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The Discovery of Polyandry in *Curculigo* (Hypoxidaceae): Implications for Androecium Evolution of Asparagoid Monocotyledons

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• *Background and Aims* Individual flowers of the monocot *Curculigo racemosa* (Hypoxidaceae, Asparagales) are regularly polyandrous. To evaluate the significance of this almost unique character among Asparagales for flower evolution of asparagoid monocots, flowers of *C. racemosa* were studied comparatively.
• *Methods* Anthetic flowers as well as early floral developmental stages were studied by light and scanning electron microscopy.
• *Key Results* Despite the polyandry, floral development is similar to that of other Asparagales with a developmental gradient from adaxial to abaxial. Stamens initiate simultaneously and the diameter of staminal primordia is about half of that in species with six anthers. The number of stamens is not fixed (12–26) and varies within the same inflorescence. Surprisingly, the gynoecium can be four- or six-locular, besides the normal trimerous state.
• *Conclusions* The discovery of a polyandrous *Curculigo* reveals plasticity of stamen number at the base of Asparagales. Orchidaceae – sister to all other Asparagales – has a reduced stamen number (three, two or one), whereas in Hypoxidaceae – part of the next diverging clade – either the normal monocot stamen number (six), polyandry (this study) or the loss of three anthers (*Pauridia*) occurs. However, at present it is impossible to decide whether the flexibility in stamen number is autapomorphic for each group or whether it is a synapomorphy. The small size of stamen primordia of *Curculigo* is conspicuous. It allows more space for additional androecial primordia. Stamens are initiated as independent organs, and filaments are not in bundles, hence *C. racemosa* is not secondarily polyandrous as may be the case in the distantly related *Gethyllis* of asparagoid Amaryllidaceae. The increase in carpel number is a rare phenomenon in angiosperms. A possible explanation for the polyandry of *C. racemosa* is that it is a natural *SUPERMAN*-deficient mutant, which shows an increase of stamens, or *ULTRAPETALA* or *CARPEL FACTORY* mutants, which are polyandrous and changed in carpel number.

Key words: Monocots, lower Asparagales, floral development, SEM, floral mutants, androecium, gynoecium, Orchidaceae.

INTRODUCTION

Curculigo racemosa Ridl. is a common understorey herb of primary and secondary lowland and montane tropical rainforests in Borneo (Geerinck, 1993; pers. obs.). The genus *Curculigo* belongs to the family Hypoxidaceae and consists of approx. 20 species of exclusively tropical origin. Hypoxidaceae is part of the 'Lower Asparagales' in a grade comprising Asteliaceae, Blandfordiaceae, Doryanthaceae, Iridaceae, Ixioliriaceae, Lanariaceae, Orchidaceae, Tecophilaeaceae, Xanthorrhoeaceae *s.l.* and Xeronemataceae (Fig. 1; Rudall *et al.*, 1997; Chase *et al.*, 2006), which are characterized by predominantly simultaneous microsporogenesis and an inferior ovary. *Curculigo* shows the regular monocot pattern of floral organs: it has five trimerous organ whorls, with three sepals, three petals, two times three stamens, and three carpels. However, the author has regularly found populations of the *C. racemosa* complex that do not follow the normal androecium rule, showing instead a multiplication of the stamens.

Polyandry is common among the basal lineages of angiosperms and eudicots, and a comprehensive literature record exists on the evolution and systematic value of this feature (e.g. Ronse de Craene and Smets, 1993; Endress, 1994; Ronse de Craene *et al.*, 2003). In the pre-molecular era, polyandry has been used as a key character to define taxonomic units such as Dilleniidae or Rosidae. However, relatively few cases of polyandry are known among monocots. Documented examples are from Poaceae (*Ochlandra* with 6–120 stamens, Soderstrom and Londono, 1988; and *Pariana* with up to 21 stamens, Soderstrom and Calderon, 1979; Cocucci and Anton, 1988), Cyperaceae (*Evandra* with 15–20 stamens, Engler, 1892), Alismataceae (Sattler and Singh, 1978), Hydrocharitaceae (Cook, 1998), Velloziaceae (*Vellozia* six to numerous stamens: Kubitzki, 1998), Tofieldiaceae (*Pleea* with nine stamens, six outer and three inner, Tamura, 1998*a*), Trilliaceae (*Paris* with tetra- to octomerous whorls; Tamura, 1998*b*) and Smilacaceae (*Heterosmilax* with 6–20 stamens, Conran, 1998). Polyandry is relatively common among Arecaceae (Uhl and Moore, 1980; Endress, 1995; Rudall *et al.*, 2003). Among Asparagales, however, it is rare and, to date, only two cases of polyandry are documented: *Aspidistra dodecandra* of Ruscaceae [Asparagaceae *s.l.* (Chase *et al.*, 2006); Fig. 1] has 10–12 stamens, i.e. twice the number of perianth parts (Tillich, 2005), and *Gethyllis* of Amaryllidaceae [Alliaceae *s.l.* (Chase *et al.*, 2006); Fig. 1] shows six, 12, 18 or more stamens (Dahlgren and Clifford, 1982).

Curculigo has been repeatedly discussed as a close relative to Orchidaceae based on growth habit similarities and sympatry with the most basal orchid clade Apostasioideae

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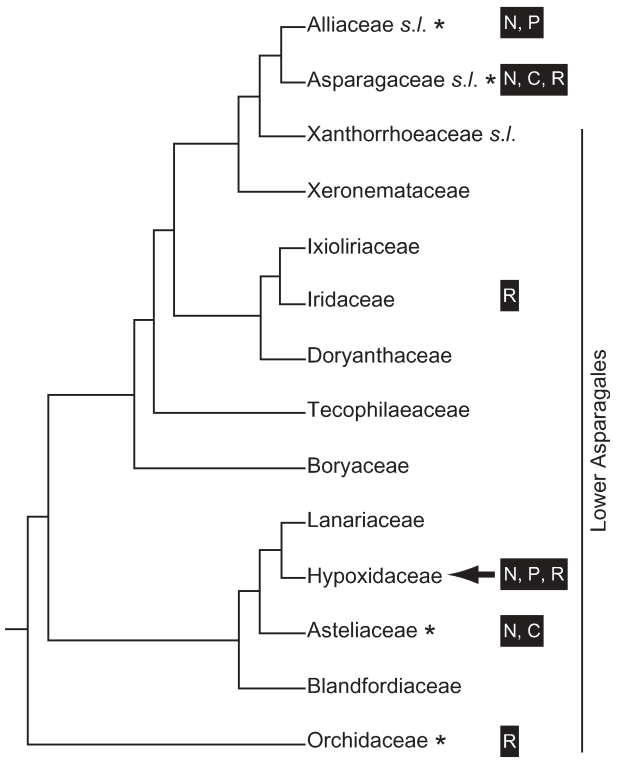

FIG. 1. Cladogram of Asparagales redrawn after Chase *et al.* (2006). The position of Hypoxidaceae is highlighted by an arrow and 'Lower Asparagales' by a bar. Orchidaceae, Asteliaceae, Iridaceae, the 'Higher Asparagales' Alliaceae *s.l.*, including Amaryllidaceae and Asparagaceae, including Ruscaceae are emphasized by asterisks. The type of stamen number variation is indicated by N [normal stamen number (6)], P (polyandrous), C (change of stamen number according to the flower merosity) and R (stamen reduction).

(Kocyan and Endress, 2001*a*; Kocyan *et al.*, 2004). Besides polyandry, the opposite situation is also known to occur in Hypoxidaceae: the South African genus *Pauridia* exhibits a reduction of the outer staminal whorl, resulting in only three functional stamens (Rudall and Bateman, 2002; A. Kocyan *et al.*, unpubl. res.). Reduction of anthers is brought to an extreme in the closely related Orchidaceae, which have lost either three, four or five stamens. The staminodial outer whorl is fused with the style, forming a gynostemium that is only known from orchids, *Pauridia* and Corsiaceae of Liliales (Rudall and Bateman, 2002). Together with molecular arguments, the loss of anthers and the gynostemium have made *Pauridia* a potentially close ally of Orchidaceae. However, more distantly related species within the Asparagales, i.e. some species of *Thysanotus* of Asparagaceae *s.l.*, have only three functional stamens, and Iridaceae has an androecial reduction to three anthers (Fig. 1). The novel finding of a polyandrous *Curculigo* species hence raises the question on the developmental plasticity of the androecium in the basal grade of Asparagales (Fig. 1) and on its potential significance for monocot flower evolution.

Here, the new finding of a polyandrous member of Asparagales is investigated and discussed. The following questions are particularly addressed. (1) What is the general pattern of androecial development and what is the general floral structure of the polyandrous *Curculigo racemosa*? (2) What are the differences from other known developmental patterns in Hypoxidaceae? (3) Which are the potentially underlying mechanisms for polyandry? (4) Is the developmental plasticity of the androecium common at the base of Asparagales?

MATERIALS AND METHODS

Samples of *C. racemosa* were collected by the author during several field trips to Sabah and Sarawak/Malaysia. For one sample collected in Tenom Agricultural Park (Sabah), detailed microtome section series and scanning electron microscope (SEM) investigations were conducted (Figs 2, Fig. 3 and Fig. 4A–I). For a sample collected in a village close to Tambunan (Sabah), additional SEM preparations of floral development were studied (Fig. 4J–M). The other samples were investigated through hand sections observed with a dissecting microscope. The living plant material was pickled in FAA [10 : 1 : 2 : 7 of ethanol (95 %), glacial acetic acid, formalin and water] and subsequently stored in 70 % ethanol. For SEM investigation, the specimens were dehydrated in an alcohol–acetone series, critical-point dried (BIO-RAD E3000 Critical Point Dryer) and sputter-coated with a gold target in a BAL-TEC SCD 050 sputter coater. SEM was performed with an updated Hitachi S-4000 or a LEO 438VP. Samples for light microscopy were gradually dehydrated, embedded in 2-hydroxyethyl methacrylate (Igersheim and Cichocki, 1996), microtome sectioned at 6 μm and stained with toluidine blue and ruthenium red. The chromosome number was counted from root tips. The preparation of the material is as recorded in Heubl and Wistuba (1997).

RESULTS

Inflorescences are produced in leaf axils and are dense, head-like racemes. At anthesis, the flowers are yellow and polysymmetric (Fig. 2A). The sepals and petals are curved backward. The anthers are sagittate and basifixed. They are free and open by latrorse dehiscence over the entire length of the thecae (Fig. 2B). The endothecium is one (to two) cell layers thick. In each stamen a single vascular bundle is present in the filament that serves the anther (Fig. 3E). The number of stamens is variable between individual plants, but also varies within the same inflorescence, from 12 to 26. The gynoecium has an inferior ovary and axile placentation (Fig. 3D), and is tetralocular (Fig. 3D). The ovaries are divided into a proximal synascidiate (Fig. 3D) and a distal symplicate region with placentae standing far apart from each other, giving the appearance of a unilocular ovary (Fig. 3C). The four-part stigma is wet and multicellular–papillate. A secretion-filled lacuna is present in the centre of the style acting as a compitum in which the pollen tubes will grow (Fig. 3F). Four vascular bundles serve the style (Fig. 3F). Gynoecia of other flowers studied by a dissecting microscope are tri-, tetra- or hexalocular; tri- or tetralocular gynoecia occur within the same inflorescence. The stigmatic partitioning as well as the

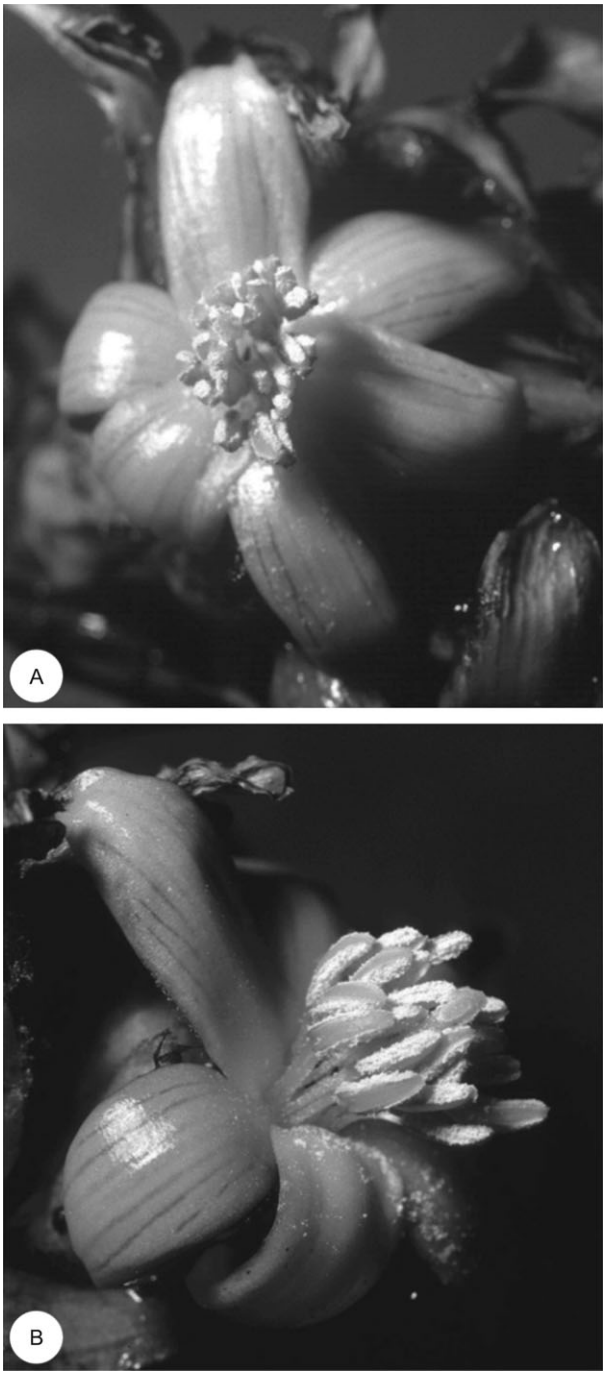

FIG. 2. Flowers of *Curculigo racemosa* at anthesis. (A) Frontal view; (B) lateral view.

bundle number supplying the style are according to the locule number.

Each flower arises in the axil of a large bract. The floral primordium emerges as a laterally expanded bulge (Fig. 4A). The first organ primordia present are the two lateral sepals followed by the median sepal (Fig. 4B). Hence, the earliest floral developmental stage is monosymmetric. The petals are initiated simultaneously between the sepal primordia (Fig. 4C), and the stamen primordia arise simultaneously in front of the incipient sepals/petals (Fig. 4D–E, J). The diameter of the stamen primordia at this stage is approx. 25 μm. The number of stamen primordia counted ranges from 19 (Fig. 4G) to 21 (Fig. 4H, I). In a second inflorescence studied by SEM, 12–14 primordia were counted (Fig. 4K–M). Up to five stamen primordia occur in an episepalous position, and one, two or three in an epipetalous position, but it is admittedly difficult to distinguish between the stamen positions. The last organ primordia to appear are those of the gynoecium (Fig. 4G, K). All young flowers investigated for floral development showed only a tripartite gynoecium, although in the adult flowers of the same inflorescences clearly a tetramerous gynoecium is visible (see above). As both gynoecial numbers may occur in the same inflorescence, it is supposed that by chance no tetramerous ontogenetic stages were detected for this work.

Raphide idioblasts were observed in all floral organs (Fig. 3G). Conspicuous concentrations occur in all parts of the style (Fig. 3F) and in the anther tips. Noticeable mucilage canals are present in the pedicel, the ovary wall and the sepals/petals (Fig. 3A–D). The flowers offer pollen as a reward (Fig. 2B); nectar has not been found. The chromosome number is $2n = 18$.

DISCUSSION

General developmental pattern

The general developmental pattern of polyandrous flowers of *C. racemosa* is similar to that of other *Curculigo* species (Kocyan and Endress, 2001*b*). The whorls of sepals and petals are initiated first, followed by the androecium and finally by the gynoecium, with a marked developmental gradient from adaxial to abaxial. The first developmental stage – after the initiation of the two lateral sepals – is monosymmetric. This character has been repeatedly found in several monocot groups that otherwise show an actinomorphic symmetry pattern at anthesis, such as *Alania*, *Asphodelus*, *Chlorophytum*, *Curculigo*, *Doryanthes*, *Hypoxis* and *Kniphofia*, all of which are in Asparagales (Kocyan and Endress, 2001*b*; pers. obs.). In *Bulbine* (Xanthorrhoeaceae *s.l.*, Asparagales) and *Veratrum* (Melanthiaceae, Liliales), zygomorphy is even more pronounced (Endress, 1995). Here, the median sepal is markedly retarded after the differentiation of the androecium (*Veratrum*) or even the gynoecium (*Bulbine*). However, the developmental gradient from adaxial to abaxial has its most extreme form in the zygomorphic orchids where the adaxial sepals and the adaxial petal (the lip) are formed first, followed by the two lateral petals and finally the abaxial sepal. In *Bulbine*, *Veratrum* and orchids, the buds are always growing in the axil of large bracts that protect them during development. However, in *Acorus* (Acoraceae), the putative sister of all other monocots (see, for example, Chase *et al.*, 2000, 2006; Savolainen *et al.*, 2000), the inflorescence spadices show no bracts to protect flower primordia. Instead, the protective function is accomplished by the massively enlarged and first

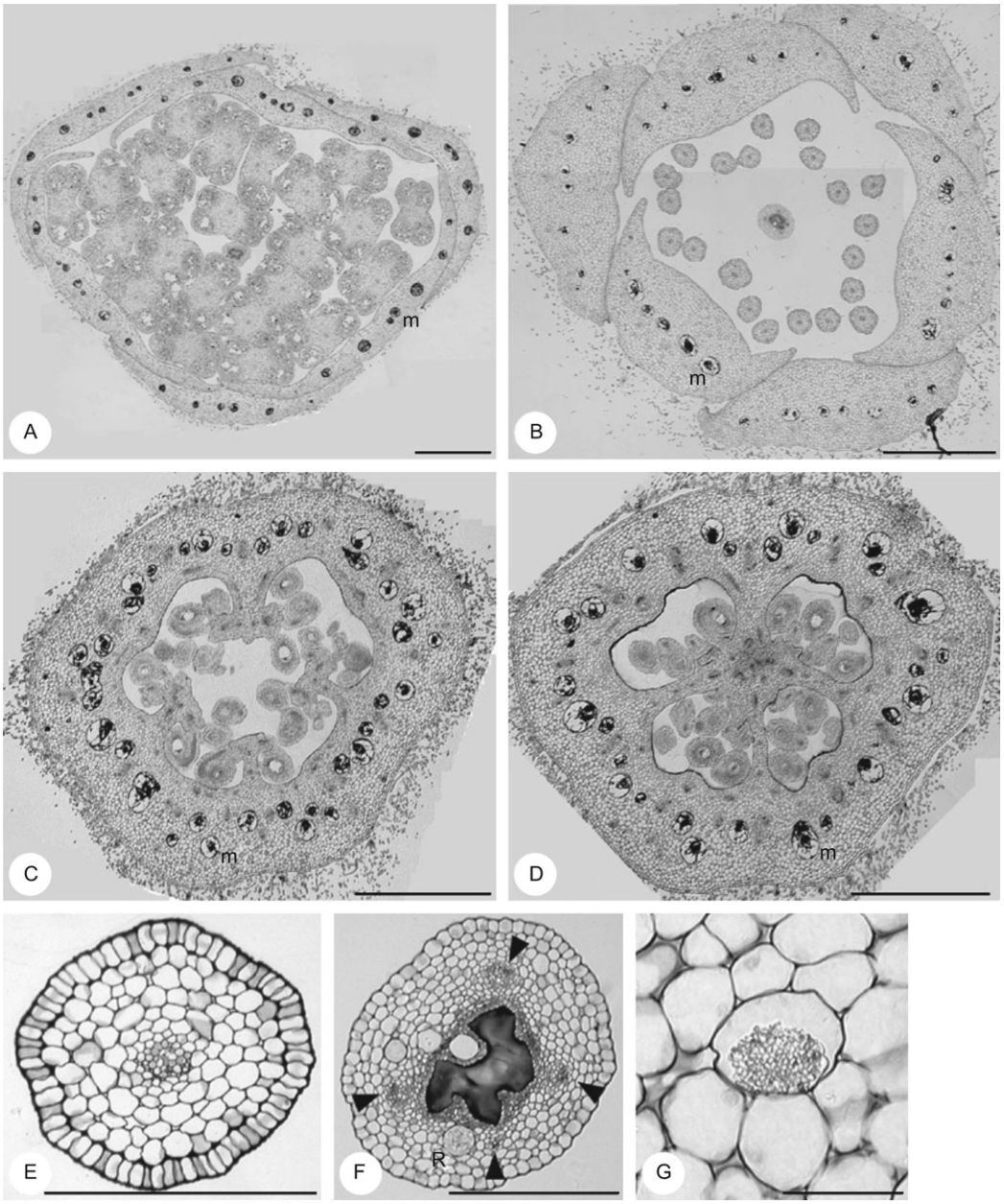

FIG. 3. Transverse sections of floral buds of *Curculigo racemosa* just before anthesis (light microscopy). (A) Superior flower part showing cross-sections through 21 anthers. (B) Cross-section through 21 filaments. (C) Cross-section of the symplicate zone of the ovary. (D) Cross-section of the synascidiate zone of the ovary. (E) Cross-section of a filament with the vascular bundle. (F) Cross-section of the four-part style with the pollen-transmitting tract forming a compitum; arrows indicate four vascular bundles. (G) Cross-section of a single raphide idioblast with raphide bundle. M, mucilage canals; R, raphide idioblast. Scale bars: A–D = 1 mm; E, F = 0·2 mm; G = 0·05 mm.

appearing abaxial sepal (Buzgo and Endress, 2000). The ongoing development gradient is similar to that of orchids: lateral sepals, median petal and finally lateral petals resulting in a monosymmetric flower at anthesis. Hence, the inversion of developmental direction from abaxial to adaxial of *Acorus* could be the result of an exhaustive consumption of the floral meristem on the abaxial side by the early formation of the large primordium of the bract or bract-like organ (Buzgo and Endress, 2000).

Androecium

With the exception of orchids, stamen formation of known Asparagales is (*a*) from outside to inside and (*b*) simultaneously within the whorls, which usually consist of three organs. However, in the case study presented here, a time lag between the antesepalous or antepetalous stamen primordia could not be detected. This contrasts with other *Curculigo* species (Kocyan and Endress, 2001*b*) in which stamen initiation is clearly sequential, though the plastochron between the stamen

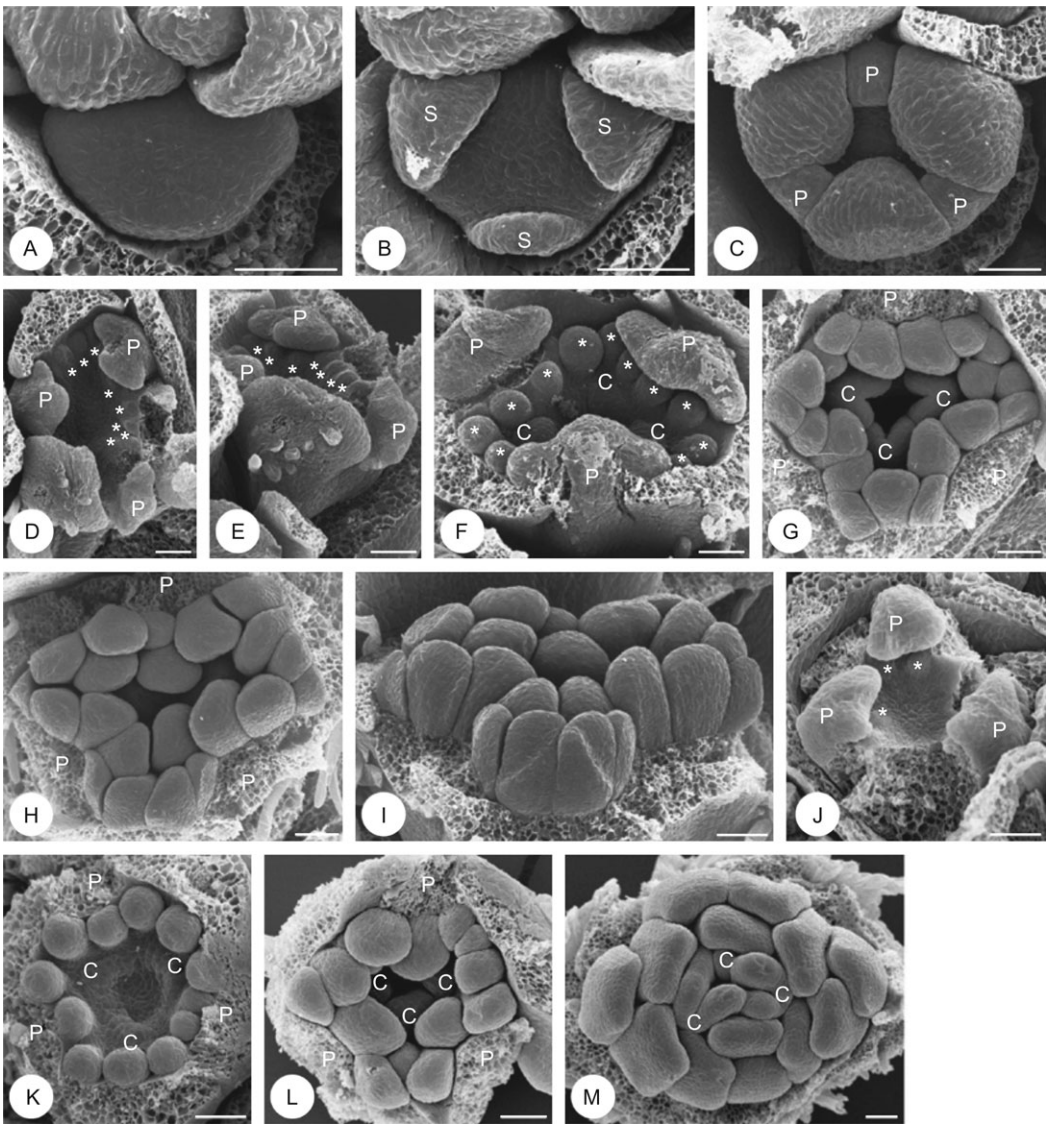

FIG. 4. *Curculigo racemosa*, early floral development (SEM). (A–I) and (J–M), respectively, are developmental series of two different individuals. (A) The first developmental stage is a laterally expanded bulge. (B) The median sepal appears last, resulting in a monosymmetric floral bud. (C) The petals arise simultaneously. (D, E) The stamen primordia appear simultaneously (sepals removed). (F) Initiation of carpel primordia (sepals removed). (G) Individual flower with 19 stamen primordia (sepals and petals removed). (H, I) The same inflorescence as in G but with 21 stamen primordia (sepals and petals removed). (J) Incipient stamen primordia (sepals removed). (K) Flower with 12 stamen primordia and three carpel primordia (sepals and petals removed). (L) Flower with 14 stamen primordia (sepals and petals removed). (M) Flower with 13 stamen primordia (sepals and petals removed). The asterisks indicate stamens; c, carpel; P, petal; S, sepal. Scale bars: 50 μm.

whorls is very short. All of the 12–26 stamens seem to be initiated simultaneously. Also, the number of stamens per flower is not fixed, even between individual flowers of the same inflorescence. The diameter of stamen primordia of the polyandrous *Curculigo* is about half of that in regular *Curculigo* flowers at comparable developmental stages (Kocyan and Endress 2001*b*), but all sepal/petal primordia have about the same dimensions. Hence, this gives more space for additional stamen primordia. A similar phenomenon is also known from some magnoliids, eudicots and monocot Alismatales where a doubling ('dédoublement') may occur if organ primordia are smaller than in the preceding whorl (Endress 1987, 1994, and references therein).

Three other genera of Asparagales are known to diverge from the normal trimerous monocot stamen number pattern. *Aspidistra* (Ruscaceae) can have more than six (but also less) stamens in accordance with the number of sepals/petals per whorl. Therefore, *Aspidistra* taxa are not strictly polyandrous, as polyandry is defined as the multiplication of stamens more than the petal number would allow (Wagenitz, 2003). There is, however, one truly polyandrous *Aspidistra* species. *Aspidistra dodecandra* shows a duplication of stamen number (10–12) in comparison with the perianth (Tillich, 2005). *Neoastelia spectabilis* of Asteliaceae has penta- to heptamerous flowers (Williams, 1987). As in *Aspidistra* the number of stamens of

Neoastelia spectabilis corresponds to the number of sepals and petals. Within Amaryllidaceae, some *Gethyllis* species are polyandrous with 12, 18 or more stamens. Unfortunately, nothing is known about the organ development patterns, especially of the androecium, of *A. dodecandra* and *Gethyllis*. It would be highly interesting to know whether the stamens are initiated sequentially or simultaneously. However, it is likely that secondary polyandry (*sensu* Endress, 1994) occurs in *Gethyllis* as the androecium of the polyandrous species is organized in stamen bundles (Meerow and Snijman, 1998; Manning *et al.*, 2002).

Pollination of polyandrous *C. racemosa* is unknown. However, the author observed pollinating *Trigona* bees on *Curculigo latifolia* in the close vicinity to specimens of *C. racemosa* (Kocyan and Endress, 2001*b*). It is therefore possible that the polyandrous *C. racemosa* is also visited by *Trigona* bees. The large number of anthers allows the production of a large quantity of pollen and is therefore a rich pollen source for pollinators. This may explain the high frequency of the polyandrous form of *C. racemosa*, as pollinators may favour these individuals due to the large pollen reward offered.

Gynoecium

The first developmental stages visible in the specimens investigated are three carpel lobes. However, at anthesis, the inferior gynoecium is three-, four- or six-partite. The variabilty of carpel numbers came as a surprise because the series of floral ontogenetic stages led to the expectation of a trimerous gynoecium, but young tetra- or hexamerous stages were not found here (see Results). With the exception of the differing carpel number, other *Curculigo* species and related Asparagales show similar gynoecial characteristics (see discussion in Kocyan and Endress, 2001*b*). The carpel number variability found here is almost unique among Asparagales. The only exceptions are *Aspidistra* and *Neoastelia* again, where the three or four locules, or 5–7, respectively, occur according to the number of organs in the other whorls. In contrast, the locule number of other monocot groups may vary considerably. In the Liliales families of Luzuriagaceae, *Drymophila moorei* is three- or four-locular (Clifford and Conran, 1987) and Trilliaceae has 3–10 carpels (Tamura, 1998*b*). Of Araceae, *Philodendron* is up to 47-locular, but the normal pattern is one- or three-locular (Mayo *et al.*, 1997). In Arecaceae trimery of the gynoecium is plesiomorphic, but seven genera possess more than three carpels (Uhl and Dransfield, 1987).

Generally, carpel number variation is rare in the angiosperms and, if found, tends to decrease (*Ipomopsis*, Polemoniaceae; Ellstrand 1983) instead of gaining new carpels as described here. A correlation between increased staminal number and increased carpel number seems not to exist as a trimerous gynoecium also occurs in polyandrous flowers. Furthermore, environmental stress as a factor in generating floral inconstancy (Ellstrand 1983) can be excluded as in the same environment tri-, tetra- and hexamerous plants were found (the same is true for the androecium).

Underlying genetic mechanism – a hypothesis

It is difficult to explain the aberrant androecium and gynoecium structures of *C. racemosa* presented here. Polyploidization may be excluded as the chromosome number ($2n = 18$) is the same as in other published *Curculigo* species (Lakshmi, 1980; Yang *et al.*, 1989). Hence, the possibility that polyandry and carpel aberration (see below) is the result of polyploidization may be excluded. However, in the last decade, molecular developmental studies have given mechanistic insights into organogenesis and superimposed gene control. In the eudicots *Arabidopsis* (Sakai *et al.*, 1995, 2000) and *Petunia* (Nakagawa *et al.*, 2004), the *SUPERMAN* (*SUP*) gene encodes a putative transcription factor that maintains the boundary between stamens and carpels. *SUP*-deficient mutants show an increase of stamens but at the cost of female fertility (Sakai *et al.*, 1995; Nakagawa *et al.*, 2004). The *SUP* gene may also be active in monocots (*Oryza*; Nandi *et al.*, 2000). Hence, the polyandrous specimens of *C. racemosa* may be natural *SUP*-deficient mutants. However, a regulative gynoecium factor should then be involved in *C. racemosa* as *Arabidopsis* and *Petunia SUP* mutants have reduced carpels and defective ovules, but the ovaries of the polyandrous examples presented here are often not regular in number but are otherwise fully functional. The increased carpel number suggests that besides the potentially deficient *SUP* gene another gene or genes may be active or inactive, respectively. Candidate mutants may be *ULTRAPETALA* (*ULT*; Fletcher, 2001) or *CARPEL FACTORY* (*CAF*; Jacobsen *et al.*, 1999). *ULT* and *CAF Arabidopsis* mutants show an increase of all floral elements. However, the three mutants just mentioned are possible candidates and only thorough research on the floral genetics may allow final conclusions. Answering this question would be of great interest because there seems to be some flexibility of stamen number in the basal groups of Asparagales (see below).

Comparison with Orchidaceae

Regarding the overall phylogeny of Asparagales, it is interesting that three basal families display distinct variation in the number of stamens. Orchidaceae, which are sister to all remaining Asparagales (Chase *et al.*, 2006), are characterized by stamen reduction to three, two or one, whereas in Hypoxidaceae a reduction to three (*Pauridia*) or a stamen multiplication from six to numerous, and in Asteliaceae penta- to heptamerous flowers occur (Fig. 1). Polyandrous flowers of orchids are unknown, though teratological individuals of monostaminal species with up to three stamens occasionally occur (Rudall and Bateman, 2002). The reduction of orchid stamens is clearly linked to their pronounced zygomorphy. However, the nature of the lip, which represents either the modified median petal (Kocyan and Endress, 2001*a*), a compound organ of the median petal plus the two outer adaxial stamens (Lindley, 1853; Darwin, 1862, 1885), or the united adaxial stamens combined with the complete suppression of the median petal (Nelson, 1965, 1967), remains unresolved (see also

Rudall and Bateman, 2002). The more we know about floral development and its genetic control via evolutionary developmental (evo–devo) studies conducted by others, the sooner we will get an answer to this long-lasting discussion. In Hypoxidaceae, staminal multiplication or reduction is symmetrical and the flowers stay actinomorphic. In combination with the style, the staminodial outer whorl of *Pauridia* forms a gynostemium (Rudall and Bateman, 2002). A gynostemium is otherwise only known in orchids and *Corsia* (Corsiaceae, Liliales). The reason why androecium plasticity is found at the base of Asparagales cannot be solved at present. However, it is unlikely that modern orchids represent the 'ancient' floral state of Asparagales. Hence, if androecium plasticity is not autapomorphic for each group where it occurs, then it is either because a lily-like orchid progenitor (sometimes also referred to as an 'ur-orchid') showed some androecium plasticity or a lost Asparagales sister group showed this phenomenon.

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