

The Relationship Between *Anisosperma* and *Fevillea* (Cucurbitaceae), and a New Species of *Fevillea* from Bolivia

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Communicating Editor: Andrea Schwarzbach

Abstract—We describe and illustrate the new species *Fevillea anomalosperma* from the semideciduous forests of northwestern Bolivia. Analysis of chloroplast DNA sequences representing most genera of Cucurbitaceae, including *Fevillea* with four of its seven species, supports placing the new species in *Fevillea* despite its small (10–11.5 × 7.5–10 mm, 2–3 mm thick), flattened, and highly sculptured seeds, which are unusual in the genus. The molecular phylogeny also revealed that the recent sinking of the monotypic genus *Anisosperma* into *Fevillea* is not justified.

Resumen—Se ilustra y describe *Fevillea anomalosperma*, una nueva especie de los boques semi-decíduos del noroeste de Bolivia. Aunque las hojas y las flores son típicas de *Fevillea*, las semillas pequeñas (10–11.5 × 7.5–10 mm, 2–3 mm de grueso), aplanadas y muy esculpidas de esta nueva especie no lo son. La posición de esta nueva especie dentro de *Fevillea* ha sido apoyado por análisis filogenéticos de secuencias de ADN del cloroplasto, en los cuales se ha incluido representantes de la mayoría de los géneros de Cucurbitaceae, junto con cuatro especies de *Fevillea*. Filogenia molecular demuestra que la inclusión del género monotípico *Anisosperma* en *Fevillea* no es justificada.

Keywords—*Anisosperma*, dry forests of Bolivia, Fevilleeae, molecular phylogenetics, oil-rich fruits.

The cucurbit genus *Fevillea*, named after the French clergyman and explorer L. É. Feuillée (1660–1732), comprises tall lianas of moist or wet forests from southern Mexico and the Caribbean to northern Argentina. A recent revision (Robinson and Wunderlin 2005b) recognized seven species in two subgenera, one with six species, the other containing *Fevillea passiflora* Vell., the former *Anisosperma passiflora* (Vell.) Silva Manso. The oil-rich seeds of some *Fevillea* species can weigh three to nine g when dry (Robinson and Wunderlin 2005b) and are among the largest seeds in the Cucurbitaceae, exceeded only by those of the Old World genera *Telfairia* Hook. and *Hodgsonia* Hook. f. & Thomson. Indigenous South Americans apparently have used the oil of *F. cordifolia* L. and *F. trilobata* L., species locally known as nhandiroba, for burning and as medicine for centuries (Gentry and Wettach 1986; www.cnpf.embrapa.br/publica/folders/Nhandiroba_2004.pdf). The same is true of *Anisosperma passiflora* (*Fevillea passiflora*), known in Brazil as castanha-mineira, andiroba, castanha de bugre, or castanha de jatoba (Silva Manso 1836; Martius 1843, 1854).

A collection made in 1987 in northwestern Bolivia in the Departamento La Paz, Provincia Nor Yungas, and others made in 2005 and 2006 in the adjacent Provincia Tamayo, have brought to light a new species that is described here. The new entity appeared to be a *Fevillea*, except for its unusual fruit and seeds. We therefore tested the phylogenetic affinities of the new species with a chloroplast data set that included two accessions of the new species, four other species of *Fevillea* (including the type species, *F. trilobata* L.), representatives of all genera of Fevilleeae, and other species of Cucurbitaceae from all but one of the genera of the family.

MATERIALS AND METHODS

Morphology—The first author studied all relevant specimens in the herbaria MO, NY, and LPB and the other authors specimens in BM, K, and M. Measurements are from herbarium specimens.

Sequencing and Taxon Sampling—DNA extraction and sequencing followed standard procedures, using the *rbcl*, *matK*, *rpl20-rps12*, and *trnL* and *trnL-F* primers and polymerase chain reaction (PCR) protocols listed in Kocyan et al. (2007). Total genomic DNA was isolated from silica-dried leaves or from herbarium specimens with a commercial plant

DNA extraction kit (NucleoSpin, Macherey-Nagel, Düren, Germany), following the manufacturer's instructions. Thermal reaction products were purified with a PCR clean-up kit (PCR Wizard, Promega GmbH, Mannheim, Germany), and cycle sequencing was performed with the BigDye Terminator cycle sequencing kit on an ABI Prism 3100 Avant automated sequencer (Applied Biosystems, Foster City, California). Twelve sequences were newly generated for this study, and their Genbank accession numbers and vouchers are listed in Appendix 1. Accession numbers for all other sequences used for the analyses are given in Kocyan et al. (2007) and Schaefer et al. (2009).

Phylogenetic analyses were conducted with a 147-taxon subset of the family dataset of Schaefer et al. (2009), which includes all but one of the genera of Cucurbitaceae and 25% of the 960 species. Besides two accessions of the new species, we included four species of *Fevillea*, including the type species, and six species representing the other three genera of Fevilleeae. As outgroups, we used 15 species of Anisophylleaceae, Begoniaceae, Coriariaceae, Corynocarpaceae, Datisceae, and Tetramelaceae based on Zhang et al. (2006). The only genus of Cucurbitaceae that has not yet been sequenced is *Khmeriosicyos* W. J. de Wilde & Duyfjes, a monotypic genus from Cambodia, known only from the type. Judging from floral morphology, it is not closely related to *Fevillea*.

Sequence Alignment and Phylogenetic Analyses—Sequences were edited with Sequencher (4.6; Gene Codes, Ann Arbor, Michigan) and aligned by eye. The aligned plastid matrix comprises 4,973 nucleotides after exclusion of a TATATA microsatellite region in the *trnL-F* intergenic spacer. The data matrix and trees have been deposited in TreeBASE study number S2210 in connection with Schaefer et al. (2009).

Maximum likelihood (ML) analyses and bootstrap searches were performed using RAxML-VI-HPCL v7.0.4 (Stamatakis et al. 2008, available at <http://phylobench.vital-it.ch/raxml-bb/>). RAxML searches relied on the GTR + G + I model. Model parameters were estimated over the duration of specified runs.

RESULTS

Morphologically, the new species belongs to the tribe Fevilleeae Benth. & Hook. f., which apart from *Fevillea* comprises *Pteropepon* (Cogn.) Cogn. (probably to include *Pseudosicydium* Harms) and *Sicydium* Schltdl. (including *Chalema* Dieterle) from the New World, and *Cyclantheropsis* Harms, which has two species in East and South tropical Africa and one endemic in Madagascar (Schaefer and Renner 2009). These other genera all have single-seeded fruits, and based on chloroplast DNA, are not close to the new species (Fig. 1).

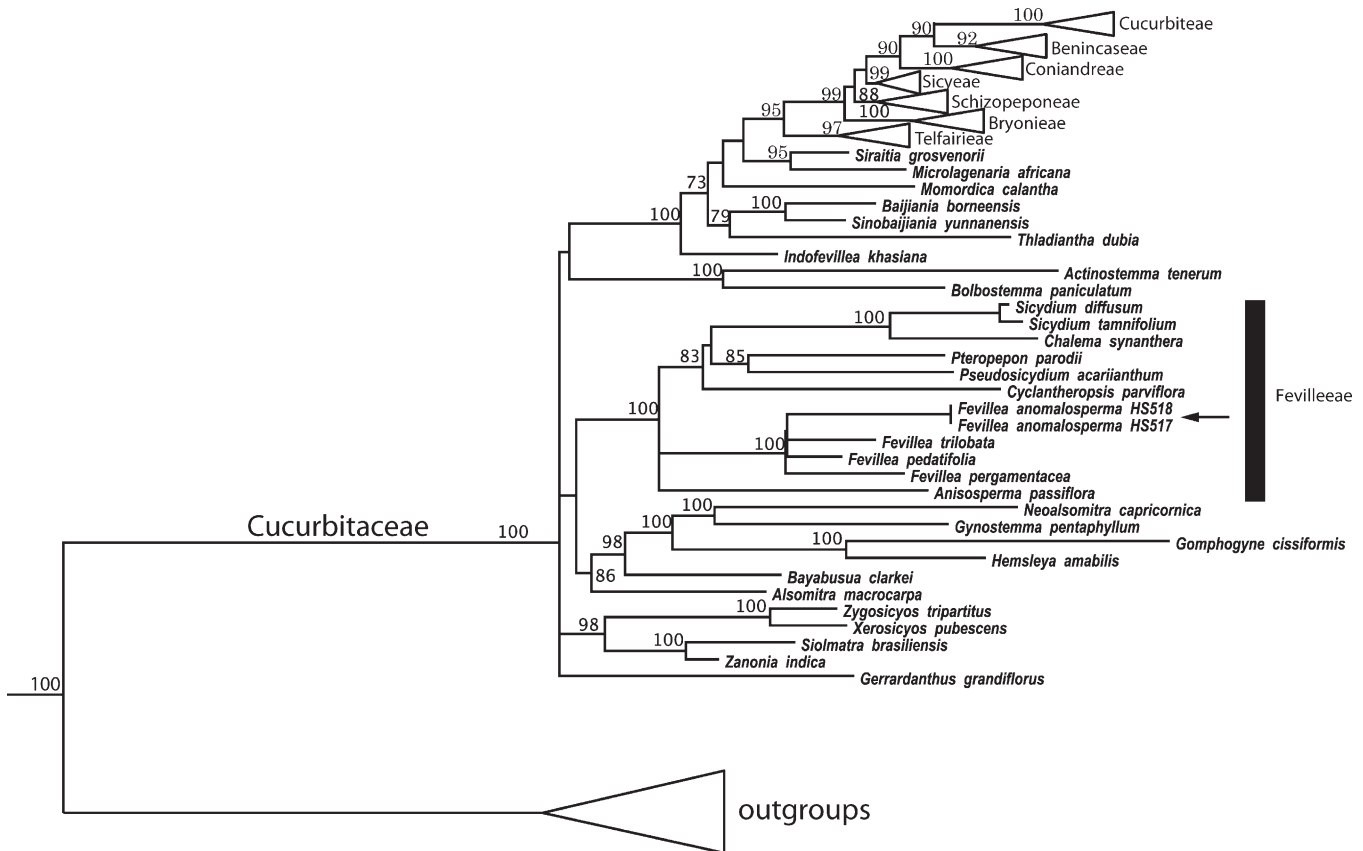


FIG. 1. Condensed version of a maximum likelihood phylogram for 147 taxa (only 24 shown), including representatives of all but one genus of Cucurbitaceae (Schaefer et al. 2009; this study). Likelihood bootstrap values >60% are shown at the nodes. The two accessions of *Fevillea anomalosperma* M. Nee are nested within the *Fevillea* clade, while the accession of *Anisosperma (Fevillea) passiflora* is not.

The tendrils of *Fevillea anomalosperma* are simple, and hence the characteristic of tendrils spiraling both above and below the point of branching, typical of many species of Fevilleeae, is not applicable. The presence of five free, bilocular anthers in *Fevillea* (and the new species) is unique for the family (Robinson and Wunderlin 2005b), but without pistillate flowers, we cannot assess whether the new species has the three free styles characterizing early-diverging Cucurbitaceae. The apparently capsular fruits of *F. anomalosperma* are similar to those of *Siolmatra* Baill. (Robinson and Wunderlin 2005a), a genus of two species that have fruits with three to six flattened, winged seeds and that occur in southern Amazonian forests as well as the dry forest to the south. Molecular data support *Siolmatra* as being sister to the monotypic Asian *Zanonia* L., with both then sister to a clade of African and Madagascan genera (Kocyan et al. 2007; Schaefer et al. 2009).

Robinson and Wunderlin (2005b) divided *Fevillea* into the typical subgenus *Fevillea*, with six species, and a monotypic subgenus *Anisosperma* (Silva Manso) G. Rob. & Wunderlin. Our new species most closely resembles species in subgenus *Fevillea*. The leaves and male inflorescences of *F. anomalosperma* are almost identical to those of *F. trilobata* from eastern Brazil. However, the pedicels in *F. trilobata* are prominently glandular in the distal half, and the flowers are greenish white, while in *F. anomalosperma* the pedicels are glabrous and the flowers are dull dark reddish (Fig. 2). Unfortunately, the fruits of *F. trilobata* are not well known (Robinson and Wunderlin

2005b). Another species in subgenus *Fevillea*, *F. cordifolia*, has flowers of exactly the same form and dull reddish-brown color as those of *F. anomalosperma*, but differs as indicated in the key.

Three species of *Fevillea* overlap the range of *F. anomalosperma* in Bolivia (Nee unpubl. data): *Fevillea cordifolia*, *F. pergamentacea* (Kuntze) Cogn., and *F. pedatifolia* (Cogn.) C. Jeffrey. All three have subglobose fruits 6–13 cm in diameter and 6–16 cm long with lenticular seeds 3.5–6 cm wide and 1–2.5 cm thick (Robinson and Wunderlin 2005b), different from the fruits of *F. anomalosperma*. The distinct testa structure, however, seems to be similar in all four species. The fruits of *F. pedatifolia* (as *F. peruviana* (Huber) C. Jeffrey) were described as dry capsules (Jeffrey 1962) based on herbarium material of *Krukoff 8466*, and in Robinson and Wunderlin (2005b) there is a personal communication from A. Gentry indicating that the fruits may have circumscissile dehiscence around the hypanthium lip scar. In the carpological collection at Kew, only fruits of *F. cordifolia* show these openings, but not the collections of *F. pedatifolia*. The fruits of *F. passiflora* might open by longitudinal splitting of the fruit walls, but this is more likely an artifact of drying. The fruit of *F. anomalosperma* appears to dehisce apically, and the few available fruits look as if a lid had fallen off (although none are preserved).

The second subgenus of *Fevillea* in the treatment of Robinson and Wunderlin (2005b) contained only *F. passiflora* Vell. (*Anisosperma passiflora* (Vell.) Silva Manso) from eastern Brazil, a species with simple, entire leaves that lacks glandular



FIG. 2. *Fevillea anomalosperma*. Leaf and a detached staminate flower. Fuentes & Miranda 10893.

calycine squamellae and medial adaxial appendages on the corolla lobes. Fruits of this species are ovoid or oblong, subtrigonal, and shortly apiculate, not zonate above the middle as in species of *Fevillea*. The ovary of *F. passiflora* is thus fully inferior, and the seeds are suborbicular, compressed, 3.5–3.5 cm long, 3–4 cm wide, and ca. 1.5 cm thick (Robinson and Wunderlin 2005b).

The 147-taxon DNA sequence matrix yielded a reasonably well-resolved phylogram of which we show a condensed version that focuses on Fevillaceae and close relatives (Fig. 1). Our new Bolivian species is nested within *Fevillea* subgenus *Fevillea*, which is sister to a clade comprising *Sicydium*, *Pteropepon*, and *Cyclantheropsis*. *Anisosperma passiflora* does not cluster with the other species of *Fevillea* but instead forms a polytomy with *Fevillea* and the *Sicydium* clade. We are therefore satisfied that the new Bolivian species *F. anomalosperma* is correctly placed in the genus *Fevillea*. The phylogenetic placement of *F. passiflora*, however, together with its morphological and genetic distinctness (the latter evident from the relative branch lengths in the phylogram, Fig. 1), requires ranking this species as a separate genus. This also has the advantage of preserving the usage accepted in numerous ecological and phytochemical studies, as well as legislation for the protection of nature in the State of São Paulo (e.g. Resolução n° 48, de 21/09/04. Publica lista preliminar das espécies da vegetação do Estado de São Paulo ameaçadas de extinção. Available online.)

TAXONOMIC TREATMENT

KEY TO THE GENERA OF TRIBE FEVILLACEAE IN SOUTH AMERICA AND TO THE SPECIES OF *FEVILLEA* IN BOLIVIA

1. Leaves compound, 3–5-foliolate; fruit with ca. 3–12 seeds. 2
2. Leaves without paired gland-like foliar outgrowths on petiole; fruit an elongate capsule 3.5–4.5 × 2–3 cm, apically dehiscent; seeds 3–6, apically attached in the single locule, strongly flattened, 3–5.5 × 0.8–1.5 cm, 2 mm thick, prominently winged. *Siolmatra*
2. Leaves with paired gland-like foliar outgrowths near apex of petiole but separate from petiolules; fruit subglobose, apparently indehiscent or perhaps circumscissile; seeds ca. 12, axile in the three locules, flattened-lenticular, 4–5 cm in diameter, 1.5–2.5 cm thick, the wing-like margin only 5 mm wide. *Fevillea pedatifolia*
1. Leaves simple, entire or (deeply) lobed; fruit with a single seed or with ca. 12–17 seeds 3
3. Fruit a berry or flattened samara with a single seed. 4
4. Fruit a fleshy, globose berry, 1–1.5 cm in diameter, dark purple-black or black at maturity. *Sicydium*
4. Fruit a dry flattened samara, surrounded by a wing, 1.5–1.6 × 1.4–1.8 cm and retuse at both ends (*P. parodii* Mart. Crov.) or 7.8–9. × 6.6–7.1 cm and acute to acuminate at both ends (*P. deltoideus* Cogn.), greenish at maturity. *Pteropepon*
3. Fruit a dry capsule or pepo with ca. 12–17 seeds. 5
5. Leaves entire, narrowly ovate, acuminate *Anisosperma*
5. Leaves entire to ± deeply lobed, or broadly cordate 6
6. Leaves with paired gland-like foliar outgrowths near apex of petiole but separate from the blade, or the outgrowths at base of blade and insertion of petiole, without thickened glandular zone at apex of leaf lobes; staminate flowers yellow-green. 7
7. Leaves with 2 paired gland-like foliar outgrowths near apex of petiole but separate from blade *Fevillea pedatifolia*
7. Leaves with 2 paired gland-like foliar outgrowths at base of blade and insertion of petiole *Fevillea pergamentacea*
6. Leaves without paired gland-like foliar outgrowths near base of blade and insertion of petiole, but with thickened glandular zones at apex of leaf lobes; staminate flowers reddish brown. 8
8. Fruit probably a capsule, narrowly campanulate, 3.5–4.5 × 3 cm, the dehiscence not certain, perhaps with a dehiscent cap; seeds ca. 17, irregularly ovate, 1.0–1.15 × 0.75–1.0 cm, 0.2–0.3 cm thick, irregularly sculptured with raised protuberances, these projected at both ends and with 2–3 similar projections per side. *Fevillea anomalosperma*
8. Fruit a coriaceous pepo, subglobose, 10–12 cm in diameter, 10–16 cm long; seeds ca. 12, suborbicular, irregularly flattened-lenticular, 3.5–5 × 4.5–6 cm, 1–2.5 cm thick, minutely pustulate *Fevillea cordifolia*

Fevillea anomalosperma M. Nee, sp. nov.—TYPE: Bolivia. La Paz: Prov. Franz Tamayo, Parque Nacional Madidi, Río Tuichi, Arroyo Pintata, 14°25'43"S, 68°35'16"W, 250 m, 5 Dec 2005 (♂ fl), A. Araujo-M., A. Poma, P. Garagorri, S. Paredes & E. Cuevas 2680 (holotype: LPB!; isotypes: MO 6100168!, NY!).

Liana, ut videtur herbacea, dioica? Folia matura membranacea, glabra, 3–5-lobata, lobi apice glandulosi. Flores masculi 5

anthera liberis, 2-locularibus. Fructus capsularis?, apice dehiscent?, campanulatus, 4.5 × 3 cm, cartaceo-coriaceus. Semina 10–11.5 mm longa, 7.5–10 mm lata, 2–3 mm crassa, complanata, grosse sculpta, fuliginosa.

Lianas, dioecious?, the stems herbaceous, 1.5–2.5 mm in diameter when dry and ridged, the youngest parts minutely furfureous-pubescent with hairs ca. 0.1 mm long, immediately glabrescent. Leaves alternate; pedicels 1.2–2.4 cm long, sometimes twisted at the base; tendrils simple, 9–12 cm long, coiled

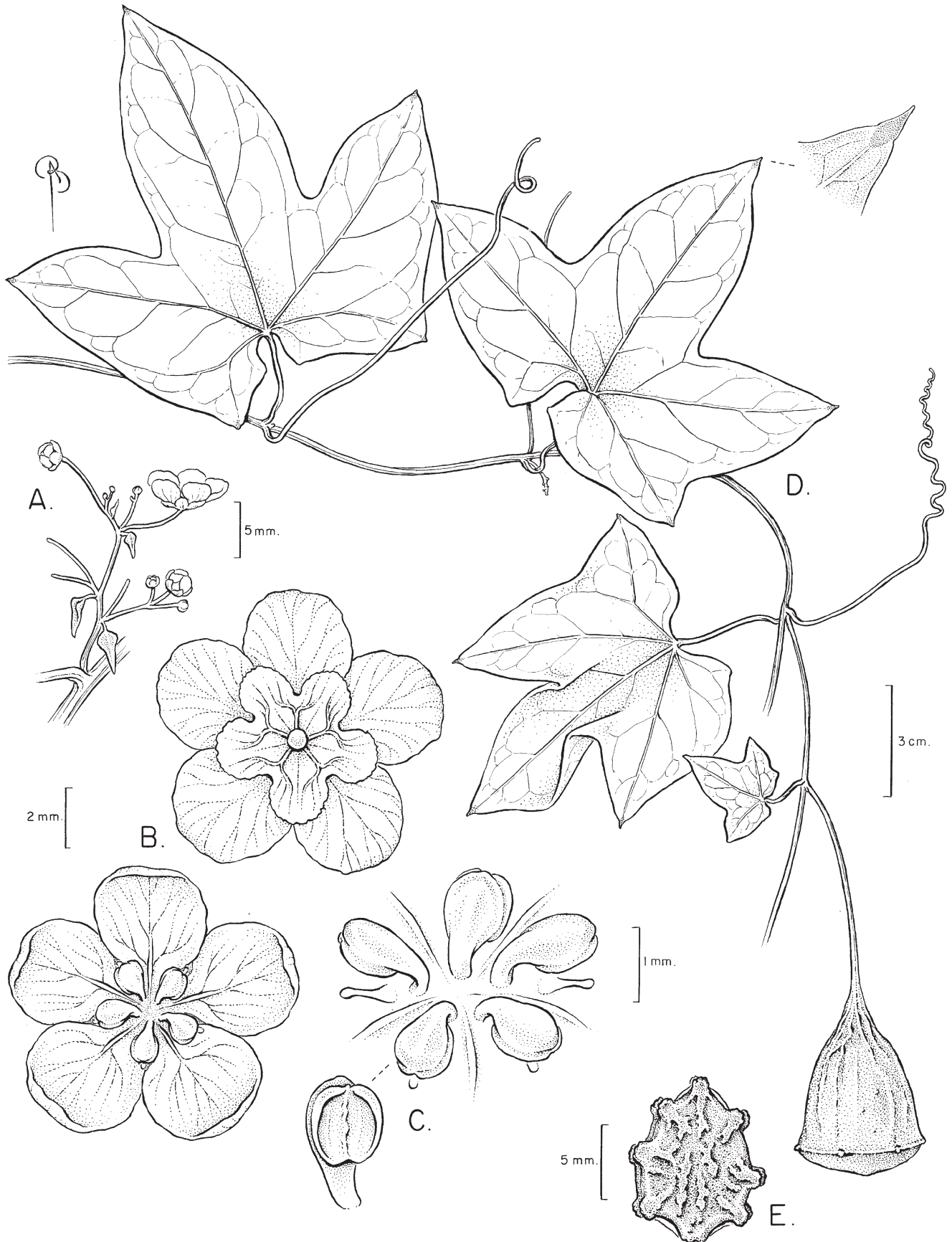


FIG. 3. *Fevillea anomalosperma*. A. Staminate inflorescence. B. Staminate flower in abaxial (above) and adaxial (below) views. C. Staminate flower detail of five free stamens and abaxial view of one anther with two locules. D. Habit of stem with one fruit. E. Seed. A–C Cayola 1729 (NY); D–E Araujo-M. et al. 2680 (isotype NY).

in the distal 1/2–1/3; blade membranaceous, 8–12 × 7–12.5 cm, deeply cordate at the base with a narrow sinus, 3-lobed, the lobes reaching about halfway or less to the base, the lobes ovate, acuminate or rounded, the terminal lobe 4.5–7 × 3–4 cm, the basal lobes again with a shallow rounded or angulate lobe at the base, the lobes apically with a slight glandular thickening, the blades very minutely appressed-pubescent with hairs 0.2 mm long when very young, immediately glabrescent. Inflorescences lateral to the base of the petiole. Male inflorescence an irregular panicle 1.5–2.5 cm long, with appearance of a developing shoot with ca. 3 branches, with 2–3 curled and only partially developed leaf-like bracts to 1.2 cm long; flowers brown (“café”) or dull dark reddish when alive, or a dull reddish brown when dry, glabrous; pedicels filiform, 4–7 mm long, articulate at the apex; calyx lobes orbicular, membranous, 1.5–2 × 1.5–2 mm, ciliate with minute gland-tipped hairs 0.05 mm long; corolla lobed about half way to base, the lobes semiorbicular 2.5–4 × 3.5–4 mm, with a central adaxial appendage, or this not obvious; stamens 5, free, the filaments curved away from center of flower, 0.6–0.7 mm long, the anthers facing the corolla surface and nearly touching it, bilocular; pistillode none. Pistillate inflorescence in flower not seen; peduncle in fruit 4.5–9 cm long, sometimes with a rachis 2 cm long extending past the fruiting pedicel, sometimes with a shallowly 3-lobed foliaceous bract 2 × 2 cm; pedicel in fruit solitary, 6–11 cm long. Fruit probably a capsule, narrowly campanulate, 3.5–4.5 × 3 cm, the pericarp chartaceous-coriaceous, glabrous, the surface minutely tuberculate and scabridulous, the calyx and petal scar apparently forming a line ca. 3 mm below the rim, but dehiscence not certain, perhaps with a dehiscent cap. Seeds ca. 17 per fruit, flattened, irregularly ovate, irregularly sculptured with raised protuberances, these projected at both ends and with 2–3 similar projections per side, brown, hard, 10–11.5 × 7.5–10 mm, 2–3 mm thick. Figures 2, 3.

Additional Specimens Examined—BOLIVIA. La Paz: Prov. Nor Yungas: Caranavi 5 km hacia Coroico, 750 m, 10 Mar 1987 (♂ fl), S. G. Beck 13523 (LPB, M, MO, NY). Prov. Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, N de Apolo, 14°19'47"S, 68°33'35"W, 700 m, 17 Jun 2005 (fl), A. Araujo-M. et al. 1974 (LPB); Parque Nacional y Área Natural de Manejo Integrado Madidi, NW de Apolo, Asariamas, Río Resina, 14°19'48"S, 68°33'35"W, 700 m, 20 May 2005 (♂ fl), L. Cayola 1716 (LPB, MO, NY); Parque Nacional y Área Natural de Manejo Integrado Madidi, NW de Apolo, Asariamas, Río Resina, 14°21'34"S, 68°32'22"W, 886 m, 7 Jun 2005 (♂ fl), L. Cayola 1729 (LPB, MO, NY); Área Natural de Manejo Integrado Madidi, entre Azariamas y Sipia, 14°20'58"S, 68°32'12"W, 800 m, 21 May 2006 (♂ fl, fr), A. Fuentes & T. Miranda 10893 (LPB, MO, NY).

Habit and Habitat—Described on labels as a “liana” or “trepadora” (climber), but without details on stem diameter or height. Known only from the eastern foothills of the Andes of northwestern Bolivia, growing in semideciduous forest with *Anadenanthera colubrina* (Vell.) Brenan (Mimosaceae), *Oxandra espiptana* (Benth.) Baill. (Annonaceae), *Swietenia macrophylla* King (Meliaceae), *Gallsia integrifolia* (Spreng.) Harms (Phytolaccaceae), *Celtis loxensis* C. C. Berg (Ulmaceae), *Trichilia elegans* A. Juss. (Meliaceae), *Cavanillesia umbellata* Ruiz & Pav. (Bombacaceae), *Phyllostylon rhamnoides* (J. Poiss.) Taub. (Ulmaceae), and *Capparis* sp. (Capparaceae).

Etymology—Named in reference to the seeds, which are decidedly anomalous in the genus *Fevillea* and the entire tribe Fevilleae.

Phenology—Flowering collections December to June (the rainy season), fruits collected in May (near end of rainy season).

Sexual System—The staminate flowering material and the fruiting material cited for *Fevillea anomalosperma* certainly belong to a single species because the leaves and stems match exactly, and no other precisely similar species is known from the region. One collection, *Fuentes & Miranda 10893* (NY), has both stami-

nate flowers and a fruit, but they are on separate, unattached stems, and it is thus not known if *F. anomalosperma* is monoecious or dioecious, as would be expected in tribe Fevilleae.

Comment on Dispersal Biology—The deeply sculptured and dark brown seeds of *Fevillea anomalosperma* superficially resemble those of New World *Cyclanthera* Schrad. and the Old World *Momordica charantia* L. which is widely naturalized in the New World, both phylogenetically distant from *Fevillea*. Perhaps the dark brown color helps to camouflage the seeds as pebbles or bits of dirt when on the ground. In *Momordica*, the orange fleshy fruit is slowly dehiscent and the seeds are enveloped in a bright red pulp; in *Cyclanthera*, the fleshy mature fruits are explosively dehiscent on contact, throwing the seeds for several meters. In *F. anomalosperma*, if the fruit is apically dehiscent at maturity, the seeds might be dispersed locally by a censer mechanism if the lianas climb high enough into the trees. Observations are needed on many basic aspects of the biology of this and most other species in the Neotropics, especially in this previously unexplored part of Bolivia.

ACKNOWLEDGMENTS. We thank Richard Wunderlin for initial confirmation, via a photo of a specimen, that this was not a known species of *Fevillea*. Bobbi Angel is responsible for the illustration. We thank Tatiana Miranda and Eric Feltz for supplying high-quality images of specimens from LPB and MO, respectively.

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APPENDIX 1. Taxa, GenBank accession numbers (*rbcl*, *matK*, *trnL*, *trnL-F*, *rpl20-rps12*; “—” = sequence not obtained), and sources of plant materials from which DNA was extracted for sequencing. Abbreviations for herbaria follow the *Index Herbariorum* at <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>.

Anisosperma passiflora (Vell.) Silva Manso, G. Hatschbach 38090 (K): —, —, — FJ665817, —; *Fevillea anomalosperma* M. Nee, L. Cayola 1716 (NY): EU436377, EU436403, —, —, EU436324; *Fevillea anomalosperma* M. Nee, A. Fuentes & T. Miranda 10893 (NY): —, FJ348683, —, —, FJ348684; *Fevillea pedatifolia* (Cogn.) C. Jeffrey, C. F. P. Martius s.n. (M): EU436378, —, —, —, EU436325; *Fevillea trilobata* L., C. F. P. Martius s.n. (M): EU436379, —, EU436351, EU436351, EU436326.