
Putranjivaceae

Putranjivaceae Endl., Ench. Bot.: 174 (1841).

G. LEVIN

Trees or shrubs, with simple trichomes or sometimes stellate on fruits. Leaves alternate or rarely opposite, spirally arranged but often appearing distichous, simple, petiolate, pinnately veined, base usually oblique, margins entire or dentate, the teeth sometimes spinose; stipules deciduous or persistent. Flowers in axillary or cauliflorous clusters, sometimes solitary, rarely cymes, pedicellate, actinomorphic, generally unisexual and the plants dioecious, but occasionally polygamodioecious or monoecious; sepals (3)4–5(6), distinct, imbricate or the pistillate rarely open in bud; petals 0. Staminate flowers: stamens (2) 3–20(–50), filaments distinct, anthers erect, dithecal, introrsely or less frequently latrorsely or extrorsely dehiscent by longitudinal slits; disk intrastaminal or absent; pistillode small or absent. Pistillate flowers: sepals deciduous or persistent; disk annular or absent; ovary superior, syncarpous, 1–3(–6)-locular, placentation axile; ovules 2 per locule, anatropous, bitegmic, embedded in a massive obturator; stylodia as many as the locules, usually short, stigmas subpeltate, reniform, discoid, bilobed, or petaloid; fruit drupaceous; seeds 1 per locule or fruit by abortion, albuminous, embryo large, straight.

Two genera and c. 225 spp., tropical and subtropical Asia, Africa, America, Australia, and western Pacific islands.

VEGETATIVE ANATOMY. The leaves are dorsiventral. Druses may be found in the mesophyll, and prismatic crystals in the mesophyll and vein bundle sheaths. Venation is brochidodromous or sometime eucamptodromous; higher order venation patterns are variable and may be systematically informative. Stomata are restricted to the abaxial side and are brachyparacytic, with the subsidiary cells overlying the guard cells (Levin 1986).

Wood is ring or diffuse porous with the vessels solitary or in radial multiples. Perforation plates are scalariform, simple, or both; intervacular and ray/vessel pitting is minute and alternate. Axial parenchyma is diffuse or apotracheal in numerous short, often interrupted bands one cell wide. Rays are uniseriate and multiseriate, heterocellular. Fibers are non-septate and very thick-walled. Prismatic crystals are found in the axial and ray parenchyma (Smith and Ayensu 1964; Hayden 1980; Mennega 1987).

EMBRYOLOGY AND SEED ANATOMY. Readers are referred to the detailed descriptions by Stuppy (1996) and Tokuoka and Tobe (1999). Systematically significant features include glandular anther tapetum; two-celled pollen grains (when shed); anatropous, bitegmic, crassinucellate ovules; a two- or three-celled archesporium; a thin, two cell-layered parietal layer in the nucellus; Polygonum type embryo sac; no nucellar beak or cap; early disintegrating nucellar tissue; a massive funicular obturator; thick, multiplicative inner and outer integuments; an endothelium; Nuclear endosperm formation; abundant endosperm in the seeds; a large, straight embryo; and generally a fibrous exotegmen.

POLLEN MORPHOLOGY. Pollen is spheroidal to prolate, 3-colporate with transversely elongate ora and often with elongate colpi, and tectate-reticulate (Punt 1962; Köhler 1965). Punt (1962) assigned the pollen of *Drypetes* and *Putranjiva* to different types based on grain shape and exine thickness, whereas Köhler (1965), who sampled a more diverse set of *Drypetes* species, assigned the two genera to the same type and recognized a second pollen type in *Drypetes* based primarily on aperture length. A broader survey could reveal

that variation in shape, apertures, exine thickness, and sculpture is systematically informative.

KARYOLOGY. Chromosome numbers have been reported for only five *Drypetes* species, four African (Hans 1973) and one southeast Asian (Oginuma et al. 1998), and they are consistently $n = 20$. In contrast, counts of $n = 7, 19, 20,$ and 21 have been reported from *Putranjiva roxburghii* (Hans 1973; Sanjappa 1979; Chattopadhyay and Sharma 1988). It is possible that the base number for the family is $x = 7$, with polyploidy and aneuploidy accounting for the other numbers. It is also possible that the counts other than $n = 20$, particularly those of $n = 7$, are in error. Broader surveys are indicated.

FRUIT AND DISPERSAL. Although all fruits of Putranjivaceae are drupaceous, there is considerable variation in the exocarp. It may be fleshy, leathery, or somewhat woody, and colors at maturity include red, orange, yellow, brown, and white. Tomlinson (1980) reported that the red fruits of *Drypetes lateriflora* are removed rapidly, whereas the white fruits of *D. alba* persist on the trees for long periods. There are almost no detailed studies of fruit dispersal in the family, but various doves and pigeons have been reported to disperse the fruits of *D. deplanchei* (Floyd 1989; Forster 1997).

PHYTOCHEMISTRY. Putranjivaceae is noteworthy for producing glucosinolates (mustard oil glucosides). Phylogenetic studies demonstrate that this evolved independently here and in the Brassicales (Rodman et al. 1998). In addition, sesquiterpene lactones and friedelanones are known from the family (Wandji et al. 2003).

PHYLOGENY. Putranjivaceae traditionally have been included in Euphorbiaceae subfamily Phyllanthoideae (Phyllanthaceae) as tribe Drypeteae, along with the African genus *Lingelsheimia* Pax (Webster 1994; Radcliffe-Smith 2001). Meeuse (1990), focusing on embryology, seed anatomy, and especially chemistry, removed the tribe from the Euphorbiaceae and placed it as a family in Brassicales. Molecular phylogenies clearly show that *Drypetes* and *Putranjiva* are closely related, belong outside the Euphorbiaceae, and are members of the Malpighiales rather than the

Brassicales (Rodman et al. 1998; APG II 2003). *Lingelsheimia* has not been included in molecular studies, but its morphology is quite different from Putranjivaceae (Léonard 1962) and consistent with Phyllanthoideae.

Affinities within Malpighiales place Putranjivaceae with strong support as the sister of *Lophopyxis* (Wurdack and Davis 2009; Soltis et al. 2011), and Xi et al. (2012) have resolved Putranjivaceae and Lophopyxidaceae, the "putranjivoids", within a larger clade, elsewhere comprising Caryocaraceae, "malpighioids" (Malpighiaceae, Elatinaceae, Centroplacaceae) and the "chrysobalanoids". For morphological traits shared by Putranjivaceae and Lophopyxidaceae, see under Lophopyxidaceae, this volume.

Various efforts have been made to fragment *Drypetes* into smaller genera. The only commonly accepted segregates are *Sibangea* and *Putranjiva*. The former, which has three African species, is distinguished by having the pistillate sepals open in bud and persistent in fruit, in contrast to imbricate and deciduous in *Drypetes* s.s. (Radcliffe-Smith 2001). Phylogenetic analysis of DNA sequence data place *Sibangea* within *Drypetes* (Wurdack et al. 2004), a placement that is adopted here. Although Hurusawa (1954) reduced *Putranjiva* to a subgenus of *Drypetes*, a treatment that has been widely followed, molecular phylogenetic studies show them to be sister taxa (Wurdack et al. 2004) and here they are treated as distinct.

DISTRIBUTION AND HABITATS. *Drypetes* grows primarily in tropical and subtropical lowland forests, woodlands, and savannas. A few species are found in tropical montane forests or warm temperate areas. Its greatest diversity is in Asia, with about 120 species. About 75 species grow in Africa and Madagascar, with only about 20 species, many of them undescribed, found in the Americas. *Putranjiva* is found in forests of tropical Asia from the Indian subcontinent to Indonesia, south China, Taiwan, and the Ryukyu Islands. Most species are narrowly distributed, but *P. roxburghii* is found in seasonal forests from Pakistan to Indonesia.

ECONOMIC IMPORTANCE. Fruit of some species of *Drypetes* are eaten locally, and the hard wood is locally used in construction. Bark extracts from

several *Drypetes* species and *Putranjiva roxburghii* are used medicinally in central Africa and India; these may have pharmacological value (Chungag Anye et al. 2003). *P. roxburghii* is widely cultivated as an ornamental tree in tropical to warm temperate regions.

CONSERVATION. Although many species of Putranjivaceae are common, in some cases dominant forest trees, others are of conservation concern. This is particularly true of some island endemics, notably *Drypetes glabra* and *D. henriquesii* from São Tomé, *D. andamanica* from the Andaman Islands, *D. leiocarpa* from the Nicobar Islands, and *D. riseleyi* from the Seychelles.

KEY TO THE GENERA

1. Disk present; stamens mostly 4 or more; stigmas somewhat swollen and subpeltate, reniform, discoid, or bilobed, but not petaloid **1. *Drypetes***
- Disk absent; stamens mostly 2 or 3; stigmas conspicuously dilated and petaloid **2. *Putranjiva***

1. *Drypetes* Vahl

Fig. 63

Drypetes Vahl, *Eclog. Amer.* 3: 49 (1810); Pax & K. Hoffm., *Pflanzenreich* 147. XV: 229–279 (1922), rev.; Airy Shaw, *Kew Bull. Addit. Series* 4: 97–108 (1975), rev. Borneo spp.; Airy Shaw, *Kew Bull.* 36: 286–292 (1981), rev. Sumatra spp.; Radcl.-Sm., *Fl. Trop. E Africa, Euphorbiaceae* I: 88–103 (1987), rev. E Afric. spp.; Radcl.-Sm., *Fl. Zambes.* 9(4): 87–93 (1996), rev. SE Afric. spp.; P.I. Forster, *Austrobaileya* 4: 477–494 (1997), rev. Australian spp.; T. Chakrab et al., *J. Econ. Taxon. Bot.* 21: 251–280 (1997), rev. S Asian spp.; McPherson, *Adansonia* III, 22: 205–209 (2000), rev. Madag. spp.; L. Phuphathanaphong and K. Chayamarit, *Flora of Thailand*, 8(1): 231–253 (2005), rev. Thai spp.

Sibangea Oliv. (1883).

Trees or shrubs, usually dioecious. Leaves alternate or rarely opposite, spiral but sometimes appearing distichous, petiolate, stipulate, pinnately veined, usually oblique at the base, margins entire or spinose-dentate. Flowers in axillary clusters or cauliflorous; sepals 4–5, imbricate or the pistillate rarely open in bud; petals none. Staminate flowers: stamens 3–20(–50); disk intrastaminal; pistillode small or none. Pistillate flowers: disk annular; ovary 1–3(–6)-locular; stigmas subpeltate, reniform, discoid, or shallowly bilobed. Fruit drupaceous. Seeds 1 per locule or fruit. $n = 20$.

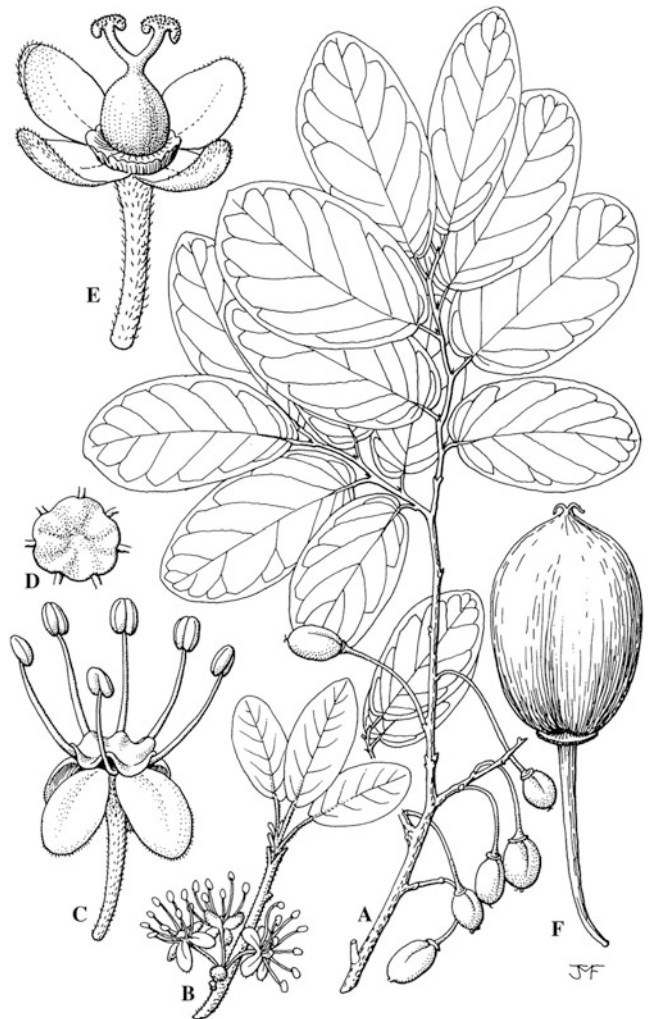


Fig. 63. Putranjivaceae. *Drypetes mossambicensis*. A Part of distal branch with immature fruits. B Staminate inflorescence. C Staminate flower. D Disk thereof. E Pistillate flower. F Fruit. (Radcliffe-Smith 1996; drawn by J.-M. Fothergill)

About 220 spp.; subsaharan Africa, southern and eastern Asia, Australasia, and tropical America.

2. *Putranjiva* Wallich

Putranjiva Wall., *Tent. Fl. Nepal.*: 61 (1826); Hurus., *J. Fac. Sci. Univ. Tokyo* III, Bot. 6: 335–338 (1954), reg. rev.

Trees, dioecious. Leaves alternate, spiral, petiolate, stipulate, pinnately veined, usually oblique at the base, margins entire or dentate. Flowers in axillary clusters or the pistillate solitary; sepals 3–6,

imbricate; petals none; disk none. Staminate flowers: stamens 2–3(–4), anthers extrorsely dehiscent; pistillode none. Pistillate flowers: ovary 2–3-locular; stigmas dilated, petaloid. Fruit drupaceous. Seed 1. $n = 20$ (and possibly 7, 19, and 21).

Four spp., tropical Asia, from Pakistan and Ceylon to Taiwan and Ryukyu Islands.

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