et al. 2001), the information gathered for different species of the *Restio*-clade provides a sufficiently broad coverage of the different flower structures for analysing the evolution of individual characters in the African Restionaceae. In this way it becomes possible to pick out phylogenetically significant character sets and to understand their evolutionary patterns.

The expression of characters at maturity depends on shifts (a matter of gradual changes in growth patterns) during the development of the flower. Changes are rarely induced by a sudden mutation, rather by subtle changes in growth rates between different or homologous organs. The build-up of these changes results in diverse expressions at maturity.

Characters of the spikelet. Spikelets are in essence racemose with an acropetal development. Switches in the timing of initiation of

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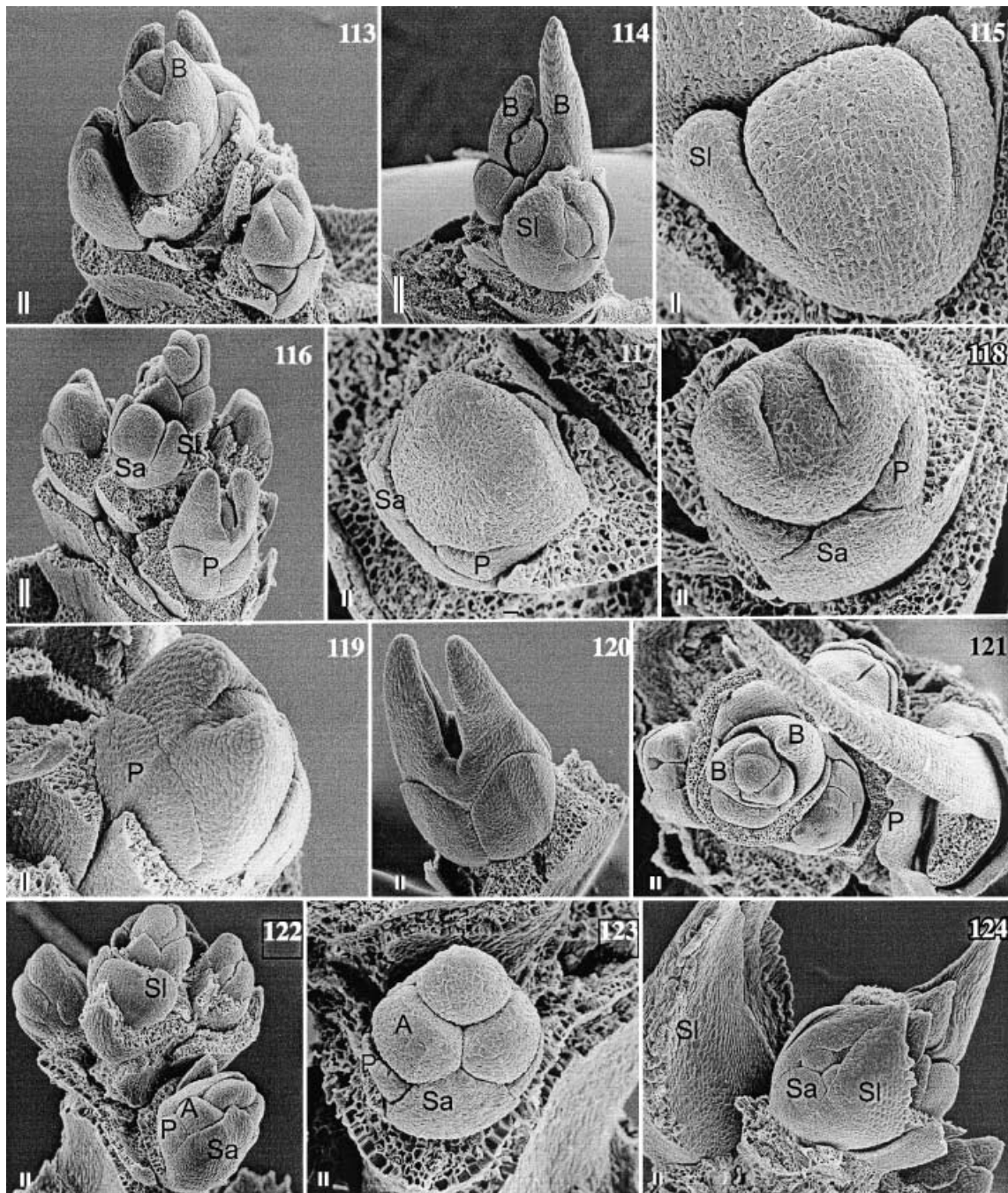
Figs. 101–104. *Staberoha cernua*. Development of staminate spikelet and flowers. **Fig. 101.** Upper part of spikelet with fewer flowers. Flower in front with initiation of petals. **Fig. 102.** Flower with early petal formation. **Fig. 103.** Flower with stamens initiated. **Fig. 104.** Development of the stamens and pronounced growth of the sepals; lateral sepals removed. Note the spearlike abaxial sepal. A, stamen; P, petal; Sa, abaxial sepal; Sl, lateral sepal. All bars = 100 μ m



Figs. 105–112. *Askidiosperma paniculatum*. Development of pistillate spikelet and flowers. **Fig. 105.** View of upper part of spikelet with elongate bract. **Fig. 106.** Partial view of spikelet with flowers at different stages of development. Note the elongate lateral sepals. **Fig. 107.** Flower with formation of petals. **Fig. 108.** Flower with staminode initiation. **Fig. 109.** Lateral view of bud at a similar stage of development. **Fig. 110.** Similar stage; lateral sepals removed. **Fig. 111.** Flower after gynoecium initiation. **Fig. 112.** Lateral view of postanthetic flower with dehiscent carpels. Ovules removed and inside view of the locules. A, staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bars = 10 μm , except Fig. 112 = 100 μm and Figs. 105, 106 = 20 μm

subsequent flowers may lead to a decussate pattern, possibly induced by the pressure of the enclosing bract. In several species studied the lowermost flowers of the spikelet have a truncated growth and abort after gynoecium

initiation. The upper flowers abort more rarely, or they do not reach maturity because the apical growth of the spikelet becomes truncated. As mentioned by Linder (2001), the number of spikelets and flowers per



spikelet is highly variable. The numbers given in this paper are just a sample of the existing variability. Abortion of flowers is an inherent economic process, leaving sufficient nutrients only for a few, or even a single flower. This is especially visible in the *Willdenowia* clade with several genera with a single terminal

flower per spikelet at anthesis (e.g. *Ceratocaryum*, *Willdenowia*, *Mastersiella*, *Hypodiscus*). Bracts tend to affect the initiation and development of the flowers either by a variable growth rate or by pressures on the flowers. A slow growth or loosely positioned bracts will have the same effect in more

regular, trimerous flowers (e.g. *Elegia capensis*, staminate *Staberoha vaginata*). Strongly compressed spikelets with enwrapping bracts will lead to curved flower primordia and reductions of organs in a median plane (e.g. *Thamnochortus lucens*, *Staberoha vaginata*, *Ischyrolepis ocreata*).

The bracts usually bear a *Vorläuferspitze* (an “awn”). A *Vorläuferspitze* as defined by Kaplan (1975) is the development of an unifacial tip above a bifacial sheath. It is a characteristic common to the Restionaceae, where it is considered as homologous to a modified leaf blade (Dahlgren et al. 1985). In some genera the *Vorläuferspitze* is almost not developed (e.g. *Restio*, *Chondropetalum*, *Thamnochortus*) or lost (e.g. *Dovea*, *Elegia*), this being obviously a derived character since these are not basal genera in the phylogeny (Eldenäs and Linder 2000). In *Rhodocoma* the distinction between the unifacial tip and the bifacial sheath becomes obvious by the displacement of the *Vorläuferspitze* to the abaxial side of the bract.

The structural variation of the perianth. A distinction between sepals and petals makes sense when discussing the phylogeny of the Restionaceae, even though the perianth tends to be morphologically homologous in the family as for the whole of the monocotyledons (e.g. Dahlgren et al. 1985). Differences between the perianth parts are often minor and are gradually built up, but they finally affect the flower in a marked way. Sepals and petals behave differently especially in their respective growth rates. Sepals tend to grow faster and

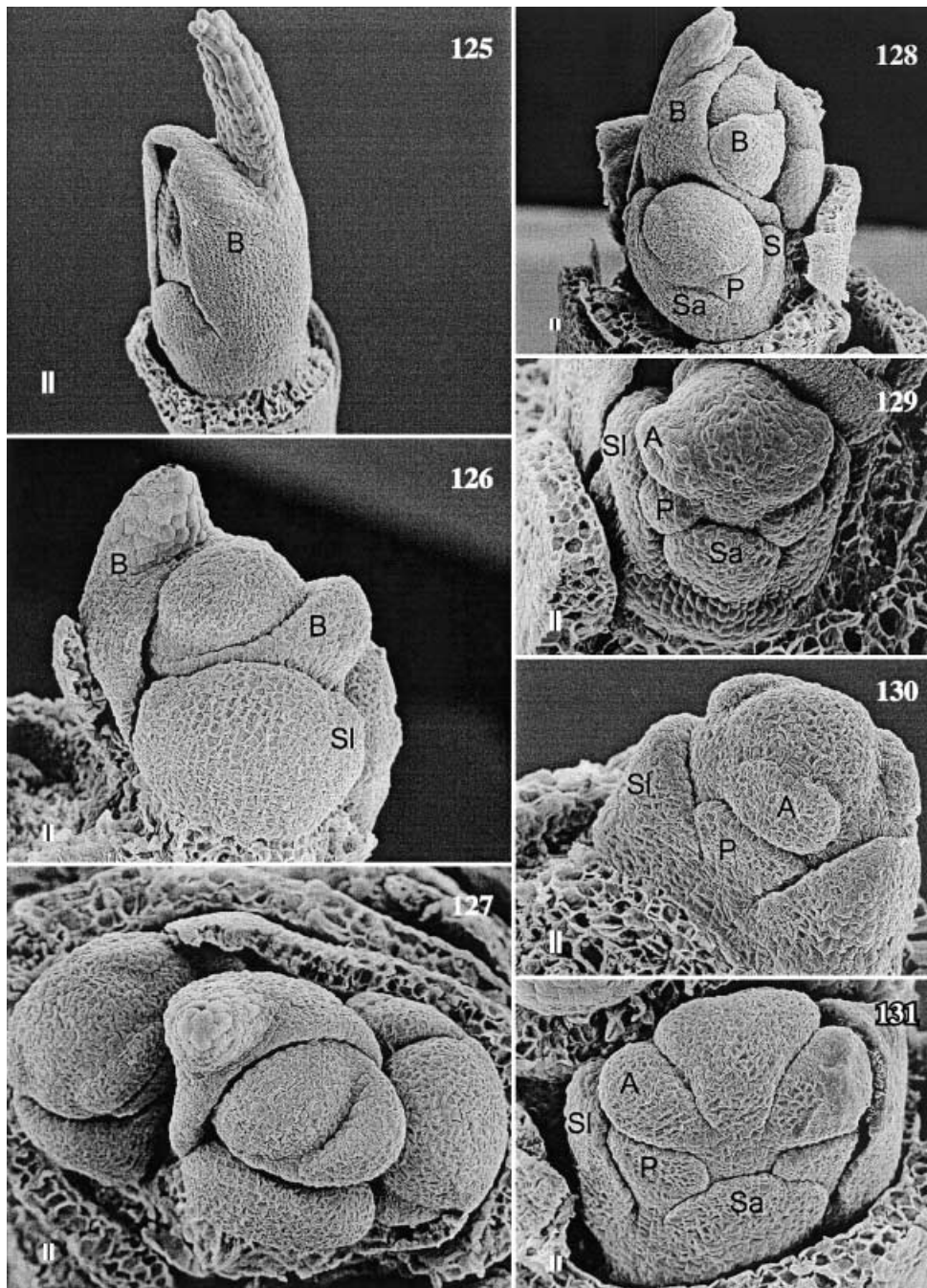
protect the flower bud, they are often compressed or keeled, and there is a marked distinction between the lateral sepals and the odd abaxial sepal. Petals tend to be more equal in size; they have a retarded growth in early stages (possibly related to the superposition of staminodes), but tend to grow faster after the initiation of the gynoecium, even reaching beyond the sepals at anthesis (Linder 2001; e.g. *Askidiosperma*, *Elegia cuspidata*, *E. racemosa*).

The differentiation between the lateral and the abaxial sepals is obviously linked with the compression of the flower between the bract and the spikelet axis. As a result the whole flower becomes flattened in early stages, sometimes curving around the spikelet axis, or remaining flattened until anthesis (e.g. *Staberoha vaginata*, *Nevillea*, *Hydrophilus*). There is a whole range of variations between well developed abaxial sepals arising after the laterals (e.g. *Dovea*, *Chondropetalum*), to a progressive retardation of the abaxial sepal that even arises together or after the petals (e.g. *Rhodocoma capensis*, *Elegia grandispicata*, *E. capensis*).

The unequal differentiation and growth of the sepals affects the initiation of the gynoecium, as the first formed, more strongly developed sepal stands at the side of the fertile carpel. If any carpels are sterilised or lost, then they are opposite the retarded sepals. Thus the retardation is distinctly manifested over the whole flower-side. The abaxial carpel opposite the weaker sepal is often lost, but this may be caused by the compression of the flower. The

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Figs. 113–124. *Ischyrolepis ocreata*. Development of pistillate (Figs. 113–121) and staminate (Figs. 122–124) spikelets and flowers. **Fig. 113.** Top of spikelet with sequential development of flowers. **Fig. 114.** Lateral view of a spikelet. **Fig. 115.** Flower with the lateral sepals formed. **Fig. 116.** Spikelet with flowers at different stages. **Fig. 117.** Flower with petals initiated; lateral sepals removed. **Fig. 118.** Flower with two carpels formed. **Fig. 119.** Older flower with apical increase in size of the gynoecium. **Fig. 120.** Development of two equal styles above the short petals. **Fig. 121.** Apical view of spikelet. Note the long erect style and small petals in the flower on the right. **Fig. 122.** Staminate spikelet with several stages of flower development; stage similar to Fig. 116. **Fig. 123.** Flower with the stamens formed and gynoecial residue. **Fig. 124.** Older flowers. Note the compressed lateral sepals. A, stamen; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. Bars: Figs. 113, 115, 117–119, 123 = 10 µm; Fig. 116 = 15 µm; Figs. 120–122, 124 = 20 µm; Fig. 114 = 50 µm



Figs. 125–131. *Rhodocoma capensis*. Development of pistillate spikelet and flowers. **Fig. 125.** Uppermost part of young spikelet, showing the shape of the subtending bract. **Fig. 126.** Lateral view of uppermost part of spikelet with younger bracts and a flower at lateral sepal initiation. **Fig. 127.** Apical view of spikelet apex. Note the sequential sepal formation in the flower on the right. **Fig. 128.** Lateral view of spikelet apex with flower in front after petal initiation. **Fig. 129.** Apical view of flower at stamen initiation. **Fig. 130.** Adaxial view of slightly older flower. **Fig. 131.** Abaxial view of flower after gynoecium initiation. A, staminode; B, bract; P, petal; Sa, abaxial sepal; Sl, lateral sepal. All bars = 20 μ m

unequal development of the lateral sepals leads in some cases to asymmetric flowers, as in *Restio dispar* or *Nevillea obtusissima*.

The petals also show a differentiation between the lateral and median (adaxial) members, although the difference is less clear-cut than for the sepals. At a certain stage of their development the adaxial petals may be bilobed, which can be caused by the compression of the petal between spikelet axis and staminode (e.g. in *Elegia cuspidata*, *Restio dispar*, *Dovea macrocarpa*, *Chondropetalum ebracteatum*).

In most genera of the *Willdenowia* clade the growth of the perianth is truncated at an early stage (Ronse Decraene et al. 2001). A consequence of this is that the perianth tends to vanish at anthesis, which is a logical consequence when the perianth has become reduced in a wind-pollinated system and where the protective function is fulfilled by the bract (Linder 1998).

Staminode reduction. In this study we encountered four possibilities for staminode reduction. (1) In a number of cases the stamens abort only after anthers have been formed and sometime before microsporogenesis (e.g. *Chondropetalum*, *Restio dispar*). (2) Species of *Restio*, *Askidiosperma*, *Calopsis*, and *Thamnochortus* share the development of a filament mostly without anther tissue. The staminodial filament is equal in size to the filament of staminate flowers. This suggests the existence of two distinct gene activities in the control of the process of anther abortion, one that affects anther formation, and one that triggers filament growth. In the case both gene activities are affected the staminode remains primordial. (3) In the most common case staminode growth ceased soon after initiation, leaving a small hump that eventually disappears at anthesis. All species of *Elegia*, *Staberoha*, and *Dovea* share this character. (4) In *Ischyrolepis* the process of inception appears to be totally lost and there is no trace of the staminodes. This is suggestive of a progressive reduction series, first affecting the anthers, and only later switching to the filaments. That the process of staminode reduction

has occurred independently and on several occasions is supported by the presence in the *Willdenowia* clade of strongly reduced staminodes as well as staminodes with aborting anthers (Ronse Decraene et al. 2001), thus indicating parallel reduction series in the *Willdenowia* and *Restio* clades.

Reduction of the carpels. Contrary to the perianth and stamens the gynoecium tends to show an amazing variation in the extent of development of the carpels. Almost all possible reductions from a trimerous gynoecial Bauplan are found in the Restionaceae.

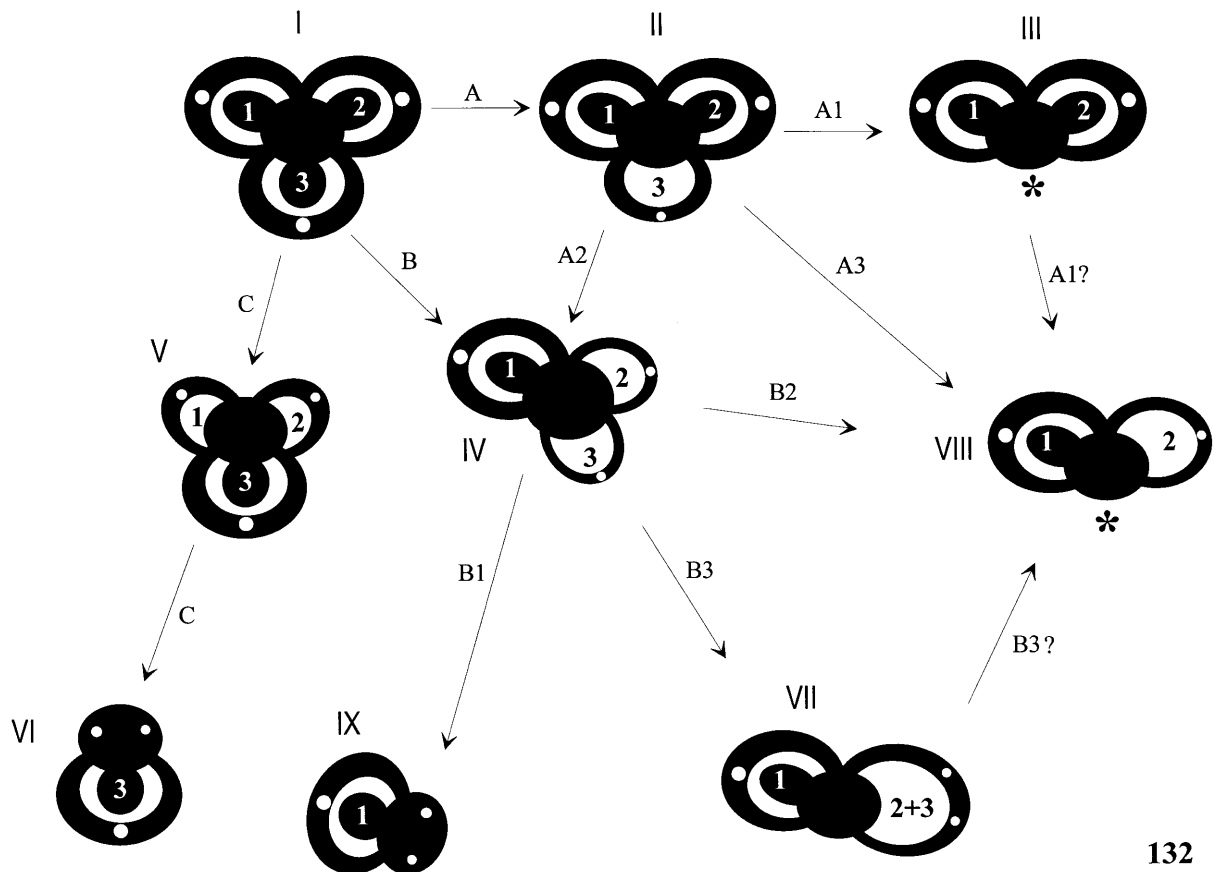
Philipson (1985) described two possible routes for ovary reduction in grasses: either by fusion of carpels, or by loss of fertility of some of the carpels. Linder (1992b) presented the reduction of carpels in the Restionaceae as an unidirectional pathway, viz. once organs have been lost, they cannot be regained. A first step is the loss of fertility of one or more carpels, which means that those carpels bear no ovules. In a few cases the sterile carpels may have an occasional sterile ovule (Kircher 1986). This is followed by the loss of locules (the carpellary tissue with dorsal trace is still present), and finally by the total loss of the carpel (with its dorsal bundle). Locular chambers that are visible in young stages may either persist (e.g. *Restio*, *Calopsis membranacea*, *Elegia capensis*, *Chondropetalum*) or they may be lost completely at anthesis (*Elegia cuspidata*). The presence of the sterile carpels at anthesis can be deduced either by the presence of styles and dorsal traces (*E. cuspidata*, *Restio multiflorus*, *Staberoha vaginata*), or only dorsal traces (e.g. *Thamnochortus lucens*) (Linder 1992b).

Linder (1992b: 417) showed in a survey of species that there are never fewer styles than locules (cf. Kircher 1986). This indicates that the process of reduction is one of ontogenetic gradations, starting with the initiation and later truncation of growth of locules, followed by the loss of the style. The vasculature is remarkably conservative and mostly persists when all other traces of carpels have vanished.

Kircher (1986) and Linder (1992a, b) indicated that a number of genera have one fertile carpel (carpel 1) with carpels 2 and 3 represented by a single combined bundle and a sterile locule. The presence of the combined bundle is intermediate between the two expected positions (opposite an inner tepal), and the sterile locule is much wider than expected. This pattern is said to occur in the genera of the *Willdenowia* clade (*Cannomois*, *Nevillea*, *Hypodiscus*, *Willdenowia*, *Mastersiella*, and *Ceratocaryum*), indicating an affinity between these genera. However, by a close inspection of the position of the carpels during ontogeny, we could neither find evidence for a displaced position of the sterile locule, nor for their larger size (Ronse Decraene et al. 2001). In general the flower tends to be much compressed against the spikelet axis, often taking the contours of it. As a consequence the whole flower appears bent and the carpels may appear displaced in relation to the other organs, especially when viewed by anatomical sections. On the other hand, the hypothesis of a fusion of two carpels can be substantiated in *Elegia*, where two subgroups are recognised on branching culms and persistent sheaths, but weakly correlated with style number, one with three styles (“*Elegia*”), and the other with mostly two styles (“*Lamprocaulis*”). In *E. racemosa* with two (three) carpels, the sterile carpel has two dorsal bundles that are close to each other, while there is a single bundle or two bundles in *E. neesii* (Linder 1992b; Ronse Decraene unpubl.). In the specimen of *Elegia racemosa* that we studied the abaxial carpel is missing and there is no ontogenetic evidence for fusion of two sterile carpels. In *E. neesii* one of the styles appears much bigger than the other (Ronse Decraene unpubl.). However, we lack the relevant stages of development to know whether this fusion occurs in an early stage. *E. stipularis* is occasionally trigonous in section, but there are only two bundles present in the ovary, and not on the abaxial side (Ronse Decraene pers. obs.).

It would be of interest to know whether the transition of trimerous to dimerous ovaries, and further to monomerous ovaries, always proceeds by this pathway. It is also possible that trimerous ovaries become dimerous by simple loss of one carpel – without intervening sterile carpels – as can be substantiated for several taxa (e.g. Ronse Decraene and Smets 1998) and could even be suggested for the loss of the abaxial carpel in the *Willdenowia* clade (Ronse Decraene et al. 2001). Truly dimerous flowers are absent in the African Restionaceae, contrary to some Australian genera (*Balaskion*, *Loxocarva*). The transition of a trimerous to a dimerous flower is a different genetic process that may be the result of a different mutation from those causing carpel loss or stamen reduction. Our observations also indicate that the process of reduction does not necessarily pass through a dimerous stage, as the sterile carpels occasionally fail to be initiated in trimerous gynoecia (e.g. *Thamnochortus*, *Elegia capensis*, *Elegia grandispicata*).

In trimerous ovaries the fertile carpel can be either situated in an abaxial position (as in *E. cuspidata*), both adaxial lateral positions (*Restio multiflorus*, *Ischyrolepis*) or one of the adaxial lateral positions (*Elegia capensis*, *Restio dispar*), either left or right. As we could observe in the *Willdenowia* clade (Ronse Decraene et al. 2001) the floral ontogeny shows that there is no preference for the position of fertile adaxial carpels (e.g. *Thamnochortus lucens*, *Staberoha vaginata*, *Elegia capensis*, *E. grandispicata*). That this position can be variable is not surprising and is related to the sequence of development of the outer tepals or sepals, where the first-formed sepal (and occasionally the largest) seems to influence the fertility of the gynoecium. Indeed the fertile carpel is initiated on the side of the first-formed and consequently largest sepal. In other floral ontogenetic studies it has been demonstrated that bracteoles arise likewise, either left or right without preferential position, with the sepals emerging clockwise or counterclockwise (e.g. Sattler 1973, Erbar and



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Fig. 132. Possible routes for gynoecial reduction in the South African Restionaceae. Letters refer to the evolutionary steps (see text for details). White dots, dorsal vasculature of the carpels; numbers refer to carpel positions; asterisks refer to lost carpel positions.

Note: Confusion may arise at anthesis as locules may not be visible any more, although they were initiated. The presence of vascular bundles is an indication of this, as well as tanniferous areas in the position of the locules. This should be kept in mind in order not to set up too many states.

(I) Basic trimerous gynoecium with all carpels fertile: *Dovea*, *Askidiosperma*, *Rhodocoma*, *Chondropetalum*; (II) Trimerous gynoecium with abaxial carpel sterile, three-styled at anthesis: *Restio multiflorus*, *R. callistachyus* (Kunth) Linder, *R. egregius* Hochst.; (III) Dimerous gynoecium without trace of the abaxial carpel, two-styled at anthesis: *Ischyrolepis*; (IV) Trimerous gynoecium with two sterile carpels and one lateral fertile carpel (either 1 or 2), three-styled at anthesis: *Elegia capensis*, *E. grandispicata*, *Restio dispar*, *Staberoha banksii* Pillans, *S. aemula* (Kunth) Pillans, *S. cernua* – it also contains cases with the locule absent at anthesis, but with the vasculature present: *Calopsis membranaceus* (Pillans) Linder, *C. paniculatus* (Rottb.) Desv., *Restio dodii* Pillans, *R. triticeus* Rottb.; (V) Trimerous gynoecium with two lateral sterile carpels and the abaxial carpel fertile, three-styled at anthesis: *Elegia cuspidata*, *Calopsis andreana* (Pillans) Linder; (VI) Pseudomonomerous gynoecium with only the abaxial fertile carpel and vascular remnants of the lost carpels (This is a theoretical possibility that has not been encountered by us yet); (VII) Dimerous gynoecium with one lateral fertile carpel and one lateral sterile carpel (either 1 or 2), bundle of lost carpel persistent, two-styled at anthesis: *Elegia neesii*, *E. racemosa*, *Thamnochortus muirii* Pillans (Kircher 1986); (VIII) Dimerous gynoecium with one lateral fertile carpel and one lateral sterile carpel (either 1 or 2), no trace of bundle of lost carpel, two-styled at anthesis: *Willdenowia* clade; (IX) Pseudomonomerous gynoecium with one lateral fertile carpel (either 1 or 2) and vascular remnants of the lost carpels; one-styled at anthesis; locules may be present as islands of tannins: *Thamnochortus*

Leins 1988, Ronse Decraene et al. 1997). The Restionaceae do not escape to this rule.

By comparing different ontogenies it becomes possible to reconstruct the different processes of carpel reduction in the South African Restionaceae. Linder (1992b) recognised six informal groups of taxa on the basis of the configuration and reduction of the ovary. These could be extended to nine groups (Fig. 132). The basic gynoeceum consists of three equally developed carpels, as in *Askidiosperma*, *Rhodocoma*, *Dovea*, and *Chondropetalum* (I). In *Chondropetalum* the abaxial style tends to be shorter than the other, and this could represent a precursory state to a further reduction. Figure 132 shows the possible pathways of ovary reduction. Three main routes can be distinguished (indicated with A, B, C):

1. The abaxial carpel becomes sterile (II; e.g. *Restio multiflorus*) and is finally completely lost (III; e.g. *Ischyrolepis*) (route A1).

2. One of the adaxial carpels remains fertile, while the other two abort (eventually at unequal rates) (IV; e.g. *Elegia capensis*, *Staberoha*, *Thamnochortus*). If the two sterile carpels regress at an equal rate one ends with a single carpel without remaining traces except for the vasculature (IX; e.g. *Thamnochortus lucens*, *Restio* sp., *Calopsis* sp.) (route B1). Evidence for the second pathway is the case of *Restio dispar*, suggesting the possibility of an independent process within the genus (A2 or B).

3. The abaxial carpel is fertile and the two adaxial carpels become sterile (V; e.g. *Calopsis andreaeana*, *Elegia cuspidata*). Finally, they disappear completely, except for their vasculature (VI; e.g. *Elegia stipularis*). (Route C).

These reductive trends do not explain for the occurrence of two lateral carpels, one of which is sterile (VIII, as e.g. in *Ceratocaryum*, *Hypodiscus*, *Cannomois*, *Nevillea*, *Hydrophilos*, *Willdenowia*). Here again three pathways are possible:

1. From a prototype as *Ischyrolepis* (III), one of the lateral carpels becomes sterile (route A1).

2. From a prototype as *Restio multiflorus* (route A3) or *Elegia capensis* (route B2), the abaxial carpel disappears completely and one lateral remains sterile.

3. From a prototype with two sterile carpels as in *Elegia capensis* the two sterile carpels become fused except for the respective vascular traces (VII; e.g. *Elegia racemosa*, *E. neesii*). Next the vascular bundles fuse (route B3).

Support for the third pathway tends to be substantiated by the fact that some *Elegia* species have one fertile and one sterile lateral carpel (e.g. *Elegia racemosa*, *E. neesii*), and by the occasional occurrence of a third abaxial carpel in *Hydrophilos* and *Nevillea* (Ronse Decraene et al. 2001). However, this appears to be irrelevant by the fact that sterile carpels never arise as double structures in the *Willdenowia* clade.

As the *Willdenowia* clade is well supported and all taxa share the same gynoeceal configuration (see Linder 2000, Ronse Decraene et al. 2001), one can confidently accept one reduction to have occurred at the base of the clade.

These processes also indicate the following. *Elegia* and *Restio* are either polyphyletic, or one has to accept the independent origin of several reductive lines within each genus. The existence of a phylogenetic framework (Eldenäs and Linder 2000) makes the eventuality to explore these routes of carpel evolution a real possibility. We plan to explore this option shortly (Linder and Ronse Decraene in prep.).

Differentiation of the sexes. All Restionaceae show a differentiation of staminate and pistillate spikes on different plants (see also Linder 2001). The sterilisation of one of the genders occurs at different stages between different species and is thus progressive¹. At

¹ Bisexual flowers are occasionally present. The type of *Anthochortus insignis* (Mast.) H.P. Linder, which is Schlechter 995b, has hermaphrodite flowers and *Restio mahonii* (N.E. Br.) Pill. ssp. *humbertii* (Cherm.) H.P. Linder from Madagascar has most flowers hermaphrodite.

one extreme stands a very late abortion of either the stamens or the carpels (e.g. *Chondropetalum ebracteatum*, *Restio dispar*, *R. multiflorus*, *Hydrophilus*, *Nevillea*); at the other the differentiation between the genders is such that the other sex is not initiated or that the floral morphologies are highly divergent (e.g. *Ischyrolepis*, *Staberoha vaginata*, *Willdenowia*). In the staminate flowers of a number of genera the gynoecium develops as a tubular structure with a rim that is higher on one side (e.g. *Elegia neesii*, *E. racemosa*, *Staberoha vaginata*). In other there is still formation of distinct carpels (e.g. *Chondropetalum ebracteatum*, *Elegia grandispicata*, *Hydrophilus*, *Nevillea*, *Ceratocaryum*, *Dovea*). This suggests that in some species the gene activity has become restricted to the upward growth of the gynoecial primordium, while a differentiation of carpels is abandoned. This is more or less comparable to the fate of the staminodes (see before), indicating a similar gene activity. The degree of reduction may be different between staminate and pistillate flowers of a same species (e.g. *Elegia grandispicata*). More research regarding the differentiation of the genders is obviously needed.

Comparison with other Restionaceae and related families. Similar ongoing reductive trends occur in the other Australian Restionaceae (Linder 1992a) and related families. In *Leptocarpus similis* two carpels appear to be totally reduced except for their dorsal bundles (Kircher 1986). In *Centrolepis fascicularis* (Centrolepidaceae) the abaxial and one lateral carpel are sterile. Abaxial sepals of staminate *Leptocarpus* often go missing, as this trend is obvious in the African Restionaceae studied. It is most probably the pressure of the flowers between bract and spikelet axis that brings about this loss. It may also induce the loss of the adaxial petal and abaxial carpel and lead to a dimerous gynoecium.

Reductions of the carpels are straightforward and appear to reach different levels of advancement spread over different species. *Thamnochortus* with a single style has appa-

rently evolved furthest in the South African Restionaceae. Similar trends have been operating in the Australian Restionaceae with several genera having monocarpellate gynoecia.

Although there seems to be an implicit assumption that the genera are homogenous for gynoecial patterns, it is possible that there is more variation within the genera, and that we have underestimated the number of reductions. Our sampling was not designed to critically test variation patterns within the genera, and so this might contradict the claim at the beginning that our sampling is adequate. We can only illustrate a limited number of reductions, and cannot pronounce on the systematic value of the carpel reductions in an unambiguous way. We recapitulate the reductive trends shown in Fig. 132 in a phylogenetic framework of the African Restionaceae. Route A1 is straightforward; most species of *Restio* have a sterile abaxial carpel and this is totally lost in the genus *Ischyrolepis*. *Restio* and *Ischyrolepis* appear closely related on other evidence (e.g. Eldenäs and Linder 2000). The pathway A2 is possible if trimerous *Restios* with two sterile carpels (e.g. *Restio dispar*) are derived by the sterilisation of a second carpel. Further reduction may eventually lead to a single carpel with one style (as in *Thamnochortus*). In a number of *Restio* species (e.g. *R. egregius*: Ronse Decraene unpubl.) the presence of locules can be detected as patches of tannin-filled tissue at anthesis (cf. Linder 1992b). However, if *Restio* is not monophyletic different independent derivations from a trimerous gynoecium are possible. Derivations of condition VIII from III (route A1) or VII (route B3) appear questionable although strictly spoken not impossible (but see comments in Ronse Decraene et al. 2001). The route B2 is the most probable route for the derivation of the homogenous *Willdenowia*-clade and is supported by the occasional presence of a second sterile carpel. Route B3 is relevant for some species of *Elegia* where two sterile carpels get fused (*E. neesii*). Route B1 occurs in the genus *Thamnochortus* by a complete reduction

of the sterile locules. Route C occurs occasionally in *Elegia* and *Calopsis* and appears to have systematic value at the generic level.

Although some genera are characterized by a stable pattern of reduction of the carpels (e.g. *Staberoha*, *Thamnochortus*, *Ischyrolepis*), some appear to be highly variable (e.g. *Calopsis*, *Elegia*, *Restio*). Whether this variability is an intrinsic generic pattern, or a reflexion of bad taxonomy should be elucidated by further study. In the study of Eldenäs and Linder (2000) *Restio* and *Calopsis* are paraphyletic, while *Elegia* is monophyletic. However, few species were studied and this does not give evidence for the evolution of the gynoecium. All species of *Elegia* share a number of conspicuous features (synapomorphies?): winglike petals with rapid growth, petal initiation starting with the adaxial petal, staminodes that abort readily after initiation, gynoecial basal rim development, and erect diverging styles. The two species of *Restio* that we studied also show a number of developmental similarities: Bracts with weakly developed *Vorläuferspitze*, strongly developed staminodes which occupy considerable space in early stages, circinate styles, and the formation of a dehiscence slit. In their tree based on combined morphological and molecular data Eldenäs and Linder (2000) recognised within the *Restio* clade two other subclades, viz. an *Elegia* clade and a *Thamnochortus* clade. The *Elegia* clade comprises the genera *Askidiosperma*, *Chondropetalum*, *Dovea* and *Elegia*. Except for *Elegia* the genera under consideration have three fertile carpels, suggesting the existence of the pathway B from a tricarpellate precursor. However, the two species of *Elegia* that we studied were not considered by Eldenäs and Linder. The *Thamnochortus* clade consists of the genera *Thamnochortus* (with a single carpel only) and *Rhodocoma* (with three fertile carpels) but the support is weak. This could suggest the presence of a single switch with the simultaneous abortion of two carpels (route B–B1).

In the morphological analysis of Eldenäs and Linder (2000) *Staberoha* stands with

Thamnochortus, while the molecular and combined analyses place the genus with *Elegia* with little resolution. There are, indeed, a number of ontogenetic similarities between *Thamnochortus* and *Staberoha*, such as the keeled lateral sepals and small adaxial sepal (compare Figs. 84–86 with Figs. 96–97), the erect fertile carpel with lateral position, and bract ontogeny. A better resolved cladogram including the same species that we studied ontogenetically would be helpful to explain trends in the flower.

There is much analogy between reductive trends affecting the gynoecium of the Restionaceae and the grasses, with repeated reductions. Philipson (1985) demonstrated that the pseudomonomerous gynoecium of the grasses can be linked to a tricarpellate ancestral condition. In most Bambusoideae (e.g. *Bambusa longispiculata*) the ovule arises adaxially opposite an abaxial fold giving rise to three growth centers developing into three distinct styles. The abaxial carpel appears to be the fertile one, as in *Elegia cuspidata*. However, in other grasses the development of the single ovule appears to have become independent of the development of carpellary tissue. In *Zea mays* the ovule arises on the abaxial side of the flower and only two styles develop (Irish and Nelson 1993). The two-styled arrangement is the predominant one in the grasses and Philipson (1985) gives a functional explanation for this. The distichous arrangement of the bracts, linked with a median compression of the spikelet leads to lateral gaps from which the feathery styles can emerge. Grasses with a single style and stigma (e.g. *Nardus*, *Lygeum*) appear to have tubular (viz. non-compressed) spikelets. In these species the fertile carpel appears to be in a median abaxial position and the laterals have vanished; the ovule is situated in an adaxial position. As we have discussed for the *Willdenowia* clade of the Restionaceae (Ronse Decraene et al. 2001), most taxa have compressed spikelets and the abaxial carpel is permanently lost. The compression of the flower between bract and axis – at least in the basal taxa (e.g. *Nevillea*, *Hydrophilus*) – is

responsible for the loss of the adaxial carpel, and this configuration is retained in the derived taxa with less compressed terminal flowers, such as *Ceratocaryum* and *Willdenowia*. It would be fruitful to perform similar ontogenetic studies in the grasses to know about the fate of the carpels that become reduced or lost.

Conclusions. Although the Restionaceae have a basically simple flower consisting of four whorls of organs, there is a remarkable variation in the mature floral structure as well as development, within a single genus or even species (e.g. in *Elegia*, *Restio*, *Staberoha*). Ontogenetic characters have a number of major advantages: (1) they are complementary to mature structures in assessing the position of reduced and fertile carpels, adding support to Linder's (1992a, b) assumption of specific losses; (2) they represent a whole set of new (cryptic) characters which are not visible in mature stages and are generally overlooked. The inversed initiation sequence of the petals in *Elegia* is one example; (3) They reveal the existence of primordia that are overlooked at anthesis. For example, staminodes can be invisible at anthesis (e.g. in *Elegia*, *Willdenowia*), because truncation of growth occurs early. On the other hand the total loss of staminodes in *Ischyrolepis* can be ontogenetically examined; (4) they can be more explicit than mature stages on the homology of certain structures, as the conditions at anthesis do not necessarily reflect the developmental processes and may be misleading. Ontogeny shows the effective stages of abortion and helps in deciding whether losses are homologous.

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