## Studies in Capparaceae XXII. Capparis sclerophylla, a Novelty from Arid Coastal Peru and Ecuador

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Abstract. Capparis sclerophylla (subg. Cynophalla), Capparaceae, a sharply distinct new species of shrub or small tree, differs from other, often dominant, related, but often difficult to distinguish species of subgenus Cynophalla by thick, hard, stiff, xerophyllous leaves, these subsessile on short (1-4 mm), dark-brown to black, rigid and fragile petioles; by large white flowers spirally disposed with reflexed petals usually borne on thick, congested, short, and rigid raceme axes; by long-gynophored, usually slender siliques with white pulp, white seed arils and green embryos; and by its restriction to arid deciduous thornscrub near the Pacific Ocean from northwestern-most Peru to west-central Ecuador. Its closest relative appears to be C. verrucosa of Mexico to Venezuela. A cytotaxonomic survey of subgenus Cynophalla proves it to be a polyploid series, with base number of n = 14, 2n = 28 (x = 14, 28, 56, 84), represented by C. flexuosa and other species; several of these chromosome numbers are reported here for the first time, but the number for C. sclerophllya is as yet unknown.

Resumen. Capparis sclerophylla (subg. Cynophal-la), Capparaceae, es una nueva y claramente distinta especie de arbusto o arbolillo que difiere de las otras especies del subg. Cynophalla, frecuentemente dominantes, relacionadas, pero usualmente dificiles de distinguir, por poseer hojas xerófilas, rígidas, gruesas, subsésiles, con pecíolos muy cortos (1–4 mm), rígidos, frágiles, de color café-obscuro a negro; grandes flores blancas con pétalos reflexos que nacen en los ejes gruesos, cortos, rígidos y sésiles de los racimos congestos; silicuas delgadas con ginóforos largos, pulpa y arilo de la semilla blancos y embriones verdes; y por estar restringida al monte espinoso y bosque muy seco deciduo, cerca del Oceano Pacífico, en la costa del norocciden-

te de Perú hasta el oeste-central de Ecuador. Su pariente más cercano parece ser C. verrucosa, distribuida desde México hasta Venezuela. Un estudio citotaxonómico del subg. Cynophalla demuestra que es una serie poliploide, con un número base de n=14, 2n=28 (x=14, 28, 56, 84), representada por C. flexuosa y otras especies; se presenta algunos de estos números cromosómicos aquí por primera vez, pero el número de C. sclerophylla es aún desconocido.

Key words: Capparaceae, Capparis, chromosome number, coastal Peru and Ecuador, endemic, extra-floral nectaries, myrmecotrophic, subgenus Cynophalla, xerophyte.

As a consequence of the dramatic rainshadow created by the upwelling cold waters of the Peru (or Humboldt) Current precipitating the humid, Pacific "westerlies," the coastal regions of western Peru and Ecuador south of the Equator are covered by a widespread arid belt of xerophytic vegetation: mostly deciduous thornscrub with columnar ceroid cacti, semideciduous woodlands and seasonally dry tropical forests, in which various species of Capparis are not only common, but characteristic and often dominant. Here one finds such highly distinct, stellate- or lepidote-pubescent species as C. scabrida Kunth (C. angulata Ruiz & Pavón ex DC.), C. crotonoides Kunth (C. cordata Ruiz & Pavón ex DC.), and C. avicennifolia Kunth (C. ovalifolia Ruiz & Pavón ex DC.), as well as many species of the glabrous or barely pilose taxonomically difficult Capparis subg. Cynophalla (DC.) Eichler (Eichler, 1865), this nevertheless a well-defined group characterized by: (1) distichous and divergent, evenly spaced out, subsessile leaves; (2) each leaf subtending an ascending series of one to three, char-

acteristic axillary, nectar-producing glands (Poulsen, 1879-1880; Di Sapio et al., 2001) visited by ants; (3) large, round, cup-shaped sepals in two unequal decussate series, with the inner the larger; (4) elongate, torulose, dehiscent siliques, each with several to many seeds embedded in a fleshy orange, red, or white pulp (endocarp); (5) seeds covered by a paper-thin testa, and this in turn enclosed by a white aril, with both together readily slipping off the naked green embryo; and (6) plants that are mostly glabrous or at best only minutely puberulent or pilose with simple short, soft trichomes. Included here are two closely related, rather thin-leaved species, C. heterophylla Ruiz & Pavón ex DC. and C. ecuadorica Iltis (Iltis, 1978). In addition there are several taxa of a notoriously variable complex of intergrading taxa from western Ecuador (the polyploid C. flexuosa (L.) L., s.l. complex; cf. Iltis, below and 1978; Madsen et al., 2001), the nomenclature of which in many regions has yet to be worked out: the infrequent C. didymobotrys Ruiz & Pavón ex DC.; the ubiquitous and enormously variable C. guayaquilensis Kunth and the usually more southern, less common variant of the latter; C. mollis Kunth; and their diverse segregating progenies of some putative, presumably ancient, hybridization events.

Intermixed and hidden in all this impossible diversity within Capparis subg. Cynophalla was an unknown, usually a sterile member of Cynophalla, superficially resembling in leaf shape Capparis guayaquilensis ( = Capparis lanceolata Ruiz & Pavón ex DC., and so cited by Madsen et al., 2001: 153-155), one that heretofore had escaped notice and is herewith newly described as Capparis sclerophylla. A closer examination revealed that its leaves are remarkably hard, stiff, and evergreen, and are subsessile, when dry on dark brown or black, short, thick, rigid, fragile petioles. As a consequence, its leaf blades do not hang loosely down as in some other, sympatric species in this subgenus, but diverge laterally and break off when dry at the slightest touch. Most significantly, its large, pure white flowers with reflexed petals are usually borne on thick, congested, stubby short shoots or spurs (i.e., peduncles) mostly no more than a centimeter long, these produced at the end and sides of older branches and unique in subgenus Cynophalla. Occasionally, flowers are spaced out on young leafless long shoots more typical of the subgenus. Finally, the scarce pulpy endocarp is said to be white rather than red, a condition duplicated only in the widespread C. verrucosa Jacquin of Mexico to Venezuela, for this and other reasons the closest relative of C. sclerophylla. Abundantly distinct, it is thus gratifying to be able to segregate still another species out of the polyploid taxonomic jungle that is the *Capparis* subg. *Cynophalla* (Iltis, 1978; Ruíz-Zapata & Iltis, 1998: 139; Iltis, unpublished).

Capparis sclerophylla is relatively uncommon, flowers infrequently, and only rarely sets fruit. When sterile specimens were collected by the first author near Bahía de Caráquez, these were initially taken to be aged, xeromorphic extremes of a variable population of the similar C. guayaquilensis, a much more common species with which it grew intermixed. But once the taxon is recognized, the petiolar characters alone readily distinguish it. Finally, the recent splendid fertile collections of Ecuadorean capparids, sent to the University of Wisconsin Herbarium (WIS) from the rejuvenated Universidad de Guayaquil Herbarium (GUAY) by Carmen Bonifaz and the second author, have made it obvious that this taxon deserves a binomial of its own. Focusing on its distinctive sclerophyllous leaves, we name it:

Capparis sclerophylla Iltis & X. Cornejo, sp. nov. TYPE: Ecuador. Manabí: Bahía de Caráquez a 8 km, alrededores de Univ. Católica, 80°32′W, 00°45′S, monte espinoso/bosque muy seco tropical deciduo, fuertemente intervenido, 30 m, 27 Oct. 1997 (fl, fr), X. Cornejo & C. Bonifaz 5822 (holotype, WIS; isotypes, AAU, B, COL, DAV, F, GB, GH, GUAY, K\*, LOJA, MA, MEXU, MO\*, MY, NY\*, P, QCA, QCNE\*, RSA\*, SBT, UC, US\*, USM, VEN, WIS [3]. [Some specimens incomplete, but all supplemented by a suite of xerox reproductions of flowering and/or fruiting isotypes; specimens with an asterisk (\*) include a wood sample.] Figures 1–3.

Fruticosa 0.5–5 m alta, *C. guayaquilensi* similis, sed foliis insigniter duris, petiolis atrofuscis vel nigris, brevioribus (2–3 mm longis) et fragilibus in sicco, floribus grandibus (20–30 mm longis) cum petalis reflexis et axibus floriferis brevibus, densis et condensatis differt.

Xeromorphic shrubs to small slender trees, 0.5 to 5 m tall and 10 cm DBH, with many leaves evenly spaced on the current year and several previous years' growth, somewhat distichous to mostly irregularly stiffly diverging in all directions but never all drooping together, the branchlets lenticellate; plants glabrous when mature, but young branches, petioles, and leaves sometimes with a fine pubescence of very short, simple trichomes. Leaves evergreen, thick, hard, stiff, entire, narrowly oblong to elliptic, less often linear-lanceolate to oblanceolate or obovate, highly variable in size and shape (e.g., in one extreme case, 8 × 1.4 cm leaves

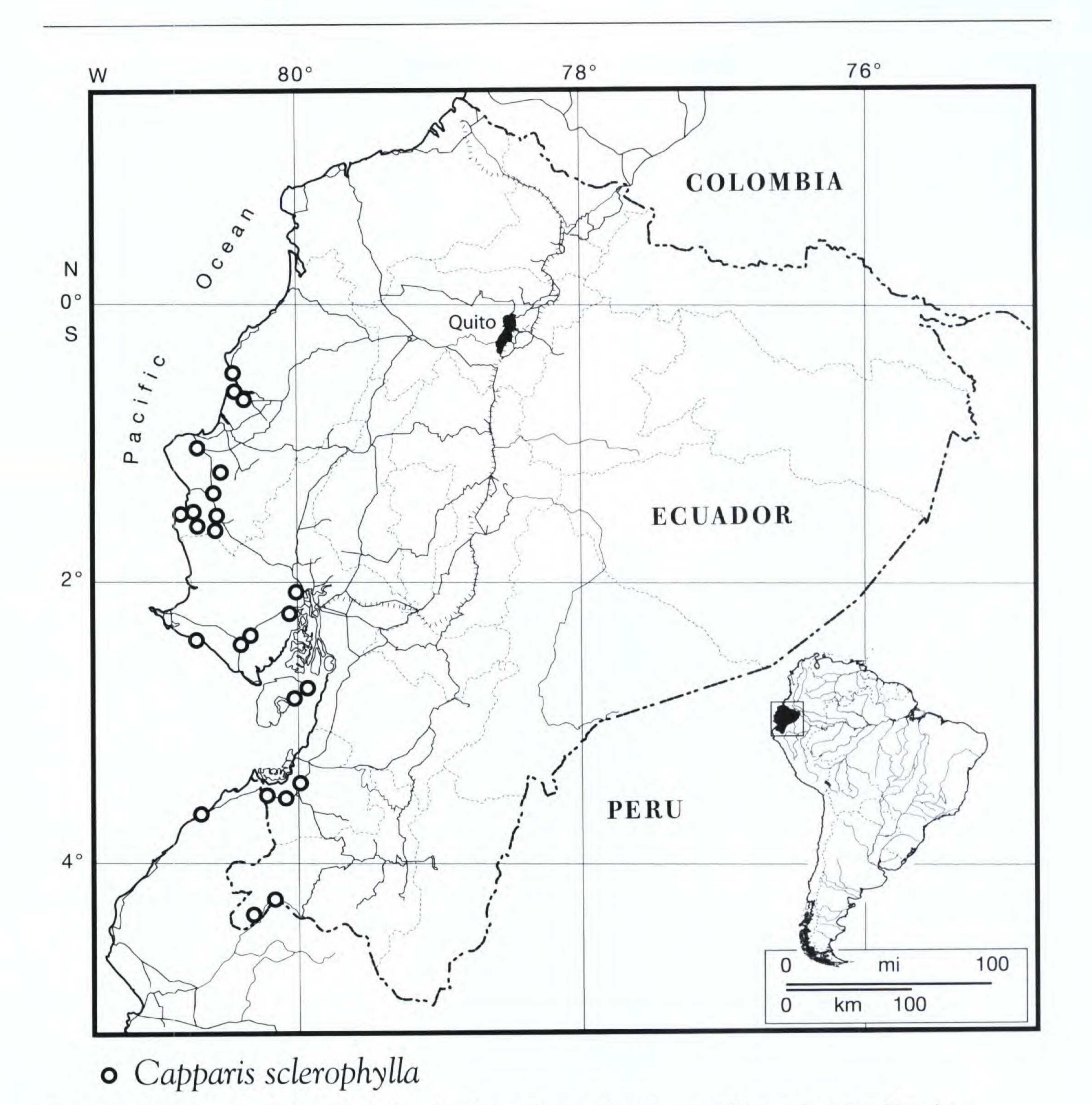


Figure 1. Capparis sclerophylla. Geographic distribution from northwesternmost Peru and western Ecuador.

adjoining some  $28 \times 5.5$  cm), those on sproutshoots often narrowly to broadly linear,  $(5-)7-9(-15) \times (1-)2-3(-4)$  cm or even  $20 \times 1$  cm, dark olive-green above, very light pale green beneath, glabrous when mature, or occasionally with a soft short dense puberulence on midrib and blade beneath but barely so above, the apex acute to obtuse, rarely rounded or emarginate, apiculate, the base subsessile, cuneate to rounded or subcordate (i.e., viewed from above, subpeltate, with leaf lobe margins overlapping and almost confluent below the petiole insertion); lateral veins 7 to 12 on each side of the midrib, somewhat elevated on both sides, the midrib beneath strongly elevated, yellow, changing abruptly into the dark brown to black petiole (rarely

green, at least in the herbarium); petioles very short, (1–)2–3(–4) mm, when fresh with 20 or more deep transverse fissures, when dry extremely brittle and readily breaking from the branch at the slightest touch (hence many if not most herbarium specimens leafless), subtended by paired, thin, triangular, apiculate, ± caducous stipules ca. 1–2 mm wide; glands above the leaf axils on very young branches 1(to 3), increasing in size upward in a vertical row, sessile, subspherical, 1–2 mm diam., composed of 2 pairs of decussate, fleshy bracts (the outer larger) enclosing a brown, nectar-producing center, subtended by a pair of round-apiculate, pale and marcescent stipules, on the older, pale gray to pale brown branches often solitary and soon becom-

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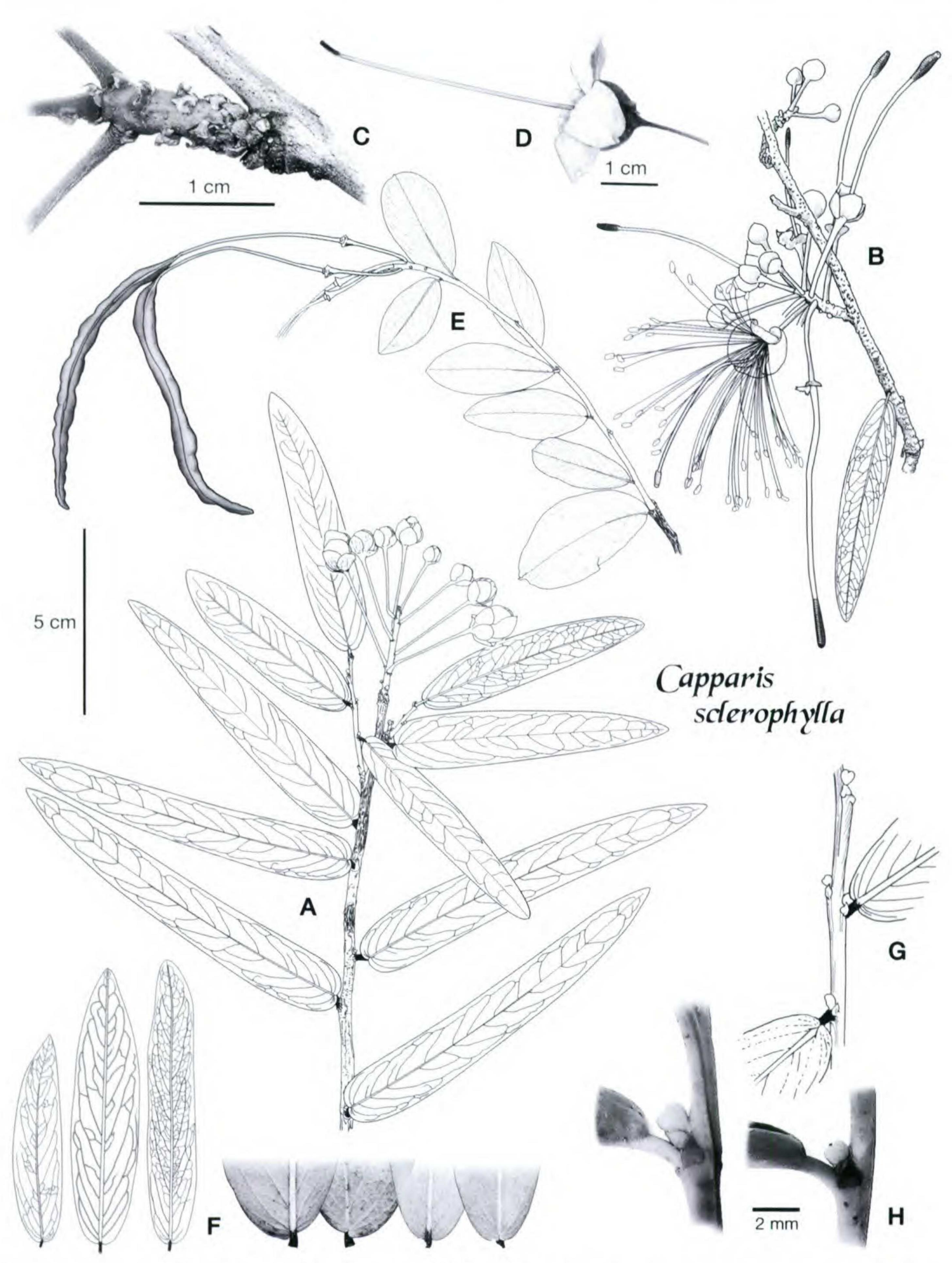


Figure 2. Capparis sclerophylla Iltis & X. Cornejo. —A. Branch with flower buds on short leafless terminal long shoot. —B. Detail, with flowers on condensed short-shoot raceme axis or peduncle. —C. Condensed short-shoot peduncle showing 3 terminal pedicels and many old spirally disposed pedicel bases with associated stipules and bracts. —D. Open flower with stamens fallen off one day after anthesis. —E. Leafy, elongate, long-shoot branch bearing four fruits (only two shown). —F. Leaves showing short black petioles: three drawings (left) and photos of two paired leaves (right), left of each pair showing underside, right of each pair, upper surface with subpeltate insertion. —G. Leaf bases, with underside (right), and upper surface (left) with subpeltate insertion. —H. Close-up photo of 2 leaf nodes of very young shoot, each with a stipulate petiole, its leaf base, axillary bud, and extra-floral nectary. (A–H, from the type, Cornejo & Bonifaz 5822.)

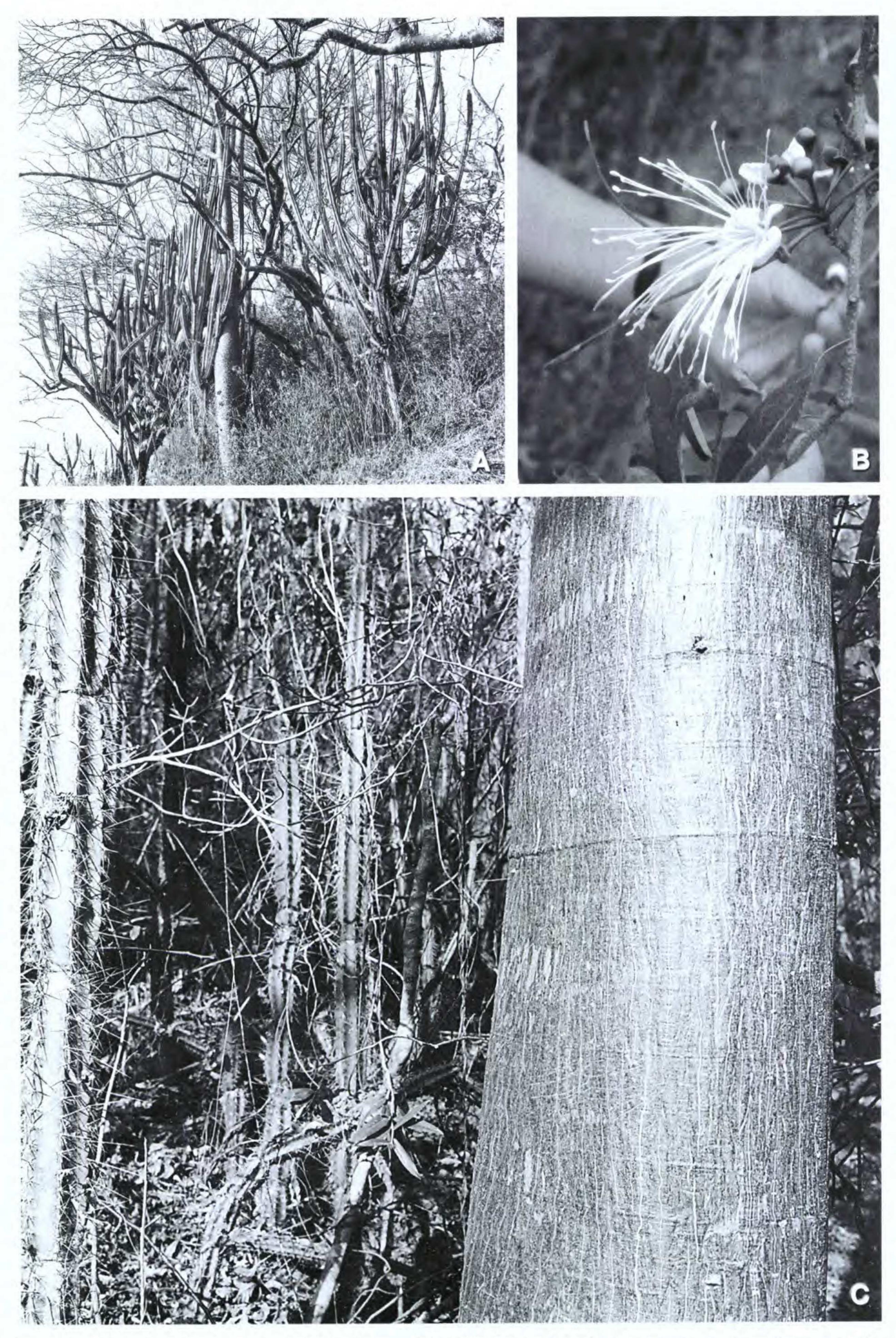


Figure 3. Capparis sclerophylla.—A, C. Habitat, ca. 5 km ESE of Bahía de Caráquez, at Sitio Mauricio, close to the type locality in Ecuador. View of vegetation with *Pilosocereus tweedianus* (Britton & Rose) Byles & G. D. Rowley (Cactaceae), the smooth bark of *Cochlospermum vitifolium* (Willdenow) Sprengel (Bixaceae), *Ceiba trichistandra* (A. Gray) Bakhuizen (Bombacaceae, shown in center of A), and leafy branch of C. sclerophylla (lower center of C). —B. Flowers on short-shoot raceme axis. (Photos: A, C, Iltis; B, Cornejo.)

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ing obsolete and barely recognizable as small, eroded axillary pits. Racemes terminal, subterminal and/or lateral, mostly on old branches, their axes (peduncles) of two sorts: most commonly (1) lateral or subterminal short shoots or spurs on old wood of leafy branches, ± highly condensed and congested, thick, stubby and sessile (never slenderly zig-zag), 5-11(-22) mm long, 2-4 mm thick, green when young or, if old, grayish and scruffy or scaly and covered with paired, round to triangular, apiculate stipules and bract surrounding (3 to)6 to 12 or more old pedicel scars or aborted flower buds; when peduncles lateral, then solitary or in twos or threes, when terminal or subterminal, solitary or in twos to fives, these often then tightly clustered on the old wood, each bearing up to 3 to 6 or more flower buds, the larger peduncle clusters at anthesis with as many as 25 flower buds arranged in a compound umbelliform false "panicle," but with only a single flower of each individual peduncle open at one time; or finally, less commonly and sometimes together with, but exceeding in length, the above condition: (2) slender and uncongested, solitary, leafless new-growth (long shoots) terminating new leafy branches or old leafy branches, in either case the peduncles (raceme axes) slender and smooth, uncondensed and mostly 20-50 mm long, ca. 2 mm thick, and ending in ca. 8 to 14 flower buds or flowers and/or pedicel scars arranged distichously as in a fan, and in addition, each with 3 to 6 axillary nectariferous glands (see above) clustered at or near the peduncle base, these not subtended by pedicels but only by minute, paired, pale, scarious, round to triangular stipules. Flowers showy, white, spirally disposed on ascending pedicels (14-)20-30(-44) mm long; calyx of 4 sepals in 2 unequal decussate-imbricate series, the smaller, outer ones  $4-6 \times 6-8$  mm, the larger, inner  $7-8 \times 9-10$  mm, green on the back, with thin, hyaline-papery, translucent margins, strongly cupulate, in bud nearly completely covering corolla, but just before anthesis tightly covering only 1/2 to 1/3; corolla buds at anthesis obovoid, ca. 15 mm diam., glabrous; receptacle obconic, topped by a circular fleshy disk 5-6 mm diam., its flat top with 4 nectar-producing depressions, the nectar very sweet. Corolla cruciform; petals pure white within, light green at base without, ovate to oblong,  $23-29 \times 9-17$  mm, with rounded apex, the base broadly cuneate to rounded, subsessile and inserted into the disk by a short peg, the open flower ca. 15-20 mm across, with the upper half of the petals at nightfall becoming sharply reflexed over, and almost to the base of, the sepals; androgynophore absent, the androecium base forming a ring around the base of the gynophore in the

center of the disk; stamens 40 to 70, filaments pure white, glabrous to the very base, subequal, 45-70 mm long, in bud spirally disposed around the style, at anthesis in a pincushion funnel with ca. 90° divergence; anthers 2-3 mm long; gynophore white, becoming dark purple with maturity, 45-65 mm long; ovary green, narrowly oblongoid, 5-7 mm long, with a hemispherical stigma, the gynophore and ovary exceeding the stamens. Siliques 1 to 4 (rarely to 6) per raceme, usually densely clustered on the short shoots (or more distant on the more uncommon slender terminal peduncles), linear-cylindric,  $6-14(-20) \times 0.8-1.2(-1.5)$  cm, smooth and glabrous, usually ± torulose (constricted around seeds, but see below), yellow-brown to purple, or green streaked with dark red to purple, when mature each continuous with its slightly curved, slender to stout, 6-9 cm long gynophore and its (1.3-)2-3(-4) cm long pedicel, with the 2-4 mm long, 6-8 mm wide receptacle in between; seeds mostly (2-)6-12(-14), usually single-rowed or occasionally 2- or 3- or rarely 4-rowed and square in cross section, gigantic to 20 × 1.5 cm, ca. 60 [Cornejo & Bonifaz 7154 (WIS)]; seeds 6-15  $\times$  ca. 5-7 mm, the testa paper thin, dark brown, surrounded by a white, oily aril, both together (unlike seeds of all other species in subg. Cynophalla, except C. verrucosa) embedded in the apparently white pulpy endocarp, with aril and testa together presumably slipping off easily under pressure exposing the naked, green, ready to germinate embryo; seeds sometimes hanging on for a short period by a slender thread from the thin, valve-embedded replum; embryo slightly curved, but essentially straight.

Peru (Tumbes) to northwestern coastal Ecuador (Provinces of Loja, El Oro, Guayas, and Manabí as far north as "El Recreo" [(just south of Canoa and north of Bahía de Caráquez), a beach house labeled "El Recreo" on the second floor and still standing in 1977, made famous by the Danish plant explorer Baron von Eggers (Eggers, 1894; Iltis, 1978)], in a variety of xerophytic, super-dry coastal vegetation types, from deciduous thornscrub or monte espinoso, to semi-evergreen dry forest (bosque muy seco-seco), savanna or bushwood, to tropical deciduous forest, from sea level to 600 m.

"The habitat of Cornejo & Bonifaz 5822 (the type collection) is a very disturbed, open, sunny, very dry tropical forest, with dense scrubby shrubs less than 2 m high and very few scattered trees, in which C. sclerophylla is a frequent shrub associated with Cordia lutea [Lamarck], Mimosa debilis var. aequatoriana [(Rudd) Barneby], Capparis crotono-

ides, C. scabrida, C. heterophylla, C. guayaquilensis, C. didymobotrys, Cucurbita ecuadorensis [Cutler & Whitaker], Ipomoea nil [(L.) Roth], I. hederifolia [L.], and Jacquemontia [Choisy] sp. In other small remnant forests nearby, mature individuals of C. sclerophylla ranged from shrubs to 4–5 m tall and 10 cm dbh treelets, that are associated with Tabebuia chrysantha [Nicholson], Caesalpinia glabrata [Kunth], Achatocarpus pubescens [C. H. Wright], Bursera graveolens [Triana & Planchon], Eriotheca ruizii [(K. Schumann) A. Robyns], Geoffroea spinosa [Jacquin], and Bonellia sprucei [(Mez) Ståhl & Källersjö]" (letter to Iltis from Cornejo & Bonifaz, 5 Nov. 1997).

Phenology. Flowering from October into March (May), fruiting mostly from (October) December to April.

Local names. Fresno (Spanish), Vivar et al. 883 (Loja); Patacón (Spanish), Iltis 168 (Manabí); Sebastián (Spanish), Iltis 168 (Manabí), Madsen 63781, 63782 (Guayas); Vaina morada (Spanish), Hernández et al. 222 (Manabí).

Local uses. For construction, firewood, and charcoal (Madsen et al., 2001).

Discussion. Capparis sclerophylla is vegetatively easily recognized by the thick, stiff, variously divergent, dark olive-green leaves on short (1-4) mm) dark brown to black petioles. In other respects it is rather similar to various forms of C. guayaquilensis, but the latter have relatively thinner and more flexible leaves that on drying become dark reddish brown or mahogany, and are borne on more flexible, slender petioles 6–10 mm long, from which the leaves usually hang down loosely, on either side of the branch. When in flower or fruit, or leafless, the densely congested, short-shoot peduncles, 2-4 mm thick and usually less than 20 mm long, immediately identify C. sclerophylla, while most others in subgenus Cynophalla have slender, flexible, often pronounced flexuous (zig-zag) raceme axes on which the flowers or flower buds are well-spaced out and 5-10 mm apart. Like all species of Cynophalla, C. sclerophylla is characterized by 1 to 3 cauline "glands" or extra-floral nectaries (Poulsen, 1879-1880) in the axil of leaves and/or at the base of the leafless terminal raceme axis (see above), which together with the young leaves are visited by vast numbers of ants of at least three taxa (Cornejo, pers. obs.).

Among its close relatives, *Capparis sclerophylla* is morphologically the most highly specialized xerophyte, judging from the thick, evergreen leaves, the congested short-shoot peduncles and the short

petioles, the latter shared only by another mostly coastal species, *Capparis verrucosa*, widespread from western Mexico to coastal Venezuela. This species not only shares with *C. sclerophylla* the strongly recurved petals of the open flower, but also the color of the fruit pulp, which in both species is apparently white rather than the typical bright orange, red, or purple of all the other *Cynophalla* species. Whether this white pulp reflects an adaptation to bat seed dispersal during the night is not known, but deserves investigation.

The unique relationship of these two clear-cut species, Capparis sclerophylla and C. verrucosa, is strengthened by an easily overlooked floral character, the presence or absence of pubescence at the base of the staminal filaments. While most of the taxa of the Capparis flexuosa s.l. complex (e.g., C. flexuosa s. str., C. polyantha Triana & Planchon, C. declinata Vellozo, C. mollis, C. guayaquilensis, C. didymobotrys, C. tarapotensis Eichler, C. retusa Grisebach, etc.) have a dense, short, glandular pubescence covering the basal ½ or so of the staminal filaments, C. sclerophylla and C. verrucosa lack this peculiarity, what with their filaments being completely glabrous to the very base.

There are two exceptions within the Capparis flexuosa s.l. complex. First of all, the condition is variable in C. hastata Jacquin f. coccolobifolia (Martius) Dugand & Iltis, a relative of C. flexuosa s. str. that appears to hybridize with it (Iltis, 1991), with staminal filaments pubescent in ca. one-fifth of the specimens and totally glabrous in the rest. Capparis hastata is apparently the only species in the C. flexuosa group that regularly has glandular pubescent ovaries and gynophores. Second, and more interesting, is the lack of filament pubescence in a closely related, but quite distinct, species pair of subgenus Cynophalla: C. heterophylla and C. ecuadorica (Iltis, 1978). Though related to subgenus Cynophalla, they do not belong with the C. flexuosa s. str. alliance, and their relationship to C. sclerophylla and C. verrucosa is rather distant. It may be worth mentioning, however, that much like C. sclerophylla, both C. heterophylla and C. ecuadorica are also restricted to the lowlands on the western side of the Andes and nearly endemic to Ecuador.

Finally, similar in leaf shape is *Capparis flexuosa* s. str., a shrub widespread from Florida, the Caribbean and Central America to Venezuela and the Brazilian Islas de Noronha in the Atlantic Ocean. While the leaves of *C. flexuosa* are generally quite flexible, the fruit shape resembles that of *C. sclerophylla*. It is of interest that *C. flexuosa* is also characterized by a few large flowers at the end of its

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branches and weak, lianoid "leaning" stems, which may also occur in *C. sclerophylla*, with one of its collections (*Plowman et al. 4610*) even called a "vine." Considering that the habitat of *C. sclerophylla* is often heavily disturbed by the gathering of firewood, animal grazing, or forest clearing through burning, we also have often seen its flexible slender branches sprawling like a vine over nearby vegetation (Cornejo, pers. obs.).

The relative rarity of Capparis sclerophylla, and the infrequency of its flowering or fruiting, may be related to such disturbance. Furthermore, the second author has often observed its firewood-trimmed shrubs in secondary vegetation overwhelmed by dense layers of vines, often of the endemic Cucurbita ecuadorensis, which, whenever such nest-like tangles were lifted off from these bushes, revealed the presence of usually sterile specimens of our new species underneath. Evidently, the treelet growth form is more to its reproductive optimum.

Biological interactions. The flowers of Capparis sclerophylla are visited by bees and ants in the early evening (Cornejo, pers. obs., 6:05 p.m.–6:30 p.m.) and also by bumblebee nectar thieves that do not penetrate the flower but bite a hole at the base of the flower to get at the nectar. The flowers produce a very sweet nectar by 7:30 p.m., becoming fragrant around 8:00 p.m., and stay open all night. Next day, once the sepals, petals, and stamens have fallen, the nectaries, as well as the axillary glands, are extensively visited by ants (Cornejo, pers. obs.). The pollinators are unknown, but probably include bats.

Cytotaxonomy of Capparis subg. Cynophalla. Clear evidence for hybridization or introgression with other species is lacking, even though C. sclerophylla quite frequently occurs together with one or more species of the subgenus. Some species groups within subgenus Cynophalla appear to be part of a polyploid series, and others are homoploid. Herein may lie the cause of both the distinctness of C. sclerophylla, whose chromosome number is as yet unknown, and the taxonomic problems due to putative hybridization between the closely related C. guayaquilensis and C. mollis of the Pacific slope of Ecuador and Peru. Despite Capparis chromosomes being very small and difficult to study, counts by Batia Pazy (in Iltis, 1978, vouchered in WIS) for C. ecuadorica indicated ca. n = 25-26(probably 28, i.e., a tetraploid 2n = 56, based on Iltis 196) and for the related C. heterophylla, ca. 2n = 70–80? (perhaps a hexaploid 2n = 84, based on Iltis 207), these two an isolated species pair essentially endemic to Ecuador.

A similar species pair of Capparis subg. Cynophalla from Pernambuco in eastern Brazil, both part of the Capparis flexuosa complex, revealed a plant with fruits similar to those of C. hastata f. coccolobifolia (listed in Costa e Silva, 1995, as "C. cynophallophora") with a chromosome count of 2n = 28, while another sympatric species within the C. flexuosa complex from eastern Brazil, C. declinata (listed as "C. flexuosa"), had a tetraploid count of 2n = 56 chromosomes (Costa e Silva, 1995: 58– 61). Finally, n = 14 has been reported for C. flexuosa s. str. from Dominica (Ernst in Iltis, 1991). Previously unreported are the following additional n = 14 counts by Batia Pazy for species of subgenus Cynophalla (Iltis et al., 1985, unpublished, all vouchered in WIS): C. flexuosa s. str., Jalisco, Mexico (Iltis 29195); C. declinata (C. flexuosa s.l.), Bahia, Brazil (Mori 11241); C. guayaquilensis, Guayas, Ecuador (Iltis E-10); and C. verrucosa, Chamela, Jalisco, Mexico (Bullock s.n., counted by S. Bullock, pers. comm. to Iltis). These chromosome numbers suggest genetic isolation of a putative diploid C. sclerophylla as supported by the morphological uniformity of C. sclerophylla, in contrast to the incredible intergrading variability observed among other sympatric taxa.

Paratypes. PERU. Túmbes: Küstenhalbwüste und Trockenwald-region, Tonnenbaum Mischwald [Ceiba trichistandra mixed forest], Cienego, just along coast S of Tumbes, H. Ellenberg 1408 (U, GUAY photo, WIS); Zarumilla, pampas de Hospital, entre El Caucho y Cóndor Flores, C. Díaz & R. Vázquez 3044 (MO, WIS fragm.); Zarumilla, region below El Caucho, T. Plowman 5489 (GH, WIS photocopy). ECUADOR. Loja: In sector algodonal, entre Macará y Zapotillo, P. Lozano & G. Lewis 702 (LOJA); Zapotillo, La Ceiba, F. Vivar 883 (LOJA). El Oro: near Santa Rosa [fide catalogue], F. Lehmann 7649 (K, WIS); 18 km SW of Santa Rosa, C. Johnson 4238 (MO, WIS); rd. from Arenillas to Huaquillas, T. Plowman, L. Jacobs & E. Davis 4610 (GH, S, WIS): 1 km NW of Arenillas on rd. to Huaquillas, L. Albert de Escobar 705 (QCA, TEX, WIS); 2 km al sur de Chacras cerca a la entrada a Balsalito en la carretera de la Reserva Militar Arenillas, H. Vargas, C. Canaday & R. Miranda 1171 (MO, QCNE, WIS). Guayas: Capeira, km 21 on rd. Guayaquil to Daule, C. Dodson & A. Gentry 12619 (MO, SEL, WIS); Finca La Gloria, km 53 carr. Guayaquil-Playas, X. Cornejo & H. Grochowski 7797 (GUAY, WIS); Guayaquil-Salinas rd., 1-5 km E of El Progreso, G. Harling & L. Andersson 21118, 21129 (GB, WIS photocopy); G. Harling & L. Andersson 21105 (GB, QCA); km 20 Guayaquil-Salinas rd, G. Harling & L. Andersson 21041 (GB, QCA, WIS); Playas, Guayaquil, G. Sánchez 2, 3 (WIS); km 17 de la vía Playas-Posorja, C. Bonifaz 3639 (GUAY, WIS); Chanduy prope Guayaquil, [Feb.-Aug. 1862], R. Spruce s.n. (K, GUAY photo, WIS); Isla Puná, trail from Puná Nueva to Concordia, J. Madsen, E. Madsen & E. Montero 85367 (AAU, QCA, WIS photo); vic. Puná Nueva tow. Zapote, J. Madsen 64106 (AAU, WIS photo); El Placer, 0-5 km tow. Río Hondo, J. Madsen 63942 (AAU, WIS

photo); path from Campo Alegre to Midway Río Hondo, J. Madsen 63781, 63782 (AAU, WIS photo). Manabí: Cuenca del Río Ayampe, Cerro Cabeza de Vaca, X. Cornejo & C. Bonifaz 818 (GUAY, WIS); Barbasmonte, X. Cornejo & C. Bonifaz 1027 (GUAY, QCNE, WIS); Portoviejo-Jipijapa rd., 1 km S of La Pila, G. Harling & L. Andersson 24824 (GB, WIS photocopy); rd. from Colimes de Paján to Jipijapa, C. Dodson & L. Thien 1693 (WIS); Cerro Montecristi, 200 m, X. Cornejo & C. Bonifaz 5917 (GUAY, WIS); N of Manta, 2 km from Montecristi, C. Dodson & L. Thien 1750 (UC, WIS); Quevedo-Manta rd., 50.9 km W of El Empalme, R. Sauleda, M. Ragan, H. Luther, R. Wunderlin, B. Hansen, L. Davenport & J. Wiersema 4023 (USF, WIS photocopy): Par. Nac. Machalilla, N de Puerto López, X. Cornejo & C. Bonifaz 2322 (GUAY, QCNE, WIS): Estero Manta Blanca, S of Agua Blanca, A. Gentry & G. Josse 72718 (MO, QCNE, WIS); Las Goteras, C. Hernández 222 (QCA); Bahía de Caráquez, predios de la Univ. Católica, X. Cornejo & C. Bonifaz 7154 (GUAY, WIS [2]); hills above Río Chone, just in back of Sitio Mauricio along main rd. 4 km SSE of Bahía de Caráquez, H. H. Iltis & M. Iltis E-168 (QCA p.p., w/ C. lanceolata); 9 km N of San Vicente, H. H. Iltis & M. Iltis E-208 (WIS [3]); Heda. El Recreo, ca. 2 km along coast from Canoa, 18 km N of Bahía de Caráquez, H. H. Iltis & M. Iltis E-216 (WIS [2]).

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