

**ADVANCES IN  
LEGUME  
SYSTEMATICS  
Part 2**

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## Tribe 24. BRONGNIARTIEAE (Benth.) Hutch.\*

Galegeae subtribe Brongniartiinae Benth. (1865), as 'Brongniartieae'

Trees, shrubs or subshrubs; leaves pinnately many-foliolate, sometimes gland-dotted; stipules and stipels present, the stipules sometimes very large; flowers in axillary racemes, leafy panicles or subcorymbose panicles, rarely solitary, sometimes resupinate; calyx 2-lipped, the tube short, upper 2 vexillary lobes united high up or entirely; lower 2 carinal lobes united for less than  $\frac{1}{2}$  the length to entirely united; vexillary filament free, or united with the others into an adaxially split sheath; anthers uniform or alternately shorter; pollen operculate; style glabrous; stigma terminal or oblique; fruit dehiscent (often elastically), bivalved, 1-many seeded, valves within smooth to the seeds surrounded by spongy tissue or separated by transverse elastic septa, seeds obovate to oblong, arillate; hilum minute; embryo with straight radicle.  $2n=18$  (1 sp. of *Brongniartia*). 2 genera in southern North America, Central and South America.

The Brongniartieae constitute a small probably relictual American group, with ancient austral roots. Characteristics of the tribe are imparipinnate leaves, a strongly bilabiate calyx, glabrous style, dehiscent legumes with spongy tissue between the seeds, seeds arillate, and embryos with straight radicles, the latter perhaps underlining the ancient nature of the assemblage. Phyletic affinities of the Brongniartieae perhaps lie with the Australian Bossiaeeae, now also known to possess several members with straight radicles (Polhill, 1976). The Brongniartieae and Bossiaeeae share close technical affinity and their taxonomic separation rests on the grounds of convenience, plus arguments to the effect that such groups probably represent endpoints of a once widespread austral complex of ancient papilionates.

Bentham (1865) associated *Harpalyce* and *Brongniartia*, both American genera, and *Lamprolobium* of Australia in the subtribe Brongniartiinae of the Galegeae. Taubert (1894) added the genus *Plagiocarpus*. Full tribal status was accorded the Brongniartieae by Hutchinson (1964), but *Plagiocarpus* was relegated to his Lotononideae. Lee (1973) questioned Hutchinson's placement of *Plagiocarpus*, suggesting affinity with the Australian Bossiaeeae. Subsequently, Polhill (1976) verified Lee's suspicion, demonstrating that both the Australian genera are equally well accommodated in Bossiaeeae as in Brongniartieae. Removal of *Plagiocarpus* and *Lamprolobium* to Bossiaeeae is fully supported here, and on these criteria, Brongniartieae is restricted to the wholly American genera *Brongniartia* and *Harpalyce*.

Both *Harpalyce* and *Brongniartia* have amphitropical disjunct distributions, which are considered to have arisen by way of physical interruption of populations across the American tropics, rather than by long-distance dispersal (Arroyo, 1976). Species of *Harpalyce* (Irwin & Arroyo, 1973; Arroyo, 1976; Borhidi & Muñiz, 1977) occur in Brazil, Cuba and taken together Mexico and Central America, where they cluster into three discrete sections based on the geographical provinces just mentioned. *Brongniartia* is heavily concentrated in Mexico with extensions into Central America, and southern U.S.A., and two have been described from the South American Andes in Chile and Bolivia. Both genera contain shrubs, subshrubs and small trees, notorious for seasonal dimorphism and each genus is tightly circumscribed morphologically. In *Harpalyce* the stamens are monadelphous with the vexillary filament united with the other into an adaxially split sheath, whereas in *Brongniartia* the stamens are supposedly always diadelphous. South American *Brongniartia* is anomalous in having monadelphous stamens, but otherwise seems to accord with the rest of the genus with respect to technical characteristics.

The orange-red flowers in *Harpalyce* (fig. 1/2,3) are resupinate and uniquely structured. The calyx is deeply 2-lipped with the two vexillary

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lobes and the three carinal lobes entirely united, and the entire staminal column and style included in the keel helically contorted through 180°. The calyx of *Brongniartia* is likewise 2-lipped, but neither the vexillary nor the carinal lobes are entirely united (fig. 1/1). The mostly red corollas are not resupinate and the broad keels are straight.

*Harpalyce* and *Brongniartia* are mostly pollinated by large, polylectic bees of the genus *Xylocopa*, but ornithophily has appeared secondarily in several Cuban species of *Harpalyce*. In *Brongniartia* bees land on the broad keels and pollen is deposited nototribically, whereas in *Harpalyce* the inverted banners serve as landing platforms and the helically contorted keels explode as a result of tension produced by downward displacement of the banner. The large anthers dehisce first, whereas the small anthers initially act as pistons forcing pollen into the beak-keel. In ornithophilous species of *Harpalyce* (fig. 1/3), the wings and banners are much reduced, the styles strongly exerted and the pollen sticky and warty (Arroyo, 1976). Pollen is tricolporate and characterised by a well-developed operculum lacking an endopore (Ferguson & Skvarla, this volume). The tectum is finely punctate in bee-pollinated species of *Harpalyce* and *Brongniartia* but coarse and warty in the sticky pollen grains of ornithophilous species of *Harpalyce* (Arroyo, 1976).

Legumes and seeds in *Harpalyce* and *Brongniartia* are quite similar (fig. 2), and on this basis the genera are clearly related. Each exhibits characteristic variation in legume size, seed number and degree of internal septation of the legume. Spongy tissue may be absent to well developed and in section *Brasilianae* of *Harpalyce* compacted into false, elastic partitions (fig. 2/4). *Brongniartia* seeds are more compressed than those of *Harpalyce*, but this is largely a reflection of the degree of compaction of the legume. The arils are either collar-like or partially interrupted (fig. 2).

Chemical data for Brongniartieae are meagre and of little value in interpreting relationships of the tribe. Both genera lack canavanine (Bell et al., 1978), while *Brongniartia* lacks cytosine (Harborne et al., 1971).

Goldblatt (this volume) reports  $n=9$  for one species of *Brongniartia*. Counts are unavailable for *Harpalyce*.

Turner in Harborne et al. (1971) first intimated that the Brongniartieae s.l. might be polyphyletic given the presence of cytosine in *Lamprolobium* and its absence in *Brongniartia*. In spite of Polhill's (1976) fully supported suggestion of removing *Lamprolobium* and *Plagiocarpus* to the Bossiaeeae, the fact remains that Brongniartieae and Bossiaeeae are technically inseparable on conventional criteria. Ferguson & Skvarla (this volume) draw attention to two well defined groups of genera in Bossiaeeae based on pollen morphology, of which pollen of *Harpalyce* and *Brongniartia* is essentially indistinguishable from that of the group including *Hovea*, *Templetonia*, *Plagiocarpus* and *Lamprolobium*. Interestingly these genera, but not all Bossiaeeae, possess collar-like arils and straight radicles characteristic of Brongniartieae (Polhill, 1976) and it becomes evident that the taxonomic distance separating Brongniartieae from Bossiaeeae is narrower than that separating constituent genera of the Bossiaeeae itself.

If the technical similarity of Brongniartieae and Bossiaeeae reflects a phylogenetic tie, some explanation for the separation of the tribes on different continents is required. Migration across an austral corridor between Australia and South America was feasible until about 38 m.y. BP (Raven & Axelrod, 1974). Primitive Bossiaeeae and Brongniartieae, however are largely tropical, and although there is no definitive evidence for rejecting this possibility, it remains unlikely. The Brongniartieae and Bossiaeeae might, on the other hand represent the tail ends of a once widespread group, the intermediate parts of which became extinct or acquired new expressions of characteristics that were maintained in, and today provide the taxonomic similarity of the two tribes. Such an ancestral



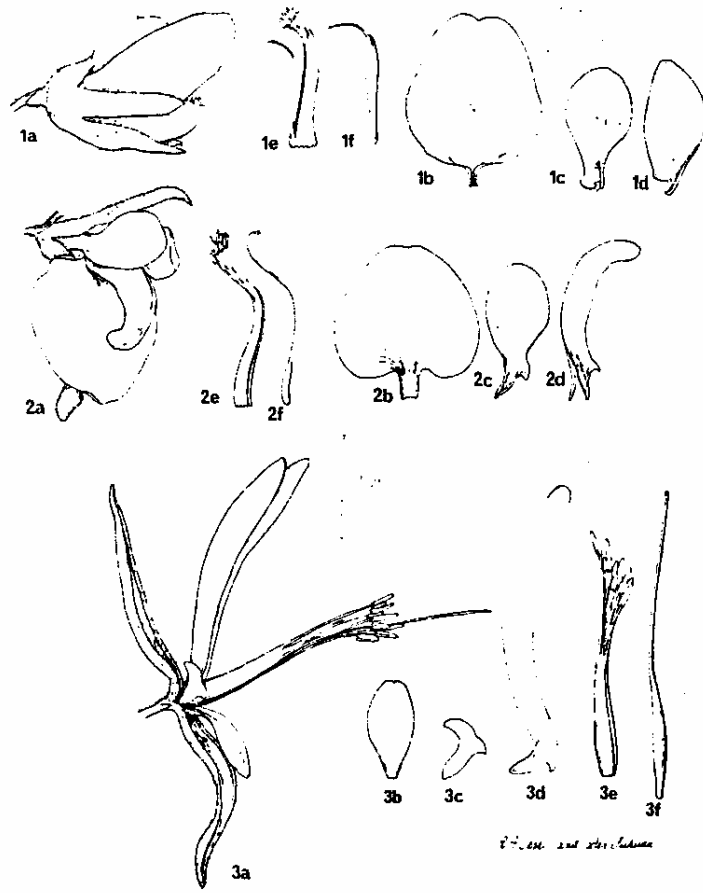


Fig. 1 Flowers of Brongniartieae. 1 *Brongniartia goldmanii*; 2 *Harpalyce lepidota*; 3 *H. villosa*.

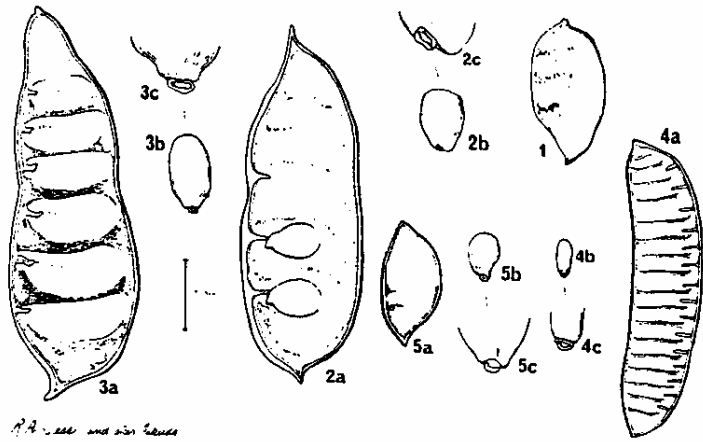


Fig. 2 Fruits and seeds of Brongniartieae. 1 *Brongniartia oligosperma*; 2 *B. intermedia*; 3 *Harpalyce sousai*; 4 *H. brasiliana*; 5 *H. cubensis*.

complex might have been centred on Africa-South America, leaving the Brongniartieae in South America as the continents separated further and eventually spreading into Australia at the other extreme, as the latter moved northward in relatively recent times (20–30 m.y.BP; Raven & Axelrod, 1974). Polhill (1976) stresses the many shared features of the Sophoreae, Podalyrieae, Crotalariaeae and Liparieae in South Africa and perhaps a detailed search in Sophoreae might reveal links to the Bossiaeeae and Brongniartieae. In summary, present evidence is all too meagre to trace the true phylogenetic affinities of the Brongniartieae. As an ancient group, moreover, it is fair to assume that many intermediate links may no longer exist.

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Plants eglandular; calyx lobes not united entirely; vexillary filament free (except *B. ulbrichiana*) 24.1 *Brongniartia*  
 Plants beset with peltate glands; calyx strongly bilabiate, upper 2 and lower 3 lobes entirely united; vexillary filament united 24.2 *Harpalyce*

24.1 BRONGNIARTIA Kunth (1823); Rydberg in N. Am. Fl. 24: 186 (1923); Hutch. 393 (1964). 56 spp., southern U.S.A., Mexico, Central America, South American Andes.

As in Hutchinson (1964) if South American *B. ulbrichiana* Harms is excluded, otherwise include 'vexillary stamen free or sometimes united'.  $2n=18$ .

24.2 HARPALYCE Moc. & Sesse ex DC. (1825), non *Harpalyce* D. Don (1829); Rydberg in N. Am. Fl. 24: 197 (1923); Hutch. 394 (1964); Arroyo in Mem. N.Y. Bot. Gard. 26(4): 1–80 (1976) (revision). 20 spp., Mexico and Central America, Cuba and Brazil.