



**PROGRAMA DE PÓS-GRADUAÇÃO EM
CIÊNCIAS BIOLÓGICAS (BIOLOGIA VEGETAL)**

**DESENVOLVIMENTO, ANATOMIA E VASCULARIZAÇÃO FLORAL:
IMPLICAÇÕES NA EVOLUÇÃO DE ERIOCAULACEAE (POALES)**

ARTHUR DE LIMA SILVA



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TÍTULO DA TESE: DESENVOLVIMENTO, ANATOMIA E VASCULARIZAÇÃO FLORAL: IMPLICAÇÕES NA EVOLUÇÃO DE ERIOCAULACEAE (POALES)

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Resumo

Eriocaulaceae emerge como grupo-irmão de Xyridaceae em Poales, sendo caracterizada por possuir flores geralmente unissexuadas dispostas em inflorescências capituliformes. Eriocaulaceae inclui cerca de 1200 espécies distribuídas em duas subfamílias, Eriocauloideae e Paepalanthoideae. Estudos morfológicos, anatômicos e ontogenéticos têm auxiliado no entendimento da relação entre gêneros e espécies de Eriocaulaceae, bem como da origem e função de suas estruturas florais. Contudo, estudos em grupos-chave, especialmente nos gêneros de Eriocauloideae, são necessários para compreender a evolução floral na família. A tese teve como objetivos estudar o desenvolvimento, a anatomia e a vascularização floral de espécies de Eriocauloideae e compará-los com os dados disponíveis para Paepalanthoideae e Xyridaceae, buscando levantar caracteres com valor sistemático e evolutivo. No Capítulo 1, foi estudada a morfologia, anatomia e vascularização floral de *Mesanthemum radicans*. *Mesanthemum* distingue-se por possuir pétalas com três feixes vasculares em vez de um. As peças florais neste gênero crescem congestionadas, restringindo a fusão completa das pétalas, que são livres na base e unidas da região mediana até o ápice. Além disso, a falta de espaço nas flores resulta em estames externos mais curtos que os internos, provavelmente um passo em direção à perda do verticilo externo em Paepalanthoideae. No Capítulo 2, foi estudado o desenvolvimento, a anatomia e a vascularização floral de espécies de *Eriocaulon*. *Eriocaulon* possui grande diversidade floral devido a diferentes graus de redução e fusão de peças do perianto. O desenvolvimento floral de Eriocaulaceae e Xyridaceae e a otimização de caracteres morfológicos indicam que Eriocaulaceae deriva de um ancestral com flores bissexuadas, dois verticilos de estames e gineceu semelhante ao de outras Poales. O primeiro passo em direção às flores de Eriocaulaceae foi o aparecimento de flores unissexuadas com carpelódios nectaríferos nas flores estaminadas. Em seguida, em Eriocauloideae, surgiram glândulas nas pétalas. Em Paepalanthoideae, o verticilo externo de estames foi perdido, os ápices dos carpelos se modificaram em ramos nectaríferos, e as margens dos carpelos tornaram-se ramos estigmáticos comissurais. Por fim, os resultados apresentados na tese contribuem para o entendimento da evolução floral em Poales e reforçam a necessidade de estudos comparativos em outros grupos de plantas.

Palavras-chave: carpelódios, Eriocauloideae, *Eriocaulon*, evolução floral, glândulas nectaríferas, *Mesanthemum*, monocotiledôneas, nectários, Paepalanthoideae, Xyridaceae, xyridíadas.

Abstract

Eriocaulaceae belongs to Poales emerging as a sister group of Xyridaceae, being distinguished by their usually unisexual flowers arranged in bisexual capituliform inflorescences. Eriocaulaceae comprises ca. 1,200 species distributed in two subfamilies, Eriocauloideae and Paepalanthoideae. Morphological, anatomical, and developmental studies have helped to understand the relationship between genera and species of Eriocaulaceae, as well as the origin and function of floral structures. However, studies on key groups, especially in the genera belonging to Eriocauloideae, are still needed to understand the floral evolution in the family. This thesis investigated the floral development, anatomy, and vasculature of species of Eriocauloideae and compared them with the data available for Paepalanthoideae and Xyridaceae to find characters of systematic and evolutionary significance. In Chapter 1, the floral morphology, anatomy, and vasculature of *Mesanthemum radicans* are presented. *Mesanthemum* is distinguishable by its petals with three vascular bundles, instead of one. In this genus, the floral parts grow tightly packed, constraining the complete fusion of petals, which are free at their base and fused from the middle region up to the apex. Besides, the lack of space in the flowers results in outer stamens shorter than the inner ones. This may indicate a pathway toward the loss of the outer stamens in Paepalanthoideae. In Chapter 2, the floral development, anatomy, and vasculature of species of *Eriocaulon* are presented. *Eriocaulon* has great floral diversity due to distinct degrees of perianth reduction and fusion. The floral development of Eriocaulaceae and Xyridaceae and the optimization of morphological characters indicate that Eriocaulaceae derive from an ancestor with bisexual flowers, two stamen whorls, and gynoecium like that of other Poales. The first step toward the flowers of Eriocaulaceae was the shift to unisexuality and the appearance of nectariferous carpellodes in the staminate flowers. After that, petal glands appeared in Eriocauloideae. In Paepalanthoideae, the outer stamen whorl was lost, the carpel apices developed into nectariferous branches, and the carpel margins became commissural stigmatic branches. Finally, the results presented in the thesis helped to understand the floral evolution in Poales and stress the importance of comparative studies in other groups of plants.

Keywords: carpellodes, Eriocauloideae, *Eriocaulon*, floral evolution, *Mesanthemum*, monocotyledons, nectaries, nectariferous glands, Paepalanthoideae, Xyridaceae, xyrids.

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INTRODUÇÃO GERAL

Um breve histórico da importância dos estudos morfológicos florais

A morfologia floral tem um papel histórico importante na classificação das angiospermas (Constance, 1955). Com o surgimento e desenvolvimento da teoria da evolução, as afinidades morfológicas passaram a ser explicadas com base na relação de parentesco entre as espécies, e a classificação dos seres vivos—e consequentemente das plantas—passou a ser baseada em descendência com modificação (Darwin, 1859; Constance, 1955). Dessa forma, estudos morfológicos florais tornaram-se cruciais não apenas para agrupar as espécies de plantas em categorias, como também para elucidar as relações evolutivas entre os diferentes grupos possibilitando sempre reavaliar os diferentes sistemas de classificação (Constance, 1955).

A comparação morfológica e anatômica entre diferentes grupos de plantas refletiu na criação de teorias em relação à origem das estruturas florais. Goethe (1790), em sua obra *A Metamorfose das Plantas*, apresentou a teoria de que as flores seriam ramos caulinares com folhas modificadas. Posteriormente, estudos buscaram compreender o significado sistemático e evolutivo de determinados caracteres morfológicos e anatômicos, como número e disposição das peças florais (Payer, 1857), tipos de placentação (Eames, 1951; Puri, 1952), e presença e tipos de nectários (Brown, 1938).

O aumento do número de estudos anatômicos florais mostrou a importância da vascularização como suporte para hipóteses evolutivas. Henslow (1888) formulou a teoria de conservação da vascularização em relação à morfologia externa, que postula que feixes vasculares indicam a presença de estruturas que desapareceram por processos de redução, adnação ou conação. Contudo, evidências mostraram que essa premissa nem sempre se sustentava devido às inúmeras exceções a essa regra (Arber, 1933; Carlquist, 1969; Schmid, 1972). Apesar disso, a vascularização floral é bastante informativa para

compreender redução, fusão e conseqüentemente a evolução de estruturas florais (Arber, 1933). Devido à interpretação isolada da vascularização por alguns autores, Arber (1933) enfatizou a importância da combinação de análises ontogenéticas e anatômicas, devido à indissociabilidade da estrutura interna e externa das plantas. Além disso, Bancroft (1935) discutiu a importância dessas diferentes abordagens, além da utilização de dados paleontológicos e teratológicos, na solução de problemas relacionados à forma e função das plantas.

Na segunda metade do século XX, o surgimento de técnicas como a microscopia eletrônica de varredura permitiu observar de forma detalhada as estruturas das plantas (Endress et al., 2000). Isso contribuiu para o incremento no número de estudos sobre desenvolvimento floral por permitir a análise da estrutura tridimensional das flores, complementando os dados fornecidos pela microscopia de luz (Endress et al., 2000). A utilização de ferramentas computacionais e o desenvolvimento da sistemática filogenética permitiram também analisar grande quantidade de dados morfológicos, e a combinação de dados morfológicos e moleculares resultaram na construção de filogenias mais robustas, que se tornaram fontes confiáveis para testar hipóteses de evolução morfológica (Endress et al., 2000). Baseado nisso, diferentes estudos têm buscado compreender as bases ontogenéticas que levaram às inovações evolutivas em diferentes grupos de plantas (ex: Bull-Hereñu et al. 2016; Dos Santos e Ronse De Craene, 2016; Ronse De Craene, 2016; Sokoloff et al., 2018; El Ottra et al., 2019). Além disso, o desenvolvimento e a vascularização têm sido importantes para a definição de homologias, de acordo com a posição e particularidades de estruturas florais (ex: Sajo et al., 2010; De-Paula et al., 2011; Xue e Saunders, 2013; Rudall et al., 2013).

Nesse contexto, o estudo da morfologia, anatomia e desenvolvimento torna-se crucial para o entendimento e para a reconstrução da evolução floral nas angiospermas.

Atualmente, a morfologia por si só não constitui mais a base de estudos filogenéticos, mas seu estudo comparativo é necessário para a correta interpretação e discussão dos dados moleculares (Endress et al., 2000).

A ordem Poales e a família Eriocaulaceae

As monocotiledôneas são um grupo de angiospermas composto por 11 ordens e 77 famílias (APG IV, 2016). A ordem Poales inclui mais de um terço de todas as monocotiledôneas, com aproximadamente 20000 espécies distribuídas em 14 famílias (Linder e Rudall, 2005; Bouchenak-Khelladi et al., 2014; APG IV, 2016) que, por sua vez, estão agrupadas em cinco grupos: bromeliídias, xyrídias, cyperídias, restiídias e graminídias (Linder e Rudall, 2005; Bouchenak-Khelladi et al., 2014). Embora as cyperídias, as restiídias e as graminídias sejam monofiléticas, as bromeliídias e xyrídias frequentemente emergem parafiléticas devido à posição inconstante das famílias Rapateaceae, Mayacaceae e Typhaceae (Bouchenak-Khelladi et al., 2014; Givnish et al., 2018; Hochbach et al., 2018).

As xyrídias incluem as famílias Eriocaulaceae, Mayacaceae e Xyridaceae. Eriocaulaceae emerge como grupo-irmão de Xyridaceae na maioria dos estudos filogenéticos, mas a posição de Mayacaceae é variável dentro de Poales, sempre com baixo suporte (Bouchenak-Khelladi et al., 2014; Givnish et al., 2018; Hochbach et al., 2018). De todo modo, a relação entre Eriocaulaceae e Xyridaceae é constante na maioria dos estudos filogenéticos, tanto naqueles mais antigos (Givnish et al., 1999, 2006; Bremer, 2002; Davis et al., 2004), quanto nos mais recentes (Bouchenak-Khelladi et al., 2014; Givnish et al., 2018; Hochbach et al., 2018), o que permite a análise evolutiva de caracteres de forma confiável.

Eriocaulaceae é uma família pantropical com cerca de 1200 espécies (WCSP, 2021) e apresenta dois importantes centros de diversificação na América do Sul: a Cadeia do Espinhaço, que abrange os estados de Minas Gerais e Bahia, no sudeste do Brasil e o Escudo das Guianas, que abrange parte da região norte do Brasil e países como Venezuela e Guiana (Giulietti e Hensold, 1990). A família tem grande importância na composição florística das regiões de campo rupestre no Brasil, apresentando grande variedade morfológica vegetativa, com espécies que crescem em locais arenosos secos, pantanosos ou dentro de corpos d'água (Giulietti e Hensold, 1990; BFG, 2015). A família é caracterizada por apresentar inflorescências capituliformes geralmente brancas sustentadas por longos escapos (Ruhland, 1903; Giulietti e Hensold, 1990; Stützel, 1998).

As inflorescências de Eriocaulaceae conservam a aparência de estruturas vivas mesmo depois de serem removidas das plantas e, por conta disso, algumas espécies são comumente conhecidas como “sempre-vivas” (Giulietti et al., 1987). Devido a essa característica, muitas espécies possuem importância econômica—principalmente nos estados da Bahia e Minas Gerais—, sendo comercializadas na forma de arranjos ou artesanato junto a partes vegetativas e reprodutivas de integrantes de outras famílias de Poales, como Cyperaceae, Poaceae e Xyridaceae (Giulietti et al., 1987).

Morfologia e classificação infrafamiliar em Eriocaulaceae

Eriocaulaceae apresenta inflorescências capituliformes nas quais estão dispostas flores diminutas e geralmente unissexuadas (Ruhland, 1903). As flores estaminadas possuem estames funcionais e gineceu reduzido e modificado em carpelódios nectaríferos (Rosa e Scatena, 2003, 2007; Silva et al., 2016). Já as flores pistiladas possuem gineceu sincárpico funcional e estames reduzidos a estaminódios (Rosa e Scatena, 2003, 2007; Silva et al., 2016). A morfologia floral das espécies de Eriocaulaceae tem sido

historicamente importante para a delimitação das subfamílias, dos gêneros e de categorias infragenéricas na família (Ruhland, 1903). Atualmente, Eriocaulaceae inclui duas subfamílias, Eriocauloideae e Paepalanthoideae, que, embora apresentem morfologia vegetativa variada, possuem características florais particulares (Ruhland, 1903; Stützel, 1998).

Eriocauloideae tem como características a presença de flores estaminadas com dois verticilos de estames, flores pistiladas com gineceu portando apenas estigmas e flores de ambos os tipos apresentando glândulas nectaríferas nas pétalas (Ruhland, 1903). Nessa subfamília, estão incluídos dois gêneros: *Eriocaulon* L. (c. 470 spp.), maior gênero da família e o único com distribuição pantropical (Giulietti e Hensold, 1990; WCSP, 2021); e *Mesanthemum* Körn. (16 spp.), pequeno gênero endêmico do continente africano (Liang et al., 2019).

Eriocaulon possui flores estaminadas e pistiladas com pétalas livres, enquanto *Mesanthemum* possui flores estaminadas com pétalas completamente conadas e flores pistiladas com pétalas livres na base e conadas da região mediana ao ápice (Ruhland, 1903; Stützel, 1998). Apesar da descrição geral de *Eriocaulon*, esse gênero apresenta grande diversidade morfológica floral, principalmente devido à variação no merisma floral—que pode ser trímero ou dímero—, no número de sépalas e pétalas, e nos graus de fusão das sépalas (Ruhland, 1903). Por outro lado, *Mesanthemum* apresenta poucas espécies, e a revisão taxonômica do gênero foi feita recentemente incluindo a descrição morfológica das flores de todas as espécies (Liang et al., 2019). As flores de *Mesanthemum* apresentam morfologia relativamente uniforme, sempre com flores trímeras e sépalas livres (Liang et al., 2019). Apesar disso, análises ontogenéticas e anatômicas florais ainda não foram realizadas neste gênero, embora sejam necessárias para o entendimento da morfologia floral de Eriocaulaceae.

Paepalanthoideae, por sua vez, é caracterizada por apresentar flores estaminadas com um único verticilo de estames, flores pistiladas com gineceu portando ramos nectaríferos e estigmáticos em posição alternada, e ambos os tipos de flores desprovidos de glândulas nas pétalas (Ruhland, 1903). Essa subfamília inclui os demais oito gêneros de Eriocaulaceae: *Actinocephalus* (Körn.) Sano (c. 50 spp.) (Costa e Sano, 2020), *Comanthera* L.B. Sm. (c. 30 spp.) (Echternacht e Parra, 2020), *Lachnocaulon* Kunth (7 spp.) (Kral, 1989), *Leiothrix* Ruhl. (39 spp.) (Giulietti, 2020), *Paepalanthus* Mart. (c. 400 spp.) (Giulietti e Hensold, 1990; Costa et al., 2018), *Rondonanthus* Herzog (5 spp.) (Hensold e Giulietti, 1991), *Syngonanthus* Ruhl. (c. 150 spp.) (Giulietti e Hensold, 1990; Echternacht et al., 2014) e *Tonina* Aubl. (1 sp.) (Ruhland, 1903). Os gêneros de Paepalanthoideae ocorrem, em sua maioria, na América do Sul e Central, com exceção de *Lachnocaulon*, que ocorre na América do Norte e em parte da América Central (Kral, 1966, 1989; Giulietti e Hensold, 1990), e de *Paepalanthus* e *Syngonanthus*, que possuem também representantes na América do Norte e na África (Ruhland, 1903; Kral, 1989; Phillips, 1998).

Alguns gêneros de Paepalanthoideae possuem características diagnósticas marcantes. *Rondonanthus*, por exemplo, possui estaminódios lineares nas flores pistiladas (Hensold e Giulietti, 1991); *Leiothrix* possui flores pistiladas com gineceu portando ramos estigmáticos e nectaríferos em alturas diferentes (Stützel, 1998); *Lachnocaulon* possui flores estaminadas e pistiladas sem pétalas (Stützel, 1998); e *Tonina* possui flores pistiladas com pétalas reduzidas (Stützel, 1998). Outros gêneros são caracterizados por um conjunto de características florais. Como exemplo, *Comanthera* e *Syngonanthus* possuem flores pistiladas com pétalas unidas na região mediana e livres na base e no ápice (como em *Mesanthemum*), e gineceu com ramo estigmático simples (Stützel, 1998; Parra

et al., 2010). Já *Paepalanthus* e *Actinocephalus* possuem flores pistiladas com pétalas livres e gineceu com ramos estigmáticos simples ou bífidos (Stützel, 1998; Sano, 2004).

Devido à grande variedade morfológica presente nas flores de Eriocaulaceae, por bastante tempo, houve dificuldade no entendimento das relações entre os gêneros da família, e diferentes hipóteses evolutivas foram levantadas com base na morfologia floral das espécies. *Eriocaulon*, por exemplo, já foi considerado o gênero que concentra estados de caráter plesiomórficos em Eriocaulaceae (Stützel, 1985a). *Rondonanthus* foi considerado um gênero basal por possuir características também presentes em Eriocauloideae, além de possuir estaminódios alongados (Hensold e Giulietti, 1991). Entretanto, estudos filogenéticos utilizando análises morfológicas e moleculares mostraram que as subfamílias Eriocauloideae e Paepalanthoideae são monofiléticas e formam grupos-irmãos (Andrade et al., 2010; Giulietti et al., 2012; Trovó et al., 2013). Nesse contexto, a definição de caracteres e seus estados e a reconstrução da história evolutiva floral em Eriocaulaceae tornam-se tarefas complexas, necessitando da utilização de dados morfológicos, ontogenéticos e anatômicos combinados com os dados filogenéticos disponíveis.

Estudos ontogenéticos e anatômicos florais em Eriocaulaceae

Estudos florais em Eriocaulaceae têm sido realizados buscando a resolução de questões taxonômicas, ecológicas e evolutivas. Estudos anatômicos comprovaram a natureza nectarífera das glândulas das pétalas de Eriocauloideae, dos ramos do gineceu de Paepalanthoideae e do gineceu estéril das flores estaminadas das duas subfamílias (Rosa e Scatena, 2003, 2007). Essa confirmação contribuiu para melhor entendimento sobre a biologia reprodutiva e tem fomentado estudos de polinização em Eriocaulaceae (Ramos et al., 2005; Oriani et al., 2009; Del-Claro et al., 2019). Tradicionalmente, a

anemofilia era considerada a principal síndrome de polinização em Eriocaulaceae (ex.: Kral, 1966), embora a produção de néctar tivesse sido reportada previamente em flores da família (ex.: Hare, 1950).

Em Eriocauloideae, estudos anatômicos estão restritos à análise das flores de *E. elichrysoides*, que foram comparadas àsquelas de *Syngonanthus caulescens* para a delimitação da posição dos ramos do gineceu (Rosa e Scatena, 2003). Estudos do desenvolvimento floral ainda são escassos, realizados em poucas espécies de *Eriocaulon*. Inicialmente, Smith (1910) investigou flores de *E. septangulare* e reportou a presença de gineceu estéril nas flores estaminadas e de estaminódios nas flores pistiladas. Posteriormente, estudos em *E. megapotamicum* descreveram o desenvolvimento das glândulas do perianto (Stützel, 1984) e o desenvolvimento floral inicial do gênero (Stützel 1990). Recentemente, estudo realizado com enfoque taxonômico analisou o desenvolvimento floral de espécies africanas de *Eriocaulon* para avaliar a estabilidade no número de peças do perianto em *E. redactum*—espécie descrita com flores possuindo sépalas reduzidas e desprovidas de pétalas (Sokoloff et al., 2020). Sokoloff et al. (2020) mostraram que as pétalas de *E. redactum* surgem durante o desenvolvimento inicial das flores, mas não se desenvolvem.

Em Paepalanthoideae, estudos anatômicos foram realizados na maioria dos gêneros da subfamília (Rosa e Scatena 2003, 2007), com exceção de *Comanthera*, *Lachnocaulon* e *Tonina*. Como já mencionado, os estudos pioneiros de Rosa e Scatena (2003, 2007) contribuíram para o entendimento da estrutura do gineceu e das estruturas nectaríferas de Eriocaulaceae. Também foram realizados estudos ontogenéticos em alguns gêneros de Paepalanthoideae com enfoque em características florais. *Tonina* e *Lachnocaulon*, por exemplo, apresentam diferentes graus de redução no perianto e os estames foram descritos com anteras bisporangiadas (Ruhland, 1903). O

desenvolvimento das flores estaminadas de *Tonina* mostrou que diferentes padrões de formação do androceu podem ocorrer em uma mesma flor (Stützel, 1985b). Neste gênero, são encontrados estames com anteras bitecas tetrasporangiadadas, comuns em Eriocaulaceae e outras monocotiledôneas, ou anteras monotecas bisporangiadadas, formadas a partir de reduções laterais da antera (Stützel, 1985b). Já em *Lachnocaulon*, as anteras apresentam redução facial, resultando apenas em anteras bitecas bisporangiadadas (Stützel e Gansser, 1995), o que parece ser uma característica constante no gênero. Em estudo posterior, foi verificado que espécies com anteras tetra- e bisporangiadadas podem ocorrer em *Paepalanthus* e, portanto, o número de esporângios não deve ser utilizado como caráter único para a classificação genérica em Eriocaulaceae (Andrade et al., 2011).

Em *Paepalanthus*, o estudo ontogenético de espécies dímeras apontou importantes sinapomorfias para algumas categorias infragenéricas do gênero (Silva et al., 2016). Espécies pertencentes à *Paepalanthus* seção *Diphyomene* e à *P.* série *Dimeri* apresentam flores com estrutura do gineceu similar àquela de outros gêneros de Paepalanthoideae—com estilete dividido em ramos estigmáticos livres e nectaríferos alternados, inseridos na mesma altura (Silva et al., 2016). Contudo, *P. echinoides*, pertencente à *P.* seção *Conodiscus*, distingue-se pela presença de ramos estigmáticos unidos, semelhante aos observados em *Leiothrix* (Silva et al., 2016). Essa característica foi considerada sinapomórfica para *P.* sect. *Conodiscus*, o que foi confirmado após a descrição de novas espécies para seção (Silva et al., 2016, 2020; Silva e Trovó, 2020). *Paepalanthus scleranthus*, por sua vez, é uma das duas espécies inseridas em *P.* subgênero *Thelxinöe* e possui ramos estigmáticos unidos (como as espécies de *P.* sect. *Conodiscus*), mas não possui ramos nectaríferos (Silva et al., 2016). O desenvolvimento floral dessa espécie mostrou que os ramos nectaríferos surgem durante a formação do

gineceu, mas se tornam superficialmente ausentes devido à supressão do seu desenvolvimento (Silva et al., 2016).

Os nectários presentes em Eriocaulaceae, assim como aqueles de Xyridaceae, são incomuns entre as monocotiledôneas e têm levantado discussões sobre a sua origem e evolução (Stützel, 1990; Rosa e Scatena, 2003, 2007; Sajo et al., 2017). As glândulas do perianto de Eriocauloideae surgem a partir da modificação apical das pétalas (Stützel, 1984). De forma semelhante, os ramos nectaríferos do gineceu de Paepalanthoideae surgem a partir da modificação do ápice dos carpelos (Stützel, 1990; Silva et al., 2016). Estudos ontogenéticos e anatômicos florais comparativos apontaram semelhanças entre os ramos nectaríferos do gineceu de Paepalanthoideae (Eriocaulaceae) e os apêndices nectaríferos do gineceu de Abolbodoideae (Xyridaceae), sugerindo que essas estruturas seriam homólogas (Stützel, 1990; Oriani e Scatena, 2012). Contudo, o estudo do desenvolvimento e da vascularização das flores de Xyridaceae levantou uma hipótese alternativa, de que essas estruturas teriam se originado independentemente nas duas famílias (Sajo et al., 2017). Já os carpelódios nectaríferos, como mencionado anteriormente, são resultado da modificação dos carpelos de um provável ancestral com flores bissexuadas, mas estudos ainda são necessários para compreender a relação deles com os ramos nectaríferos das flores pistiladas.

Estudos da morfologia, anatomia e desenvolvimento floral têm sido realizados em Eriocaulaceae, mas principalmente em gêneros de Paepalanthoideae. Com o avanço de estudos filogenéticos, torna-se possível reconstruir a história evolutiva de alguns caracteres florais importantes da família. Entretanto, a condição ancestral das flores de Eriocaulaceae ainda é difícil de ser apontada devido às lacunas no conhecimento da morfologia, do desenvolvimento e da anatomia floral de alguns grupos-chave. Nesse contexto, destaca-se a necessidade de estudos nos gêneros de Eriocauloideae, de forma

que a comparação de aspectos florais das duas subfamílias possibilite uma análise mais detalhada da evolução floral de Eriocaulaceae.

Objetivo geral e estrutura da tese

A tese teve como objetivo geral contribuir para o entendimento morfológico e anatômico de Eriocaulaceae e compreender a evolução floral da família. A tese encontra-se estruturada em dois capítulos:

I) Floral structure of *Mesanthemum radicans* (Eriocaulaceae, Poales): morphological and anatomical novelties

Neste primeiro capítulo, foi estudada a morfologia e a anatomia floral de *Mesanthemum radicans* buscando contribuir para o conhecimento do gênero e avaliar caracteres com valor taxonômico e evolutivo. Esse capítulo foi publicado no periódico *South African Journal of Botany* e contribuiu com resultados importantes de Eriocauloideae que serviram de subsídio para a discussão da evolução floral de Eriocaulaceae apresentada no Capítulo 2.

II) Floral diversity, development and vasculature of *Eriocaulon* (Eriocaulaceae, Poales) provides insights into the evolution of the xyrids

Neste segundo capítulo, foram estudados o desenvolvimento, a anatomia e a vascularização floral de 13 espécies de *Eriocaulon*, incluindo representantes da África, da América do Norte, da América do Sul e da Ásia. Além disso, caracteres florais chave foram otimizados em uma árvore filogenética consensual incluindo Eriocaulaceae e Xyridaceae. O objetivo desse capítulo foi investigar a diversidade floral no gênero e auxiliar no entendimento da evolução floral em Eriocaulaceae. Ao fim do capítulo, foi proposta uma hipótese de evolução floral para a família com base em estudos anteriores e nos dados obtidos nos capítulos 1 e 2.

Por fim, no Anexo I, são apresentados os trabalhos e colaborações paralelos publicados no período de desenvolvimento da tese de Doutorado. Embora os artigos não tenham relação direta com os objetivos propostos, eles contribuíram para a compreensão de táxons pertencentes às Poales, em especial Eriocaulaceae. Nesse sentido, destacam-se o artigo referente à morfologia e anatomia floral de Thurniaceae, que serviu como subsídio para as interpretações das flores de outros grupos; e as contribuições nas descrições de espécies novas de *Paepalanthus*, gênero complexo e com grande diversidade morfológica floral, mas com características comuns às Paepalanthoideae.

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CAPÍTULO 1: Floral structure of *Mesanthemum radicans* (Eriocaulaceae, Poales): morphological and anatomical novelties

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Abstract

Mesanthemum is a genus of Eriocaulaceae endemic to Africa whose petals are free at the base and fused from the middle region up to the apex. Detailed studies on its floral morphology are scarce and based only on exsiccates, while the floral anatomy remains understudied. However, information regarding its floral structure is key to understanding the evolution of Eriocaulaceae. We provided details on the floral morphology and anatomy of *M. radicans* to evaluate characters with taxonomic and evolutionary importance. The flowers of *M. radicans* have tightly packed floral parts and reduced vasculature. They have petals with three vascular bundles, in contrast to a single bundle in petals of other Eriocaulaceae. Each petal receives three vascular traces, as in Xyridaceae, but they diverge from common petal-inner stamen traces. The type of petal fusion and the presence of stamens at two heights in *M. radicans* are probably related to space constraints in the floral buds of this species. However, further studies are necessary to comprehend the developmental processes that lead to petal fusion in *Mesanthemum*. The fact that the outer stamens are shorter than the inner ones can be interpreted as a step towards their loss in Paepalanthoideae. Furthermore, the petal glands and the carpellodes share characteristics, such as shape and the presence and location of papillae, that may be diagnostic for Eriocaulaceae.

Keywords: carpellode, petal fusion, petal gland, Xyridaceae, xyrids.

Introduction

Eriocaulaceae are a Monocot family of Poales diversified in the tropics with ca. 1,250 species (WCSP, 2020) and characterized by their capituliform inflorescences with minute, usually diclinous flowers. The floral morphology of Eriocaulaceae is highly diverse, with distinct degrees of fusion between floral parts, organ reductions, and unusual floral specializations. Such floral variation is important for the delimitation of infrafamilial groups, serving as basis for generic segregation in the current classification system (Ruhland, 1903; Stützel, 1998). The family is historically divided into two subfamilies recently tested as monophyletic: Paepalanthoideae (ca. 740 spp.), primarily diversified in the Neotropics but with some species in Africa; and Eriocauloideae (ca. 500 spp.), with wide geographic distribution and representatives in tropical areas of all continents (Giulietti and Hensold, 1990; Andrade et al., 2010; WCSP, 2020). Although floral studies have been conducted on the Eriocaulaceae, most of the species studied belong to the Paepalanthoideae and originate from South and North America (Stützel, 1985a, 1990; Stützel and Gansser, 1995; Rosa and Scatena, 2003, 2007; Silva et al., 2016), with few studies including Eriocauloideae species (Stützel, 1990; Sokoloff et al., 2020). Therefore, further analysis on the Eriocauloideae, as well as on the Paepalanthoideae from Africa, are still necessary.

The flowers of the Eriocauloideae differ from those of Paepalanthoideae by the presence of petal glands and a two-whorled androecium, and by the absence of nectariferous branches on the gynoecium in pistillate flowers (Ruhland, 1903; Giulietti and Hensold, 1990; Stützel, 1998). This subfamily includes two genera: *Eriocaulon* L., with about 480 species and the only one with a truly pantropical distribution, including a single species in Europe, *E. aquaticum* (Hill) Druce (Giulietti and Hensold, 1990; WCSP, 2020); and *Mesanthemum* Körn., with 16 species restricted to Africa (Liang et al., 2019).

The species of *Eriocaulon* have free petals in both staminate and pistillate flowers, while those of *Mesanthemum* have petals usually fused into a tube in the staminate flowers and fused from the mid region to the apex in the pistillate ones (Stützel, 1998).

Floral studies have been carried out on the Eriocauloideae to understand the nature and origin of floral structures. The floral development of *Eriocaulon septangulare* With. helped to understand the basic floral morphology of Eriocaulaceae, evidencing the occurrence of a rudimentary pistil (sterile gynoecium) in staminate flowers and rudimentary stamens (staminodes) in the pistillate ones (Smith, 1910). Later, the floral development of *E. megapotamicum* Malme showed the origin of petal glands in *Eriocaulon* (Stützel, 1984). Moreover, a study compared the floral development of *E. megapotamicum* to that of species of *Leiothrix* (Körn.) Ruhland, *Paepalanthus* Mart., *Syngonanthus* Ruhland (Paepalanthoideae) and Xyridaceae (to which Eriocaulaceae frequently emerge closely related), and hypothesised the origin of nectariferous structures in the gynoecium of both families (Stützel, 1990). Recently, three Indian species of *Eriocaulon* were studied to resolve taxonomic issues on a group of species with apparent heteromerous whorls (Sokoloff et al., 2020).

Floral anatomical studies in Eriocauloideae are restricted to the comparative analysis of *E. elichrysoides* Bong. (Eriocauloideae) and *Syngonanthus caulescens* (Poir.) Ruhland (Paepalanthoideae) (Rosa and Scatena, 2003). In this study, the floral vasculature and position of gynoecial structures indicated the homology between the stigmas of Eriocauloideae and the nectariferous branches of Paepalanthoideae.

Although studies on Eriocauloideae have helped to elucidate the floral structure of Eriocaulaceae, they include few species, all of them belonging to *Eriocaulon*. The general vegetative and reproductive morphology of species of *Mesanthemum* was described in floristic studies conducted in Africa (e.g., Meikle, 1968; Phillips, 1998),

having been complemented in the recent revision of the genus (Liang et al., 2019). In phylogenetic analyses, *Mesanthemum* emerges as sister to *Eriocaulon* (Andrade et al., 2010; Liang et al., 2019), a reasonable position according to their floral morphology. However, details regarding the floral morphology, anatomy, and vasculature of *Mesanthemum* remain absent.

Mesanthemum radicans (Benth.) Körn. is the most widespread species of *Mesanthemum*. It is quite common in West Africa, but also occurs in southern and eastern African countries, such as Angola, Mozambique, Uganda, and Tanzania (Liang et al., 2019). This species is robust, with leaves arranged in rosettes like most species of the genus, but with a flat-topped capitula with involucre bracts surpassing the floral disc (Liang et al., 2019). Here, we study the floral morphology and anatomy of *M. radicans* and compare it with the available data for the other genera of Eriocaulaceae to evaluate characteristics in a taxonomic and evolutionary scenario.

Material and methods

Inflorescences of *Mesanthemum radicans* (Benth.) Körn. were obtained from the spirit collection of the Ruhr-Universität Bochum (RUB), Germany: Kohlmeyer 2358. The material had been previously collected in Liberia and stored in 70% ethanol. Additional samples were obtained from the *ex situ* collection of the Botanical Garden of the Ruhr-Universität Bochum (RUB) (cultivated from material obtained from the Botanical Garden of the Technische Universität Dresden, from a collection made in Angola): Lautenschläger 151. This material was fixed in FAA 50 (Johansen, 1940), and stored in 70% ethanol.

For the morphological analysis, inflorescences were carefully dissected. Both staminate and pistillate flowers were dehydrated in formaldehyde dimethyl acetal (FDA)

and then critical-point dried. The samples were mounted on metal stubs and coated with gold for observation using scanning electron microscope (SEM) (Zeiss Sigma VP). For the anatomical analysis, flowers were dehydrated in a butyl alcohol series and embedded in historesin (Leica Historesin Embedding kit). The samples were cross-sectioned at 6–8 μm on a rotary microtome (Leica DM2245). The sections were then stained with periodic acid-Schiff reagent (PAS reaction) and Toluidine Blue (Feder and O'Brien, 1968). Permanent slides were mounted with Entellan and photomicrographs were taken using a microscope (Leica DM4000) with coupled camera (Leica DFC450). The floral diagrams were made using the Floral Diagram Generator (Kebert, 2020) and edited using the software program Inkscape[®].

Results

Floral morphology

Both staminate and pistillate flowers of *M. radicans* are pedicellate, with floral parts tightly arranged. The staminate flowers are trimerous, pentacyclic, and subtended by a floral bract (Fig. 1A). The sepals are free (Fig. 1A, B) and have trichomes on their apices (Fig. 1B). An anthophore subtends the corolla, the androecium, and the sterile gynoecium (Fig. 1C). The petals are free at the base (Fig. 1C – arrowhead) and fused into a tube from the middle region up to the apex (Fig. 1B); they have trichomes on their apices (Fig. 1B). Each petal bears a nectariferous gland on its upper adaxial surface (Fig. 1A, D). These glands are attached to the petals by their base and are papillose on their distal portion (Fig. 1D). The androecium consists of six stamens arranged in two whorls. The outer stamens are free (Fig. 1A, C), while the inner ones are adnate to the petals at the basal-most part (Fig. 1A, C). The stamens are also arranged at two heights, with the inner stamens above the outer ones, surpassing the corolla tube (Fig. 1B). The anthers are

dorsifixed, bithecate (Fig. 1E) and tetrasporangiate (Fig. 4 A). The gynoecium is sterile, with three nectariferous carpellodes (Fig. 1A, C), which are cylindrical and papillose at their tip (Fig. 1C, F).

The pistillate flowers of *M. radicans* are also trimerous, pentacyclic, and subtended by a floral bract (Fig. 2A, B). The sepals are free and have trichomes on their apices (Fig. 2A, B). The petals are free at their base (Fig. 2C, D – arrowhead) and fused into a tube from the middle region up to the apex (Fig. 2A–D); they have trichomes on their apices (Fig. 2B, C). A nectariferous gland occurs on the upper adaxial surface of each petal, as in the staminate flowers (Fig. 2E). The androecium is reduced to scale-like staminodes; the outer staminode whorl is located opposite to the locules, below the ovary (Fig. 2D), while the inner whorl is located opposite to the ovary septa (Fig. 2F). The gynoecium is tricarpellate and syncarpic, with a short style and three filiform simple stigmas in dorsal position (Fig. 2F). The outer staminodes and the ovary are visible in the openings of the corolla tube, between the free petal bases (Fig. 2C, D).

Floral anatomy

The staminate flowers of *M. radicans* have sepals formed by the epidermis and a single central vascular bundle (Fig. 3A). In some flowers, the sepals have two small vascular bundles (Fig. 3B). The petals are free at the base, adnate to the inner stamens (Fig. 3C), and fused into a tube from the middle region up to the apex (Fig. 3D). The petals are formed by a single-layered epidermis with tabular cells up to four times higher than wide, a reduced mesophyll with one cell layer, and three vascular bundles (Fig. 3C, D). The petal glands are formed by a papillose nectariferous epidermis, nectariferous parenchyma (with dense cytoplasm), and a vascular bundle with several transport cells (Fig. 3E). The inner stamens are adnate to the petals (Fig. 3C) and distally free, while the outer ones are entirely free (Fig. 3D, F). The filaments are formed by a single-layered

epidermis, parenchymatic tissue, and one vascular bundle that reaches the connective (Figs. 3C, F, 4A). The anthers are tetrasporangiate, and both sporangia of each theca open with a common slit (Fig. 4A). The anther wall comprises a papillose epidermis and endothecium with band-like thickenings (Fig. 4A, B). The stamens of pre-anthetic flowers are tightly packed inside the flower (Fig. 4C). On the other hand, the stamens of anthetic flowers are exerted (Fig. 1B). The sterile gynoecium has three carpellodes that consist of a single-layered nectariferous epidermis and nectariferous parenchyma (Fig. 4D). Each carpellode is vascularized by a vascular bundle, with few transport cells, that ramifies at the median region (Fig. 4D).

The pistillate flowers of *M. radicans* have sepals formed by the epidermis and a single vascular bundle (Fig. 5A). The petals are formed by a single-layered epidermis with tabular cells up to four times higher than wide, a 1-2-layered mesophyll, and three vascular bundles (Figs. 5B, C, 6A). The petals are free at their base (Fig. 5C) and fused from the middle region up to the apex (Fig. 6A). The petal glands are formed by a single-layered epidermis, a nectariferous parenchyma, and a vascular bundle (Fig. 6B). The staminodes of both whorls are formed by the epidermis and lack vasculature (Fig. 6C). The gynoecium is trilocular with complete septa at its median region and has one ovule per locule (Fig. 5C). The ovary wall is formed by the epidermis, a single-layered mesophyll (Fig. 6D), and is vascularized by three dorsal carpellary bundles (Fig. 6D), three ventral bundles (Fig. 6E), and the vascular cylinder (Figs. 5C, 6E). Furrows are present in the commissural region (Figs. 5C, 6E). The placentation is axile (Fig. 6F). Some crystalliferous idioblasts with druses are observed in the pedicel and in the ovary (Fig. 6G). The style is hollow, formed by the epidermis, parenchyma, and three reduced dorsal bundles (Fig. 6H). The stigmas consist of a papillose epidermis and parenchyma and lack vasculature at their middle region (Fig. 6I).

Floral vasculature

The pedicel of the staminate flower has a central vascular cylinder (Fig. 7A) from which diverge the vascular bundles of all floral parts. At the flower base, three sepal traces diverge (Fig. 7B). At the anthophore, six vascular traces diverge from the vascular cylinder (Fig. 7C). The vascular traces opposite to the sepals enter the outer stamens, while the alternate ones divide into the petal and the inner stamen traces (Fig. 7C, D). Each petal trace divides into three traces that enter the petal at their base (Fig. 7D, E). The median vascular bundle divides radially at the distal part of the petal. One part enters the petal gland (Fig. 7E) and the other continues until the petal apex (Fig. 7F). The remaining vascular cylinder divides into three vascular bundles that enter the sterile gynoecium, vascularizing each one of the carpellobes (Figs. 4D, 7G). Furthermore, the floral centre is visible in the sterile gynoecium as a remnant of the undeveloped ovary septum (Fig. 7G).

The pedicel of the pistillate flowers has a central cylinder (Fig. 8A) from which diverge the vascular traces of all floral parts, as occurs in the staminate flowers. The vascular traces of distinct whorls diverge at the same height due to the reduced internodes between the floral parts. Three vascular traces diverge from the central cylinder at the flower base, corresponding to the sepal traces (Fig. 8B). Three traces alternate to the sepals diverge above them, corresponding to the common traces shared by the inner staminodes and petals (Fig. 8C). Three vascular traces opposite to the sepals diverge and reach the base of the outer staminodes (Fig. 8D). Each common petal-inner staminode trace divides tangentially into three petal traces (Fig. 8E); another trace diverges radially from it and reaches the base of the inner staminodes (Fig. 8E, F). At the distal region of the petals, the median vascular bundle divides radially. The inner part of it enters the petal

gland, while the outer one reaches the petal apex (Fig. 9A). The median vascular bundle enters completely the petal gland in some flowers (Fig. 9B).

At the base of the ovary, the three carpellary vascular traces diverge alternate to the inner staminodes and divide into the ventral and the dorsal carpellary bundles (resulting in six bundles) (Fig. 9C–E). The dorsal traces vascularize the ovary wall and the style (Figs. 6H, 9E). The ventral traces diverge radially opposite to the ovary locules and vascularize the placenta and the ovules (Fig. 9C–G). At the distal region of the ovary, each ventral bundle divides into two smaller bundles that fuse laterally with the vascular bundles of the adjacent carpels in the commissural region (Fig. 9F, G). The vascular cylinder remains conspicuous at the middle region of the ovary (Fig. 9F) and become inconspicuous more distally (Fig. 9G).

A comparative schematic drawing of the vasculature system of staminate and pistillate flowers of *M. radicans* is presented in Fig. 10.

Discussion

The floral morphology and anatomy of *Mesanthemum radicans* shows high similarity with those of other Eriocaulaceae (Stützel, 1998; Rosa and Scatena, 2003, 2007; Silva et al., 2016). Like all genera of the family, *M. radicans* has flowers with a reduced vascular system; sepals of both staminate and pistillate flowers formed solely by epidermis; staminate flowers with inner stamens adnate to the petals and sterile gynoecium with nectariferous carpellodes; and pistillate flowers with staminodes. However, the species presents peculiarities that add important information to the general knowledge of the Eriocaulaceae and characteristics that may be important to distinguish *Mesanthemum* from other genera.

The sepals of *M. radicans* are morphologically and anatomically similar to the sepals of other Eriocaulaceae (Rosa and Scatena, 2003, 2007). The presence of a single vascular bundle and the absence of mesophyll are reductions related to the minute flowers in the family (Rosa and Scatena, 2007). Nevertheless, the petals of *M. radicans* present a particular type of fusion, in which the petals are free at their base and fused from the middle to the apex. This type of fusion, known as syngonanthoid fusion (*sensu* Stützel 1985b), also occurs in *Comanthera* L.B.Sm., *Rondonanthus* Herzog and *Syngonanthus*—all belonging to Paepalanthoideae (Stützel, 1998; Rosa and Scatena, 2003, 2007).

The occurrence of syngonanthoid fusion in both Eriocauloideae and Paepalanthoideae implies that this characteristic had independent origins in the family. The presence of tightly packed floral parts in the flowers of *M. radicans* suggests that the lack of space in the minute flowers of *Mesanthemum* may constrain the complete cohesion of adjacent petals, especially when they have narrow bases. This is particularly noticeable in the pistillate flowers because of the space required for the ovary to develop (e.g. in Figs. 2D and 5C). This hypothesis would also explain why completely fused petals do not occur in pistillate flowers of any Eriocaulaceae (Ruhland, 1903; Stützel, 1998), although this feature is common in staminate flowers of Paepalanthoideae (Rosa and Scatena, 2003, 2007; Silva et al., 2016). Future ontogenetic studies in *Mesanthemum*, as well as in *Comanthera*, *Rondonanthus*, and *Syngonanthus*, are therefore necessary to comprehend the ontogenetical processes that lead to the syngonanthoid fusion in Eriocaulaceae.

We report petals with tabular cells, mesophyll (although reduced) and three vascular bundles for the first time in Eriocaulaceae. The petals are also vascularized by three or several vascular bundles in Xyridaceae (Sajo et al., 1997, 2017; Oriani and Scatena, 2012; Remizowa et al., 2012), a family considered a sister group of

Eriocaulaceae (Givnish et al., 2018; Hochbach et al., 2018). However, in *M. radicans* the three vascular traces diverge from the common traces shared by the petals and the inner stamens, while in Xyridaceae, they diverge at different floral levels in distinct species and from two different vascular rings (Sajo et al., 2017). This difference does not allow us to conclude whether there is a phylogenetic relation between the petal vasculature of *Mesanthemum* and Xyridaceae. However, the presence of three petal traces and three petal bundles seems to be diagnostic to distinguish *Mesanthemum* from *Eriocaulon* and from other genera of Eriocaulaceae.

The presence of nectariferous glands in the petals is a singular feature of Eriocauloideae (Stützel, 1998). The developmental study of petal glands in *E. megapotamicum* showed that they originate from the modification of the petal apex in *Eriocaulon* (Stützel, 1984). Stützel (1984) considered that the petal glands of *Eriocaulon* and *Mesanthemum* are homologous, although there is no developmental study on *Mesanthemum*. The petal glands of *M. radicans* are vascularized by a single vascular bundle that originates from the division of the median petal bundles or that enters the gland without branching. The single vascular bundle of the petals of *E. megapotamicum* also enters the petal gland without branching (Stützel, 1984), but this should be investigated in other *Eriocaulon* species to verify whether this is a constant feature in the genus.

In *M. radicans*, the petal glands of the staminate and pistillate flowers are papillose on their apical region, like the nectariferous carpellodes of the staminate ones. Likewise, in *Paepalanthus* (Paepalanthoideae), the carpellodes of staminate flowers and the nectariferous branches of the pistillate ones share epidermal characteristics in a same species, which was considered of taxonomic importance by Silva et al. (2016). In *Eriocaulon*, the colour of petal glands frequently matches that of anthers and of

carpellodes, and is used to distinguish infrageneric taxa (Ruhland, 1903; Stützel, 1984). However, detailed analyses of these structures are absent. Although the petal glands and the carpellodes have clear distinct origins in Eriocauloideae regarding their position in the flowers, their similarity indicates that micromorphological features of nectaries may be important to distinguish taxa in Eriocaulaceae.

The androecium of *M. radicans* is two-whorled, which is usual for Eriocauloideae. In Monocot families with a two-whorled androecium, especially in those belonging to Poales, the stamens are commonly at equal or nearly equal heights in the flower, e.g. Bromeliaceae (Santa-Rosa et al., 2020), Rapateaceae (Oriani and Scatena, 2013), and Thurniaceae (Silva et al., 2020). In contrast, the inner stamens of *M. radicans* are longer than the outer ones in preanthetic and anthetic flowers, which indicates that the two anther heights are not related to a temporal difference in anther dehiscence between the androecium whorls. This arrangement of the androecium parts may also be related to the lack of space within the floral bud, precluding the stamens from developing side by side—as observed in Fig. 4C.

In contrast to what occurs in Eriocauloideae, Paepalanthoideae has a single-whorled androecium, formed solely by the inner stamen whorl (Rosa and Scatena, 2003, 2007). Sajo et al. (2017) made a character state reconstruction regarding the current phylogenetic placement of both subfamilies and discussed the ancestral condition of the androecium in Eriocaulaceae. However, the results were inconclusive. Shorter outer stamens were also reported for *Eriocaulon* (Rosa and Scatena, 2003; Sokoloff et al., 2019), which belongs to the same lineage as *Mesanthemum*, in Eriocauloideae. The shorter outer stamens in this subfamily can be interpreted as a first step towards the loss of this whorl in Paepalanthoideae. This implies that two-whorled androecium is a plesiomorphic character state in Eriocaulaceae.

Mesanthemum radicans has inner stamens adnate to the petals and anthers formed by epidermis and endothecium with band-like thickenings. These characteristics are common in angiosperms and are constant in Eriocaulaceae (Scatena and Bouman, 2001; Rosa and Scatena, 2003, 2007; Coan and Scatena, 2004; Coan et al., 2007a, b, 2010). Moreover, petals and stamens of *M. radicans*—or staminodes, in the pistillate flowers—share a vascular trace, from which their independent vascular bundles diverge. This petal-stamen association was reported for *Paepalanthus* (Silva et al., 2016) and is probably common in the family.

The gynoecium of *M. radicans* is syncarpic and formed by the ovary, a short style, and filiform stigmas inserted in dorsal position. These characteristics are congruent with the general description of Eriocauloideae (Stützel, 1998; Rosa and Scatena, 2003). However, the presence of druses at the base and in the middle region of the ovary, and furrows opposite to the ovary septae are novel features in Eriocaulaceae, distinguishing *M. radicans* from the other species studied so far.

The dorsal carpellary bundles of *Eriocaulon* reach the stigmas (Rosa and Scatena, 2003). On the other hand, nectariferous branches of Paepalanthoideae are in dorsal position and are vascularized, while stigmatic branches are in commissural position and lack vascularization (Rosa and Scatena, 2007). This difference between the gynoecium structure of the two subfamilies implies that the stigmas of Eriocauloideae and the nectariferous branches of Paepalanthoideae are homologous structures, as stated in the study conducted by Rosa and Scatena (2007). Despite that, the stigmas of *M. radicans* lack vasculature. This feature is probably because of a reduction of vasculature, regarding its phylogenetic position and the dorsal position of the stigmas in this species.

The gynoecium of Eriocaulaceae has heterocarpellary ventral bundles in commissural position (Rosa and Scatena, 2003, 2007; Silva et al., 2016). In *M. radicans*,

the ventral bundles shift position according to the distinct ovary regions. At the ovary base, the ventral bundles are opposite to the locules, indicating that they correspond to the fusion of lateral bundles of a single carpel. At the distal region, these ventral bundles divide and fuse with the bundles of the adjacent carpels in commissural region, indicating that they are heterocarpellary. Furthermore, the vascular cylinder remains conspicuous in the central region of the ovary and may help vascularize the placenta and the ovules. These characteristics are described for the first time for Eriocaulaceae and must be verified in other taxa. Moreover, the shift of position of ventral bundles was recently described in Thurniaceae (Silva et al., 2020)—also belonging to Poales—and may be an overlooked characteristic in the order.

In staminate flowers of Eriocaulaceae, the gynoecium is sterile and the carpels are modified into nectaries. These nectaries are commonly defined as pistillodes (Rosa and Scatena, 2003, 2007), but they originate from the carpel walls and were reinterpreted as carpellodes (Silva et al., 2016). In staminate flowers of *M. radicans*, the gynoecium is also sterile and has three nectariferous carpellodes, as is usual for the family. In addition, the sterile gynoecium of this species has a central bulge. This structure was also observed in *Paepalanthus* (Silva et al., 2016) and *Eriocaulon* (Sokoloff et al., 2020). Although the nature of this central bulge was considered problematic due to distinct possible interpretations (Sokoloff et al., 2020), we interpret it as the undeveloped ovary septum, as it develops into the septum and raises the placenta and the ovules in pistillate flowers (Coan et al., 2010; Silva et al., 2016).

In conclusion, this is the first research study on the detailed floral morphology and anatomy of *Mesanthemum*, contributing to the general understanding of the floral structure in Eriocaulaceae. *Mesanthemum radicans* shares floral morphological and anatomical features with *Eriocaulon*, which was expected since both genera are sister

groups comprising the Eriocauloideae. However, the floral structure of *M. radicans* shows variation of the floral anatomy and vasculature known for the family. The lack of space in the floral buds of *M. radicans* are likely related to certain morphological features of Eriocaulaceae, such as the syngonanthoid fusion and stamens at two heights. Moreover, aspects of the nectaries of *M. radicans* may have taxonomic value and should be investigated in other genera of Eriocaulaceae.

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Figures

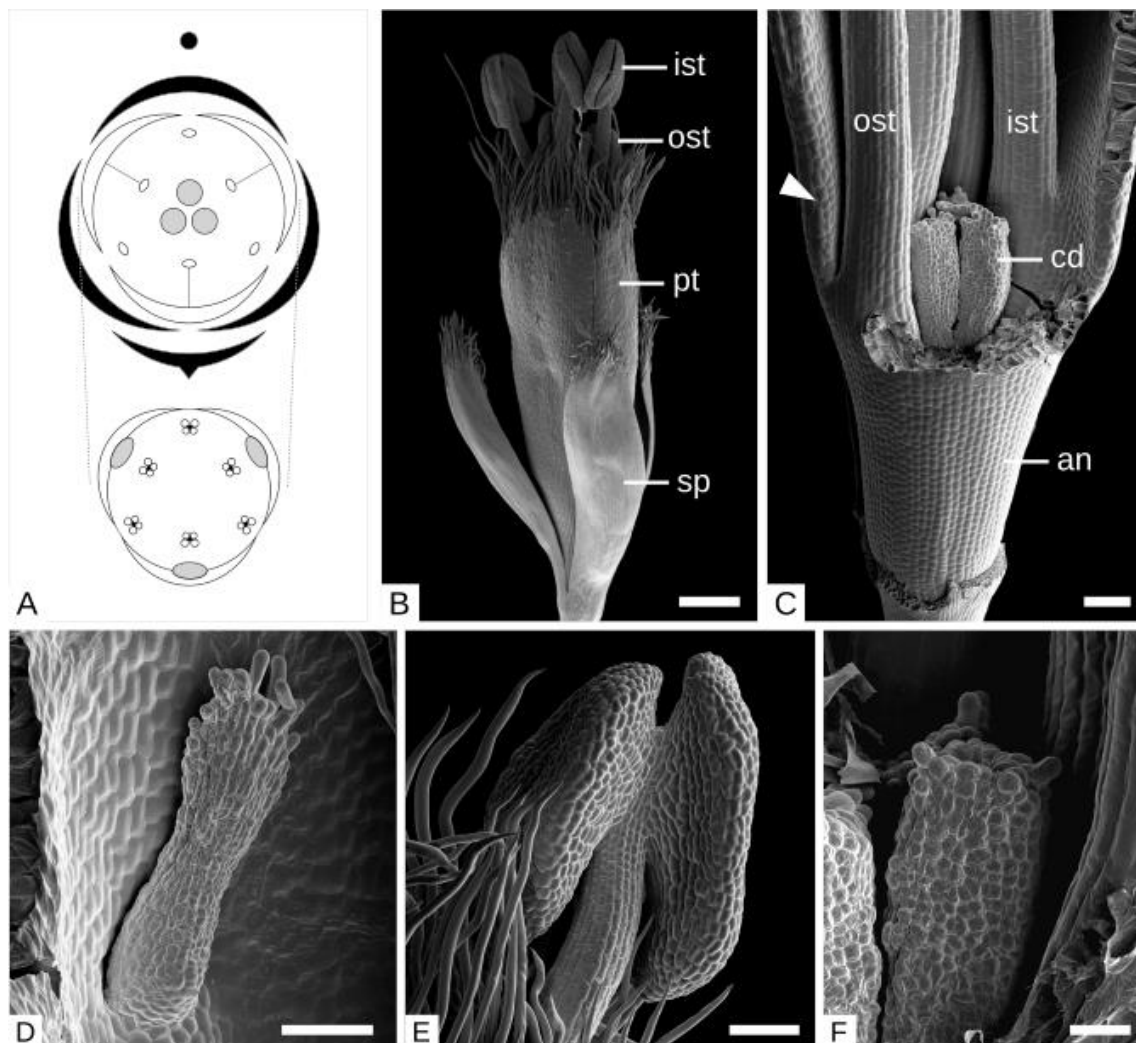


Fig. 1. Staminate flower of *Mesanthemum radicans*—in scanning electron microscopy (SEM). A. Superposing floral diagrams illustrating the flower base and the flower apex. B. General aspect of the flower. C. Detail of a flower with all sepals and a petal removed to show the anthophore, the free margins of a petal (arrowhead), the filaments, and the nectariferous carpellodes. D. Detail of a petal gland. E. Detail of an anther. F. Detail of a carpellode with papillose epidermis. Labels: an – anthophore, cd – carpellode, ist – inner stamen, ost – outer stamen, pt – petal, sp – sepal. Scale bars: B – 400 μm ; C–E = 100 μm ; F = 50 μm .

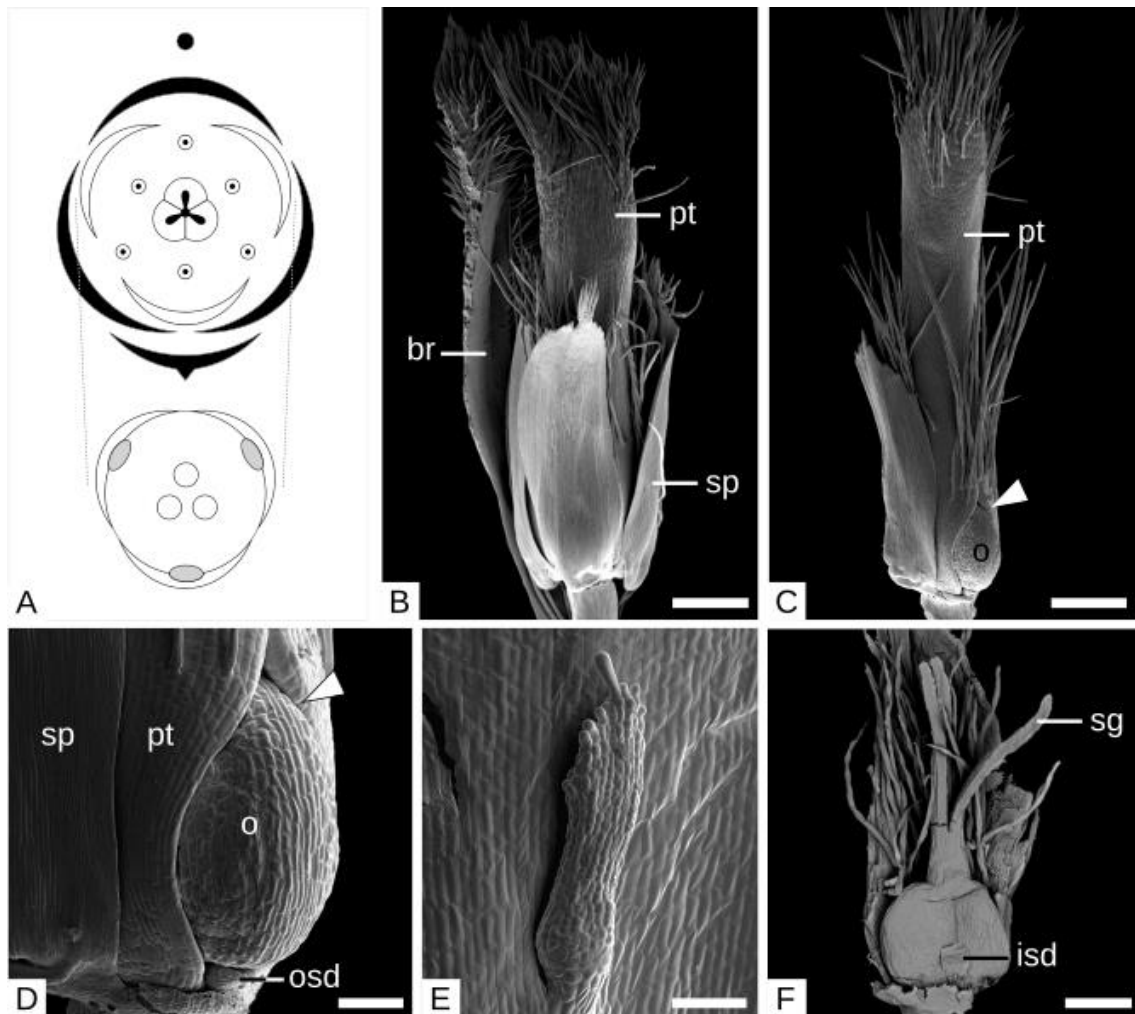


Fig. 2. Pistillate flower of *Mesanthemum radicans*—in SEM. A. Superposing floral diagrams, illustrating the flower base and the flower apex. B. General aspect of the flower. C. Flower with a sepal removed and showing petals with their free margins at their base (arrowhead) and fused from the middle region up to the apex. D. Detail of the flower base showing the free petal margins (arrowhead), the ovary, and an outer staminode. E. Detail of a petal gland. F. Detail of the gynoecium and an inner staminode. Labels: br – floral bract, isd – inner staminode, o – ovary, osd – outer staminode, pt – petal, sg – stigma, sp – sepal. Scale bars: B, C = 400 μ m; D, E = 100 μ m; F = 200 μ m.

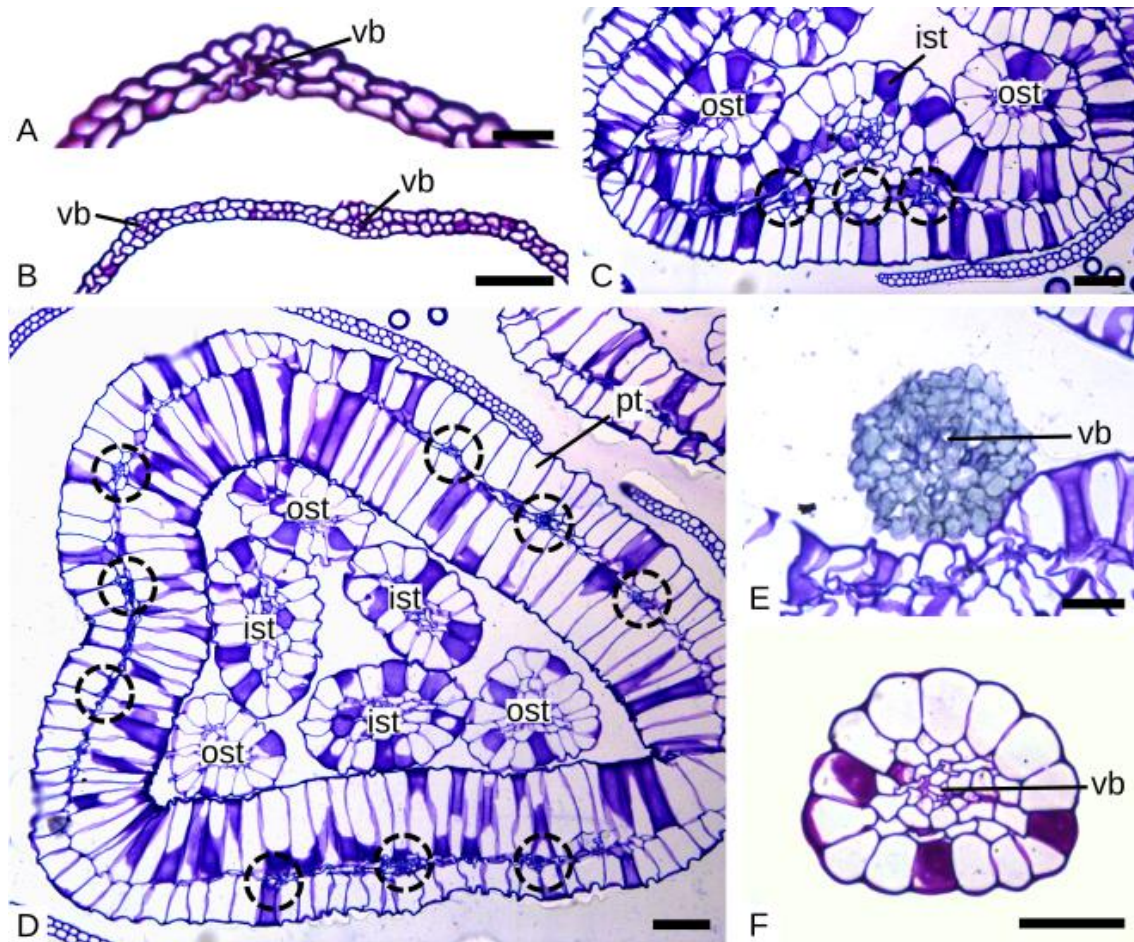


Fig. 3. Anatomical aspects of the staminate flower of *M. radicans*—in cross sections. A, B. Sepals with one (A) and two vascular bundles (B). C. Detail of a petal free at the base with three vascular bundles, an adnate inner stamen, and two free outer stamens. D. Middle region of a flower, with petals fused into a tube, and free inner and outer stamens. E. Detail of a petal gland. F. Detail of a filament. Labels: dashed circle – petal bundle, ist – inner stamen, ost – outer stamen, vb – vascular bundle. Scale bars: A, B, F = 50 μm ; C = 100 μm ; D, E, G = 200 μm .

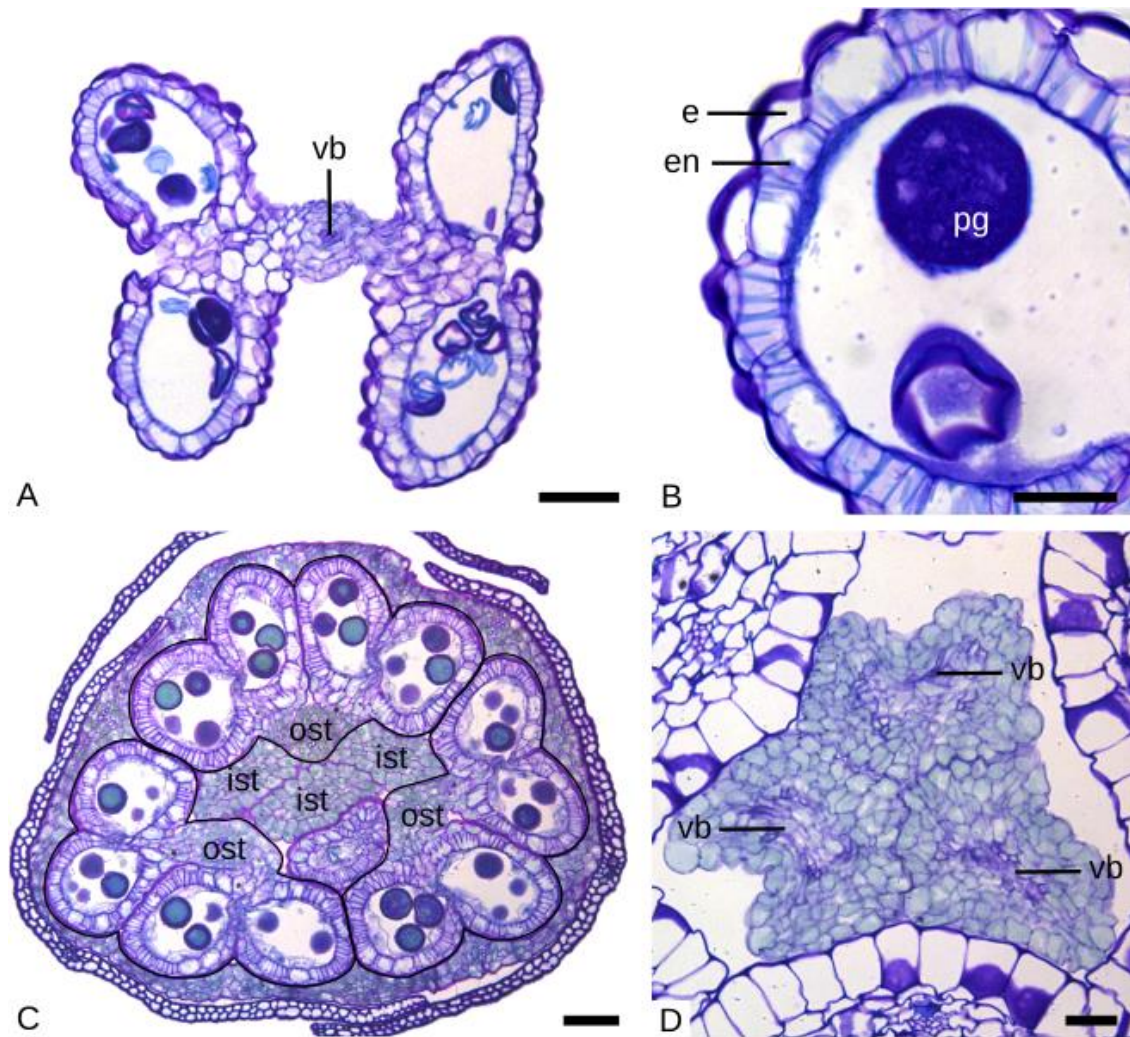


Fig. 4. Anatomical aspects of the staminate flower of *M. radicans*—in cross sections. A. Detail of a dehiscent anther. B. Detail of the anther wall. C. Pre-anthetic flower at the height of the outer stamens (outlined). D. Sterile gynoecium with three nectariferous carpellodes. Labels: e – epidermis, en – endothecium, ist – inner stamen, ost – outer stamen, pg – pollen grain, vb – vascular bundle. Scale bars: A, C, D= 200 μm ; B= 25 μm .

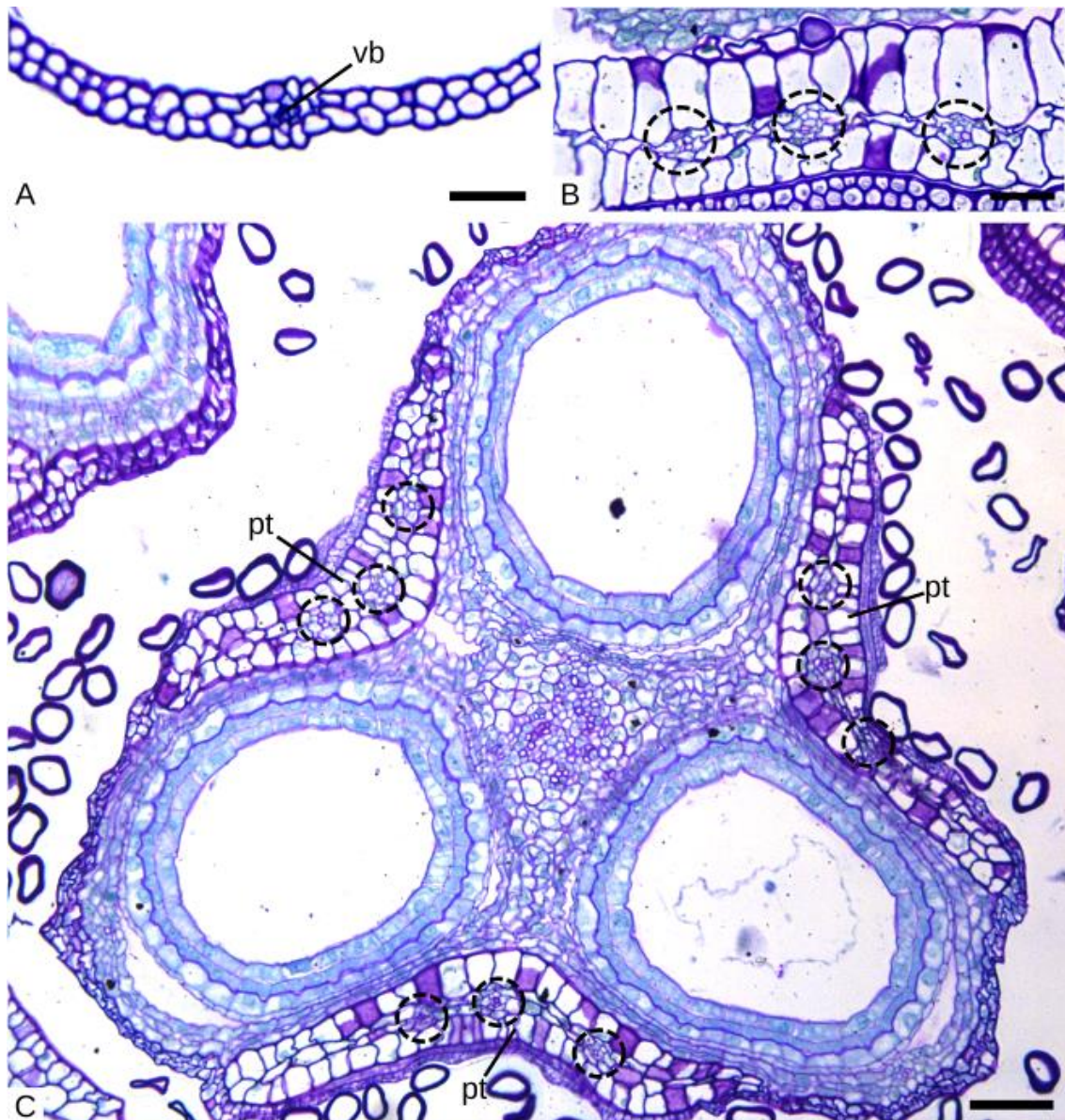


Fig. 5. Anatomical aspects of the pistillate flower of *M. radicans*—in cross sections. A. Detail of the sepal. B. Petal with three vascular bundles. C. Flower base showing the free petals and the syncarpic gynoecium. Labels: dashed circle – petal bundle, pt – petals, vb – vascular bundle. Scale bars: A, B = 100 μ m; C = 200 μ m.

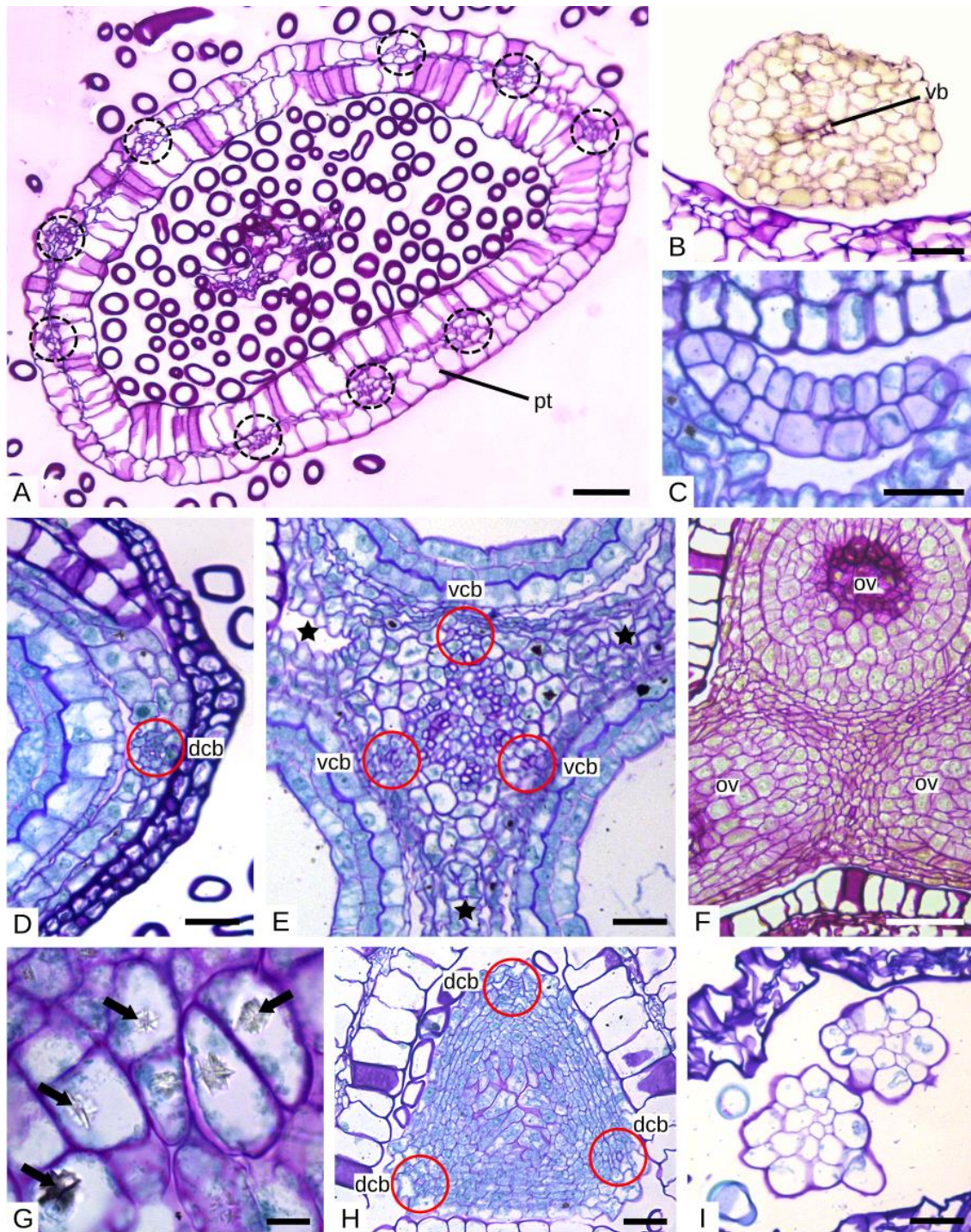


Fig. 6. Anatomical aspects of the pistillate flower of *M. radicans*—in cross sections. A. Middle region of a flower (below the petal glands) showing the petals fused into a tube. B. Detail of a petal gland. C. Detail of a staminode of the inner whorl. D. Detail of the ovary wall with the dorsal carpellary bundle. E. Detail of the central region of the ovary showing furrows (stars) and ventral carpellary bundles. F. Detail of the ovules at the ovary septum. G. Crystalliferous idioblasts containing druses (arrows). H. Style. I. Detail of stigmas. Labels: dashed circle – petal bundle, dcb – dorsal carpellary bundle, ov – ovules, pt – petal, vb – vascular bundle, vcb – ventral carpellary bundle. Scale bars: A, B = 50 μ m; C, G = 20 μ m; D, H, I = 200 μ m; E, F = 100 μ m.

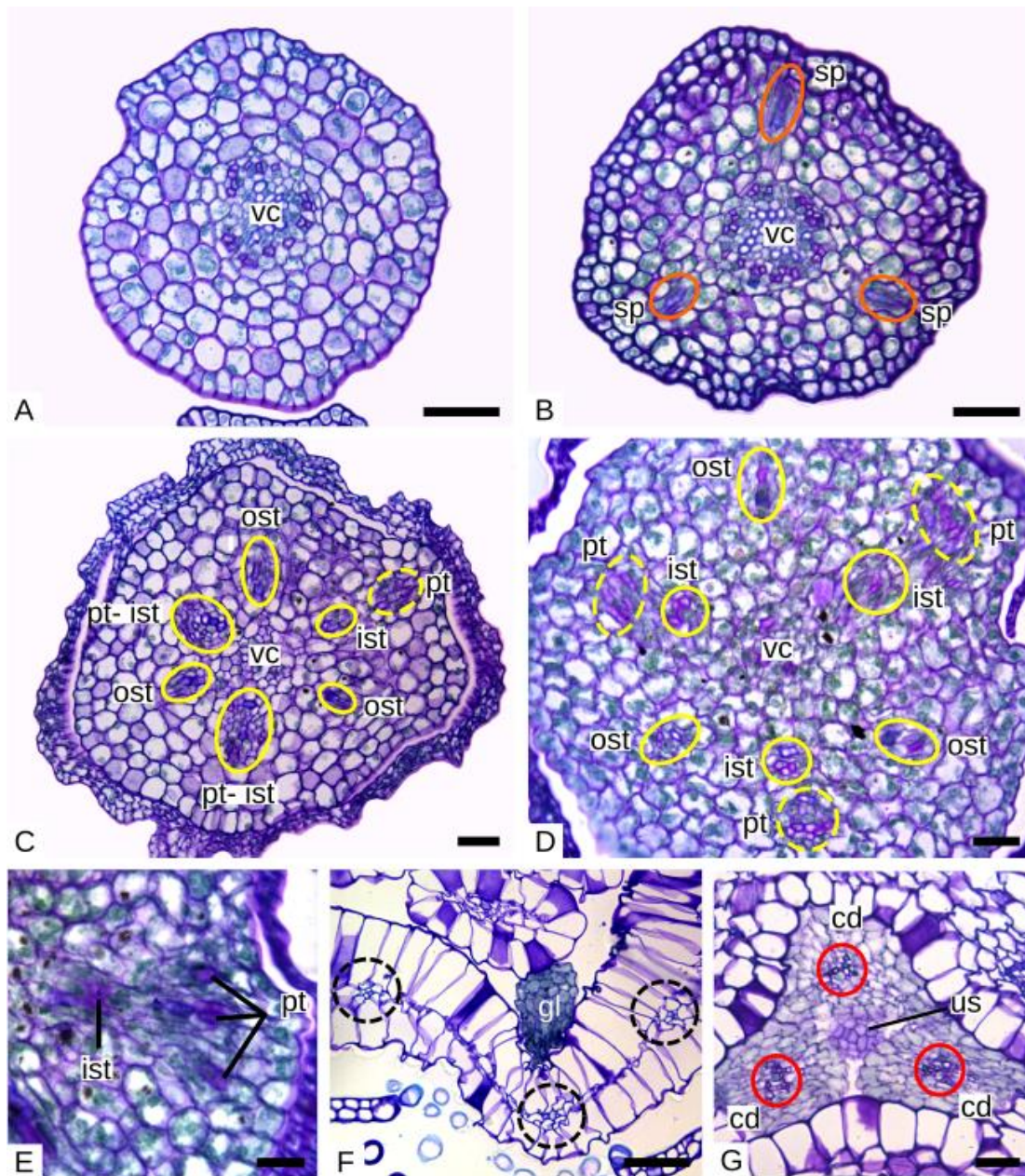


Fig. 7. Vasculature of the staminate flower of *M. radicans*—in cross sections. A. Pedicel with central vascular cylinder. B. Pedicel with diverging sepal traces. C. Anthophore with traces of the outer stamens and common traces of petals and inner stamens. D. Anthophore with separate traces of petals and inner stamens. E. Detail of the three traces of a petal. F. Detail of a petal above the gland with three vascular bundles. G. Sterile gynoecium with three nectariferous carpellodes and the undeveloped septum. Labels: cd – carpellode bundle, dashed circle – petal bundle, gl – petal gland, ist – inner stamen trace, ost – outer stamen trace, pt – petal trace, pt-ist – common trace of a petal and an inner stamen, sp – sepal trace, us – undeveloped septum, vc – central vascular cylinder. Scale bars: A-C, G = 200 μ m; D, E = 100 μ m; F = 50 μ m.

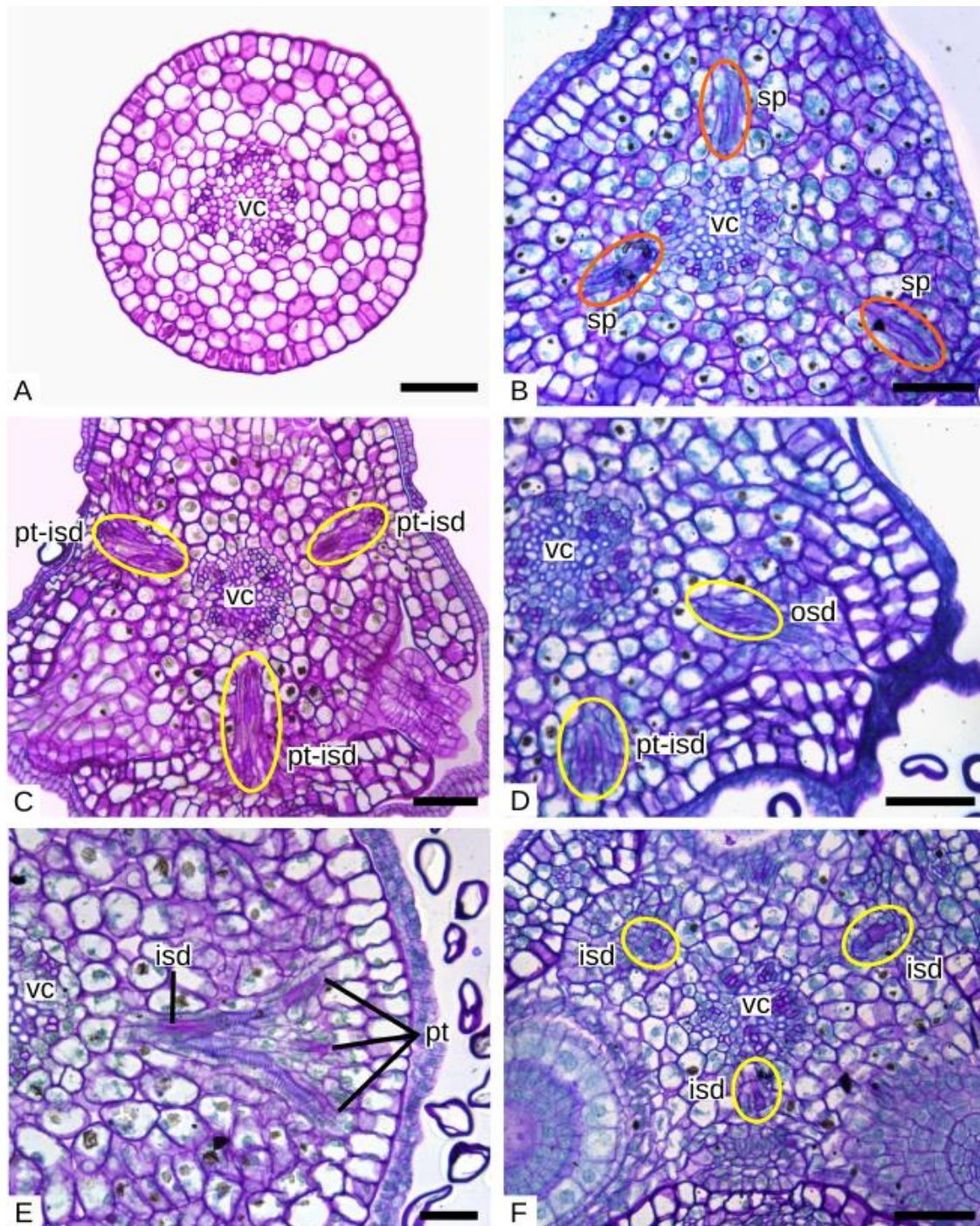


Fig. 8. Vasculature of the pistillate flower of *M. radicans*—in cross sections. A. Pedicel with central vascular cylinder. B. Pedicel with diverging sepal traces. C. Flower base showing common traces of petals and inner staminodes. D. Detail of an outer staminode trace. E. Detail of the three traces of a petal. F. Diverging inner staminode traces. Labels: isd – inner staminode trace, osd – outer staminode trace, pt – petal trace, pt-isd – common trace of a petal and an inner staminode, sp – sepal trace, vc – central vascular cylinder. Scale bars: A-C, F = 50 μ m; D, E = 25 μ m.

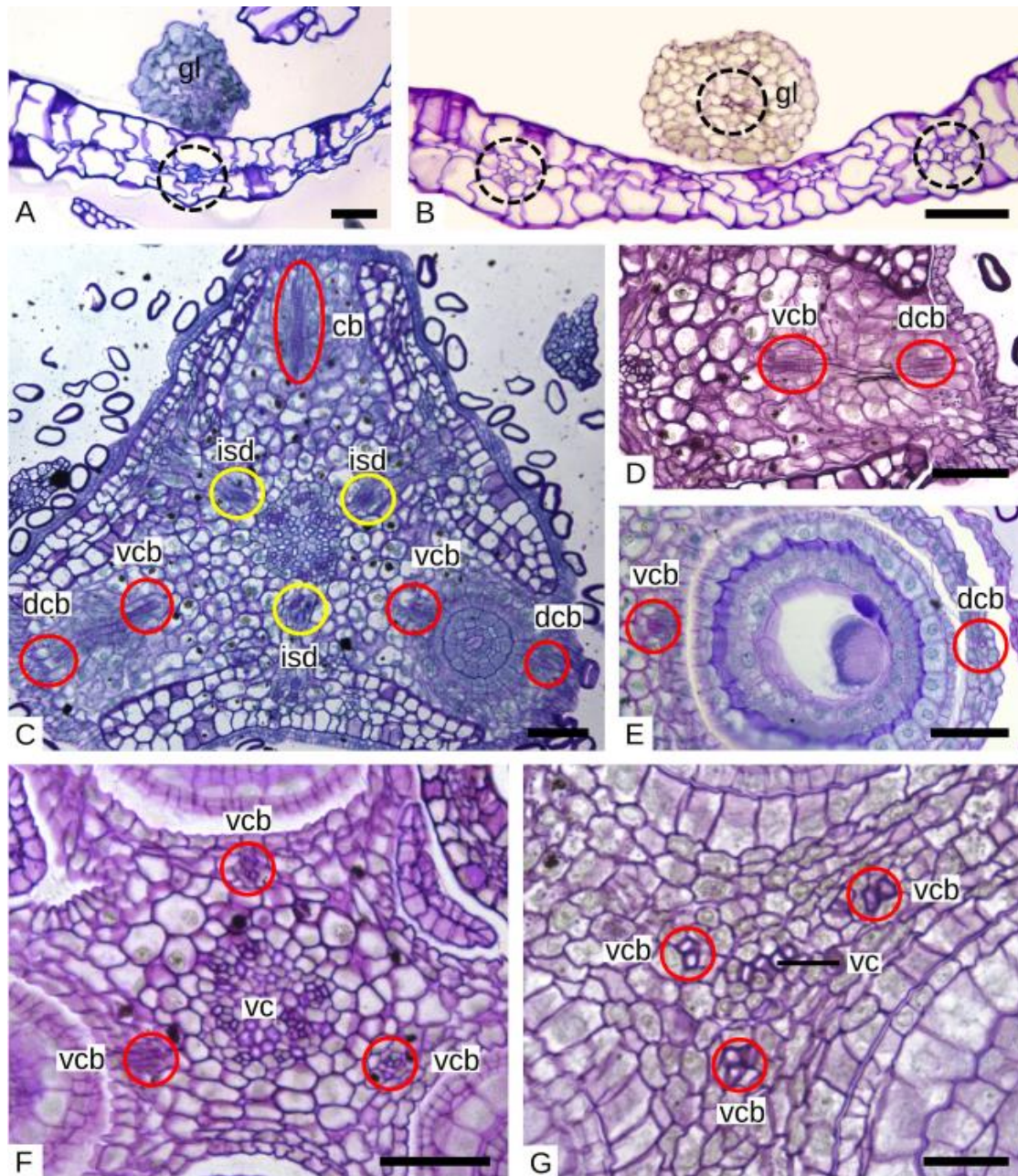


Fig. 9. Vasculature of the pistillate flower of *M. radicans*—in cross sections. A. Apical region of the petal showing the median vascular bundle above the nectariferous gland. B. Apical region of the petal with the median vascular bundle in the nectariferous gland. C. Base of the ovary with a carpellary bundle (up) diverging dorsal and ventral carpellary bundles (left), and separate dorsal and ventral carpellary bundles (right). D, E. Details of diverging (D) and of separated (E) dorsal and ventral carpellary bundles. F. Detail of the middle region of the ovary, with ventral carpellary bundles opposite to the ovarian locules. G. Detail of the distal region of the ovary with ventral carpellary bundles in commissural position. Labels: cb – carpellary bundle, dashed circle – petal bundle, dcb – dorsal carpellary bundle, gl – petal gland, isd – inner staminode trace, vc – vascular cylinder, vcb – ventral carpellary bundle. Scale bars: A, B, D-G = 50 μ m; C = 200 μ m.

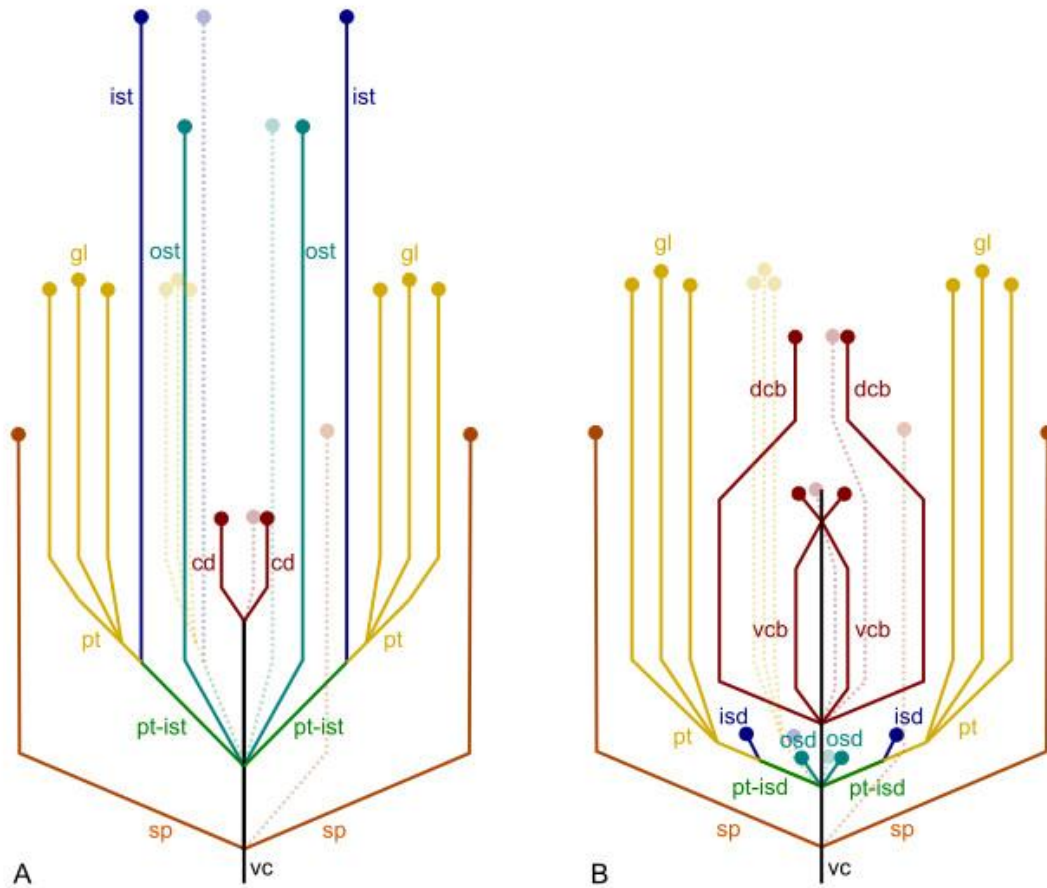


Fig. 10. Schematic drawing of the floral vascular system of *Mesanthemum radicans*. A. Vascular system of the staminate flower. B. Vascular system of the pistillate flower. Dotted lines represent the vascular traces and bundles of the third element of each floral whorl. Labels: cd – carpellode bundle, dcb – dorsal carpellary bundle, gl – petal gland, isd – inner staminode trace, ist – inner stamen bundle, osd – outer staminode trace, ost – outer stamen bundle, pt – petal traces, pt-isd – petal-inner staminode trace, pt-ist – petal-inner stamen trace, vc – vascular cylinder, vcb – ventral carpellary bundle.

**CAPÍTULO 2: Floral development and vasculature in *Eriocaulon* (Eriocaulaceae)
provide insights into the evolution of the xyrids**

Running title: Floral development and vasculature of *Eriocaulon* (Eriocaulaceae)

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ABSTRACT

Backgrounds and aims: Eriocaulaceae have generally unisexual flowers bearing unusual nectaries and consist of two subfamilies, Eriocauloideae and Paepalanthoideae. Floral developmental studies were carried out in Paepalanthoideae, but studies on Eriocauloideae are necessary to discuss the origin and evolution of the androecium, gynoecium, and floral nectaries of Eriocaulaceae. Thus, we analysed the floral development and vasculature of *Eriocaulon*, the largest genus of Eriocauloideae, under an evolutionary context to understand the floral variation in the genus and to help to elucidate the floral evolution of Eriocaulaceae and Xyridaceae.

Methods: Thirteen species of *Eriocaulon* were studied. The developmental analysis was carried out using Scanning Electron Microscopy (SEM), and vasculature analysis was carried out using light microscopy (LM). Fresh material was also analysed using SEM with Cryo function. The character evolution was reconstructed over well-resolved phylogenies.

Key Results: Perianth reductions occur due to delayed development and/or loss of vascular bundles of the median sepals. Nectariferous petal glands stop developing and are vestigial in some species. In some staminate flowers, the inner stamens emerge before the outer ones, and carpels turn completely into nectariferous carpellodes. In pistillate flowers, stamens of both whorls are reduced to staminodes, and the gynoecium has dorsal stigmas.

Conclusions: The floral morphology of *Eriocaulon* is highly variable as a result of fusion, reduction or loss of perianth parts. Dimerous flowers of *Eriocaulon* probably evolved from the loss of the median sepal. The comparative floral morphology of Eriocauloideae and Paepalanthoideae corroborates that the ancestor of Eriocaulaceae had bisexual flowers with two-whorled androecium and dorsal stigmas. The nectariferous carpellodes

of staminate flowers originated first, in the ancestor of Eriocaulaceae; petal glands and nectariferous branches of pistillate flowers originated independently in Eriocaulaceae through transfer of function. Based on that, we present a hypothesis of floral evolution for the family.

Keywords: dimery, *Eriocaulon*, Eriocaulaceae, Eriocauloideae, floral anatomy, floral development, floral evolution, floral ontogeny, floral vasculature, nectary, Poales, xyrids.

INTRODUCTION

Poales is a highly diverse order of ca. 20,000 species, representing more than a third of all monocots (Givnish et al., 2010). Within this order, Eriocaulaceae emerge as the sister group of Xyridaceae in the xyrid clade (Givnish et al., 2010, 2018; Bouchenak-Khelladi et al., 2014), and both families share some floral characters, such as the presence of staminodes and unusual floral nectaries (Stützel, 1990; Oriani and Scatena, 2012). However, Eriocaulaceae differ by their compact bisexual capituliform inflorescences (Fig. 1A–D) with generally unisexual flowers. Eriocaulaceae (ca. 1,200 spp.) consist of two subfamilies, Eriocauloideae and Paepalanthoideae, which are strongly supported by phylogenetic studies (Andrade et al., 2010). Eriocauloideae includes *Eriocaulon* L. (c. 400 spp.), the single genus of Eriocaulaceae with pantropical distribution; and *Mesanthemum* Körn. (16 spp.), a small genus endemic to Africa (Giulietti and Hensold, 1990; Stützel, 1998; Liang et al., 2019). Paepalanthoideae includes the eight remaining genera of the family, with most of their species occurring in America (Giulietti and Hensold, 1990).

In the last few decades, anatomical and developmental studies have discussed the homologies of the floral structures of Eriocaulaceae and Xyridaceae, as well as those of the two subfamilies of Eriocaulaceae (Stützel, 1990; Rosa and Scatena, 2003, 2007; Sajo et al., 2017; Silva et al., 2021). These studies have focused mainly on the number of androecium whorls and on the presence and position of nectaries. However, the evolutionary significance of these characters remains controversial due to the complex floral morphology in the family.

In Eriocaulaceae, an inner androecial whorl is present in both Eriocauloideae and Paepalanthoideae (Rosa and Scatena, 2003, 2007; Silva et al., 2021), but an outer androecial whorl is present only in Eriocauloideae (Stützel, 1990; Rosa and Scatena,

2003; Silva et al., 2021). In Paepalanthoideae, outer staminodes had been described in staminate flowers together with the functional inner fertile stamens, suggesting that the ancestor of the subfamily had a two-whorled androecium (Rosa and Scatena, 2003, 2007). However, these outer staminodes were later reinterpreted as late-developing petals, discarding this hypothesis (Silva et al., 2016). Sajo et al. (2017) studied the floral development and vasculature of Xyridaceae to reconstruct androecial evolution in the xyrids; however, they pointed out the need for further comparative studies on Eriocaulaceae to elucidate this question.

Regarding the nectariferous structures, in Eriocauloideae perianth glands are frequently present on the adaxial epidermal surface of the petals, but they are apical, subapical, or even absent in some species of *Eriocaulon* (Ruhland, 1903; Oliveira and Bove, 2015). In *E. megapotamicum* Malme, these glands appear on the petal apex in the floral primordia and change position during flower development (Stützel, 1984). Although gland formation has not yet been studied in *Mesanthemum*, development is probably similar in this genus (Stützel, 1984).

The gynoecium of Eriocaulaceae has puzzling characteristics that make it difficult to reconstruct floral evolution in the family. In Paepalanthoideae, the gynoecium has nectariferous branches that were considered homologous to the nectariferous appendages found in some Xyridaceae, since both structures have a dorsal position, similar ontogenetic stages, and are vascularized by a dorsal carpellary bundle (Stützel, 1990; Rosa and Scatena, 2003; Oriani and Scatena, 2012). However, differences in both development and vasculature of the gynoecium indicate that they may have originated independently (Sajo et al., 2017).

In Eriocauloideae, the stigmas have a dorsal position and receive the dorsal carpellary bundle, like the nectariferous branches of Paepalanthoideae (Rosa and Scatena,

2003). Based on this, Rosa and Scatena (2007) suggested that the nectariferous branches originated from an evolutionary shift in stigma function. The stigmatic branches of Paepalanthoideae have a commissural position and are formed through the rise and fusion of adjacent carpel margins (Stützel, 1990), but their evolution has been inadequately discussed.

In staminate flowers of Eriocaulaceae, the gynoecium is sterile and has nectariferous carpellodes. In Paepalanthoideae, the carpellodes are in the same position as the nectariferous branches of their pistillate flowers and are vascularized by the dorsal carpellary bundle (Rosa and Scatena 2003, 2007); their development is also similar, and they share morphological and anatomical characteristics, at least in the species studied so far (Silva et al., 2016), which could indicate a single evolutionary origin. However, the presence of carpellodes in staminate flowers of Eriocauloideae and the lack of nectariferous branches in their pistillate flowers suggest that nectariferous branches were absent in the ancestor of Eriocaulaceae and appeared only in Paepalanthoideae. The floral anatomy of *Mesanthemum radicans* showed that the carpellodes are in the same position as the carpellodes of Paepalanthoideae (Silva et al., 2021). Despite that, developmental data about the carpellodes of Eriocauloideae, are lacking and may help to understand the relation between these structures and the nectariferous branches of Eriocaulaceae.

To date, developmental and anatomical studies in Eriocaulaceae have mostly included species of Paepalanthoideae, but further comparative studies including species of Eriocauloideae are needed to clarify floral evolution in Eriocaulaceae. *Eriocaulon* is the largest genus of Eriocauloideae with ca. 470 spp. (WCSP, 2021) and highly variable floral morphology. The genus has pantropical distribution, with representatives in North and South America, Africa, Asia, and a single species in Europe (Giulietti and Hensold, 1990). Studies on *Eriocaulon* have been carried out on a few species, focusing on early

floral development (Smith, 1910; Stützel, 1990), the origin of the petal glands of *E. megapotamicum* (Stützel, 1984), and perianth reduction of some close related Indian species (Sokoloff et al., 2020). In the present work, we study the floral development of *Eriocaulon* in a phylogenetic context to address floral morphological variation in the genus, the possible ancestral characters of Eriocaulaceae, and the evolution of the androecium, gynoecium and the nectariferous structures in the xyrids.

MATERIAL AND METHODS

For this study, we selected 13 species of *Eriocaulon*. Part of the material was collected during scientific expeditions in Brazil (Fig. 1A–C) and vouchers were deposited in the Herbário Rioclarense (HRCB). The North American species were obtained from the *ex situ* collection of the Botanical Garden of the Ruhr-Universität Bochum (RUB) in Germany (Fig. 1D). The African species and the single Asian species were obtained from the spirit collection of the Royal Botanic Gardens Kew, United Kingdom. Details of the collections and data analysed are listed in Table 1.

Inflorescences at distinct developmental stages were collected in the field or in the Botanical Garden of the RUB, fixed in FAA 50 (Johansen, 1940) and stored in ethanol 70%. Material obtained from the Kew spirit collection was already fixed in FAA 50. For morphological and developmental analyses, flowers and inflorescences were dehydrated in formaldehyde dimethyl acetal (FDA) and critical-point dried. The material was mounted on metallic stubs with adhesive tape and coated with gold for observation using a scanning electron microscope (SEM) (Zeiss Sigma VP). For detection of secretory activity, fresh inflorescences of *E. decangulare* and *E. compressum* were collected from the Botanical Garden of the Ruhr-Universität Bochum. The flowers were dissected under a stereomicroscope, mounted on metallic stubs, and rapidly cooled with liquid nitrogen.

The samples were analysed using SEM (Zeiss Sigma VP). Images were taken using the software Smart SEM. The floral diagrams were generated using the Floral Diagram Generator (Kebert, 2020) and edited using the software program Inkscape®.

For anatomical analysis, mature flowers were dehydrated in n-butyl alcohol series and embedded in histological resin (Leica Histoiresin Embedding kit). The material was serial cross-sectioned with disposable steel knives using a rotary microtome at 8–10µm (Leica DM2245), and the sections obtained were stained with periodic-acid Schiff reagent (PAS reaction) and Toluidine Blue (Feder and O'Brien, 1968). Permanent slides were mounted in Entellan, and photomicrographs were taken using a light microscope (Leica DM4000) with a coupled camera. The image plates were made using the software program Inkscape®.

Characters and their respective states were established on a binary matrix of primary homologies using Mesquite 3.61 (Maddison and Maddison, 2019) according to topographical and ontogenetic principles. All characters were mapped over a comprehensive consensual tree from recent phylogenies (Andrade et al., 2010; Trovó et al., 2013; Bouchenak-Khelladi et al., 2014; Echternacht et al., 2014; Givnish et al., 2018; Andrino et al., 2021) applying the 'Trace Character History' option implemented in Mesquite 3.61 (Maddison and Maddison, 2019). All characters were considered as unordered and the optimization follows accelerated transformations. The morphological matrix with characters and states for each species is available in Appendix 1.

RESULTS

Organography

Floral diagrams of the *Eriocaulon* species studied are presented in Figure 2. Most species present pentacyclic trimerous flowers (Fig. 2A–D, G–J). However, *E. decangulare* (Fig. 2E, K) and *E. guyanense* (Fig. 2F, L) have dimerous flowers.

Staminate flowers

The staminate flowers of *Eriocaulon* have sepals that are free (Fig. 2A, D–F) or fused (Fig. 2B, C). The sepals are entirely free in *Eriocaulon decangulare*, *E. kunthii*, *E. sellowianum*, and *E. teusczii* (Figs. 2A, E, 3A), and fused into a spathaceous calyx in *E. cinereum* (Fig. 3B), *E. modestum*, and *E. nigericum*. In *E. twaitesii*, the sepals are mostly free, but fused at their basalmost parts, with a reduced median sepal (Fig. 2D). In *E. guyanense* the sepals are free or fused up to their median region (Fig. 2F) and bear an abaxial midrib keel (Fig. 3C). In *E. abyssinicum*, *E. aquatile*, *E. compressum*, and *E. xeranthemoides*, the sepals are fused up to their median region (Fig. 2B, C). Sepals have many trichomes at their apex, on the margin and dorsal side (Fig. 3A), except in *E. abyssinicum*, *E. cinereum* (Fig. 3B), *E. guyanense*, *E. nigericum*, and *E. xeranthemoides*.

The internode between the sepals and petals is elongated; we refer to it as an anthophore (Fig. 3A, B), as usually described for Eriocaulaceae (Stützel, 1998). Petals are free and similar in size in most species (Fig. 3B), but the median petal is larger than the lateral ones in *E. modestum* (Fig. 3D), *E. sellowianum*, and *E. teusczii*. Petals bear a nectariferous gland on their upper adaxial surface (Fig. 3E); this gland is vestigial in *E. abyssinicum*, *E. guyanense* (Fig. 3F), *E. nigericum*, and *E. xeranthemoides*. Trichomes occur at the petal apex (Fig. 3D, E), except in *E. abyssinicum*, *E. cinereum* (Fig. 3B), *E. guyanense* (Fig. 3F), *E. nigericum*, and *E. xeranthemoides*.

The androecium is two-whorled (Fig. 2A–F). Stamens are inserted at two heights—with the inner stamens above the outer ones (Fig. 3D), and the anthers are bithecate (Fig.

3F). The gynoecium is stalked and sterile, with three carpellodes in the trimerous species (Figs. 2A–D, 3G, H) and two carpellodes in the dimerous ones (Fig. 2E, F); the carpellodes are nectariferous (Fig. 3I).

Pistillate flowers

The pistillate flowers of *Eriocaulon* have free sepals in all species studied (Figs. 2G–L, 4A–D), but sepals may be fused at their basalmost part (noticeable only under light microscope). Sepals are keeled only in *E. guyanense* (Fig. 4B). They have trichomes at their apex (Fig. 4A, C), except in *E. abyssinicum*, *E. cinereum*, *E. guyanense* (Fig. 4B), *E. nigericum*, and *E. xeranthemoides*. In *E. cinereum* the median sepal is reduced (Figs. 2I, 4D), while in *E. twaithesii* it is absent (Fig. 2J).

An elongated anthophore is present in *E. aquatile*, *E. cinereum*, *E. compressum*, *E. guyanense*, *E. modestum* and *E. teuschii* (Fig. 4A). Petals are free (Fig. 4C) and present a nectariferous gland like those of staminate flowers (Fig. 4E). This gland is vestigial in *E. abyssinicum* (Fig. 4F), and absent in *E. cinereum*, *E. guyanense* (Fig. 4G), *E. nigericum*, and *E. xeranthemoides*. In *E. cinereum*, the petals are reduced and scale-like (Fig. 4H) or linear (Fig. 4I). Petals have trichomes at their apex (Fig. 4A, C, E), except in *E. abyssinicum* (Fig. 4F), *E. cinereum* (Fig. 4I), *E. guyanense* (Fig. 4G), *E. nigericum* and *E. xeranthemoides*.

The sterile androecium consists of two whorls of scale-like staminodes located at the ovary base (Figs 2G–L, 4H). The outer staminodes are inserted opposite the sepals, while the inner staminodes are opposite the petals (Fig. 4H). The gynoecium consists of a superior ovary and a style with three filiform stigmas in trimerous species (Fig. 4I) and two in dimerous species (Fig. 4B). In all species, stigmas are papillose and in a dorsal position (Fig. 4I).

Ontogeny

Early development

Staminate and pistillate flowers of *Eriocaulon* are indistinguishable at early developmental stages (Fig. 5A–F). The flowers develop centripetally in the inflorescence and are each subtended by a floral bract (Fig. 5A). In the floral primordia, the sepals emerge almost simultaneously (Fig. 5B). The two lateral sepals emerge at an 180° angle in both trimerous and dimerous flowers; the median sepal of the trimerous flowers emerge on the adaxial position (Fig. 5B). The stamen primordia emerge almost simultaneously (Fig. 5C, D), but in some flowers, the inner stamens emerge shortly before the outer ones (Fig. 5C). The gynoecium primordium emerges at the floral apex and divides into two or three prominences, which correspond to the carpel walls, and a central prominence, which corresponds to the undifferentiated placenta (Fig. 5E–H). Petals have late development and emerge by division of the common petal-stamen primordia (Fig. 5E–G).

At this developmental stage, the lateral sepals are similar in size in trimerous flowers, while the median adaxial sepal is smaller (Fig. 5G). In dimerous flowers, the two lateral sepals are the same size (Fig. 5H).

Staminate flower

In staminate flowers, the sepals elongate and cover the floral primordia (Fig. 6A, B). In species with a fused calyx, the sepals fuse through late congenital fusion (Fig. 6A). In *E. cinereum* (Fig. 6B), *E. modestum*, and *E. nigericum*, sepals fuse into a spathaceous calyx but remain free and distinguishable at their uppermost parts. In *E. twaitesii*, the two lateral sepals develop completely (Fig. 6C, D), but development of the median sepal is arrested at an early stage (Fig. 6D). In *E. guyanense*, sepals grow free (Fig. 6E) or fused

(Fig. 6F). In this species, each sepal develops a keel on its abaxial surface (Fig. 6E, F). The anthophore starts elongating, and the stamen primordia differentiate into filament and anther (Fig. 6B-D). The apex of each petal modifies into a prominence (Fig. 7A), which will later become the petal gland. The apical petal margins develop into two lateral prominences that fuse abaxially (Fig. 7B, C), dislocating the central apical prominence to the adaxial petal surface (Fig. 7C). However, in *E. abyssinicum*, *E. guyanense* (Fig. 7D), *E. nigericum* and *E. xeranthemoides*, the petal apex stops developing, resulting in an aborted gland.

In all species, the inner stamens become longer than the outer ones (Fig. 6A, B). Carpels start closing around the undeveloped septum (Fig. 7E), but they develop into carpellobes shortly afterwards (Fig. 7F-H). During their development, the carpellobes fold slightly inwards forming a median slit, which may be more prominent (Fig. 7G) or less prominent (Fig. 7H). In *E. sellowianum*, the carpellobes have an ascidiate shape at some stages of development (Fig. 7G).

Pistillate flower

In pistillate flowers, the sepals grow and remain free in all species (Fig. 8A-C). In *E. guyanense*, sepals develop a dorsal keel, as in staminate flowers (Figs. 3B, 6E, F). In *E. cinereum*, the lateral sepals develop completely, but development of the median sepal is arrested at an early developmental stage and it is reduced in mature flower (Figs. 2I, 8D). We were unable to analyse sepal development in *E. twaithesii* due to the lack of pistillate flowers at younger developmental stages, but it seems that the median sepal aborts during early development and is thus no longer distinguishable.

In species that possess an anthophore, this structure starts elongating after all floral parts are differentiated, with a higher growth rate immediately before anthesis (Fig. 8C).

In most species, the apex of each petal modifies into a prominence that will later become the nectariferous gland (Fig. 9A), and the apical petal margins raise and fuse abaxially, dislocating the central prominence to the adaxial petal surface (Fig. 9B, C); this process is similar to that in staminate flowers. In *E. cinereum*, petal development ceases at an early stage, forming scale-like (Fig. 4F, 8D) or linear structures (Fig. 4G). In this species, nectariferous glands do not appear at any moment. In *E. abyssinicum* (Fig. 4F) and *E. guyanense* (Figs. 4G, 9D–F), the petal apex does not develop into a gland, but the apical petal margins grow normally, which results in an emarginate petal.

In all species examined, the stamen primordia cease development and become scale-like staminodes at the ovary base (Figs. 4H, 8D, 9D). The outer staminodes are inserted opposite the ovary locules, while the inner staminodes are opposite the ovary septa (Figs. 4H, 9F–H). In the gynoecium, the carpels close into an ovary (Fig. 8A, B, D) and stigmas differentiate at their apices in a dorsal position (Fig. 9A, D). The style is formed by zonal growth (Fig. 9F–H) and the stigmas elongate and become filiform (Fig. 9G, H). None of the species display vestigial structures in the commissural position.

Vasculature

Staminate flower

The pedicel of the staminate flower has a central vascular cylinder from which diverge the floral vascular traces (Fig. 10A). Each sepal receives a single vascular trace (Fig. 10B), but in *E. cinereum* (Fig. 10C), *E. decangulare*, *E. guyanense*, and *E. twaitthesii*, two lateral sepal traces diverge from the vascular cylinder with no remnant of a median sepal trace. In all species, each sepal is vascularized by a single vascular bundle (Fig. 10D, E), except for *E. cinereum* (Fig. 10F) and *E. twaitthesii*, in which the median sepal lacks vasculature. In *E. guyanense*, the sepal keel is formed solely by the epidermis

and is opposite the sepal vascular bundle (Fig. 10E). In *E. cinereum*, the sepals are fused into a spathaceous calyx with only two vascular bundles, corresponding to the lateral sepal bundles (Fig. 10F).

At the anthophore, the vascular cylinder divides into six vascular traces in trimerous species (Fig. 11A) and four traces in dimerous ones (Fig. 11B). The traces opposite the sepals enter the outer stamens (Fig. 11C, D); the traces alternating with the sepals divide radially into petal and inner-stamen traces (Fig. 11C, E, F). The petals are each vascularized by a single vascular bundle that reaches the base of the petal gland (Figs. 11F, 12A). In *E. xeranthemoides*, the vascular bundle does not reach the gland, which is vestigial (Fig. 12B). In *E. abyssinicum*, *E. nigericum*, and *E. guyanense*, the vestigial glands are indistinguishable under light microscopy. The stamens are vascularized by a single vascular bundle that reaches the connective (Fig. 12C, D). The remaining vascular cylinder divides into the vascular bundles that enter the carpellodes (Fig. 12D, E). The ventral carpellary bundles are absent, so the undifferentiated septum lacks vasculature (Fig. 12D, F)

Pistillate flower

The pedicel of the pistillate flower has a central vascular cylinder, from which diverge the traces of all floral parts (Fig. 13A). As in the staminate flowers, each sepal receives a single vascular trace (Fig. 13B). In *E. decangulare*, *E. guyanense*, *E. cinereum* (Fig. 13C, D), and *E. twaitesii*, the lateral sepals receive vascular traces, but there is no remnant of a median sepal trace. In *E. guyanense*, the sepals of the pistillate flower have a keel like that of the staminate flower (Fig. 10E).

In *E. aquatile*, *E. cinereum*, *E. compressum*, *E. guyanense*, *E. modestum* and *E. teuschii*, the vascular cylinder does not divide at the anthophore (Fig. 13D). Divergence

of the petal traces from the vascular cylinder alternates with the sepals (Fig. 13E, F). The petals are each vascularized by a single vascular bundle that reaches the base of the petal glands (Fig. 14A, B). In species that lack petal glands, no differentiated tissue was observed (Fig. 14C). In *E. aquatile*, *E. kunthii*, *E. modestum* and *E. nigericum* (Fig. 14D), a vascular trace alternating with the petals reaches the base of each outer staminode. In these species, a small vascular trace diverges from the petal trace and reaches the base of each inner staminode (Fig. 14E, F).

At the ovary base, dorsal carpellary traces diverge from the vascular cylinder (Fig. 15A, B). More distally, the remaining vascular cylinder divides into ventral vascular bundles, which are in the commissural position (Fig. 15C, D). Overall, the gynoecium vasculature consists of two or three dorsal carpellary bundles and two or three synlateral ventral bundles (Fig. 15B–D), the number depending on the number of carpels. In *E. abyssinicum*, *E. cinereum*, *E. nigericum*, and *E. xeranthemoides*, the remaining vascular cylinder usually does not divide into ventral bundles but remains in the central region of the ovary (Fig. 15E). The ventral bundles, or the remaining vascular cylinder, reach the placenta and vascularize the ovules (Fig. 15D). The dorsal carpellary bundles vascularize the style in all species studied (Fig. 15F). In some flowers, the dorsal bundles are reduced, resulting in a non-vascularized style (Fig. 15G). The stigmas usually lack vasculature in all species (Fig. 14B, C), but the dorsal carpellary bundles reach their base in some flowers (Fig. 15H).

DISCUSSION

Floral diversity and reduction in *Eriocaulon*

Early floral development of *Eriocaulon* is similar to that observed in other Eriocaulaceae (Stützel, 1990; Stützel and Gansser, 1995; Silva et al., 2016; Sokoloff et

al., 2020). The sepals are the first floral parts to emerge in the floral primordium, followed by the stamens and the gynoecium; the petals differentiate from the division of common petal-stamen primordia (Stützel, 1990; Silva et al., 2016; Sokoloff et al., 2020). Despite this relatively stable general pattern in *Eriocaulon*, there is variation in floral merism, size and number of perianth parts, and presence of petal glands. Our comparative analysis of floral development and vasculature in several species provides clues to possible evolutionary processes.

Eriocaulon decangulare and *E. guyanense* differ from the other species examined by their dimerous flowers. In both species, the median sepal does not emerge, and the two equal lateral sepals resemble the lateral sepals of trimerous species in morphology and position. In a developmental study of dimerous *Paepalanthus* (Paepalanthoideae), Silva et al. (2016) hypothesized that dimery evolved in this genus from the loss of an entire floral sector, including the median sepal, so that the floral parts shifted position, and the flowers became zygomorphic. In *Eriocaulon*, trimerous flowers are slightly zygomorphic due to the position of the lateral sepals, but the other floral parts are not dislocated, as also observed by Sokoloff et al. (2020). However, in dimerous flowers, all floral parts and their vascular bundles have shifted position so that the flowers are zygomorphic. Therefore, it is likely that dimery in *Eriocaulon* also evolved from the loss of a median sepal, as in *Paepalanthus*.

In *Eriocaulon*, sepals are free at earlier developmental stages of the staminate flowers. The sepals may remain free or become fused through late congenital fusion at later stages, resulting in considerable diversity in calyx morphology. *Eriocaulon guyanense* has staminate flowers either with free or fused sepals, and the sepal keel may be more or less conspicuous. These morphological variations were also reported in an African dimerous species of *Eriocaulon* and are apparently related to distinct zones in the

capitulum (S Phillips, Kew Gardens, UK, pers. comm.). This variation is novel to Brazilian species of Eriocaulaceae, so we emphasise the importance of studying floral morphological variation in other species to address morphological and taxonomic problems in the family.

In *E. cinereum* and *E. twaitesii*, late development differs considerably from the other species studied and indicates distinct degrees of perianth reduction. In *E. cinereum*, the calyx is spathaceous in staminate flowers and has only two lateral vascular bundles, which correspond to the vascular bundles of lateral sepals. The median sepal lacks vasculature, but the tripartite tip of the spathaceous calyx shows that the median sepal develops to some degree and becomes incorporated in the calyx.

In pistillate flowers of *E. cinereum*, the median sepal has an arrested development and is reduced and non-vascularized. The petals emerge in the same way as those of other species, but they are reduced and lack vasculature. This pattern of perianth reduction also occurs in *E. redactum* (Sokoloff et al., 2020), a species closely related to *E. cinereum*. Although flowers of both species develop similarly, *E. redactum* differs by its smaller sepals with trichomes at their apices (Sokoloff et al., 2020). Sokoloff et al. (2020) also noted the importance of studying other species that belong to the *E. cinereum* group to understand its morphological variation.

In *E. twaitesii*, the median sepal is reduced in comparison with the lateral ones and lacks vasculature. The reduced median sepal is noticeable in staminate flowers of this species because sepals are free at their median region. In pistillate flowers, the median sepal is superficially absent in the mature flower, but a complete development series is still missing. Based on data from species with dimerous and apparently heteromerous flowers, there seems to be a tendency that, when outer-perianth reduction occurs in

Eriocaulaceae, the median sepal is reduced or lost. Furthermore, reduction in perianth parts is frequently accompanied by complete loss of their vasculature.

The presence of petal glands is a variable character state in *Eriocaulon*. They are commonly present in the genus but are absent in five out of the 13 species studied here. Development of the petal glands is quite uniform in *Eriocaulon* and is in accordance with what was previously reported for the genus (Stützel, 1984). However, glands are lacking in both staminate and pistillate flowers of *E. abyssinicum*, *E. guyanense*, *E. nigericum*, *E. xeranthemoides*, and in pistillate flowers of *E. cinereum*. In *E. cinereum*, the lack of petal glands in pistillate flowers is likely related to petal reduction, since these glands develop fully in staminate flowers. In the remaining species, vestigial glands are found either in staminate or in pistillate flowers, indicating that petal glands were secondarily lost. In *E. abyssinicum* and *E. guyanense*, the apical petal margins arise but do not fuse together in the pistillate flowers, so petals become emarginate as a result of gland abortion.

Vasculature of the androecium and gynoecium

Androecium and gynoecium morphology are quite uniform in the species studied, but some variation was observed regarding their vasculature. Staminalodes are generally vascularized in Eriocaulaceae, at least to some degree. In Paepalanthoideae and in *Mesanthemum* (Eriocauloideae), vascular bundles reach the base of staminalodes (Rosa and Scatena, 2007; Silva et al., 2016, 2021). In *Eriocaulon*, staminalodes are vascularized in *E. aquatile*, *E. kunthii*, *E. modestum*, and *E. nigericum*, but not in the other species studied, indicating that the presence of staminal vascularization is variable in *Eriocaulon*, and its absence displays a higher degree of stamen reduction.

The gynoecium of Eriocaulaceae is generally vascularized by both dorsal and ventral carpellary bundles (Rosa and Scatena 2003, 2007; Silva et al., 2016, 2021). In *Mesanthemum*, the dorsal carpellary bundles reach the style, but the stigmas are non-

vascularized probably because of reduction of vasculature (Silva et al., 2021). Similarly, in *Eriocaulon*, the dorsal vascular bundles reach the style but rarely the stigmas. The lack of vasculature in stigmas of Eriocauloideae indicates that the dorsal vascular bundle is reduced and is probably related to the presence of filiform stigmas, which do not require large vascular supply.

The remaining central vascular cylinder divides into the ventral vascular bundles in the ovary of *Eriocaulon* and are in a commissural position. However, in *E. abyssinicum*, *E. cinereum*, *E. nigericum* and *E. xeranthemoides*, the central vascular cylinder does not divide, and ventral vascular bundles are absent probably because of vascular reduction. In *Mesanthemum*, the ventral vascular bundles are opposite the locules, but they shift position along the ovary regions and become commissural, indicating distinct types of carpel fusion occur in this genus (Silva et al., 2021). The comparative analysis of Eriocauloideae flowers shows that the gynoecium vasculature varies in the subfamily and, although morphological reductions are apparently lacking in the gynoecium, vascular reductions occur frequently.

Evolutionary implications for the xyrids

The floral development of *Eriocaulon* allows us to discuss in greater detail the floral homologies between Eriocaulaceae and Xyridaceae. Character optimization also improves our understanding of these structures in Eriocauloideae and Paepalanthoideae.

Our character optimization shows that Eriocaulaceae and Xyridaceae could have evolved from an ancestor with either bisexual or unisexual flowers (Fig. 16A). Although most species of Eriocaulaceae are unisexual, flowers of all species are bisexual at early developmental stages and become unisexual as a result of carpel or stamen abortion (Smith, 1910; Stützel, 1990; Stützel and Gansser, 1995; Silva et al., 2016; this paper). A

few species with bisexual flowers occur in *Syngonanthus* (Watanabe et al., 2015), *Rondonanthus* (Hensold and Giulietti, 1991) and *Eriocaulon* (Prajaksood et al., 2017), but our analysis indicates that bisexuality is a reversal in Eriocaulaceae that appeared multiple times independently (Fig. 16A). Therefore, we assume that the ancestor of the xyrids had bisexual flowers and that the shift to unisexuality occurred in the ancestor of Eriocaulaceae. The adaptive significance of this shift is not clear, but could be related to the small flowers and compact inflorescence in the family and also to floral behavior; further studies on the reproductive biology of the family are needed to elucidate this question.

Most species of Eriocaulaceae are trimerous, while Xyridaceae are exclusively trimerous. In Xyridaceae, the lateral sepals emerge before the median adaxial sepal, in contrast to what occurs in *Eriocaulon*. Our character optimization shows that dimery has evolved at least six times in Eriocaulaceae (Fig. 16B). As previously discussed, in *Paepalanthus* (Silva et al., 2016) and *Eriocaulon*, dimery has evolved from the loss of an entire floral sector, without vestigial remnants of floral parts, and is associated with a shift in floral symmetry. We predict that further analyses of dimerous *Syngonanthus* and *Comanthera* will indicate a similar process within these genera.

In Eriocaulaceae and Xyridaceae, stamens may be reduced to staminodes, but the origin of the staminodes differs between the two families. In Eriocaulaceae, the presence of staminodes is associated with a shift to unisexuality, as stamen development is arrested only in pistillate flowers; in Paepalanthoideae a whorl is lost entirely. In contrast, flowers in Xyridaceae are bisexual; when staminodes are present, the fertile stamens correspond with the inner androecium whorl and staminodes with the outer whorl.

Our character optimization was inconclusive regarding the evolution of the outer androecium whorl in the xyrids (Fig. 16C), but floral development of Eriocaulaceae and

Xyridaceae indicates possible interpretations. Across angiosperms, whorled staminodes tend to occur in more recently diversified groups in which the ancestor possessed two-whorled stamens (Walker-Larsen and Harder, 2000). In Xyridaceae, the outer androecial whorl is staminodial in *Xyris* and some species of *Abolboda*, and tends to be lost in more recently diversified genera (Fig. 16C), which also suggests that the ancestor of the family likely had a two-whorled androecium. The complete loss of whorled staminodes seems to be irreversible (Walker-Larsen and Harder, 2000), implying that flowers with a two-whorled androecium could not be derived from flowers like those of Paepalanthoideae (Eriocaulaceae), *Aratityopea*, *Orectanthe*, and some species of *Abolboda* (Xyridaceae), in which the outer androecium whorl is lost from inception (Stützel, 1990; Stützel and Gansser, 1995; Silva et al., 2016; Sajo et al., 2017). Therefore, we can assume that the presence of two androecium whorls is a plesiomorphic character state in both Eriocaulaceae and Xyridaceae.

In *Eriocaulon*, stamens are arranged in two whorls that emerge simultaneously in the floral primordia (Stützel, 1990), but we show that the outer stamens emerge slightly later than the common petal-inner stamen in a few flowers. In all species of *Eriocaulon*, the inner stamens are longer than the outer ones throughout floral development. In contrast, in Paepalanthoideae, the inner stamens are the same height and outer stamens are completely lost (Stützel, 1990; Stützel and Gansser, 1995; Rosa and Scatena, 2007; Silva et al., 2016). Delayed development of the outer androecial whorl was also observed in *Mesanthemum* and is probably related to lack of space for the stamens to develop side by side and could represent a step towards their loss in Paepalanthoideae (Silva et al., 2021).

In staminate flowers of *Eriocaulon*, carpels start to close at early developmental stages, sometimes becoming ascidiate; they develop into nectariferous carpellobes, while

the septum remains as a central nonvascularized prominence. A similar developmental pattern was described in *Paepalanthus* (Silva et al., 2016), but also occurs in other genera of Paepalanthoideae (AL Silva, UNESP, Brazil, unpubl. res.). In *Paepalanthus*, carpels do not close during development of the sterile gynoecium (Silva et al., 2016), but this difference is related to the point when the carpels start to differentiate. Our character reconstruction was inconclusive about the plesiomorphic state in the xyrids (Fig. 16D). However, the occurrence of a sterile gynoecium with nectariferous carpellobes in both Eriocauloideae and Paepalanthoideae indicates that these structures appeared only once, in the Eriocaulaceae ancestor, and is clearly associated with the shift to unisexuality.

In pistillate flowers of *Eriocaulon*, the stigmas are in a dorsal position and emerge as an apical bulge shortly after carpel closure leading to ovary formation. In *Eriocaulon*, commissural structures do not emerge, and the overall gynoecium structure resembles that of many other Poales, consisting of ovary, style and dorsal stigmas, as in Cyperaceae (Vrijdaghs et al., 2009), Juncaceae (Oriani et al., 2012), Restionaceae (Ronse De Craene et al., 2002), Thurniaceae (Silva et al., 2020), and Xyridaceae (Remizowa et al., 2012; Sajo et al., 2017). In Paepalanthoideae, the nectariferous branches are in a dorsal position and follow the same developmental pattern as the stigmas of *Eriocaulon*, while stigmatic branches arise in a commissural position by fusion of adjacent carpel margins (Stützel, 1990; Stützel and Gansser, 1995; Rosa and Scatena, 2003; Silva et al., 2016). However, in *Syngonanthus* and *Paepalanthus*, species without nectariferous branches may occur because of abortion of the carpel apex (Stützel and Gansser, 1995; Silva et al., 2016). This gynoecium complexity observed in Eriocaulaceae shows that evolutionary interpretations should consider modifications of the different carpellary regions.

In Xyridaceae, the nectariferous appendages emerge later, only after style formation (Sajo et al., 2017). Previous studies have reported that the nectariferous branches of

Paepalanthoideae and the stigmas of Eriocauloideae are vascularized by the dorsal carpel bundle (Rosa and Scatena, 2003, 2007; Silva et al., 2016), while the nectariferous appendages of Xyridaceae are vascularized by ramifications of the dorsal carpel bundles (Sajo et al., 2017). Data on vasculature should be discussed with caution, as reductions occur frequently in Eriocaulaceae, as exemplified in the present work. In any case, comparative analysis of flowers of *Eriocaulon* shows that gynoecium development in Eriocauloideae is more similar to that of Xyridaceae than Paepalanthoideae. Comparative gynoecium development also supports the suggestion that the nectaries of Xyridaceae and Paepalanthoideae are not homologous (Sajo et al., 2017).

Our character optimization considering gynoecium development (Fig. 16E) also agrees with the hypothesis of Rosa and Scatena (2007) that the nectariferous branches of Paepalanthoideae are derived by morphological and functional modification of the dorsal region of the carpel, and that species of Paepalanthoideae without nectariferous branches have lost them secondarily. Like the nectariferous appendages of Paepalanthoideae, commissural stigmas appeared only once in this subfamily. Moreover, character optimization confirms that the nectaries of Eriocaulaceae and Xyridaceae had independent origins (Fig. 16F), as suggested by Sajo et al. (2017).

In previous morphological studies, the gynoecial nectaries of Eriocaulaceae and Xyridaceae are commonly referred to as “nectariferous appendices” (Rosa and Scatena, 2003, 2007), “nectariferous appendages” (Oriani and Scatena, 2012; Sajo et al., 2017) or “nectariferous branches” (Silva et al., 2016, 2021; this paper), but we note the importance of using distinct and standardized terminologies in these families since the structures are not homologous. In Xyridaceae, the term “nectariferous appendages” is commonly used (Stützel, 1990; Oriani and Scatena, 2012; Sajo et al., 2017), and we agree it should be maintained. In Eriocaulaceae (Paepalanthoideae), we propose the usage of the terms

“nectariferous branches” and “stigmatic branches” to refer to the nectariferous and stigmatic portions of the style, respectively, since they have been used in taxonomic descriptions by several authors and in several genera—e.g., in *Actinocephalus* (Echternacht et al., 2011), *Comanthera* (Echternacht et al., 2015), *Leiothrix* (Giulietti and Silva, 2016), *Paepalanthus* (Sano et al., 2015; Trovó et al., 2015), and *Syngonanthus* (Watanabe et al., 2015). In addition, in Eriocauloideae, we propose the usage of the term “stigmas”, as commonly used (Prajaksood and Chantaranonthai, 2002; Phillips and Masterházy, 2015; Prajaksood et al., 2017; Sokoloff et al., 2020), to make clear that they have different origin from the stigmatic branches of Paepalanthoideae.

Finally, species of Eriocauloideae usually have petals with glands in both staminate and pistillate flowers. As previously discussed, although these glands are absent in some *Eriocaulon*, they were secondarily lost in the genus. In Paepalanthoideae, petal glands are also absent, but, in contrast to *Eriocaulon*, they do not emerge at any stage of development (Silva et al., 2016). Although we did not optimize this character in the phylogeny, we have no reason to infer that petal glands were present in Paepalanthoideae. Instead, we assume that they appeared only once, in Eriocauloideae.

Hypothesis of floral evolution of Eriocaulaceae

The ancestor of Eriocaulaceae probably had trimerous, bisexual flowers with a two-whorled androecium (Fig. 17A). Its gynoecium resembled the gynoecium of Eriocauloideae and many other Poales, which is syncarpous and has dorsal stigmas (Fig. 17A). The first and key evolutionary step toward the floral types of Eriocaulaceae was a shift from bisexual to functionally unisexual flowers (Fig. 17B, C). In staminate flowers, the carpels became sterile, changed their function and became nectariferous (Figs. 17A). In pistillate flowers, the stamens became staminodes (Fig. 17C).

The current patterns found in Eriocauloideae and Paepalanthoideae were both derived from an intermediate ancestor with unisexual flowers and nectariferous carpellobes.

(I) In Eriocauloideae, the androecium remained two-whorled (Fig. 17D, E) and the gynoecium retained its dorsal stigmas (Fig. 17E). However, Eriocauloideae developed petal glands in both staminate and pistillate flowers (Fig. 17D, E), originating from modification of the petal apex (Fig. 17B). As carpellobes and petal glands have a distinct position in the flower and distinct development, they are clearly not homologous. Instead, a transference of function could have occurred from carpellobes to petal glands. This hypothesis would also explain the morphological and anatomical similarities between these structures. The appearance of petal glands in Eriocauloideae seems to have been a key change in the subfamily, as they are apical and make nectar more readily available to floral visitors than the carpellobes.

(II) In Paepalanthoideae, the androecium became single-whorled, as a result of complete loss of the outer stamen whorl (Fig. 17F, G). In pistillate flowers, the stigmatic branches arise in the commissural region of adjacent carpels, while the nectariferous branches originate in the dorsal region by differentiation of the carpel apex (Fig. 17G). Although nectariferous carpellobes and nectariferous branches have a similar position and originate from the gynoecium primordium, they cannot be considered homologous, since their development and evolutionary timing is distinct. Nectariferous carpellobes originate from entire carpels and were already present in the Eriocaulaceae ancestor, while nectariferous branches originate from the carpel apex and appear only in the Paepalanthoideae lineage. The stigmatic branches likely originated concurrently with the nectariferous branches. As the carpel apex became nectariferous in the gynoecium of Paepalanthoideae, the absence of stigmatic function would prevent the plant from

reproducing. Thus, the apical carpel margins took over the stigmatic function to compensate the appearance of a dorsal nectary (Fig. 17C).

CONCLUSIONS

The floral morphology of *Eriocaulon* is highly diverse, with different degrees of fusion and reduction of floral parts. Our study provides clues to some of the developmental processes underlying this floral variation. Further developmental and anatomical studies including more species of *Eriocaulon*, combined with a robust phylogenetic analysis, will allow greater understanding of the evolution of floral characters within the genus.

Comparative floral development of *Eriocaulon* has also added important information about the floral structure of Eriocauloideae, allowing us to infer homologies between Eriocaulaceae and Xyridaceae, and helping us to reconstruct the evolutionary history of some floral characters in these families. The major evolutionary steps towards the flowers of Eriocaulaceae encompassed both a sexuality shift, and morphological and functional changes in the carpels or parts of the carpels in both pistillate and staminate flowers. Finally, our study helps us to understand floral evolution of Eriocaulaceae in a broader context within the order Poales and emphasises the importance of comparative morphological and developmental studies to comprehend floral evolution.

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TABLE

Table 1. List of species of *Eriocaulon* selected for the study and their respective collection data.

Species	Collector number	Local of origin
1. <i>Eriocaulon abyssinicum</i> Hochst.	Wood 446	Uganda
2. <i>E. aquatile</i> Körn.	Coan et al. 100	Brazil
3. <i>E. cinereum</i> R. Br.	Silva et al. 52	Brazil
4. <i>E. compressum</i> Lam.	Cultivated (RUB)	United States of America
5. <i>E. decangulare</i> L.	Cultivated (RUB)	United States of America
6. <i>E. guyanense</i> Körn.	Silva et al. 54	Brazil
7. <i>E. kunthii</i> Körn.	Scatena et al. 199	Brazil
8. <i>E. modestum</i> Kunth	Silva et al. 59, 61, 67	Brazil
9. <i>E. nigericum</i> Meikle	Jones 20718	Nigeria
10. <i>E. sellowianum</i> Kunth	Silva et al. 62	Brazil
11. <i>E. teuschii</i> Engl. & Ruhland	Taylor 9163	Tanzania
12. <i>E. twaitesii</i> Körn.	Barnes 89	India
13. <i>E. xeranthemoides</i> Bong.	Stanfield 117	Nigeria

FIGURES

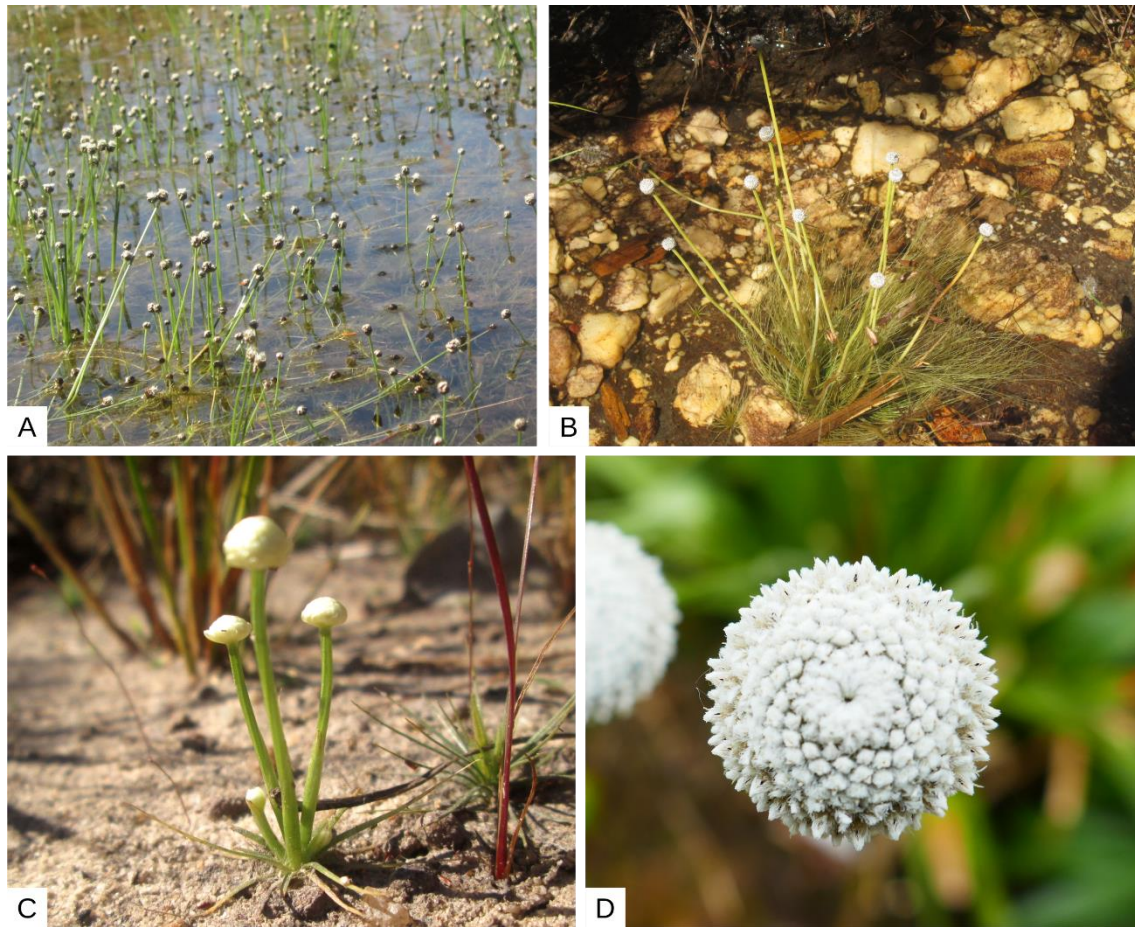


Fig. 1. Photographs of *Eriocaulon* representatives. A. A population of *E. cinereum*. B. *Eriocaulon aquatile*. C. *Eriocaulon guyanense*. D. Detail of a capituliform inflorescence of *E. decangulare*. Photos: A.L. Silva.

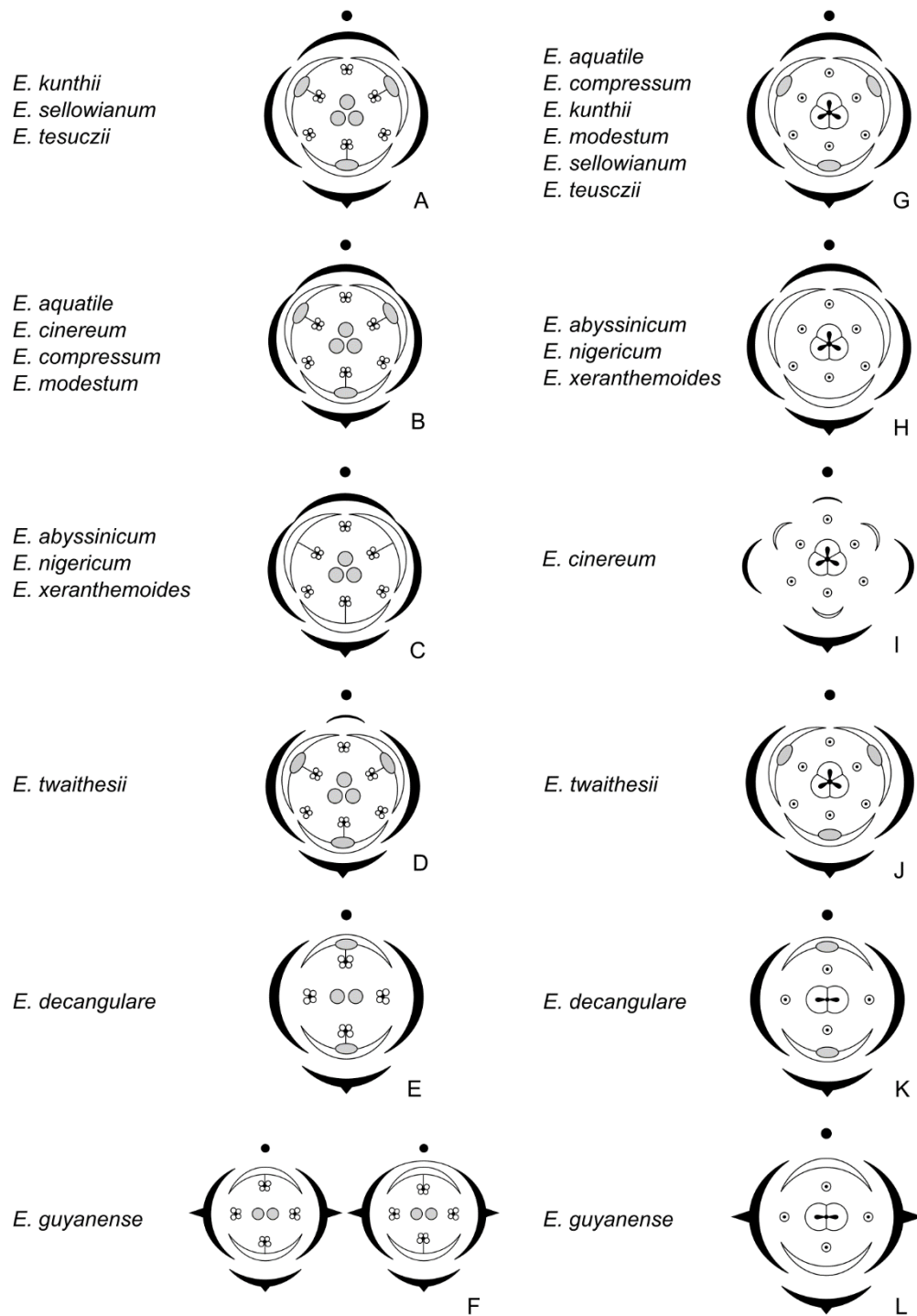


Fig. 2. Floral diagrams of staminate and pistillate flowers of *Eriocaulon*. A–D. Trimerous staminate flowers. E, F. Dimerous staminate flowers. G, H. Trimerous pistillate flowers. I, J. Heteromerous pistillate flowers. K, L. Dimerous pistillate flowers.

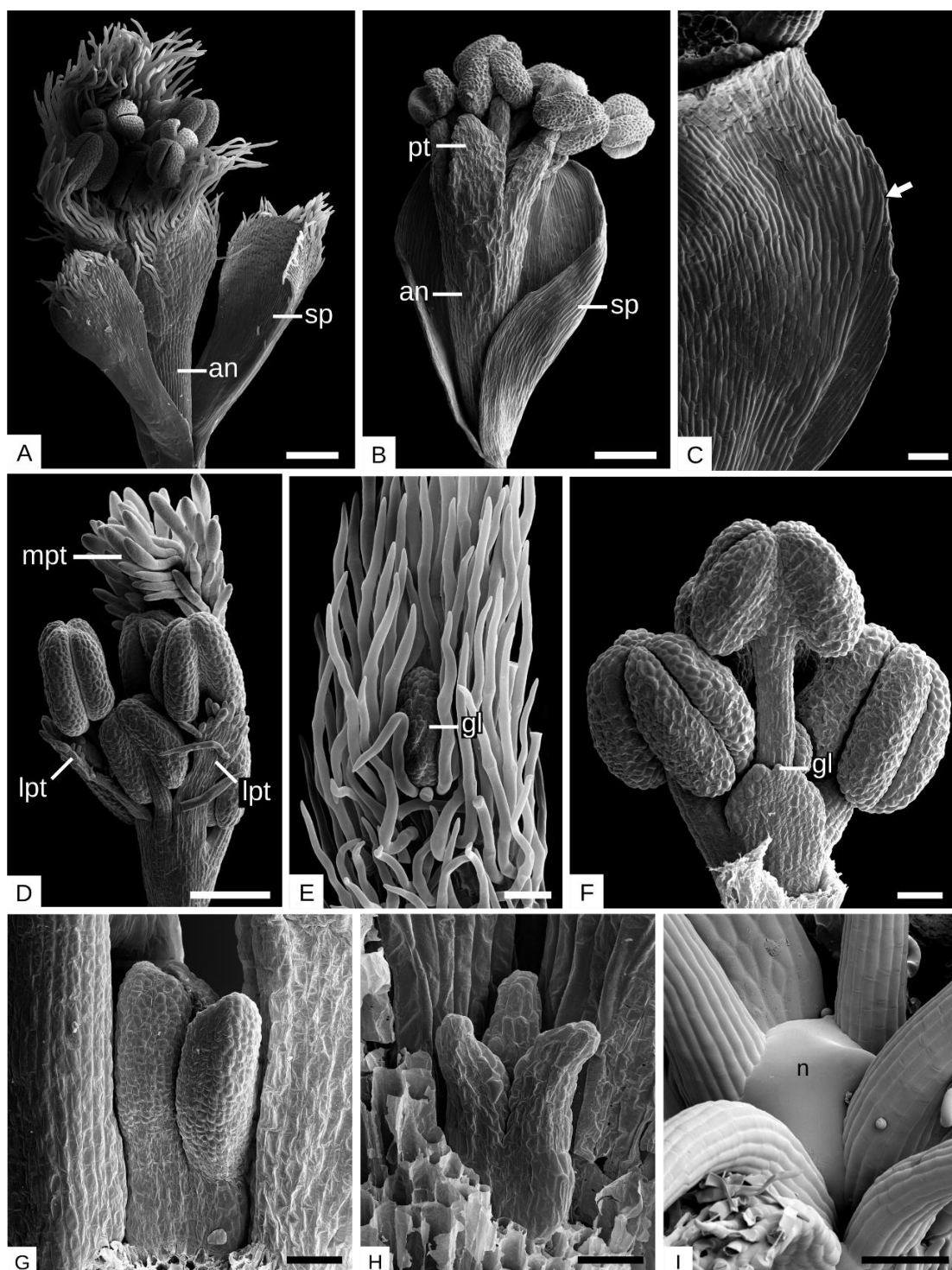


Fig. 3. Organography of staminate flowers of *Eriocaulon*. A, B. General aspects of *E. sellowianum* (A) and *E. cinereum* (B). C. Lateral view of a sepal of *E. guyanense* showing the midrib keel (arrow). D. Young flower of *E. modestum* with sepals removed and showing petals with different sizes. E. Detail of a petal apex of *E. modestum* with a gland. F. Young flower of *E. guyanense*, indicating a petal with aborted gland. G. Detail of a sterile gynoecium of *E. kunthii*. H, I. Nectariferous carpellodes of *E. compressum* without (F) and with (G) nectar drop covering it completely. Abbreviations: arrow – midrib keel, an – anthophore, gl – petal gland, lpt – lateral petal, mpt – median petal, n – nectar drop, pt – petal, sp – sepal. Scale bars: A= 400 μ m; B, D, I = 200 μ m; C, E, F, G = 100 μ m; H= 80 μ m.

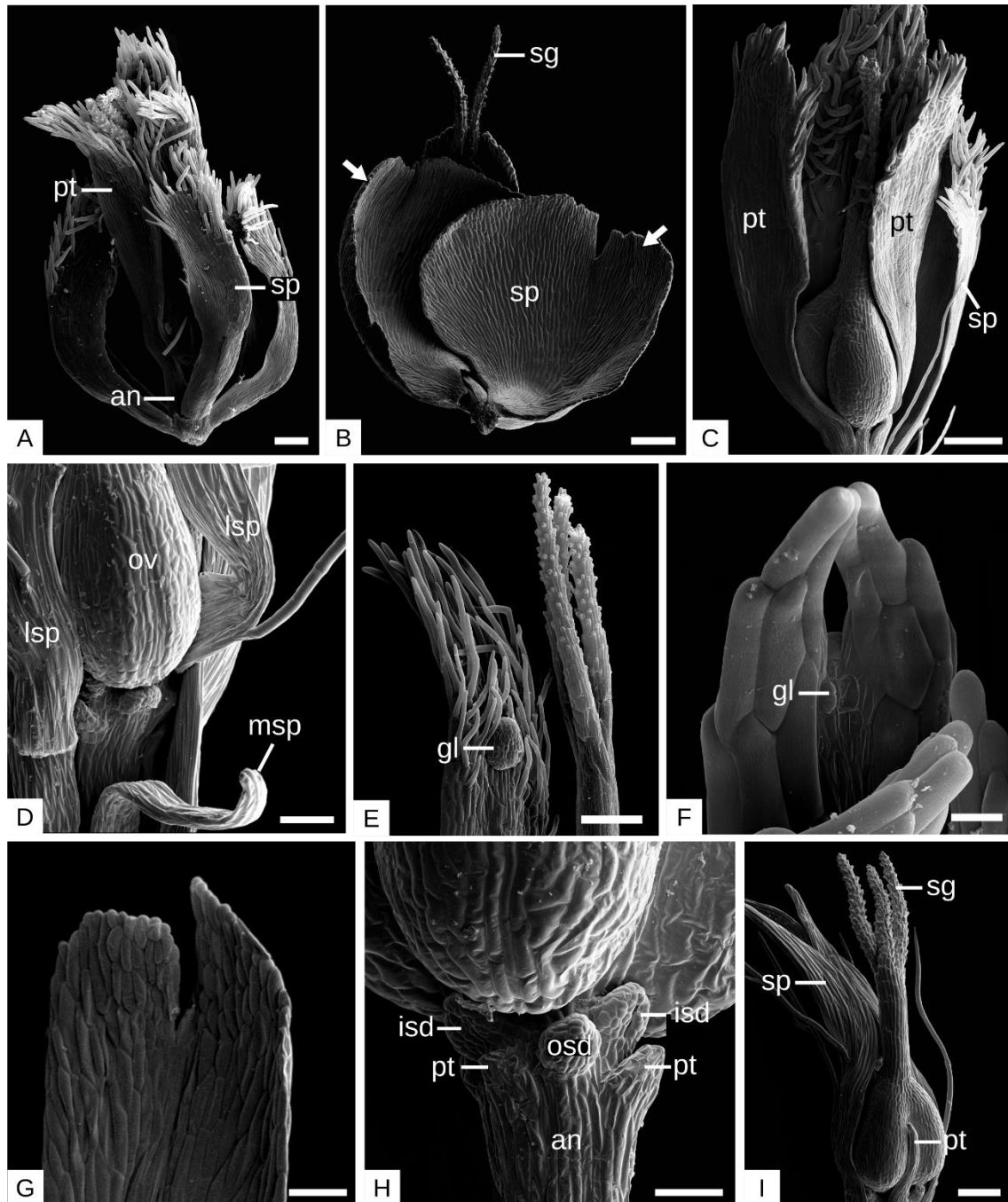


Fig. 4. Organography of pistillate flowers of *Eriocaulon*. A–C. General aspects of *E. teusczii* (A), *E. guyanense* (B), and *E. modestum* (C). D. Flower base of *E. cinereum* showing the reduced median sepal. E. Detail of a petal apex of *E. teusczii*, indicating a nectariferous gland. F. Detail of a vestigial gland on a petal apex of *E. abyssinicum*. G. Detail of the petal apex of *E. guyanense* lacking the petal gland. H. Detail of the ovary base of *E. cinereum* indicating vestigial petals and staminodes from the inner and outer whorls. I. Flower of *E. cinereum* indicating a linear petal. Abbreviations: arrow – sepal keel, gl – petal gland, isd – inner staminode, lsp – lateral sepal, msp – median sepal, osd – outer staminode, ov – ovary, pt – petal, sg – stigma, sp – sepal. Scale bars: A–C, E= 200 µm; D, G, I= 100 µm; F= 20 µm; H= 40 µm.

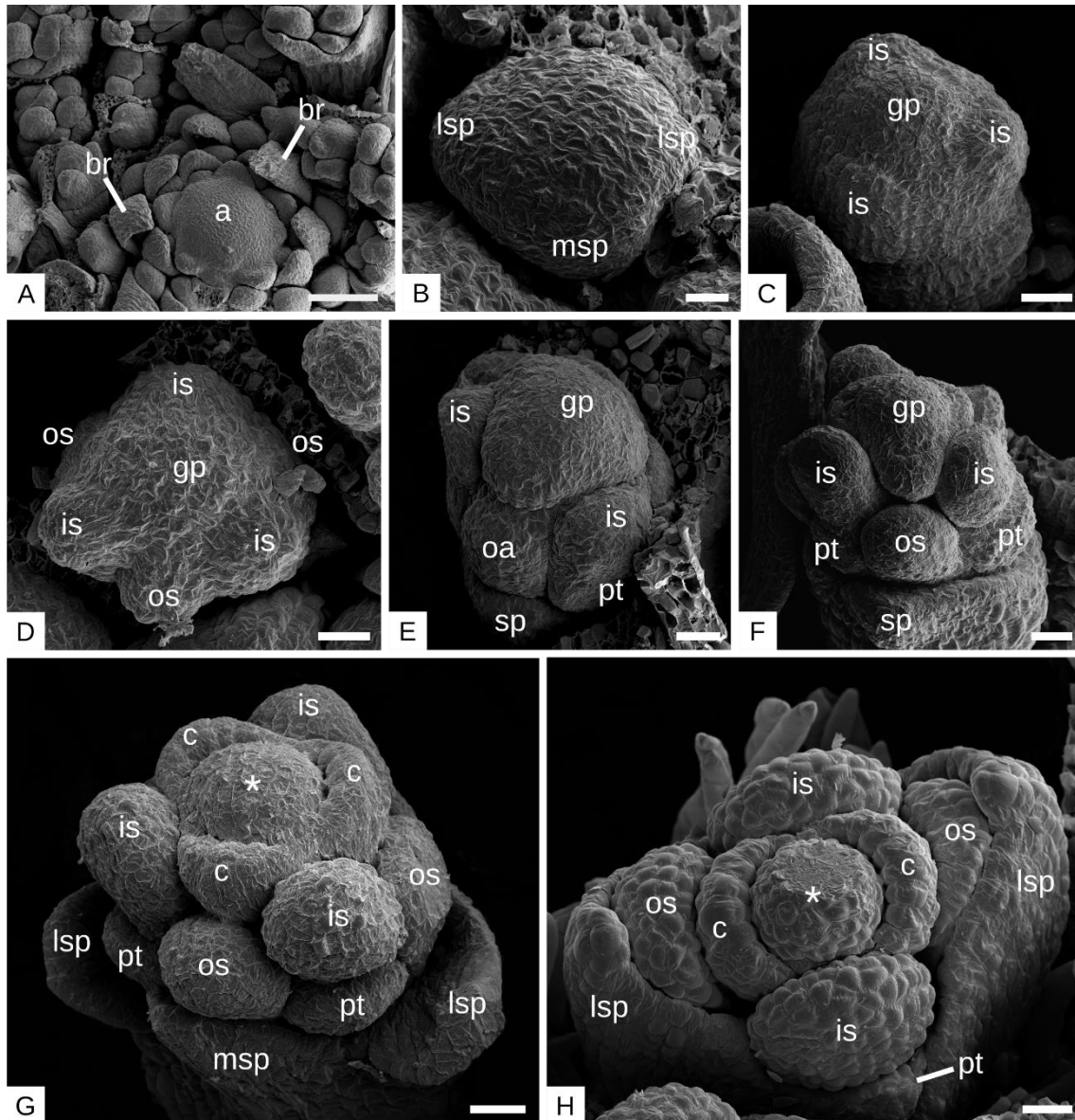


Fig. 5. Early developmental stages of staminate and pistillate flowers of *Eriocaulon*. A. Inflorescence apex of *E. aquatile*, indicating the centripetal development of flowers. B. Floral primordium of *E. aquatile* indicating the sepals' inception (abaxial view). C. Floral primordium of *E. compressum*, indicating primordia of the inner stamens and the gynoecium. D. Floral primordium of *E. modestum*, showing the initiation of the outer stamens (abaxial view). E, F. Floral primordia of *E. kunthii* (E) and *E. compressum* (F) showing the initiation of the petals. G, H. Floral primordia of *E. compressum* (G) and *E. decangulare* (H) showing the initiation of the carpels. Abbreviations: a – inflorescence apex, asterisk – undeveloped septum, br – floral bract, c – carpel, gp – gynoecium primordium, is – inner stamen, os – outer stamen, pt – petal, sp – sepal. Scale bars: A= 100 μ m; B–H= 20 μ m.

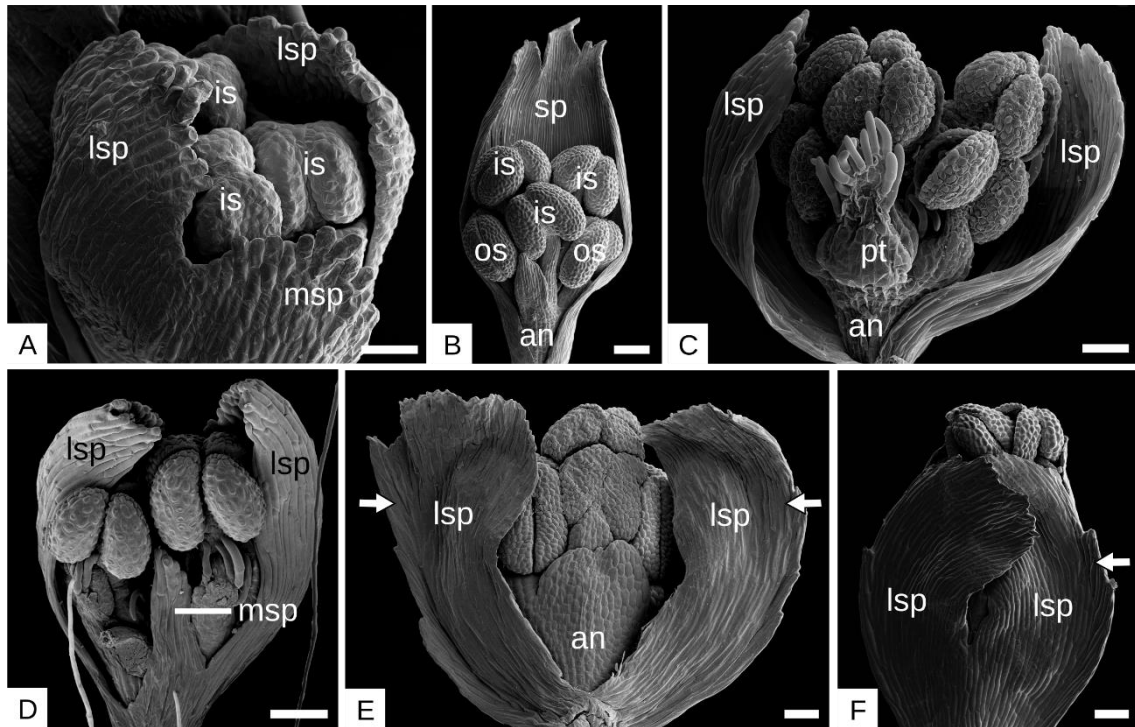


Fig. 6. Development of staminate flowers of *Eriocaulon*. A. Young flower of *E. aquatile* showing fusion of sepals. B. Young flower of *E. cinereum* showing developing anthophore and spathaceous sepals. C, D. Flowers of *E. twaitesii* showing developing anthophore, lateral sepals (C, D), and reduced median sepal (D). E, F. Flowers of *E. guyanense* showing developing gibbose sepals. Abbreviations: an – anthophore, arrow – sepal protrusion, is – inner stamen, os – outer stamen, lsp – lateral sepal, msp – median sepal, pt – petal, sp – sepal. Scale bars: A= 40 μm ; B–E = 100 μm .

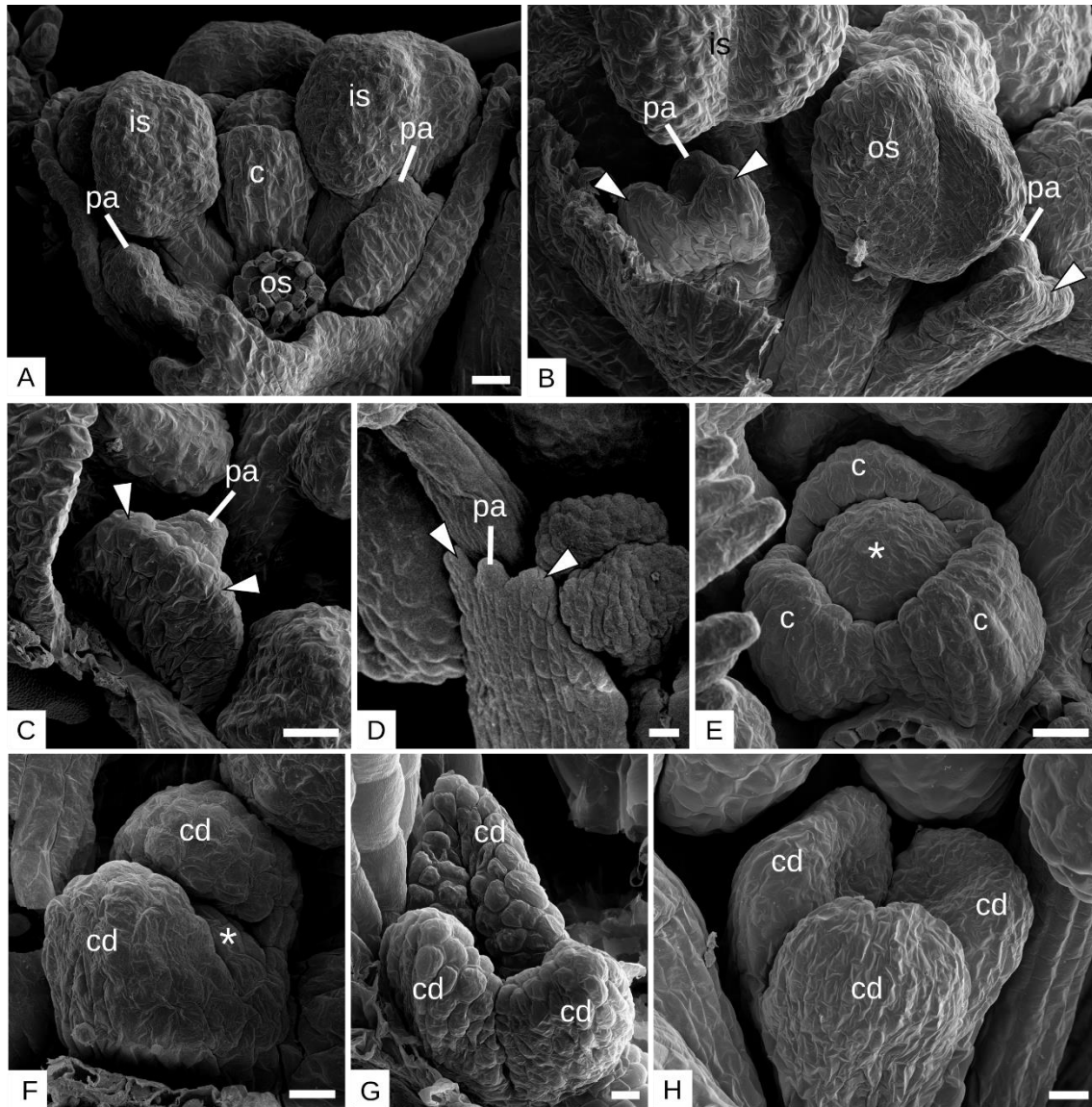


Fig. 7. Development of staminate flowers of *Eriocaulon*. A. Young flower of *E. aquatile* with developing petals and showing the modifying petal apex. B. Young flower of *E. cinereum* with developing petals and showing the petal apex and raising petal margins (arrowheads). C. Detail of a developing petal of *E. aquatile* showing the dislocated petal apex and fused petal margins. D. Detail of a developing petal of *E. guyanense* showing the aborted petal apex and the petal margins. E. Detail of the developing gynoecium of *E. modestum* with carpels closing around the undeveloped septum. F. Detail of a developing sterile gynoecium of *E. guyanense* with three carpellodes and the undeveloped septum. G. Detail of developing ascidiate carpellodes of *E. sellowianum*. H. Detail of the developing carpellodes of *E. aquatile*. Abbreviations: arrowhead – petal margins, asterisk – undeveloped septum, c – carpel, cd – carpellode, gl – petal gland, is – inner stamen, os – outer stamen, pa – petal apex. Scale bars: A, C–E, G, H = 20 μ m; B, F = 10 μ m.

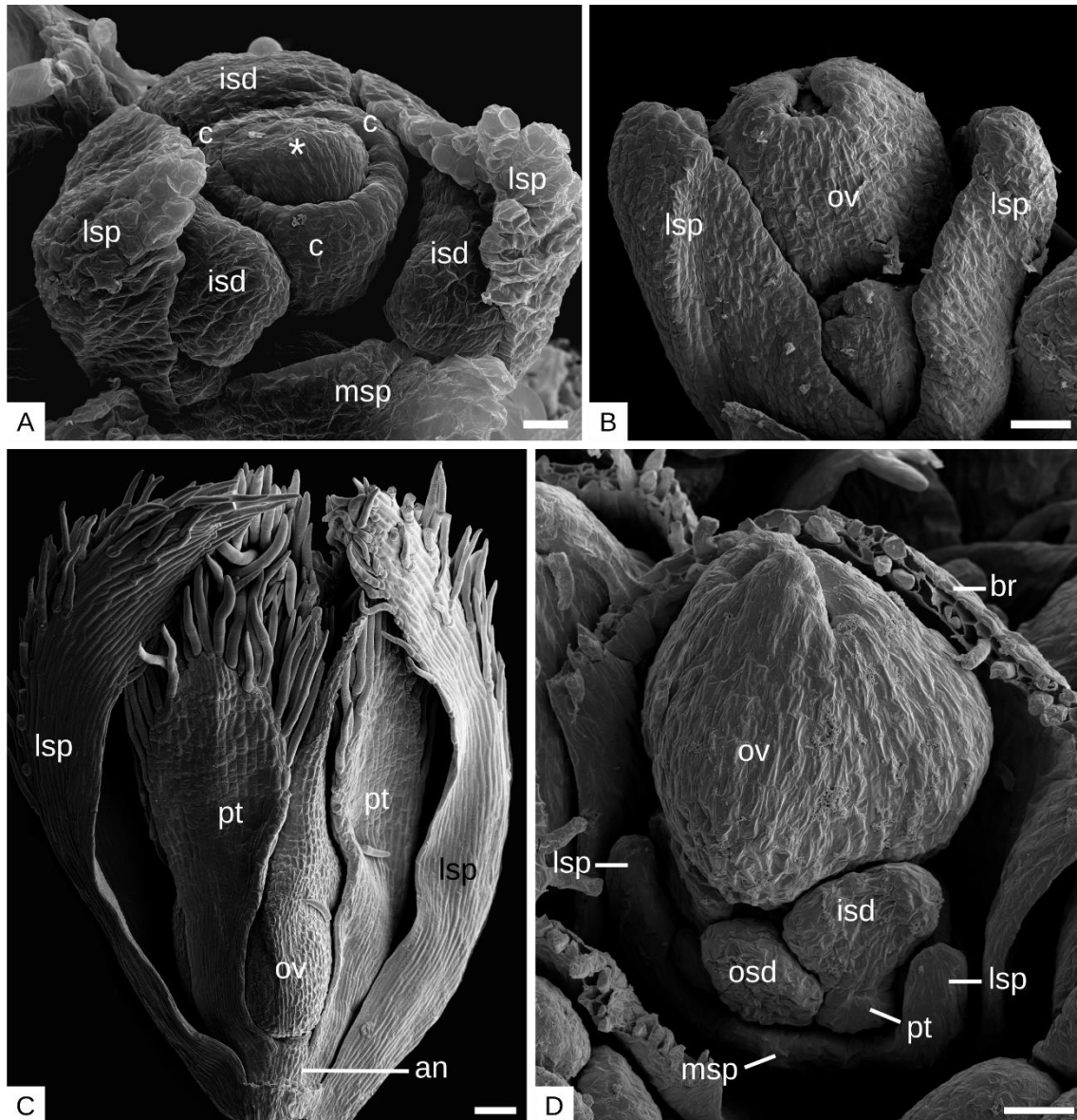


Fig. 8. Development of pistillate flowers of *Eriocaulon*. A, B. Young flowers of *E. teusczii* (A) and *E. decangulare* (B) showing developing sepals and carpels closing into the ovary. C. Young flower of *E. modestum* showing the free sepals. D. Young flower of *E. cinereum* showing developing lateral sepals, the aborted median sepal, an aborted petal and staminodes. Abbreviations: asterisk – undeveloped septum, c – carpel, isd – inner staminode, lsp – lateral sepal, msp – median sepal, osd – outer staminode, ov – ovary, pt – petal. Scale bars: A, D = 20 μ m; B = 40 μ m; C = 100 μ m.

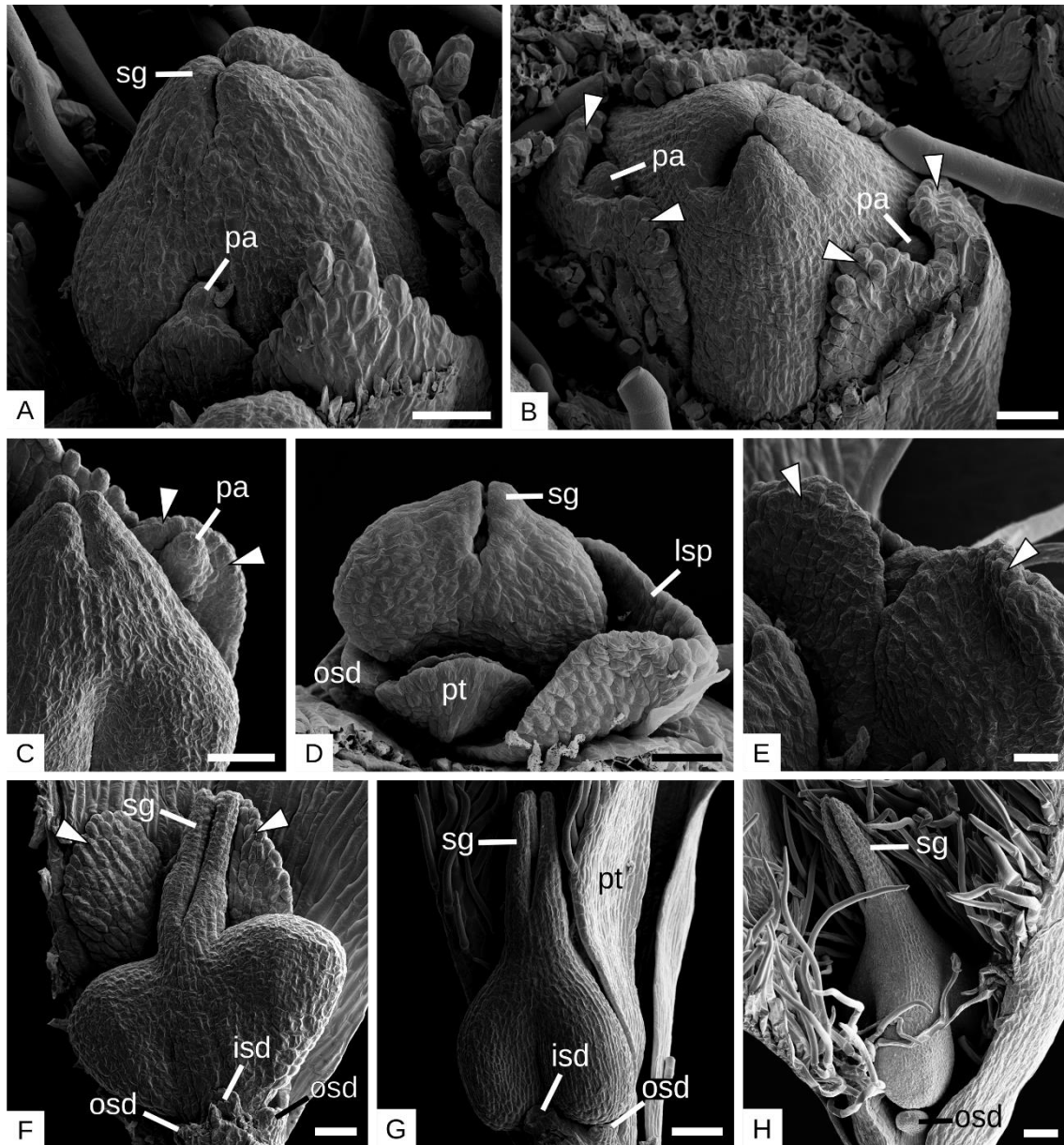


Fig. 9. Development of pistillate flowers of *Eriocaulon*. A–C. Young flowers of *E. aquatile* (A), *E. kunthii* (B), and *modestum* (C) showing successive development of petals and young stigmas. D. Young flower of *E. guyanense* showing developing petal and stigma. E. Detail of a developing petal of *E. guyanense* in frontal view. F. Young flower of *E. guyanense* showing an emarginate petal, staminodes at the base of the ovary and developing stigmas. G, H. Young flowers of *E. modestum* (G) and *E. kunthii* (H) showing staminodes at the base of the ovary and developing stigmas. Abbreviations: arrow – petal margin, isd – inner staminode, isp – lateral sepal, osd – outer staminode, pa – petal apex, pt – petal, sg – stigma. Scale bars: A, B = 40 μ m; C, F = 50 μ m; D, E = 20 μ m; H = 100 μ m.

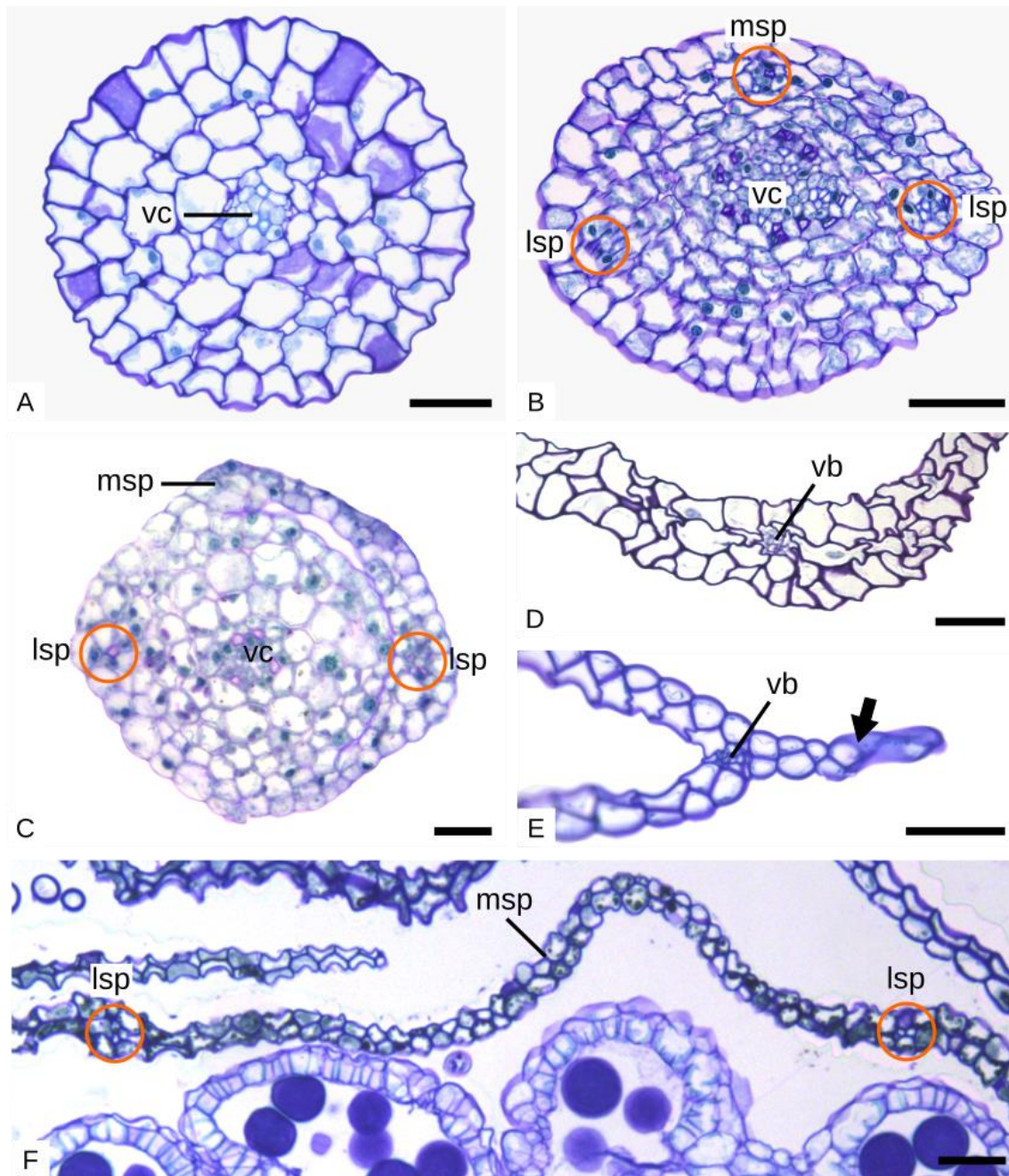


Fig. 10. Vasculature of staminate flowers of *Eriocaulon* – cross sections. A. Pedicel of *E. compressum*. B. Sepal traces of *E. modestum*. C. Sepal traces of *E. cinereum*. D. Sepal of *E. decangulare*. E. Sepal of *E. guyanense*. F. Spathaceous calyx of *E. cinereum*. Abbreviations: arrow – sepal protrusion, lsp – lateral sepal, msp – median sepal, vb – vascular bundle, vc – vascular cylinder. Scale bars: A, B, D–F = 50 μm ; C = 25 μm .

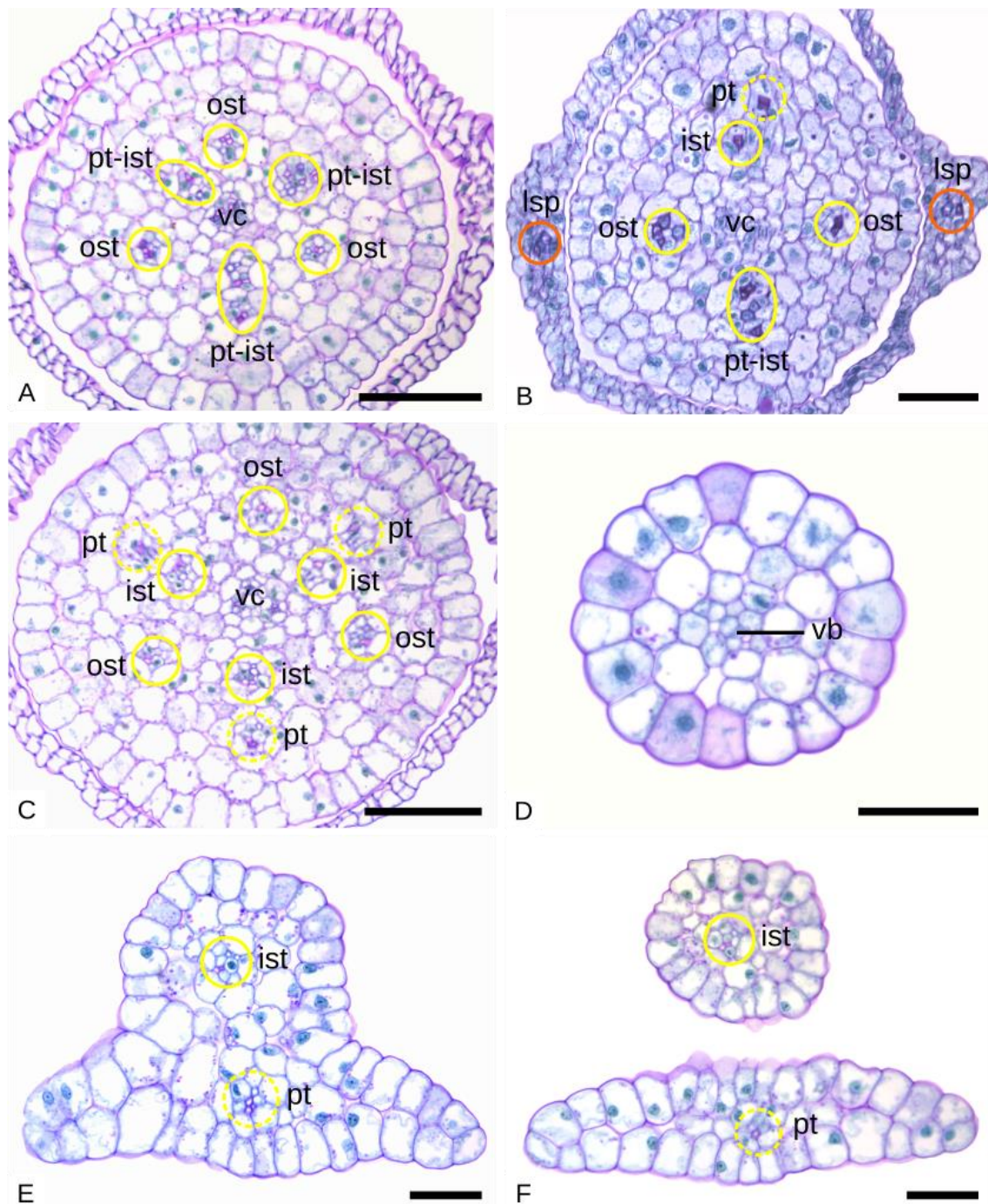


Fig. 11. Vasculature of staminate flowers of *Eriocaulon* – cross sections. A, B. Antophore of *E. teuschii* (A) and *E. decangulare* (B) showing the outer stamens traces and common petal-inner stamens traces. C. Anthophore of *E. teuschii* showing the outer stamens traces and separate traces of petals and inner stamens. D. Detail of the filament of an outer stamen of *E. teuschii* showing the vascular bundle. E, F. Inner stamen of *E. compressum* with the base of a filament adnate to a petal (E) and the same filament free at its median region (F). Abbreviation: ist – inner stamen, ost – outer stamen, pt – petal, pt-ist – common trace of a petal and inner a stamen, vb – vascular bundle, vc – vascular cylinder. Scale bars: A–F = 50 μ m.

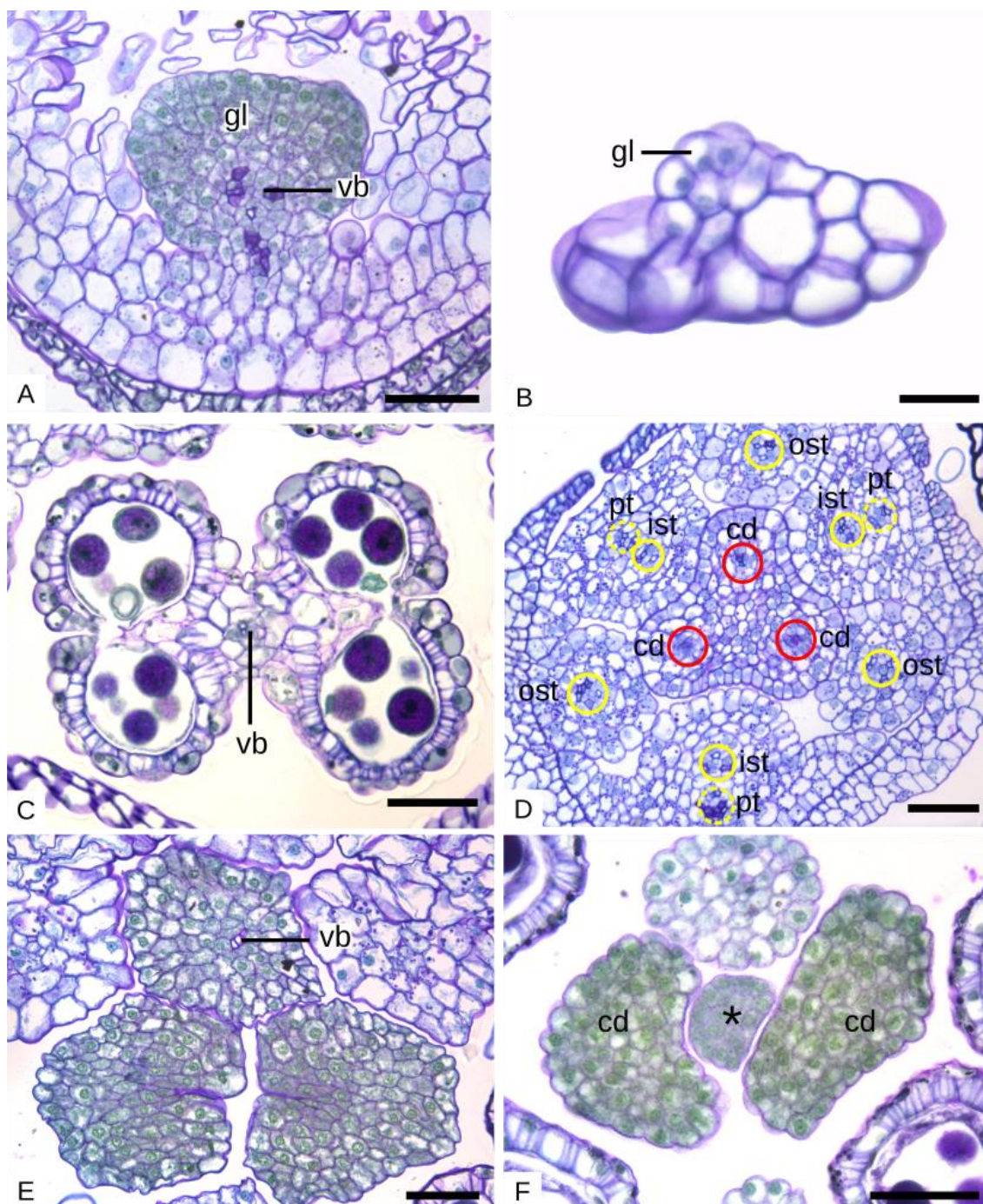


Fig. 12. Vasculature of staminate flowers of *Eriocaulon* – cross sections. A. Detail of a petal gland of *E. kunthii* showing the vascular bundle. B. Detail of a petal of *E. xeranthemoides* showing a vestigial petal gland without vasculature. C. Detail of an anther of *E. nigericum* showing the vascular bundle in the connective. D. Region above the anthophore in *E. kunthii*, showing vascular bundles of stamens and vascular bundles of the carpellodes at the stalk of the sterile gynoecium. E. Detail of a sterile gynoecium of *E. modestum* showing the median carpellode with a vascular bundle and lateral carpellodes folded inwards. F. Detail of a sterile gynoecium of *E. guyanense* showing the two carpellodes and the undeveloped septum. Abbreviations: asterisk – undeveloped septum, cd – carpellode, gl – petal gland, ist – innerstamen, ost – outer stamen, pt – petal, vb – vascular bundle. Scale bars: A, C-F = 50 μm ; B = 25 μm .

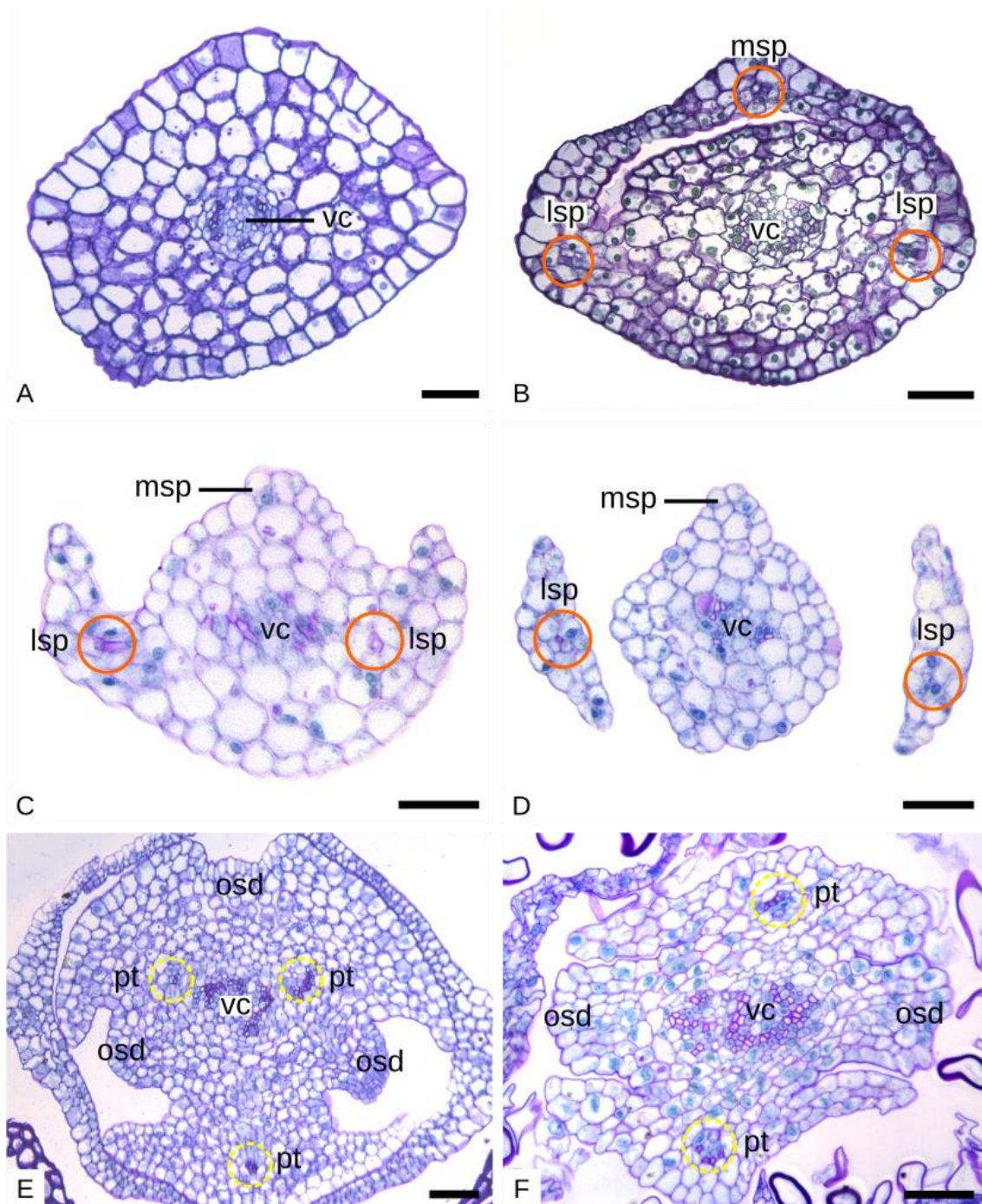


Fig. 13. Vasculature of pistillate flowers of *Eriocaulon* – cross sections. A. Pedicel of *E. kunthii*. B. Sepal traces of *E. aquatile*. C. Sepal traces of *E. cinereum*. D. Anthophore *E. cinereum* with vascular cylinder. E, F. Flower base of *E. kunthii* (E) and *E. decangulare* (F) showing the vascular traces of petals and the outer staminodes. Abbreviations: lsp – lateral sepal, msp – median sepal, osd – outer staminode, pt – petal, vc – vascular cylinder. Scale bars: A, E = 100 μ m; B = 200 μ m; C, D = 25 μ m; F = 50 μ m.

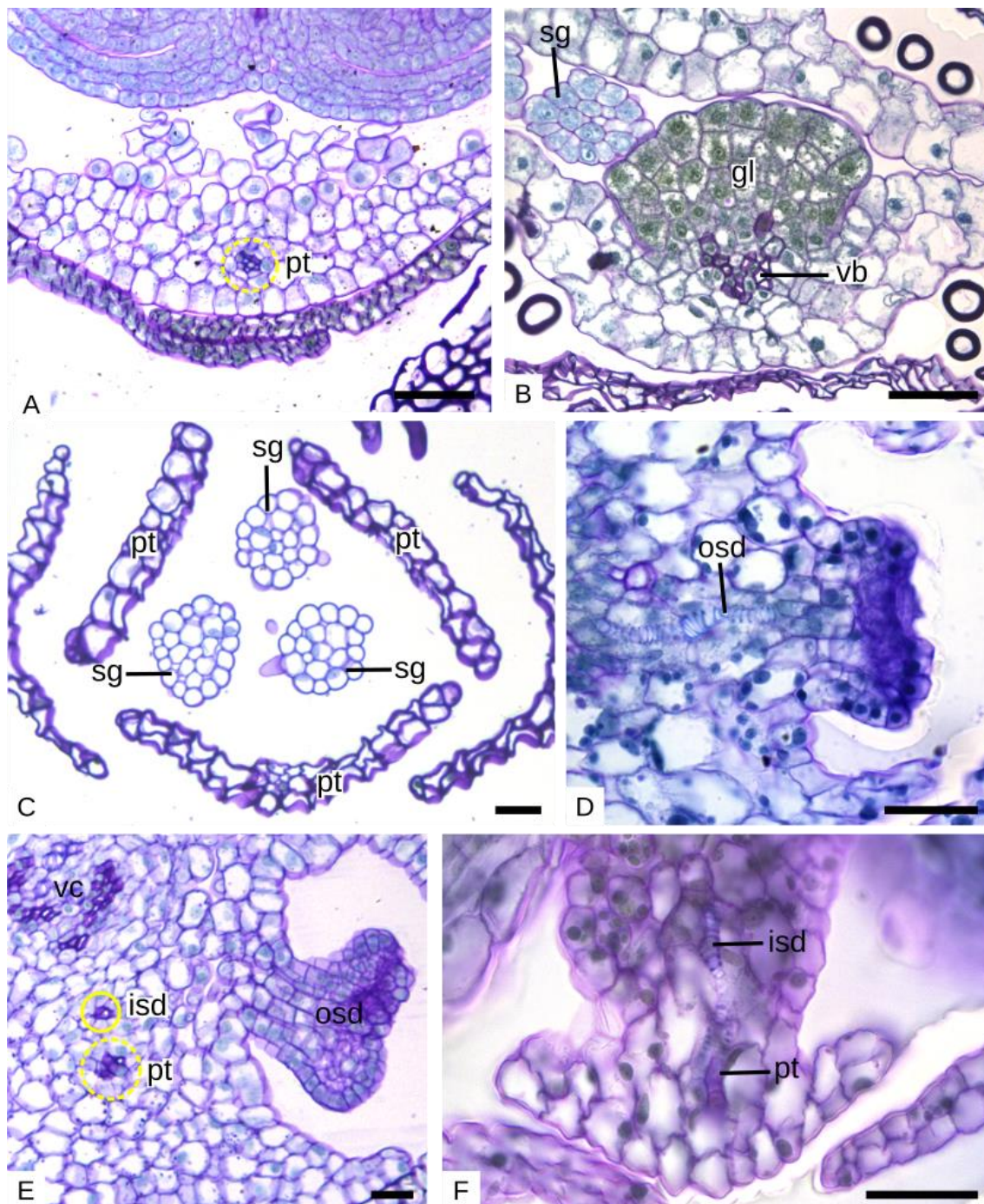


Fig. 14. Vasculature of pistillate flowers of *Eriocaulon* – cross sections. A. Detail of a petal of *E. kunthii* showing the vascular bundle. B. Detail of a petal gland of *E. decangulare* showing the vascular bundle. C. Apical region of a flower of *E. xeranthemoides* showing petals without glands and stigmas. D. Detail of a vascular trace reaching the base of an outer staminode in *E. nigericum*. E. Detail of the flower base of *E. kunthii* showing a petal trace and an inner staminode trace. F. Detail of an inner staminode trace diverging from a petal trace in *E. nigericum*. Abbreviations: gl – petal gland, isd – inner staminode, osd – outer staminode, pt – petal, sg – stigma, vb – vascular bundle, vc – vascular cylinder. Scale bars: A, B = 200 μm ; C, E = 50 μm ; D, F = 25 μm .

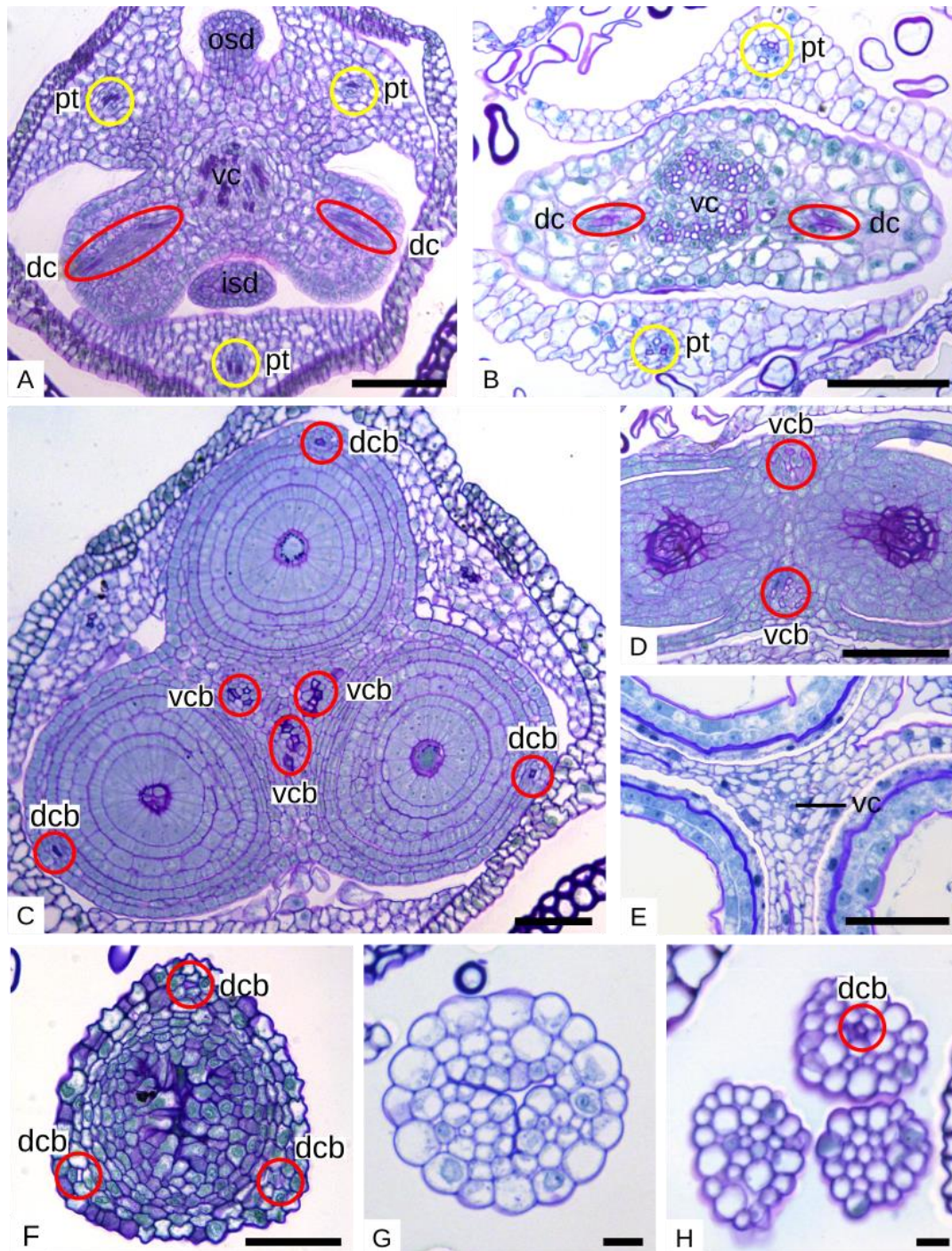


Fig. 15. Vasculature of pistillate flowers of *Eriocaulon* – cross sections. A. Ovary base of *E. kunthii* showing two out of three dorsal carpellary traces alternate to the petals (oblique section). B. Ovary base of *E. decangulare* showing the two dorsal carpellary traces alternate to the petals. C. Middle region of the ovary of *E. kunthii* showing the dorsal carpellary bundles and vascular cylinder dividing into ventral carpellary bundles. D. Distal region of the ovary of *E. decangulare* showing the two ventral carpellary bundles in commissural position. E. Middle region of the ovary of *E. tesczii* showing the undivided central vascular cylinder. F. Style of *E. modestum* showing dorsal carpellary bundles. G. Style of *E. cinereum* without vasculature. H. Stigmas of *E. xeranthemoides* showing a single vascular bundle. Abbreviations: dc – dorsal carpellary trace, dcb – dorsal carpellary bundle, isd – inner

staminode, osd – outer staminode, pt – petal, vc – central vascular cylinder, vcb – ventral carpellary bundle. Scale bars: A = 200 μ m; B, D–H = 50 μ m; E = 100 μ m.

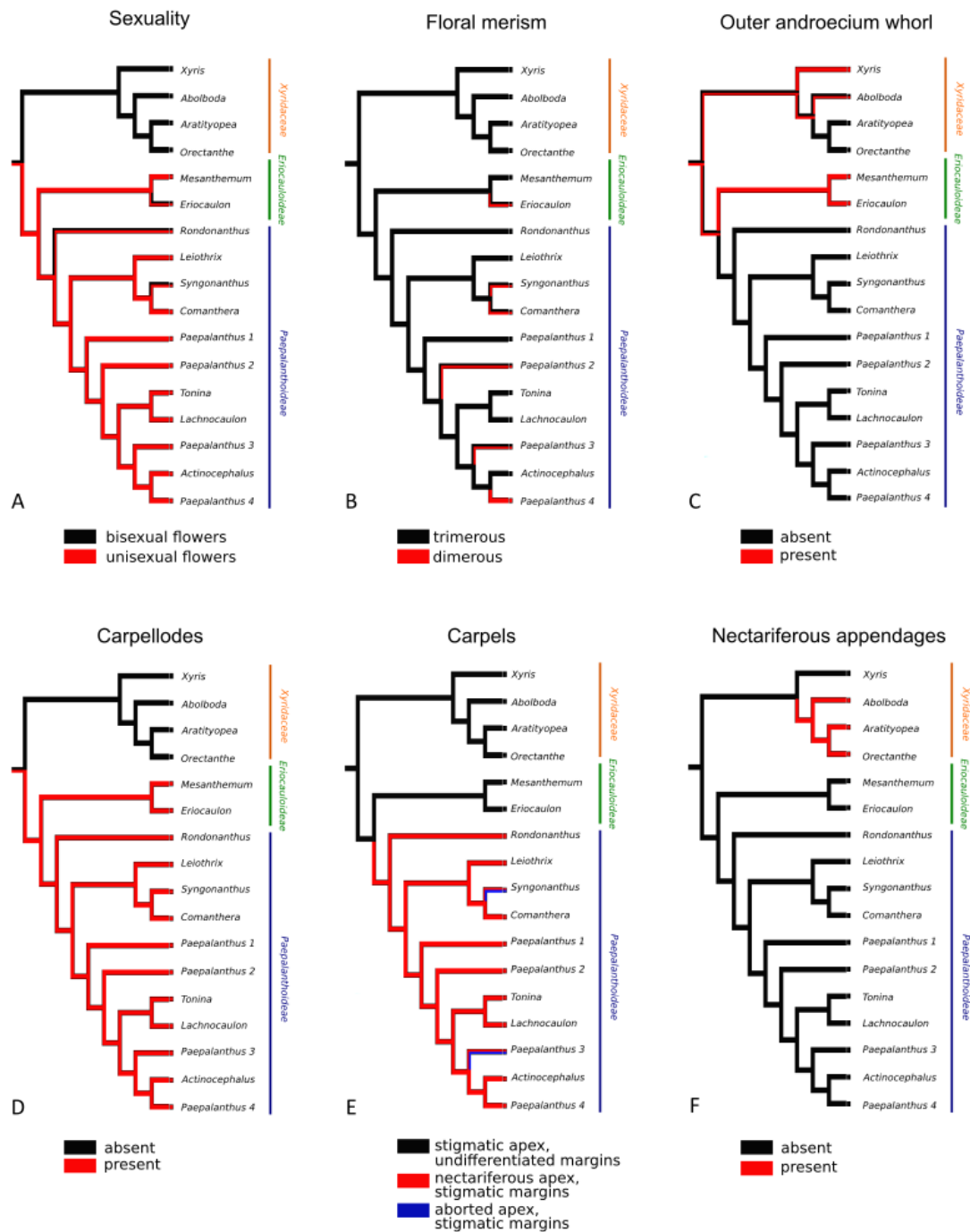


Fig. 16. Optimization of six floral characters onto a combined phylogenetic tree of the xyrids. A. Sexuality. B. Floral merism. C. Outer androecium whorl. D. Carpellodes. E. Carpels. F. Nectariferous appendages.

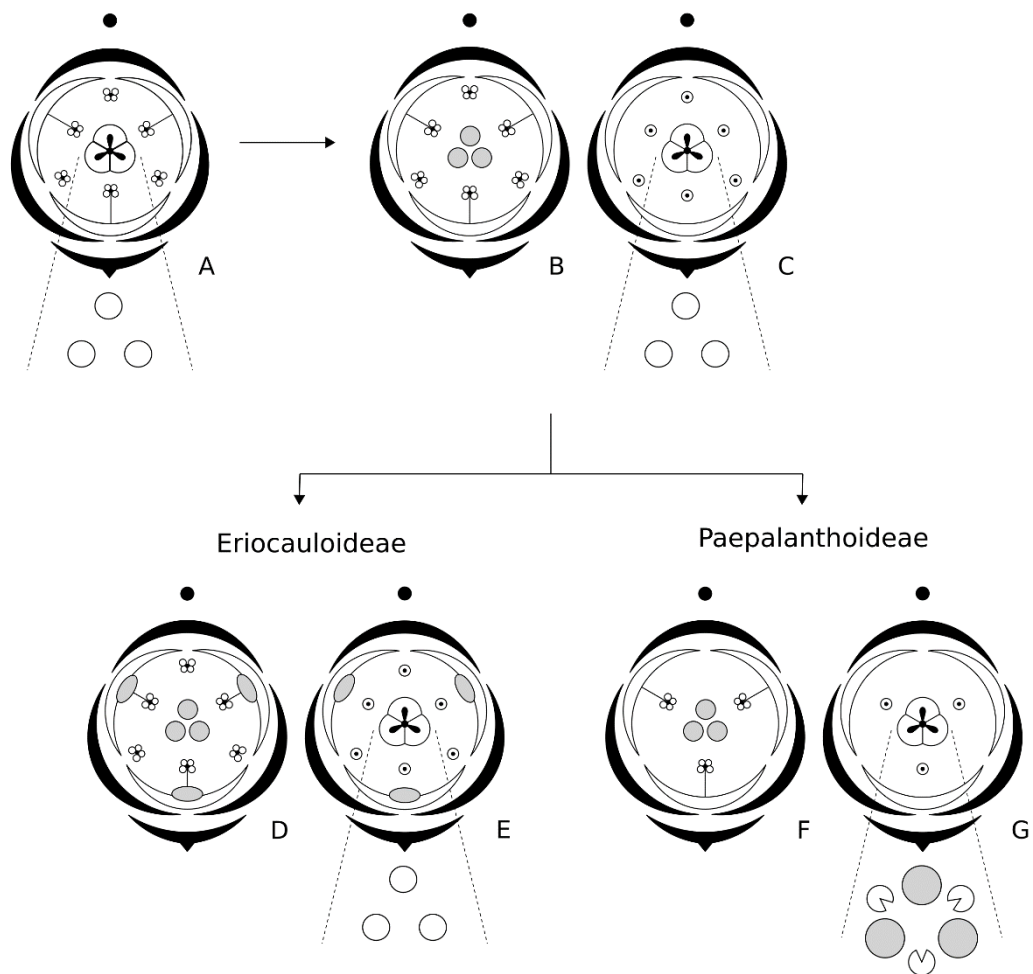


Fig. 17. Floral diagrams illustrating a hypothesis of floral evolution in Eriocaulaceae. A. Ancestor of Eriocaulaceae with bisexual flowers. B, C. Staminate (B) and pistillate (C) flowers of an intermediate ancestor. D, E. Staminate (D) and pistillate (E) flowers of Eriocauloideae. F, G. Staminate (F) and Pistillate (G) flowers of Paepalanthoideae.

APPENDIX 1

Morphological matrix with morphological characters and their respective states. (1) Sexuality: 0 bisexual flowers, unisexual flowers; (2) floral merism: 0 trimerous, 1 dimerous; (3) outer androecium whorl: 0 absent, 1 present; (4) carpelloses: 0 absent, 1 present; (5) carpels: 0 stigmatic apex and undifferentiated margins, 1 nectariferous apex and stigmatic margins, 2 aborted apex and stigmatic margins; (6) nectariferous appendages: 0 absent, 1 present.

Taxa/character	1	2	3	4	5	6
<i>Xyris</i>	0	0	1	0	0	0
<i>Abolboda</i>	0	0	0/1	0	0	1
<i>Aratitiyopea</i>	0	0	0	0	0	1
<i>Orectanthe</i>	0	0	0	0	0	1
<i>Mesanthemum</i>	1	0	1	1	0	0
<i>Eriocaulon</i>	0/1	0/1	1	1	0	0
<i>Rondonanthus</i>	0/1	0	0	1	1	0
<i>Leiothrix</i>	1	0	0	1	1	0
<i>Syngonanthus</i>	0/1	0/1	0	1	1/2	0
<i>Comanthera</i>	1	0/1	0	1	1	0
<i>Tonina</i>	1	0	0	1	1	0
<i>Lachnocaulon</i>	1	0	0	1	1	0
<i>Actinocephalus</i>	1	0	0	1	1	0
<i>Paepalanthus</i> 1	1	0	0	1	1	0
<i>Paepalanthus</i> 2	1	0/1	0	1	1	0
<i>Paepalanthus</i> 3	1	0/1	0	1	1/2	0
<i>Paepalanthus</i> 4	1	1	0	1	1	0

CONSIDERAÇÕES FINAIS

A presente tese contribui para o conhecimento da morfologia, da anatomia, do desenvolvimento e da vascularização floral de Eriocaulaceae. Além disso, a comparação dos dados florais de Eriocauloideae presentes neste trabalho com aqueles disponíveis na literatura para Paepalanthoideae e Xyridaceae permitem discutir o valor taxonômico e evolutivo dos caracteres florais.

A estrutura floral de *Mesanthemum radicans* é congruente com o já reportado para a subfamília Eriocauloideae. Contudo, dados florais inéditos são apresentados, especialmente relacionados à vascularização, como a presença de pétalas com três feixes vasculares e estigmas sem vascularização. Além disso, a vascularização do gineceu ilustra diferentes graus de fusão dos carpelos nas flores pistiladas.

Do ponto de vista evolutivo, a morfologia floral de *Mesanthemum* sugere que o arranjo congestionado das peças florais no gênero restringe a fusão total das pétalas das flores pistiladas, que permanecem com as bases livres, e o desenvolvimento do verticilo externo de estames, que é mais curto que o verticilo interno. Possivelmente, a presença de estames externos mais curtos seja um passo intermediário em direção à perda deste verticilo em Paepalanthoideae.

A comparação do desenvolvimento floral de Eriocauloideae e Paepalanthoideae e a otimização de caracteres morfológicos mostram que as estruturas nectaríferas de Eriocaulaceae—glândulas das pétalas, carpelódios e ramos nectaríferos—surgiram independentemente. Além disso, as espécies de *Eriocaulon* possuem estames externos mais curtos que os internos, semelhante ao observado em *Mesanthemum*, e que surgem após os estames internos em algumas flores. Esses dados corroboram a hipótese levantada

no primeiro capítulo de que a presença de dois verticilos de estames é um estado de caráter plesiomórfico.

Por fim, é apresentada uma hipótese de evolução floral para Eriocaulaceae com base nos dados apresentados na tese para Eriocauloideae e no que havia sido discutido em estudos previamente em Eriocaulaceae e Xyridaceae. O ancestral de Eriocaulaceae provavelmente possuía flores bissexuadas com dois verticilos de estames e gineceu com estigma dorsal. O primeiro passo evolutivo foi o surgimento da unissexualidade, que resultou na modificação do gineceu estéril em carpelódios nectaríferos, nas flores estaminadas, e ao surgimento de estaminódios, nas flores pistiladas. Em seguida, em Eriocauloideae, surgiram glândulas nectaríferas nas pétalas. Em Paepalanthoideae, o verticilo externo de estames foi perdido, e os ramos nectaríferos dorsais surgiram concomitantemente aos ramos estigmáticos comissurais.

Apêndice I: Comparative floral morphology and anatomy of Thurniaceae, an early-diverging family in the cyperids (Poales, Monocotyledons)

Artigo publicado como primeiro autor no periódico *Plant Systematics and Evolution*:

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ORIGINAL ARTICLE



Comparative floral morphology and anatomy of Thurniaceae, an early-diverging family in the cyperids (Poales, Monocotyledons)

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Abstract

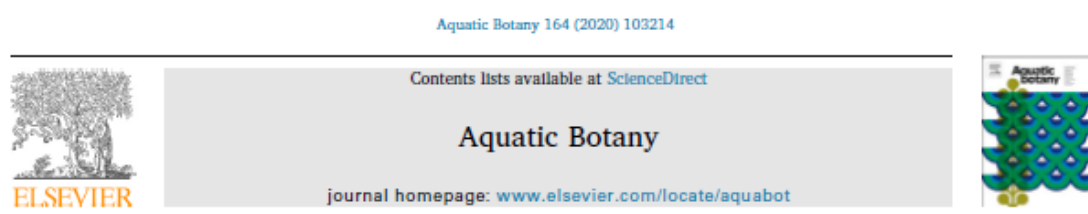
Thurniaceae are positioned at the base of the cyperids, in Poales, as a sister group of Cyperaceae + Juncaceae. However, Rapateaceae + Mayacaceae have emerged related to these families in a recent phylogenetic study. Although Thurniaceae are morphologically similar to Juncaceae, studies are needed to evaluate characters with systematic value and that may help comprehend the reproductive biology in the family. In this regard, we investigate the floral morphology and anatomy of *Prionium serratum* and *Thurnia sphaerocephala* using standard techniques of scanning electron microscopy and light microscopy. The flowers of both species are trimerous, pentacyclic, with diplostemonous androecium and tricarpellate syncarpous gynoecium. Nevertheless, dimerous flowers with an inconsistent number of stamens also occur in *T. sphaerocephala*. Most floral traits of Thurniaceae are shared with Juncaceae and indicate putative plesiomorphies in the cyperids. However, no consistent data corroborates a link between Rapateaceae and Mayacaceae and the cyperids. The perigonium of Thurniaceae has diagnostic characters for the family, but also for each one of the species studied. The androecium is similar in *P. serratum* and *T. sphaerocephala*. In the gynoecium, the number of ovules, the length of the ovary zones, and the occurrence of ovary wall intrusions distinguish *P. serratum* from *T. sphaerocephala* and may have a correlation in the cyperids. Furthermore, the type of inflorescence, the color of flowers, and the type of stigma suggest that *P. serratum* is wind-pollinated and that *T. sphaerocephala* is insect-pollinated.

Keywords Dimery · Floral biology · Floral structure · Gynoecium · *Prionium* · *Thurnia*

Apêndice II: Morphological and anatomical plasticity of a rare amphibious species of Eriocaulaceae (Poales, Monocotyledons)

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Morphological and anatomical plasticity of a rare amphibious species of Eriocaulaceae (Poales, Monocotyledons)

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ABSTRACT

Phenotypic plasticity is common in aquatic monocots, but is sometimes mistaken with heteroblasty. In Eriocaulaceae, aquatic and amphibious species may present interesting adaptive morphological features. However, *Paepalanthus saxicola* var. *pilosus* is unusual by having two leaf morphotypes and scapes that can be partially submerged or completely exposed. This taxon also presents an uncertain identity due to its incomplete morphological description. Here, we studied the morphology and anatomy of both leaf morphotypes and of scapes of *P. saxicola* var. *pilosus* to understand if the morphological differences in leaves correspond to phenotypic plasticity or heteroblasty; and the ecological and systematic significance of its leaves and scapes. Besides, we describe its morphology to evaluate its identity. The short curved leaves show supporting tissue and three vascular bundles, while the long filiform ones lack supporting tissue and have a single vascular bundle. All specimens share anatomical characteristics of scape. We raised this taxon to the species level, giving it a replacing name, *Paepalanthus amphibius*. We observed that *P. amphibius* is the first confirmed report of heterophylly in Eriocaulaceae. The anatomy of its short leaves and scapes reflects adaptations to a xeric environment, while the anatomy of the long leaves shows characteristics adapted to an aquatic habit. Possibly, such degree of plasticity is underreported in the family, so we stress the importance of seasonal studies to understand the morphology and taxonomy of the amphibious species.

Apêndice III: Taxonomic and morphological notes on a tiny new species of *Paepalanthus* (Eriocaulaceae) from central Brazil

Artigo publicado como coautor no periódico *Phytotaxa*:

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Article



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Taxonomic and morphological notes on a tiny new species of *Paepalanthus* (Eriocaulaceae) from central Brazil

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Abstract

We describe and illustrate *Paepalanthus campanulatus*, a new species of Eriocaulaceae from the Chapada dos Veadeiros National Park (Goiás, Brazil). The species is known from a single population with many individuals growing under rocks and in small caves, sometimes upside down attached to the top of the cave. The new species is mainly distinguished by its usually tiny, unbranched stem bearing a fasciculate inflorescence composed of mostly glabrous, campanulate capitula surrounded by whitish hyaline involucre bracts. Due to its very restricted distribution, the species may be considered endangered. It is compared with *Paepalanthus albidus* and *P. subtilis*, the morphologically most similar species. We provide details on the leaf and scape anatomy of these species, as well as comments on the distribution, habitat, ecology, and morphological variation, along with line drawings and photos of the new species.

Keywords: Anatomy, Chapada dos Veadeiros National Park, Endemism, Goiás, Paepalanthoideae

Apêndice IV: Root, rhizome and scape anatomy of Amazonian species of *Mapania* Aubl. (Mapanioideae, Cyperaceae) and its taxonomic and ecological significance

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RESEARCH PAPER

Root, rhizome and scape anatomy of Amazonian species of *Mapania* Aubl. (Mapanioideae, Cyperaceae) and its taxonomic and ecological significance

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Cyperaceae are a cosmopolitan Monocot family comprising about 5,700 species divided into two subfamilies: Cyperoideae and Mapanioideae. Within Mapanioideae, *Mapania* is the largest genus, with about 90 species. Anatomical studies on Mapanioideae are of great importance but still scarce. Here, the anatomy of roots, rhizomes and scapes of five Amazonian species of *Mapania* is studied. The species have two types of roots, which differ anatomically: thick roots, serving mainly for fixing, and thin ones, mainly for nutrient absorption. Rhizomes show a uniform anatomical pattern, with amyloplasts and phenolic idioblasts in the cortex and in the vascular cylinder, without aerenchyma. In this organ, the collateral vascular bundles are similar to those found in *Hypolytrum*, a genus closely related to *Mapania* within Mapanioideae, suggesting that this feature may be diagnostic for the tribe Hypolytreae. The scape anatomy of the species is taxonomically important at species level but does not corroborate precisely the infrageneric classification of the genus. Finally, the aerenchyma found in roots and scapes is an adaptive character state for a humid forest environment. This work contributes valuable information for the anatomical characterization of vegetative organs of *Mapania* and discusses its taxonomic and ecological relevance.

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Keywords:

Hypolytreae, *M. sect. Mapania*, *M. sect. Mapaniopsis*, *M. sect. Pycnocephala*, Poales

Apêndice V: *Paepalanthus modestus* (Eriocaulaceae), a new dimerous species from Goiás, Brazil, with notes on leaf and scape anatomy

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***Paepalanthus modestus* (Eriocaulaceae), a new dimerous species from Goiás, Brazil, with notes on leaf and scape anatomy**

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Abstract

Paepalanthus modestus, a new species of Eriocaulaceae with dimerous flowers, is described and illustrated. The species is placed in *P.* [unranked] *Dimeri* based on floral and vegetative characters. A detailed comparison with *P. harleyi* and *P. oxyphyllus* is given. The hemispherical mature capitula, the relatively short involucral bracts slightly surpassing the floral disc, and the vestiture of leaves, scapes, and floral parts distinguish *P. modestus*. Large populations of the species occur on rocky soils in the municipalities of Alto Paraíso de Goiás and Teresina de Goiás, Brazil. Some of these populations were found in Chapada dos Veadeiros National Park, and the species is considered endangered according to the IUCN criteria. Anatomical details of leaves and scapes, along with photos and comments on etymology, morphological variation, and ecological aspects related to fire tolerance are provided.

Keywords: Central Brazil, Poales, Paepalanthoideae, Taxonomy, Endemism