

# STUDIES IN THE CAPPARACEAE XXIX: SYNOPSIS OF QUADRELLA, A MESOAMERICAN AND WEST INDIAN GENUS

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## ABSTRACT

*Quadrella* (DC.) J. Presl (Capparaceae) is validated as an American genus of 25 species, characterized by the stellate to lepidote-peltate indumenta, flowers with valvate calyces, dehiscent fruits bearing seeds with green, white or cream embryos, a haploid chromosome number of  $n = 8$ , and a diploid one of  $2n = 16$ . The following taxa are transferred from New World *Capparis* L. s.l. to *Quadrella*: ***Quadrella* subg. *Breyniastrum* (DC.) Iltis, comb. nov., *Quadrella antonensis* (Woodson) Iltis & Cornejo, comb. nov., *Quadrella asperifolia* (K. Presl) Iltis & Cornejo, comb. nov., *Quadrella calciphila* (Standl. & Steyerl.) Iltis & Cornejo, comb. nov., *Quadrella filipes* (Donnell Smith) Iltis & Cornejo, comb. nov., *Quadrella indica* (L.) Iltis & Cornejo, comb. nov., *Quadrella lundellii* (Standl.) Iltis & Cornejo, comb. nov., *Quadrella mirifica* (Standl.) Iltis & Cornejo, comb. nov., *Quadrella pringlei* (Briquet) Iltis & Cornejo, comb. nov., *Quadrella steyermarkii* (Standl.) Iltis & Cornejo, comb. nov.; *Quadrella* subgenus *Intutis* (Raf.) Iltis, comb. et stat. nov., *Quadrella angustifolia* (Kunth) Iltis & Cornejo, comb. nov., *Quadrella domingensis* (Spreng. ex DC.) Iltis & Cornejo, comb. nov., *Quadrella domingensis* subsp. *grisebachii* (Eichler) Iltis & Cornejo, comb. nov., *Quadrella ferruginea* (L.) Iltis & Cornejo, comb. nov., *Quadrella ferruginea* subsp. *cubensis* (R. Rankin) Iltis & Cornejo, comb. nov., and *Quadrella singularis* (R. Rankin) Iltis & Cornejo, comb. nov. Lectotypes are designated for *Octanema* Raf., *Pleuteron* Raf., *Quadrella asperifolia*, *Q. filipes*, *Q. lundellii*, and *Capparis intermedia* Kunth. Neotypes are designated for *Quadrella* and *Intutis* Raf. All species of *Quadrella* are geographically restricted to southern North America (Texas and Florida), Central America to northern South America (Colombia and Venezuela) and the West Indies. Keys to all the subgenera, species and subspecies of *Quadrella* are herewith provided.**

## RESUMEN

Se valida *Quadrella* (DC.) J. Presl (Capparaceae), un género que comprende 25 especies, caracterizadas por presentar un indumento de tricomas estrellados hasta lepidoto-peltados, flores con cálices valvados, frutos dehiscentes con semillas de embriones verdes, blancos o cremas y un número cromosómico haploide de  $n = 8$ , y uno diploide de  $2n = 16$ . Se transfieren las siguientes taxa de *Capparis* L. s.l. del Nuevo Mundo a *Quadrella*: ***Quadrella* subg. *Breyniastrum* (DC.) Iltis, comb. nov., *Quadrella antonensis* (Woodson) Iltis & Cornejo, comb. nov., *Quadrella asperifolia* (K. Presl) Iltis & Cornejo, comb. nov., *Quadrella calciphila* (Standl. & Steyerl.) Iltis & Cornejo, comb. nov., *Quadrella filipes* (Donnell Smith) Iltis & Cornejo, comb. nov., *Quadrella indica* (L.) Iltis & Cornejo, comb. nov., *Quadrella lundellii* (Standl.) Iltis & Cornejo, comb. nov., *Quadrella mirifica* (Standl.) Iltis & Cornejo, comb. nov., *Quadrella pringlei* (Briquet) Iltis & Cornejo, comb. nov., *Quadrella steyermarkii* (Standl.) Iltis & Cornejo, comb. nov.; *Quadrella* subgenus *Intutis* (Raf.) Iltis, comb. et stat. nov., *Quadrella angustifolia* (Kunth) Iltis & Cornejo, comb. nov., *Quadrella domingensis* (Spreng. ex DC.) Iltis & Cornejo, comb. nov., *Quadrella domingensis* subsp. *grisebachii* (Eichler) Iltis & Cornejo, comb. nov., *Quadrella ferruginea* (L.) Iltis & Cornejo, comb. nov., *Quadrella ferruginea* subsp. *cubensis* (R. Rankin) Iltis & Cornejo, comb. nov., y *Quadrella singularis* (R. Rankin) Iltis & Cornejo, comb. nov. Se lectotifican *Octanema* Raf., *Pleuteron* Raf., *Quadrella asperifolia*, *Q. filipes*, *Q. lundellii*, y *Capparis intermedia* Kunth. Se neotifican *Quadrella* y *Intutis* Raf. Todas las especies de *Quadrella* están geográficamente restringidas al Sur de América del Norte (Texas y Florida), América Central hasta el norte de América del Sur (Colombia y Venezuela) y las Indias Occidentales. Se proveen claves de identificación para todos los subgéneros, especies y subespecies aquí tratadas.**

KEY WORDS: *Quadrella*, subgenera *Breyniastrum*, *Intutis*, Capparaceae, Mesoamerica, West Indies

*Quadrella* (DC.) J. Presl (Capparaceae) is an American genus characterized by the combination of complex, tufted, stellate to peltate, or candelabroid to dendroid trichomes, a valvate or reduplicate calyces and dehiscent capsules bearing seeds with green, white or cream embryos. *Quadrella* comprises three subgenera linked by their inter-digitating morphologies (Table 1), and 25 species distributed from southern North America (Texas and Florida) through Central America to Panama, northern Colombia and Venezuela, and throughout the West Indies (Iltis & Cornejo 2007a: 452).



TABLE 1. Morphological comparison of *Quadrella* subgenera *Quadrella*, *Breyniastrum* and *Intutis*.

	Quadrella	Breyniastrum	Intutis
Pubescence complex	peltate	usually tufted or stellate, few times to peltate	stellate to candelabroid
Calyx aestivation (valvate)	closed until anthesis	open when young	open or covering the petals in bud
Sepal shape	oblong, lanceolate to ovate	triangular to linear or filiform	triangular to linear, or oblong to lanceolate
Stamens number	16 to 60	8 to 40	usually 8, ca. 16 (in <i>Q. singularis</i> )
Fruit shape, dehiscence, and length	linear to oblong, ± torulose, to 60 cm	linear to linear-oblong, ± torulose rarely ovoid, to 40 cm	ovoid or obovoid to oblongoid or shortly ellipsoid, usually to 3 cm (to 10 cm only in <i>Q. angustifolia</i> )
Embryo color	green	green	white or cream
Testa	thin and soft	thin and soft	hard and brittle

Calyx characters in New World capparid taxonomy have been important. Used first by de Candolle (1824) for closed vs. open calyx aestivation, then by Eichler (1865) for his stellate- to peltate-pubescent subgenera, and since then by subsequent workers (e.g., Hutchinson 1967). As an example we may take valvate calyx aestivation, the condition in which the four sepals develop in a single series with their parallel margins adjoining one another to tightly appressed or even reduplicate, but with the margins never overlapping. The calyx may then a), either stop growing from early on, to be rapidly exceeded by the corolla bud and thus ending up with small, ± triangular sepals producing a calyx aestivation that is open (“aperta,” Robert Brown 1826: 220), this the hallmark of *Quadrella* subg. *Breyniastrum* (DC.) Iltis and half of the species in *Quadrella* subg. *Intutis* (Raf.) Iltis; or b), continue to grow and enclose the corolla bud and result with a calyx aestivation that is closed until shortly before anthesis, this the hallmark of *Quadrella* subgenus *Quadrella*.

The valvate calyx is one of the primary unifying characters of *Quadrella*, with the closely adjoining sepals meeting exactly but never overlapping. Although, this character is present in *Quadrella* subg. *Quadrella* and half of the species of *Q.* subg. *Intutis* (*Q. angustifolia* [Kunth] Iltis & Cornejo, *Q. alaineana* Cornejo & Iltis and *Q. singularis* [R. Rankin] Iltis & Cornejo), where the relatively large sepals result in a valvate or reduplicate calyx with closed aestivation until anthesis, in the majority of species (subg. *Breyniastrum* and the remaining three species of subg. *Intutis*), the calyx aestivation is open, with the very short, triangular to linear sepals not enclosing the petal bud. Admittedly, while calyx aestivation is distinctive, nevertheless those calyx types are valvate, and the differences are subtle and not significant enough to break up the genus *Quadrella* into two genera, as has been done, whether at the sectional level by de Candolle (1824) or at the generic level by Hutchinson (1967).

The complex lepidote-peltate pubescence that unites *Quadrella* subg. *Quadrella* is clearly a specialization of once stellate or tufted pubescence types fused into lepidote or peltate, multicelular scales as they occur in great diversity in *Quadrella* subg. *Breyniastrum*. Nevertheless, comparing *Q. odoratissima* (Jacq.) Hutch. and *Q. cynophallophora* (L.) Hutch. of *Quadrella* subg. *Quadrella*, their respective peltate trichomes are so distinctive that we must conclude that they most probably evolved independently in these two taxa. Similarly, we can separate out the stellate or peltate pubescent groups from those that are characterized by stellate-tufted (e.g., *Quadrella* subg. *Breyniastrum*) or the stellate-candelabra types of pubescence (e.g., *Quadrella* subg. *Intutis*). Much like the basic ubiquitous ( $n = 8$ ) chromosome number, these are conservative characters not easily subject to change (Iltis & Cornejo 2007b).

Stellate to peltate pubescence evolved, especially in *Quadrella*, into an astonishing diversity of morphological trichome types that obliterate the sectional division (de Candolle 1824) imposed by the closed vs. open aestivation of the calyx. Pubescence varies from simple stellate hairs to complex, stemmed, bottlebrush hairs in subg. *Intutis*, in a continuum from ca. 20 plus, simple, unbranched but tufted hairs on a short stem through complex intermediates to semi-peltate or peltate trichomes in subg. *Breyniastrum* (e.g., *Q. indica* [L.]



Iltis & Cornejo), to end in the massive shield-shaped peltate hair types of subg. *Quadrella*, reminiscent of the indumenta in the Brassicaceae Burnett and *Croton* L. of the Euphorbiaceae Juss. (Webster et al. 1996). Close examination of trichomes types has not been studied in Capparaceae since Vesque in the late 1800s (Vesque 1882) and recently by Rankin & Greuter (2004, as *Capparis* sect. *Breyniastrum* [DC.] Eichler), for *Quadrella* subg. *Intutis*.

The number of stamens in *Quadrella* varies from eight to ca. 60, with eight-staminate species scattered throughout subgen. *Breyniastrum* (three of 13 species), and predominant in subgen. *Intutis* (all species except *Q. singularis*). The eight-staminate condition, otherwise infrequent in Capparaceae, is considered here to be the basic primitive condition often linked with stellate pubescence (see above). The multi-staminate condition may reflect a derived state due to “dedoublement” (chorosis) of eight staminal initials and a specialization that in its extreme is often linked to peltate pubescence, e.g., in *Quadrella isthmensis* (Eichler) Hutch.

In *Quadrella*, the seed is often surrounded by a bright red or orange aril (or sarcotesta and/or pulp), but exactly what that structure is, and from what it is derived, we must leave to the morphological insights of others.

One character related to seed dispersal is the nature of the testa. In *Quadrella* subg. *Intutis*, seeds have a hard testa that encloses a white or cream embryo that is presumably ingested and then expelled with the feces. In contrast, in species of subg. *Quadrella* and *Breyniastrum*, the testa is relatively thin and in some species easily removed to expose a naked green embryo that, apparently acrid and bad tasting, is soon spit out. This suggests a short embryo viability (Linnaeus 1779, 4: 9–10) that made horticultural introduction from the New World across the Atlantic via sail ship unsuccessful.

Even though only sparingly investigated, the number of chromosomes has turned out to be, as in many angiosperm groups, one of the most significant characters defining the stellate-pubescent Capparaceae (Iltis & Cornejo 2007b). In *Quadrella*, the chromosome number of  $n = 8$  (or  $2n = 16$ , from root tips) is herewith reported for *Q. antonensis* (Woodson) Iltis & Cornejo, *Q. isthmensis* (Eichler) Hutch. subsp. *isthmensis*, and *Q. odoratissima* (Jacq.) Hutch. In addition to this cytological information, the following other Neotropical genera of Capparaceae, all characterized by having a stellate or peltate pubescence, have the same chromosome number: *Atamisquea emarginata* (DC.) Miers ex Hook & Arn. (Kers 2003), *Beautempsia avicennifolia* (Kunth) Gaudich. (Iltis & Iltis E-20, WIS), *Capparicordis crotonoides* (Kunth) Iltis & Cornejo (Iltis & Iltis E-15, WIS), *Colicodendron yco* Mart. (Mori et al. 11218, WIS), *C. scabridum* (Kunth) Seem. (Iltis & Iltis 243, WIS), *Neocalyptocalyx longifolium* (Mart.) Cornejo & Iltis (Mori et al. 11205, WIS), and *Preslianthus pittieri* (Standl.) Iltis & Cornejo (Judziewicz 4555, WIS). On the other hand, the generic type of *Capparis*, *Capparis spinosa* L. has reportedly  $2n = 38$  (Al-Turki et al. 2000), with base numbers that are neither  $n = 8$  nor 16.

#### TAXONOMIC TREATMENT

***Quadrella*** (DC.) J. Presl in Berchtold & J. Presl, *Prir. Rostlin* 2:260. 1825. BASIONYM: *Capparis* sect. *Quadrella* DC., *Prodr.* 1:251. 1824. *Capparis* subg. *Quadrella* (DC.) Eichler in Martius, *Fl. Bras.* 13:269. 1865. TYPE: *Quadrella jamaicensis* (Jacq.) J. Presl (= *Capparis jamaicensis* Jacq.) (NEOTYPE, designated here).

Shrubs to small trees, pubescent throughout, with abundant lepidote-peltate to variously stellate or tomentose tufted hairs, with several trichomes types often intermixed at least when young, especially on the underside of the leaves. Leaves various, lanceolate to narrowly to broadly elliptic or oblong. Calyx valvate, with the 1-seriate 4 sepals either larger, lanceolate and with closed aestivation, covering the corolla until anthesis (subg. *Quadrella* and *Q. angustifolia*, *Q. alaineana* and *Q. singularis*, of subg. *Intutis*), or small, triangular to linear and with an open aestivation, exposing the corolla from early on (subg. *Breyniastrum* and the remaining species of subg. *Intutis*). Disk of 4 separate and erect episepalous scales arranged on a flat receptacle; stamens 8 to 60. Capsules linear-cylindric, often torulose, to 60 cm (in subgenera *Quadrella* and *Breyniastrum*, except *Q. morenoi* Cornejo & Iltis), or fruits short and ovoid to shortly oblongoid, to 3(–10, *Q. angustifolia*) cm (in subg. *Intutis*), dehiscent (rarely tardily so) along one or both sutures; valves fleshy with reddish pulp; seeds alternating from both repla but usually arranged in a single row, oblong with shallow or



obsolete testa invagination, the embryo straight or slightly curved, green (subgenera *Quadrella*, *Breyniastrum*) or white (subg. *Intutis*).

*Quadrella* was originally established by de Candolle (1824) as a neotropical section of *Capparis* L. s.l. In *Capparis* sect. *Quadrella* DC., de Candolle accepted seven *Capparis* species (numbered 92–98), but not *C. cynophallophora*. However, under species 95, *C. breynia* L., he does list in synonymy *Breynia indica* L. (= *Quadrella indica* [L.] Iltis & Cornejo) and *C. cynophallophora* (= *Q. cynophallophora*), evidently confusing *Q. cynophallophora* and *Q. indica*.

The elevation of *Capparis* sect. *Quadrella* to generic status occurred a year later (1825), and with it the transfer of seven species in Volume 2 of a very rare Czech work, written in the rare Bohemian language, *O Pirozenosti Rostlin* by the world traveler and amateur botanist, Friedrich Berchtold (1781–1876), and his junior co-author, Jan Swatopluk Presl (1791–1849). The latter, the trained taxonomist of the pair, is the one to whom the genus and new combinations are credited. In *Flora Brasiliensis*, Eichler (1865) reduced *Quadrella* to a subgenus of *Capparis*, but 102 years later, Hutchinson (1967), in his generic realignment of *Capparaceae*, recognized *Quadrella* as a valid genus.

Hutchinson (1967) designated *Quadrella cynophallophora* as the lectotype of the genus *Quadrella*, with *Quadrella jamaicensis* in synonymy under the former species. However, *Quadrella cynophallophora* was not cited by Presl when the genus was established, therefore Hutchinson's lectotypification of *Quadrella* is not valid, because was not based on Presl's original material for the name. We designate *Quadrella jamaicensis* the neotype for this genus, which was previously cited by de Candolle (1824), in *Capparis* sect. *Quadrella*, by Eichler (1865) under *Capparis* subg. *Quadrella*, by Presl (1825) under *Quadrella*, and by Hutchinson (1967) as a synonym of his lectotype *Quadrella cynophallophora*.

Inocencio et al. (2006) state that *Quadrella crotonoides* (Kunth) Presl (= *Capparicordis crotonoides* [Kunth] Iltis & Cornejo) is the type of *Quadrella*. However, in the cited literature, there is no such designation of this species as type for this genus. Their typification was not explicitly cited with the phrase "designate here" (as must be for accepted lectotypifications on or after 1 Jan 2001, in accordance to the Art. 7.11 of the Vienna Code [McNeill et al. 2006]), therefore *Quadrella crotonoides* is not the type for this genus. Finally, in our concept of *Quadrella*, which follows most of the species cited by de Candolle and Presl, and all of Eichler's and Hutchinson's, *Quadrella crotonoides* doesn't belong to the genus *Quadrella* at all (see rejected names).

A molecular work (Hall 2008) has demonstrated that the genus *Quadrella* is related to some Neotropical taxa of *Capparaceae* characterized by the presence of stellate to peltate indumenta, such as: *Capparicordis* Iltis & Cornejo, *Calanthea* (DC.) Miers, *Colicodendron* Martius, *Morisonia* L., and *Steriphoma* Spreng.; and that those genera, jointly with all remaining Neotropical species also formerly placed in *Capparis*, represent a separate lineage that is not closely related to that of the Old World *Capparis*, including *C. spinosa* L., the generic type. That molecular evidence is also consistent with the morphology of all Neotropical genera of *Capparaceae* (including *Quadrella*), in which, in contrast, it is evident the absence of the following characters that are present in *Capparis spinosa*: 1) A pair of retrorse stipular spines; 2) flowers with one galeate (helmet-shape) sepal; 3) only a single nectary gland with its apex directed towards the interior of the flower; and 4) two of the four petals having an irregular shape, with their asymmetrical bases laterally connate to each other and folded, forming a petaloid hood-like structure that partially envelops and protects the solitary nectary gland (Cornejo & Iltis 2009a). Thus, those morphological and molecular differences make it impossible to continue using the name *Capparis* for the Neotropical species traditionally assigned to that generic name. A key to *Quadrella* and related Neotropical genera with stellate to lepidote-peltate indumenta is provided in Cornejo & Iltis (2009b).

#### KEY TO THE SUBGENERA OF QUADRELLA

1. Indument of terminal branches and leaf blades (at least abaxially) of peltate-lepidote trichomes; calyx with closed aestivation, the sepals lanceolate to oblong or ovate, covering the corolla until anthesis

1. *Quadrella* (DC.) J. Presl subg. *Quadrella*



1. Indument of terminal branches and leaf blades (at least abaxially) of stellate to candelabra trichomes; calyx usually with open aestivation and much exceeded by the corolla bud, the sepals usually triangular to linear, distinctively smaller than the petals from buds (except *Q. angustifolia*, *Q. alaineana* and *Q. singularis*).
2. Seeds oblongoid or ellipsoid, sometimes cleomoid-reniform, with  $\pm$  green embryo; fruits usually linear to linear-oblong, (1.3–)5–40 cm, usually several to many-seeded (except *Q. morenoi*); stamens 8 to 60 \_\_\_\_\_ **II. *Quadrella* subg. *Breyniastrum* (DC.) Ittis**
2. Seeds cleomoid-reniform, with white or cream embryo; fruits ovoid to obovoid or shortly oblongoid, 1–3 cm, 1- to 6-seeded; stamens usually 8, or ca. 16 (*Q. singularis*). \_\_\_\_\_ **III. *Quadrella* subg. *Intutis* (Raf.) Ittis**

**I. *Quadrella* (DC.) J. Presl subg. *Quadrella***

The subgenus *Quadrella* is characterized by the combination of the following characters: Closed valvate calyx aestivation, with oblong, lanceolate u ovate sepals, that at or after anthesis tend to recurve and fall off; peltate-lepidote trichomes; usually  $\pm$  torulose capsules; and seeds with green embryos. It comprises 7 species and 3 subspecies.

Distribution. Mexico, Central America, Florida, the West Indies and northern-most South America, mostly of arid places.

KEY TO SPECIES IN *QUADRELLA* SUBG. *QUADRELLA*

1. Calyces  $\pm$  quadrate, with 4 fairly sharp ridges; peltate indumentum rusty brown or golden brown; gynophores 1 to 8 cm (absent or to 5 mm only in *Q. quintanarooensis*).
2. Ovaries at anthesis 3–6.5 mm; sepals 5–10(–11) mm; receptacle in fruits (2–)3–5(–6) mm wide; stamens 16–35(–40); leaf blades mostly lustrous above, usually uniformly lepidote or peltate green or brownish beneath. Florida, through the West Indies to Trinidad and Barbados; disjunct to Mexico's Yucatan Peninsula and Quintana Roo, not uncommon locally on Cozumel Island and on the immediate adjoining north-eastern coastal mainland.
3. Flowers large, with petals 8–17 mm and sepals (5–)7–11 mm; stamens with simple or few-branched stellate trichomes at the base of the filament; anthers (2–)3–4 mm; southern Florida, West Indies and northeastern Yucatan Peninsula, Mexico.
4. Gynophores in flower conspicuous, 10–50 mm, to 80 mm in fruits; filaments 20–50 mm; petals 10–17 mm; common throughout the West Indies and southern Florida.
5. Leaf blades 3–8(–10)  $\times$  1–4(–4.5) cm, elliptic to narrowly obovate or oblong, rarely lanceolate (linear to lanceolate [to 17 cm] in juvenile leaves or stump sprouts), stiffly coriaceous and revolute, lustrous above; petioles 1–2 cm; seeds 5–8  $\times$  4–6 mm, packed in near each other in mostly barely torulose siliques; throughout the West Indies and southern Florida, in Jamaica, as elsewhere, mostly in coastal lowlands.
6. Leaf blades  $\pm$  elliptic, mostly 5–10  $\times$  2–6 cm, with apex acuminate or acute, sometimes obtuse to rounded but then often apiculate and not emarginate; central and eastern West Indies, from the Bahamas and Hispaniola to Puerto Rico and on to Trinidad and Barbados, sympatric with the following in Hispaniola \_\_\_\_\_ ***Quadrella cynophallophora***
6. Leaf blades mostly oblong or oblong-elliptic, mostly 3–7(–9)  $\times$  1–3(–3.5) cm, with apex usually emarginate (notched) to rounded; southern Florida, Cuba, Jamaica, and the Cayman and Swan islands, sympatric with the preceding species in Hispaniola and rarely in the Bahamas \_\_\_\_\_ ***Quadrella jamaicensis***
5. Leaf blades 7–15(–20)  $\times$  4–9 cm,  $\pm$  broadly elliptic,  $\pm$  chartaceous, rather opaque above, on petioles (1.5–)2–4 cm; seeds 7–15  $\times$  6–9 mm, spaced out in strongly torulose siliques; highlands of Jamaica at 200–800 m (500–2600 feet), in mesic to moist montane woodlands and limestone savannas \_\_\_\_\_ ***Quadrella siliquosa***
4. Gynophores in flower and fruit highly reduced to 5 mm or less or lacking; filaments 6–15 mm; petals 8–9 mm; endemic to Cozumel Island and immediately adjoining mainland of Quintana Roo, northeastern Yucatan Peninsula, Mexico \_\_\_\_\_ ***Quadrella quintanarooensis***
3. Flowers small, delicate, with petals 6–7 mm and sepals 5 mm; stamens with densely lepidote-radiate or lepidote-stellate (many-branched) trichomes at filament base; anthers 1–2 mm; very rare, scattered eastern half of Hispaniola (Haiti and easternmost Dominican Republic) \_\_\_\_\_ ***Quadrella gonaievensis***
2. Ovaries at anthesis 6.5–10 mm; sepals (9–)10–18 mm; receptacle in fruits 5–10 mm wide; stamens ca. 30–60; leaf blades opaque above (except *Quadrella isthmensis* subsp. *mexicana*), silvery lepidote peltate beneath, with scattered darker bronze hairs giving the lower surface a peppered appearance. Panama



and Costa Rica, and disjunct to the central Yucatan Peninsula (northern Guatemala and Belize) north to the Caribbean coast of Mexico's Yucatan State.

7. Petals completely glabrous without, sepals tomentulose within; very rare, on or near the crest of the Cordillera Central of western Panama, at 500–1200 m. ***Quadrella isthmensis* subsp. *glabripetala***
7. Petals densely lepidote without, sepals tomentose within; eastern Mexico, from northern Yucatan and Campeche south into Guatemala and Belize; and, disjunct, to Costa Rica and the lowlands of Panama.
8. Flower larger, with petals 12–18 × 7–10 mm, stamens 4–7 cm, and gynophores 4–8 cm; fruits to 60 cm, on gynophores 4–8 cm, and pedicels (1.3–)2–4.5 cm; mature leaf blades (5–)8–21(–26) cm, opaque above (when dry); Costa Rica and lowlands of Panama. ***Quadrella isthmensis* subsp. *isthmensis***
8. Flowers smaller, with petals 9–13 × 6–7.5 mm, stamens 2–4(–4.5) cm and gynophores 1–4.5 cm; fruits to 23 cm long, on gynophores 2–4(–5.5) cm and pedicels 1–2 cm; mature leaf blades 6–15 cm, often lustrous above (when dry); northern and central Yucatan Peninsula of Mexico to adjacent Guatemala and Belize. ***Quadrella isthmensis* subsp. *mexicana***
1. Calyx ± round, not ridged; peltate indumentum golden to silvery; gynophores absent. ***Quadrella odoratissima***

**1a. *Quadrella cynophallophora* (L.) Hutch.**, Gen. Fl. Pl. 2:309. 1967, sensu stricto. BASIONYM: *Capparis cynophallophora* L., Sp. Pl. ed. 1, 504. 1753; ed. 2:721, 1762, non *Capparis cynophallophora* Jacq., Select. Stirp. Amer. t. 98. 1763, which is *C. flexuosa* (L.) L., = *Cynophalla flexuosa* (L.) J. Presl, 1825. TYPE: JAMAICA?: Left hand specimen, "*Capparis* 2," Hortus Cliffortianus Hb. (LECTOTYPE, designated by Iltis & Cornejo 2010, BM-628728).

*Quadrella cynophallophora* is a widespread, polymorphic species, ranging from the Bahamas through the Dominican Republic (Hispaniola) and the Lesser Antilles to Trinidad and Barbados (in the latter two apparently known mostly from cultivated or escaped plants), generally at low elevations near the ocean, but to 400 m in Dominican Republic. Locally rarely sympatric with the similar *Quadrella jamaicensis* (Jacquin) J. Presl, in the Bahamas and the Dominican Republic, it can be distinguished by its mostly pointed, acute to obtuse, but not emarginate leaves.

*Quadrella cynophallophora* occurs in central and eastern West Indies, from the Bahamas to Hispaniola (where intergrades with *Quadrella jamaicensis*) and the southern coast of Puerto Rico and through the Lesser Antilles to Trinidad and Barbados (Gooding et al. 1965), mostly in coastal, seasonally dry, evergreen woodlands, but also in a great variety of habitats, often cultivated as hedges.

**1b. *Quadrella cynophallophora* (L.) Hutch., f. *linearifolia* Iltis**, J. Bot. Res. Inst Texas 4:98. 2010. TYPE: U.S.A. VIRGIN ISLANDS: St. John, East End Quarter, Hansen Bay, (eastern part of the Island at the end of Rt. 10) 0–10 m, dry scrubby coastal environment along a rocky shore, P. Acevedo-Rodríguez, A. Reilly & M. Davis 1808 (HOLOTYPE: NY).

A juvenile or stump sprout form with characteristic linear leaf blades.

**2. *Quadrella gonaievensis* (Helwig) Hutch.**, Gen. Fl. Pl. 2:308. 1967. BASIONYM: *Capparis gonaievensis* Helwig, Ark. Bot. 22A:10. 1929. TYPE: HAITI: "Peninsula sept.-occidentalis ad viam inter Les Gonaïves et Hatte-Rocher prope mangrove communis," s.d., E. Ekman 8483 (LECTOTYPE, B, B fragm. & photo at WIS; duplicates of the LECTOTYPE: GH, IJ, US).

*Quadrella gonaievensis* is a rare, highly localized but scattered endemic of Haiti and adjacent western parts of the Dominican Republic. This species has usually been ignored completely, or listed in synonymy under *Q. cynophallophora* (Urban 1920–21: 239; Al-Shehbaz 1988; Rankin & Greuter 2004). However, *Quadrella gonaievensis* differs from *Q. cynophallophora* by having small, delicate flowers, with petals 6–7 mm (vs. ca. 9–10 mm); stamens with densely lepidote-radiate or lepidote-stellate, many branched (vs. densely pilose with simple) trichomes at the filament base; and smaller anthers, 1–2 mm (vs. 2–3.5 mm).

**3. *Quadrella isthmensis* (Eichler) Hutch.**, Gen. Fl. Pl. 2:308. 1967. BASIONYM: *Capparis isthmensis* Eichler in Martius, Fl. Bras. 13:269. 1865. TYPE: COSTA RICA: "Habitat ad Costa Rica et Veraguas Americae Centralis," s.d., C. Hoffmann & Warszewicz 217 (LECTOTYPE, designated by Iltis & Cornejo 2010a, B, B fragm. at M, WIS).

**3a. *Quadrella isthmensis* (Eichler) Hutch. subsp. *isthmensis***

*Capparis chiriquensis* Woodson, Ann. Missouri Bot. Gard. 35:92, fig. 49. 1948. TYPE: PANAMA. PROVINCE OF CHIRIQUI: vic. Puerto Armuelles, 0–75 m, 28–31 Jul 1940, R. Woodson & R. Schery 846 (HOLOTYPE: MO, MO photo at WIS; ISOTYPES: GH, US, US photo at WIS).

Chromosome number.— $2n = 16$  [Pazy, from root tip]. Panama: Canal Zone, 7 m tree, 10 cm dbh, visited by



small bees, trail along Rio Petit Pie, near road to Fort Sherman, on Limestone, upland Panama, *S. Mori & J. Kallunki* 5011 (WIS).

*Quadrella isthmensis* subsp. *isthmensis* is found in Costa Rica, from sea level (Osa Peninsula) to 900 m (Cordillera de Tilarán), generally on the Pacific slope, and in coastal mostly Pacific lowlands of Panama, mostly in wet or moist tropical forests, apparently not overlapping the range of *Q. isthmensis* subsp. *glabripetala*.

**3b. *Quadrella isthmensis* subsp. *glabripetala*** Cornejo & Iltis, *J. Bot. Res. Inst Texas* 4:111. 2010. TYPE: PANAMA. CHIRIQUI: near Fortuna Dam Camp, 26 Feb 1985 (fl), *R.J. Hampshire & C. Whiteford* 111 (HOLOTYPE: MO; ISOTYPES: PMA, WIS).

Restricted to higher elevations and the crest of Cordillera Central in Panama (Cornejo & Iltis 2010a).

**3c. *Quadrella isthmensis* subsp. *mexicana*** Cornejo & Iltis, *J. Bot. Res. Inst Texas* 4:110. 2010. TYPE: MEXICO. YUCATAN: Las Bocas de Silam [Dzilám], May 1916 (fl), *G. Gaumer & sons* 23344 (HOLOTYPE: MO; ISOTYPES: BM, F, K, NY, US, US photo at WIS).

*Quadrella isthmensis* subspecies *mexicana* is one of the successional elements from mangrove borders in Yucatán (*Lira et al.* 368, MEXU) inland to “selvas medianas subperennifolias” (Rzedowski 1978), south to high forests in Guatemala and adjoining Belize.

**4a. *Quadrella jamaicensis*** (Jacq.) J. Presl, *Prir. Rostlin* 2:261. 1825. BASIONYM: *Capparis jamaicensis* Jacq., *Enum. Pl. Carib.* 23. 1760. TYPE: JAMAICA: t. 101 in Jacquin, 1763 (LECTOTYPE, designated by Al-Shehbaz in *Flora of the Lesser Antilles-Dicotyledoneae* 4(1):296. 1988).

*Capparis emarginata* A. Richard in Sagra, *Hist. Fis. Cuba* 10:28. 1845. TYPE: CUBA: s.d., *Sagra s.n.* (LECTOTYPE: P, designed by Al-Shehbaz in *Flora of the Lesser Antilles-Dicotyledoneae* 4(1):296. 1988).

*Colicodendron anceps* Shuttl., *nomen in Chapman, Fl. South. U.S.* 32. 1860.

*Quadrella jamaicensis* is an evergreen, ornamental species, known as Jamaica Caper. This species is characteristic of coastal areas from central Florida (from Cape Cañaveral on the east coast and St. Petersburg Beach on the west coast), south to Key West. It also occurs in Cuba, Jamaica, and the Cayman and Swan Islands, overlapping and intergrading with *Quadrella cynophallophora* in Hispaniola, but is rare in the Bahamas (Iltis & Cornejo 2010a).

**4b. *Quadrella jamaicensis*** (Jacq.) J. Presl, f. *longifolia* (Swartz) Iltis, *J. Bot. Res. Inst Texas* 4:98. 2010. BASIONYM: *Capparis longifolia* Swartz, *Prodr.* 81. 1788. TYPE: JAMAICA: *Swartz s.n.* (HOLOTYPE: S, S photo at WIS; ISOTYPE: C, C photos at IJ, WIS).

This strikingly different-appearing form is a stump sprout or juvenile, sterile branch with narrow elongate leaf blades, common in this species and, in a homologous form, also in *Quadrella cynophallophora* f. *linearifolia*. This form is distributed across the range of the species.

**5. *Quadrella odoratissima*** (Jacq.) Hutch., *Gen. Fl. Pl.* 2:308. 1967. BASIONYM: *Capparis odoratissima* Jacq., *Hort. Schoenbr.* 1:57, t. 110. 1797. TYPE: VENEZUELA: Caracas, “In caldario, floret Martio & Aprili” (LECTOTYPE, Tab. 110, in Jacquin, loc. cit. designated by Al-Shehbaz, in *Flora of the Lesser Antilles-Dicotyledoneae* 4(1): 1988).

*Capparis intermedia* Kunth, *Nov. Sp. Pl.* 5:98. 1821. *Quadrella intermedia* (Kunth) J. Presl, *Prir. Rostlin* 2:261. 1825. TYPE: VENEZUELA: “Crescit prope Cumaná,” Sep, *A. Humboldt & A. Bonpland* 39 (LECTOTYPE, designated here: P).

*Chromosome number*.— $2n = 16$  [!Pazy, !Przywara, from root tips]. Venezuela: Distrito Federal, shrub 3 m, tropical low deciduous forest, carretera vieja Caracas-La Guaira, 320 m, 4 Feb 1979, *P. Berry & T. Plowman* 3363 (MO, WIS).

*Quadrella odoratissima* is a common and very distinctive silvery-peltate evergreen species with beautiful flowers and sessile siliques, characteristic of arid tropical dry forests, from northern coastal Colombia and Venezuela into the Lesser Antilles, and, in Mesoamerica, from Panama to southern Mexico.

*Capparis intermedia* is herein synonymized under *Quadrella odoratissima* because both describe the same species, giving priority the older name.

**6. *Quadrella quintanarooensis*** Iltis & Cornejo, *J. Bot. Res. Inst Texas* 4:104. 2010. TYPE: MEXICO. QUINTANA ROO:



Xcaret, a 5 km S de Playa del Carmen, selva mediana, 15 Sep 1982 (fr), E. Cabrera & H. de Cabrera 3495 (HOLOTYPE: MEXU, MEXU fragm. & photo at WIS; ISOTYPES: CAS, MO).

*Quadrella quintanarooensis* occurs in dry, open, tropical forests and woodlands on or near beaches at sea level on Cozumel Island and the adjoining Mexican mainland of Quintana Roo (Iltis & Cornejo 2010a).

**7. *Quadrella siliquosa* (L.) Iltis & Cornejo, J. Bot. Res. Inst Texas 4:98. 2010.** BASIONYM: *Capparis siliquosa* L., Syst. Nat. ed. 10 (2): 1071. 1759, p.p. *Pleuteron siliquosa* (L.) Raf., Sylva Tellur. 109. 1838. TYPE: JAMAICA: road to Troy, 18 Sep 1906, W. Harris 9488 (NEOTYPE, designated by Iltis & Cornejo 2010, BM, BM fragm. & photo at WIS; ISONEOTYPES: A, GH, K, NY, US).

*Capparis torulosa* Swartz, Prodr. 81. 1788. *Quadrella torulosa* (Swartz) J. Presl, Prir. Rostlin 2:261. 1825. *Pleuteron torulosa* (Swartz) Raf., Sylva Tellur. 109. 1838. TYPE: JAMAICA: s.d. (fr), C. Wright s.n. (NEOTYPE, designated by Iltis & Cornejo 2010, S 05-9708).

Endemic to the montane woodlands and savannas of Jamaica (Iltis & Cornejo 2010).

**II. *Quadrella* subg. *Breyniastrum* (DC.) Iltis, comb. nov.** BASIONYM: *Capparis* section *Breyniastrum* DC., Prod. 1:250. 1824. *Capparis* subg. *Breyniastrum* (DC.) Eichler in Martius, Fl. Bras. 13(1):271, t. 64. 1865, p.p. (excl. *Capparis longifolia*, =*Quadrella jamaicensis* f. *longifolia*). *Breynia* L., Sp. Pl. 1:503. 1753, nom. rej. for *Breynia* J.R. Forster & G. Forster, Char. Gen. Pl., 73. 1775, nom. cons. [Euphorbiaceae]. *Linnaebreynia* Hutch., Gen. Fl. Pl. 2:310. 1967, p.p. (excl. *L. domingensis* [Spreng. ex DC.] Hutch., *L. ferruginea* [L.] Hutch., *L. grisebachii* [Eichler] Hutch., *L. incana* [Kunth] Iltis & Cornejo, =*Quadrella* subg. *Intutis* [Raf.] Iltis & Cornejo, and *Capparis* sect. *Calanthea* DC., =*Calanthea* [DC.] Miers). TYPE: *Breynia indica* L. (= *Quadrella indica* [L.] Iltis & Cornejo), lectotype, designated by Hutchinson in The Genera of Flowering Plants (Angiospermae). Dicotyledones 2:311. 1967).

*Pleuteron* Raf., Sylva Tellur. 109. 1838, p.p. (excl. *Capparis frondosa* Jacq., *C. baducca* L., *C. hastata* Jacq., *C. linearis* Jacq., *C. siliquosa* L. [= *Quadrella siliquosa*], *C. comosa* Jacq. (= *Q. ferruginea* [L.] Iltis & Cornejo), *C. torulosa* [= *Quadrella siliquosa*], *C. tenuisiliqua* Jacq.). TYPE: *Pleuteron breynia* (L.) Raf. [= *Quadrella indica* (L.) Iltis & Cornejo], lectotype designated here.

The logical choice of Hutchinson (1967) of *Breynia indica* (= *Quadrella indica*) as the subgenus lectotype (for *Capparis* subg. *Breyniastrum*) preserves traditional useage, while *Capparis ferruginea* L. (= *Quadrella ferruginea*), posteriorly designated as lectotype by Rankin & Greuter (2004: 262, for *Capparis* sect. *Breyniastrum*), introduces an extraneous element belonging to a different taxonomic group that is characterized by a capsular fruits with few seeds containing white embryos surrounded by a ± hard testa, which we now segregate in *Quadrella* subg. *Intutis* (Raf.) Iltis; see below.

Hutchinson (1967), proposed *Linnaebreynia* as a new generic name for *Breynia* L., a rejected illegal homonym, because *Breynia* J.R. Forster & G. Forster (Euphorbiaceae) is a previously established nomen conservandum. He repeated most of the species included in Eichler's broad but heterogeneous concept of *Capparis* subgenus *Calanthea* (DC.) Eichler, intermixing species with different calyx structure, dehiscent and indehiscent fruits and with seeds of green and white embryos, including *L. pulcherrima* (Jacq.) Hutch. (= *Calanthea pulcherrima* [Jacq.] Miers, the type of *Calanthea* [DC.] Miers, a valid South American small genus of Capparaceae characterized by the flowers with widely spaced, linear-ligulate to oblong sepals exposing the valvate corolla from early bud on and fleshy amphisarca, bearing seeds with uncommonly very thick cotyledons [Cornejo & Iltis 2008, 2009]); four species of *Quadrella* subg. *Breyniastrum*: *L. admirabilis* (Standl.) Hutch. (= *Q. lundellii* [Standl.] Iltis & Cornejo), *L. asperifolia* (K. Presl) Hutch. (= *Q. asperifolia* [K. Presl] Iltis & Cornejo), *L. pringlei* (Briq.) Hutch. (= *Q. pringlei* Briquet), and *L. tonduzii* (Briq.) Hutch. (= *Q. indica*); and the following taxa of *Quadrella* subg. *Intutis*: *L. domingensis* (= *Q. domingensis* [Spreng. ex DC.] Iltis & Cornejo), *L. grisebachii* (= *Q. domingensis* subsp. *grisebachii* [Eichler] Iltis & Cornejo), *L. ferruginea* (= *Q. ferruginea* [L.] Iltis & Cornejo), and *L. incana* (= *Q. incana* [Kunth] Iltis & Cornejo).

*Pleuteron breynia* (= *Quadrella indica*) is herein designated the lectotype of *Pleuteron* because Rafinesque, in the protologue, referred to it as the "main type." *Pleuteron* is synonymized under *Quadrella* subgen. *Breyniastrum* because the mentioned selected lectotype has stellate pubescence, flowers with calyx valvate and open aestivation in bud and fruits with seeds containing green embryos.

*Quadrella* subg. *Breyniastrum* is similar to subg. *Quadrella* in its peltate or stellate pubescence and capsular fruits, but with its retarded calyx growth resulting in small triangular sepals. These, valvate from very early on in development, are soon much exceeded by the corolla, thus leading to an open calyx aestivation at anthesis. Lastly, its dehiscent elongate capsules are filled with sticky red pulp and several to many seeds,



these covered by a red or orange aril or endocarp(?) and a thin testa that easily is slipped off the green embryos by the vertebrate dispersers. Twelve species are assigned to this subgenus.

Despite the calyx differences between subg. *Quadrella* (closed calyx aestivation) and subg. *Breyniastrum* (open calyx aestivation), the two sections seem very closely related indeed, considering their similar fruit, pulp, and embryo colors, the nature and color of their seed arils and seed coats, their variable tufted to stellate to peltate-lepidote pubescence and finally their distributional biogeographic coherence.

Distribution. A New World group centered on Mexico and Central America.

#### KEY TO THE SPECIES OF *QUADRELLA* SUBG. *BREYNIASTRUM*

1. Detritophilous plants, main stem with adventitious roots and spirulate leaves, densely arranged at the end of the stem or branches in pseudovercils that collect humus; androgynophores and gynophores absent.
2. Shrubs or branched treelets; leaf blades (12–)15–35(–40) × 3–10(–11) cm; inflorescence a persistent raceme, bracts soon deciduous; filaments 4–5 mm, petals 5–7 mm; Panama, west of the canal. *Quadrella antonensis*
2. Unbranched or sometimes to 2-branched treelets; leaf blades 30–70 × 9–19 cm; inflorescence paniculiform bearing to several few-flowered 2nd order bracteate racemes, soon deciduous if not pollinated, raceme bracts persistent, 3–4 mm; filaments and petals 7–8 mm; Panama, east of the canal. *Quadrella dressleri*
1. Plants not detritophilous, main stem without adventitious roots, leaves alternate to laxly-spiralate, arranged along the branches; androgynophores and gynophores present.
3. Gynophores 2–10 mm, staminal filaments 5–10 mm.
4. Petals 4–8 × 2–5 mm, anthers 1.5–2.8 mm.
5. Flowers with 8 stamens.
6. Leaf blades (2.5–)3–8.5(–10) × 1–4(–5) cm; petals 4.5–6 mm; fruits broadly ellipsoid to obovoid, 1.3–2.5 × 0.8–1.1 cm. *Quadrella morenoi*
6. Leaf blades 18–27 × 5–10.5 cm; petals 7–8 mm; fruits linear, torulose, 11–31 × 0.6–1 cm. *Quadrella steyermarkii*
5. Flowers with 14–30 stamens.
7. Leaf blades 0.8–2.5 cm wide, petioles 2–8 mm; filaments 7–10 mm, gynophores golden lepidote; fruits 4–5 mm wide, seeds 5–8 mm. *Quadrella lindeniana*
7. Leaf blades 2–5.5(–8) cm wide, petioles (15–)20–50(–74) mm; filaments 5–7 mm, gynophores lepidote-stellate; fruits 7–15 mm wide, seeds 8–12 mm. *Quadrella pringlei*
4. Petals 12–13 × 8–9 mm, anthers 3–4 mm. *Quadrella calciphila*
3. Gynophores 12–40 mm, staminal filaments 12–30 mm.
8. Inflorescences erect or suberect, panicles or corymbose racemes; leaves loosely spirulate.
8. Inflorescences pyramidal panicles, peduncles 2–5 mm wide, longitudinally costate; stamens 8; nectaries dark brown when dry, conspicuous from floral bud; leaf blades with rounded to subcordate base. *Quadrella lundellii*
9. Inflorescences corymbose racemes, peduncles 1–2 mm wide, ecostate; stamens 15–36; nectaries inconspicuous in floral bud; leaf blades with usually cuneate base.
10. Leaf blades smooth above, lepidote-peltate beneath; ovaries densely covered by appressed lepidote-peltate trichomes. *Quadrella indica*
10. Leaf blades ± scabrous above, stellate and dendroid beneath; ovaries densely covered by stellate multiradiate and lepidote-stellate trichomes. *Quadrella asperifolia*
8. Inflorescence pendulous, umbellate; leaves distichous.
11. Leaf blades usually with a reddish brown, stellate tomentose, marginal pubescence, anthers 4 mm. *Quadrella mirifica*
11. Leaf blades without a reddish brown, stellate tomentose, marginal pubescence, anthers ca. 2 mm. *Quadrella filipes*

**1. *Quadrella antonensis*** (Woodson) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis antonensis* Woodson, Ann. Missouri Bot. Gard. 35:90. 1948. TYPE: PANAMA. COCLE: hills N El Valle, 13 Jan 1942, P.H. Allen 2948 (HOLOTYPE: MO).

*Chromosome number*.— $2n = 16$  [!Pazy, !Przywara, from root tip]. Panama: Cocle, shrub 2 m, in cloud forest, ca. 3 km NE of El Valle, 2 Nov 1961, S. Mori & J. Kallunki 2961 (WIS).

A locally common shrub or treelet with subverticillate, overlapping, cordate based leaves that form a trash basket invaded by adventitious roots (detritophily) and home to a mini-botanical garden of mosses, ferns, pepperomias and a mini-zoo of amphibians and diverse invertebrates, such as Collembolas. The plant



species is endemic to tropical rain and cloud forests of eastern Panama. It is similar to *Q. dressleri* Cornejo & Iltis, for differences see Cornejo and Iltis (2010). This is apparently a case of convergent evolution allopatrically evolved in the Panamanian area in response to unknown pollinators or other factors, an evolutionary enigma in need of molecular answers (Dressler 1985; Sánchez 2001).

- 2. *Quadrella asperifolia*** (K. Presl) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis asperifolia* K. Presl, Reliq. Haenk. 2:86. 1835. *Linnaeobreynea asperifolia* (K. Presl) Hutch., Gen. Fl. Pl. 2:310. 1967. TYPE: MEXICO: "Habitat ad urbem et portum Acapulco," Jun 1834, T. Haenke s.n. (LECTOTYPE, designated here, PR; duplicates of the LECTOTYPE: MO 3835176, W, W photo at F 030115).  
*Capparis langlassei* Briquet, Ann. Jard. Bot. Geneve 17:392. 1914, syn. nov. TYPE: MEXICO. MICHOACAN: Cuesta de Cijones, 1000 m, 14 Apr 1899 (fl), E. Langlássé 993 (HOLOTYPE: G, G photo at F 27287, WIS; ISOTYPES: B, GH, K, MEXU, P, P fragm. at WIS).

A rare endemic of arid scrublands in pockets of semideserts and summer-green deciduous forests inland from the Pacific coast in southwestern Mexico. The species name is somewhat misleading because the dendritic stellate pubescent on the underside of the leaves is velvety and soft, while only the upper leaf surface is scabrous.

- 3. *Quadrella calciphila*** (Standl. & Steyermark) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis calciphila* Standl. & Steyermark, Field. Mus. Bot. 23:158. 1944. TYPE: GUATEMALA. ALTA VERAPAZ: Cerro Chinajá, betw. finca Yalpemech & Chinajá, above source of Río San Diego, ca. 200 m, 1–2 Apr 1942 (fl), J. Steyermark 45616 (HOLOTYPE: F, F photo 51609 at WIS; ISOTYPES: NY, US).  
*Capparis mayana* Lundell, Wrightia 5:356. 1977, syn. nov. TYPE: Guatemala. Petén: La Cumbre in zapotal on top of hill, S of Río Pusila rd., ca. 3.5 km, 21 Mar 1977, C.L. Lundell & E. Contreras 20630 (HOLOTYPE: LL).

*Quadrella calciphila* is a very rare endemic, known by few collections from the tropical rain forests of Guatemala. It has a pubescence seemingly closely related to *Q. pringlei*, but mainly differs by having longer petals, 12–13 × 8–9 mm (vs. 4–6 × 3–5 mm), longer filaments, 8–10 mm (vs. 5–7 mm), and longer fruit, 9–15 cm (vs. 2.5–7 cm).

- 4. *Quadrella dressleri*** Cornejo & Iltis, J. Bot. Res. Inst. Texas 4:77. 2010. TYPE: PANAMA. PANAMA: 8–12 km N of El Llano along new El Llano-Cartí rd., premontane wet forest, 400–450 m, 12 Dec 1973 (fl), M. Nee, A. Gentry & R. Dressler 8765 (HOLOTYPE: WIS; ISOTYPES: MO, US, PMA, WIS [2]).

Restricted to wet or very wet, tropical rain or submontane cloud forests of the Caribbean slopes of eastern Panama, north of the continental divide and east of the Panama Canal, in the provinces of Colon, San Blas and Panama, at 50–500(–850) m (Cornejo & Iltis 2010).

- 5. *Quadrella filipes*** (Donnell Smith) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis filipes* Donnell Smith, Bot. Gaz. 23:2. 1897. TYPE: COSTA RICA. LIMÓN: Suerre, Llanuras de Santa Clara, 300 m, Apr 1896, D. J. Smith 6433 (LECTOTYPE, designated here: US).  
*Capparis clara* Schery, Ann. Missouri Bot. Gard. 29:351. 1942, syn. nov. TYPE: PANAMÁ. BOCAS DEL TORO: Fish Creek Mts., 6 Apr 1941, H. von Wedel 2235 (HOLOTYPE: MO 1232846).

*Quadrella filipes* is uncommon but widespread from Costa Rica to Panama in tropical moist to wet forests. It differs from *Quadrella antonensis* mainly in its longer gynophores (22–42 vs. sessile to 4 mm), and the distichous leaves (vs. trash-collecting leaf funnels).

- 6. *Quadrella indica*** (L.) Iltis & Cornejo, comb. nov. BASIONYM: *Breynea indica* L., nom. rej., Sp. Pl. 1:503. 1753. *Capparis breynia* L. Syst. Pl. ed. 10:1071. 1759, nom. illeg. *Quadrella breynia* (L.) J. Presl, Priur. Rostlin 2:261. 1825. *Pleuteron breynia* (L.) Raf., Sylva Tellur. 109. 1838. *Uterveria breynia* (L.) Bertoloni, Pl. nov. H. Bonon. 2:10. 1839. *Capparis indica* (L.) Druce, Bot. Exch. Club Soc. Brit. Isles 3:415. 1914. *Linnaeobreynea indica* (L.) Hutch., Gen. Fl. Pl. 2:311. 1967, nom. illeg. TYPE: "Habitat in Caribaeis & in continente vicina" (neotype, designated by Rankin & Greuter in Willdenowia 34:262. 2004, t. "Breynea Eleaegni foliis Plum." in Breynia, 1739: t. ad p. 13).  
*Capparis amygdalina* Lam., Encycl. 1:608. 1785. TYPE: ANTILLES: J. Surian 123 (LECTOTYPE: P-JU, designated by Al-Shehbaz, in Flora of the Lesser Antilles-Dicotyledoneae 4(1):299. 1988).  
*Pseudocroton tinctorius* Müller Argoviensis, Flora 55:24. 1872. TYPE: NICARAGUA: Near Managua, E. Friedrichstahl 1072 (HOLOTYPE: W; ISOTYPE: F).  
*Capparis tonduzii* Briquet, Ann. Conserv. Jard. Bot. Genève 17:391. 1914. *Linnaeobreynea tonduzii* (Briquet) Hutch., Gen. Fl. Pl. 2:310. 1967. TYPE: COSTA RICA. Forêts de Nicoya, Apr 1900, A. Tonduz 13970 (HOLOTYPE: G-DC, G-DC photo, F 008476).



*Capparis furfuracea* Ruiz & Pavón ex DC., Prodr. 1:252. 1824. *Capparis furfuracea* Sessé & Mociño, Fl. Mex. ed. 2, 129. 1894. *Quadrella furfuracea* (Ruiz & Pavón ex DC.) J. Presl, Priř. Rostlin 2:260. 1825. TYPE: PUERTO RICO: seashore near Ponce (fide McVaugh 2000: 116).

*Quadrella indica* is a common species, widespread from Pacific coastal western Mexico and Central America and from the Dominican Republic and Puerto Rico through the West Indies to Venezuela.

- 7. *Quadrella lindeniana*** Cornejo & Iltis, J. Bot. Res. Inst. Texas 4:83. 2010. TYPE: MEXICO. QUINTANA ROO: Isla de Cozumel, a 1 km NO del Faro de la Punta Celarain, 4 Jun 1986 (fl), E. Cabrera & H. de Cabrera 11433 (HOLOTYPE: MEXU [MEXU photocopies at AAU, B, BM, COL, DAV, F, GH, GUAY, K, MA, NY, P, QCA, QCNE, S, U, UC, US, WIS]; ISOTYPES: MO, TEX).

*Quadrella lindeniana* is restricted to Mexico's Yucatan Peninsula, where it occurs through dry thorn scrub to subdeciduous lowlands and subevergreen forests in the south, often growing on coastal dunes or rocky soils, and persisting in disturbed forests (Cornejo & Iltis 2010).

- 8. *Quadrella lundellii*** (Standl.) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis lundellii* Standl., Carnegie Inst. Wash. Publ. 461:57. 1935. TYPE: GUATEMALA. PETÉN: San Andrés, 3 May 1933 (fl), C.L. Lundell 3115 (LECTOTYPE, designated here: F 706.401, F photo 51611; duplicate of the LECTOTYPE: US).

*Capparis admirabilis* Standl. in Yuncker, Field Mus. Nat. Hist., Bot. Ser. 9:291. 1940, syn. nov. *Linnaeobreyenia admirabilis* (Standl.) Hutch., Gen. Fl. Pl. 2:310. 1967. TYPE: HONDURAS. YORO: in woodland in semi-arid region near Coyoles, 29 Jun 1938, T.G. Yuncker, J.M. Koepper & K.A. Wagner 8130 (HOLOTYPE: F, F photo 051607; ISOTYPES: S, US).

*Quadrella lundellii* is a rare and local, in pockets of aridity near the coast, from southern Mexico to Guatemala. This species has the ability to produce stump sprouts and juvenile branches with strongly hastate leaves (ditto for species 10, *Q. morenoi*).

- 9. *Quadrella mirifica*** (Standl.) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis mirifica* Standl. in Woodson & Schery, Ann. Missouri Bot. Gard. 27:311. 1940. TYPE: PANAMA. CANAL ZONE: Vic. Salamanca Hydro. Station, Rio Pequeni, ca. 80 m, 28–29 Jul 1938 (fr), R.E. Woodson, Jr., P.H. Allen & R.J. Seibert 1591 (HOLOTYPE: F; ISOTYPES: MO, NY).

*Quadrella mirifica* is a gorgeously golden, softly and velvety pubescent shrub, especially on the leaf margins, extremely rare and endemic to the tropical forests in the vicinity of the Canal Zone of Panama. It is similar in inflorescence structure by virtue of the elongate filiform peduncles of the pendulous umbels to the sometimes sympatric *Q. filipes*. Its stellate pubescence corresponds to that seen in two other species as *Q. steyermarkii* and *Q. asperifolia*.

- 10a. *Quadrella morenoi*** Cornejo & Iltis, J. Bot. Res. Inst. Texas 4:86. 2010. TYPE: NICARAGUA. BOACO: km 7 carr. al Rama, 12°24'N 85°45'W, 180–200 m, 19 Jun 1982 (fr), P. Moreno 16555 (HOLOTYPE: WIS; ISOTYPES: HNMM, MO, VDB).

*Quadrella morenoi* is scattered from southern Mexico (Michoacan) to southwestern Costa Rica, but is especially common in Central Nicaragua. It ranges from sea level to 930 m, in deciduous thorn scrub, gallery forests and semi-deciduous tropical dry forests and woodlands, persists in secondary vegetation and grazed areas, often on rocky and volcanic soils, and overlaps parapatrically the range of the similar but more common *Q. incana* (of subg. *Intutis*) from southern Mexico to Guatemala and rarely into central Honduras, mostly in the seasonally arid climates of the Pacific slope, with their sympatry apparently only at Tehuantepec in southern Oaxaca, Mexico (Cornejo & Iltis 2010).

- 10b. *Quadrella morenoi* f. *hastata*** Iltis, J. Bot. Res. Inst. Texas 4:90. 2010. TYPE: NICARAGUA: Vic. Hac. San Jacinto, NE of Managua, stump sprouts from disturbed shrub and small tree savanna, ca. 100 m, 14 Oct 1991 (st), H.H. Iltis & P. Anderson 30875 (HOLOTYPE: WIS; ISOTYPES: MO, NHNM, US).

A juvenile form characterized by the radically different, strongly hastate leaves, resembling those of *Q. lundellii* (Cornejo & Iltis 2010).

- 11. *Quadrella pringlei*** (Briquet) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis pringlei* Briquet, Ann. Conserv. & Jard. Bot. Genève 17:390. 1914. *Linnaeobreyenia pringlei* (Briquet) Hutch., Gen. Fl. Pl. 2:310. 1967. TYPE: MEXICO. OAXACA: Tomellin Canyon, ca. 3000 ft, 18 May 1894 (fr), C. Pringle 4639 (HOLOTYPE: G; ISOTYPES: B, B photo at WIS, BKL, BM, BR, CM, F, GH, GOET, IA, IA fragm. at WIS, K, LE, M, MEXU, MIN, MO, MSC, ND, NY, P, PR, UC, US, UT, UT fragm. & photo at WIS, VT, VT photos at WIS & XAL, Z).



*Capparis langmaniae* Standl. & L. Williams, Ceiba 14:5. 1968. TYPE: MÉXICO. CHIAPAS: betw. San Fernando & Plan de Ayala, barranca W of Tuxtla, "Chirimay de montaña," 17 Apr 1949 (fl, fr), I.K. Langman 3912 (HOLOTYPE: EAP; ISOTYPES: F, US, US fragm. at WIS).

*Quadrella pringlei* is distributed from southern Mexico to Guatemala with disjunct local populations in Nicaragua (Sierra de Managua) and Costa Rica (below Monteverde). Due to the similar appearance, *Quadrella pringlei* is often confused with *Q. indica*, but has somewhat broader leaves, these  $\pm$  spirally disposed on subverticillate petioles highly variable in length on the same branch. The flowers of *Q. pringlei* are smaller and less attractive with shorter petals and stamens and with shorter, subsessile, fewer-seeded capsules.

**12. *Quadrella steyermarkii*** (Standl.) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis steyermarkii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:140. 1940. TYPE: GUATEMALA. IZABAL: Río Dulce, betw. Livingston & 6 mi. up river, on N side, near sea level, 14 Apr 1940 (fl), J.A. Steyermark 39387 (HOLOTYPE: F, F photo 51613 at WIS).

*Quadrella steyermarkii* is a rare Guatemalan rainforest endemic, similar in its obovate to obovate-elliptic leaf shape, but with shorter petals (7–8  $\times$  3–5 mm vs. 12–13  $\times$  8–9 mm) to the sympatric *Q. calciphila*, also in subg. *Breyniastrum*. *Quadrella steyermarkii* is exceedingly similar in leaf pubescence to *Quadrella mirifica*, but the pubescence is soft and velvety underneath, similar to that of *Q. asperifolia*.

**III. *Quadrella* subg. *Intutis*** (Raf.) Iltis, comb. et stat. nov. BASIONYM: *Intutis* Raf., Sylva Tellur. 108. 1838, p.p. (excl. *Capparis amygdalina* Lam., =*Quadrella indica*). TYPE: *Intutis ferruginea* (L.) Raf. (= *Quadrella ferruginea* [L.] Iltis & Cornejo) (NEOTYPE, designated here).

*Capparis* sect. *Pseudocrataeva* Grisebach, Fl. Brit. W.I., 17. 1864, p.p. (excl. *Capparis amygdalina* Lam., =*Quadrella indica*). TYPE: *Capparis ferruginea* L. (= *Quadrella ferruginea*) (lectotype, designated by Rankin & Greuter in Willdenowia 34:262. 2004).

*Octanema* Raf., Sylva Tellur. 112. 1838, p.p. (excl. *O. crotonoides* [= *Capparicordis crotonoides* (Kunth) Iltis & Cornejo], and *O. scabrida* [= *Colicodendron scabridum* (Kunth) Seeman]). TYPE: *Capparis angustifolia* Kunth (= *Quadrella angustifolia* [Kunth] Iltis & Cornejo) (LECTOTYPE, designated here).

Shrubs to small trees, stellate throughout, with small, subsessile, densely stellate to candelabroid leaves, small flowers with calyces with open aestivation, the sepals linear to triangular, far exceeded by the corolla in bud, or calyces with closed aestivation, the sepals oblong to lanceolate, covering the petals in bud nearly to anthesis; stamens usually 8, or ca. 16 (in *Q. singularis*); fruits ovoid to obovoid capsules, 1.5–3(–10 cm in *Q. angustifolia*), often tardily dehiscent, 1 to 6-seeded, with red pulp, splitting open with 2 to 4 recurved thin valves, exposing red arillate seeds dangling from funicles, the seeds with white or cream embryos. Whether the tissue around the seed is arillate in origin or part of the pulp or mesocarp is an unanswered question. In *Quadrella incana* it appears as if there is no pulp and the seed is enclosed by its own aril. This subgenus comprises 6 species, 6 subspecies and one variety.

When Hutchinson (1967) validated the genus *Quadrella*, he cited the Rafinesquean *Intutis* in synonymy and lectotypified both with *Quadrella cynophallophora*. However, similar to the lectotypification of *Quadrella* (op. cit.), Hutchinson's lectotypification of *Intutis* is not valid because *Quadrella cynophallophora* was not mentioned by Rafinesque in the protologue of *Intutis*, and is not original material for the name. *Capparis ferruginea* (= *Quadrella ferruginea*) is herein designated the neotype of *Intutis* because was the first syntype designed by Rafinesque in the protologue. Hutchinson (1967) placed *Quadrella ferruginea* within his heterogeneous *Linnaeobreynia* (= *Quadrella* subg. *Breyniastrum*), but *Q. ferruginea* is kept in *Quadrella* subgenus *Intutis* because the eight stamens and seeds with white embryos.

*Quadrella angustifolia*, the first syntype cited by Rafinesque in the protologue of *Octanema*, is the herein designated lectotype of *Octanema* because of its flowers with eight stamens and seeds with a white embryo. *Quadrella angustifolia* and *Q. incana*, both species placed by Rafinesque in *Octanema* were included by Hutchinson (1967) within *Linnaeobreynia*.

**Distribution.**—*Quadrella* subgenus *Intutis* ranges from southern North America (Texas) through Mexico to northern Honduras, and in the West Indies from Cuba to Hispaniola.

#### KEY TO THE SPECIES OF QUADRELLA SUBGENUS INTUTIS

1. Calyx with open aestivation, sepals triangular to linear, distinctively shorter than petals from buds.



- 2. West Indies species.
  - 3. Branches and leaves, especially beneath, with a dense,  $\pm$  rusty cover of stellate trichomes; sepals triangular, 1–2.5 mm, distinctively smaller to half of the petals length.
    - 4. Leaf blades lanceolate; sepals linear-triangular; the common subspecies of Jamaica and Dominican Republic \_\_\_\_\_ *Quadrella ferruginea* subsp. *ferruginea*
    - 4. Leaf blades spatulate-lanceolate; sepals triangular; Cuba \_\_\_\_\_ *Quadrella ferruginea* subsp. *cubensis*
  - 3. Branches and leaves covered by yellowish white trichomes, the leaves beneath with a mixed tomentum of stellate and dendritic hairs; sepals linear, (2–)3–5(–6) mm, two third to as long as the petals.
    - 5. Leaf blades above covered with soon deciduous sessile stellate trichomes, shaped like a sea-urchin or a stout bottlebrush, and with persistent, sharply pointed conical protuberances \_\_\_\_\_ *Quadrella domingensis* subsp. *domingensis*
    - 5. Leaf blades above initially dense, stellate, yellow, velvety pubescent, becoming glabrous, smooth and shiny, sharply pointed conical protuberances on the leaf blades absent \_\_\_\_\_ *Quadrella domingensis* subsp. *grisebachii*
- 2. Continental species, from southeastern Texas, south to Guatemala and rarely into northern Honduras.
  - 6. Sepals linear to filiform, 2–5  $\times$  0.5–0.9 mm; staminal filaments 6–9 mm.
    - 7. Leaf blades lanceolate or narrowly elliptic to oblanceolate or obovate \_\_\_\_\_ *Quadrella incana* subsp. *incana*
    - 7. Leaf blades broadly obovate to rhomboid; mostly in Yucatan but scattered across the range of the species \_\_\_\_\_ *Quadrella incana* subsp. *yucatanensis*
  - 6. Sepals triangular, 1–1.5  $\times$  1–1.3 mm; staminal filaments ca. 4 mm; Mexico, in western Jalisco \_\_\_\_\_ *Quadrella incana* var. *triangularis*
- 1. Calyx with closed aestivation, sepals oblong, covering the petals in bud nearly to anthesis.
  - 8. Leaf blades narrowly oblong to oblong-lanceolate; petioles 1–5 mm; calyx valvate-reduplicate in flowerbud; southern Mexico \_\_\_\_\_ *Quadrella angustifolia*
  - 8. Leaf blades ovate to elliptic or slightly obovate; petioles 6–15 mm; calyx valvate but not reduplicate in flowerbud; West Indies.
    - 9. Stamens 8, filaments ca. 8 mm; gynophores 6–9 mm; Dominican Republic \_\_\_\_\_ *Quadrella alaineana*
    - 9. Stamens ca. 16, filaments 12–14 mm; gynophores 12–18 mm; eastern Cuba \_\_\_\_\_ *Quadrella singularis*

**1. *Quadrella alaineana*** Cornejo & Iltis, J. Bot. Res. Inst. Texas 4:75. 2010. TYPE: DOMINICAN REPUBLIC [Hisp.]. Azua: Monte Río Azua, sandy soil, in thickets, 22 Aug 1964 (fl), Bro. Basilio Augusto Lavastre 1730 (HOLOTYPE: JBSD; ISOTYPES: NY, WIS).

Endemic to the Dominican Republic (Cornejo & Iltis 2010).

**2. *Quadrella angustifolia*** (Kunth) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis angustifolia* Kunth, Nov. Gen. Sp. Pl. 5:46 t. 438. 1821. *Octanema angustifolia* (Kunth) Raf., Sylva Tellur. 112. 1838. *Colicodendron angustifolium* (Kunth) Hutch., Gen. Fl. Pl. 2:309. 1967. TYPE: MEXICO: "Crescit in Cañada de Sopilote, inter Mexico at Acapulco," Apr, A. Humboldt & A. Bonpland s.n. (LECTOTYPE, designated here, P).

*Quadrella angustifolia* is a rare, highly local endemic in two super arid desert pockets inland from the Pacific coast in the southern Mexican states of Michoacan and Guerrero. This species has xerophyllous, linear leaves and thick-walled, often tardily dehiscent siliquiform capsules, the latter a condition which induced Eichler (1865) to place it in *Capparis* subg. *Colicodendron*. The species is placed in *Quadrella* because of its calyx with closed reduplicate valvate aestivation and eight stamens. The capsules are similar to those of *Q. asperifolia* and *Q. indica* in subg. *Breyniastrum*, which suggests that our classification of *Quadrella* is somewhat arbitrary. Molecular biology is needed to understand the true relationships.

**3. *Quadrella domingensis*** (Spreng. ex DC.) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis domingensis* Spreng. ex DC. Prodr. 1:253. 1824. TYPE: Dominican Republic. Hispaniola: Santo Domingo, Azua, s.d., C. Bertero s.n. (HOLOTYPE: G-DC, ISOTYPES: BM, M).

**3a. *Quadrella domingensis*** (Spreng. ex DC.) Iltis & Cornejo subsp. *domingensis*

*Quadrella domingensis* subsp. *domingensis* is a local taxon on Hispaniola, with the type collection (fide Urban 1920–21) from Azua, Santo Domingo. It is characterized by having persistent, sharply pointed conical protuberances above the leaf blades (Rankin & Greuter 2004).

**3b. *Quadrella domingensis*** subsp. *grisebachii* (Eichler) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis grisebachii*



Eichler in Martius, Fl. Bras. 13:275. 1865. *Linnaeobreynia grisebachii* (Eichler) Hutch., Gen. Fl. Pl. 2:310. 1967. *Capparis domingensis* subsp. *grisebachii* (Eichler) R. Rankin in R. Rankin & Greuter, Willdenowia 34:263. 2004. TYPE: CUBA: "In Cuba Orientali," 1856–1857, C. Wright 9b (HOLOTYPE: G, G fragm. at WIS; ISOTYPES: BR, BR photo at WIS, GH p.p. [with C. Wright 1869], K, K photo at WIS).

*Quadrella domingensis* subsp. *grisebachii* is a local subspecies of Cuba and Hispaniola. It is characterized by having a dense but more brightly yellow pubescence than *Q. domingensis* subsp. *domingensis*, and mainly by the absence of the persistent, sharply pointed conical protuberances above the leaf blades (Rankin & Greuter 2004).

**4. *Quadrella ferruginea* (L.) Iltis & Cornejo, comb. nov.** BASIONYM: *Capparis ferruginea* L., Syst. Nat., ed. 10, 1071. 1759. *Linnaeobreynia ferruginea* (L.) Hutch., Gen. Fl. Pl. 2:310. 1967. TYPE: JAMAICA: P. Browne s.n. (LECTOTYPE, designated by Rankin & Greuter in Willdenowia 34:263. 2004; 664.6 [LINN]).

*Capparis octandra* Jacq., Select Stirp. Amer. Hist. 160 t. 100. 1763. TYPE: HISPANIOLA: "Habitat in Domingo ad Portum Principis in fruticosis maritimis" (lectotype, designated by Rankin & Greuter in Willdenowia 34:263. 2004; t. 100 in Jacquin 1763).

*Capparis comosa* Jacq., Select Stirp. Amer. Hist. 160. 1763. *Pleuteron comosa* (Jacq.) Raf., Sylva Tellur. 109. 1838. *Uterveria comosa* (Jacq.) Bertoloni, Pl. nov. H. Bonon. 2:9. 1839. TYPE: HISPANIOLA. SANTO DOMINGO: "Habitat passim in inundatis maritimis Jaquesi in Domingo" (LECTOTYPE, not designated).

**4a. *Quadrella ferruginea* (L.) Iltis & Cornejo subsp. *ferruginea***

*Quadrella ferruginea* subsp. *ferruginea* is a common subspecies of Jamaica. The lanceolate leaf blades and linear-triangular sepals characterize this subspecies (Rankin & Greuter 2004).

**4b. *Quadrella ferruginea* subsp. *cubensis* (R. Rankin) Iltis & Cornejo, comb. nov.** BASIONYM: *Capparis ferruginea* L. subsp. *cubensis* R. Rankin, Willdenowia 34:263, 2004. TYPE: CUBA. CAMAGÜEY: "Nuevitas, falda sur de la Península Pastelillo," 11 May 1976, Areces et al. HFC 31382 (HOLOTYPE: HAJB; ISOTYPES: B, JE).

*Quadrella ferruginea* subsp. *cubensis* is a local endemic of eastern Cuba. It is characterized by the spatulate-lanceolate leaf blades and triangular sepals (Rankin & Greuter 2004: 274).

**5. *Quadrella incana* (Kunth) Iltis & Cornejo, Novon 17:452. 2007.** BASIONYM: *Capparis incana* Kunth, Nov. Gen. & Sp. 5:94. 1821. *Octanema incana* (Kunth) Raf., Sylva Tellur. 112. 1838. *Linnaeobreynia incana* (Kunth) Hutch., Gen. Fl. Pl. 2:310. 1967. TYPE: MEXICO. GUERRERO: "Crescit in declivitate occidentali montium Mexicanorum, inter Mescala et Estola, 300 m," Apr. A. Humboldt & A. Bonpland s.n. (LECTOTYPE: P, designated in Iltis & Cornejo 2007a; ISOTYPE: B–W 10,045, B–W photo 9479 at WIS).

*Capparis karwinskiana* Schlechter, Linnaea 10:237. 1836. TYPE: MEXICO: San Bartolo, 1830, W.F. Karwinski s.n. (HOLOTYPE: M; ISOTYPE: BR, BR photo at WIS).

*Quadrella incana* is the only species of subg. *Intutis* in the Mesoamerican flora. Except for its variable leaf shape, *Quadrella incana* is a rather uniform species as for flowers and fruits. It can be identified by its white cream cochleate-reniform embryo surrounded by a hard brittle testa, the leaves with fewer (3 to 8) lateral veins and the rusty stellate pubescence of the young buds.

**5a. *Quadrella incana* (Kunth) Iltis & Cornejo subsp. *incana***

*Quadrella incana* subsp. *incana* is widespread from Texas, eastern and southwestern Mexico to Guatemala (Contreras 11084) and barely into Honduras (Molina & Molina 26028) (Iltis & Cornejo 2007a).

**5b. *Quadrella incana* var. *triangularis* Cornejo & Iltis, J. Bot. Res. Ins. Texas 4:80. 2010.** TYPE: MEXICO. JALISCO: ca. 8 km NW of Chamela, 19°33'N 105°08'W, 2 m, 22 Jun 1984, H.H. Iltis & S. Wisniewski 29194 (HOLOTYPE: WIS; ISOTYPE: MEXU).

*Quadrella incana* var. *triangularis* is known by only two collections from Chamela (Mexico, Jalisco). The distinctive smaller (1–1.5 × 1–1.3), triangular sepals and smaller filaments (ca. 4 mm), characterize this variety (Cornejo & Iltis 2010).

**5c. *Quadrella incana* subsp. *yucatanensis* (Lundell) Iltis, J. Bot. Res. Ins. Texas 4:83. 2010.** BASIONYM: *Capparis yucatanensis* Lundell, Bull. Torrey Bot. Club 69:389. 1942. TYPE: MEXICO [Yucatán]: Chichen Itzá, off Kaua road, 8 Jun 1938 (fr), C. Lundell & A. Lundell 7452 (HOLOTYPE: MICH; ISOTYPES: DS, F [not seen], GH, LL-TEX [2], NY, US).

*Quadrella incana* subsp. *yucatanensis* is most commonly represented in specimens from the Yucatan Pen-



insula, but scattered beyond, throughout much of the range of *Q. incana*. It is characterized by its broadly obovate to rhomboid leaves.

**6. *Quadrella singularis*** (R. Rankin) Iltis & Cornejo, comb. nov. BASIONYM: *Capparis singularis* R. Rankin, Willdenowia 34:263. 2004. TYPE: CUBA. GUANTÁNAMO: U.S. Naval Base, Guantánamo Bay, windward side, Cuzco Beach, 19°58'23.4"N 75°08'45.1"W, 3 Dec 1996, Areces et al. 6496 (HOLOTYPE: MNHN; ISOTYPE: MAPR).

*Quadrella singularis* is a rare endemic of eastern Cuba, known only from the type specimen. Although the flower buds of *Quadrella singularis* are unknown, this species is placed in *Quadrella* subg. *Intutis* because the stellate pubescence. The similar length of its sepals and petals (7 and 7 to 8 mm, respectively), suggest that "the sepals appear to tend to the valvate condition" (Rankin & Greuter 2004).

#### REJECTED NAMES

*Quadrella crotonoides* (Kunth) J. Presl, in Berchtold & J. Presl, Prir. Rostlin 2:260. 1825 (= *Capparicordis crotonoides* [Kunth] Iltis & Cornejo).

*Quadrella sidaefolia* (Ruiz & Pavon ex DC.) J. Presl, in Berchtold & J. Presl, Prir. Rostlin 2:260. 1825 (= *Capparicordis crotonoides* [Kunth] Iltis & Cornejo).

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