ANDRODECIDUA ENDRESSII GEN. ET SP. NOV., FROM THE LATE CRETACEOUS OF GEORGIA (UNITED STATES): FURTHER FLORAL DIVERSITY IN HAMAMELIDOIDEAE (HAMAMELIDACEAE)

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The early history of Hamamelidaceae is currently documented by several reproductive structures from Late Cretaceous sediments of the Northern Hemisphere. Recently discovered floral remains from the late Santonian (Late Cretaceous) Allon locality, in central Georgia (United States), represent an additional extinct taxon, *Androdecidua endressii* gen. et sp. nov., which documents further floral diversity within Hamamelidaceae. The remains of *A. endressii* comprise the androecium and corolla of a whorled, pentamerous, and actinomorphic flower. Calyx and gynoecium are unknown. The androecium consists of 10 stamens arranged in two alternating whorls of five, with the stamen filaments fused at their bases. The five petals are fusiform and slightly dorsiventrally flattened. They are opposite and basally fused to the filament bases of the inner whorl of stamens. The stamens and petals detach as a unit from the floral receptacle. The stamens have distinct filament and anther and a prominent apical extension of the anther connective. Filaments are massive, broad, and nearly parallel-sided. Anthers are short and abaxially rounded, but radially elongate. The long apical extension of the connective is flattened and directed toward the center of the flower, where the connective extensions of the 10 stamens converge to form a low conical peak. Stamens of the outer whorl have bithecal and bisporangiate anthers in which the adaxial pollen sac of each theca is missing. Thecal dehiscence is through a single valve. Stamens of the inner whorl have bithecal and tetrasporangiate anthers that dehisce through two valves. Pollen grains are spheroidal and tricolpate, with a coarse and moderately heterobrochate exine reticulum and a line of gemmae on the aperture membrane. The presence of a long apical extension of the connective and the valvate anther dehiscence indicate the affinity of *A. endressii* with the genera of subtribe Loropetalinae (Hamamelideae; Hamamelidaceae). The level of synorganization of the corolla and androecium and the presence of two structural types of anthers are characters previously unknown among Hamamelidaceae.

Keywords: fossil, floral morphology, floral groundplan, calyx, corolla, androecium, core eudicots, basal eudicots, Saxifragales, hamamelids, systematics, paleobotany.

Introduction

Ongoing studies of three-dimensional, charcoalified flowers, recovered from Cretaceous sediments, have significantly amplified both the geological range and morphological diversity of several angiosperm families, including Chloranthaceae (e.g., Pedersen et al. 1991), Laurales s.l. (Drinnan et al. 1990; Friis et al. 1994), Platanaceae (Friis et al. 1988; Crane et al. 1993; Magallón et al. 1997), Buxaceae (Drinnan et al. 1991), Fagales s.l. (Herendeen et al. 1995; Sims et al. 1998), and other "higher hamamelids" (e.g., Friis 1983; Sims et al. 1999). These studies have contributed significantly toward a better understanding of the evolution of particular angiosperm lineages.

Recently, the known floral diversity of Hamamelidaceae has been increased by the recognition of floral remains from the Late Cretaceous, including *Archamamelis*, from the late Santonian to early Campanian of Sweden (Endress and Friis 1991), and

Allonia, from the late Santonian of Georgia (United States) (Magallón et al. 1996). Newly discovered floral remains from late Santonian sediments of the Allon locality, in central Georgia, represent an extinct taxon with features indicating an affinity with subfamily Hamamelidoideae (Hamamelidaceae). Detailed comparisons reveal substantial similarities with genera of tribe Hamamelideae, particularly with those of subtribe Loropetalinae. Nevertheless, in other features, and in its combination of floral characters, this extinct taxon is unique and displays a level of floral synorganization previously unknown among extant and extinct Hamamelidaceae.

The most recent formal suprageneric classification for Hamamelidaceae was presented by Endress (1989*c*; table 1). This system is a modification of the treatment by Harms (1930) and by Schulze-Menz (1964), and it integrates new infrafamilial taxa described by Chang (1973). Four subfamilies are recognized: Hamamelidoideae, Exbucklandioideae, Rhodoleioideae, and Altingioideae.

Hamamelidoideae is the largest subfamily. Its circumscription coincides substantially with that of Harms (1930) and Schulze-Menz (1964) but also includes more recently discov-

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Table 1

Suprageneric Classification of Hamamelidaceae according to Endress (1989c)

Taxon	No. of species	Geographical distribution
Family Hamamelidaceae R. Br.:		
Subfamily Hamamelidoideae Reinsch:		
Tribe Hamamelideae A. DC.:		
Subtribe Hamamelidinae Endress:		
Hamamelis L.	ca. 5	China, Japan, E North America
Subtribe Loropetalinae Endress:		
Loropetalum R. Br. ex Reichb.	2–3	India, China
Tetrathyrium Benth.	1	Hong Kong
Maingaya Oliv.	1	Malayan Peninsula
Embolanthera Merr.	2	Philippines, Tonkin
Subtribe Dicoryphinae Endress:		
Dicoryphe Du Petit-Thouars	10–22	Madagascar and Comores
Trichocladus Pers.	ca. 4	Tropical E Africa, S Africa
Ostrearia Baill.	1	NE Queensland
Neostrearia L.S. Smith	1	NE Queensland
Noahdendron Endress, Hyland & Tracey	1	NE Queensland
Tribe Corylopsideae Harms:		
Corylopsis Sieb. & Zucc.	7–20	Assam to Japan
Tribe Eustigmateae Harms:		
Eustigma Gardn. & Champ.	2	Hong Kong, Taiwan, Tonkin
Fortunearia Rehd. Wils.	1	Central and E China
Sinowilsonia Hemsl.	1	Central China
Tribe Fothergilleae A. DC.:		
Molinadendron Endress	3	Costa Rica to NW Mexico
Fothergilla Murray in L.	2	E North America
Parrotiopsis Schneider	1	NW Himalaya
Parrotia C.A. Mey.	1	Caspian Sea region and Caucasus
Sycopsis Oliv.	2–3	Assam, China, Taiwan
Distyliopsis Endress	6	S China, Taiwan, Malesia to New Guinea
Distylium Sieb. & Zucc.	10–18	Japan, SE Asia, Malesia
Matudaea Lundell	2	Honduras to central Mexico
Shaniodendron Deng et al.	1	China
Subfamily Exbucklandioideae Reinsch:		
Disanthus Maxim.	1	E China, Japan
Mytilaria Lecomte	1	Kwangsi (China) and Laos
Chunia H.-T. Chang	1	Hainan
Exbucklandia R.W. Br.	2–4	E Asia, Malesia
Subfamily Rhodoleioideae Reinsch:		
Rhodoleia Champ.	1–10	E Asia, Malesia
Subfamily Altingioideae Reinsch:		
Liquidambar L.	ca. 5	E Asia, Mediterranean region, SE North America to Central America
Altingia Nor.	ca. 8	E Asia and Malesia
Semiliquidambar H.-T. Chang	ca. 3	E China, Hainan

Note.   Species diversity and geographical distribution after Endress (1993).

ered genera (Endress 1969, 1970; Endress et al. 1985; Deng et al. 1992). Endress (1989c) introduced substantial rearrangements within the subfamily by recognizing four tribes (Hamamelideae, Corylopsideae, Eustigmateae, and Fothergilleae; table 1) and by subdividing tribe Hamamelideae into three subtribes (Hamamelidinae, Loropetalinae, and Dicoryphinae; table 1).

Exbucklandioideae was modified by Endress (1989c) to include, in addition to the genus *Exbucklandia*, the former subfamilies Disanthoideae (including *Disanthus*) and Mytilarioideae (including *Mytilaria* and *Chunia*). Rhodoleioideae includes the single genus *Rhodoleia*. Altingioideae is equivalent to Liq-

uidambaroideae *sensu* Harms, except in including *Semiliquidambar* (Chang 1973), and is considered morphologically divergent with respect to other members of the family.

Monophyly and Phylogenetic Placement

Whereas traditional taxonomic studies have considered Hamamelidaceae to be transitional between the "lower hamamelids" (e.g., Cercidiphyllaceae, Daphniphyllaceae, Trochodendraceae) and the "higher hamamelids" (i.e., the Amentiferae, including Fagales, Juglandales, Myricales [Takhtajan 1969], or related "lower" rosid taxa [Endress 1993]), results of higher-level phy-

logenetic analyses based on molecular sequence data have unambiguously placed Hamamelidaceae in the saxifragalean clade, within the core eudicots (e.g., Chase et al. 1993; Soltis et al. 1997, 2000; Qiu et al. 1998; Hoot et al. 1999; Savolainen et al. 2000). In addition to Hamamelidaceae, this clade includes the "lower hamamelid" genera *Cercidiphyllum* and *Daphniphyllum*, the Saxifragaceae s. str. (equivalent to Saxifragoideae of Harms 1930 and Schulze-Menz 1964), several saxifragoid genera, *Paeonia*, Haloragaceae, and Crassulaceae.

Although placement of Hamamelidaceae within the saxifragalean clade is consistently supported, the monophyly of the family has not been confirmed. On the contrary, all available higher-level phylogenetic studies indicate that Hamamelidaceae is paraphyletic. Altingioideae represents a unit that is distinct and independent from Hamamelidoideae (e.g., Chase et al. 1993; Soltis et al. 1997, 2000; Qiu et al. 1998; Hoot et al. 1999; Savolainen et al. 2000), whereas those members of Exbucklandioideae sampled so far, as well as *Rhodoleia*, tend to group with Hamamelidoideae. A consistent and usually strongly supported result is the placement of *Disanthus* (Exbucklandioideae) as the sister taxon to Hamamelidoideae (e.g., Hoot et al. 1999 [combined *rbcL*, *atpB*, and 18S tree]; Savolainen et al. 2000 [combined *rbcL* and *atpB* tree]).

Cretaceous Representatives

The fossil record of Hamamelidaceae extends to the Late Cretaceous. Some of its oldest representatives are floral remains of three different fossil taxa from Coniacian-Santonian strata of Georgia (Upatoi Creek locality; Crane and Herendeen 1996). These are (1) partially epigynous flowers with a bicarpellate and basally syncarpous gynoecium with moderately long and apically divergent styles, which resemble some epigynous genera of Fothergilleae (e.g., *Sycopsis*) or some species of *Corylopsis* (e.g., *Corylopsis veitchiana*); (2) a tiny fragment of an infructescence with closely spaced, dehisced capsules, very similar to *Liquidambar*; and (3) a spheroidal infructescence with crowded fruits, reminiscent of Altingioideae. These fossils await formal description, but spheroidal altingioid infructescences very similar to those from Upatoi Creek are also found in the slightly younger Allon locality and were illustrated and preliminarily described by Herendeen et al. (1999, fig. 16, "Taxon 19, Capitate infructescence, cf. Hamamelidaceae subfamily Altingioideae"). Similar altingioid infructescences, as well as a different type of clustered flowers from Turonian sediments of New Jersey, have been preliminarily reported (Borgardt et al. 2000). The affinity of presumed hamamelidaceous flowers from Turonian sediments (Crepet et al. 1992) has been discussed in detail elsewhere (Magallón et al. 1997).

Cretaceous fossil flowers with a probable affinity with subfamily Hamamelidoideae are three-dimensional, lignitized or fusainized flowers of *Allonia decandra*, from the late Santonian Allon locality of Georgia (Magallón et al. 1996) and *Archamamelis bivalvis*, from the late Santonian to early Campanian Höganäs quarry in Scania, Sweden (Endress and Friis 1991). *Allonia decandra* has pentamerous, probably bisexual flowers, with distinct calyx and corolla. Petals are narrow, parallel margined, and ribbon-like. The androecium is formed by 10 stamens arranged in two alternating whorls of five, and each stamen is characterized by an extremely long connective ex-

tension. The failure to find carpels in the single known complete fossil flower may be the result of pronounced protandry. Phylogenetic analysis based on floral characters placed *Allonia* within Loropetalinae, as sister to the extant genus *Maingaya* (Magallón et al. 1996).

Archamamelis bivalvis (Endress and Friis 1991) has six- or seven-merous flowers, except for the gynoecium, which is trimerous. The perianth is differentiated into calyx and corolla, and a whorl of stamens alternates with the petals. Each stamen has only two pollen sacs, corresponding to the adaxial sac of each theca (figs. 7–10, 13, 14 in Endress and Friis 1991). Lobed structures arranged in a whorl internal to, and alternating with, the stamens may represent staminodes, or the lobes of a (nectariferous) disk. Apparently, each carpel contains two ovules. Endress and Friis (1991) considered *Archamamelis* to be most similar to *Hamamelis*, especially with regard to the structurally and morphologically similar bithecal anthers. Nevertheless, they point out that the fossil flower may represent a separate phylogenetic line within Hamamelidales.

In this article, we describe *Androdecidua endressii* gen. et sp. nov., a fossil taxon based on floral remains, and compare it in detail with living and fossil Hamamelidaceae, particularly with members of Hamamelidoideae. A subsequent article will provide a phylogenetic analysis based on characters of floral form, in which the relationships within Hamamelidoideae and the phylogenetic placement of *Androdecidua*, *Allonia*, and *Archamameli*s are addressed (Magallón 2000; S. Magallón, unpublished manuscript).

Material and Methods

The fossil floral remains were discovered among charcoalified plant organs that comprise the abundant mesofossil flora of the Allon locality, in central Georgia (United States). The mesofossils occur in a microlaminated, carbonaceous clay lens of the Buffalo Creek Member of the Gaillard Formation (Huddlestun and Hetrick 1991). The age of the sediments is late Santonian, according to biostratigraphic correlation of palynomorphs (R. A. Christopher, unpublished data, in Herendeen et al. 1999). The Allon locality represents a single site of deposition, probably a floodplain pond (Herendeen et al. 1999; R. Lupia, personal communication, 1999). Its diverse fossil plant assemblage includes bryophytes, ferns, conifers, and angiosperms exquisitely preserved as three-dimensional lignitic or fusainized mesofossils. In addition to the mesofossils, the Allon locality contains a macrofossil assemblage mostly of leaf impressions (Herendeen et al. 1999) and a microfossil assemblage that includes a diverse palynoflora (R. Lupia, unpublished data). Fossil taxa from the Allon flora that have been studied in detail include capsules and gametophytes of Polytrichaceae and Dicranaceae (Konopka et al. 1997, 1998), flowers of Hamamelidaceae (Magallón et al. 1996), flowers and associated reproductive structures of Fagaceae s.l. (Herendeen et al. 1995; Sims et al. 1998), flowers with Normapolles pollen grains (Sims et al. 1999), and flowers of Actinidiaceae (Keller et al. 1996).

Mesofossils were isolated from clay samples by bulk sieving in water. Samples were rinsed through a coarse-mesh sieve to eliminate the bulk of the clay sediments, soaked in a detergent solution to dissolve remaining lumps of clay, and then rinsed
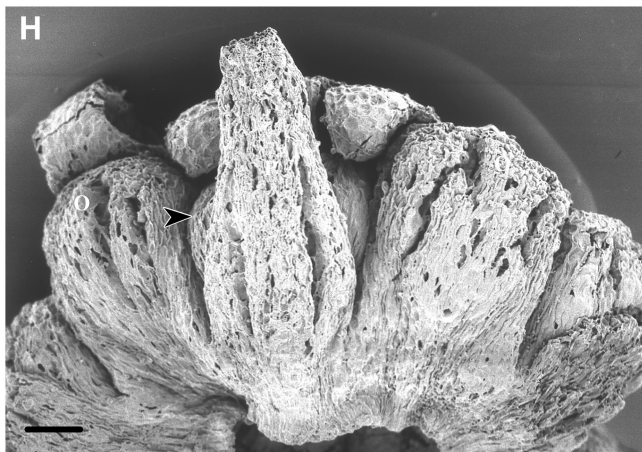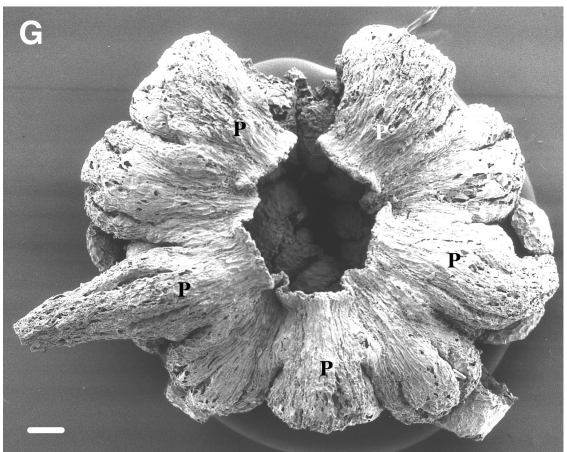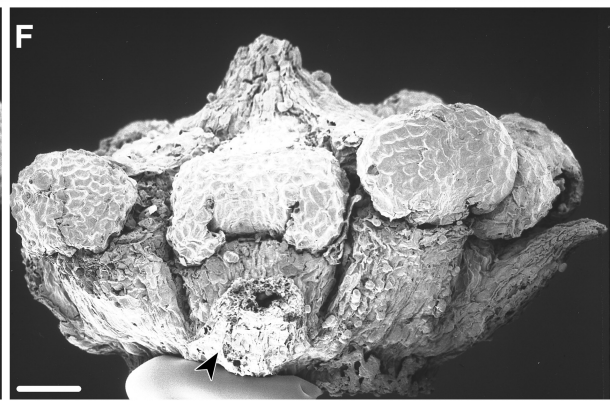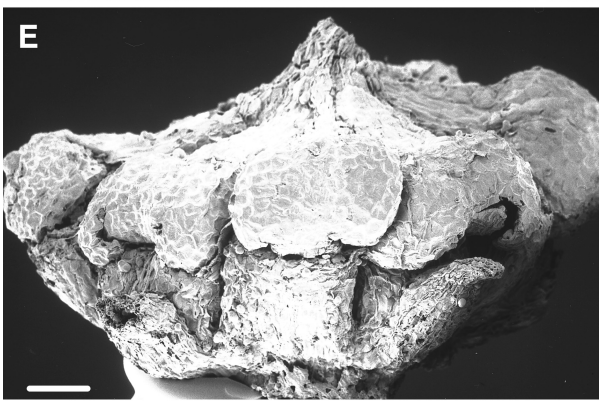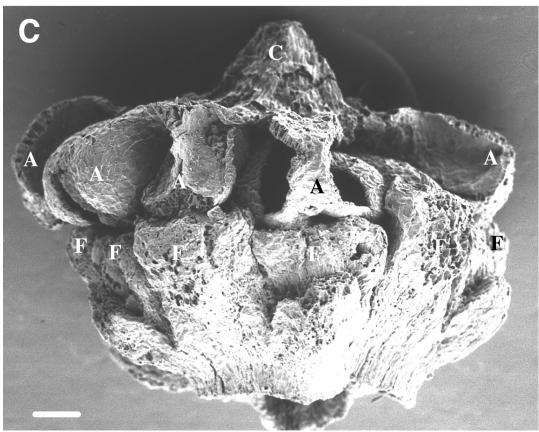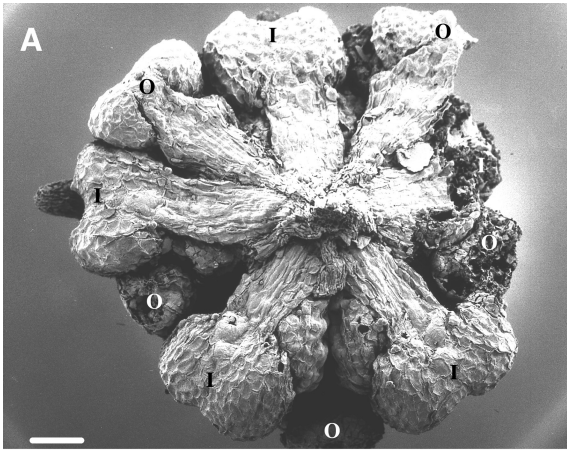
through a fine-mesh sieve, which retained the charcoalified fossils. The fossils were soaked in a solution of HCl, rinsed in water, and subsequently soaked in concentrated HF to eliminate remaining minerals. Mesofossils were then thoroughly rinsed in water, dried in air, and sorted using a stereoscopic microscope. Selected specimens were examined using a stereoscopic microscope and were then mounted on stubs and coated with gold for examination with a scanning electron microscope (SEM; AMRAY 1810). Initially, *Androdecidua endressii* gen. et sp. nov. was known from only a single specimen, which was described and illustrated by Herendeen et al. (1999). Subsequently, six more specimens of this fossil taxon were discovered. Specimens are housed in the paleobotanical collection of the Field Museum.

Flowers of extant Hamamelidaceae were collected from living plant collections (see Acknowledgments section) or were kindly provided by P. K. Endress, J. Horn, and P. Manos. Living flowers were preserved in 70% EtOH. The flowers were dehydrated in an ethanol series (70%–100% EtOH) and subsequently critical-point dried. Complete and dissected flowers were mounted on stubs, coated with gold, and examined using the SEM.

Systematics

Family—Hamamelidaceae R. Brown

Subfamily—Hamamelidoideae Reinsch

Tribe—Hamamelideae A. DC.

Subtribe—Loropetalinae Endress

*Genus—*Androdecidua *Magallón, Herendeen et Crane, gen. nov.*

*Type species—*Androdecidua endressii *Magallón, Herendeen et Crane, sp. nov.*

Generic diagnosis. Flowers actinomorphic, pentamerous; androecium formed by two alternating whorls of stamens, which detach as a unit from the floral receptacle; stamens consisting of a massive, dorsiventrally flattened filament, a short anther, and an elongate apical extension of the connective directed toward the center of the flower; stamens of the outer androecial whorl with bithecal and bisporangiate anthers in which only the abaxial pollen sac of each theca is present; stamens of the inner androecial whorl with bithecal and tet-

rasporangiate anthers; thecae dehisce through valves; pollen grains tricolpate, exine reticulate.

Derivation of generic name. From the Latin *andros-* and *-deciduum*, in reference to the deciduous androecium, which is the best-known part of this fossil flower.

Remarks on the genus. *Androdecidua* gen. nov. is distinguished from extant and fossil genera of Hamamelidaceae by a unique combination of morphological characters, the fusion of stamens and petals, which detach as a unit from the rest of the flower, and the occurrence of tetrasporangiate and bisporangiate stamens in the same androecium.

Species. *Androdecidua endressii* Magallón, Herendeen et Crane, sp. nov. (figs. 1–5).

Specific diagnosis. Corolla pentamerous, with petals opposite and basally fused to stamens of the inner androecial whorl; petals fusiform, thick, abscising from the floral receptacle together with the androecium; stamen filaments basally fused; anthers of the inner androecial whorl dehiscing through abaxial thecal valves that open extrorsely and upward and adaxial thecal valves that open introrsely and downward; pollen grains spheroidal, exine moderately heterobrochate with tall muri and broad lumina.

Derivation of the specific epithet. In recognition of Peter K. Endress, whose substantial and detailed work has significantly advanced knowledge of Hamamelidaceae and understanding of angiosperm floral evolution.

Holotype. PP45947 (fig. 1A, 1E, 1F; fig. 2C; fig. 5B, 5C)

Paratypes. PP45232 (fig. 15A–H in Herendeen et al. 1999; our fig. 1D, 1G, 1H; figs. 2D, 3B), PP45942 (fig. 3C; fig. 5E, 5G), PP45943 (fig. 3C; fig. 5E, 5G), PP45944 (fig. 1B, 1C; figs. 2B, 3A, 5F), PP45945 (fig. 5D), and PP45946 (figs. 2A, 3D; fig. 4B, 4D–4F; fig. 5A).

Type locality. Allon quarry, south pit of the Atlanta Sand and Supply Company, Gaillard, ca. 9.5 km southeast of Roberta, Crawford County, Georgia (Knoxville Quadrangle, 32°37′47″N, 83°59′10″W).

Age. Late Santonian (Late Cretaceous), based on biostratigraphic correlation of terrestrial palynomorphs (Herendeen et al. 1999; R. A. Christopher, personal communication).

Material. *Androdecidua endressii* is known from seven specimens. Four specimens show the complete androecium and petals or petal bases. The remaining specimens are fragments of androecia.

Description. The fossil flowers are actinomorphic, pentamerous, and have a whorled phyllotaxy (fig. 1A–1C). It is not known whether the flowers were hypogynous or partially or fully epigynous, although features of the androecium indicate the existence of a hypanthium and partial epigyny (see

Fig. 1 *Androdecidua endressii* gen. et sp. nov. Androecium and corolla. Scale = 100 μm. *A*, Top view of androecium, with an outer (*O*) and an inner (*I*) whorl of stamens. The anthers of four stamens are missing. The connective extension of stamens converges at the center of the flower. PP45947. *B*, Oblique lateral view of androecium, showing connective extensions (*C*), anthers (*A*), and upper part of filaments (*F*). PP45944. *C*, Lateral view, showing connective extensions (*C*), anthers (*A*), and upper part of filaments (*F*). PP45944. *D*, Oblique lateral view from below of strongly compressed specimen, showing anthers (*A*), filaments (*F*), and petals (*P*). PP45232. *E*, Lateral view, with stamen of the outer androecial whorl in frontal view. PP45947. *F*, Lateral view, with stamen of the inner androecial whorl and opposing petal (arrow) in frontal view. PP45947. *G*, View from below, showing connate filament bases forming an undulating ring and petals or remains of petals (*P*) adnate to filaments of the inner androecial whorl. PP45232. *H*, View from below showing two filaments of the outer androecial whorl (*O*) on either side of a filament of the inner androecial whorl (arrow) and an opposite petal (*P*). PP45232.
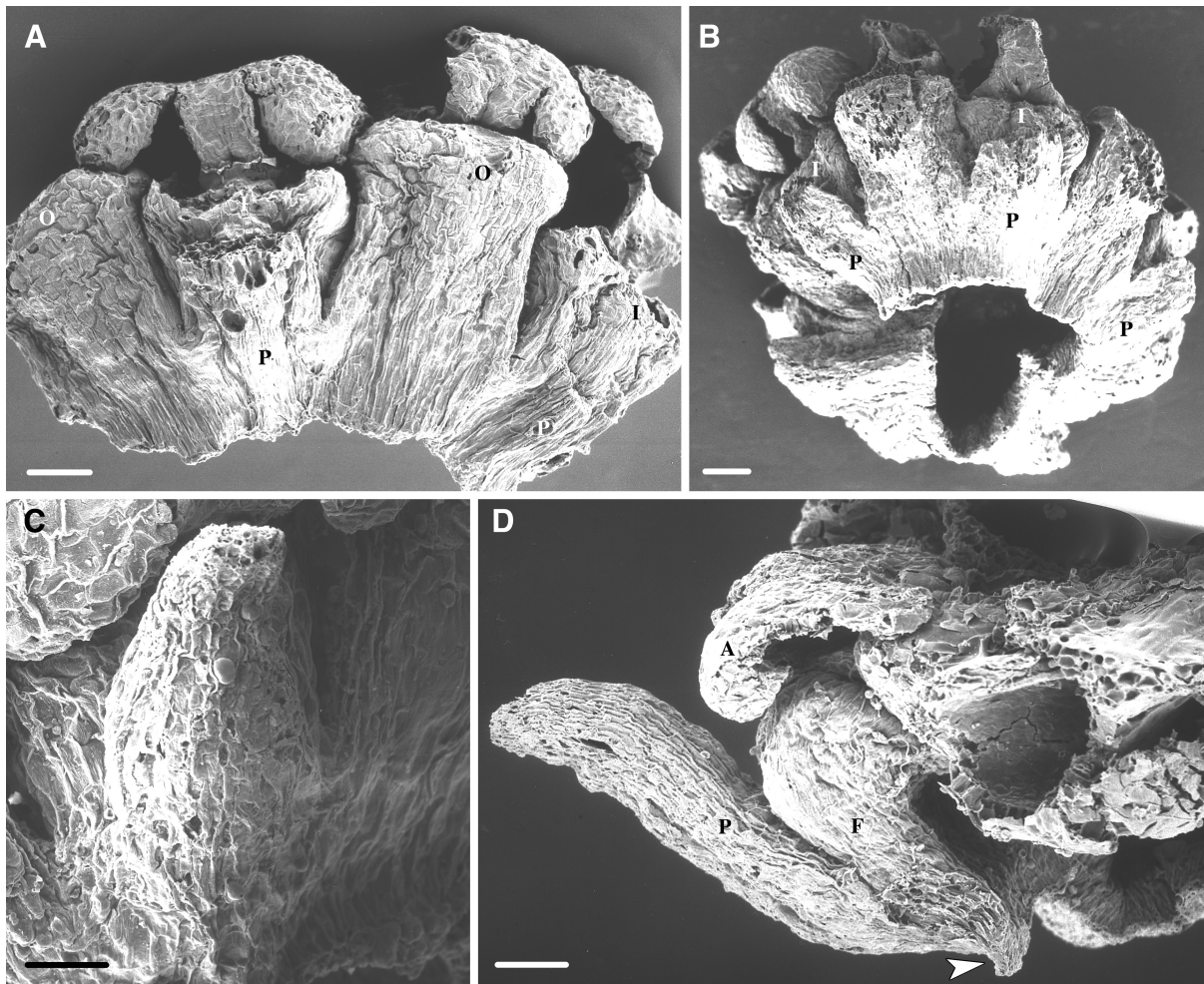
Fig. 2 *Androdecidua endressii* gen. et sp. nov. Androecium and petals. *A*, Lateral view of two outer stamens (*O*) and two inner stamens (*I*) with fused bases of petals (*P*). PP45946. Scale = 100 μm. *B*, Oblique view from below, showing fused filament bases, with bases of petals (*P*) opposite the stamens of the inner androecial whorl (*I*). PP45944. Scale = 100 μm. *C*, Abaxial view of petal. PP45947. Scale = 50 μm. *D*, Radial plane of flower, showing one petal (*P*) fused to the base of one stamen from the inner androecial whorl (arrow). F = filament. A = anther. PP45232. Scale = 100 μm.

"Interpretation of Floral Structure"). The floral receptacle, calyx, and gynoecium are not preserved. The corolla consists of five petals. The androecium consists of two alternating, pentamerous whorls of stamens. The petals are opposite and basally fused to the filaments of the inner androecial whorl (fig. 1*D*–1*H*). Each stamen is fused basally to adjacent stamens of the alternating whorl, and the fused bases of the 10 stamens form a shallow, slightly undulating ring (fig. 1*G*, 1*H*). The androecium and the petals apparently detached as a unit from the floral receptacle.

Petals, fragments of petals, or scars indicating their placement opposite the stamens of the inner androecial whorl are present in all available fossil specimens (fig. 1*C*–1*H*; fig. 2*A*, 2*B*). Petals are spindle shaped, with constricted base and apex (fig. 2*C*), ca. 430–870 μm long ($\overline{X}$ = 720 μm), and 140–400 μm at their widest region ($\overline{X}$ = 280 μm). The petals are thick but dorsiventrally flattened (fig. 2*D*). Although the proximal region of each petal is narrower than its distal portion, the base is not differentiated as a claw (fig. 2*C*). The tip of each

petal is moderately tapering to rounded (fig. 2*C*, 2*D*). Epidermal cells are elongate and longitudinally aligned (fig. 2*C*, 2*D*).

The androecium is 975–1310 μm in diameter ($\overline{X}$ = 1190 μm). Stamens of the inner and outer androecial whorls are morphologically similar (fig. 1*A*, 1*E*, 1*F*), although they differ in anther structure. All stamens consist of a massive filament, a short anther, and a prominent apical extension of the anther connective that extends toward the center of the flower (fig. 1*A*–1*C*). Filaments of stamens in both androecial whorls are similar in size and shape. Each is broad, thick, and massive, with parallel or slightly apically divergent lateral margins. Filaments are dorsiventrally flattened, but with a convex abaxial surface and a concave adaxial surface (figs. 1*E*, 1*F*; fig. 2*A*, 2*D*). Filaments are thin at their base but distally become considerably thicker and are expanded in radial direction, especially immediately below the junction with the anther (fig. 2*D*). The filaments of the 10 stamens are proximally fused for one-third or less of their length, forming an undulating basal ring
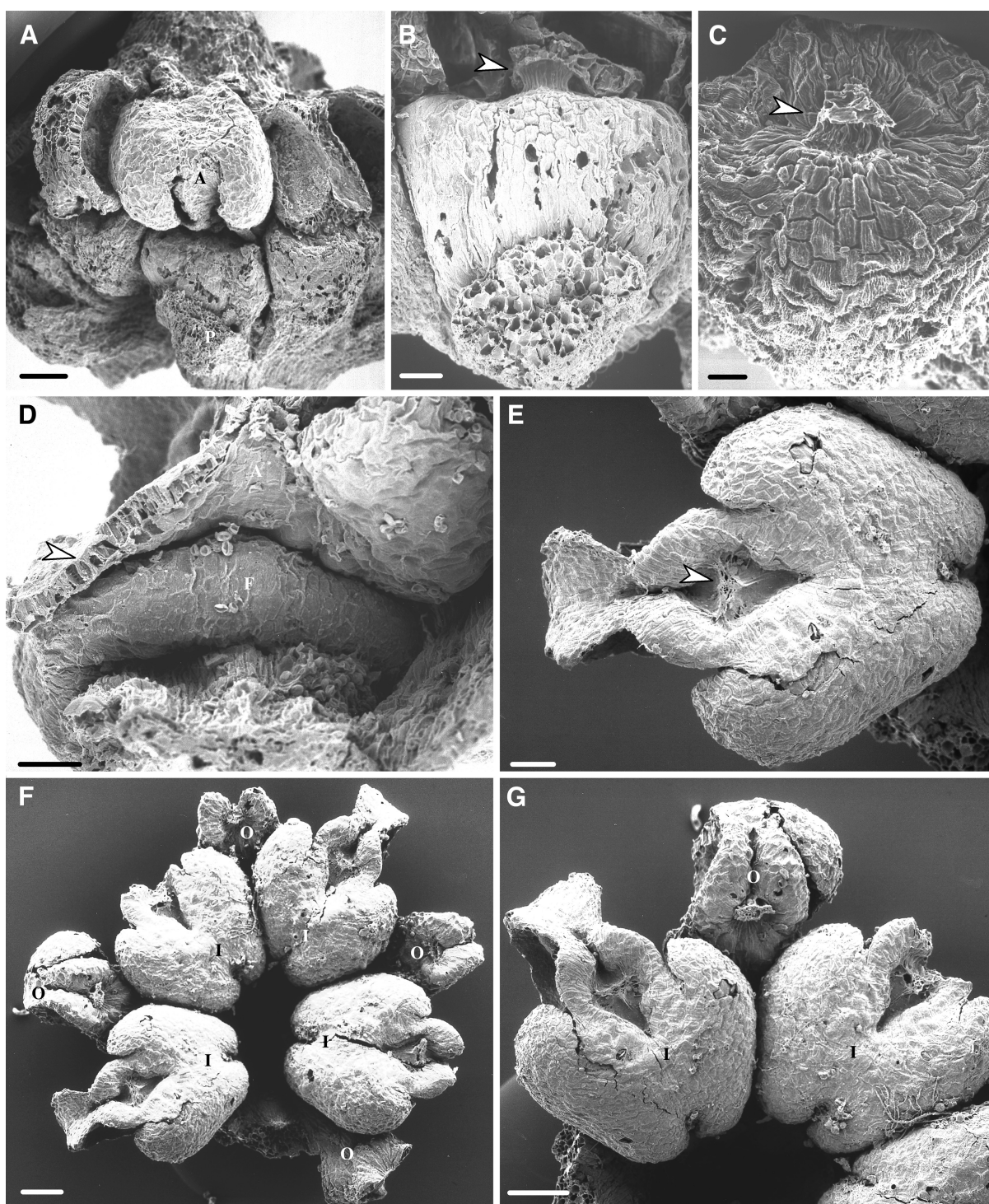
Fig. 3 *Androdecidua endressii* gen. et sp. nov. Androecium and stamens. *A*, Abaxial view of stamen of the inner whorl with partially dehisced anther (*A*) and fragment of base of petal (*P*). PP45944. Scale = 100 μm. *B*, Abaxial view of upper part of filament, with anther detached, showing narrow junction between filament and anther (arrow). A fragment of the petal opposite the stamen remains attached to the base of the filament. Expanded petal cells are apparent. PP45232. Scale = 50 μm. *C*, Abaxial-top view of filament with anther detached, showing narrow junction with anther (arrow) and rectangular to square epidermal cells. PP45943. Scale = 25 μm. *D*, Adaxial view of stamen, showing concave filament (*F*) and anther (*A*). One valve is not preserved, but endothecial cells are exposed (arrow). PP45946. Scale = 50 μm. *E*, View of anther of the inner whorl from below, showing attachment scar (arrow). Valves of the abaxial pollen sacs are not preserved. PP45942. Scale = 50 μm. *F*, View of the androecium from below, showing four anthers of the inner whorl (*I*) and four anthers (some fragmentary) of the outer whorl (*O*). PP45942. Scale = 50 μm. *G*, View from below of two anthers of the inner whorl (*I*) and one anther of the outer whorl (*O*). The valves of the adaxial pollen sacs of the anthers of the inner whorl are not preserved. PP45942. Scale = 10 μm.
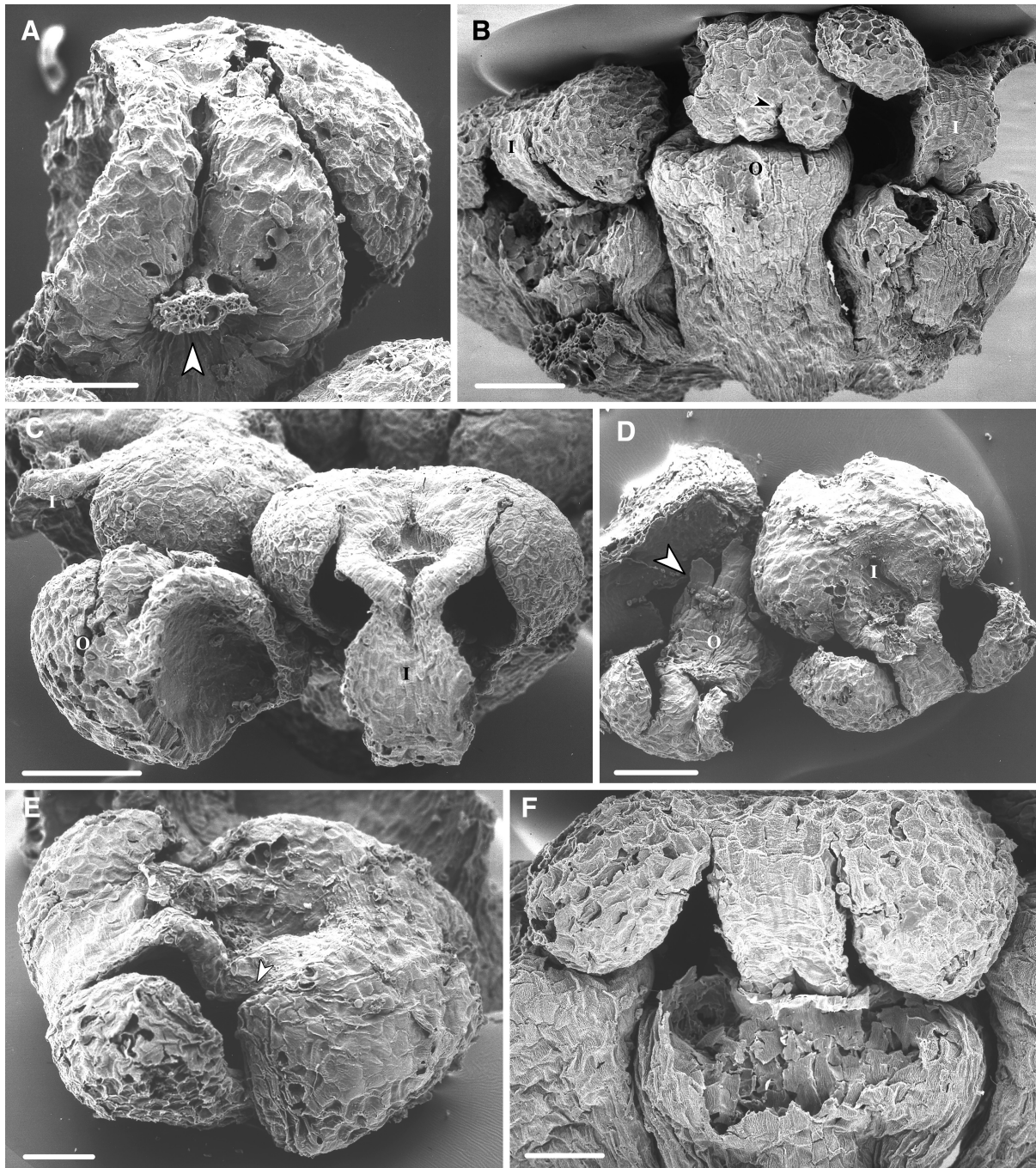
Fig. 4 *Androdecidua endressii* gen. et sp. nov. Anthers. *A*, View from below of anther of the outer androecial whorl, showing attachment scar (arrow). One pollen sac valve (left) is not preserved. Pollen sacs are placed abaxially with respect to site of attachment of the filament to the anther. PP45942. Scale = 50 μm. *B*, Abaxial view of stamen of the outer whorl (*O*), showing partially dehisced anther with proximal segment of the stomium extending on the abaxial surface of the anther (arrow). The anthers of the inner stamens (*I*) are dehisced, with valves opening upward. PP45946. Scale = 100 μm. *C*, Abaxial view of anthers of the inner whorl (*I*) and outer whorl (*O*). The bottom of anthers faces the top of the figure. Some pollen sac valves are not preserved. PP45942. Scale = 100 μm. *D*, View from the bottom of anthers of the inner whorl (*I*) and outer whorl (*O*). The adaxial half of the anther of the outer whorl is not developed (arrow) because pollen sacs are not formed in it. PP45946. Scale = 100 μm. *E*, Radial view of anther of the inner whorl, showing asymmetric stomium. The bottom of the anther faces the top of the figure. The segment directed toward the abaxial side (left) is long, but the one directed adaxially (right) is much shorter (arrow). PP45946. Scale = 50 μm. *F*, Abaxial view of dehisced anther of the inner whorl. The proximal segment of the stomium extends upward on the abaxial side of the anther, and the valve opens upward. PP45946. Scale = 50 μm.
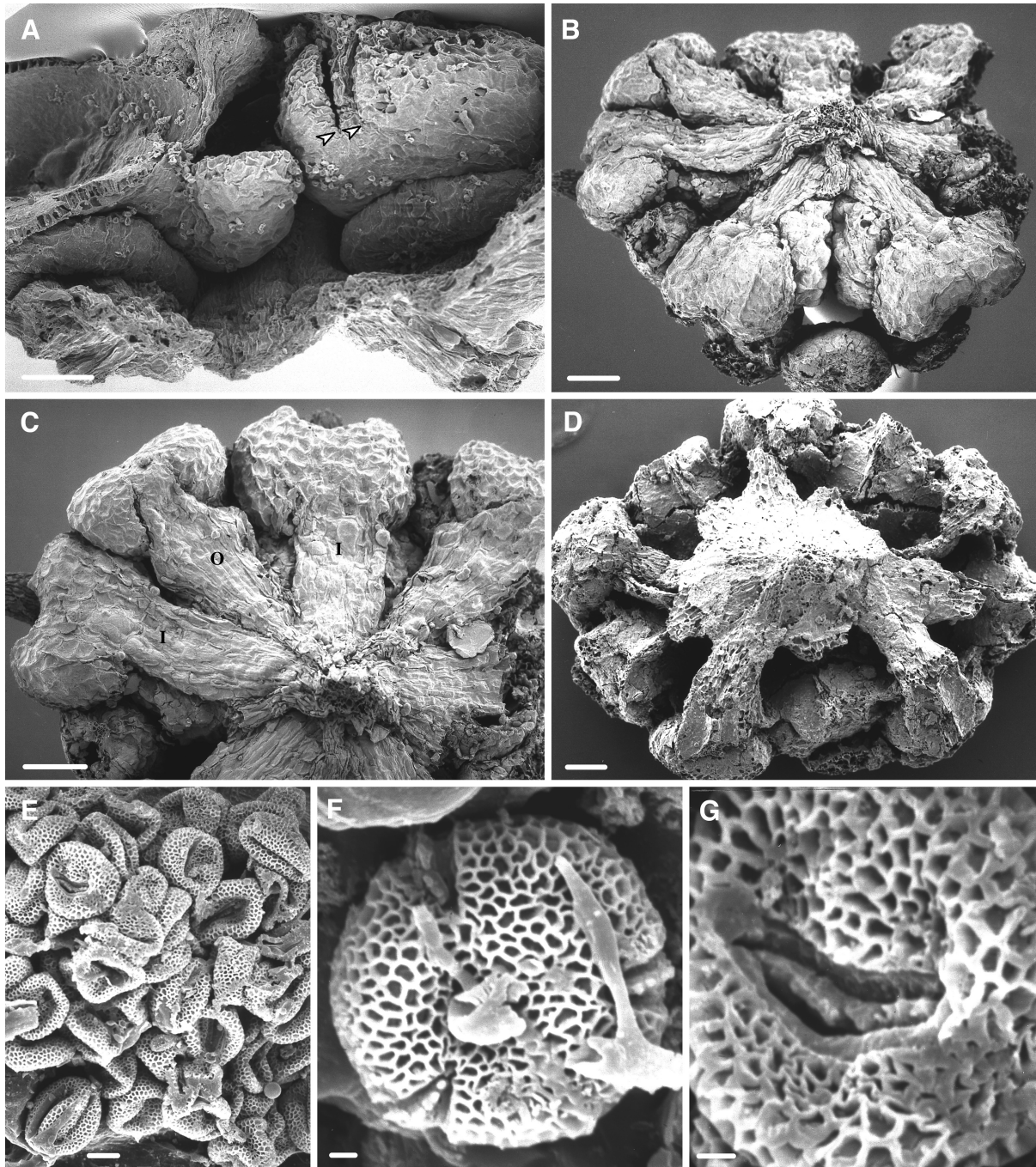
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Fig. 5 *Androdecidua endressii* gen. et sp. nov. Androecium, stamens, and pollen grains. *A*, Adaxial view of two stamens of the inner whorl. The one on the right shows the distal segment of the stomium extending on the adaxial surface of the anther (arrows), and the stamen on the left shows the valves of the inner pollen sacs opening downward. PP45946. Scale = 100 μm. *B*, View of the androecium from the top with apical extensions of the anther connective converging above the center of the flower. PP45947. Scale = 100 μm. *C*, Apical view of connective extensions of anthers of the outer (*O*) and inner (*I*) androecial whorls. The connective extensions are in close proximity but remain distinct. PP45947. Scale = 50 μm. *D*, Apical view of androecium with partially abraded anthers and connectives. Connective extensions appear fused, probably as a result of charcoalification. PP45945. Scale = 100 μm. *E*, Pollen grains showing apertures and exine reticulum. PP45943. Scale = 5 μm. *F*, Polar view of pollen grain showing the ends of three colpi and exine reticulum. The colpi membranes have a line of gemmae. PP45944. Scale = 1 μm. *G*, Pollen grain with line of gemmae on colpus membrane and reticulate exine. PP45943. Scale = 1 μm.
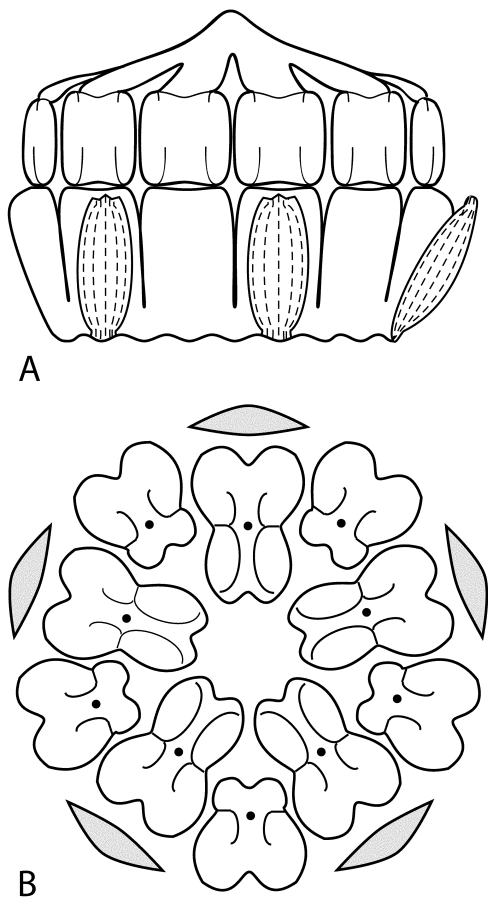
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Fig. 6 *Androdecidua endressii* gen. et sp. nov. Reconstruction of androecium and corolla. *A*, Lateral view of androecium and petals. The petals are opposite stamens of the inner androecial whorl. *B*, Diagram of staminal whorls and petals. Stamens are represented only by anthers; the connective extensions are not shown. Anthers of the outer whorl are bithecal but have only two pollen sacs, situated abaxially with respect to the site of attachment of the anther to the filament (dot). The distal stomial extensions are short. Anthers of the inner whorl are bithecal and tetrasporangiate. The distal, abaxially directed stomial extensions are short, but the distal, adaxially directed extensions are longer and reach the adaxial surface of the anther. Petals are opposite the inner stamens.

(fig. 1*G*, 1*H*; fig. 2*A*, 2*B*; fig. 3*A*). Epidermal cells on the abaxial and adaxial surfaces of the filament are elongate and longitudinally aligned, with approximately parallel margins and transverse or slightly oblique end walls (figs. 2*A*, 3*B*). Epidermal cells near the tip of the filament are nearly square, with deep grooves between contiguous cells (fig. 3*C*). Filament and anther are distinctly delimited (fig. 3*A*, 3*D*). Anthers are basifixed with an extremely short and narrow junction to the filament (fig. 3*B*, 3*C*). When broken at the junction, the filament leaves a distinct small scar at the base of the anther (fig. 3*E*).

Anthers are short, nearly as broad as the filaments in the tangential plane (fig. 1*E*, 1*F*; fig. 3*A*), and radially elongate (fig. 1*A*; fig. 3*F*, 3*G*). Anthers of the outer androecial whorl are smaller and slightly rounder than those of the inner an-

droecial whorl (fig. 3*F*, 3*G*; fig. 4*A*–4*C*). They have two thecae, but each theca has only one pollen sac, placed abaxially with respect to the site of attachment of the filament (fig. 4*C*, 4*D*; fig. 6*B*). Thecae are moderately protuberant on the abaxial side of the anther (fig. 4*A*, 4*D*). The adaxial half of the anther is underdeveloped, reflecting the absence of the inner pollen sacs of each theca (fig. 4*C*, 4*D*), but the distal side of the anther is not obviously modified (fig. 1*A*). Anthers of the outer androecial whorl rarely show an intact stomium. The stomium is approximately C-shaped, with the vertical segment placed approximately at the level of the attachment of the filament and the proximal and distal segments directed toward the abaxial side of the anther (figs. 4*D*, 6*B*, 7*A*). The proximal stomial segment extends a short distance up on the abaxial side of the anther (fig. 4*B*, 4*D*). The distal segment is shorter, extending onto the apex of the anther but not reaching its abaxial side (fig. 1*A*). Each theca dehisced through a single valve, which apparently opened extrorsely and upward. Valves of anthers of the outer whorl are not preserved in most of the available material.

Anthers of the inner androecial whorl are bithecal and tetrasporangiate. Thecae protrude on the adaxial, abaxial, and lateral sides of the anthers (fig. 4*B*, 4*D*, 4*E*). The stomium consists of a vertical segment placed at the level of the attachment of the filament and approximately horizontal proximal and distal segments that extend abaxially and adaxially (fig. 4*E*). The stomium is asymmetric (figs. 6*B*, 7*C*). The proximal abaxially directed part of the stomium is long; it reaches and curves upward on the abaxial side of the anther (fig. 4*D*, 4*F*). The distal, abaxially directed part of the stomium is shorter; it extends onto the upper side of the anther but does not reach the abaxial side (fig. 1*A*). The proximal adaxially directed stomial segment is very short (fig. 4*D*, 4*E*), whereas the adaxially directed, distal segment is substantially longer, reaching and extending downwardly on the adaxial side of the anther (fig. 5*A*). Thecae dehisced through two valves, but given the elaborate stomial configuration, dehiscence was complex. The outer (abaxial) valve of each theca opened extrorsely and upward (fig. 4*B*, 4*F*), but the inner (adaxial) valve opened introrsely and apparently downward (fig. 5*A*). Endothecial cells of anthers of both whorls are rectangular with thickened walls (figs. 3*D*, 4*C*). Epidermal cells of all anthers are polygonal to round in outline (fig. 3*A*; fig. 4*A*, 4*B*, 4*D*–4*F*).

Each stamen has a prominent extension of the connective that extends from the top of each anther toward the center of the flower, where it converges with the connective extensions of all other stamens (fig. 5*B*, 5*C*). The connective extensions are broad and flattened, taper in width only near their ends, and are tightly packed together so as to leave no empty spaces between them (fig. 5*B*, 5*C*). Connective extensions of the anthers of the outer androecial whorl are slightly longer and narrower, especially at their end, than the connective extensions of anthers of the inner androecial whorl (fig. 5*C*). The connective extensions converge above the center of the flower to form a low conical peak (fig. 1*B*, 1*C*). In some specimens, the connective extension of adjacent stamens appears to be postgenitally fused, especially at their tips, although it is not clear whether this apparent fusion is the result of the fossilization process (fig. 5*D*). In other specimens, connective extensions are very closely set but are apparently distinct (fig. 5*C*).
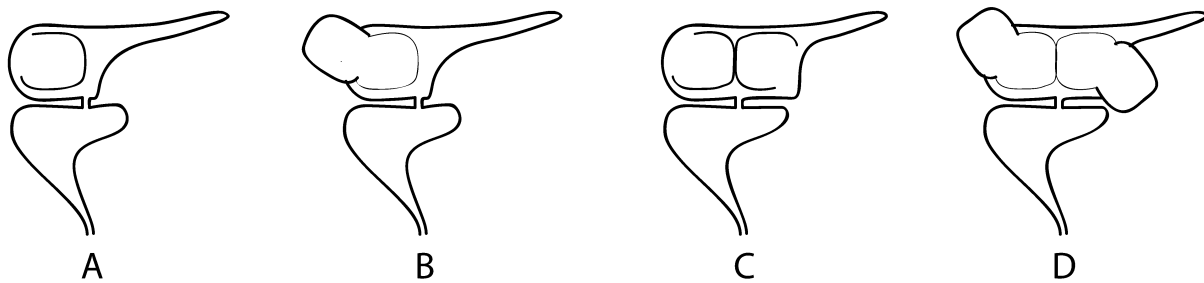
Fig. 7 *Androdecidua endressii* gen. et sp. nov. Reconstruction of stamens. Adaxial side of stamen faces right, abaxial side of stamen faces left. *A*, Lateral view of stamen of the outer whorl, with undehisced anther. The adaxial half of the anther is not developed, and pollen sacs are missing. The vertical part of the stomium is aligned with the attachment of anther and filament. The distal horizontal stomial extension is relatively short, but the proximal horizontal extension is longer and reaches the abaxial side of the anther. *B*, Lateral view of stamen of the outer whorl, with dehisced anther. The valves of dehisced pollen sacs open extrorsely and upward. *C*, Lateral view of stamen of the inner whorl, with undehisced anther, showing asymmetric stomium. The vertical stomial segment is aligned with the attachment between the anther and filament. The distal, abaxially directed horizontal segment is short, but the proximal, abaxially directed segment is long, reaching the abaxial side of the anther. The distal, adaxially directed segment is long, reaching the adaxial side of the anther, but the proximal, adaxially directed segment is short. *D*, Lateral view of stamen of the inner whorl, with dehisced anther. As a result of the unequal proximal and distal length of stomial segments, the valves of dehisced abaxial pollen sacs open extrorsely and upward, and the valves of dehisced adaxial pollen sacs open introrsely and downward.

Pollen grains are present in the pollen sacs of anthers of both androecial whorls. Pollen grains are spheroidal, 13.2–13.9 μm in diameter ($\overline{X} = 13.5$ μm), and tricolpate (fig. 5*E*, 5*F*). Each colpus is lens shaped to elliptic, does not extend to the polar areas, and has a line of gemmae on the aperture membrane (fig. 5*F*, 5*G*). The exine is coarsely reticulate and slightly heterobrochate, with broad lumina and muri of moderate height. A distinctly differentiated exine pattern along the border of apertures is not present (fig. 5*F*, 5*G*).

Discussion

Interpretation of Floral Structure

Reconstructions of the androecium, corolla, and stamens of *Androdecidua endressii* are presented in figures 6 and 7. A pentamerous floral merosity is indicated by the presence of a whorl of five perianth organs and the androecium, interpreted as consisting of two alternating, pentamerous whorls. The alternative possibility, that the androecium consists of a single decamerous whorl, is rejected based on the slightly displaced placement of the filament bases. Five filaments are slightly more internal and alternate with five filaments that are more external, forming an undulating ring with their fused bases (fig. 1*G*). The alternating external-internal placement of anthers corresponds with the positions of the filaments (fig. 1*C*–1*F*), and the regular radial alternation of bisporangiate and tetrasporangiate anthers also indicates that each structural anther type corresponds to a different whorl.

The organs of the perianth whorl are interpreted as petals, rather than sepals, because they are relatively large and conspicuous. The placement of the five perianth organs immediately external to, and alternating with, the outer whorl of stamens (fig. 1*E*–1*H*) also indicates that the perianth organs correspond to the inner whorl of the perianth, i.e., the corolla. If this interpretation is correct, then an additional, external perianth whorl, the calyx, may also be inferred. Therefore, the flowers of *A. endressii* probably had a perianth composed of

an outer whorl of sepals, which is not preserved in the available material, and an inner whorl of petals.

Proximal fusion among stamen filaments is documented by the continuous ring formed by their bases. Proximal fusion of petals with filaments of the inner whorl of stamens is strongly indicated by the very close association between these organs (fig. 1*H*; fig. 2*A*, 2*B*, 2*D*) and additionally by the fact that in all cases, petal bases remain attached to the filaments (e.g., fig. 1*C*, 1*D*, 1*H*), indicating that petals were more easily torn off, rather than separated, from the opposite stamen filament, as it would occur if these organs were only closely appressed.

The base of the flower, including the floral receptacle, is unknown. The fused stamen bases form a relatively broad attachment perimeter, perhaps indicating that they were attached to the rim of a hypanthium (figs. 1*G*, 2*B*) rather than to a narrow floral receptacle. A gynoecium is not preserved in the available material, but based on comparisons with flowers of closely related taxa (Magallón 1999, 2000; S. Magallón, unpublished manuscript), it is assumed that a gynoecium was present and was surrounded by a partially or completely fused receptacular cup that formed a hypanthium. The flowers of *A. endressii* were probably bisexual and partially or fully epigynous.

The thickness of petals and filament bases indicates that these structures may have been inflated. Support for this idea is provided by the expanded cell cavities observed in abraded or broken petals and stamen filaments (fig. 3*B*). Other taxa of Hamamelidoideae also have inflated filaments (e.g., *Fothergilla*) that appear to play a role in attracting potential pollinators.

The organs of both androecial whorls are interpreted as fertile stamens because identical pollen grains have been found in all anthers. The anthers of the outer androecial whorl are interpreted as bithecal and bisporangiate, in which the adaxial pollen sac of each theca is missing. The two pollen sacs of the anthers of the outer androecial whorl are interpreted as corresponding to the abaxial pollen sac of each theca because they are on opposite sides and are abaxially placed with respect to the site of attachment of the filament to the anther (fig. 2*A*,

2*D*). This interpretation is also supported by the configuration of the stomium, which has its vertical segment placed at the level of the site of filament attachment and proximal and distal segments extending toward the abaxial side of the anther (fig. 2*A*). This interpretation is further supported by the presence of the partially undeveloped inner half of the anther (fig. 2*D*), in which pollen sacs are not formed.

The androecium probably became detached from the floral receptacle after the anthers had dehisced and shed most of their pollen grains. If the flowers are correctly interpreted as bisexual, the close placement of the anther connectives (figs. 1*A*, 5*C*) may have blocked the access of pollinators or of airborne pollen, and thus, the gynoecium of a particular flower could be reached by "outcrossing" pollen only after its own androecium became detached. If this is the case, then it is likely that the development of the gynoecium lagged behind that of the androecium, in order to avoid self-fertilization. The flowers of *A. endressii* may have been protandrous, as is the case in many extant Hamamelidaceae.

Comparative Morphology

Summary of floral diversity in extant Hamamelidaceae. Morphological diversity of flowers of Hamamelidaceae is relatively wide, but nevertheless, most flowers conform to a structural groundplan characterized by whorled phyllotaxy, fixed merosity (frequently pentamerous perianth and androecium), radial alternation of adjacent floral whorls, and a perianth consisting of two types of morphologically distinct organs (sepals and petals) arranged in two whorls (calyx and corolla). This floral groundplan is found exclusively in the flowers of the core eudicots (Magallón 1999; Magallón et al. 1999). Recent studies on molecular evolution of the genes that control flower development provide a genetic basis for some of the distinctive features of the core eudicot floral groundplan (i.e., a perianth formed by strictly defined petals and sepals; Kramer et al. 1998). In this context, an explicit clarification becomes necessary: the terms "petals" and "sepals" are here used only to refer to a perianth that conforms to the core eudicot floral groundplan.

The genera included in subfamily Hamamelidoideae share the presence of a single functional ovule in each carpel of the bicarpellate gynoecium as well as a sophisticated mechanism of seed ejection that involves specialization of seeds and fruits. Seeds are elliptical to fusiform and have a hard and smooth outer wall. Fruits are capsules with an extremely smooth and rigid endocarp, which at maturity detaches from the outer fruit walls and forcefully ejects the single seed in each ovary locule. Variations in floral merosity and perianth features are found among the four tribes within the subfamily (table 1). Whereas the genera within tribes Hamamelideae and Corylopsidea have a perianth consisting of calyx and corolla and a fixed merosity, tribe Eustigmateae includes some genera with inconspicuous or absent petals, and in tribe Fothergilleae, one or both perianth whorls may be absent, with concomitant alteration in stamen number.

Most flowers of tribe Hamamelideae are pentamerous, and a few genera have tetramerous flowers. The petals of several genera are parallel margined, straplike, and circinately coiled in bud. *Hamamelis*, the single genus in subtribe Hamamelid-

inae, has tetramerous flowers and bisporangiate stamens (see "Comparative morphology for *Androdecidua*"). The four genera of subtribe Loropetalinae have stamens with a conspicuous centripetal protuberance of the anther connective and very short styles. Subtribe Dicoryphinae includes five genera with a unique mode of thecal dehiscence, in which a single valve opens introrsely, uncovering the two pollen sacs of each theca.

The flowers of *Corylopsis*, the single genus in tribe Corylopsideae, have a well-developed calyx and corolla and petals that are clawed and conspicuous. There are three ovules in each carpel, but only one reaches maturity (Endress 1989*a*). Flowers of tribe Eustigmateae are pentamerous; the perianth is formed by calyx and corolla, but the petals are small and inconspicuous in *Sinowilsonia* and *Fortunearia* (Endress 1989*b*, 1993; Magallón 1999). The three genera in the tribe share long, decurrent stigmas, which are extremely conspicuous in *Eustigma*. Flowers of tribe Fothergilleae have a single perianth whorl, probably corresponding to the calyx, or the perianth is absent altogether. Floral merosity is not fixed (Endress 1989*a*).

Subfamily Exbucklandioideae includes four genera that comprise a somewhat broad range of floral morphological diversity. Exbucklandioideae includes forms with a well-developed perianth, formed by calyx and corolla (i.e., *Disanthus*), to forms in which the perianth is absent (i.e., *Chunia*). *Exbucklandia* has bisporangiate anthers (see "Comparative morphology for *Androdecidua*"). The number of ovules ranges from five to eight in each of the two carpels that conform the gynoecium (Endress 1989*c*, 1989*a*, 1993).

Rhodoleia, the single genus in subfamily Rhodoleioideae, has pseudanthial inflorescences formed by a cluster of zygomorphic, bisexual flowers. The perianth consists of a small calyx and a conspicuous corolla formed by more or less clawed petals. The number of petals varies from flower to flower, presumably as a result of clustering in the inflorescence. Each carpel in the bicarpellate gynoecium contains 10 or more ovules.

Subfamily Altingioideae has unisexual flowers clustered in dense spherical unisexual partial inflorescences. Staminate flowers have been reported to have vestigial carpels (Wisniewski and Bogle 1982; Bogle 1986), and pistillate flowers have staminodes, although these stop developing when flowers are very young. Each carpel in the bicarpellate gynoecium contains 20 or more ovules, some of which develop into winged seeds.

Comparative morphology for Androdecidua. *Androdecidua endressii*, with its radially alternating floral whorls, fixed merosity (i.e., pentamerous corolla and androecium), and perianth presumably consisting of calyx and corolla, conforms to the core eudicot floral groundplan. Within the saxifragalean clade, which includes Hamamelidaceae, not all the taxa display the core eudicot floral groundplan. For example, it does not occur in *Cercidiphyllum* (Cercidiphyllaceae), *Daphniphyllum* (Daphniphyllaceae), and perhaps Haloragaceae and Paeoniaceae. However, this basic pattern of floral construction occurs in all other members of the saxifragalean clade (i.e., some Hamamelidaceae, Saxifragoideae, Penthoroideae, Iteoideae, Pterostemonoideae, Ribseoideae, Tetracarpoideae, and Crassulaceae).

Among Hamamelidaceae, the core eudicot floral groundplan occurs in genera of Hamamelideae and Corylopsideae as well

Table 2

Morphological Comparison of *Androdecidua endressii* with Selected Extant and Fossil Genera of Hamamelidaceae

	Merosity	Fusion of petals and stamens	Fusion of stamens	Petal form	No. of androecial whorls	Merosity, differentiation into stamens and staminodes	Filament thickness	Narrow junction between filament and anther	No. of pollen sacs per anther	Pollen sacs in bisporangiate anthers	Valvate anther dehiscence	No. of valves, no. of pollen sacs per theca	Prominent extension of connective	Deciduous androecium
Androdecidua[a]	5-merous	Present	Present	Fusiform	2	Fixed, not differentiated	Very fleshy	Present	4 and 2	Abaxial	Present	2, 2 and 1, 1	Present	Present
Allonia[a]	5-merous	Absent	Absent	Ribbon-like	2	Fixed, not differentiated	NA	NA	4	NA	Present	2, 2	Present	Absent
Archamamelis[a]	6- or 7-merous	Absent	Absent	?	?	?	Moderately fleshy	Absent	2	Adaxial	Present	1, 1	Absent	Absent
Hamamelis	4-merous	Absent	Absent	Ribbon-like	2	Fixed, differentiated	Moderately fleshy	Absent	2	Adaxial	Present	1, 1	Absent	Absent
Loropetalum	4- or 5-merous	Absent	Absent	Ribbon-like	1	NA	Moderately fleshy	Absent	4	NA	Present	2, 2	Present	Absent
Manigaya	5-merous	Absent	Absent	Ribbon-like	2	Fixed, differentiated	Fleshy	Absent	4	NA	Present	2, 2	Present	Absent
Tetrathyrium	5-merous	Absent	Absent	Ribbon-like	1	NA	Moderately fleshy	Absent	4	NA	Present	2, 2	Present	Absent
Embolanthera	5-merous	Present	Absent	Ribbon-like, lobed at the base	1	NA	Moderately fleshy	Absent	4	NA	Present	2, 2	Present	Absent
Noahdendron	5-merous	Absent	Absent	Ribbon-like	1	NA	Fleshy	Present	4	NA	Present	1, 2	Present	Absent
Ostrearia	5-merous	Absent	Absent	Ribbon-like	2	Fixed, differentiated	Fleshy	Present	4	NA	Present	1, 2	Present	Absent
Dicoryphe	4-merous	Present	Present	Fleshy, tapering apex	2	Fixed, differentiated	Moderately fleshy	Absent	4	NA	Present	1, 2	Absent	Absent
Matudaea	Not fixed	Absent	Absent	Absent	2	Not fixed, not differentiated	Moderately fleshy	Absent	4	NA	Present	2, 2	Absent	Absent
Fothergilla	Not fixed	Absent	Absent	Absent	1	NA	Fleshy, inflated	Absent	4	NA	Present	2, 2	Absent	Absent
Rhodoleia	Not fixed	Absent	Absent	Clavate	2, inner incomplete	Not fixed, differentiated	Fleshy	Slight constriction	4	NA	Present	2, 2	Absent	Absent
Exbucklandia	Not fixed	Absent	Absent	Fleshy, flattened	1 or 2	Not fixed, not differentiated	Moderately fleshy	Absent	2	Abaxial	Present	1, 1	Absent	Absent

Note.   NA = not applicable condition.

[a] Fossil genera.
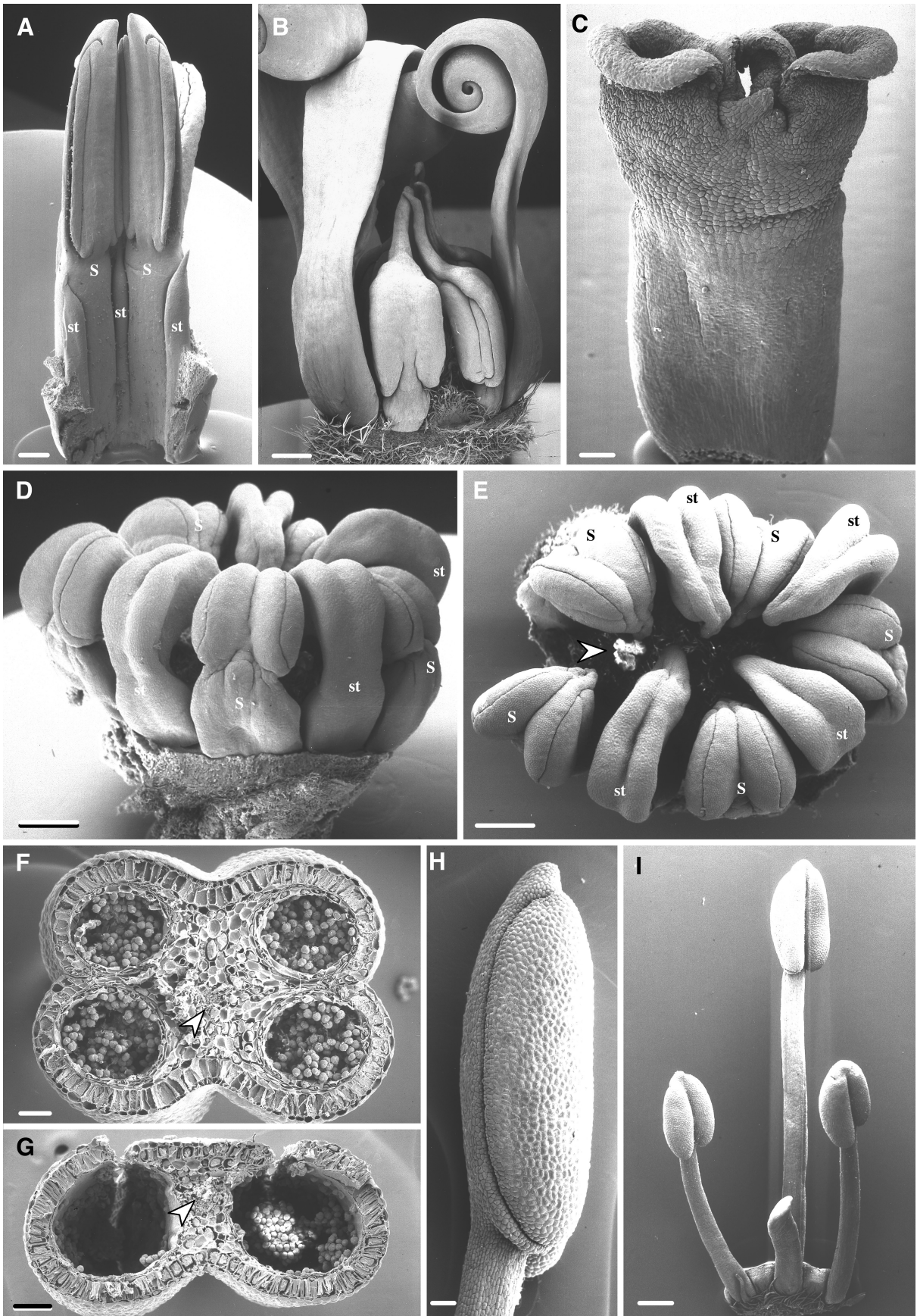
as in *Disanthus*. In other taxa of Hamamelidaceae, it apparently became modified by the reduction of petals (Eustigmateae), by reduction or absence of petals and sepals, with a concomitant variation and increase (usually) in the number of androecial organs (Fothergilleae), by absence or modification of calyx and corolla (e.g., *Exbucklandia*), by asymmetric reduction in the number of organs in the corolla and in the androecium as a result of lateral crowding of flowers in inflorescences (*Rhodoleia*), and by absence of perianth and crowding of flowers in unisexual inflorescences (Altingioideae). A summary of floral characters of *A. endressii* and of selected extant and fossil Hamamelidaceae is presented in table 2.

Fusion among stamens and petals of *Androdecidua*, although restricted to proximal regions, results in a functional association that allows the androecium and corolla to detach as a unit from the floral receptacle. In this respect, *Androdecidua* is unusual with respect to members of the saxifragalean clade, as well as other less derived core eudicots (e.g., the Cornales), which usually have free perianth and androecial organs, except sometimes at their most proximal regions. Functional associations resulting from fusion of organs of one or several floral whorls are more common among particular derived core eudicot taxa (e.g., Papilionoideae, Asteridae s.l., and Lamiidae s.l.).

Fusion among stamens and among stamens and petals is known in a few extant genera of Hamamelidaceae (table 2). *Dicoryphe* has two tetramerous androecial whorls, the outer one consisting of stamens and the inner one consisting of staminodes. The bases of all androecial elements are fused, forming a shallow ring (fig. 8*A*). Petals are opposite and are basally fused to the staminodes. Because the petals are significantly wider than the staminodes, they are apparently also fused to the alternating stamens. Additionally, the sepals of *Dicoryphe* are fused, forming a long calyx tube. The flowers of *Embolanthera* have a single pentamerous androecial whorl in which the five stamens are proximally fused to the petals. However, the stamens themselves are apparently free from each other (Endress 1989*b*). In terms of the fusion among organs of different whorls, *Androdecidua* is more like *Dicoryphe*, in which fusion between petals and androecial organs occurs on radial planes, whereas in *Embolanthera*, because of the radial alternation of petals and stamens, fusion between these organs occurs on oblique planes. However, in general, the degree of functional association among stamens and petals exhibited by *Androdecidua* is unparalleled among extant or extinct Hamamelidaceae.

The petals of *Androdecidua* differ from those of extant and fossil members of Hamamelidaceae. Several Hamamelidaceae,

for example, *Hamamelis* and the genera of Loropetalinae, including the fossil *Allonia*, have narrow, parallel-margined, ribbon-like petals that are circinate in bud and that uncoil (at least partially) at maturity (e.g., *Noahdendron*; fig. 8*B*). Nevertheless, variability in petal morphology among members of Hamamelidaceae is extensive, including, for example, clawed petals in *Corylopsis*; geniculate and distally bilobed petals in *Eustigma*; very fleshy, spatulate petals in *Dicoryphe*; dorsiventrally flattened, long, and longitudinally outwardly curled petals in *Trichocladus crinitus*; as well as small, cylindrical petals (e.g., *Fortunearia* and *Sinowilsonia*). Although fleshy, spindle-shaped, dorsiventrally flattened petals like those of *Androdecidua* do not occur among extant genera of Hamamelidaceae, fleshy petals of different forms do occur and are relatively common. In terms of the extensive morphological plasticity of petals that exists within the family, particularly within Hamamelidoideae, the petals of *Androdecidua* are not unusual.

The androecium of *Androdecidua* consists of two alternating whorls of stamens. Flowers with two androecial whorls, in which either both whorls consist of stamens or the external whorl has stamens and the internal one has staminodes, are common among core eudicots. Two androecial whorls are present in several extant genera of Hamamelidaceae as well as in the fossil *Allonia* (table 2). The flowers of *Rhodoleia* and *Matudaea* have two androecial whorls, but merosity is irregular, and the inner androecial whorl may be incomplete, especially in *Rhodoleia*. The flowers of *Exbucklandia* apparently have two alternating androecial whorls, but merosity is also irregular. *Trichocladus crinitus* has a single complete whorl of five stamens, but one or two additional stamens sometimes occur internal to, and alternating with, members of complete staminal whorl, in what would correspond to the placement of organs of an inner androecial whorl. In these four extant genera, androecial organs are not differentiated into stamens and staminodes.

The flowers of *Dicoryphe*, *Ostrearia*, *Hamamelis*, and *Maingaya* also have two androecial whorls, and floral merosity is fixed: *Dicoryphe* and *Hamamelis* are tetramerous, and *Ostrearia* and *Maingaya* are pentamerous. In these genera, the androecial whorls are functionally differentiated: the outer one consists of stamens, and the inner one consists of staminodes (table 2). *Androdecidua* resembles these last four genera in having two complete androecial whorls in which the number of organs is fixed, but it differs in that the androecial organs are not differentiated into stamens and staminodes. *Allonia* is similar to *Androdecidua* in having two whorls of stamens.

Fig. 8 Extant Hamamelidaceae. *A*, *Dicoryphe stipulacea*. Adaxial view of basally fused stamens (*S*) and staminodes (*st*). Scale = 1 mm. *B*, *Noahdendron nicholasii*. Partially dissected flower, showing circinately coiled petals and stamens. Stamens have a distinct junction between anther and filament and a long connective extension. Scale = 0.5 mm. *C*, *Disanthus cercidifolius*. Adaxial view of dehisced stamen, with thick, dorsiventrally flattened filament. Scale = 100 μm. *D*, *Ostrearia australiana*. Lateral view of flower with perianth removed, showing stamens (*S*) and staminodes (*st*). Filaments are thick, and there is a clear junction between filament and anther. Scale = 0.5 mm. *E*, *Ostrearia australiana*. Top view of flower with perianth removed, showing stamens (*S*), staminodes (*st*), and one style (arrow). One staminode is missing. Scale = 0.5 mm. *F*, *Corylopsis veitchiana*. Bithecal and tetrasporangiate anther in transverse section, showing placement of the pollen sacs of each theca with respect to the main vascular strand of the anther (arrow). Scale = 100 μm. *G*, *Exbucklandia populnea*. Anther in transverse section, showing two pollen sacs placed abaxially with respect to the main vascular strand of the anther (arrow). Scale = 100 μm. *H*, *Exbucklandia populnea*. Anther on side view, with abaxial side facing right. The ends of the stomium point abaxially. Scale = 100 μm. *I*, *Exbucklandia populnea*. Abaxial view of three stamens and one perianth organ. Pollen sacs are protuberant on the abaxial side of anthers. Scale = 0.5 mm.
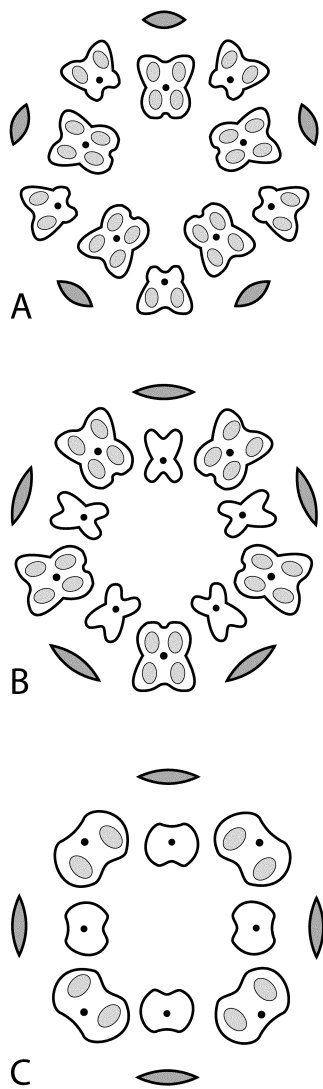
Fig. 9 Floral diagrams of extant and fossil Hamamelidaceae, showing androecium and corolla. *A*, *Androdecidua*. Stamens of the inner androecial whorl are bithecal and tetrasporangiate, but those of the outer androecial whorl are modified by the absence of the inner pollen sac in each theca. Petals are opposite the tetrasporangiate (inner) stamens. *B*, *Maingaya*. Outer androecial whorl is formed by stamens, and inner whorl is staminodial. Petals are opposite the staminodes. *C*, *Hamamelis*. Outer androecial whorl consists of functional stamens that have two pollen sacs, corresponding to the inner one of each theca. The inner androecial whorl is staminodial. Petals are opposite the staminodes.

These two fossil genera are unique with respect to extant Hamamelidaceae in having two androecial whorls in which the number of organs is fixed (pentamerous), but the organs are not differentiated into stamens and staminodes. The presence of an inner whorl of staminodes in the fossil *Archamamelis* is uncertain (Endress and Friis 1991).

The stamens of *Androdecidua* are morphologically distinctive, particularly in their massive filaments and apical extension of the anther connective. Stamen diversity within Hamamelidaceae is broad, and thick, fleshy filaments are not uncommon (fig. 8*A*–8*D*). *Rhodoleia* has thick, fleshy filaments that are substantially longer than those of *Androdecidua*. Filaments of *Exbucklandia* are dorsiventrally flattened, whereas those of *Rhodoleia* are rounded and vary in width along their length. *Disanthus* has short, fleshy, dorsiventrally flattened filaments that are as broad as the anthers at the time of dehiscence (fig. 8*C*). Nevertheless, they differ from *Androdecidua* in lacking a narrow junction with the anther.

Among genera of Hamamelidoideae, *Fothergilla* has long, thick filaments that become inflated and constitute the most conspicuous organs of the flower. It is possible that at least part of the thickness of the filaments of *Androdecidua* resulted from similar inflation. However, the filaments *Fothergilla* are cylindrical and very long. *Hamamelis* has relatively short, dorsiventrally flattened, fleshy filaments.

Stamen filaments in Dicoryphinae and Loropetalinae (Hamamelideae) are thick and fleshy. *Dicoryphe* and *Trichocladus* have relatively long stamens, which are dorsiventrally flattened in the former genus (fig. 8*A*) and are more or less cylindrical in the latter. Both differ from the filaments of *Androdecidua* in lacking a distinct narrow attachment to the anther. The filaments of *Noahdendron* and *Ostrearia* are short, broad, dorsiventrally flattened, and have a distinct narrow attachment to the anther (fig. 8*B*, 8*D*). The filaments of *Ostrearia* especially resemble those of *Androdecidua* in their general proportion, their variability in radial thickness, and in being as broad as the anther. Among the genera of Loropetalinae, *Loropetalum* and *Maingaya* have short, broad, and thickened filaments. The filaments of *Maingaya* are especially thick and are as broad as the anthers (Endress 1989*b*). However, at least in *Loropetalum*, the filament and the anther are broadly attached.

Short anthers, similar to those of *Androdecidua*, occur in several genera of Hamamelidaceae (e.g., *Hamamelis*, *Ostrearia*, and *Tetrathyrium*). Although the anthers of these extant genera are relatively thick in the radial plane (fig. 8*D*, 8*E*), none are as radially extensive as those of *Androdecidua*. Whereas differences in anther morphology between *Androdecidua* and members of Hamamelidaceae are relatively minor, *Androdecidua* is unique in having two structurally different types of anthers, each occurring in one of the two androecial whorls. Several genera in the family have two types of androecial organs: stamens on the outer whorl, and staminodes in the inner whorl (table 2). The androecial condition of *Androdecidua* differs from this pattern in two ways. First, the organs of both whorls were presumably fertile, as indicated by the abundance of pollen grains in the anthers of all of them. Second, the organs of the *outer* androecial whorl, rather than those of the *inner* whorl, are modified, as in extant genera of Hamamelidaceae (e.g., *Ostrearia*, *Hamamelis*, and *Maingaya*; fig. 9).

The anthers of the inner androecial whorl of *Androdecidua* conform to a bithecal and tetrasporangiate groundplan found in most angiosperms, but the anthers of the outer androecial whorl differ in having only two pollen sacs, each of which corresponds to the abaxial sac of one theca (see "Interpretation of Floral Structure"). Most genera of Hamamelidaceae have bithecal and tetrasporangiate anthers (e.g., *Corylopsis*; fig. 8*F*; table 2), but *Exbucklandia*, *Hamamelis*, and the fossil *Archamamelis* differ in having bisporangiate anthers. In these three genera, each pollen sac is placed laterally with respect to the
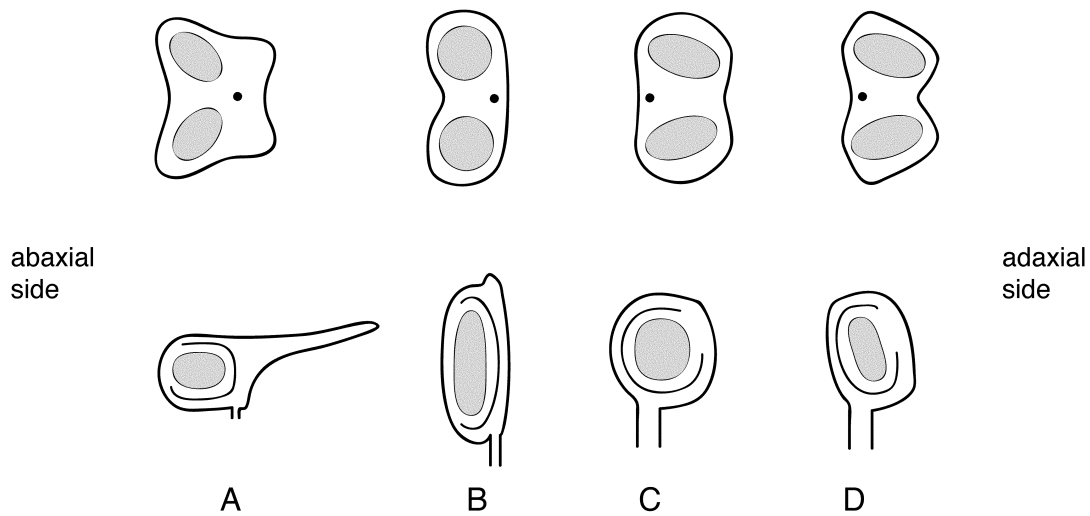
Fig. 10 Extant and fossil Hamamelidaceae with bisporangiate anthers. In all cases, the abaxial side of anthers faces left, and the adaxial side faces right. The upper row shows anthers in transverse section, including placement of pollen sacs (gray areas) with respect to main vascular strand of the anther (black dot). The lower row shows anthers in lateral view, including the placement of the stomium (solid line) with respect to the pollen sacs (gray areas). A, *Androdecidua*. Anthers of the outer androecial whorl. Pollen sacs are placed abaxially with respect to main vascular strand. B, *Exbucklandia*. Pollen sacs are placed abaxially with respect to main vascular strand. C, *Hamamelis*. Pollen sacs are placed adaxially with respect to main vascular strand. D, *Archamamelis*. Pollen sacs are placed adaxially with respect to main vascular strand.

main vascular strand of the anther, indicating a bithecal condition.

The pollen sacs of *Exbucklandia* correspond to the abaxial sac in each theca, as documented by their abaxial placement with respect to the main vascular strand of the anther (fig. 8G). This interpretation is supported by the bulging of the pollen sacs on the abaxial side of the anther (fig. 8I) and also by the orientation of the curved stomia, with their long vertical segment placed on, or close to, the adaxial surface of the anther (fig. 8G) and with their ends pointing toward the abaxial side (figs. 8H, 10B). At dehiscence, each stomium forms a valve that opens extrorsely. The possibility that the long filaments of *Exbucklandia* may be twisted is rejected on the grounds that the filaments are dorsiventrally flattened, thick, fleshy, and not prone to twisting (fig. 8I). Examination with the SEM showed that filaments of *Exbucklandia* may bend moderately to their sides but did not reveal evidence of twisting.

The pollen sacs of *Hamamelis* and *Archamamelis* correspond to the adaxial one of each theca, as indicated by their placement on the adaxial side of the vascular strand of the anther (fig. 10C, 10D; fig. 11A; Endress 1989a; Endress and Friis 1991). The stomium is curved and oriented with its vertical section approximately at the level of the anther's vascular strand (fig. 11A), close to the abaxial side of the anther (fig. 11C), with its ends pointing toward the adaxial side of the anther (fig. 11B, 11C). The single valve of each theca opens introrsely at dehiscence (fig. 11C).

The bithecal and bisporangiate anthers of the outer androecial whorl of *Androdecidua* are structurally similar to those of *Exbucklandia* in having the abaxial pollen sac of each theca preserved, and they are different from those of *Hamamelis* and *Archamamelis*, in which each theca has the adaxial pollen sac (fig. 10). However, the anthers of *Androdecidua* resemble those of *Hamamelis* and *Archamamelis* in being short

and rounded, whereas those of *Exbucklandia* are elongate and somewhat dorsiventrally flattened. The bithecal and bisporangiate anthers of *Androdecidua* are unique in preserving part of the inner half of the anther, although pollen sacs are not formed in it.

Stomia formed by a vertical segment with horizontal proximal and distal prolongations, which form valves at dehiscence, are relatively rare among angiosperms as a whole but are present in several taxa of early-diverging angiosperm lineages (e.g., *Nuphar*, *Eupomatia*, *Degeneria*, and Annonaceae), as well as in some basal eudicots (e.g., *Platanus* and Trochodendrales). They also occur frequently among genera of Hamamelidaceae (e.g., *Corylopsis*, Loropetalinae, Eustigmateae, and some Fothergilleae and *Rhodoleia*). Stomia of *Androdecidua* form valves at dehiscence; however, the pattern is modified as a result of the asymmetry on the horizontal segments of the stomium in both inner and outer stamens and because of the absence of the inner pollen sacs in the outer stamens. Stomia of anthers of the outer androecial whorl have a short distal segment and a long proximal segment, which extends upward close to the abaxial side of the anther. As a result of the different lengths of the proximal and distal stomial segments, the single valve of each theca opens extrorsely and upward (fig. 7A, 7B). A similar stomial configuration, resulting in a slight upward opening of the thecal valve, occurs in *Hamamelis* and in *Archamamelis*. However, because the single pollen sac in each theca corresponds to the adaxial one, the valves in *Hamamelis* and *Archamamelis* open introrsely (fig. 10C, 10D; Endress and Friis 1991). Stomia of the anthers of the inner androecial whorl of *Androdecidua* are also asymmetric. The abaxial portion of the stomium has a short distal segment and a long proximal segment, and the resulting valve opens extrorsely and upward, as in the anthers of the outer androecial whorl (fig. 7C, 7D). The adaxial portion of the stomium has a long distal segment
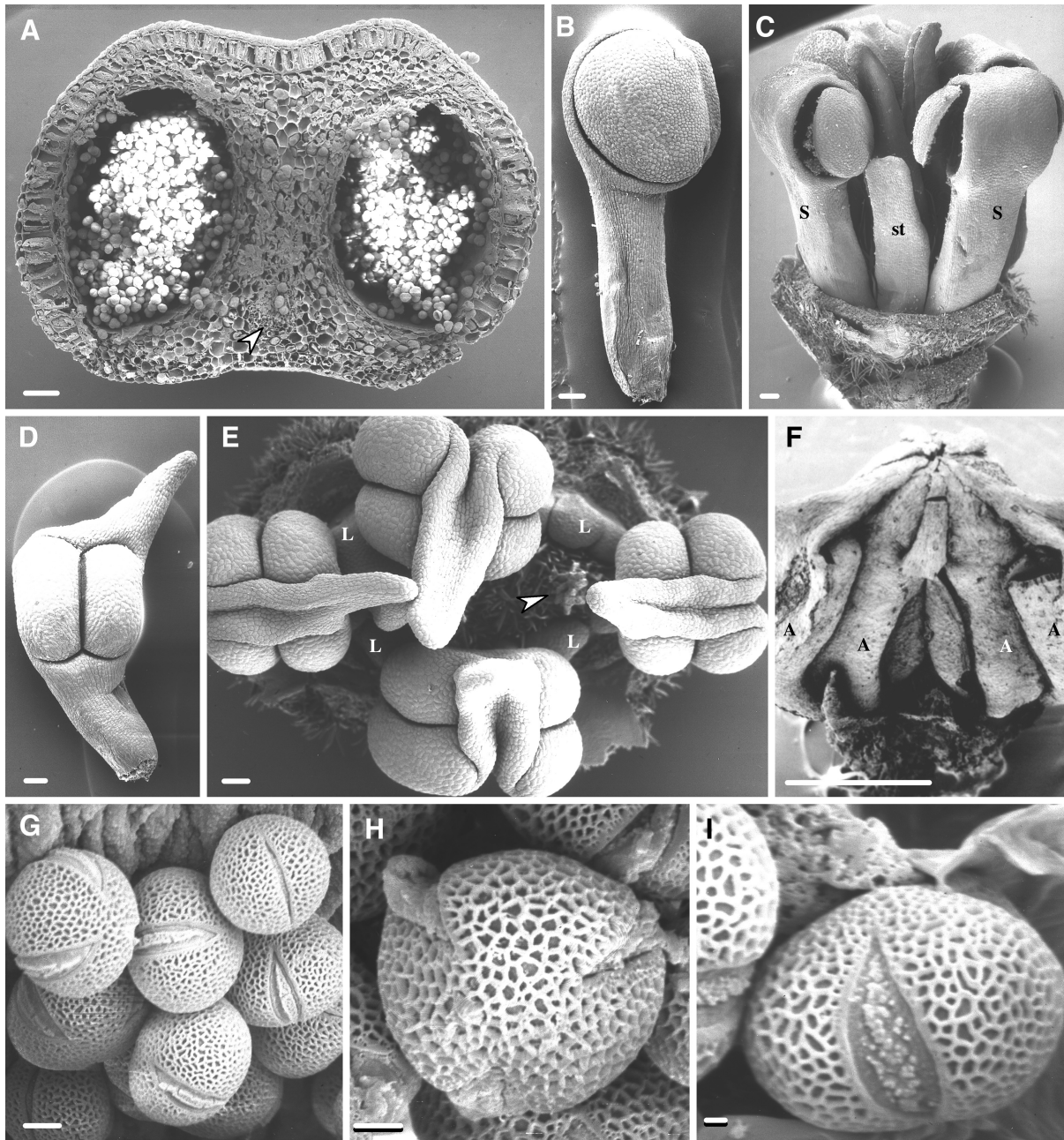
Fig. 11 Extant and fossil Hamamelidaceae. *A, Hamamelis vernalis*. Anther in cross section, showing two pollen sacs placed adaxially with respect to main vascular strand of anther (arrow). Scale = 100 μm. *B, Hamamelis vernalis*. Stamen in side view, with abaxial side facing right. Ends of the stomium point adaxially. Scale = 100 μm. *C, Hamamelis vernalis*. Flower with perianth removed, showing dehisced stamens (*S*), with valves opening introrsely, and staminodes (*st*). Scale = 250 μm. *D, Loropetalum chinense*. Lateral view of stamen with partially dehisced theca and prominent apical extension of connective. Scale = 100 μm. *E, Loropetalum chinense*. Top view of partially dissected tetramerous flower, showing four stamens, one style (arrow), and lobes of disc (*L*) placed between gynoecium and androecium. Connective extensions of all stamens are flattened, prominent, and converge above the center of the flower. Scale = 100 μm. *F, Allonia decandra*. Top-lateral view of flower. Stamens with elongated anthers (*A*) and prominent apical extension of connectives directed toward the center of the flower. Scale = 500 μm. *G, Disanthus cercidifolius*. Pollen grains with reticulate exine and gemmae on colpi membrane. Scale = 5 μm. *H, Noahdendron nicholasii*. Pollen grain in polar view showing three colpi with gemmae on aperture membrane and reticulate exine. Scale = 5 μm. *I, Hamamelis vernalis*. Pollen grain showing reticulate exine and gemmae on aperture membrane. Scale = 1 μm.

and a short proximal segment, and the resulting valve opens introrsely and downward (fig. 7C, 7D). A similar pattern of anther dehiscence is unknown among extant genera of Hamamelidaceae.

Anthers with a long and massive prolongation of the connective, which extends from the top of the anther toward the center of the flower, similar to those in *Androdecidua*, characterize the genera of subtribe Loropetalinae (fig. 11D, 11E), including the fossil *Allonia* (fig. 11F). Such an extension also occurs in *Noahdendron* (Dicoryphinae; fig. 8B). Other genera of Hamamelidaceae (e.g., *Ostrearia* and some species of *Trichocladus*) also have an apical, centripetal connective extension, but it is substantially less prominent. Among genera of Loropetalinae, the connective extensions of all stamens converge above the center of the flower and cover, at least partially, the gynoecium, which has very short styles (fig. 11E). Endress (1989b) suggested that the convergent connective extensions play a role in pollination biology. The connective extensions of the anthers of *Androdecidua* are flattened and massive and resemble those of *Loropetalum* (fig. 11E). A feature shared by *Androdecidua* and *Allonia*, one which is rare among extant Hamamelidaceae, is the close lateral proximity among connective extension of radially adjacent stamens (figs. 5C, 11F). In these two fossil genera, there are no gaps between adjacent connective extensions. This lateral proximity is probably the result of the inevitable close spacing of 10 androecial organs, as it occurs in *Ostrearia* (fig. 8D, 8E). In spite of their close lateral association, the connective extensions of *Androdecidua* and *Allonia* were most likely free from each other, and the lateral coalescence observed in some specimens of *Androdecidua* probably resulted from the fossilization process.

Tricolpate pollen grains occur mostly among taxa of early-diverging lineages of eudicots (e.g., some ranunculids, Platanaceae, Nelumbonaceae, some species of *Buxus*, Trochodendrales, as well as a few core eudicot taxa). One of these is Hamamelidoideae, in which tricolpate pollen grains with reticulate exine ornamentation are widespread, particularly among insect-pollinated genera. The grains of *Androdecidua* have the greatest overall similarity with those of *Trichocladus*, particularly in the pattern of the exine reticulum and in the presence of a distinct line of gemmae on the aperture membrane (Bogle and Philbrick 1980, pl. 15). There is also considerable similarity with the grains of *Loropetalum* (Bogle and Philbrick 1980, pl. 16), *Disanthus* (fig. 11G), *Ostrearia*, *Noahdendron* (fig. 11H), *Corylopsis*, and *Hamamelis* (fig. 11I).

The androecium of *Androdecidua* resembles that of *Ostrearia* in general form and proportions. Both genera have two androecial whorls, and androecial organs are short, broad, and converge at the center of the flower (cf. fig. 1A, 1E, 1F vs. fig. 8D, 8E). However, important differences between both genera include a specialized stomial configuration and mode of anther dehiscence in *Ostrearia*, in which each theca opens through a single valve that uncovers the two pollen sacs. Additionally, stamens of *Ostrearia* lack a prominent connective extension, and the inner whorl is staminodial. *Androdecidua* shares with genera of Loropetalinae, including *Allonia*, the massive anther connective extensions as well as the mode of anther dehiscence. The fusion of an-

droecial organs and petals into a unit that detached from the floral receptacle, as well as the presence of two structurally different types of anthers, is unique to *Androdecidua*.

Conclusion

The morphological features of *Androdecidua* indicate a relationship to subfamily Hamamelidoideae (Hamamelidaceae). The presence of an elongated centripetal connective extension together with a generalized mode of anther dehiscence indicate the presence of a particularly close affinity with the genera of tribe Hamamelideae, subtribe Loropetalinae. This affinity, based on a general assessment of floral features, is also supported by morphology-based phylogenetic analyses (Magallón 1999, 2000; S. Magallón, unpublished manuscript).

Most of the morphological characters of *Androdecidua* are found in isolation, or in partial combination, in genera of subfamily Hamamelidoideae, tribe Hamamelideae, and subtribe Loropetalinae. Flowers with fixed merosity and an androecium formed by two whorls of stamens are unknown among extant Hamamelidaceae. However, this androecial configuration is present in the fossil *Allonia decandra*, which belongs to crown group Loropetalinae (Magallón et al. 1996). With its unique androecial organization, comprising two structural types of functional anthers, *Androdecidua* increases the known floral diversity of Hamamelidaceae. Furthermore, the fusion of stamens and petals, and their detachment as a unit from the receptacle, represents a level of floral synorganization previously unknown among Hamamelidaceae and among taxa of the saxifragalean clade.

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