EVOLUTIONARY BIOLOGY OF *ACACIA CAVEN* (LEGUMINOSAE, MIMOSOIDEAE): INFRASPECIFIC VARIATION IN FRUIT AND SEED CHARACTERS[1]

James Aronson[2]

Abstract

Six varieties are recognized in *Acacia caven* (Leguminosae, Mimosoideae; *Acacia* subg. *Acacia*, subsection *Polyseriae*), based on herbarium studies of vegetative characters, population-level studies of fruit and seed characters, and a map of the species' distribution and morphological variation patterns in southern South America. Two new varieties are described. Ecological and evolutionary aspects of carpological variations are discussed, and a framework is established for further studies in this and related species.

Within the huge pantropical genus *Acacia* Miller, subgenus *Acacia* sensu Vassal (= series *Gummiferae* Bentham, excluding *Faidherbia albida* (Del.) A. Chev.) appears to be a natural phyletic unit (Bentham, 1842; Pedley, 1986; Vassal, 1972). Its members occur primarily in the thornscrub and savannas of the Neotropics (ca. 50 species) and Africa (ca. 115 species) (Guinet & Vassal, 1978; Ross, 1979; Vassal, 1981; Rico Arce, 1984), but there are also 5–10 endemic species in western and northern Australia. The South American members of this subgenus (ca. 15 species) are among the least well known, despite the recent revision of the genus *Acacia* in Argentina by Cialdella (1984).

Although most abundant and variable in the warm temperate to subtropical biogeographical region known as the Chaco (Hueck & Seibert, 1972; Cabrera & Willink, 1973), one member of subgenus *Acacia, A. caven* (Molina) Molina, appears to have spread relatively recently into other biogeographical regions in northern Argentina, eastern Bolivia, western Paraguay, southern Brazil, Uruguay, and central Chile. This paper attempts to clarify infraspecific taxonomy of the species and set the stage for ecological, biogeographical, and other studies of *A. caven* and related species.

Historical Systematic Treatment

Acacia caven was originally described (as *M. caven*) from central Chile by Molina (1782), who considered it very similar to *A. farnesiana* (L.) Willd., a species described over 29 years previously and widely cultivated in Italy and France during the eighteenth and nineteenth centuries. Unfortunately, leaflet size (and "a shorter pod") was the basis on which Bentham (1875: 502) separated the two taxa, thereby paving the way for subsequent authors, e.g., Kuntze (1898), Arechavaleta (1901), Hassler (1909), Spegazzini (1923), and Clos (1930), to lump the two together. By contrast, Hooker & Arnott (1830), Wight & Arnott (1834),

[1] Rupert Barneby, Paul Berry, Jan Gillett, Philip Guinet, Bruce Maslin, Gwilym Lewis, David Mabberley, Lourdes Rico Arce, Amy Scheuler, Sara Tressens, and Charles Stirton made valuable comments on early versions of the manuscript. I thank them as well as A. M. Cialdella, C. Cristobal, D. H. Janzen, M. Kalin Arroyo, J. Ebinger, A. Krapovickas, the late P. Legname, J. Morello, R. Nash, C. Ovalle, R. Palacios, R. M. Polhill, A. Radcliffe-Smith, P. H. Raven, C. Saravia Toledo, and D. Seigler for help and encouragement. The curators and staff of the following herbaria kindly provided access to materials: BA, BM, CONC, CORD, CTES, FCQ, G, ICN, K, LP, LIL, LPB, MCNS, MERL, MO, MVHC, MVM, NY, SGO, and SI. An unpublished manuscript by Arturo Burkart (1959–1975) was made available by Nélida Bacigalupo (SI). Permission was granted by the Instituto Darwinion (SI) to reproduce two drawings of pods from that manuscript and to reproduce three others that appeared in *Darwiniana* (1984). Additional figures were drawn by René Ferris, CEFE, Montpellier. This study was made possible by financial support of the National Geographic Society.

[2] Centre d'Ecologie Fonctionnelle et Evolutive L. Emberger, CNRS, B.P. 5051, 34033 Montpellier, France.

Arata (1891), Burkart (1952, 1967, unpublished), Tortorelli (1956), Vassal (1972), Lombardo (1982), Cialdella (1984), Rodriguez et al. (1984), and Bernardi (1984) maintained separation of the two taxa on the basis of length to width ratio and anatomy of the pods, pericarp striations, length and pubescence of petioles, size of leaflets, and other morphological characters. Only Spegazzini (1923) and Cialdella (1984) treated *A. caven* in detail.

Position Within Subgenus *Acacia*

The small subsection *Polyseriae* (Vassal, 1972) is considered evolutionarily advanced compared to the far larger subsection *Uniseriae*, which contains all other members of the subgenus. *Acacia caven* and *A. farnesiana* are the only South American members of this subsection (*A. erioloba* E. Mey and *A. sphaerocephala* Cham. et Schldl. are the sole African and Mesoamerican representatives). Species of subsection *Polyseriae* have two, rarely three, rows of seeds per pod, as compared to only one row per pod in subsection *Uniseriae* (Vassal, 1972). This character led Wight & Arnott (1834) to propose the segregate genus *Vachellia*, a proposition accepted by Spegazzini (1923) but rejected by most subsequent workers. Many modern workers consider the subsection unnatural (D. Seigler & J. Ebinger, pers. comm.). Yet, it should be noted that indehiscent (or tardily dehiscent) pods are a diagnostic trait cited by Vassal (1972) for subsection *Polyseriae*, and that the group corresponds in part to the subseries *Summibracteatae* defined by Bentham (1875: 499) on the basis of floral as well as carpological characters.

Infraspecific Treatment

Cialdella (1984) recognized four varieties within *Acacia caven*. Three of these were characterized by pod size and shape (vars. *caven*, *microcarpa*, and *stenocarpa*) and corresponded to "forms" recognized by Spegazzini (1923) under *Vachellia farnesiana*. The fourth, *A. caven* variety *dehiscens* Burkart ex Cialdella, recognized the unusual populations with dehiscent pods in the hills between Córdoba and San Luis, Argentina. Three more of Spegazzini's (1923) "forms," characterized by short peduncles, small anthers, and large leaflets, respectively, were rejected by Burkart (unpublished) and Cialdella (1984). Furthermore, Burkart labeled several specimens var. *macrocarpa* or var. *sphaerocarpa*, but never prepared formal descriptions for them. Typical fruit types of the six putative varieties are shown in Figure 1.

Habitat and Distribution

Acacia caven is one of the most widespread arboreal species of extra-tropical South America, occurring ca. 37°–18°S in six countries, where it is variously known as "espino," "espinillo," "aromita," and "churqui" (Fig. 2). It is a natural component of the deciduous thorn forest in all but the driest areas of the Chaco. This region covers more than 1,000,000 km^2 between 15° and 35°S in north-central Argentina, adjacent parts of Bolivia, a tiny portion of Mato Grosso, Brazil, and nearly half of Paraguay (Ragonese & Castiglioni, 1970; Cabrera & Willink, 1973; Ramella & Spichiger, 1989). Outside of the Chaco, it is considered invasive.

Like some other widespread acacias, e.g., *A. nilotica* (L.) Willd., *A. farnesiana*, *A. macracantha* Humbl. & Bonpl. ex Willd., and *A. karroo* Hayne, *A. caven* shows remarkable climatic tolerance and ecological adaptability, as well as a propensity to invade disturbed habitats. In central Chile, encroachment by *A. caven* affects over 2,000,000 ha, including natural ecosystems in the semiarid and subhumid portions of the mediterranean climate zone (Parsons, 1976; Fuentes et al., 1989; Ovalle et al., 1990). It occurs from sea level to nearly 3,200 m at its northern limits in central Bolivia. In Argentina and Chile it rarely occurs above 1,200 m, and in Bolivia it is sparse above 1,900 m. Freezing temperatures would appear to be a limiting factor. For unknown reasons, *A. caven* does not occur in close proximity to the sea. It occurs not only in diverse continental-climate areas but also in the mediterranean-climate region in Chile, both in seasonally inundated plains and on very dry slopes or inselbergs. Preferring open cow pastures or abandoned fields, it also enters clearings in various types of natural vegetation wherever livestock roam. Although usually seen as a much-coppiced shrub 1–3 m tall, *A. caven* can attain 8–10 m in height, with DBH of 80 cm, when left uncut in deep soils (Ovalle, 1986; pers. obs.).

Reproductive Biology

Similar to several Australian and African acacias, *A. caven* possesses both hermaphroditic and masculine flowers, and thus should be considered an andromonoecious species (Spegazzini, 1923; Burkart, 1967; León et al., in prep.). These flowers occur in varying proportions, both within and among populations, possibly in response to changes in water availability (León et al., in prep.). *Acacia caven* seems to be largely allogamous, as more than 50 individuals tested have proven to be highly self-

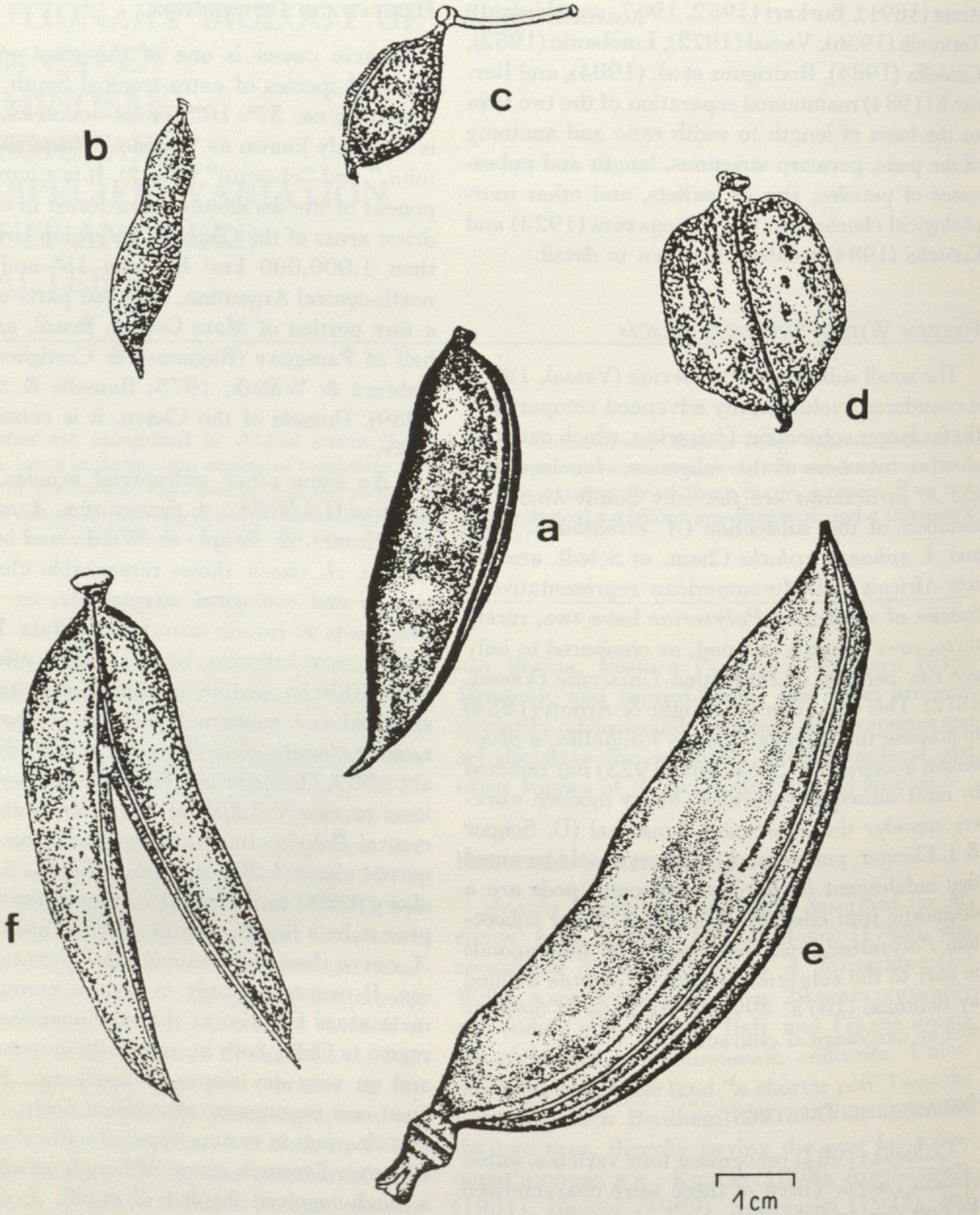

FIGURE 1. Typical fruits of the six varieties of *Acacia caven.*—a. Variety *caven Burkart 29343.*—b. Variety *stenocarpa Krapovickas 983.*—c. Variety *microcarpa Rojas 7697.*—d. Variety *sphaerocarpa Tressans & Radovancich 3539.*—e. Variety *macrocarpa Burkart 17577.*—f. Variety *dehiscens Burkart 15730.* All drawings life size.

incompatible, both in an Argentinian population near Córdoba (A. Anton, pers. comm.) and a Chilean population near Santiago (Peralta et al., in press). Pollination appears to be achieved—at least in central Chile—by small, crawling beetles, especially *Actylus trifaciatus* (Peralta et al., in press) rather than or in addition to, honey bees: the latter pollinator group is the most common for the genus (Arroyo, 1981).

SEED DISPERSAL

Most *Acacia caven* pods float in water, and some seeds are presumably dispersed in this fashion. For this reason, it has been suggested that its primary habitat within the Chaco was near seasonally active waterways, where it is often seen today (C. Saravia Toledo, pers. comm.). At the same time, most varieties of *A. caven* seem adapted for long-dis-

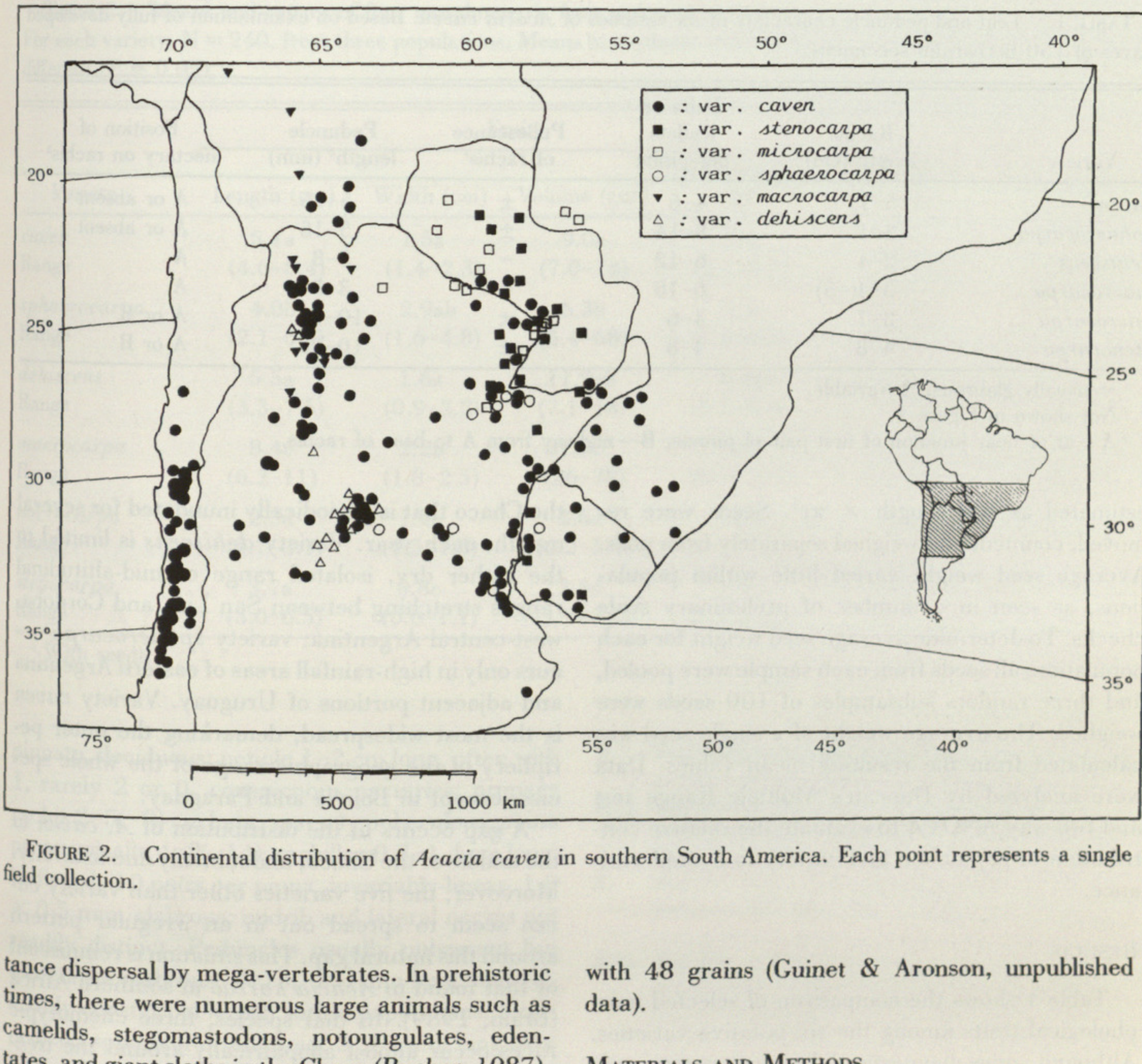

FIGURE 2. Continental distribution of *Acacia caven* in southern South America. Each point represents a single field collection.

tance dispersal by mega-vertebrates. In prehistoric times, there were numerous large animals such as camelids, stegomastodons, notoungulates, edentates, and giant sloths in the Chaco (Bucher, 1987). At present, domestic livestock are undoubtedly the most important agents of dispersal (Gutierrez & Armesto, 1981). Medium-sized birds such as "charata" (*Ortalis canicollis*), and "corzuela" (*Mazama americana*, *M. rufa*), as well as tapir (*Tapirus terrestris*), guanaco (*Lama guanicoe*), and sury (*Rhea americana*) are all probable dispersers of seed (C. Saravia Toledo, pers. comm.).

CYTOLOGY AND PALYNOLOGY

Chromosome numbers for *Acacia caven* have been recorded as $2n = 26$ (Castronovo, 1945) and $2n = 26, 52$ (Atchison, 1948). Similarly variable numbers occur in the closely related *A. farnesiana*, which is said to have $2n = 52, 104$ (Atchison, 1948). Pollen is shed in relatively large polyads consisting of ca. 32 grains (Caccavari, 1970; Heusser, 1971; Peralta et al., in press). Exceptions are *Rojas 7694* (SI) (var. *microcarpa*) with 16 grains and *Aronson 7977* (MO, SGO) (var. *macrocarpa*) with 48 grains (Guinet & Aronson, unpublished data).

MATERIALS AND METHODS

FRUITS AND SEEDS

Collections of seeds and pods were made at 49 sites covering the current range of distribution of *Acacia caven*. In addition, more than 750 herbarium fruit-bearing specimens of *A. caven* were compared for carpological and vegetative traits. Several fruit (pod) and seed characters appeared relatively constant within populations, and the three largest fruit samples from populations of each of the six putative varieties were selected for analysis. A total sample of 80 pods from each of five or more individuals was sufficient to represent each population, since the addition of further pods failed to alter the generalized variance (Tatsuoka, 1971; Farrell & Ashton, 1978). Only ripe pods free of bruchid damage were used. Voucher specimens for each population are deposited at herbaria in Chile (CONC, SGO), at Kew (K), and in Missouri (MO).

Length and width of 80 fully ripe pods per population were measured, and pod volume was

TABLE 1. Leaf and peduncle characters in six varieties of *Acacia caven*. Based on examination of fully developed leaves of 750 herbarium specimens.

Variety	Rachis length (cm)	Pairs of leaflets per pinna	Pubescence of rachis[1]	Peduncle length[2] (mm)	Position of nectary on rachis[3]
caven	5–7	4–6	±	5–15	A or absent
sphaerocarpa	3–4	8–14	±	5–15	A or absent
dehiscens	2–4	6–12	–	5–8	A
macrocarpa	3–4(–5)	6–10	–	3–5	A
microcarpa	3–7	4–6	±	10–15	A or B
stenocarpa	4–8	4–8	±	10–25	A or B

[1] – usually glabrous; ± variable.
[2] Not shown in Figure 1.
[3] A—at or near junction of first pair of pinnae; B—midway from A to base of rachis.

estimated as pod length × πr^2. Seeds were removed, counted, and weighed separately from pods. Average seed weight varied little within populations, as seen in a number of preliminary scale checks. To determine average seed weight for each population, all seeds from each sample were pooled, and three random subsamples of 100 seeds were weighed. The average weight of a single seed was calculated from the resulting mean values. Data were analyzed by Duncan's Multiple Range test and two-way ANOVA to evaluate the relative contribution of population and variety to overall variance.

RESULTS

Table 1 shows the comparison of selected morphological traits among the six putative varieties. Although some diagnostic differences occur, vegetative organs clearly do not display the most distinctive infraspecific variation. Table 2 shows intervarietal means of four pod and seed characters in 17 populations representing the six putative varieties. On the basis of pod volume and seed number per pod, three varietal groups can be distinguished: (i) *caven*, *sphaerocarpa*, and *dehiscens*, (ii) *macrocarpa*, and (iii) *microcarpa* and *stenocarpa*, which is further distinguished by narrow pod shape and small seed size.

Figure 2 shows collection localities for the six varieties. Partial geographic isolation occurs in some varieties, notably variety *dehiscens* in west-central Argentina, and variety *microcarpa* + variety *stenocarpa* in the Río Pilcomayo area of northeast Argentina and southern Paraguay. Geographic separation is correlated to ecological differentiation in most cases. Thus, variety *macrocarpa* is not only circumscribed geographically but also limited to sites above 2,000 m. Both variety *microcarpa* and variety *stenocarpa* are restricted to the portion of the Chaco that is periodically inundated for several months each year. Variety *dehiscens* is limited to the rather dry, isolated range of mid-altitudinal ranges stretching between San Luis and Córdoba, west-central Argentina; variety *sphaerocarpa* occurs only in high-rainfall areas of eastern Argentina and adjacent portions of Uruguay. Variety *caven* is the most widespread, demarking the outer periphery of the geographic range of the whole species, except in Bolivia and Paraguay.

A gap occurs in the distribution of *A. caven* in the middle of the Chaco, undoubtedly due to aridity. Moreover, the five varieties other than variety *caven* seem to spread out in an irregular pattern around this natural gap. This situation is reminiscent of that found in *Acacia karroo* in southern Africa (Brain, 1989). In that species, three chemotypic races occur almost allopatrically around the treeless Drakensberg massif. The geographic distribution of these races appears correlated with changes in the quantity and distribution of precipitation. In 818 specimens of *A. caven*, polymorphism in a peroxidase banding pattern has been determined and a clear distinction was found between Chilean and non-Chilean populations (Brain & Aronson, in prep.). Further studies are needed in this area.

TAXONOMIC TREATMENT

Acacia caven (Molina) Molina, in Sag. Stor. Nat. Chili, 2nd ed., 163; 299, 1810.

Shrub or tree to 10 m high, but usually much smaller; single-stemmed or with 5–20 or more densely crowded basal stems, depending on history of cutting and burning; young branchlets mottled gray, sparingly puberulous, lenticels not prominent. Stipular spines 0.4–2.5 cm long, slender, not swollen at the base, white or gray, rarely brown, often mottled, borne in pairs at every node. Leaves bi-

TABLE 2. Means and ranges of four morphometric fruit and seed traits in six putative varieties of *Acacia caven*. For each variety, N = 240, from three populations. Means in a column followed by the same letter are not significantly different ($P = 0.05$).

	Fruits				Seeds	
Variety	Length (cm)	Width (cm)	Volume (cm³)	Dry weight (g)[1]	Seeds per pod	Dry seed weight (g)
caven	5.1a	1.5a	9.0a	5.4a	21.3a	1.23a
Range	(4.6–8.4)	(1.4–2.3)	(7.0–14)	(3.7–9.7)	(9–39)	(1.2–1.3)
sphaerocarpa	4.0b	2.9ab	6.3b	3.5a	22.9a	1.15a
Range	(2.1–6.5)	(1.6–4.8)	(5.4–68)	(1.5–6.0)	(11–31)	(1.0–1.3)
dehiscens	5.5a	1.6a	11.9ab	6.3ab	18.4a	0.91b
Range	(3.3–7.5)	(0.9–2.2)	(7.1–18)	(5.2–8.3)	(4–28)	(0.90–0.93)
macrocarpa	8.4c	2.2b	31.9c	9.8b	30.2b	1.26a
Range	(6.2–11)	(1.8–2.5)	(26–38)	(8.4–12.7)	(16–41)	(1.25–1.27)
microcarpa	2.3d	1.2c	2.6d	0.9d	11.2c	0.47c
Range	(1.7–3.1)	(0.5–1.5)	(2.2–3.0)	(0.7–1.4)	(7–15)	(0.4–0.5)
stenocarpa	3.7a	0.8c	2.4d	1.4d	12.4c	0.51c
Range	(3.0–6.5)	(0.6–1.1)	(1.9–3.6)	(0.8–2.4)	(8–17)	(0.4–0.56)

[1] With seeds.

pinnate, deciduous; petiole 1–2 cm long, often with 1, rarely 2 or 0, conspicuous nectaries; primary rachis 2–5(–8) cm long, sparsely puberulous; pinna pairs typically 4–8(–14); rachillae 0.7–1.4 cm long; leaflets 4–10 pairs per pinna, invariably linear, 1.0 × 0.5 mm, glabrous; midrib and lateral nerves not readily distinct. Peduncles usually pubescent but sometimes glabrous, 3–15(–25) mm long, and relatively constant in length within populations. Flower head spherical or ellipsoid, 5–10 mm long; one or usually several per leaf axil, highly visible prior to the emergence of leaves. Flowers sessile, yellow, highly fragrant. Calyx 0.5–1.0 mm long, glabrous. Corolla 1–3 mm long, glabrous, approximately 30–55 flowers per head; stamens 44–58 per flower, with filaments free from the base and anthers eglandulate; pods brownish black or purplish brown, oblong-elongate or subglobose, straight or slightly falcate, frequently stipitate basally and/or acuminate, extremely variable in size, volume and weight; indehiscent, except in variety *dehiscens*; glabrous, usually not striate. Mesocarp ± spongy or quite sparse. Seeds olive brown, ± elliptic, 5–7 × 4–6 mm, areole 4–5 × 3–4 mm. Seeds 12–35 per pod in 2 (rarely 3) rows, or ± scattered in fully ripe pods.

KEY TO FRUITING SPECIMENS OF *ACACIA CAVEN*

1. Mature pod dehiscent ____ var. *dehiscens*
1. Mature pod indehiscent ____ 2
2(1). Pod subglobose, less than twice as broad as long, excluding beak and peduncle ____ 3
2. Pod elongate-fusiform, more than twice as broad as long, excluding beak and peduncle ____ 4
3(2). Pod usually 2.0–3.0 × 1.0–1.5 cm; mesocarp somewhat reddish, peduncle more than 15 mm long ____ var. *microcarpa*
3. Pod 2.1–6.5 × 1.6–4.8 cm; mesocarp white, peduncle less than 15 mm long ____ var. *sphaerocarpa*
4(2). Pod 3.0–4.0(–6.5) × 0.6–1.1 cm, narrowing at both ends, sometimes subtorulose, often light brown, occasionally reddish purple, peduncle usually more than 15 mm and rarely up to 30 mm ____ var. *stenocarpa*
4. Pod 5–11 × 1.5–2.5 cm, elongate, acuminate, not torulose, peduncle less than 15 mm long ____ 5
5(4). Pod dark brown, rarely black or slightly purple, 5–8 cm long, with one sutural ridge, this often indistinct; mesocarp evanescent ____ var. *caven*
5. Pod usually reddish purple, usually more than 8 cm long, with three distinct sutural ridges, these often sharply distinct; mesocarp resinous ____ var. *macrocarpa*

Acacia caven var. **caven**, *Mimosa caven* Molina, Sag. Stor. Nat. Chili 1st ed., 174. 1782. TYPE: not known. Neotype here designated: Rancagua, Chile, Oct. 1828, *Bertero s.n.* (SGO). Figure 1a.

Acacia adenopa Hook. & Arn., Bot. Miscell. 3: 206. 1833.

Acacia farnesiana (L.) Willd. var. *brachicarpa* O. Kuntze. Rev. Gen. Pl. 1:156. 1891. *Acacia farnesiana* (L.) Willd. var. *cavenia* (Hook & Arn.) O.Kuntze, Rev. Gen. Pl. 3:47. 1898. *Vachellia farnesiana* (L.) Wight & Arn. f. *cavenia* (Molina) Speg., Bol. Acad.

Nac. Cs. Córdoba 26(2): 298. 1923. *Acacia farnesiana* (L.) Willd. f. *cavenia* E. C. Clos, Bol. Min. Agric. Nac. 28(4): 455. 1930.

Shrub or tree to 10 m high, but usually much smaller; single-stemmed or with 5–20 or more densely crowded basal stems; young branchlets mottled gray, sparingly puberulous. Stipular spines 0.4–2.5 cm long, slender, white or gray, borne in pairs at every node. Leaves bipinnate, deciduous; peduncle 5–15 mm long, usually with one nectary at midpoint of petiole; primary rachis 5–7 cm long, sparsely puberulous; pinna pairs 4–6; rachillae 0.7–1.0 cm long; leaflets 4–6 pairs per pinna, linear, 1.0 × 0.5 mm, glabrous; midrib and lateral nerves not readily distinct. Peduncles usually pubescent, 3–15 mm long, and relatively constant in length within populations. Flower head spherical or ellipsoid, 0.5–1.0 cm long; one or usually several per leaf axil, highly visible prior to the emergence of leaves. Flowers sessile, yellow, highly fragrant. Calyx 0.5–1.0 mm long, glabrous. Corolla 1–3 mm long, glabrous, approximately 30–55 flowers per head; stamens 44–58 per flower; filaments free from the base; anthers eglandulate; pods brownish black or purplish brown, oblong-elongate or subglobose, straight or slightly falcate, frequently stipitate basally and/or acuminate ± 5–7 × 10–13 cm, 8–10 g; indehiscent, glabrous, usually not striate. Mesocarp ± spongy. Seeds olive brown, ± elliptic, 5–7 × 4–6 mm, areole 4–5 × 3–4 mm; 9–39 per pod in 2 rows in young pods but ± scattered in fully ripe pods.

Habit and distribution (Fig. 2). In disturbed sites in northern Argentina, southeastern Bolivia, and south-central Paraguay, occasionally an integrated element in xerophytic Chaco woodlands and along former river courses in adjacent areas. Also in the central valleys of Chile (36–27°S), parts of Uruguay, and southern Brazil. Especially frequent in much-burned, overgrazed cow pastures and in abandoned fields.

Representative specimens. ARGENTINA. CORDOBA: 32 km E of Córdoba, ca. 31°19′S, 64°57′W, 280 m, 11 Oct. 1988, *Aronson 7642* (CONC, K, MO). BOLIVIA. CHUQUISACA: 19 km S of Camargo, on road to Tarija, ca. 20°41′S, 65°15′W, 2,350 m, 26 Feb. 1989, *Aronson 7799* (CONC, MO); 53 km S of Palos Blancos, ca. 21°45′S, 63°38′W, 850 m, 28 Feb. 1989, *Aronson 7827* (MO). CHILE. 4 km E of Lo Ovalle, ca. 33°02′S, 71°22′W, 220 m, 18 Nov. 1988, *Aronson 7692* (K, MO); Cuesta de Chacabuco, 45 km N of Santiago, ca. 32°58′S, 70°42′W, 750 m, 23 Nov. 1988, *Aronson 7696* (K, MO). URUGUAY. 2 km E of Gauleguaychu, ca. 33°10′S, 58°22′W, 45 m, 23 Oct. 1988, *Aronson 7650* (CONC, MO, SGO).

Acacia caven var. **sphaerocarpa** Burkart ex Aronson, var. nov. TYPE. Argentina. Corrientes: ca. 27°27′S, 58°46′W, 60 m, "alrededores de la ciudad de Corrientes, antiguo camino a Matadero, 500 m de la ruta, 17 Feb. 1989, *S. G. Tressens & A. Radovancich 3539* (holotype, K; isotype, CTES). Figure 1d.

A varietatibus omnibus aliis var. *microcarpa* sola excepta legumine subgloboso differt, a var. *microcarpa* legumine maiore pedunculum crassum haud excedente differt.

Fruits are nearly spheroid when small (ca. 15 × 15 mm) or slightly ovoid when larger (ca. 25–30 × 20 mm), often with a sharp acuminate tip. Leaflets are numerous (8–14 pairs) and leaves are larger than in variety *caven*: 30–45 × 10–15 mm; stipular spines mostly less than 5 mm long.

Distribution (Fig. 2). In the more humid part of the Chaco and adjacent regions of Corrientes and Entre Ríos, Argentina, rarely in Santa Fe and Córdoba provinces, Argentina, and in western Paraguay and Uruguay. In damp fields where livestock roam.

Representative specimens. ARGENTINA. CORRIENTES: Empedrado, Estado La Yela, ca. 27°53′S, 58°49′W, 1954, *Pederson 3072* (K, LP); Arrocera Drews, 10 km NE of Colonia C. Pelligrini, Route 14, *Krapovickas et al. 29427* (CTES, SI). ENTRE RIOS: Depto. Islas del Ibicuy, 14.5 km N of the interprovince line with Buenos Aires, ca. 33°47′S, 58°20′W, 70 m, 22 Oct. 1988, *Aronson 7648* (MO). SANTA FE: Río Nah Tuli Piague, 9 Jan. 1937, *Ragonese 2444* (SI). URUGUAY. Laguna Guayaca, Apr. 1906, *Berro 4002* (MVFA).

In 1947, Burkart labeled one herbarium sheet (*Ragonese 2444*, SI) "forma sphaerocarpa n.f." but never described it formally. In all morphological traits except pod shape, this clearly shows affinity with variety *caven*. However, apart from carpological differences, limited geographical distribution (Fig. 2) and comparatively rapid growth rate under controlled environmental conditions (Aronson et al., 1991) support its recognition as a distinct variety. This variety seems to have unusually large leaves, regardless of water availability.

Acacia caven var. **dehiscens** Burkart ex Cialdella. Darwiniana 25: 76. 1984. TYPE: Argentina. Córdoba: Ascochinga, 22 Sep. 1936, *E. G. Nicora 962* (SI). Figure 1f.

Distribution. The mid-altitudinal hills of Córdoba and San Luis provinces, western Argentina. Very rare in the lower pre-Andean slopes of Catamarca and, according to Cialdella (1984), Salta. Tends to occur in heavily cut-over and frequently burned, heavily grazed, and otherwise disturbed sites in proximity to large, permanent human populations (Fig. 2).

Representative specimens. ARGENTINA. CATAMARCA: Las Peñas, *Brizuela 563* (LIL 206316). CORDOBA: Lago San Roque, Apr. 1945, *Hunziker 5984* (SI); Ascochinga, *Giardelli 405* (SI); 2 km E Villa de Totoral (jct. Rte. 9 and Rte. 17), ca. 31°15′S, 64°52′W, 500 m, 11 Oct. 1988, *Aronson 7644* (MO, SGO). SAN LUIS: Bajo Grande, Larca, *A. Maldonado 102* (SI); Larca, *Hunziker 2097* (SI); Embalse La Florida, 2 km E of Trapiche, ca. 33°06′S, 66°02′W, 930 m, 27 Mar. 1990, *Aronson 7907* (MERL, SGO).

Fruiting material is generally required to key out this variety. Variety *dehiscens* displays well-opened pods (see Fig. 1f) on the tree, especially at Embalse La Florida. Special caution is required with specimens from Lago San Roque, near Córdoba and from San Luis, since natural hybridization appears to occur between this variety and *A. atramentaria*. Moreover, pods on some herbarium sheets appear dehiscent due to crushing of specimens.

Acacia caven var. **macrocarpa** J. Aronson, var. nov. TYPE: Argentina. Salta: Chicoana, El Carril, 19 Oct. 1948, *Burkart 17577* (SI). Figure 1e.

A varietatibus aliis leguminibus multo maioribus pilis minutis glandulosis rubropurpureis omnimoobsitis et suturis prominentibus differt.

Mesocarp spongy and whitish.

Distribution. This variety has only been found at high altitudes (2,000–3,200 m) on the eastern flanks of the Andes, in Catamarca, Salta, Tucumán, and Jujuy provinces, northwestern Argentina and in Chuquisaca, Cochabamba, and La Paz departments of southern Bolivia. This variety is generally only found in dry streambeds and alluvial plains where groundwater is relatively near the surface (Fig. 2).

Representative specimens. ARGENTINA. CATAMARCA: Andalgalá, *Jorgensen 960* (MVM); Depto. Capital, "La Quebrada," *Krapovickas 1748* (SI). SALTA: between Guachipas y Alemania, ca. 25°38′S, 65°37′W, Jan. 1957, *Job 1511* (LP); Tolombón, 20 Oct. 1948, *Real 12084* (MERL); Quebrada de las Conchas, 14 Aug. 1936, *Cabrera 3758* (SI); Valle Santa María, Los Arcos, *Spegazini 5983* (SI). JUJUY: Villa El Perchal, ca. 23°20′S, 65°30′W, 2,490 m, 7 Nov. 1988, *Aronson 7677* (MO, SGO). BOLIVIA. LA PAZ: Prov. Murillo, Mallasa, 16°32′S, 68°08′W, 3,200 m, 7 Aug. 1986, *Solomon 15483* (LBP, MBM). COCHABAMBA: Prov. Capinota, Santibañez to Capinota road, ca. 17°45′S, 66°17′W, 2,500 m, 1 Feb. 1985, *Pedrotti et al. 87* (LPB). CHUQUISACA: 27 km S of Las Careras, ca. 21°16′S, 65°17′W, 3,080 m, 26 Feb. 1989, *Aronson 7808* (K, MO).

Although Burkart had a drawing prepared for this variety in 1949 (Fig. 2e), he did not write a description. The three sutural ridges, the reddish purple pericarp, and the spongy, resinous mesocarp of the pod are unusual in *Acacia caven* and are reminiscent of some forms of *A. farnesiana*. Nevertheless, some Chilean, Bolivian, and one Uruguayan specimen of variety *caven* show morphologically intermediate pods that suggest possible gene flow with variety *macrocarpa*.

Acacia caven var. **microcarpa** (Speg.) Burkart ex Cialdella, Darwiniana 25(1–4): 77. 1984. TYPE: Argentina. Formosa. Depto. Patiño, Fortín Soledad, *A. Krapovickas 1283* (SI; isotype, LIL). Figure 1c.

Vachellia farnesiana (L.) Wight & Arn. f. *microcarpa* Speg., Bol. Acad. Nac. Ci. Córdoba 26: 301. 1923. fig. 20f, 3.

Compared to all other varieties except variety *stenocarpa*, the pod here is much smaller (2–3 × 1–2 cm) and the peduncle much longer (usually > 15 mm). The variety differs from variety *stenocarpa* by its much shorter, somewhat spherical or subglobose fruit, less than twice as long as broad. Mesocarp is white and evanescent.

Distribution. On heavy soils in the seasonally inundated portions of central Paraguay and northeastern Argentina (Formosa and Chaco provinces), in relative proximity to the Río Pilcomayo. Isolated specimens have also been collected in the small Brazilian portion of the Chaco. Found under relatively pristine as well as secondary, disturbed conditions in that region.

Representative specimens. ARGENTINA. CHACO: Pto. Barrangueras, 5 Dec., 1939, *Poiraberi 77* (LP, MVM). FORMOSA: R. Juarez, 10 Jan. 1957, *Burkart 201698* (SI); Río Pilcomayo, 12 Nov. 1986, *Vergara s.n.* (CTES). SALTA: between Colonia Castelli y Rivadavia, Mar. 1967, *Morello & Adamoli s.n.* (SI). BRAZIL. MATO GROSSO DO SUL: Mun. Porto Murtinho, estrada ao Fazenda Jererê, ca. 21°30′S, 57°44′W, 22 Dec. 1985, *Loureiro 161* (NY). MATO GROSSO: 20 km E of Pôrto Murtinho, 23 Oct. 1980, *Pires & Furtado 17287* (NY). PARAGUAY. PRESIDENTE HAYES: Palmas Chicas, near Puerto Mastinho, Dec. 1937, *Rojas 7694* (SI); Colonia, Menno, Misión Nueva, ca. 23°05′S, 59°40′W, *Arenas 200* (SI). BOQUERON: Mariscal Estigarribia, 23 Oct. 1980, *F. Casas & Molera 4431* (MO).

Acacia caven var. **stenocarpa** (Speg.) Burkart ex Cialdella, Darwiniana 25: 78, 1984. *Vachellia farnesiana* (L.) Wight & Arn. f. *stenocarpa* Speg., Bol. Acad. Nac. Ciencias Córdoba 262: 301. 1923. fig. 20. TYPE: Argentina, Misiones. Dept. Candelaria, Santa Ana, *Burkart 14734* (SI). Figure 1b.

Distribution. This variety is seen primarily in Formosa and Misiones provinces, Argentina and in adjacent Paraguay, especially within the area periodically flooded by the Río Pilcomayo. However, the few specimens from the Rió Uruguay collected before 1930 suggest that its former distribution, and possibly that of variety *microcarpa*, formerly included parts of Uruguay and possibly the Río Paraná region as well. Both of these areas are now transformed by agriculture and urban sprawl. There also exists one specimen from Tucumán, Argentina, nearly 800 km to the west of its current area of distribution.

Representative specimens. ARGENTINA. CHACO: Colonel Benitez, 7 July 1937, *Schinini 1987* (SI). CORRIENTES: 75 km N of Merced, Laguna Trinidad, Culantrillar, *Schinini et al. 11761* (MBM). FORMOSA: between Formosa and Mosou de Fierro, 7 Jan. 1945, *Ragonese & Cosso 2658* (SI); Clorinda, banks of the Río Pilcomayo, 14 Nov. 1944, *T. Rojas 12298* (LIL). ENTRE RIOS: 5 km S of Colón, ca. 32°20'S, 58°06'W, 20 m, *Aronson 7882* (CONC, K, MO). PARAGUAY. Trinidad, Bahia Caballero, Depto. Central, 11 Nov. 1950, *Sparre & Vervoorst 57* (K). PRESIDENTE HAYES: Mariscal Estigarribia, 11 Dec. 1987, *Schinini & Palacios 25934* (CORD, CTES, G); Presidente Hayes, 1 Dec. 1877, *Rojas 6979* (SI); Capitan López de Filippis, Oct. 1938, *Rojas 8419* (SI); Bajo Chaco, 30 km from Río Aguaray Guazu, 4 Jan. 1980, *P. Arenas 1571* (CTES). CAAGUAZU: *Hassler 9085* (LIL). URUGUAY. PAYSANDU: Santa Lucia, Bañado del Río Uruguay, ca. 34°28'S, 56°22'W, Nov. 1919, *J. Schroder 8865* (MVM).

This variety is distinguished by its short, narrow pod (> 10 mm) and long peduncle (≥ 15 mm). Fresh pods are usually light brown and often bear three strongly delineated suture ridges as in variety *macrocarpa* (and in much material of *A. farnesiana*). Leaves are big (80 × 50 mm), with pinnae up to 30 mm long. As in variety *stenocarpa*, trees tend to be weak and spindly compared to other varieties. Some introgression apparently takes place between variety *stenocarpa* and variety *microcarpa* (e.g., in *Sparre & Vervoorst 57*, K). Much more collection is needed in the Río Pilcomayo basin and in western Paraguay.

The few, rather old specimens of variety *stenocarpa* collected from Uruguay bear witness to the wider distribution of this variety in earlier times. They also raise the possibility that *A. caven* var. *stenocarpa* populations that existed in eastern Argentina and western Uruguay were eradicated, only to be replaced more recently by *A. caven* var. *caven*.

DISCUSSION

An infraspecific revision of a widespread and polymorphic *Acacia* based in large part on differences in shape and volume of pods and seed weight and number recalls the taxonomic revision of Brenan (1957) for *A. nilotica* (L.) Willd., the type species of *Acacia*. In *A. nilotica*, nine subspecies were delimited by Brenan, mainly on differences in the shape, size, and pubescence of the pods. Only fruiting specimens can be readily placed to subspecies, but geographic separation tends to confirm the validity of the infraspecific system proposed. Brenan's (1957) elaborate system for *A. nilotica* has been maintained by Ross (1979, 1981).

On a higher taxonomic level, Britton & Rose's (1928) subdivision of Bentham's (1875) series *Gummiferae* into 12 genera, partly on the basis of fruit characters, has been rejected by most subsequent workers. Moreover, for generic and tribal-level revisions throughout the Leguminosae, it has been argued that far too much emphasis in the past was placed on obvious fruit features, and that in the future these should be replaced, or at least supplemented, by consideration of flowers, inflorescences, seed, and seedlings in attempts to produce natural classification systems (Polhill et al., 1981: 25). However, at the specific and particularly the subspecific level in *Acacia caven*, fruit and seed parameters seem more conservative within populations than leaf pubescence, size of leaflets, capitulum diameter, and stipular spine length, all of which have been used to split up species complexes or to erect infraspecific categories within some widespread acacias and other Mimosoideae. For *A. caven*, and many related species, most pinnae, leaflet, and spinescent stipule parameters show such considerable infraspecific, and even within-population, variation that they gain taxonomic value only when substantiated by greenhouse or common-garden experiments, or when they are shown to be genetically fixed traits (cf. Aronson, 1992).

By contrast, the shape of mature legumes and the number and average weight of fully developed seeds per legume appear to be conservative within most populations of *A. caven*, though contrasted among varieties, and thus can play a role in systematic and other types of studies. Lewis & Elias (1981) consider that fruit characters provide excellent generic markers within the Mimoseae.

With regard to the evolutionary and ecological aspects of variation within *Acacia caven*, it seems that fruit and seed characters are subject to more intense selective pressure than other vegetative ones. At least four different types of seed dispersal strategies may have evolved in the varieties of *A. caven* described herein (Fig. 1). Variety *sphaerocarpa*, variety *microcarpa*, and variety *stenocarpa* may have undergone selection for seed dispersal by water in the regularly inundated regions they occupy. By contrast, high in the Andes, the unusually large pods of variety *macrocarpa* could have been selected for long distance dispersal by megavertebrates. Finally, variety *dehiscens* has possibly undergone selection for seed dispersal by rodents, ants, or avian granivores (Aronson, in prep.).

Studies on variation in polyad grain number among varieties of *Acacia caven*, e.g., those of Kenrick & Knox (1982) for *A. retinodes*, reveal a correlation between pollen grain number and maximum seed number per pod. Yet, there is no obvious correlation between seed number and average seed size in *A. caven*, such as predicted by Harper et al. (1970) and others. A related question is the possible correlation between ovule number in *Acacia caven* flowers and the number of seeds borne per pod (Lewis & Elias, 1981; Ph. Guinet, pers. comm.).

In Hispañola, Barneby & Zanoni (1989) used pod dehiscence as one of the diagnostic features for distinguishing *A. tortuosa* from *A. macracantha*. At a higher taxonomic level, the occasional occurrence of pod indehiscence is considered a diagnostic feature of subgenus *Acacia*, since nowhere in subgenus *Aculeiferum* or *Phyllodinae* can it be found (Elias, 1981). Within subgenus *Acacia*, as well as in various other legume taxa, it is observed that once pod indehiscence has arisen, it remains firmly fixed (B. Verdcourt, pers. comm.). The question arises whether *A. caven* variety *dehiscens* is the most primitive of the six varieties or a case of evolutionary "reversion." This latter hypothesis seems more likely in view of the fact that seed arrangement in variety *dehiscens* is polyseriate, just as in all the other varieties.

The significance of polyseriate seeds in a given pod should be noted in this context. In contrast to uniseriate seeded pods, pod length of *A. caven* (and of its close relative *A. farnesiana*) bears no correlation with seed number. Thus pod volume and dry weight are required, in addition to pod width and length, in order to adequately describe variation in reproductive output and therefore in evolutionarily significant phyletic groups. As Vassal (1972) put it: "The genus *Acacia* is endowed with great evolutionary dynamism; apparently it has not yet exhausted all its potentialities." Systematic treatments within the genus need to take this dynamism into account.

Literature Cited

Arata, P. N. 1891. Ciencias Naturales XXXVII. *Acacia cavenia* Hook y Arn. Anales Dept. Nac. de Hygiene (Argentina) 1(2): 43–44.

Arechavaleta, J. 1901. Flora Uruguayana, III: 436–437. Anales Museo Nac. Montevideo, Montevideo.

Aronson, J. 1992. Description and distribution of *Acacia macracantha* Humb. & Bonpl. (Leguminosae, Mimosoideae) in northern Chile. Gayana, Bot. 48: 81–87.

———, C. Ovalle & J. Avendaño. 1991. Early growth rate and nitrogen fixation potential in 44 legume species grown in an acid and a neutral soil from central Chile. Forest Ecol. Managem. 47: 225–244.

Arroyo, M. T. K. 1981. Breeding systems and pollination biology in Leguminosae. Pp. 723–769 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics, Volume 1. Royal Botanic Gardens, Kew.

Atchison, E. 1948. Studies in the *Leguminosae*. II. Cytogeography of *Acacia* (Tourn.) L. Amer. J. Bot. 35: 651–656.

Barneby, R. C. & T. A. Zanoni. 1989. Las Acacias (*Acacia*, Mimosaceae) de la Española: dos nuevas, una mejor descrita, y una clave para todas, las indigenas así como las cultivadas. Moscosoa 5: 4–27.

Bentham, G. 1842. Notes on Mimosaceae, with a synopsis of species. Hooker's J. Bot. Kew Gard. Misc. 1: 318–392.

———. 1875. Revision of the suborder *Mimoseae*. Trans. Linn. Soc. London 30: 335–667.

Bernardi, L. 1984. Contribución a la Dendrología Paraguaya. I. Boissiera 35: 1–341.

Brain, P. 1989. Genetic races in a ring species, *Acacia karroo*. S. African J. Sci. 85: 181–185.

Brenan, J. P. M. 1957. Notes on Mimosoideae: III. Kew Bull. 12: 75–96.

Britton, N. L. & J. N. Rose. 1928. Mimosaceae. North Amer. Fl. 23 (Part 2): 1–194.

Bucher, E. 1987. Herbivory in arid and semi-arid regions of Argentina. Rev. Chilena Hist. Nat. 60: 265–273.

Burkart, A. 1952. Las Leguminosas Argentinas Silvestres y Cultivadas, 2nd edition. Acme Agency, Buenos Aires.

———. 1967. Flora de la Provincia de Buenos Aires, Volume IV, 3A. Leguminosas. INTA, Buenos Aires.

Cabrera, A. L. & A. Willink. 1973. Biogeografía de América Latina. Organization of the Americas, Washington, D.C.

Caccavari, M. A. 1970. Granos de polen de Leguminosas de la Argentina. I. *Mimosoideae*; Tribu *Acacieae*. Darwiniana 16: 144–174.

Castronovo, A. 1945. Estudio cariológico de doce especies de Leguminosas. Darwiniana 7: 38–57.

Cialdella, A. M. 1984. El género *Acacia* (Leguminosae) en la Argentina. Darwiniana 25: 59–111.

Clos, E. C. 1930. Segunda contribución al conocimiento de los arboles y arbustos cultivados en la Argentina (Leguminosae-Mimosoideae). Bol. Minist. Agric. de la Nacion 28: 442–468.

Elias, T. S. 1981. Mimosoideae. Pp. 143–152 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics, Volume I. Royal Botanic Gardens, Kew.

Farrell, T. P. & D. H. Ashton. 1978. Population studies on *Acacia melanoxylon* R. Br. I. Variation in seed and vegetative characteristics. Austral. J. Bot. 26: 365–380.

Fuentes, E. R., R. Aviles & A. Seguro. 1989. Landscape change under indirect effects of human use: the savanna of Central Chile. Landscape Ecol. 2: 73–80.

GUINET, PH. & J. VASSAL. 1978. Hypotheses on the differentiation of the major groups in the genus *Acacia* (Leguminosae). Kew Bull. 32: 509–527.

GUTIERREZ, J. & J. J. ARMESTO. 1981. El rol del ganado en la dispersión de las semillas de *Acacia caven* (Leguminosae). Ci. & Invest. Agríc. (Chile) 10: 3–8.

HARPER, J. L., P. H. LOVELL & K. G. MOORE. 1970. The shapes and sizes of seeds. Annual Rev. Ecol. Syst. 1: 327–355.

HASSLER, E. 1909. Contribuciones a la Flora del Chaco Argentino-Paraguayo. I Parte. Flórula pilcomayensis. Trab. Mus. Farmacol. No. 21. Buenos Aires, Argentina.

HEUSSER, C. J. 1971. Pollen and spores of Chile. Univ. of Arizona Press, Tucson.

HOOKER, W. J. & G. A. W. ARNOTT. 1830–1841. The Botany of Captain Beechey's Voyage. Henry G. Bohn, London.

HUECK, K. & P. SEIBERT. 1972. Vegetationskarte von Sudamerika. Gustave Fischer, Stuttgart.

KENRICK, J. & B. KNOX. 1982. Function of the polyad in reproduction of *Acacia*. Ann. Bot. (London) 50: 721–727.

KUNTZE, O. 1898. Revisio Generum Plantarum 3: 47.

LEWIS, G. P. & T. S. ELIAS. 1981. Mimoseae, Pp. 155–168 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics, Volume I. Royal Botanic Gardens, Kew.

LOMBARDO, A. 1982. Flora Montevidensis, Volume I: 126–127. Intendencia Municipal de Montevideo, Uruguay.

MOLINA, G. I. 1782. Saggio Sulla Storia Naturale del Chili, 1st edition Bologna.

———. 1810. Saggio Sulla Storia Naturale del Chili, 2nd ed. Bologna.

OVALLE, C. 1986. Etude du Système Ecologique Sylvo-Pastoral à *Acacia caven* (Mol.) Hook. et Arn.: applications à la gestion des ressources renouvables dans l'aire climatique méditerranéenne du Chili. Ph.D. Université de Sciences et Techniques du Languedoc, Montpellier, France.

———, J. ARONSON, A. DEL POZO & J. AVENDAÑO. 1990. The Espinal: agroforestry systems of the mediterranean-type climate region of Chile: state of the art and prospects for improvement. Agroforest. Systems 10: 213–239.

PARSONS, D. J. 1976. Vegetation structure in the mediterranean scrub communities of California and Chile. J. Ecol. 64: 435–447.

PEDLEY, L. 1986. Derivation and dispersal of *Acacia* (Leguminosae) with particular reference to Australia, and the recognition of *Senegalia* and *Racosperma*. Bot. J. Linn. Soc. 92: 219–254.

PERALTA, I., J. G. RODRIGUEZ & M. T. KALIN ARROYO. Breeding systems and aspects of pollination of *Acacia caven* (Mol.) Mol. (Leguminosae: Mimosoideae) in the mediterranean-type climate zone of central Chile. Bot. Jahrb. Syst. (in press).

POLHILL, R. M., P. H. RAVEN & C. H. STIRTON. 1981. Evolution and Systematics of the Leguminosae. Pp. 1–26 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legumes Systematics, Volume I. Royal Botanic Gardens, Kew.

RAMELLA, L. & R. SPICHIGER. 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco I. Candollea 44: 639–680.

RAGONESE, A. E. & J. C. CASTIGLIONI. 1970. La vegetación del Parque Chaqueño. Bol. Soc. Argent. Bot. 11: 133–160.

RICO ARCE, L. 1984. The genus *Acacia* in Mexico. Bull. Int. Group Study Mimosoideae 12: 50–59.

RODRIGUEZ, R., M. QUEZADA & O. MATTHEI. 1984. Flora Arbórea de Chile. Universidad de Concepción, Concepción.

ROSS, J. H. 1979. A conspectus of the African *Acacia* species. Memoirs of the Bot. Survey of South Africa 44: 1–155.

———. 1981. An analysis of the African *Acacia* species: their distribution, possible origins and relationships. Bothalia 13: 89–413.

SPEGAZZINI, C. 1923. Acacieas Argentinas. Bol. Acad. Nac. Ci. Córdoba 26: 161–334.

TATSUOKA, M. M. 1971. Multivariate Analysis. John Wiley & Sons, New York.

TORTORELLI, L. A. 1956. Maderas y Bosques Argentinos. Editorial Acme, Buenos Aires.

VASSAL, J. 1972. Apport des recherches ontogéniques et séminologiques à l'étude morphologique, taxonomique et phylogénétique du genre *Acacia*. Bull. Soc. Hist. Nat. Toulouse 108: 1–115.

———. 1981. Acacieae. Pp. 169–171 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics, Volume I. Royal Botanic Gardens, Kew.

WIGHT, R. & G. A. W. ARNOTT. 1834. Prodromus Florae Peninsulae Indiae Orientalis, Volume 1. London.