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HOMOLOGIES OF FLORAL STRUCTURES IN VELLOZACEAE WITH PARTICULAR REFERENCE TO THE CORONA

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New data on floral morphology, development, and vasculature in two Brazilian genera of the monocot family Velloziaceae (Pandanales) are used to explore the homologies of their unusual floral structures, especially the corona of *Barbacenia* and the corona-like appendages and multiple stamens of some *Vellozia* species. All Velloziaceae have epigynous flowers. Some species of *Vellozia* are polyandrous, and stamen number can be variable within species. In *Vellozia jolyi*, there is a single stamen opposite each sepal and a stamen fascicle (of three secondary stamens) opposite each petal. Each stamen possesses a single vascular bundle, and these are united into a single aggregate bundle in proximal regions of the fascicle. Stamens mature centripetally within each fascicle. The coronal appendages of both genera are closely associated with the stamens, but they share some vasculature with the tepals and develop late in ontogeny. The coronal organs cannot readily be homologized with any of the typical floral organs, but they show partial homology with both tepals and stamens. They are most readily interpreted as a late elaboration of the region between the petals and stamens associated with epigyny and the hypanthium.

Keywords: corona, flower, monocot, Pandanales, Velloziaceae.

Introduction

With their beautiful, showy flowers, species of the monocot family Velloziaceae (~250 species) represent an iconic feature of some of the most characteristic habitats of Brazil, especially cerrado vegetation. As currently circumscribed, Velloziaceae include five genera (Mello-Silva et al. 2008), of which two are mostly Brazilian (*Barbacenia* Vand. [including *Aylthia*, *Burlemarxia*, *Pleurostima*] and *Vellozia* Vand. [including *Nanuzia*]), one is Andean (*Barbaceniopsis* L.B. Sm.), one is African (*Xerophyta* Juss. [including *Talbotia*]), and one is Chinese (*Acanthochlamys* P.C. Kao). Velloziaceae are placed in Pandanales (Chase et al. 2000), a small but morphologically diverse order containing the following five families: Cyclanthaceae, Pandanaceae, Stemonaceae (including *Pentstemon*), Triuridaceae, and Velloziaceae. In contrast with the anomalous flowers of most Pandanales (Rudall and Bateman 2006), flowers of Velloziaceae resemble “typical” monocot flowers in that they are trimorous, with a petaloid perianth of six tepals in two whorls, six stamens (or multiples of six) in two whorls, and three fused carpels with septal nectaries. However, they differ from the typical monocot flower in three respects: (1) they are epigynous; (2) many species are polyandrous, especially in *Vellozia*, with from six to many stamens (predominantly 18) in different species; and (3) many species possess a corona of petaloid appendages that is usually adnate to the outer surface of the stamens.

A corona (sometimes termed a paracorolla) is a petaloid organ whorl that is additional to the typical floral organ complement that occurs in monocots (e.g., Amaryllidaceae, Bromeliaceae; Endress 1995) and many eudicots (e.g., Gentianaceae; Endress and Matthews 2006). The homologies of the corona in different angiosperms have been widely debated. On the basis of floral anatomy, especially vasculature, the “classic” corona of the monocot family Amaryllidaceae (order Asparagales) has been interpreted as being derived from the stamens in *Pancratium* and the tepals in *Narcissus* (Arber 1937). However, Scotland et al. (2008) challenged this conclusion for *Narcissus* on the basis of the expression of C-class MADS-box genes in the corona. The closely related family Alliaceae (Amaryllidaceae-Allioideae, sensu APG III 2009) also possesses a diversity of petaloid appendages that are sometimes flattened and corona-like (e.g., *Tulbaghia*) and sometimes filamentous (e.g., *Gilliesia*; Rudall et al. 2002), indicating that similar structures have evolved iteratively in Amaryllidaceae sensu lato in association with either the petals or the stamens. Schaeppi (1939) also described the diversity of appendages in *Allium* and other monocots and discussed their relationship with the corona of Amaryllidaceae. The homologies of the corona-like structures in Velloziaceae are similarly controversial (Menezes and Semir 1990). On the basis of external morphology, Noher and Cocucci (1971) suggested that the *Barbacenia* corona is staminodial, but Menezes (1973) stated that it is derived from the perianth on the basis of floral vasculature (see also Menezes 1980; Menezes and Semir 1990). However, no other authors have examined early ontogenetic stages or comparative morphology and anatomy of a broad range of species in

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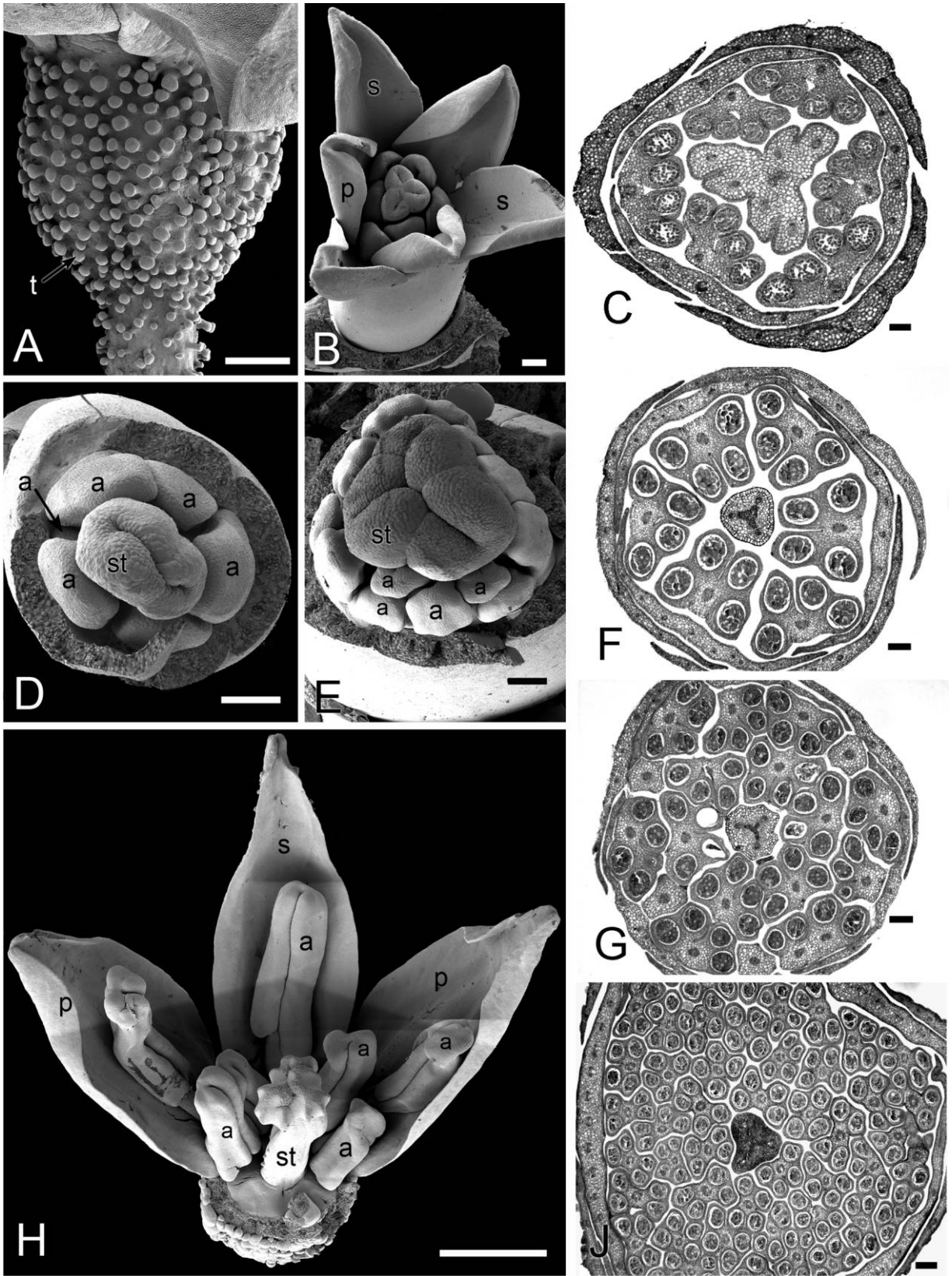


Fig. 1 A, *Vellozia jolyi*, SEM of surface of inferior ovary. Scale bar = 500 μm . B, *Barbacenia blanchetii*, SEM of young flower. Scale bar = 200 μm . C, *Barbacenia riparia*, LM transverse section (TS) of flower bud with six stamens, sectioned through anthers and style. Scale bar = 50 μm . D, *Vellozia* sp. nov. 1, SEM of young flower bud with six stamens. Scale bar = 100 μm . E, *Vellozia epidendroides*, SEM of young flower bud with 18

Velloziaceae. In the context of studies of floral evolution in other Pandanales (Rudall 2003, 2008; Rudall et al. 2005; Rudall and Bateman 2006) and other monocots (e.g., Caddick et al. 2000; Remizowa et al. 2006, forthcoming), this article examines flower anatomy and development of 13 species of the Brazilian genera *Vellozia* and *Barbacenia* in order to clarify the homologies of floral structures in Velloziaceae.

Material and Methods

Most of the material examined in this study was collected from plants in their natural habitats in Minas Gerais and Bahia, Brazil, and deposited in the cited herbaria (acronyms follow Holmgren and Holmgren 1998): *Barbacenia blanchetii* Goethart & Henrard (Mello-Silva 3096, CDBI, HUEFS, K, SPF), *Barbacenia flava* Mart. ex Schult. & Schult. f. (Sajo s.n., HUFU 45619), *Barbacenia gentianoides* Goethart & Henrard (Sajo s.n., HUFU 45621), *Barbacenia riparia* (N.L. Menezes & Mello-Silva) Mello-Silva (Menezes 1167, SPF), *Barbacenia spiralis* L.B. Sm. & Ayensu (Mello-Silva 3172, K, SPF), *Vellozia burlemarxii* L.B. Sm. & Ayensu (Mello-Silva 2148, B, CDBI, CTES, HUEFS, K, M, NY, RB, SPF), *Vellozia canelinha* Mello-Silva (Mello-Silva 2131, K, SPF), *Vellozia declinans* Goethart & Henrard (Mello-Silva 3170, B, RB, SPF), *Vellozia epidendroides* Mart. ex Schult. & Schult. f. (Sajo s.n., HUFU 48106), *Vellozia jolyi* L.B. Sm. (Mello-Silva 3093, B, HUEFS, K, SPF), *Vellozia taxifolia* (Mart. ex Schult. & Schult. f.) Mart. ex Seub. (Sajo s.n., HUFU 45620), *Vellozia* sp. nov. 1 (Mello-Silva 3167, SPF), and *Vellozia* sp. nov. 2 (Mello-Silva 3161, SPF).

Flowers were fixed in FAA (formalin–acetic acid–alcohol) and stored in 70% ethanol. For LM, flowers were embedded in Paraplast using standard methods and serially sectioned at ~13- μ m thicknesses using a rotary microtome. Sections were mounted onto microscope slides, stained in safranin and Alcian blue, dehydrated through an ethanol series to 100% ethanol, transferred to Histoclear, and mounted in DPX (distrene with dibutyl phthalate and xylene) mounting medium. Slides were examined using a Leica DMLB photomicroscope fitted with a Zeiss Axiocam digital camera. For SEM, fixed flowers and buds were carefully dissected in 70% ethanol and dehydrated in an ethanol series to 100% ethanol. They were then critical-point dried using a Bal-Tec 030 critical-point dryer, mounted onto pin stubs, coated with platinum using an Emitech K550 sputter-coater, and examined using a Hitachi S-4700 cold field emission SEM at 2 kV.

Results

Morphology and Development

Flowers of all Velloziaceae are epigynous; many species possess numerous large, multicellular, capitate glandular trichomes around the peduncle and the hypanthium (fig. 1A).

These hairs are unusual for monocots but resemble those of *Pentastemona* (Stemonaceae–Pandanales; Rudall et al. 2005) and of some Dioscoreales (e.g., *Dioscorea*, *Stenomeris*; Caddick et al. 2000). The perianth consists of six petaloid tepals in two whorls (fig. 1B). Stamen number is six in *Barbacenia*, with each stamen being placed opposite a tepal (fig. 1B, 1C), and it is six to many in *Vellozia* (fig. 1D–1J), with 18 stamens being the predominant condition (three stamens opposite each tepal). Some *Vellozia* species (e.g., *Vellozia jolyi*) possess a single stamen opposite each outer tepal and three stamens opposite each inner tepal (fig. 1H), for a total of 12 stamens. The tricarpellate ovary is inferior; the apical parts are initially free (fig. 2E) but soon fuse postgenitally (fig. 2F).

Very young floral buds with early stages of organ development are difficult to obtain for Velloziaceae (as in other Pandanales as well) because they are very small and hidden close to the axis under numerous leaf sheaths, making it necessary to dissect many stems to obtain the desired stages. For this investigation, buds at early stages were obtained only from *Barbacenia blanchetii*. In this species, buds develop in pairs enclosed within the same bract, with one bud being older than the other in each pair (fig. 2). The first primordia initiated on the floral meristem are the outer and inner tepals; these two whorls form almost synchronously, with the outer tepal primordia visible just before the inner ones (fig. 2A). The three outer tepals (sepals) soon overlap the inner tepals (petals; fig. 2B, 2C). Six stamen primordia and three free carpel primordia are formed subsequently (fig. 2E; slightly later stages are visible in the small bud in fig. 2D). Each stamen primordium becomes differentiated into an almost sessile anther, and two lateral outgrowths are formed at the base of the anther (larger flower in fig. 2D). As the anthers develop, the outgrowths elongate and become fused at their bases, forming petaloid appendages that support the mature sessile anthers (fig. 2G, 2H; fig. 3A). Even in some *Barbacenia* species in which the anthers are borne on filaments, the appendages develop in the same way (fig. 3B), becoming evident before the origin of the filament by intercalary extension.

In *Vellozia*, the trunk bundles of the stamen fascicles opposite the inner tepals (petals) diverge below those opposite the outer tepals (sepals; fig. 4H). This could suggest centrifugal development of stamen fascicles. If so, in the unusual flowers of *V. jolyi* with 12 stamens (fig. 1H), the presence of a single stamen opposite the sepals compared with a stamen fascicle (of three secondary stamens) opposite the petals could be explained by heterochrony, that is, as a delay resulting in failure of division of the outer primordia. On the other hand, stamens apparently mature centripetally within fascicles (fig. 1H).

In *Vellozia*, we were unable to obtain very early stages of organ inception, but the available stages showed that stamens mature centripetally within fascicles (fig. 1B, 1D, 1E, 1H). For example, in *V. jolyi* there are 12 stamens, one opposite each outer tepal and three opposite each inner tepal. The

stamens. Scale bar = 100 μ m. F, *Vellozia* sp. nov. 2, LM TS of flower bud with six stamens, sectioned through anthers and style. Scale bar = 100 μ m. G, *Vellozia epidendroides*, LM TS of flower bud with 18 stamens through anthers and style. Scale bar = 100 μ m. H, *Vellozia jolyi*, SEM of dissected flower bud with 12 stamens, showing one stamen opposite outer tepals (sepals) and three stamens opposite inner tepals (petals). Scale bar = 1 mm. J, *Vellozia canelinha*, LM TS of flower bud with 52 stamens, sectioned through anthers and style. Scale bar = 100 μ m. a = anther; p = inner tepal (petal); s = outer tepal (sepal); st = stamen; t = trichome.

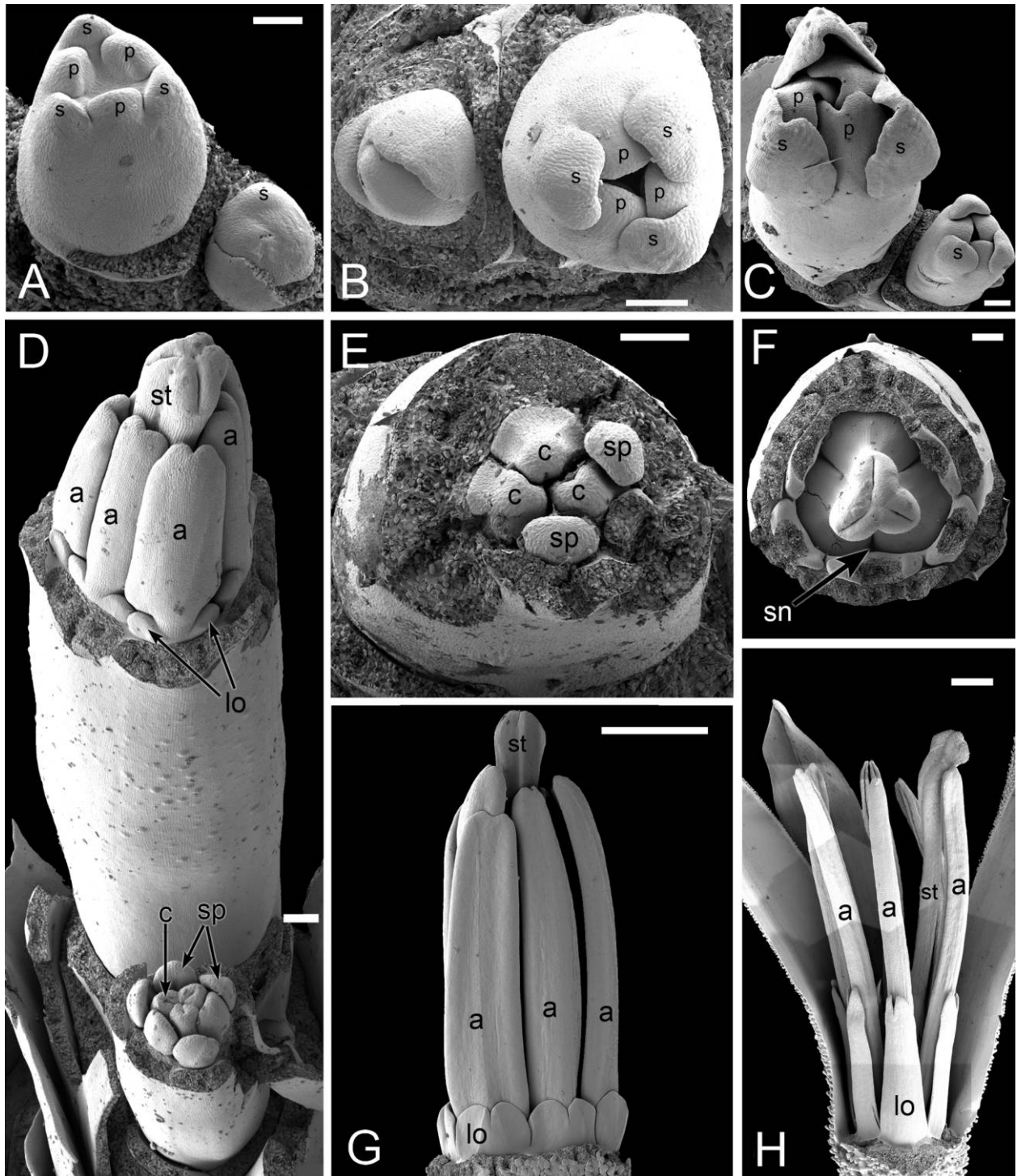


Fig. 2 *Barbacenia blanchetii*, SEM of buds dissected to show various stages of floral ontogeny. A–D, Pairs of buds showing successive stages of development. In (A), the three outer tepal primordia are just visible on the (younger) right-hand bud. E, Young bud showing three free carpels alternating with two (of three) inner stamen primordia (other stamen primordia and tepals removed). F, Older bud viewed from above, showing fused carpels and septal nectary openings. G, Sessile anthers with developing lobed appendages. H, Preanthetic flower. *a* = anther; *c* = carpel; *lo* = lateral outgrowth at base of anther, which ultimately forms a petaloid appendage; *p* = inner tepal (petal); *s* = outer tepal (sepal); *sp* = stamen primordium; *sn* = septal nectary; *st* = stamen. Scale bars in A–F = 100 μ m; scale bars in G and H = 1 mm.

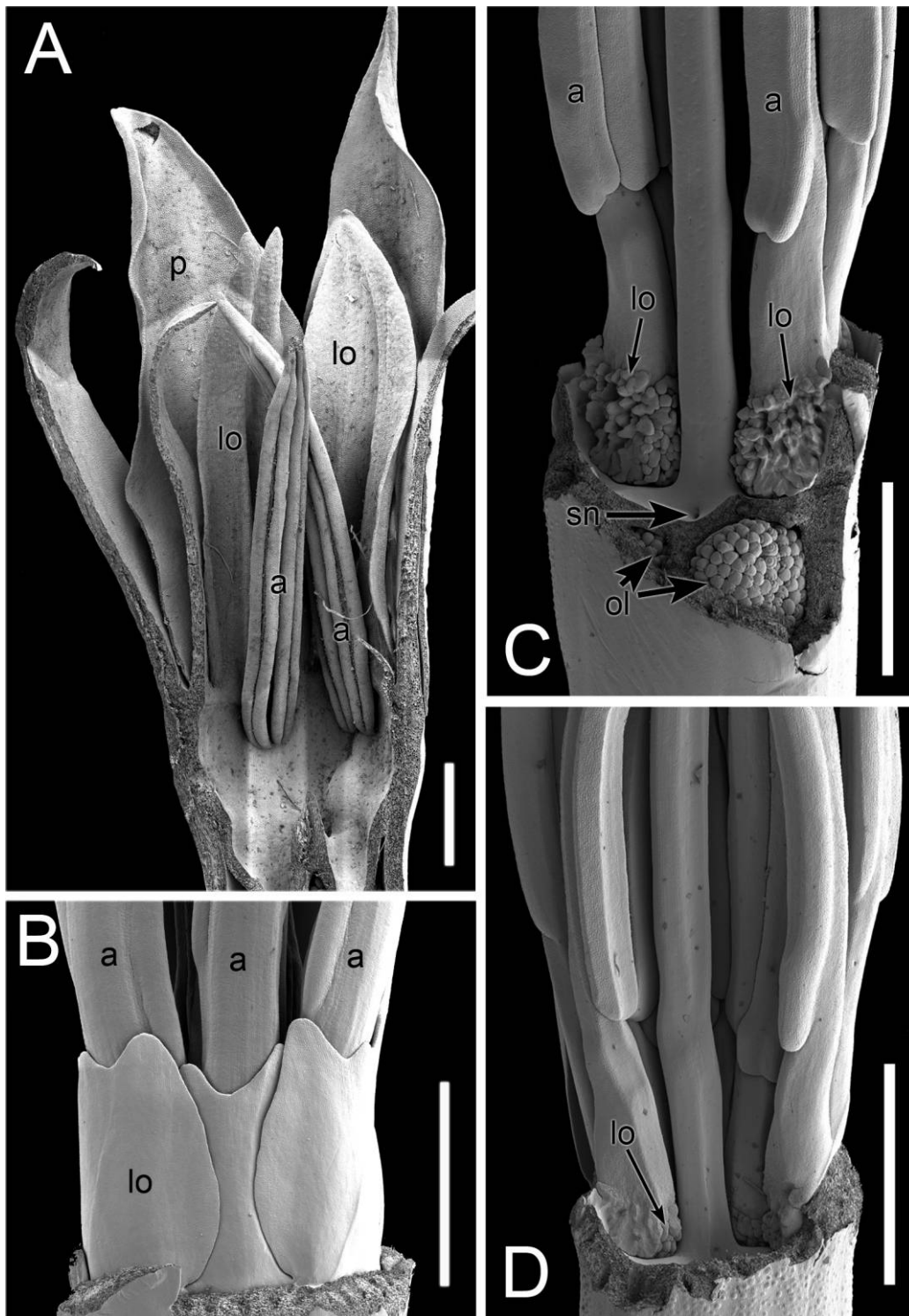


Fig. 3 SEM of dissected flower buds: A, *Barbacenia riparia*; B, *Barbacenia spiralis*; C, D, *Vellozia declinans*. a = anther; lo = lateral outgrowth at base of anther; ol = ovary locule; sn = sepal nectary opening; tr = trichomes. Scale bars = 1 mm.

group of three stamens are in a single fascicle, but the outer stamen in each fascicle matures before the inner pair (fig. 1H). In all *Vellozia* species, the stamens possess filaments that develop after the anthers (fig. 1H; fig. 3C, 3D). *Vellozia*

lacks a typical corona of flattened (petaloid) appendages, but some polyandrous species possess ramified outgrowths (fringes) on the inner side of the filament bases. These fringes differ in shape and location from those of *Barbacenia* and

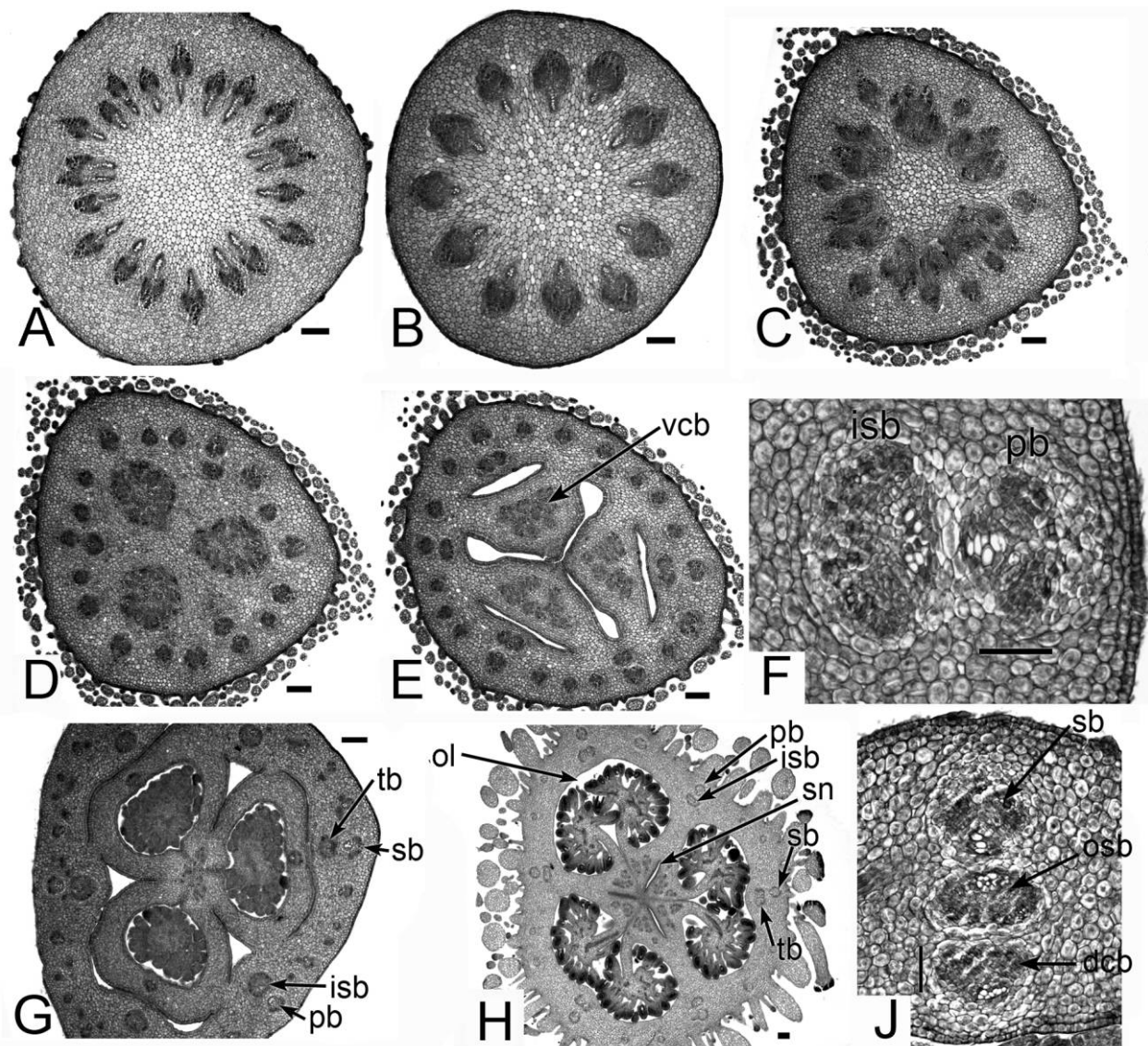


Fig. 4 *Barbacenia*, floral vasculature. A, *Barbacenia gentianoides*, transverse section (TS) of flower below ovary locules. B, *Barbacenia spiralis*, TS of ovary below locules. C–E, *Barbacenia blanchetii*, TS through the same flower from below locules (C) to level of ovary locules (E). F, *Barbacenia gentianoides*, TS just above level of divergence of inner stamen bundle; xylem pole facing the xylem of the corresponding petal bundle. G, *Barbacenia spiralis*, TS through ovary locules. H, *Barbacenia flava*, TS of flower at the level of the ovary locules. J, *Barbacenia gentianoides*, TS of flower at the level of the hypanthium apex. dcb = dorsal carpellary bundle; isb = inner stamen bundle; ol = ovary locule; osb = outer stamen bundle; pb = petal (inner tepal) bundle; sb = sepal (outer tepal) bundle; sn = sepal nectary; tb = trunk bundle, which will divide further up the flower into a dcb and an osb; vcb = ventral carpellary bundles. Scale bars = 100 μm , except in F, where it is 50 μm .

they develop after the stamens have already extended (fig. 3C, 3D). They lie close to the openings of the sepal nectaries on the hypanthium (fig. 3C). They are located primarily on the inside of the filament but sometimes reach the outer side of the filament (fig. 3C). In a few *Vellozia* species, the stamen appendages are reduced and resemble the early developmental stages of *Barbacenia* appendages in transverse section (cf. figs. 5F and 6F).

Flower Vasculature

In the pedicel, there are usually six vascular bundles at the floral base in *Vellozia* (fig. 5A), compared with 12 in *Barba-*

cenia (fig. 4B), though bundles are sometimes subdivided (figs. 4A, 5B). At this level, all bundles are collateral, with phloem external to the xylem. At the base of the hypanthium, the bundles become reorganized (figs. 4C, 5C) to form the bundles that will supply the flower parts (fig. 4D, 4E; fig. 5D). The two bundles that lie opposite the ovary locules correspond to the median bundle of the outer tepals (sepals) and the trunk bundle, which will divide further up the flower into a dorsal carpellary bundle and an outer stamen bundle (fig. 4G–4J; fig. 5D, 5H). The two bundles opposite each nectary slit are the median inner tepal (petal) bundle and the inner stamen bundle (fig. 4G, 4H; fig. 5G). In the flower center,

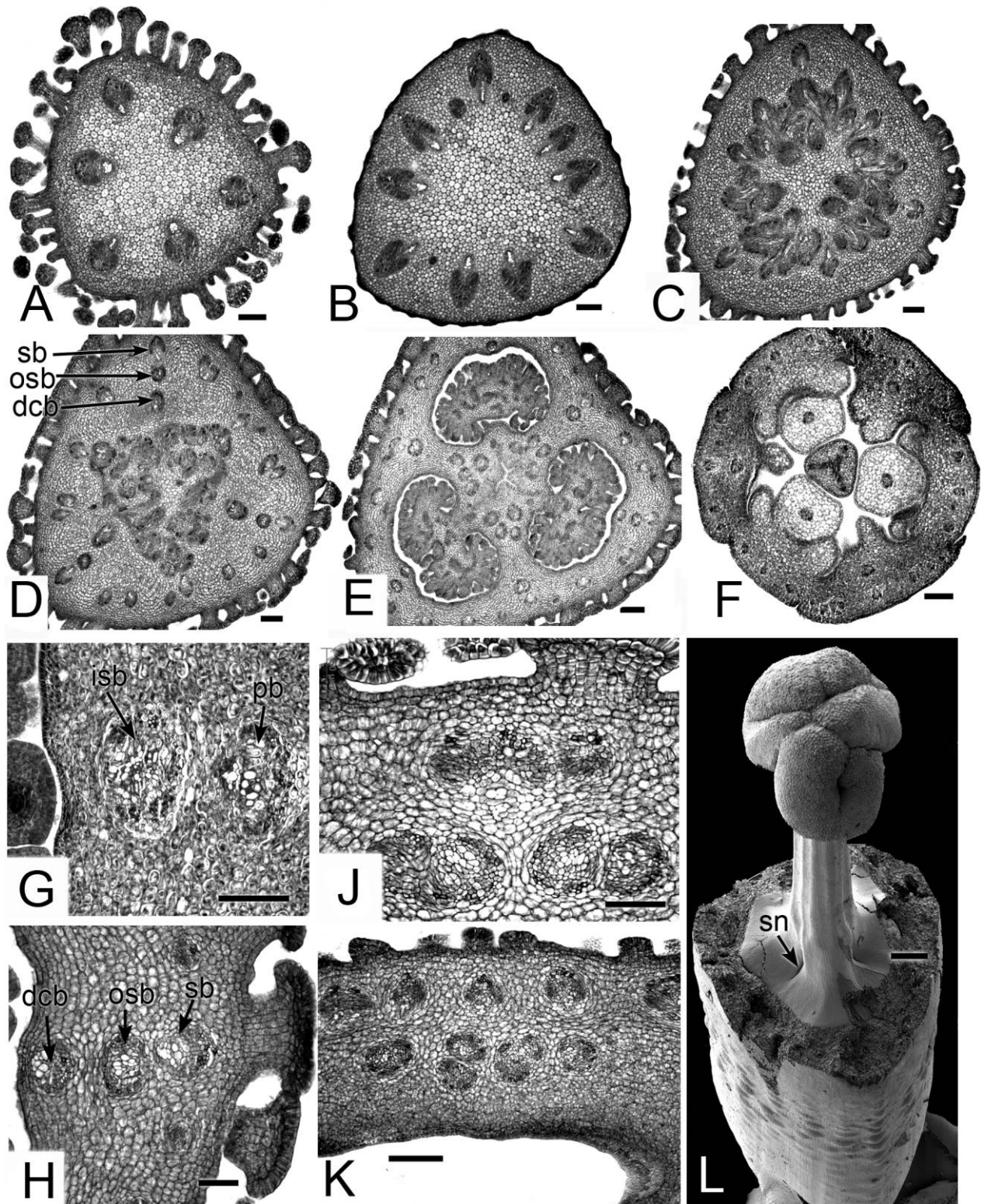


Fig. 5 *Vellozia*: A–K, LM of floral vasculature; L, SEM of floral vasculature. A, *Vellozia jolyi*, transverse section (TS) of flower below ovary locules. B–E, *Vellozia canelinha*, TS through same flower from below locules (H) to ovary locules (L). F, *Vellozia* sp. nov. 2, inconspicuous staminal appendages. G, *Vellozia epidendroides*, stamen and dorsal carpel bundles. H, *Vellozia canelinha*, dorsal carpel vasculature. J, K, *Vellozia canelinha*, stamen traces splitting. L, *Vellozia epidendroides*. dcb = dorsal carpellary bundle; isb = inner stamen bundle; osb = outer stamen bundle; pb = petal (inner tepal) bundle; sb = sepal (outer tepal) bundle; sn = sepal nectary. Scale bars = 100 μ m, except in G–J, where they are 50 μ m.

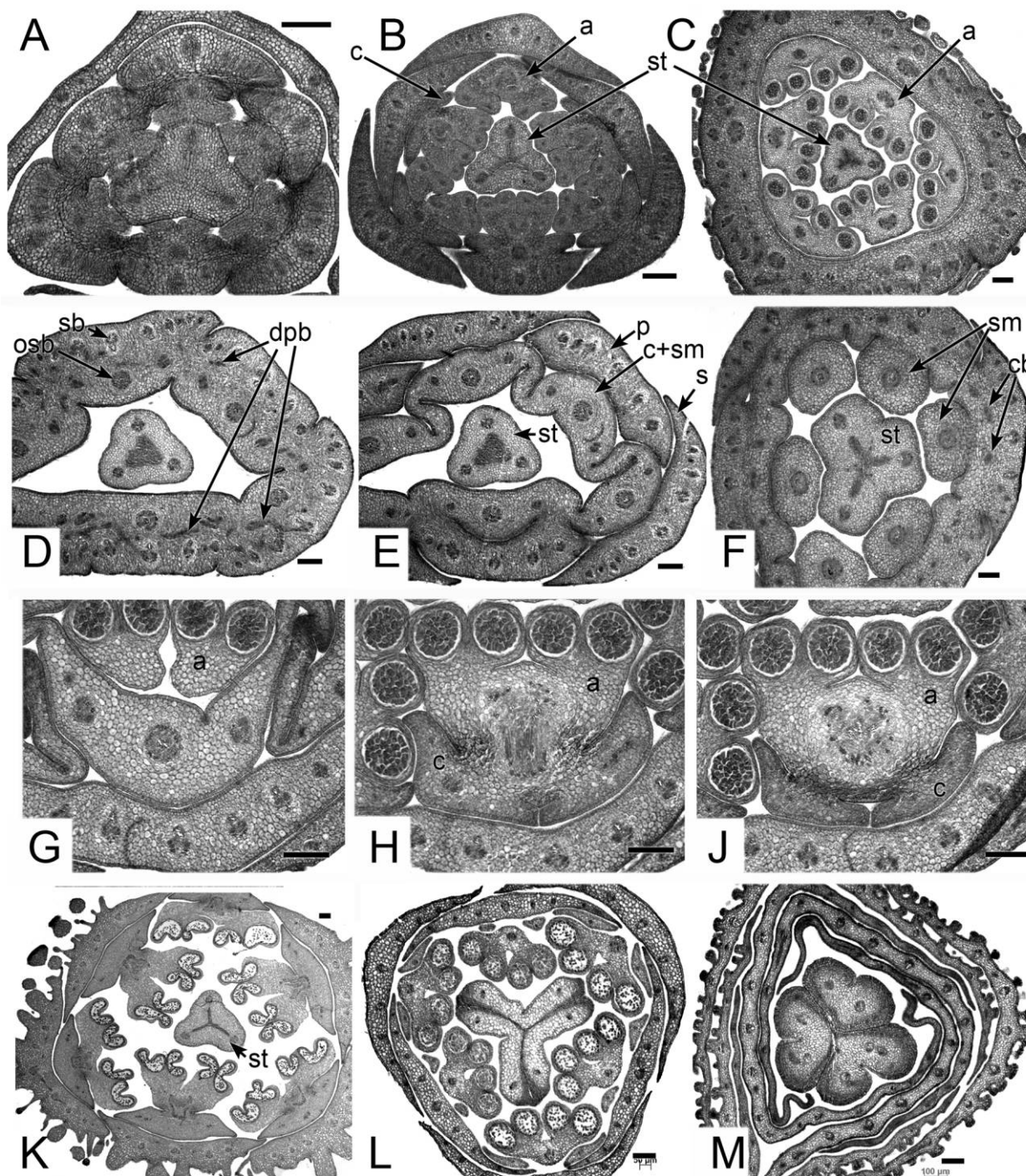


Fig. 6 Floral vasculature (all LM, transverse section [TS]). A, B, *Barbacenia blanchetii*, young buds (early stages of corona lacking vasculature visible in B). C, *Barbacenia blanchetii*. D, E, *Barbacenia gentianoides*, serial sections just below (D) and above (E) top of hypanthium. F, *Barbacenia spiralis*, corona plus stamen filaments. G–J, *Barbacenia gentianoides*, diverging corona and stamen bundles. K, *Barbacenia flava*, anthers diverging from corona. L, *Barbacenia riparia*, TS of style. M, *Vellozia canelinha*, TS of style. a = anther; c = corona; cb = corona bundle; c+sm = corona plus stamens; dpb = diverging perianth bundles; osb = outer stamen bundle; p = inner tepal (petal); s = outer tepal (sepal); sb = sepal bundle; sm = stamen; st = style. Scale bars = 100 μ m.

the ventral carpellary bundles form a group of bundles or a vascular plexus that supplies the septal nectaries and ovules (fig. 4E). When the inner stamen bundles diverge, their xylem poles face the xylem of the corresponding petal bundle

(figs. 4F, 5G). When the trunk bundles diverge above this level, their xylem is also external and faces the xylem of the corresponding sepal (figs. 4J, 5H). At the top of the hypanthium, after the divergence of the dorsal carpel bundle from

the trunk bundle, the xylem of the stamen bundle faces the xylem of the sepal bundle (figs. 4J, 5H).

At its distal part, the hypanthium contains collateral perianth bundles and near-concentric stamen bundles (fig. 5J, 5K). In *Barbacenia*, some perianth bundles diverge inward at this level (fig. 6D, 6E) to supply the lateral parts of the six petaloid coronal appendages (as also described in Menezes 1973), though in young buds the appendages possess only stamen bundles (fig. 6B). The central bundle in each appendage is concentric; at its distal part it supplies the anther (fig. 6G–6J). The lateral coronal bundles are collateral and variously oriented; in some of these bundles, the xylem is external and faces the xylem of the corresponding tepal (fig. 6G). The coronal appendages detach from the hypanthium below the level of anther attachment (fig. 6E). In *Barbacenia* species with a short filament, the concentric bundles lie in the filament and the appendage bundles are all collateral (fig. 6F). Both the filament and the corresponding coronal appendage detach together from the hypanthium. Each appendage is bifurcated above the level of anther attachment (fig. 3A, 3B; fig. 6H, 6J). Within the anthers, the bundles are collateral (fig. 6J).

In some *Vellozia* species with elaborate staminal appendages, such as *Vellozia epidendroides* (fig. 7), perianthial bundles diverge at the top of the hypanthium to supply the appendages (fig. 5F), as in the *Barbacenia* corona. In contrast to *Barbacenia*, in which a single stamen is associated with each appendage, appendages in *Vellozia* have a single concentric stamen bundle that splits at upper levels, giving rise to 18 or more collateral bundles (fig. 7G–7C). The stamens opposite the petals usually diverge before those opposite the sepals. Relatively inconspicuous appendages are usually associated with relatively few stamens (fig. 5F). In *Vellozia* species that possess more than six stamens but that lack staminal appendages, the concentric bundles diverge at the hypanthium top to give rise to other concentric bundles (fig. 5J, 5K).

The inferior ovary contains three septal nectaries (fig. 4H) leading to three openings at the top of the hypanthium (figs. 2F, 3C, 5L). The style has a central trifurcate transmitting tissue and three vascular bundles (figs. 6A–6F, 7C–7G). The stigma is trifurcate, with two vascular bundles in each branch (fig. 7L, 7M).

Discussion

Homologies of the Corona in Velloziaceae

Our investigation confirms earlier observations on floral vasculature in *Barbacenia* (Menezes 1973; Menezes and Semir 1990) that branches of the perianth bundles partly supply the corona and that lateral coronal bundles have an “inverted” orientation with respect to other collateral bundles. We also found that the fringed (corona-like) appendages of some *Vellozia* species are vascularized on the dorsal side by branches of perianthial bundles. However, in contrast to the *Barbacenia* corona, vascular tissue is not inverted in the fringed appendages of *Vellozia*. The extent and degree of vascularization of the fringed appendages are apparently correlated with stamen number. Other *Vellozia* species with only six stamens possess inconspicuous associated appendages that resemble early stages of corona differentiation in *Barba-*

cenia, before differentiation of the procambial strands. This similarity indicates a primary homology between the *Barbacenia* corona and the *Vellozia* fringed appendages, though morphological analyses suggest that these two structures are homoplasious within the family (Mello-Silva 2005; Mello-Silva et al. 2008). However, shared vasculature and anomalous vascular orientation do not necessarily imply homology. The inverted orientation of some appendage bundles observed in some Velloziaceae could be due to the late development of the appendages, because procambial development is discontinuous and bidirectional. Our investigation shows that in *Barbacenia*, procambial strands differentiate laterally from the single concentric anther bundle as the appendage grows, forming collateral bundles that are connected to the perianth vasculature at the hypanthium. Some of these lateral bundles possess external xylem facing the xylem of the opposite tepal. Puri and Agarwal (1976) also suggested that the inverted orientation of the bundles in accessory floral organs in some angiosperms is caused by their delayed initiation. Among other monocots, there is frequently overlap between organ vasculature, especially between petals and sepals; the marginal traces of both structures frequently branch into neighboring organs, especially in epigynous taxa such as orchids (Rudall and Bateman 2002).

The late development of the Velloziaceae corona mirrors the late development of similar floral structures in some other angiosperms, both distantly and closely related. For example, the petaloid coronas (sometimes termed paracorollas) of many angiosperms are late-developing structures (reviewed by Endress and Matthews 2006). Similarly, many angiosperms possess other types of appendage that are initiated relatively late in floral ontogeny. Prenner and Rudall (2007) described late-developing perianth-like structures in unisexual flowers of Euphorbiaceae and noted that late-developing structures are relatively common around the ovary base in a wide range of angiosperm flowers, including the epicalyces of some Dipsacales (Roels and Smets 1996). Among monocots, the filamentous appendages of *Gilliesia* (Amaryllidaceae-Allioideae; Asparagales) develop late in floral ontogeny. These appendages probably function as osmophores and are most readily interpreted as novel floral structures rather than modifications of preexisting organs (Rudall et al. 2002). Among other Pandanales, flattened corona-like staminal appendages also occur in *Stemona* (Stemonaceae), though in this case the appendages are initiated relatively early in stamen ontogeny (Rudall et al. 2005). Some Triuridaceae (Pandanales) possess late-developing filamentous appendages (probably osmophores) in various parts of the flower, including the tepal apices in many Triurideae, the tepal bases in *Seychellaria*, and the center of the male flower in *Triuridopsis* (Rudall 2008).

Polyandry in Velloziaceae

Differences in temporal initiation of the coronal appendages raises the question of whether other floral organs are initiated centrifugally in Velloziaceae (Rudall 2010). Unfortunately, this issue is difficult to resolve due to the problems in obtaining very early ontogenetic stages in Velloziaceae, as in other Pandanales. In our investigation of polyandrous species

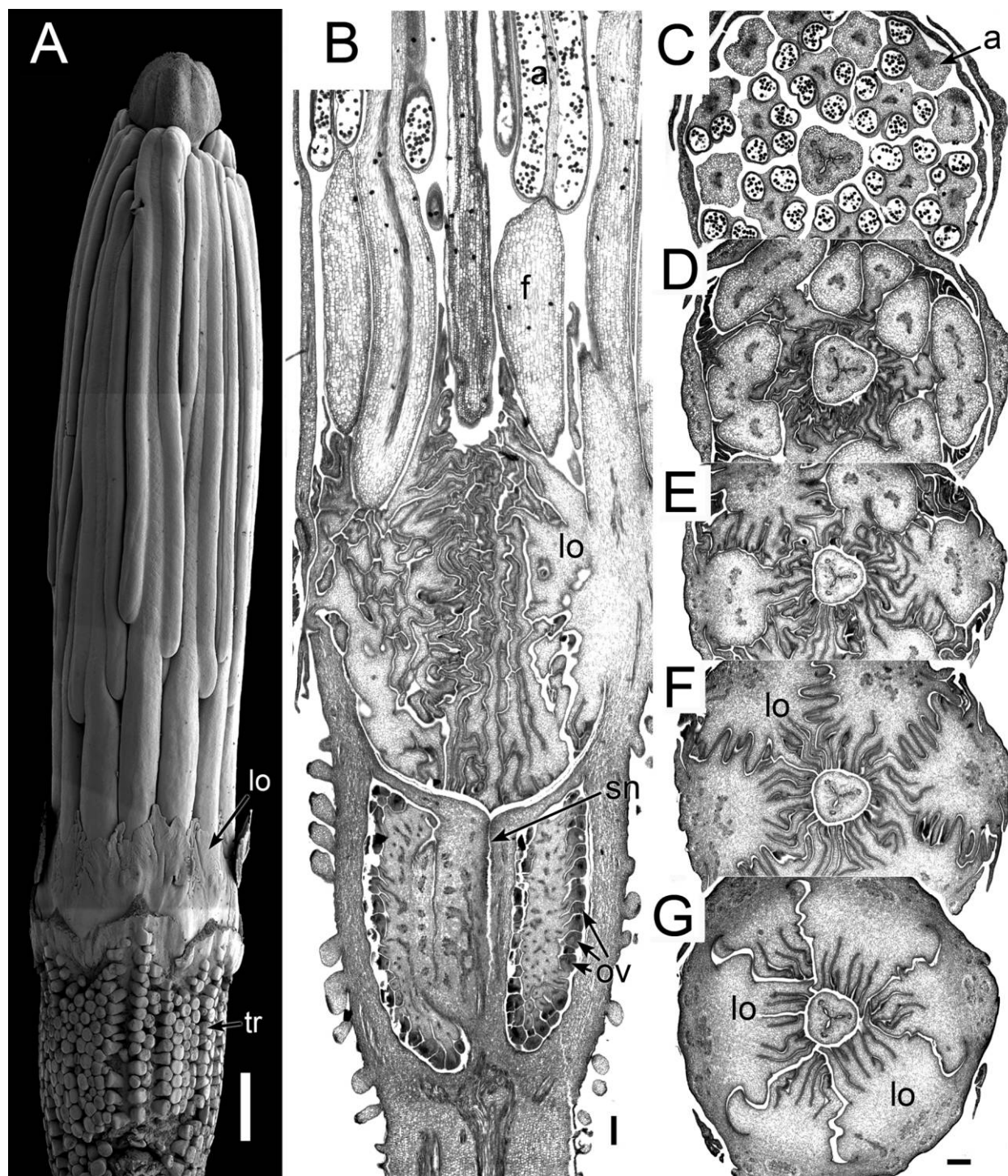


Fig. 7 *Vellozia epidendroides*. A, SEM of entire ovary with stamens removed. B, Longitudinal section of flower bud. C–G, Serial transverse sections through a single flower. a = anther; f = filament; lo = lateral outgrowth; ov = ovule; sn = sepal nectary; tr = trichome. Scale bar in A = 1 mm; scale bars in B–G = 200 μm.

of *Vellozia*, stamen initiation was not observed. The sequence of stamen initiation also remains unknown in most other polyandrous Pandanales, such as *Sararanga* (Pandanaceae) and *Carludovica* (Cyclanthaceae). However, in polycarpous

Pandanales, the multiple carpels and carpel fascicles of some Triuridaceae are initiated centrifugally (Rudall 2008).

Only six stamen primordia were observed in *Barbacenia*. Although early floral stages of *Vellozia* were not observed

here, six is probably the basic stamen number for the family, as it is in the “typical” monocot flower (Remizowa et al., forthcoming). In polyandrous species of *Vellozia*, stamen number can vary, even within the same population (Mello-Silva 1995), but the stamens are always grouped into six fascicles. Stamen fascicles (groups of stamens derived from a single primordium) are taxonomically widespread in angiosperms (Ronse Decraene and Smets 1987, 1992; Endress 1994; Prenner et al. 2008). Each fascicle possesses a single fused trunk bundle that diverges into each stamen, so that the number of trunk bundles corresponds with the number of fascicle primordia. On the basis of the arrangement of the stamen fascicles, polyandry in many species of *Vellozia* probably results from secondary primordia (i.e., stamen primordia) arising from at least some of the six primary stamen primordia (i.e., fascicle primordia). The variation in stamen number that occurs in some *Vellozia* species could be due to an unequal division in each fascicle primordium. Within each fascicle, stamens clearly mature centripetally (fig. 1H). However, the trunk bundles of the stamen fascicles opposite the inner tepals (petals) diverge below those opposite the outer tepals (sepals). This could suggest centrifugal development of stamen fascicles in *Vellozia*, though this hypothesis requires testing. If this is the case, the presence of a single stamen opposite the sepals, compared with a stamen fascicle (of three secondary stamens) opposite the petals in the unusual 12-staminate flowers of *Vellozia jolyi* (fig. 1H), could be explained by heterochrony, as a delay resulting in failure of division of the outer primordia. Since the fringed appendages of *Vellozia* are primarily located on the outer parts of the stamen fascicles, their late development would be consistent with centrifugal organ development. Interestingly, in this respect, stamen fascicles in *Vellozia* resemble carpel fascicles in some members of the closely related family Triuridaceae (Rudall 2008).

Conclusions

Menezes (1973) strongly asserted that the coronal appendages of *Barbacenia* sensu lato (including *Pleurostima*) are perianthial in origin, even though they are adnate to the stamens in some species. This conclusion was based primarily on detailed studies of floral vasculature, and hence it reflects Arber's (1937) conclusion that the *Narcissus* corona is tepal derived, a conclusion that was made partly on the basis of the bundle orientation. However, the appendages of all Velloziaceae are

late-developing structures with respect to the other floral organs. Taken in an improved phylogenetic context, our observations on both ontogeny and vasculature indicate that the Velloziaceae corona cannot readily be homologized with any of the typical floral organs (see also Endress and Matthews 2006; Rudall 2010) and may be best interpreted as a late elaboration of the region between the petals and stamens associated with epigyny and the hypanthium.

The apparently iterative evolution and ambivalent organ identity (either petal or stamen) of late-developing coronal-like structures in Velloziaceae are analogous with similar structures in Amaryllidaceae sensu lato (e.g., the coronas of *Narcissus* and *Tulbaghia*). These iterative features occurring in families that are not closely related are not homologous in the sense of true phylogenetic synapomorphies, but they can be significant in investigating the genetic bases for morphological evolution. Expression of C-class organ identity genes in the *Narcissus* corona could suggest stamen homology (Scotland et al. 2008). However, testing such homologies using developmental genetics is problematic because MADS-box genes that control floral organ identity (ABC genes; Coen and Meyerowitz 1991) are initially expressed during early stages of ontogeny, before formation of the late-developing coronal structures. The ABC model did not consider multiple stamen whorls or centrifugal organ formation in flowers (Endress 1992; Rudall 2010). Vascular overlap, which appears to be especially common in epigynous species, could invoke partial homology (Rudall and Bateman 2002). In orchids, in which overlap of sepal-petal vasculature is common, teratological forms exist in which the labellum is partially sepaline or the sepals are partially petaloid (most commonly, labellum-like). Such examples become evident only in species where individual organs differ within a single whorl, which is not the case in most monocots that possess a corona, including Velloziaceae. Our investigation underlines the general need for multiple sources of comparative data in homology assessments.

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