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Abstract

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Capparis is represented in Cuba by six species of four sections. A key for their identification is provided, their nomenclature and that of the sections in which they belong is revised, and the intricate relevant typification problems are discussed. Three species, each of a different section, are not critical taxonomically. The other three, which belong to *C.* sect. *Breyniastrum*, have been poorly understood and often confused in the past. Microcharacters of trichome and leaf surface morphology (illustrated by SEM photographs) prove useful to tell them apart. In conclusion, two Macroantillean species are recognised, each represented in Cuba by a distinct, endemic subspecies (one new, one recombined); a third species, *C. singularis*, known from a single E Cuban gathering, is described as new to science. Distribution maps are provided of these three Cuban endemics, and the relevant specimen data are included, as a searchable database, in an electronic supplement to the present paper.

Introduction

Capparis is a large and polymorphic genus, with a world-wide distribution in the tropics and subtropical zones. Infrageneric treatments have been proposed for it by various authors (Candolle 1824, Endlicher 1836-41, Grisebach 1859-64, Eichler 1865, Pax & Hoffmann 1936), but whereas Jacobs (1965) has published a revision of the S Asian and Pacific taxa, no modern global classification exists other than Hutchinson's (1967), who atomised *Capparis* into several small genera that few other than himself have accepted. In so far as they are natural units, we consider them to be sections of *Capparis*.

According to Iltis (2001) there are about 160 *Capparis* taxa (species?) world-wide, of which less than one third (c. 50) are present in the New World. From the Antillean islands, 15 species

are known (Fawcett & Rendle 1914b, Adams 1972, Alain 1983, 1985, Al-Shehbaz 1988), and of these, four (León & Alain 1951) or five (Alain 1969) are reported for Cuba, the difference depending on whether or not *C. grisebachii* Eichler is accepted as distinct from *C. ferruginea* L.

The purpose of the present paper is twofold. Its first part is a survey of the Cuban *Capparis* taxa. It starts by a key permitting their identification, then deals with their placement in sections (and Hutchinson's genera) and tackles the intricate problems of nomenclature and typification that many of them present. The second portion is devoted to the study of the *C. ferruginea* complex, in which taxa are difficult to tell apart and have often been confused in the past. New characters were found, in particular in the micromorphology of trichomes and upper leaf surface, that permit a clearer delimitation of the species and, within them, of the populations of the different Antillean islands. Detailed morphological descriptions are given of the five Caribbean taxa that we recognise in the group, and for the three Cuban endemics distribution maps are provided, based on a large bulk of herbarium material that we have revised.

Key for the identification of *Capparis* in Cuba

1. Plants glabrous; sepals \pm orbicular, imbricate 2
 - Plants with branched hairs or peltate scales; sepals triangular or lanceolate to linear, not imbricate in bud 3
2. Leaves clustered at the end of the branches, the proximal ones long-petiolate, the distal subsessile; axillary glands absent; sepals minute, subequal 2. *C. frondosa*
 - Leaves evenly spaced along the branches; petioles of \pm equal length; knob-like glands present in the leaf axils; sepals conspicuous, markedly unequal in size 1. *C. flexuosa*
3. Plants covered with peltate scales, except for the glabrous and shiny upper leaf surface; fruits cylindrical, torulose; calyx valvate, completely enclosing the corolla in bud 3. *C. cynophallophora*
 - Plants covered with branched hairs; upper leaf surface hairy at least when young; fruits ovoid to obovoid; calyx not enclosing the corolla in bud, i.e., sepal margins not contiguous 4
4. Sepals lanceolate, c. 7×2 mm, reflexed; stamens \pm 16, with 12-14 mm long filaments; gynophore 12-18 mm long in flower; upper leaf surface with minute, blunt, broadly conical protuberances 6. *C. singularis*
 - Sepals $\leq 6 \times 1.5$ mm; stamens 8, with ≤ 6 mm long filaments; gynophore ≤ 5 mm long in flower; upper leaf surface smooth 5
5. Branches and leaves, especially beneath, with a dense, \pm rusty cover of stellate hairs; sepals ovate-triangular, c. 2 mm long, stellately spreading at anthesis 4b. *C. ferruginea* subsp. *cubensis*
 - Hair cover of branches and leaves yellowish white, the leaves beneath with a mixed tomentum of stellate and dendritic hairs; sepals linear, 3-6 mm long, reflexed at anthesis 5b. *C. domingensis* subsp. *grisebachii*

Synopsis of Cuban *Capparis* taxa

Capparis L., Sp. Pl.: 503. 1753. – Type (Green in Sprague & al., Nom. Prop. Brit. Bot.: 160. 1929): *C. spinosa* L.

A. *Capparis* sect. *Cynophalla* DC., Prodr. 1: 249. 1824 \equiv *C.* subg. *Cynophalla* (DC.) Eichler in Martius, Fl. Bras. 13(1): 282. 1865. – Type: *C. cynophallophora* DC., nom. illeg. [non L.] (\equiv *Morisonia flexuosa* L. \equiv *C. flexuosa* (L.) L.).

Notes. – By using the name *Capparis cynophallophora* in a sense that excludes its original type (see below), Candolle (1824) created an illegitimate later homonym under Art. 48.1 of the International Code of Botanical Nomenclature (ICBN; Greuter & al. 2000). Furthermore he included

as a synonym *C. flexuosa*, a name that he ought to have adopted, so that *C. cynophallophora* DC. is doubly illegitimate. Nevertheless it provides the type of the sectional name (Art. 22.7).

Following Candolle's authority, the name *Capparis cynophallophora* has been applied in the sense of *C. flexuosa* throughout the 19th century and beyond, until Fawcett & Rendle (1914a) cleared up the confusion. Pax & Hoffmann (1936: 178), well aware of Fawcett & Rendle's paper and seemingly adopting its conclusions (as witnessed by synonymy), still had Candolle's illegitimate *C. cynophallophora* in mind (as is shown by its placement in *C. sect. Cynophalla*, next to *C. flexuosa*). Under *C. sect. Quadrella*, where *C. cynophallophora* L. belongs under Pax & Hoffmann's own criteria, they do not mention that species.

1. *Capparis flexuosa* (L.) L., Sp. Pl., ed. 2: 722. 1762 ≡ *Morisonia flexuosa* L., Pl. Jamaic. Pug.: 14. 1759 ≡ *C. cynophallophora* DC., Prodr. 1: 249. 1824, nom. illeg. [non L. 1753]. – Lectotype (Fawcett & Rendle 1914a: 142): [Jamaica], *Browne* in herb. Linn. 664.10 (LINN).

Note. – Typification of *Capparis cynophallophora* by LINN 664.10 has been confirmed by Al-Shehbaz (1988: 297). Fawcett & Rendle (1914a) wrote: "*C. flexuosa* ... is founded on a Jamaican specimen from Patrick Browne ... in the Linnean herbarium". Considering that the phrases "founded on" and "based on" have exactly the same meaning, and noting the Committee for Spermatophyta's majority opinion (Brummitt 1996: 671) that the phrase "based on" is equivalent to "type" for the purposes of Art. 7.11 of the ICBN, we accept Fawcett & Rendle's statement as effective type designation.

B. *Capparis* sect. *Capparidastrum* DC., Prodr. 1: 248. 1824 ≡ *Capparis* subg. *Capparidastrum* (DC.) Eichler in Martius, Fl. Bras. 13(1): 278. 1865 ≡ *Capparidastrum* (DC.) Hutch., Gen. Fl. Pl. 2: 309. 1967. – Type (designated here): *C. frondosa* Jacq.

Note. – Hutchinson (1967) proposed *Capparidastrum* as a new genus, with a Latin description and *Capparis baducca* L. (*Capparidastrum baducca* (L.) Hutch.) as type, but he also cited Eichler's *C. subg. Capparidastrum* in synonymy. Under Art. 33.6(d) of the ICBN it is possible to consider *Capparidastrum* as implicitly based on *C. sect. Capparidastrum* DC., in which case one must dismiss Hutchinson's type statement as a correctable error, because *Capparis baducca* is not among the elements of Candolle's section. In fact, Candolle does not include *C. baducca* it in any of his sections, because (as he comments under *C. rheedei* DC.) it is a mixture "in quâ plures sunt confusae". As presently typified (see below), *C. baducca* would be in conflict with Hutchinson's concept of *Capparidastrum* as a New World genus.

2. *Capparis frondosa* Jacq., Enum. Syst. Pl.: 24. 1760. – Neotype (Al-Shehbaz 1988: 295): Jacquin, Select. Stirp. Amer. Hist.: t. 104. 1763. ≡ *Capparis baducca* D. E. Prado in Taxon 42: 658. 1993 [non L. 1753]. – Holotype: Herb. Clifford: 204, *Capparis* No. 3 (BM).

Note. – Linnaeus (1753: 504) confused two species under *Capparis baducca*. The first to designate a type, Jacobs (1965: 435), chose the Old World element from which Linnaeus derived the specific epithet ("Badukka" in Rheede, Hort. Malab. 6: t. 57. 1686). This is a plant from the Malabar coast in SW India that was later redescribed as *C. rheedei* DC. Jacobs's lectotype designation was disputed by several authors, beginning with Nicolson (1978), but under the nomenclatural rules there is no way, short of conservation, in which it can be superseded. The subsequent choice, by Prado (1993), of a West Indian type specimen has no effect on the application of the Linnean name but, under Art. 48.1 of the ICBN, inadvertently resulted in the validation of a later homonym, *C. baducca* D. E. Prado.

In some floras (e.g. Iltis 1991), the name *Capparis baducca* L. is still misapplied to the New World species, but other, more recent treatments have switched to the correct *C. frondosa* (e.g. Ruiz-Zapata & Iltis 1998). Unless it is formally rejected (which would, we feel, be desirable), *C. baducca* threatens to displace the unambiguous *C. rheedei*.

C. *Capparis* sect. *Quadrella* DC., Prodr. 1: 251. 1824 ≡ *Quadrella* (DC.) J. Presl in Berchtold & Presl, Prir. Rostlin 2: 260. 1825 ≡ *Capparis* subg. *Quadrella* (DC.) Eichler in Martius, Fl. Bras. 13(1): 269. 1865. – Type (Hutchinson 1967: 309): *C. cynophallophora* L. (≡ *Quadrella cynophallophora* (L.) Hitchc.).

Note. – It is rather confusing that what appears to be the same name, *Capparis cynophallophora*, should provide the type of two different, simultaneously published sectional names, *C. sect. Quadrella* and *C. sect. Cynophalla* (see above). Linnaeus himself is at the origin of the confusion. He initially (Linnaeus 1753) had a single element in *C. cynophallophora*, but later (Linnaeus 1762) added other, discordant elements. Candolle (1824) cited the Linnaean binomial in the sense of these later additions, excluding the original element: he cites *C. cynophallophora*, “Lin. sp. ed. 1 p. ... 504” in synonymy under *C. breynia* L., a member of *C. sect. Quadrella*. As binomials that in the protologue are cited in synonymy are eligible to provide the type of a generic name (ICBN, Art. 10.3), Hutchinson’s type designation is appropriate and must stand.

3. *Capparis cynophallophora* L., Sp. Pl.: 504. 1753 ≡ *Quadrella cynophallophora* (L.) Hutch., Gen. Fl. Pl. 2: 309. 1967. – Lectotype (Fawcett & Rendle 1914a: 142): Herb. Clifford: 204, *Capparis* No. 2 (BM).

= *Capparis jamaicensis* Jacq., Enum. Syst. Pl.: 23. 1760. – Neotype (Al-Shehbaz 1988: 296): [icon] Jacquin, Select. Stirp. Amer. Hist.: t. 101. 1763.

= *Capparis emarginata* A. Rich. in Sagra, Hist. Fís. Cuba 10: 28. 1845. – Lectotype (Al-Shehbaz 1988: 296): [Cuba], Sagra (P).

Note. – Typification of *Capparis cynophallophora*, by the specimen in the Clifford Herbarium has been confirmed by Al-Shehbaz (1988: 296). Fawcett & Rendle (1914a) wrote: “*Capparis cynophallophora*... is based on the plant *Capparis*, no. 2, of Hortus Cliffortianus, 204”. We follow the advice of the Committee for Spermatophyta (Brummitt 1996: 671) in considering that the phrase “based on” is acceptable as an equivalent of the word “type” for the purposes of Art. 7.11 of the ICBN.

D. *Capparis* sect. *Breyniastrum* DC., Prodr. 1: 250. 1824 ≡ *Capparis* sect. *Pseudocrataeva* Griseb., Fl. Brit. W. I.: 17. 1859 (homotypic by type designation) ≡ *Capparis* subg. *Breyniastrum* (DC.) Eichler in Martius, Fl. Bras. 13(1): 271. 1865. – Type (designated here): *C. ferruginea* L. (≡ *Linnaeobreynia ferruginea* (L.) Hutch.)

= *Breynia* L., Sp. Pl.: 503. 1753, nom. rej. ≡ *Linnaeobreynia* Hutch., Gen. Fl. Pl. 2: 310. 1967, nom. illeg. – Type: *B. indica* L. (≡ *Capparis breynia* L., nom. illeg. ≡ *Capparis indica* (L.) Fawc. & Rendle ≡ *Linnaeobreynia indica* (L.) Hutch.).

?= *Capparis* sect. *Calanthea* DC., Prodr. 1: 250. 1824 ≡ *Calanthea* (DC.) Miers in Proc. Roy. Hort. Soc. London 4: 161. 1865. – Type (Chambers & al. in ING: card No. 33135. 1971): *C. pulcherrima* Jacq. (*Calanthea pulcherrima* (Jacq.) Miers).

Notes. – The original type of *Breynia* L. and of the homotypic *Linnaeobreynia* Hutch. is *B. indica* L., a name that has not so far been properly typified. The Plumier plate that Al-Shehbaz (1988: 299) designated as “type” is not eligible as such because it illustrates the genus as a whole and not the particular species cited by Linnaeus. A specimen collected by Sloane in Jamaica (BM-SL vol. 6: 54), identified and cited by Fawcett & Rendle (1914b), can be viewed on the World Wide Web (under *Capparis indica*, <http://internt.nhm.ac.uk/botany/sloane/lgimages/bm000593850.jpg>), but it is unlikely that Linnaeus could have studied that particular specimen during his brief visit to Sloane. What then remains is the plate cited by Linnaeus (“*Breynia Elaeagni foliis* Plum.” in Breynia, Prodr. Fasc. Rar. Pl.: t. ad p. 13. 1739), which is reproduced from an illustration by Aubriet and is an excellent likeness of *Capparis indica* (L.) Fawc. & Rendle as now understood (except for the stamen number, reduced to about half of the normal number of c. 16 by the license of the artist). As there can be no doubt on that plate’s identity, we here designate it as the lectotype of *Breynia indica*.

Candolle (1824) was of a different opinion, since he placed the plant he described as *Capparis breynia*, listing both *Breynia indica* and *C. cynophallophora* in synonymy, in *C. sect. Quadrella*. *B. indica* is therefore unavailable as type of *C. sect. Breyniastrum*. A taxonomic synonym of it, *C. amygdalina* Lam., might be chosen as type. Grisebach (1859-64) indeed left it in Candolle's section while creating a separate section for *C. ferruginea*. Our preference, nevertheless, goes to *C. ferruginea*, for two main reasons. First, the features that Candolle gives for the fruit in his sectional description ("bacca oblonga") fit *C. ferruginea* but not *C. indica* (which has the elongate, splitting "siliquae dehiscentes" that characterise *C. sect. Quadrella*). Second, *C. indica* is in our opinion marginal to *C. sect. Breyniastrum*, as it combines features of *C. ferruginea* (open calyx, stellate hairs on the upper leaf surface) to almost equal shares with those of *C. (sect. Quadrella) cynophallophora* (indumentum of peltate scales, numerous and elongate stamens, not to mention fruit shape).

Linnaeobreynia we hold to be an illegitimate name, because Hutchinson (1967) included *Calanthea* in his new genus. We do not share his view that *Calanthea* is a confusingly similar later parohomonym of *Calanthe* R. Br. (*Orchidaceae*), no more than of *Calathea* G. Mey. (*Marantaceae*). Whether the type of *Calanthea*, said to be a glabrous plant, really belongs to the same section as *C. ferruginea*, as is generally accepted (e.g. by Pax & Hoffmann 1936: 182), will have to be confirmed by further studies.

4. *Capparis ferruginea* L., Syst. Nat., ed. 10: 1071. 1759 \equiv *Linnaeobreynia ferruginea* (L.) Hutch., Gen. Fl. Pl. 2: 310. 1967. – Lectotype (designated here): herb. Linn. 664.6 (LINN). = *Capparis octandra* Jacq., Select. Stirp. Amer. Hist.: 160. 1763. – Lectotype (designated here): [icon] Jacquin, Select. Stirp. Amer. Hist.: t. 100. 1763.

Note. – In the protologue of *Capparis ferruginea*, Linnaeus cited "Brown. jam. t. 27. f. 2." [representing in fact *Canella alba* Murray], but three years later (Linnaeus 1762) he corrected the reference to "t. 28, f. 1." Fawcett & Rendle (1914a) gave a detailed and convincing explanation of the original mis-quotation, which has its roots in Browne's (1756) book itself.

4b. *Capparis ferruginea* subsp. *cubensis* R. Rankin, subsp. *nova* – Holotype: [Cuba, prov. Camagüey], "Nuevitas, falda sur de la Península Pastelillo", 11.5.1976, *Areces & al. HFC 31382* (HAJB; isotypes: B, JE).

A subspecies typica imprimis differt foliis lanceolato-spathulatis (nempe supra medium latissimis), apice rotundatis vel subacutis, nec non sepalis triangularibus, latitudine ad summum duplo longioribus.

Note. – See also the full English description of this taxon, below.

5. *Capparis domingensis* Spreng. ex DC. Prodr. 1: 253. 1824. – Holotype: [Hispaniola], "S. Domingo", *Bertero* (G-DC; probable isotype: B).

5b. *Capparis domingensis* subsp. *grisebachii* (Eichler) R. Rankin, comb. & stat. *novi* \equiv *Capparis grisebachii* Eichler in Martius, Fl. Bras. 13(1): 275. 1865. – Holotype: "in Cuba Orientali" 1856-1857, *Wright 9b* (BR; probable isotypes: G [2×]).

Note. – A full description of this taxon is given below.

6. *Capparis singularis* R. Rankin, sp. *nova* – Holotype: [Cuba, prov. Guantánamo], "US Naval Base, Guantánamo Bay, windward side, Cuzco Beach", 19°58'23.4"N, 75°08'45.1"W, 3.10.1996, *Areces & al. 6496* (MNHN; isotype: MAPR).

A speciebus affinis praecipue differt foliis supra diutius pube stellata tenuiori intertexta et insuper protuberationibus conicis subobtusis, subtus pilis radiatim stellatis densis obsitis; sepalis majoribus, lineari-lanceolatis; petalis utrinque tomentosis (nec intus glabris); gynophoro multoties longiore; staminibus numerosioribus (c. 16 nec 8) et multo longioribus.

Note. – See also the full English description of this taxon, given below.

Morphology of the *Capparis ferruginea* group

Three species of *Capparis* sect. *Breyniastrum* have been described from the Greater Antilles (extending to the Cayman Islands but not reaching Porto Rico). They form a closely knit complex, endemic to the said area, which we shall call the *C. ferruginea* group. They are, in the order in that they were published: *C. ferruginea* (Jamaica, Hispaniola, Cuba, Grand Cayman), *C. dominicensis* (Hispaniola) and *C. grisebachii* (Cuba and supposedly Hispaniola). An additional species, *C. singularis*, is newly described here from its single known, E Cuban gathering.

Few authors have attempted so far to discriminate between these species. Candolle (1824), when describing *Capparis dominicensis*, left it unplaced as to section and did not compare it with *C. ferruginea*. Some Floras of Cuba and Hispaniola, from where more than one member of the group has been reported, sidestepped the problem by recognising but a single species: León & Alain (1951) treated *C. grisebachii* as a synonym of *C. ferruginea*, Moscoso (1943) did the same for *C. dominicensis*.

Alain (1969) keyed out *Capparis ferruginea* and *C. grisebachii* by means of sepal shape and size, quality of the leaf indumentum and gynophore length. Two other works treat *C. ferruginea*, *C. dominicensis* and *C. grisebachii* side by side in a comparative way: Eichler's (1865) classical Flora Brasiliensis account and Alain's (1983) account of the Flora of Hispaniola. The distinctions used in these works concern leaf indumentum (described in general qualitative terms); size, shape and position of the sepals; filament hairiness; and gynophore length. We shall proceed to discuss these features individually, plus additional characters we found to vary within the complex.

Leaf indumentum. – In all species of the group, the leaves are initially covered by an indumentum of branched hairs on both surfaces, and permanently so underneath. The upper leaf surface is glabrescent with age, but less promptly so in *Capparis singularis* than in the other taxa. The colour of the hair cover may have some relevance: in *C. dominicensis* (both subspecies) it is dirty white, turning yellowish in the herbarium, whereas in *C. ferruginea*, especially in Jamaican material (subsp. *ferruginea*), it has the pronounced rusty tinge that gave the species its name. The ferrugineous shade is less obvious in Cuban material of the same species, where the larger rusty-coloured hairs are intermingled with tinier, colourless ones; it can also be seen in *C. singularis*, and sometimes even in old herbarium material of *C. dominicensis*.

Leaf trichomes. – The whole group is characterised by the presence of symmetrically branched hairs and concomitant absence of simple hairs and lepidote scales. The hairs are by no means uniform, however, and they provide excellent criteria for species-level distinctions. The hair cover of *Capparis ferruginea* (Fig. 1, 2), which looks evenly felted, is composed of stellate hairs in the shape of a morning star, with relatively few branches pointing in all directions from a short central axis; abaxially they are irregularly two-tiered and partly stalked. In *C. dominicensis* (both subspecies) the hairs are bottlebrush-like, with an elongate core and a large number of densely set, straight branches; on the upper leaf surface (Fig. 3A, 4A) they are relatively stout and condensed, sometimes in the shape of a sea-urchin, but abaxially (Fig. 3B, 4B) they are always long and are often two-tiered, most of them sessile but some stalked, so that the indumentum has a shaggy aspect under hand-lens magnification. Finally, *C. singularis* (Fig. 5) has stellate hairs that again are quite different: their branches are relatively thin, flexuous rather than straight, and show an almost regular radial arrangement, spreading horizontally from an upright basis, and with a clear tendency to get fused collaterally in their proximal part – perhaps a first step toward a scale-like structure?

Leaf epidermis protuberances. – The upper leaf epidermis is single-layered, formed of small, regular cells with moderately thickened outer walls, and in all but two taxa it is flat to slightly undulate (Fig. 1B, 2B, 4B). The two exceptions are *Capparis dominicensis* subsp. *dominicensis* and *C. singularis*. Eichler (1865: 275) is the first and so far only author to have noted epidermal protuberances in the type gathering of *C. dominicensis*, which he described as follows: “pilorum basibus bulbosis persistentibus minute densissimeque verruculosus scabridisque”. The protuberances he saw are not in fact the bases of deciduous trichomes (these leave virtually no trace), but

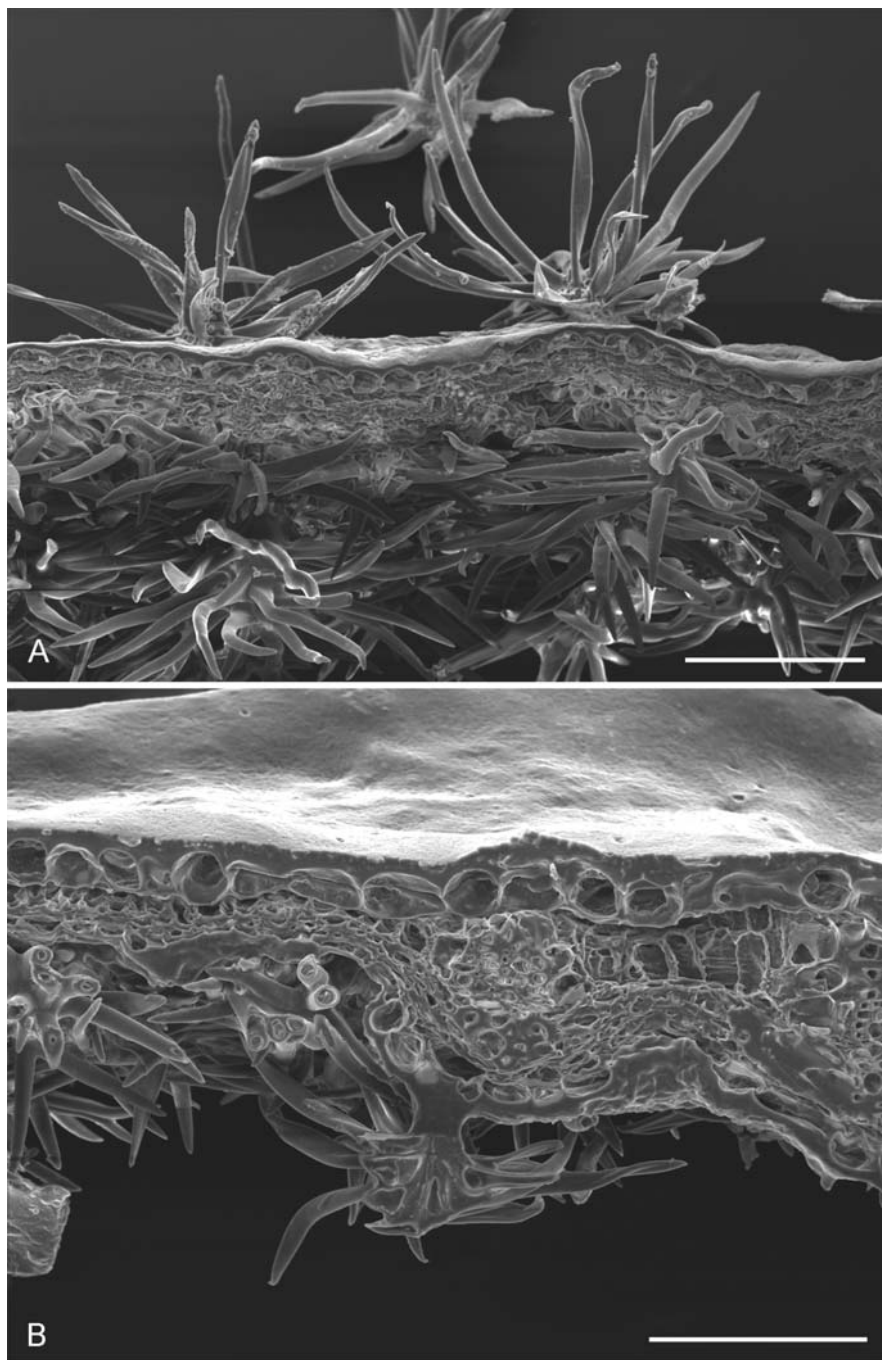


Fig. 1. SEM photographs of leaf cross sections, showing trichomes, of *Capparis ferruginea* subsp. *ferruginea*. – A: young leaf, showing stellate trichomes on both sides; B: adult leaf, smooth and glabrous above, with sessile to shortly stalked stellate hairs below. – Scale bars: A = 100 μ m, B = 90 μ m; Jamaica, Lime Cay, St Andrew, *Adams 12345* (M).

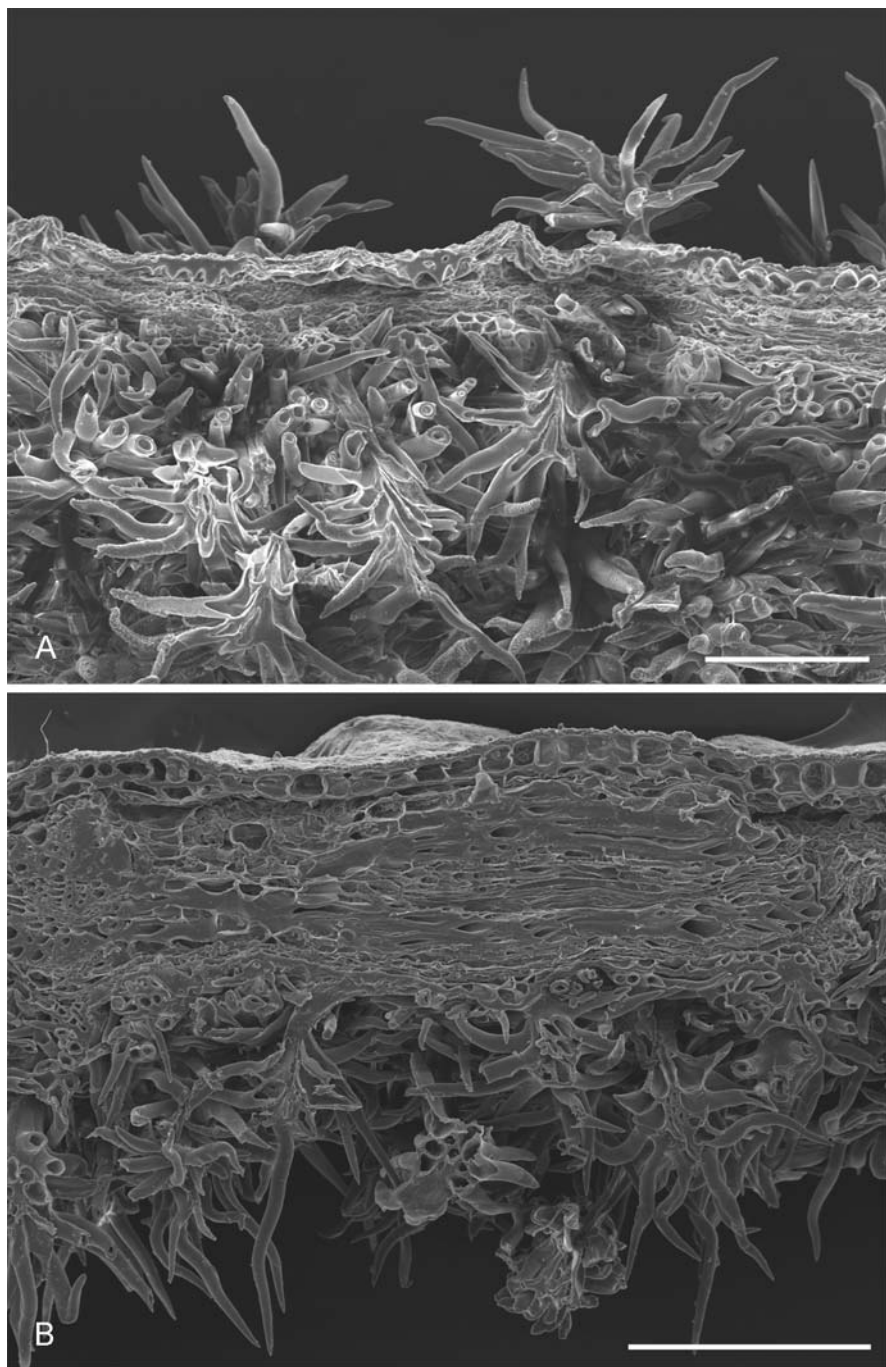


Fig. 2. SEM photographs of leaf cross sections, showing trichomes, of *Capparis ferruginea* subsp. *cubensis*. – A: young leaf, showing stellate trichomes on both sides; B: adult leaf, smooth and glabrous above, with sessile to shortly stalked stellate hairs below. – Scale bars: A = 100 μ m, B = 200 μ m; Cuba, Prov. Guantánamo, Abra del río Yumurí, HFC 27295 (B).

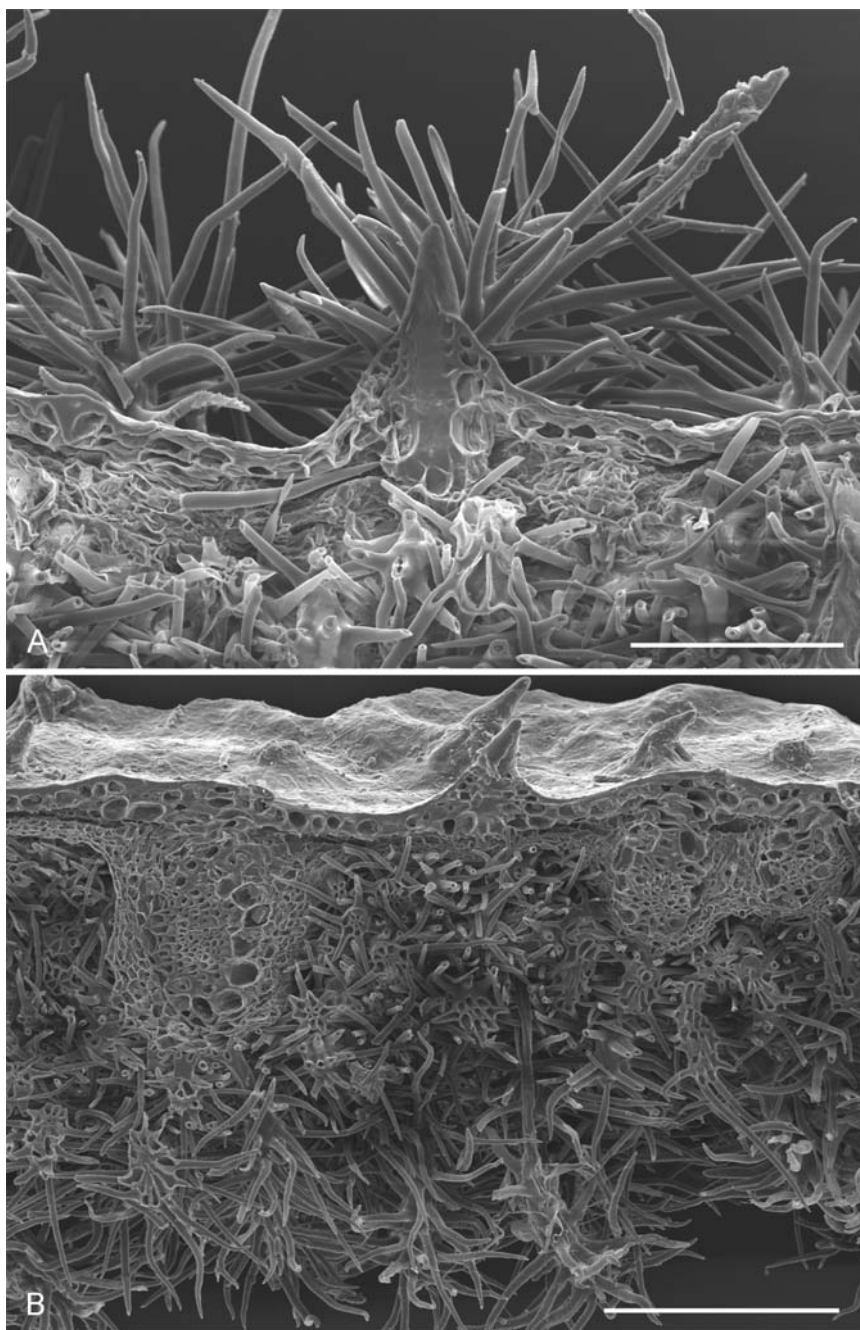


Fig. 3. SEM photographs of leaf cross sections, showing trichomes, of *Capparis domingensis* subsp. *domingensis*. – A: young leaf, upper surface showing sea-urchin-like stellate trichomes and a protuberance with sclerotic core; B: adult leaf, glabrous and with pointed protuberances above, with dense sessile and some stalked bottlebrush-like hairs underneath. – Scale bars: A = 90 μ m, B = 200 μ m; Hispaniola, Dominican Republic, Prov. Pedernales, “Fundo Paradís”, Greuter & Rankin 24757 (B).

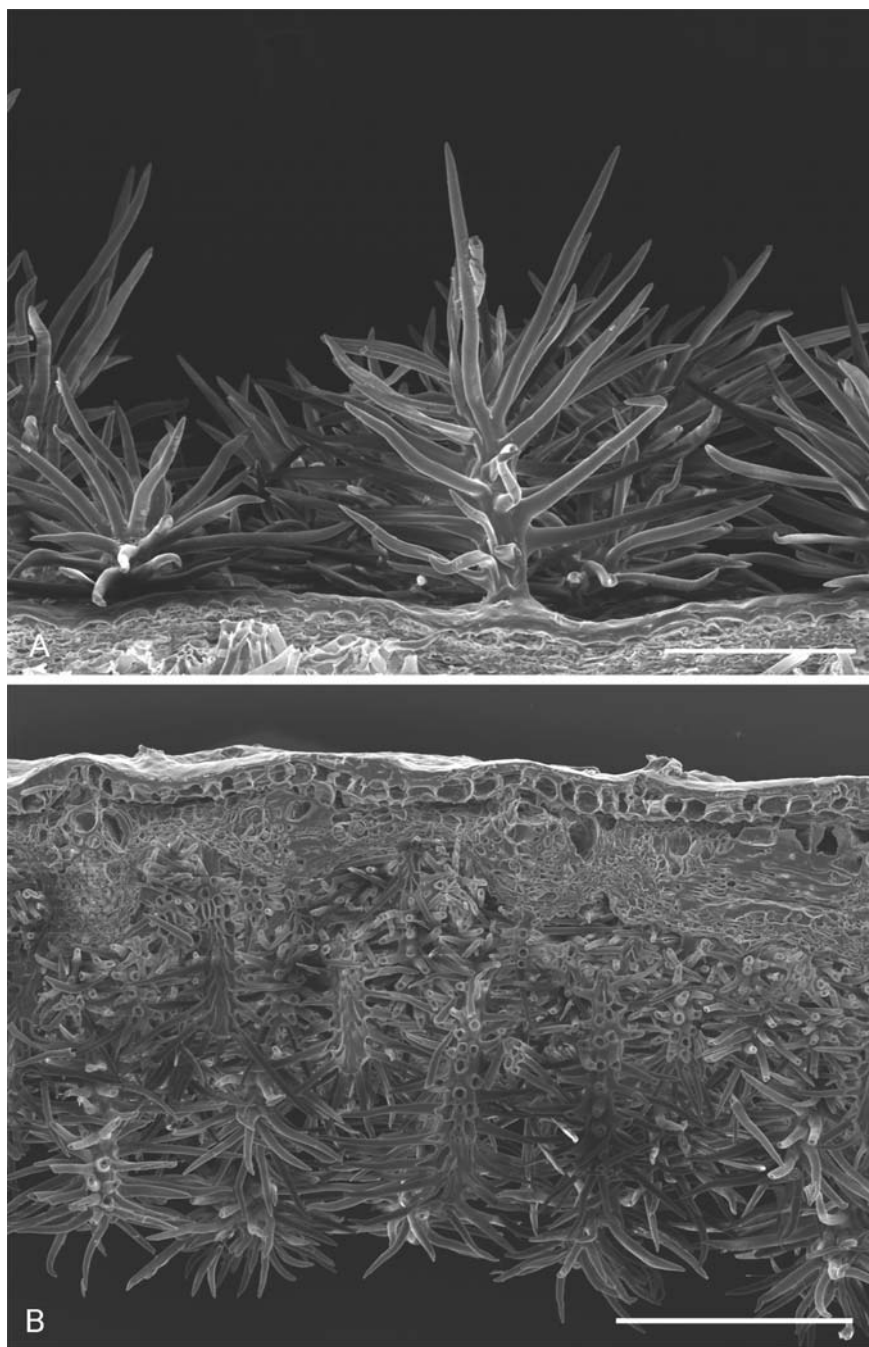


Fig. 4. SEM photographs of leaf cross sections, showing trichomes, of *Capparis domingensis* subsp. *grisebachii*. – A: young leaf, upper surface showing sea-urchin-like stellate and short bottlebrush-like sessile trichomes; B: adult leaf, smooth and glabrous above, with dense sessile bottlebrush-like hairs underneath (some with obsolete stalks). – Scale bars: A = 100 μm , B = 200 μm ; Cuba, Prov. Guantánamo, El Diamante, HFC 48089 (JE).

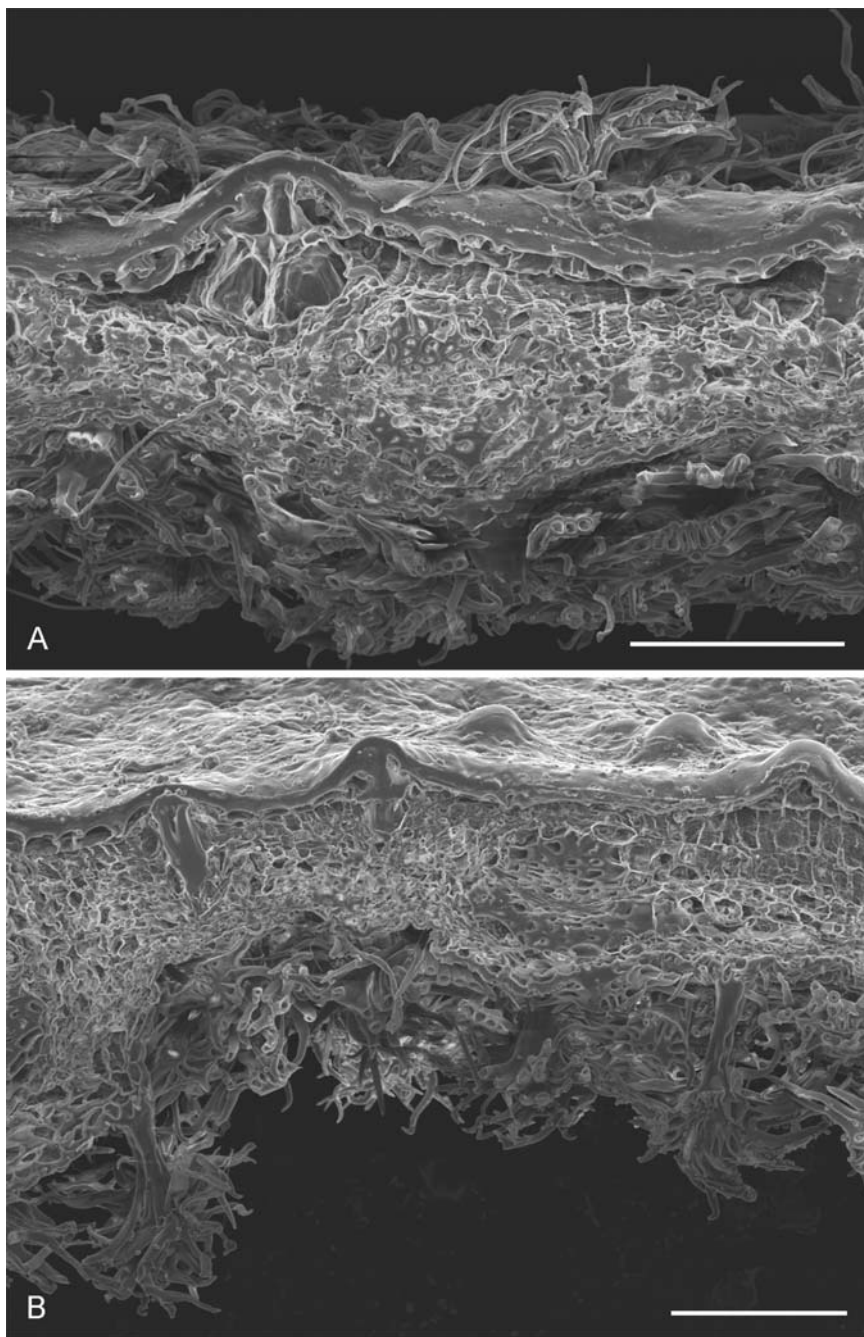


Fig. 5. SEM photographs of leaf cross sections, showing trichomes, of *Capparis singularis*. – A: young leaf, showing stellate trichomes with flexuous branches as well as a large-celled protuberance above, and cross-cuts of radiately stellate hairs with basally fused branches below; B: adult leaf, glabrous and with blunt protuberances showing sclereid cores above, with dense sessile and stalked radiately stellate hairs below. – Scale bars: A = 90 μm , B = 100 μm ; from isotype specimen (MAPR).

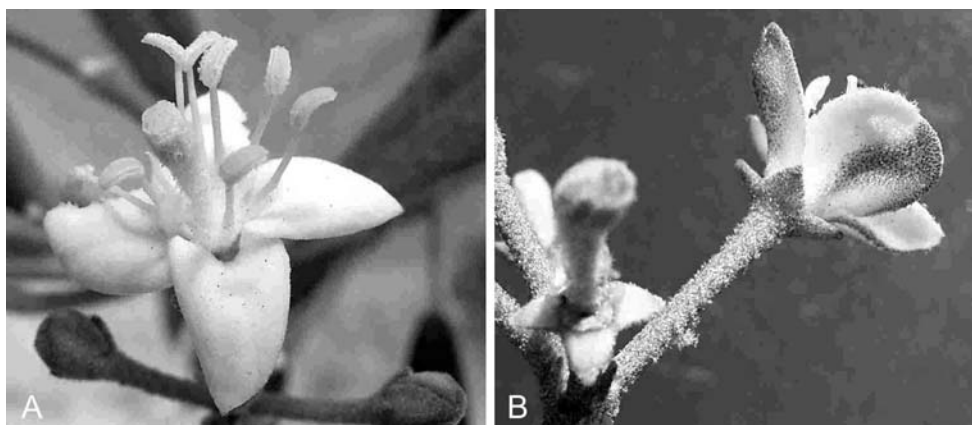


Fig. 6. *Capparis ferruginea* subsp. *cubensis*. – A: flower in front view, showing petals glabrous inside of and 9 stamens; B: flower during and past anthesis, in lateral and front view, respectively, showing stellately patent, triangular sepals and two-coloured petal indumentum. – Live plant, Cuba, Prov. Holguín, near Gibara, 1 March 2004; photograph by R. Rankin; voucher: Greuter & al. 26274 (B, HAJB, herb. Greuter, etc.).

otherwise Eichler's observations are remarkably accurate. The conical structures (Fig. 3B), which appear to be regularly present, end in a sharp point, which is the tip of a massive sclerotic pillar anchored in the mesophyll and surrounded by a crown of numerous, minute sclerified epidermal and subepidermal cells. These pillars we consider to be sclereids, which according to Pax & Hoffmann (1936) are widespread and polymorphic structures in the caper family. The blunt, broadly conical mounds scattered over the adaxial leaf face in *C. singularis* (Fig. 5B) may be homologous with the pointed cones of *C. domingensis* subsp. *domingensis*, but they differ significantly in their structure. They do at least sometimes possess a scleroid core, which appears as an irregular, perhaps often oblique, elongate structure, never excurrent beyond the leaf surface; the epidermal and subepidermal cells associated with each protuberance are, however, conspicuously enlarged rather than reduced in size. Also, to judge from the scant material at hand, the mesophyll in *C. singularis* is thicker and more robust than in the other species, but further anatomical work is needed to bear out the significance of such differences.

Petals (colour). – The petals do not appear to differ significantly in shape and size even though, in a general way, they are relatively wider in *Capparis ferruginea* than in the two other species, and slightly longer in *C. singularis*. They are \pm broadly elliptical, glabrous within and stellate-pubescent without, slightly keeled by the prominent midvein and with widely overlapping margins, showing the contorted prefloration that is widespread in the genus. Colour, however, does differ, if our observations of live material (both in the wild along the northern coast in the Holguín Province and in the National Botanic Garden in Havana) can be generalised. In *C. ferruginea* subsp. *cubensis* (Fig. 6) the petals are pure white inside and markedly two-coloured outside, as the right (outer) half of each, including the keel, is covered with rusty indumentum and the left (inner) half by a tiny, white stellate down. The petals of *C. domingensis* subsp. *grisebachii* (Fig. 7A-B) are creamy yellow, and the difference in indumentum shade between the outer and inner half is barely obvious. As herbarium material is unsuited for petal colour assessment, no data exist for *C. singularis* and for the plants of Jamaica and Hispaniola; dried material suggests that the latter might show darker colour shades, but for the time being this remains conjectural.

Sepals (size, shape, position). – As is characteristic for the whole section, the four sepals are equal and of small size, not completely enclosing the corolla in the flower bud. In *Capparis ferruginea* they are stellately patent through anthesis until they are eventually shed, either linear-triangular and several times as long as broad (subsp. *ferruginea*) or triangular, up to twice as

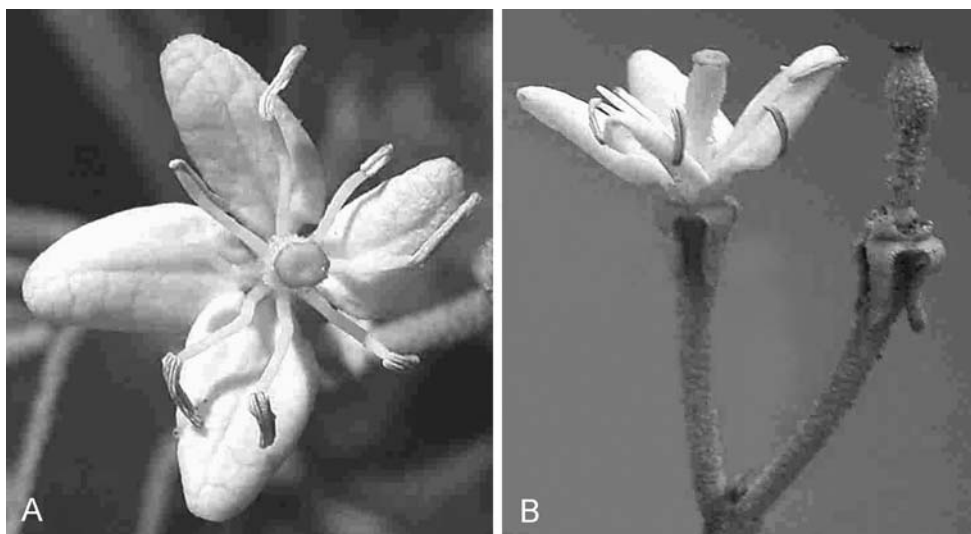


Fig. 7. *Capparis domingensis* subsp. *grisebachii*. – A: flower in front view, showing petals glabrous inside and 8 stamens; B: flowers during and past anthesis in lateral view, showing reflexed, linear sepals. – Live plant grown in the National Botanic Garden of La Habana, transplanted from La Chivera (Guantánamo province, Imías) in SE Cuba; photograph by R. Rankin.

long as broad (subsp. *cubensis*: Fig. 6). The sepals of *C. domingensis* are linear, 3–4 mm long (up to 6 mm in subsp. *grisebachii*, Fig. 7A) and 1 mm wide, become reflexed at anthesis and often persist in fruit. *C. singularis* (Fig. 8A) has the largest calyx, with linear-lanceolate, reflexed sepals of 6–7 × 2–2.5 mm.

Stamens (hairiness, number, length). – In *Capparis singularis* (Fig. 8A) the stamen number is c. 16, and filament length 12–14 mm. In all other taxa 8 stamens per flower are normally found (in *C. ferruginea* one can occasionally observe up to 3 supernumerary stamens); the filaments are much shorter, ± 3 mm long in *C. domingensis* subsp. *domingensis* and 6–5 mm in the other taxa. There appear to be differences in filament pubescence, too, which is limited to the very base in *C. domingensis* (subsp. *grisebachii*: Fig. 7B) and to the basal ¼ in *C. singularis* (Fig. 8A) but covers the lower ½ in *C. ferruginea*.

Gynophore (length). – Alain (1969) uses this as a key character to distinguish between *Capparis ferruginea* [subsp. *cubensis*] and *C. [domingensis subsp.] grisebachii*, attributing a gynophore length of 4–5 mm to the former and of 6–8 mm to the latter. He may have switched the figures, but even so they would be inaccurate. We measured c. 5 mm and 3–4 mm, respectively, for the same two taxa. The gynophore is shortest (c. 2.5 mm) in *C. domingensis* from Hispaniola and slightly more variable (3–5 mm) in *C. ferruginea* from Jamaica, but none of these differences is impressive. Once more, the one species that really sticks out is *C. singularis* with its 12–18 mm long gynophore (Fig. 8A).

Systematics and chorology of the *Capparis ferruginea* group

There are clear structural differences in trichome morphology and calyx shape, in particular, that permit the distinction of three sympatrically occurring species. Two species show differences between their populations on different islands, which, we feel, are best expressed by the recognition of subspecies. The differences are decidedly neater in *Capparis domingensis* than in *C. ferruginea*, though.

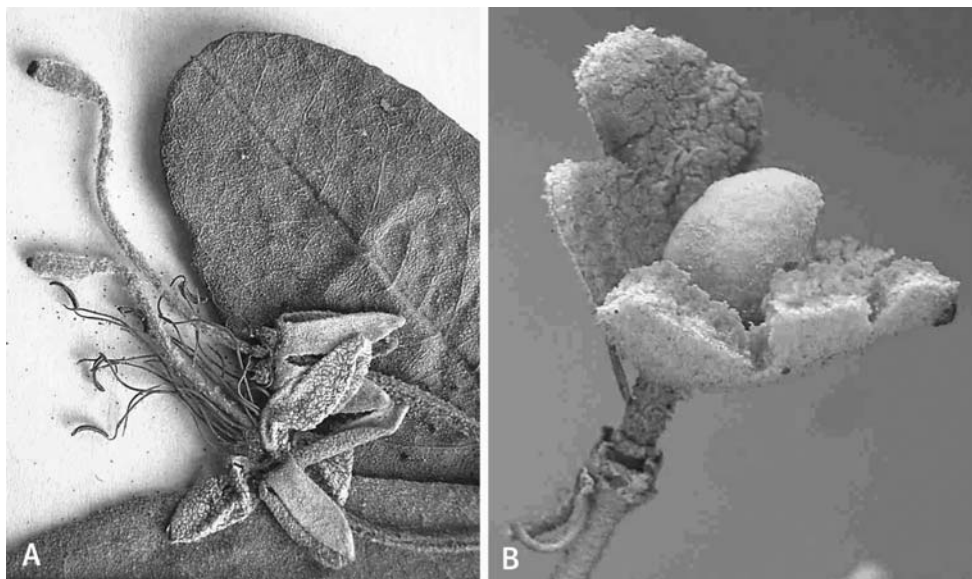


Fig. 8. A: *Capparis singularis*, flowers during and past anthesis in lateral view, showing linear-lanceolate, reflexed sepals, petals tomentose on both sides, numerous stamens with long filaments hairy in the lower $\frac{1}{4}$, and a long slender gynophore; from holotype specimen (MNHN). – B: *C. domingensis* subsp. *grisebachii*, mature, irregularly split fruit exhibiting fleshy endocarp encircling the single mature seed; live plant grown in the National Botanic Garden of La Habana, transplanted from La Chivera (Guantánamo province, Imías) in SE Cuba. – Photographs by R. Rankin.

Capparis domingensis subsp. *domingensis* and subsp. *grisebachii* differ in some quantitative features but also in at least one structural character, the presence in the former of sharply pointed, conical protuberances that we never found in subsp. *grisebachii*. The two subspecies are truly vicarious, each endemic to its island, and the alleged presence of *C. grisebachii* on Hispaniola cannot be confirmed. Alain (1983) erroneously described genuine *C. domingensis* under the name “*C. grisebachii*”, as demonstrated by the characters he describes. What he meant by “*C. domingensis*” is less clear. He so designated a plant from Azua, not seen by us, but genuine *C. domingensis* (which indeed occurs near Azua: *Rose & al.* 3903, B) does not fit Alain’s description of a plant with a valvate rather than apert calyx and stamens exceeding the petals. These features are found in *C. cynophallophora*, which is widespread on the island, but never in *C. domingensis*. Other features mentioned by Alain, such as the short gynophore (6 mm) and fruit (2 cm), do not support a hypothetical hybrid origin of the plant he describes. Rather, it might represent a new, unnamed species.

The Cuban and Jamaican plants of *Capparis ferruginea* differ chiefly in the shape of their leaves: in subsp. *ferruginea* (Jamaica) they are lanceolate, i.e. broadest in the middle on average, and acutely pointed to acuminate at the tip, whereas they tend to be spatulate, broadest above the middle and apically rounded or at best subacute in Cuban subsp. *cubensis*. We have not seen sufficient material from Hispaniola, where *C. ferruginea* also occurs (Alain 1983), and none at all from Grand Cayman (Proctor 1984), so we cannot yet decide which subspecies occurs on these islands.

Capparis singularis is an enigmatic species. It differs markedly from the two others in a number of taxonomically important features, both quantitative and qualitative. It might be interpreted as an old relic reduced to a single small population of perhaps one or a few individuals, or as a newly evolved offshoot with a hazardous evolutionary fate, but the easiest way to explain its presence in a single locality is to stipulate its hybrid origin. Two caper species occur in the immediate neighbourhood that might be considered as potential parents: *C. domingensis* subsp. *grisebachii*

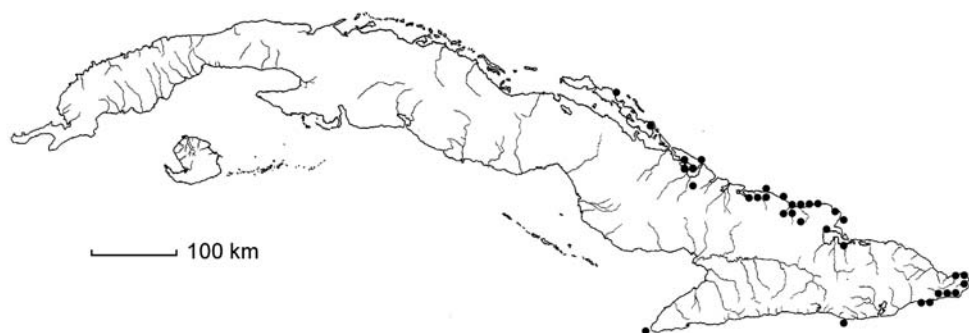


Fig. 9. Dot map showing the total known distribution of *Capparis ferruginea* subsp. *cubensis*.

and *C. cynophallophora*. The hybrid hypothesis is consistent with the fact that *C. singularis* is intermediate between these two in a number of features, in particular sepal size (no flower buds are known, but the sepals appear to tend toward the valvate condition that is characteristic of *C. sect. Quadrella*), stamen number, filament length and gynophore size. Also, the basal fusion of the rays of the stellate hairs, in *C. singularis*, can be interpreted as mediating between the bottle-brush-like hairs of *C. domingensis* and the peltate scales of *C. cynophallophora*. There are at least two characters, however, in which *C. singularis* stands apart from both its potential parents. The upper leaf surface is smooth, glabrous and shiny in *C. cynophallophora*, smooth and soon glabrescent in *C. domingensis* subsp. *grisebachii*, but tardily glabrescent and covered with blunt protuberances in *C. singularis*; and the inner petal surface is stellate-tomentose in the latter species but glabrous in the two former ones. May we, then, assume that *Capparis singularis* is a hybridogenous species that has already evolved its own set of differential characteristics? If so, it would be exceptional in providing an example of sympatric speciation, both parental taxa being present on the very spot. Decidedly, further investigations in the field are needed to study the fertility, reproductive behaviour, chromosome numbers, and population structure of the taxa concerned – but field work in the locus classicus is presently impossible for Cuban botanists. A search in other areas in which the presumed parents coexist is also a possibility, and there are many such places in various parts of Cuba – but then, no hybrids, or plants presenting the features of *C. singularis*, have yet been collected there.

To conclude, we are going to provide full descriptions of the taxa of the *Capparis ferruginea* complex that we presently recognise. The distribution we have mapped only for Cuba, from where we have studied large numbers of specimens. Relevant specimen data can be consulted in a searchable database forming an electronic supplement to the present paper (<http://www.bgbm.org/bgbm/library/publikat/willd34/rankin&greuter.htm>).

Capparis ferruginea subsp. *ferruginea* (Jamaica). – Shrub or small tree to c. 5 m tall. *Young shoots* covered with rust-coloured, felted indumentum. *Leaves* with 1-1.5 cm long petiole; blade lanceolate, 5.5-9 × 1.7-2.5 cm, widest at or slightly below the middle, with an acute to acuminate tip; base subpeltate, cuneate to rounded; adaxial surface covered with sessile stellate trichomes when young, dull, soon glabrescent; abaxial surface with a dense, persistent, felted cover of morning-star-shaped stellate hairs c. 0.2-0.3 mm in diameter, some sessile, other borne on stalks of up to 0.2 mm; lateral veins not prominent adaxially but strongly raised abaxially. *Sepals* linear-triangular, 2-3 × 0.5-0.7 mm, 4-6 times as long as wide, stellately patent at anthesis. *Episepalous disk scales* triangular, upright, 0.5-0.7 mm long, tomentose on the back. *Petals* broadly elliptic, 5-5.5 × 4-5 mm, with a rusty tomentum on the back, inside glabrous and brownish when dry. *Androgynophore* very short, glabrous. *Stamens* 8; filaments 4-5 mm long, hairy in their lower half; anthers c. 2 mm long. *Gynophore* 3-5 mm long, stellate-tomentose. *Fruit* ellipsoidal, attenuate into the carpophore, ± 1.5 cm long (including the carpophore) and 1 cm in diameter, irregu-



Fig. 10. Dot map showing the total known distribution of *Capparis domingensis* subsp. *grisebachii*.

larly ruptured at maturity; seeds not seen. – The only taxon of the section found growing in Jamaica; whether the populations of Hispaniola and the Grand Cayman belong here or rather separate taxa, or even to the following subspecies, remains to be seen.

Capparis ferruginea subsp. *cubensis* (Cuba). – Shrub or small tree to c. 6 m tall. *Young shoots* covered with pale, greyish yellow, and rust-tinged, felted indumentum. *Leaves* with 0.6-1 cm long petiole; blade spatulate-lanceolate, 4-9 × 1.2-2 cm, widest in the distal half, with a rounded to subacute tip; base subpeltate, cuneate to rounded; indumentum, trichome morphology and venation same as in subsp. *ferruginea*. *Sepals* triangular, 1.5-2 × c. 1 mm, up to twice as long as broad, stellately patent at anthesis. *Episepalous disk scales* triangular, upright, 0.5-1 mm long, tomentose on the back. *Petals* broadly elliptic, 6 × 5 mm, with a two-coloured, rusty and white indumentum outside, inside glabrous and pure white (brownish red when dry). *Androgynophore* very short, glabrous. *Stamens* 8; filaments 5-6 mm long, hairy in their lower half; anthers 1.5-1.7 mm long. *Gynophore* c. 5 mm long, stellate-tomentose. *Fruit* ellipsoidal, attenuate into the carpophore, 1.5-2.5 cm long (including the carpophore) and 1 cm in diameter, irregularly ruptured at maturity; seeds 3, reniform, 4-5 mm long. – Presumably endemic to E Cuba (but see note under the previous taxon), being most frequent along the northern coast where it reaches the keys of Camagüey Province; completely absent from the west and from inland localities (Fig. 9).

Capparis domingensis subsp. *domingensis* (Hispaniola). – Shrub to c. 2 m tall (Alain 1983: 318). *Young shoots* covered with yellowish grey, velvety indumentum. *Leaves* with 0.5-0.6 cm long petiole; blade narrowly elliptic to spatulate, 5.5-7 × 1.9-2 cm; tip rounded, obtuse or mucronulate; base subpeltate, rounded to slightly cordate; adaxial surface covered with soon deciduous, sessile stellate trichomes shaped like a sea-urchin or a stout bottlebrush and with persistent, sharply pointed, conical protuberances; abaxial surface with a dense, shaggy tomentum of bottlebrush-like trichomes c. 0.3 mm in diameter, mostly sessile but some shortly stalked; lateral veins not raised adaxially but prominent abaxially. *Sepals* linear, 3-4 × 1 mm, accumbent to the flower bud but reflexed at anthesis, often persistent. *Petals* elliptic, 5 × 3 mm, adaxial surface glabrous, dark reddish brown when dry, and abaxial surface tomentose, brownish yellow. *Episepalous disk scales* irregularly shaped, blunt, c. 0.7 mm long, tomentose on the back. *Androgynophore* very short, glabrous. *Stamens* 8(-11), drying dark; filaments c. 3 mm long, glabrous except at the very base; anthers c. 3 mm long. *Gynophore* c. 2.5 mm long, with a shaggy stellate tomentum. *Fruit* ellipsoidal, attenuate into the carpophore, 2.5-4 cm long (including the carpophore), irregularly ruptured at maturity; seeds not seen. – The taxon is endemic in Hispaniola, where it grows along the southern coast of the island (Alain 1983).

Capparis domingensis subsp. *grisebachii* (Cuba). – Shrub to c. 5 m tall. *Young shoots* covered with yellowish grey, velvety indumentum. *Leaves* with 0.5-1 cm long petiole; blade narrowly el-



Fig. 11. Dot map showing the total known distribution of *Capparis singularis*.

liptic to subspathulate, 4–8 × 1.2–2.8 cm; apex rounded to retuse and slightly mucronulate; base subpeltate, rounded-truncate to slightly cordate; adaxial surface initially stellate-pubescent, becoming glabrous, smooth and shiny; trichomes on either side, tomentum below and venation as in subsp. *domingensis*. *Sepals* same as in subsp. *domingensis* but 3–6 mm long. *Petals* elliptic, 6–7 × 3 mm, adaxial surface glabrous, creamy yellow, becoming light brown on drying, and abaxial surface tomentose, the right half dirty cream coloured (brownish yellow when dry) the left half paler. *Episepalous disk scales* ± triangular, c. 1 mm long, tomentose on the back. *Androgynophore* very short, glabrous. *Stamens* (7–)8–9, whitish, drying light brown; filaments 4–5 mm long, glabrous except at the very base; anthers 3–4 mm long. *Gynophore* 3–4 mm long, with a shaggy stellate tomentum. *Fruit* ellipsoidal, attenuate into the carpophore, c. 1.5 cm long (carpophore included), irregularly rupturing to show the orange-red, fleshy endocarp; ovules 3, two generally aborting; mature seed displayed in the open fruit, dull, yellow, reniform, 5–6 mm long (Fig. 8B). – This taxon is widespread in Cuba, being most frequent along the SE coast and rare in the interior as well as in the west, being absent from the Isla de la Juventud (Fig. 10).

Capparis singularis. – Shrub or small tree 3–4 m tall (according to label information). *Young shoots* covered with a thin, pale, slightly ferruginous indumentum, later glabrescent. *Leaves* with 0.7–1 cm long petiole; blade elliptic, 4.3–5 × 2–2.1 cm; tip rounded and mucronulate; base subpeltate, rounded; adaxial surface pubescent with stellate, tardily deciduous, accumbent hairs with thin, flexuous branches and with blunt conical protuberances, dull; abaxial surface greyish tomentose with sessile or stoutly stalked stellate trichomes c. 0.2 mm in diameter with radiately disposed, basally fused, flexuous branches; lateral veins not raised on either surface or but slightly prominent abaxially. *Sepals* linear-lanceolate, c. 7 × 2 mm. *Petals* elliptic, 7–8 × 4 mm, yellowish tomentose on both surfaces. *Episepalous disk scales* ± semicircular, blunt, c. 1 mm long, tomentose on the back. *Androgynophore* very short, glabrous. *Stamens* c. 16; filaments 12–14 mm long, hairy in their basal ¼; anthers 2.5–3 mm long. *Gynophore* 12–18 mm long, stellate-tomentose. *Fruit* unknown. – The species so far is known only from the Guantánamo Bay in SE Cuba (Fig. 11).

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