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WERNER GREUTER[1] & ROSA RANKIN RODRÍGUEZ[2]

Notes on some endemic Cuban species of *Ruelliinae (Acanthaceae)*, on their seeds, pollen morphology and hygroscopic features

Abstract

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Ruellia shaferiana, a seldom collected and incompletely known species, is described in detail and compared with two vegetatively similar Cuban endemics, *Dyschoriste bayatensis* and the recently described *Hygrophila urquiolae,* and with the two Cuban species of *Apassalus (A. cubensis* and *A. parvulus).* All are placed by Scotland and Vollesen, in their classification of *Acanthaceae,* in the newly circumscribed subtribe *Ruelliinae.* Contrary to *Dyschoriste,* the other taxa studied have anther thecae that lack basal awns. Absence of these awns is the single character distinguishing *Apassalus* from *Dyschoriste,* and it has been suggested that both be combined. Our results lend support to that suggestion and prompt the transfer of *A. parvulus* to *Dyschoriste*. Study of pollen by SEM confirms the generic placement of the species studied, again associating *Apassalus* with *Dyschoriste.* Seed indumentum was studied by LM and REM, complementing earlier studies of the remarkable hygroscopic mucilaginous hairs, which apparently characterise the subtribe. Hygrochastic capsule dehiscence was detected in all four species. Pre-dawn anthesis and flowers withering by noon were observed in *R. shaferiana*. *H. urquiolae,* only known from a small area in W Cuba, is newly reported from E Cuba, and conversely, W Cuban occurrences of *R. shaferiana* are put on record. For three of the names lectotypes are designated, as Urban's original material was destroyed in Berlin in World War II.

Additional key words: *Apassalus, Dyschoriste bayatensis, Dyschoriste parvula, Hygrophila urquiolae, Ruellia shaferiana,* mucilage, bionics, hygrochasy, pre-dawn anthesis

Introduction

When describing a new Cuban species of *Hygrophila* R. Br., *H. urquiolae* Greuter & al. (2010), we pointed out that tropical and subtropical wetland habitats, those of Cuba in particular, had been relatively neglected by botanists. We might have added that this is particularly true of *Acanthaceae* Juss. Indeed, we were then already working on another member of this family that appeared to present special interest. We had first collected that plant in 2000, and earlier this year (February 2010) we were able to study it again in the living state. It turned out to be *Ruellia shaferiana* Urb., an incompletely known and seldom collected Cuban endemic, superficially similar to *Dyschoriste bayatensis* (Urb.) Urb. and of which we are offering a new, detailed description here.

Our paper will focus on the study of some scarcely collected, presumably rare, Cuban endemic species: the three already mentioned plus two currently placed in *Apassalus* Kobuski: *A. cubensis* (Urb.) Kobuski and *A. parvulus* Alain & Leonard. They are currently placed in four different genera, but it is debatable whether *Apassalus* is distinct or should rather, as has been suggested, be merged in *Dyschoriste* Nees. By our observations we hope, among other things, to help answering that question. Among the aspects studied are seed indumentum, pollen morphology and capsule dehiscence.

Seeds. — Seed hairs of *Acanthaceae* were first described in considerable detail by Kippist (1842) and again stud-

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ied by Schaffnit (1906) and Oehm (1932), who, taken together, provide a pretty good coverage of the family. In recent studies these structures were by and large neglected, even though they appear to be of taxonomic value, as we hope to demonstrate. The seed hairs found in many representatives of the *Ruelliinae* Nees can be characterised as follows. They are slender, very numerous, covering the whole seed or only its marginal portion, and almost invariably present spiral or annular wall thickenings, or both. In the dry seed they cannot be discerned as discrete structures even under the microscope, appearing to be glued down as by a varnish to form a compact layer on the testa. Instantly upon contact with water the hairs are set free from their former confinement, to form a dense spreading pelt. At the same time a mucilaginous substance is released, which upon drying will attach the seed firmly to the substratum. All species studied here present such mucilage hairs (Fig. 2–3).

Pollen morphology. — *Acanthaceae* pollen is extremely diverse and the morphology of pollen grains has been used for the purpose of classification ever since Radlkofer's (1883) and Lindau's (1893) seminal work. Raj's (1961) extensive study of *Acanthaceae* pollen makes reference to two of the species here treated. More recently, scanning electron microscopy (SEM) has much improved our knowledge of the subject, as evidenced by excellent photographs in many recent papers (e.g. Daniel 1998; Scotland & Vollesen 2000).

Hygroscopic features. — The most visible function of hygroscopy in *Acanthaceae* (only the *Acanthoideae,* not the two other subfamilies) is expressed in their explosive capsules, which, assisted by the peculiar structures known as retinacula (or "jaculators", as proposed by Lindau (1895) for semantic reasons; Sell (1969) prefers the neutral term "hooks"), disseminate the seeds in the surroundings of the mother plant. One tends to assume that the capsules tear open when drying (xerochasy), but Bremekamp (1926) came to the contrary conclusion, that acanthoid capsules open hygrochastically. He discovered that hygrochasy is so to say a phenomenon superimposed on xerochasy, insofar as first a tension must build up in the fruit as a result of desiccation, only then can wetting of the capsule beak, which holds the capsule halves together, trigger the release. Bremekamp was wrong, however, when he generalised his findings to the whole family (according to Sell (1969), he had been studying a single species, *Ruellia tuberosa* L.). Sell proved that xerochastic capsules are the usual condition in *Acanthaceae,* from which hygrochasy has evolved at least twice and probably repeatedly and/or reversibly. In hygrochastic *Ruelliinae* species (some of *Ruellia* L., *Hygrophila* and *Phaulopsis* Willd.), an apical cap of lignified cells clamps the capsule halves together and imbibition of two subapical tissue pads with pectinised cell walls triggers the release. In hygrochastic species of *Barleriinae* Nees (*Barleria* L., *Crabbea* Harv.) and *Acantheae* Dumort. (*Blepharis* Juss., *Crossandra* Salisb.), it is the apical cap that has pectinised cell walls that lose cohesion when wetted. Subsequent studies in *Acanthaceae* have paid scant attention to the conditions, wet or dry, triggering capsule dehiscence.

Systematics. — Due to recent, including molecular, studies, the classification of *Acanthaceae* is undergoing considerable change. The traditional subdivision of the family goes back to the pioneer work of Nees (1847), modified by Bentham (1876) then Lindau (1895), and is artificial to a considerable degree. Bremekamp (1965), whose main experience was with the palaeotropical groups, proposed a new classification, which, however, failed to gain general acceptance. For our purpose we adopt the recent rearrangement by Scotland & Vollesen (2000) as the best currently available system of classification. According to it, the 23 *Acanthaceae* genera recognised for Cuba by Alain (1957), reduced to 21 under Scotland & Vollesen's (2000) criteria (they include *Phidiasia* Urb. in *Odontonema* Nees and *Drejerella* Lindau in *Justicia* L.), represent all recognised subdivisions of *Acanthaceae:* the three subfamilies, but very unevenly (*Thunbergioideae* Kostel. by *Thunbergia* Retz., widely naturalised; *Nelsonioideae* Lindl. by *Elytraria* Michx.; *Acanthoideae* Kostel. by the remaining 19 genera); both tribes of the latter (*Acantheae* with *Stenandrium* Nees; *Ruellieae* Dumort., 18 genera); and the four *Ruellieae* subtribes: *Andrographinae* Nees with *Andrographis* Nees; *Barleriinae* with *Teliostachya* Nees (now *Lepidagathis* Willd.) and *Barleriola* Oerst.; *Justiciinae* Nees and *Ruelliinae* with eight and seven genera, respectively.

The subtribe *Ruelliinae,* with which this paper is concerned, is characterised by contorted aestivation of the corolla lobes and by the four didynamous stamens being connate pairwise. It is by and large congruent with Lindau's (1895) unranked subdivision *"Retortae",* comprising six of its seven tribes (*Barlerieae* Nees being excluded). The seven *Ruelliinae* genera present on Cuba are: *Bravaisia* DC., *Blechum* P. Browne, *Apassalus, Dyschoriste, Ruellia, Hygrophila* and the naturalised *Eranthemum* L. We will focus on the four to which our target species belong, which we shall briefly introduce.

Dyschoriste is a pantropical genus of perhaps 50 or 60 species (Wasshausen & Wood 2004; Furness 1995). The New World representatives were monographed by Kobuski (1928b), who recognised 40 species, to which those from Asia and Africa must be added. The generic name is typified by an Old World element. If the American species were treated as generically distinct (which no one presently does), they would have to be placed in *Calophanes* D. Don. The genus is characterised by the presence of a mucro or awn-like process at the base of the anther thecae (the other genera lack such a process, except sometimes *Hygrophila,* in which the thecae may be "mucronulate", Wasshausen 2005). The corolla limb

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is (almost) regular to (slightly) bilabiate. The capsule has a short sterile stipe and is spindle-shaped. Seed number is (2–)4. Chromosome counts are available for five species (Anonymous 2010) and indicate a consistent basic chromosome number of $x = 15$ at the diploid or tetraploid level.

Mucilaginous seed hairs have been described by Kippist (1842) for *Dyschoriste erecta* (Burm. f.) Kuntze (as *D. cernua* Nees) and *D. litoralis* Nees, by Schaffnit (1906) for *D. linearis* (Torrey & A. Gray) Kuntze (as *Calophanes linearis* (Torrey & A. Gray) A. Gray) and by Oehm (1932) for *D. microphylla* (Cav.) Kuntze (as *C. jasminum-mexicanum* Nees) and *D. nagchana* (Nees) Bennet (as *C. fasciculiflora* (Fenzl ex Sond.) Martelli). The hairs cover the whole seed surface, which is described as dull when dry, and have annular and/or spiral thickenings. Hairs limited to the thickened seed margin were reported by Stopp (1958) for the S African *D. depressa* (L. f.) Nees and other (unspecified) species from that area.

The pollen of 34 species (including the three previously placed in *Chaetacanthus* Nees) was studied by Furness (1995): grains prolate spheroidal to prolate, 3-colporate, with a variable number of prominent longitudinal, microechinate exine ribs separated by pseudocolpi; the colpi are shorter than most pseudocolpi and the rib sides bordering the aperture bulge up on either side to form an atrium around the ± circular endopore (Scotland 1993: fig. 42; Furness 1995: pl. I–V; Daniel 1998: fig. 4A–C). This pollen type is remarkably uniform (Furness distinguishes seven subtypes based on pseudocolpi number) and, disregarding one anomalous sample, diagnostic for the genus.

In Cuba *Dyschoriste* (when kept separate from *Apassalus*) is represented by the single *D. bayatensis,* which was not included by Kobuski (1928b) in his revision, because it had been described in *Hygrophila* and not yet transferred to *Dyschoriste* at the time.

Apassalus was established by Kobuski (1928a) as a genus of three species segregated from *Dyschoriste: A. diffusus* (Nees) Kobuski endemic to Hispaniola (providing the type), Cuban *A. cubensis* (Urb.) Kobuski and *A. humistratus* (Michx.) Kobuski of the SE United States. Subsequently, a second Cuban species was described, *A. parvulus* (Alain 1956). The genus is characterised by creeping habit, the small size of all parts of the plants and principally the fact that the base of the anther thecae is not mucronate but rounded. The corolla limb is almost regular. The capsule has a short sterile stipe and is spindle-shaped. The seeds are 2 or 4 per capsule. Chromosome number is $2n = 30$ in *A. humistratus* (Hilsebeck 1976). The seed hairs had not so far been described and the pollen is only known through the brief characterisation of *D. cubensis* by Raj (1961).

The taxonomic status of *Apassalus* is controversial. Long (1970: 295) writes: "The absence of anther appendages appears to be the only consistent character for the genus [*Apassalus*], and this hardly warrants recognition of a new genus in the *Acanthaceae*". Alain (1995) accepts Long's opinion. On the other hand, Scotland & Vollesen (2000) maintain *Apassalus*. Current usage, as documented by Web-based treatments, is split, with e.g. Wasshausen (2010) maintaining *Apassalus* but Wunderlin & Hansen (2010) merging it under *Dyschoriste*.

Hygrophila is pantropical, comprising 20–30 species (Wasshausen 2005; Mabberley 2008) rather than the previously estimated 100 (Mabberley 1987). The nomenclatural type, provided by *Ruellia ringens* L., is an Old World element. *Hygrophila* species consistently have a bilabiate corolla limb, often strongly so. The anther thecae have a blunt base or may be mucronulate (Wasshausen 2005). Seed number (4–32 per capsule) varies but is usually high. The capsule shape is ± cylindrical, with a truncate base not narrowed into a sterile portion. Chromosome counts are available for seven species (Anonymous 2010) and indicate a prevalent basic number of $x = 16$ at the diploid or tetraploid level, but $x = 6$, 11 (or 22) and 12 have also been reported.

Mucilaginous seed hairs have been described by Kippist (1842) for five species and by Schaffnit (1906) for 14 species (including one he placed in *Cardanthera* Buch.-Ham. ex Benth. and another one in *Nomaphila* Blume). The hairs cover the whole seed surface, which when dry is said to have a silky sheen, and have annular and/or spiral thickenings. Kippist mentions a single species, *H. polysperma* (Roxb.) T. Anderson (as *Hemiadelphis polysperma* (Roxb.) Nees), among those with seed hairs lacking mucilage and devoid of thickenings, but verification of this assessment is desirable.

The pollen (Scotland 1993: fig. 9–11; Scotland & Vollesen 2000: fig. 9A–B [same images with different species identities]; Furness 1994: pl. I–III) has been described in some detail, for 34 species, by Furness (1994). *Hygrophila* and the closely related *Brillantaisia* P. Beauv. share a unique general pollen morphology: suboblate to prolate spheroidal, 4-colporate grains with a distinctive pattern of raised longitudinal exine ribs separated by the colpi and interjacent pseudocolpi. The apertures are usually equatorial, but opposite pairs are sometimes ± shifted toward opposed poles. The general pattern is reminiscent of that found in *Dyschoriste* (see above) but differs in aperture number, in colpi which are not shorter than average pseudocolpi, and in the absence of exine bulges collateral to the pores. Exine sculpture also differs, but is variable in *Hygrophila* and was used by Furness (1994) to define several different pollen types.

According to Sell (1969), *Hygrophila auriculata* (Schumach.) Heine (as *spinosa* T. Anderson; a widespread palaeotropical species) has hygrochastic but a majority of its congeners has xerochastic fruits.

In Cuba the genus is represented by *Hygrophila costata* Nees & T. Nees, a widespread and variable American species also known under numerous synonyms, and *H. urquiolae*.

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Ruellia, with its 250 or perhaps 300 species (Wasshausen & Wood 2004; McDade & Tripp 2007), is the second largest genus in the family after *Justicia.* It is also pantropical in distribution but is based on a New World nomenclatural type, provided by *R. tuberosa* L. As currently defined, *Ruellia* encompasses at least 21 generic synonyms, which is a good indication of its polymorphism. Ezcurra's (1993) revision of the southern South American species, even though limited in geographical coverage, conveys a fair impression of that variability. Typically the corolla is large and showy, often vividly coloured, and its limb is usually ± regular but sometimes distinctly bilabiate. The anther thecae are rounded at both ends, lacking a basal mucro. Seed number (2–26) varies but is typically high. The capsule is ± spindle-shaped, being narrowed at the base into a sterile, solid stipe of variable length, but *R. tuberosa* and its relatives (i.e. *Ruellia* in the strict sense) have cylindrical, many-seeded, non-stipitate capsules (Long 1973). Chromosome counts are available for c. 40 species (Anonymous 2010) and indicate a prevalent basic number of $x = 17$, rarely 16 or (11–)12, almost invariably at the diploid level.

Mucilaginous seed hairs have been described by Kippist (1842) for many, mostly unspecified species, and three named ones he placed in *Dipteracanthus* Nees; and by Schaffnit (1906) for 13 species. Variability is greater than in the other genera. The hairs usually cover the whole seed surface, but in several species (including the three that Kippist placed in *Dipteracanthus,* said to have narrowly winged seeds, plus *Ruellia ochroleuca* Mart. ex Nees, *R. rubicaulis* Cav. and *R. solitaria* Vell. mentioned by Schaffnit), they are confined to the margin. The annular and spiral wall thickenings are usually well developed but may be weak or absent. Finally, in two of the species studied by Schaffnit (1906: 460–461), *R. elegans* Poir. (*R. formosa* "Andrews") and *R. squarrosa* (Fenzl) Schaffnit, the hairs are replaced by mucilage cells closely resembling those found in *Blechum.*

The pollen of *Ruellia* and its close relatives differs conspicuously from that of the preceding three genera. According to Lindau's (1895) classification, it belongs to the category of honeycomb pollen ("Wabenpollen"), whereas *Dyschoriste, Hygrophila* and, by implication, *Apassalus* have ribbed pollen ("Rippenpollen"). The pollen grains of *Ruellia* are spheroidal, lacking obvious polarity, 3(–5)-porate or 3-colporate to poly-pantoporate. With minor exceptions (neglected here) they are surrounded by a coarse net of high exine structures best described as "reticulate handrails" supported by robust, simple or branched columellae. Good examples can be seen in Long (1973: fig. 6–11), Ezcurra (1993: fig. 4), Scotland (1993: fig. 21–24) and Furness & Grant (1996: fig. 13–36).

Sell (1969) mentions hygrochastic capsules for *Ruellia tuberosa* (Neotropics, including Cuba), *R. ciliatiflora* Hook. (as *R. lorentziana* Griseb.; South America) and *R. prostrata* T. Anderson non Poir. (Africa), and xerochastic fruits for an equal number of other species.

Alain (1957) reports 10 *Ruellia* species from Cuba, which number, if one follows Ezcurra & Daniel (2007) in synonymising *R. tweedieana* Griseb. with *R. simplex* C. Wright, is reduced to 9 (but see Ward 2007). Under Bremekamp's generic concept, as outlined by Long (1973), only two of them would remain in *Ruellia: R. tuberosa* and *R. nudiflora* (Engelm. & A. Gray) Urb.; a third, *R. geminiflora* Kunth, provides the type of *Ulleria* Bremek.; whereas the "microgeneric" placement of the remaining 6, including *R. shaferiana,* is unsettled. If, on the contrary, one accepts the recent synthetic, molecule-based approach by Tripp (2007) and Tripp & al. (2008), one must add *Ruellia blechum* L. (formerly *Blechum pyramidatum* (Lam.) Urb. and *B. blechioides* (Sw.) Hitchc.) to the count.

In the present paper, we propose to (1) present and compare the five target species, their known distribution and habitat, based on available herbarium material, adding a detailed morphological description of *Ruellia shaferiana,* a seldom collected and incompletely known species; (2) study the seeds, with emphasis on mucilaginous hairs; (3) perform an REM-based study of the pollen; and (4) discuss hygroscopic features, capsule dehiscence in particular, and other traits potentially relevant to reproductive biology, such as daily flowering rhythm.

Material and methods

Plant material collected by us has been deposited in the herbaria B, HAJB, HIPC, JE and PAL-Gr (in due course, available duplicates will be distributed to further herbaria). Specimens kept in the herbaria B, HAC, HAJB, HIPC, JE and S, as well as digital photographs from FLAS, FSU, NY, S and USF, have been studied for comparison.

For *Ruellia shaferiana* and *Hygrophila urquiolae,* morphological details of the flowers were observed on FAA-fixed material. Details of flowers of live plants were documented with the aid of a Canon digital camera IXUS 9515. In *R. shaferiana,* diurnal flowering rhythm was observed, on three consecutive days, on cut branches kept in a vase.

Seeds were obtained from herbarium specimens, wetted in plain water and observed in incident light under a stereomicroscope WILD M5A. Seed and other close-up photographs were taken with a digital camera Leica DFC 290.

Pollen was extracted from FAA-fixed buds *(Ruellia shaferiana* and *Hygrophila urquiolae)* or sampled on herbarium material *(Dyschoriste bayatensis, Apassalus parvulus)*, then acetolysed following the standard procedure described by Erdtman (1960). When the pollen sample was scant, it was not centrifuged after acetolysis but concentrated manually in a watch glass, and the solvent pipetted off, as described by Leuenberger (1976).

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For scanning electron microscopy (SEM), pollen and seeds were coated with a 20 nm layer of gold-palladium in a Low Voltage Cool Sputter Coater EMITECH K 550, at 20 mA under a vacuum of c. 0.2 mbar. They were studied, partly under a FEI Quanta 200 SEM at the Department of Zoology and partly under a Zeiss LEO 430 SEM at the Department of Systematic Botany, Free University of Berlin.

Results

Dyschoriste bayatensis (Urb.) Urb. in Ark. Bot. 24A (4): 35. 1932 ≡ *Hygrophila bayatensis* Urb., Symb. Antill. 9: 127. 1923. – Holotype: Cuba, "Prov. Oriente, prope Bayate in fruticetis densis ad marginem Savanna Miranda, solum hic observata!, 22.3.1917, *Ekman 8566* (?B†); lectotype (designated here): S [photo], isolectotypes: F 47389F [photo], NY 1185563 [photo], US 955934 [photo]).

Morphology. — We refer to the full original description of Urban (1923) for details. Important diagnostic features, as verified by us, are summarised in Table 1.

Additional specimens seen. — Cuba: [Prov. & Munic. Camagüey]: Caminos al sur de C. Camagüey, 20.12.1925, *Acuña 13797* (HAC). – [Prov. Granma, Munic. Bayamo]: Bayamo, in thickets at Rio Bayamo, 23.1.1923, *Ekman 16196* (S [n.v.]); [Munic. Guisa]: Guisa, in living fences along the road, a Spreizklimmer up to 2 m, fl. pale lila, 3.1.1923, *Ekman 16061* (HAC, NY 1185564 [photo], S [photo]); Guisa, 3.1.1923, *Ekman* [*16061*] ex Herb. Cañizares 15a (HAJB). – [Prov. Santiago de Cuba, Munic. Mella]: Prope Bayate in fruticetis densis ad marginem Savanna Miranda rara, 5.2.1915, *Ekman 4549* (S [photo], NY 1185565 [photo]); Bayate, Sabana Miranda, in thickets, 30.10.1922, *Ekman 15595* (S [n.v.]); same data, 8.12.1922, *Ekman 15849* (S [photo], NY 1185566 [photo]); en Bayate, 3.12.1922, *Ekman* [*15849*] ex herb. Cañizares 15 (HAJB); en Sabana Miranda, s.d., *Ekman* ex herb. Cañizares 15b (HAJB).

Distribution. — According to Alain (1957), *Dyschoriste bayatensis* occurs in E Cuba, the Camagüey Province in Central Cuba and the neighbouring island of Hispaniola, but the latter indication is definitely erroneous, as Alain (1995) himself does not mention the species in his Flora of Hispaniola. The main area of the species is in the Cauto river basin in E Cuba, from where six gatherings exist, all made by the Swedish collector Ekman in three localities between 1915 and 1923: near Bayate (the locus classicus), Bayamo and Guisa. Alain's record from Camagüey is based on a single specimen, collected by Acuña, which we have studied and found not to deviate in any significant detail from the E Cuban plants. – Fig. 1.

Habitat. — Thickets and fences, scrub margins, occasionally a straggling climber; lowland below 200 m of altitude.

Seeds. — There are normally 4 seeds per capsule. They are lenticular-compressed, broadly elliptic in outline, with blunt wingless margins, measuring c. 2×1.4 mm. The dry seeds (Fig. 2A) are covered by a light-grey, silky layer of tightly packed, parallel, antrorsely appressed hairs that are discernible only towards the distal end, where the densely set annular thickenings of the cell wall become evident. When wetted, the hairs immediately spread and surround the seed as a dense down, releasing mucilaginous matter which, in water, can be seen as a milky, unstructured cloud (Fig. 2B). The mucilage hairs are 0.4–0.5 mm long, erecto-patent except at the seed base.

Pollen morphology. — The pollen grains (Fig. 4) are typical for the genus: subprolate 3-colporate "Rippenpollen" with equatorial pori. Average dimensions (polar axis, equatorial diameter and their ratio) are: P=42.5 (40.6–44.7) µm, E=35.5 (33.6–37.6) µm, P/E=1.19 (1.11–1.29). The pseudocolpi are fairly variable in number (6–8 per intercolpium) and often somewhat irregular in size (both length and width), which places our species in "subtype *e*" as defined by Furness (1995), together with a number of Old World (predominantly African) species. However,

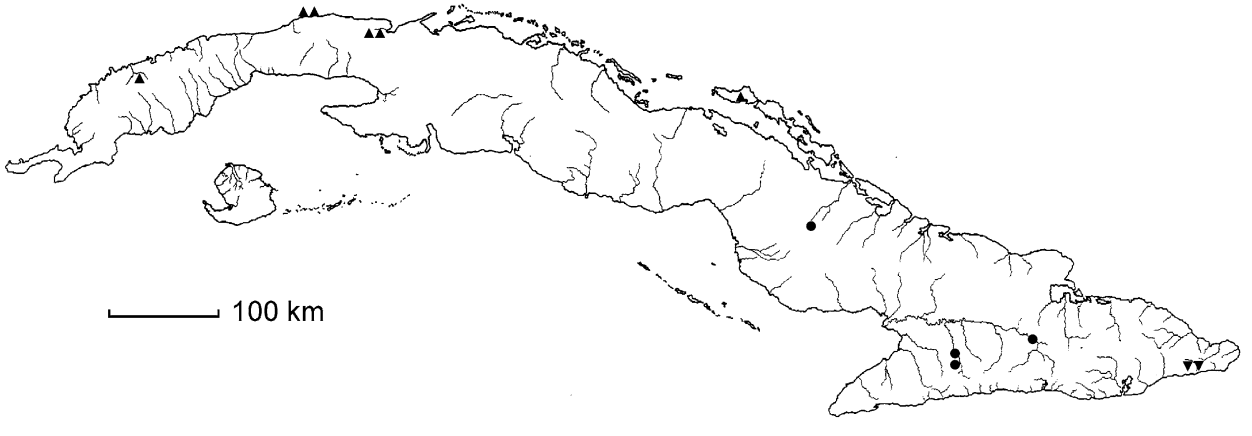


Fig. 1. Known distribution of *Dyschoriste bayatensis* (●), *Apassalus cubensis* (▲) and *A. parvulus* (▼).

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Furness' subtypes are but an artificial, arbitrary classification device. The colpi are small and narrow, so that the pore appears to open in the centre of one medially split twin rib (Fig. 4A, C). The exine lips on either side of each circular endopore are well developed, regular, protruding above the surface by c. 2 µm, and occasional fractured pollen (Fig. 4D) shows that they enclose a distinct atrium. The tectum is densely and regularly microgranulate (granule size: 0.2–0.8 µm), otherwise compact, with no apparent reticulum and hardly any microperforations (Fig. 4B). Raj (1961: 30, under *Hygrophila*) gives a detailed description of the exine structure, based on light microscopic study of sectioned pollen grains, but his measurements are slightly at variance with ours.

Hygroscopic features. — Exposing apparently mature capsules of herbarium specimens to the vapour of boiling water did not suffice to trigger dehiscence. The capsule surface, including the tip, is water repellent. Nevertheless, when a water droplet was placed atop a capsule tip, the capsule after c. 5 minutes opened explosively and ejected two of its seeds to some distance (5–10 cm). The open capsules are eventually shed from an abscission layer at their base, and when this happens the void calyx segments, in their distal half, curve slightly but perceptibly inward. This is a reversible hygroscopic movement: when wetted, the calyx segments straighten within a matter of minutes to diverge stellately from above the base. (All observations were made on the specimen *Ekman* ex herb. Cañizares 15a, HAJB).

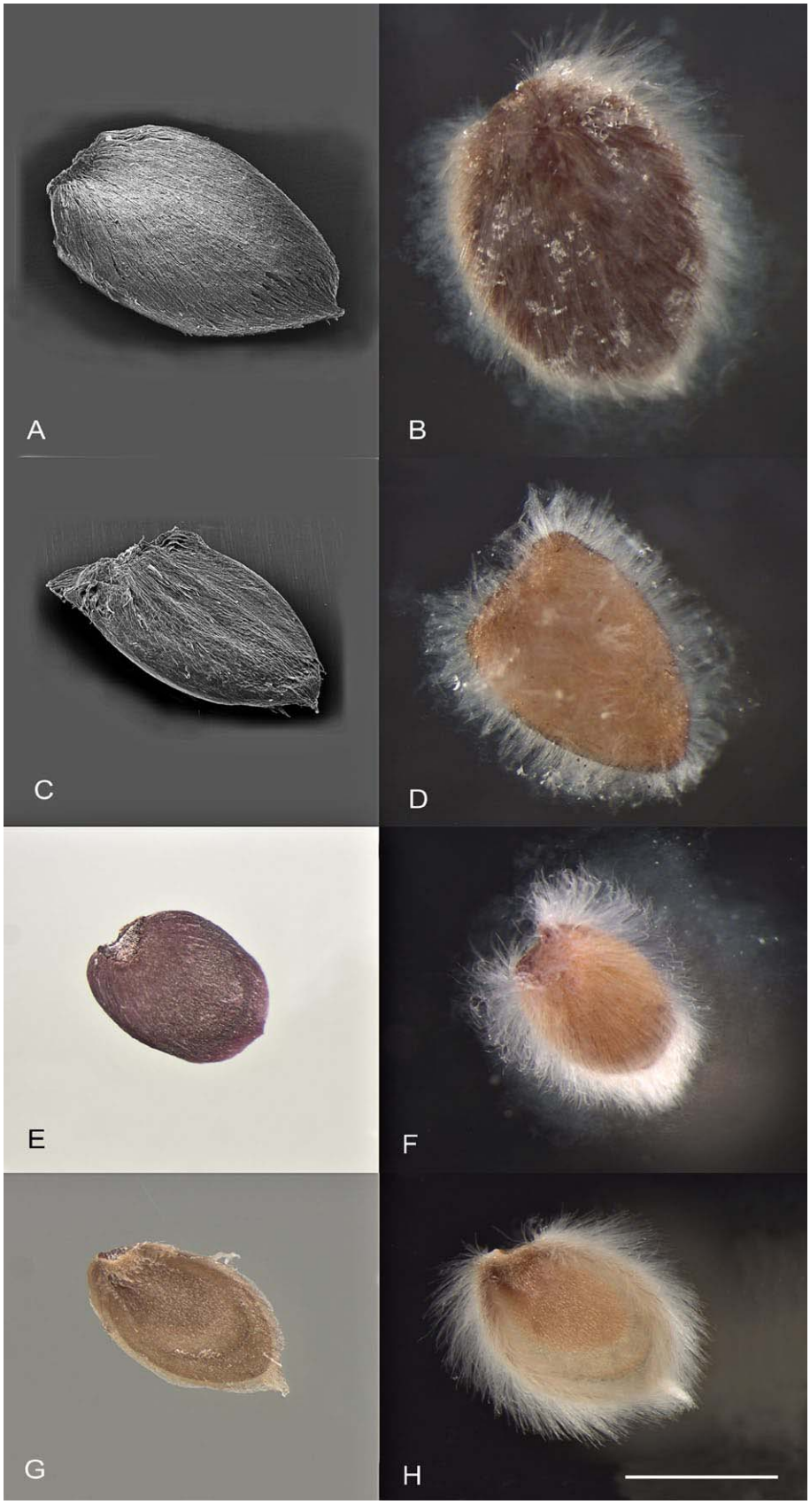


Fig. 2. SEM (A, C) or incident light photographs (B, D–H) of dry (left) and wetted (right) seeds – A–B: *Dyschoriste bayatensis* (*Ekman* [*16061*]); C–D: *Apassalus parvulus (HFC 46906)*; E–F: *Hygrophila urquiolae (Greuter & al. 26662)*; G–H: *Ruellia shaferiana* (*Greuter & al. 25199)*. – Scale bar = 1 mm.

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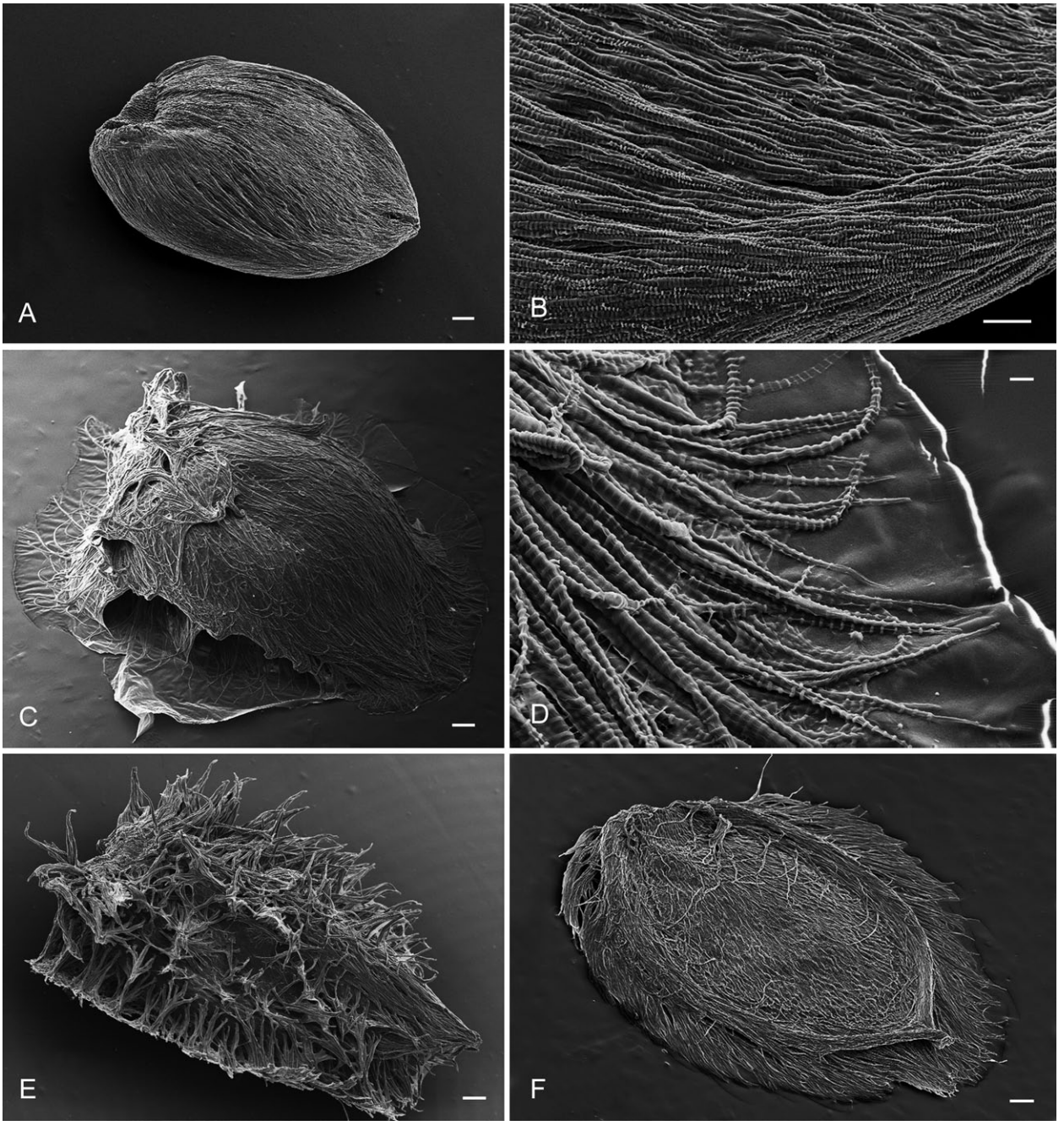


Fig. 3. SEM photographs of dry (A–B) and once-wet (C–F) seeds – A–D: *Hygrophila urquiolae (Greuter & al. 26662)*; E: *Apassalus parvulus (HFC 46906)*; F: *Ruellia shaferiana (Greuter & al. 25199)*. – Scale bars: A, C, E–F = 100 µm, B = 50 µm; D = 10 µm.

Apassalus cubensis (Urb.) Kobuski in Ann. Missouri Bot. Gard. 15: 2. 1928 ≡ *Dyschoriste cubensis* Urb., Symb. Antill. 7: 381. 1912. – Holotype: [Cuba, Prov. Ciudad de la Habana, Munic. Habana del Este], Cojimar, 14.3.1906, *Baker 2894* (?B†); lectotype (designated here): NY 114981 [photo]; isolectotype: HAJB ex herb. Canizares).

Apassalus parvulus Alain & Leonard in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 15: 20. 1956. – Holotype: [Cuba, Prov. Guantánamo, Munic. Imías], subida al Puntón del Cuero, Imías, 11.1.1956, *Alain & Morton 4991* (HAC); isotypes: Puntón del Cuero, Imías, 11.1.1956, *Alain A-4991* (HAC); el Puntón del Cuero, Via Azul, 11.1.1956, *Alain, Morton & López Figueras A-4991* (HAC).

Morphology. — We refer to the full descriptions of Urban (1912), Kobuski (1928a) and Alain (1956) for details. Important diagnostic features, as verified by us, are summarised in Table 1. Pubescence is very variable in density and length. The square stems are often shortly pubescent on two opposite faces (those corresponding to the leaf axils of the proximal node) and glabrous on the two others.

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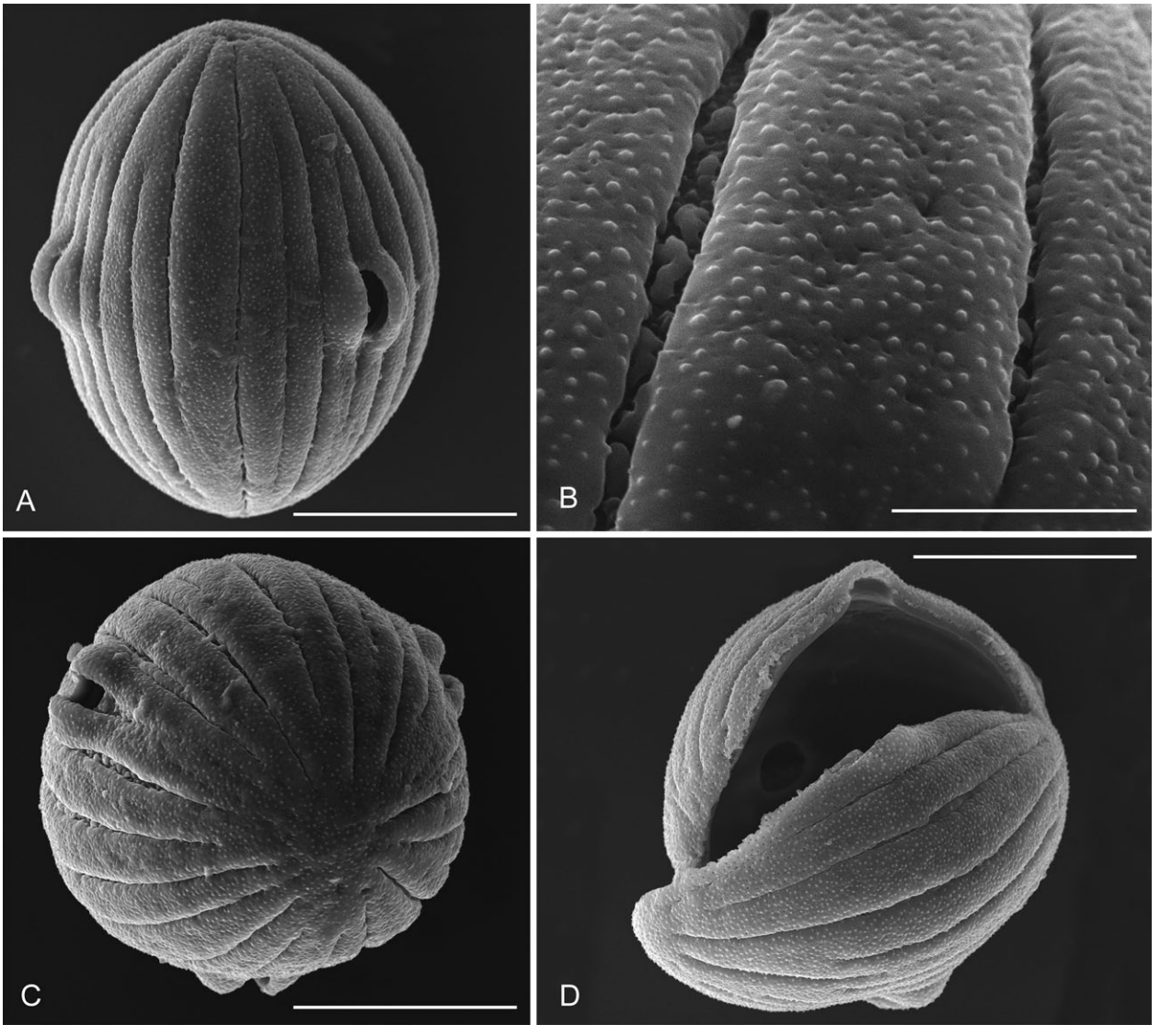


Fig. 4. Pollen of *Dyschoriste bayatensis* (*Ekman* [*16061*]), SEM micrographs – A: equatorial view; B: id., detail of exine ribs and pseudocolpi; C: subpolar view; D: fractured grain, showing atrium formation and, from within, circular endopore. – Scale bars: A, C–D = 20 µm; B = 5 µm.

Additional specimens seen. — ***Apassalus cubensis:*** Cuba: Prov. Pinar del Río, Munic. Viñales: En el agua del río [?], finca El Ancón, Viñales, 19.5.1955, *Alain 4258* (HAC). – Prov. Ciudad de la Habana, Munic. Habana del Este: lectotype, Cojimar, 10.1.1905, *Baker & O'Donovan 4421* (NY 1185575 [photo]); playa de Cojímar, 7.5.1951, *Daudinet 16833* (HAC); Cojimar, coastal thicket, 24.8. 1910, *Britton & al. 6300* (NY 1185574 [photo]); manigua costera / coastal thickets, Cojímar, 14.2.1953, *Alain 2756* (HAC, NY 1185569 [photo]); manigua costera, Cojímar, 2.3.1931, *León & Alain* (HAC); id., 6.7.1957, *Alain 6304* (HAC); in coastal thickets between Morro and Cojímar, 5.4.1922, *Ekman 13693* (MO 807432 [photo], NY 1185567 [photo]); El Morro to Cojimar, prostrate in shady places, under shrubs; fls. white, 8.12.1910, *Wilson 9143* (NY 1185570, 1185572 [photo]); Casa Blanca, in coastal thickets between Morro and Cojímar, 6.7.1923, *Ekman 16886* (K 534044 [photo], NY 1185568 [photo]); between Rio Cojímar and Playa de Bacuranao, vine; fls. white; shady places in coastal sands, 26.12.1910, *Wilson 9533* (NY 1185571 [photo]); cerca de Playa entre / sea coast between Cojímar y / and Bacuranao, 29.12.1910, *Wilson & León 1912* (HAC, NY 1185573 [photo]). – Prov. Habana, Munic. Santa Cruz del Norte: Boca de Canasí (Matanzas), on rocks, 7.12.1927, *León 13192* (HAC). – Prov. Matanzas: ad rupes supra Matanzas, [1849], *Rugel 109* (NY 1185577 [photo]); ad rupes maritimas prope Matanzas, [1849], *Rugel 741* (NY 1185576 [photo]). – Prov. Ciego de Ávila, Munic. Morón: Camino a la cueva del Jabalí, Cayo Coco, Ciego de Ávila, 19.2.1995, *Herrera & al.* (HAC 40681).

Apassalus parvulus: [Prov. Guantánamo, Munic. Imías]: Veguita del Sur, alrededores del río Jojo [= Jobo], monte galería semicaducifolio [20°06'50"N, 74°28'52"W], 24.5.1982, *Bässler & al. HFC 46906* (B,

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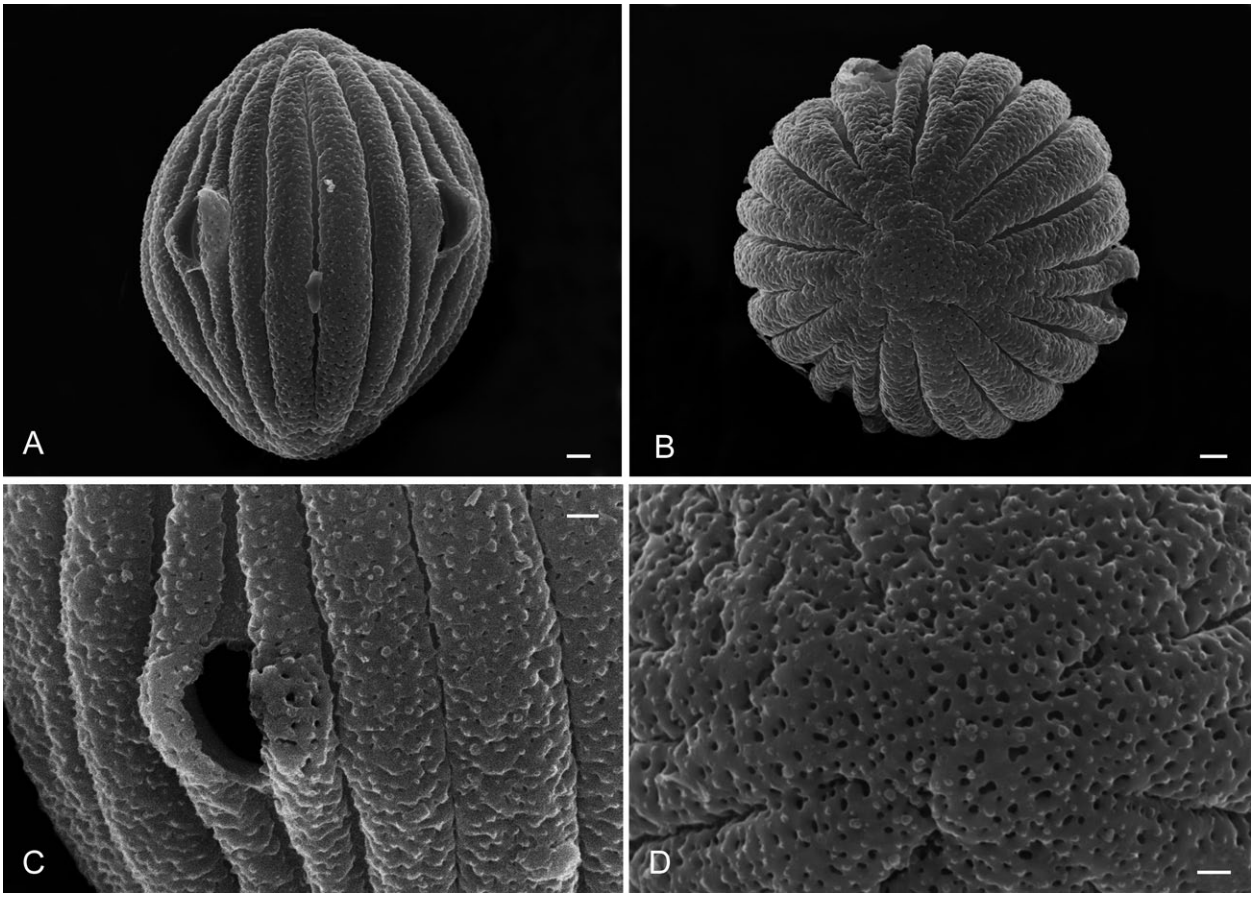


Fig. 5. Pollen of *Apassalus parvulus (HFC 46906)*, SEM micrographs – A: equatorial view; B: polar view; C: some exine ribs and aperture, showing part of circular endopore and atrium; D: polar cap, detail of tectum with perforations and microgranules. – Scale bars: A–B = 2 μm; C–D = 1 μm.

JE); id., esquistos cristalinos, 24.5.1982, *Bisse & al. HFC 46906* (HAJB).

Distribution. — According to Alain (1957), *Apassalus cubensis* has a fairly wide distribution along the coasts of Cuba, being reported from the provinces of Pinar del Río, [Ciudad de] la Habana and Matanzas, and also from "Oriente". As we did not find E Cuban material identified as *A. cubensis* in any of the herbaria we consulted (which include those with which Alain was working), we consider the "Oriente" record as due to a slip of memory. *A. parvulus* is only known from the municipality of Imías (Fig. 1).

Habitat. — Both species are apparently restricted to shady places, either on coastal sands or in gallery woods, below 100 (or occasionally 300) m of altitude.

Variation. — *Apassalus parvulus* was based on a single gathering made in easternmost Cuba at the beginning of 1956. In the protologue, Alain (1956) failed to compare it with *A. cubensis,* considering it closest to *A. diffusus* of Hispaniola on account of seed number (2 rather than 4 per capsule). This is a questionable criterion, as he described *A. parvulus* as "4-seeded, one pair abortive", and occasional seed abortion is frequent in *Acanthaceae.* One year later, Alain (1957) keyed out *A. parvulus* against *A. cubensis,* based on indumentum, leaf crenation and dimensions, and calyx and corolla length. The second, copious gathering of *A. parvulus, HFC 46906,* from near the locus classicus, shows that the vegetative characters of that species are fully congruent with those of *A. cubensis,* whereas for calyx, corolla and capsule length, the values for the E Cuban plants do not fall within the variation range of *A. cubensis.* The differences are slight, but added to the geographical disjunction they just suffice to recognise distinct species, as we shall argue in the concluding part of our paper. In the following discussion, unless otherwise stated, we refer to both species together.

Seeds. — There are normally 4 seeds per capsule. They are similar in shape to those of *Dyschoriste bayatensis,* with blunt wingless margins, but with a markedly oblique base, and somewhat smaller (c. 1.5 × 1 mm). The dry seeds (Fig. 2C) are covered by a brownish shell that consists of tightly packed, parallel, antrorse hairs glued together by a kind of lacquer and discernible only towards the distal end and sometimes at the bend beside the hilum. The annular thickenings of the cell wall are

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less pronounced than in the previous species, because the wall between the thickenings is more robust and does not cave in. When wetted, the hairs immediately spread at a right angle and surround the seed, releasing a conspicuous mucilage cloud (Fig. 2D). Being stouter than in the other species studied, they remain ± upright and do not collapse upon drying (Fig. 3E). Their length is c. 0.25 mm.

Pollen morphology. — Same as *Dyschoriste bayatensis, Apassalus parvulus* has subprolate, 3-colporate Rippenpollen with equatorial pori (Fig. 5). Average dimensions are: P = 31.4 (27.7–36.5) µm, E = 25.4 (22.6–29.4) µm, P/E = 1.24 (1.11–1.30). There are 6–8 pseudocolpi per intercolpium (Fig. 5B), which are somewhat irregular in size (both length and width), so that under Furness' (1994) classification the *Apassalus* pollen falls within the same subtype as that of *D. bayatensis*. The shape and dimensions of the colpi and of the characteristic exine lips protruding on either side of the pores (Fig. 5A, C) do not deviate from those seen in the latter species. However, there are minor differences. The grains are spindle-shaped rather than broadly ellipsoidal, i.e. they taper ± conically toward the poles (Fig. 5A). The tectum is rugulose-scrobiculate underneath the microgranular pattern and is microperforate, especially on the lips and at the poles (Fig. 5C–D). Raj (1961) characterised the pollen of *Dyschoriste cubensis* somewhat differently, namely as prolate (47 × 28 µm); he did not, however, provide an illustration or detailed description.



Fig. 6. *Apassalus parvulus (HFC 46906)*, incident light photographs – A: capsule with tip burnt off, exploded to eject one seed; B: dry post-fruiting calyx with hygroscopically incurved segments; C: same calyx, expanded after wetting, displaying the axial stump on which the now shed capsule was articulated. – Scale bars: A–B = 1 cm; C = 2 cm.

Hygroscopic features. — The tip of one of the few available ± mature capsules of *Apassalus parvulus* (from the specimen *HFC 46906,* JE) was burnt off by means of a red-hot needle. The capsule readily exploded, ejecting one of its seeds to a distance of c. 10 cm (Fig. 6A, where the seed has been re-positioned). The same result was obtained by placing a droplet of water, for about 10 min, on the tip of a mature capsule of *A. cubensis* (specimen *Herrera & al.,* HAC 40681). Reversible hygroscopic bending of post-fruiting calyx segments was observed in several specimens. The void capsule, disarticulating at the base, is shed; by the time this happens the proximal portion of the calyx, having become hardened, splits to the base, from where the formerly upright segments now diverge, then curve inward in their proximal third, with the distal part remaining straight. This bending is not very obvious in *A. cubensis* but is extreme in plants of *A. parvulus* from both E Cuban localities and results in an awkward, "spidery" look of the old calyces (Fig. 6B), which upon wetting inverts to a regularly stellate

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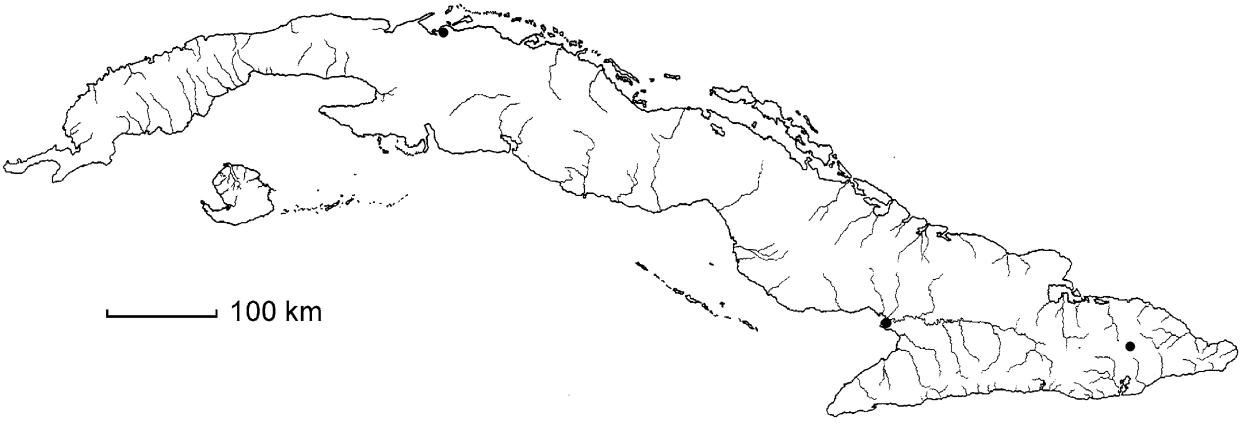


Fig. 7. Known distribution of *Hygrophila urquiolae.*

shape (Fig. 6C). This feature, not so far described, lends further support to the recognition of both species as distinct.

Hygrophila urquiolae Greuter & al. in Willdenowia 39: 288. 2010.

Morphology. — This rare Cuban endemic was described only recently (Greuter & al. 2010). We refer to the full original description for details and include the characteristic features in Table 1.

Specimens seen. — Cuba: As *"Dyschoriste bayatensis"* [lacking label data] (HAC). – Prov. Matanzas, Municipio Martí: Ciénaga del Majaguillar al NO de Martí, Ciénaga de Gonzalito cerca del Canal de Blanquizal, alt. 5 m, 22°59'39"N, 80°58'06"W, herbazales de ciénaga, 28.2.2009, *Greuter & al. 27013* (holotype: HAJB; isotypes B, JE, NY, PAL-Gr); same locality, 22°59'45"N, 80°58'45"W, bosque secundario de ciénaga, 10.2.2007, *Palmarola & al. HFC 84651* (HAJB); same locality, flores lila pálido con tubo blancuzco, 27.2.2007, *Greuter & al. 26662* (B, HAJB, PAL-Gr). – Prov. Granma [Munic. Río Cauto]: Monte Atejito, Ciénaga de Biramas, 29.1.1998, *Méndez 9692* (HIPC, PAL-Gr). – Prov. Guantánamo, [Munic. Yateras]: camino a Felicidad de Yateras (7–10 km al N), Montecristo, pluvisilva montana sobre caliza, 600–800 m/nm, 23.1.1996, *Méndez & Romano 8626* (HIPC).

Distribution. — When we described *Hygrophila urquiolae* from a single, restricted locality in the Ciénaga de Majaguillar of Matanzas Province, we already suspected that it might be more widely distributed but was so far overlooked. We thought of similar habitats in W Cuba, but when revising the *Acanthaceae* of the HIPC herbarium had the surprise of finding two E Cuban specimens unmistakeably representing *H. urquiolae*. The first is from the Ciénaga de Biramas, Granma Prov., an area in which similar, suitable habitats are to be expected. The second, from the Monte Cristo region of Guantánamo Prov., is puzzling. The labelling is apparently reliable, but one might suspect a recent introduction as a casual roadside weed, because that very same area had been repeatedly explored by previous botanical expeditions, which failed to collect the species. – Fig. 7.

Habitat. — Marshy flat coastal grassland areas interspersed with copses and patches of shrubbery, near sea level. An entirely different habitat, montane rainforest above 600 m of altitude, is indicated for the Monte Cristo specimen. We cannot presently explain this very unusual ecological discrepancy (see above, under distribution).

Seeds. — There are normally 32 seeds per capsule. They are similar in shape to those of *Dyschoriste bayatensis,* with blunt wingless margins, but relatively broad and somewhat smaller (c. 1.2×1 mm). The dry seeds (Fig. 2E) are covered by a compact brown shell consisting of parallel, antrorse hairs glued together as if lacquered over and not discernible individually (Fig. 3A, B). The annular thickenings of the cell wall are very numerous and pronounced (Fig. 3D). When wetted, the hairs immediately spread in the same way and with the same orientation as in *D. bayatensis,* amidst a dense mucilage cloud (Fig. 2F). They are long (0.4–0.5 mm) and slender, collapsing completely upon drying (Fig. 3C).

Pollen morphology. — The pollen grains are typical for the genus: spheroidal to suboblate, 4-colporate "Rippenpollen" (Fig. 8) with apertures that are either equatorial or displaced by opposite pairs toward opposed poles (Fig. 8A). Average dimensions are: P = 32 (31.3–32.8) µm, E = 34 (30.8–39.5) µm, P/E = 0.94 (0.79–1.03). There are usually 4 (rarely 3 or 5) fairly regular, smooth, narrow pseudocolpi per intercolpium, which together with the colpi delimit a total of (17–)20 exine ribs per grain (Fig. 8B). The colpi are almost as long as the pseudocolpi, much widened and distinctly granulate in their medial part; there are no marked, lip-like exine protrusions on either side of the circular endopores, which

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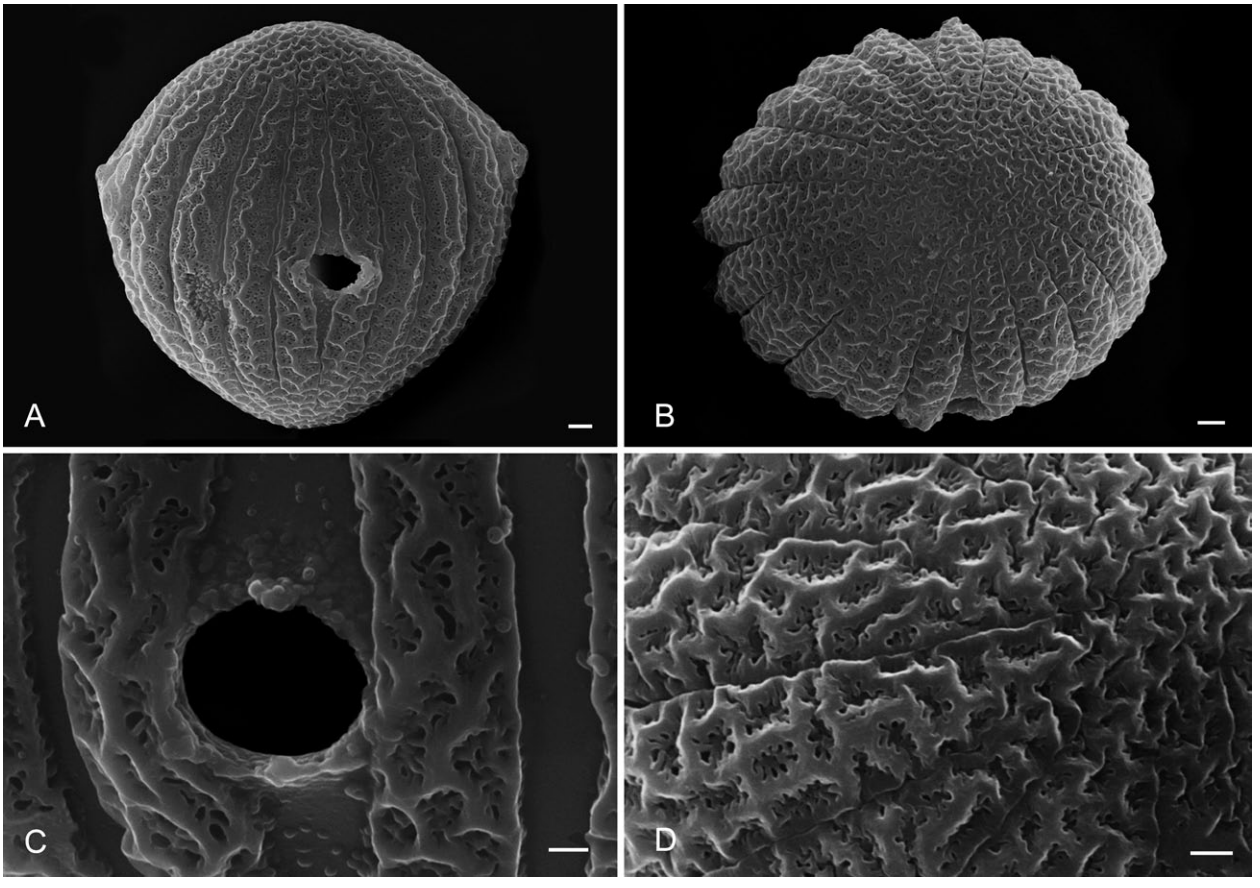


Fig. 8. Pollen of *Hygrophila urquiolae (Greuter & al. 26662)*, SEM micrographs – A: equatorial view; B: polar view; C: aperture, showing granular colpus, smooth adjacent pseudocolpi and circular endopore; D: subpolar exine portion. – Scale bars: A–B = 2 µm; C–D = 1 µm.

are, however, bordered by a granular rim (Fig. 8C). The tectum, on ribs and pole areas, shows a pronounced reticulate pattern with rather few but coarse perforations inside the primary lumina, which decrease in size from the equator to the poles (Fig. 8D). According to Furness' (1994) classification, our species groups with four others of *Hygrophila* and one of *Brillantaisia,* all Palaeotropical, which share the *Hygrophila salicifolia* pollen type.

Hygroscopic features. — Exposure of mature but still closed capsules of the type specimen to the vapour of boiling water almost immediately triggered their explosive opening. Wetting the tip by a drop of water, however, did not function unless some detergent was added. Not only the seeds but the capsule halves were ejected in this species, breaking free at the basal articulation point. The firm, tubular calyx does not show any hygroscopic properties.

Daily flowering rhythm. — Hygrophila urquiolae appears to be a normal day-flowering species. We did not attempt to establish its exact flowering cycle, but it was certainly in full bloom in the early afternoon hours when we took pictures of it.

Ruellia shaferiana Urb., Symb. Antill. 9: 128. 1923. – Holotype: Cuba, Prov. Camagüey [Munic. Nuevitas], vicinity of Tiffin [c. 21°33'N, 77°20'W], 1.–5.11.1909, *Shafer 2880* (?B†); lectotype (designated here): NY 114918 [photo]).

Morphology. — Urban (1923) described *Ruellia shaferiana* rather briefly, based on an incomplete specimen bearing flower buds and immature capsules only. Thanks to our new material, complemented by observations in the field, we can here provide a full and detailed description. The main characteristics are summarised in Table 1.

Perennial herb, 20–40 cm tall, procumbent below and rooting at the nodes, the fertile portion ± erect. *Epidermis* covered with linear cystoliths raised in the dry state, which are parallel along the veins on the abaxial leaf surface, stems and calyces, but irregularly arranged on the adaxial face of the leaves; in fresh material they are barely visible, apparently sunk rather than protruding. *Stems* initially quadrangular, later almost terete, not sulcate, glabrous, inflated at the nodes. *Lower leaves* shed by flowering time, the middle and upper ones decussate, thin, undivided, the middle measuring up to 8×3 cm, the

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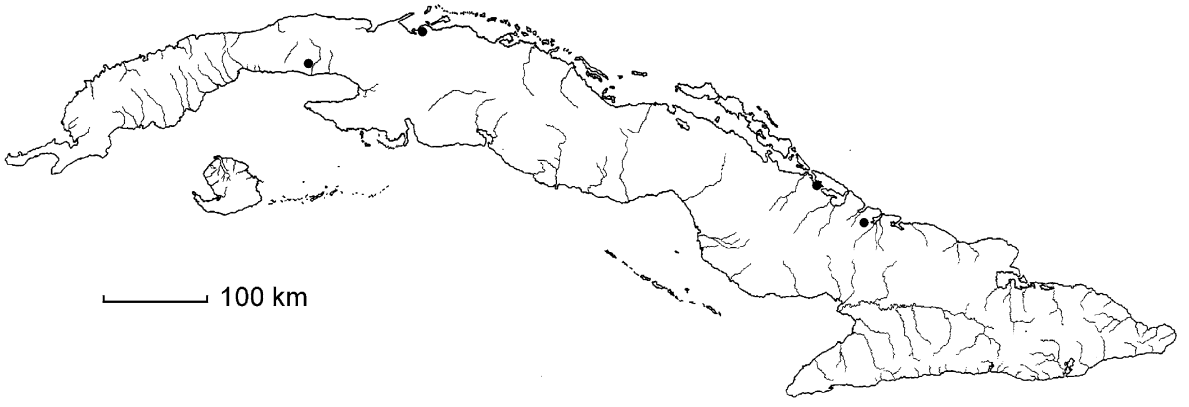


Fig. 9. Known distribution of *Ruellia shaferiana.*

upper much smaller; lamina broadly lanceolate to ovate-lanceolate, acute or subacute, tapering basally into a short petiole, with entire but often undulate margins that are ciliolate when young, otherwise glabrous on both faces, pinnately veined with 6–7 pairs of abaxially prominent main veins and a loosely reticulate tertiary venation. *Inflorescences* dichasial; flowers sessile, mostly in threes (the lateral borne by linear-spatulate bracteoles) in the axils of foliaceous to linear-spatulate bracts, ± spaced or densely crowded on axillary side branches of which only the lowermost are ± elongate but the upper very short. *Calyx* 7–8 mm long at anthesis, accrescent to 10–11 mm, split to the base into 5 subequal, green, linear segments narrowing gradually to a setaceous tip; segments devoid of a membranous margin, glabrous inside, outside on the midvein and especially along the margins with a mixture of long (up to twice as long as the segment width) gland-tipped and scattered slender, short, eglandular patent hairs (Fig. 10A). *Corolla* c. 14 mm long, exceeding the calyx by half, with left-contort aestivation, divided into tube and limb (including throat) by the insertion point of stamens; tube cylindrical, straight except at the ± outward bent top, as long as the limb (7 mm), glabrous, pale; limb obliquely inserted on the tube then imperceptibly upward curved (Fig. 10A) but otherwise subregular, glabrous inside but outside glandular- and eglandular-puberulent (Fig. 10C), especially apically and along the veins, bright blue at anthesis turning pale burgundy on withering, marked with 5 darker veins that do not attain the margin; throat narrowly campanulate, the 5 ± equal, truncate-obovate or rounded-squarish lobes (3.5×2.5 mm) curved outward and patent distally. *Stamens* 4; filaments glabrous, fused pairwise at the base, each pair inserted obliquely at the tip of the corolla tube, the pairs not united by a transverse membrane or fold; staminode absent; anthers bithecic, dorsifix, elliptic, c. 1.6 mm long, parallel, appressed to the dorsal side of the throat, the anterior (outer) ones overtopping the posterior by half their length and reaching the mouth of the corolla throat (Fig. 10A–C); thecae parallel, free in the proximal third, rounded at both ends and lacking basal awns; pollen and anthers white. *Ovary* cylindrical, glabrous, bilocular; style filiform, glabrous, apically recurved in bud, becoming straight at anthesis, its tip reaching the opening of the corolla throat; stigmatic branches bluish in bud, diverging from the style at right angles in the sagittal plane, the anterior filiform, c. 1 mm long, eventually becoming porrect, the posterior usually reduced to a small tooth (Fig. 10Da) but occasionally of the same length and shape as the anterior one (Fig. 10Db). *Capsule* loculicidal, straight, narrowly spindle-shaped, acute and mucronate, equalling or slightly exceeding the calyx, measuring 9–11× c. 1.5 mm, with a sterile basal and apical portion; valves brown; placental suture a narrow groove; retinacula robust, biseriate.

Additional specimens seen. – Cuba: Prov. Habana [Munic. Melena del Sur or Güines]: Batabanó, La Mora, in palm savannas behind the manglares [ca. 22°43'N, 82°06'W], 11.12.1920, *Ekman 12631* (S). – [Prov. Matanzas, Municipio Martí]: Circuito Norte, Man. Gómez y Martí, 19.8.1956, *Acuña, Roig & Acosta 20360* (HAC). – Prov. Camagüey, [Munic. Nuevitas]: Tiffin, in pastures [c. 21°33'N, 77°20'W], 7.10.1922, *Ekman 15400* (S, 2×); costa antes del puente de Cayo Sabinal, alt. 0–1 m, 21°36'10"N, 77°22'45"W, 3.3.2000, *Greuter & al. 25199* (B, HAJB, HIPC, PAL-Gr); costa antes del puente de Cayo Sabinal, alt. 1–2 m, 21°35'46"N, 77°22'38"W, 22.2.2010, *Greuter & al. 27118* (B, HAJB, HIPC, PAL-Gr, etc.). – Prov. Las Tunas, [Munic. Manatí]: Sabanas de Manatí, 24.11.1951, *Acuña 17161* (HAC).

Distribution (Fig. 9). — The area of distribution, as indicated by Alain (1957), comprises E Cuba (the former Prov. Oriente) and Camagüey Province. A large majority of the material seen, including our own gatherings, comes from the latter. In fact, no specimen from any of the four traditional "Oriental" provinces (Granma, Santiago de Cuba, Holguín, Guantánamo) has been traced, and it is doubtful whether the species was ever collected there. However, the eastern half of Prov. Las Tunas (including Manatí) also belonged to the old Oriente Province, a fact that is sometimes overlooked, and it is reasonable to assume that Alain's mention of "Or." is based solely on Acuña's Manatí specimen. The westward ex-

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Fig. 10. *Ruellia shaferiana* – A: flower in lateral view; B: corolla in front view, showing white pollen packages in the dehisced thecae and all around the mouth; C: flower in dorsal view; D: variation of stigmatic branches: a, normal, unequal branches, style protruding from corolla bud; b, exceptional, equal branches, style protruding from calyx (corolla removed). – Photographs R. Rankin.

tension of the area of *Ruellia shaferiana* to the provinces of Matanzas and Habana, so far unrecorded, requires confirmation because the material on which it is based is exceedingly poor. Neither of the two specimens cited bears a corolla. That of *Acuña & al.* is badly damaged by insects; it only has scant remains of two calyces and one half of a capsule (which is too short and was probably less than 8-seeded, but may have been malformed). Ekman's gathering from Batabanó is not in much better shape; Urban (1923) did not cite it in the protologue of *R. shaferiana,* and it is not certain that he even saw it (nor is there any statement of who identified it). That specimen deviates in having densely pubescent (not glabrous) floriferous side branches; the calyx segments are shortly antrorse-strigulose ventrally and on the back and along the margins, densely covered with short eglandular and scarcely longer, robust glandular hairs; finally the capsule, rather than being completely glabrous and smooth, is shortly patent-strigulose along the suture distally. Neither specimen fits any other species known from Cuba, but they might conceivably represent a new taxon and their identification as *R. shaferiana* is therefore tentative.

Habitat. — Moist grassland used for grazing, near sea level. At our collecting locality, the species occurs locally but plentiful in the shade of *Bucida* trees, at the margin of wet coastal grassland, on rich black crumbling soil, and appears to be an element of the gallery forest undergrowth.

Seeds. — There are up to 8 seeds per capsule. They are similar in shape to those of the three other species, measuring 1.5–2×0.9–1.2 mm, but have a narrowly winged margin. In the dry state (Fig. 2G) the surface is light brown, smooth and apparently glabrous throughout, as the lateral faces indeed are. When wetted, the previously obsolete hairs along the winged margin immediately spread to form a of dense, white aureole (Fig. 2H, 3F). These hairs are obliquely forward directed, 0.5 mm long near the base but decreasing toward the tip of the seed.

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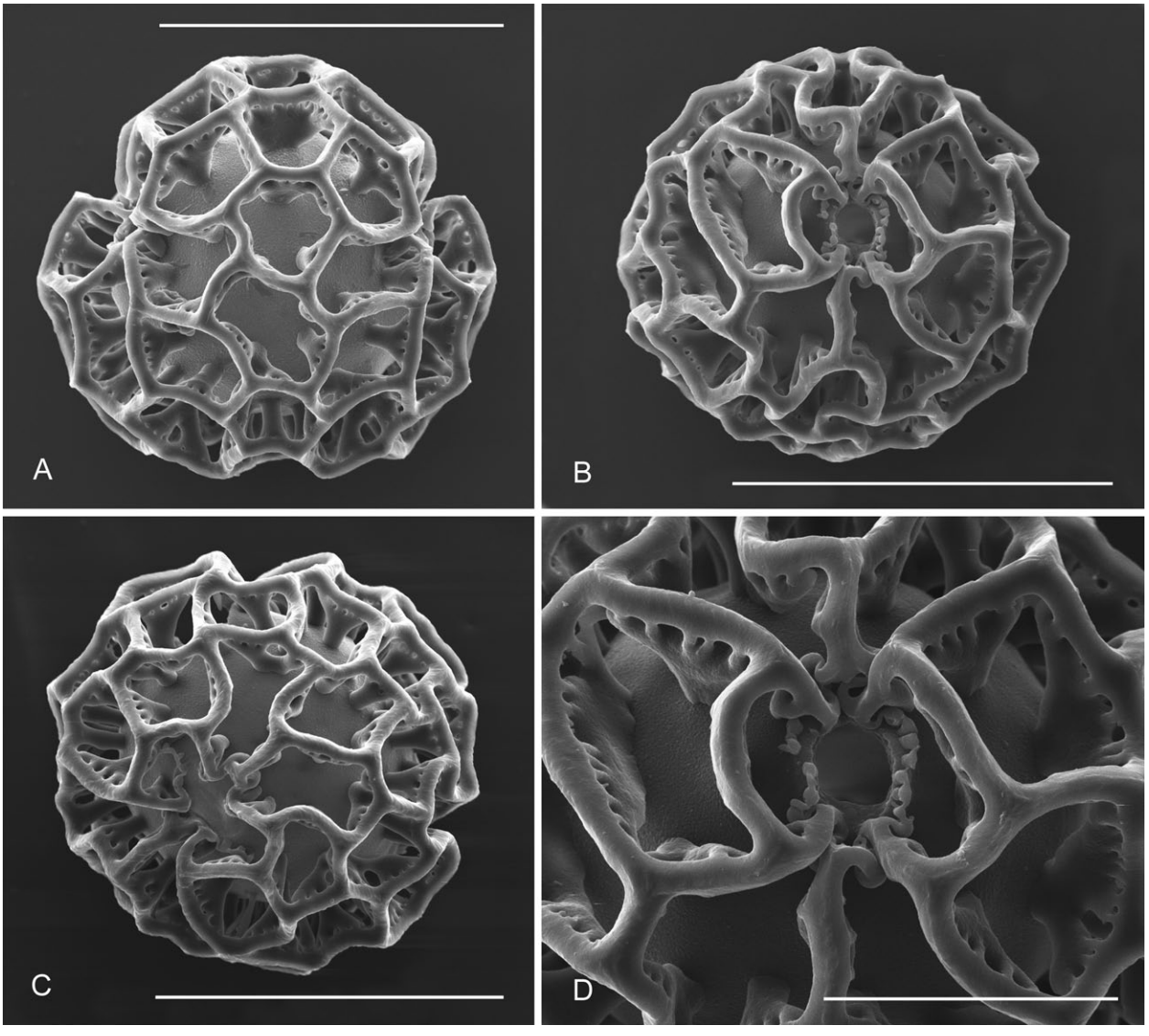


Fig. 11. Pollen of *Ruellia shaferiana (Greuter & al. 27118)*, SEM micrographs – A: grain viewed from a presumed pole; B & D: view upon an aperture: note the triplets of "handrails" plunging to the nexine surface at either end, the small, free, knob-headed columellae bordering the short colpus, and the circular endoaperture; C: grain with a similar structure not linked to an aperture. – Scale bars: A–C = 50 µm; D = 20 µm.

They are slender, collapse upon drying (Fig. 3F), and show weak annular to spiral wall thickenings.

Pollen morphology. — The pollen (Fig. 11) is spheroidal, not distinctly polar, 3-colporate "Wabenpollen" with (not easily discerned) apertures that may be taken to define the equatorial plane. The grains (see Furness & Grant 1996 for standardised character definitions) are small, with an average diameter (including the c. 10 µm high muri) of D = 59.6 (51.1–64.8) µm. No granules are present. The lumina of the reticulum are medium-sized (15 µm across on average in the ± isodiametric lumina). The reticulum is subregular above the poles and intercolpi, where each lumen is surrounded by 6 other lumina to form a hexagonal pattern (Fig. 11A); the lumina adjacent to the apertures are irregularly shaped. The muri are rounded and smooth. The columellae supporting the muri are tall, with a massive base distally divided like a candelabrum into a varying number (2–9) of branches (Fig. 11A); when two neighbouring candelabra fuse, a two-tiered columellar structure may result. Apertures are peculiar, with very short, ill differentiated colpi almost coextensive with the pore. At either end of the colpus, three muri ("handrails") dip down to the nexine surface, their bases becoming irregularly intertwined (Fig. 11B, D; this may also, on occasions, occur where no aperture is found: Fig. 11C). From there, two dense rows of free, apically expanded, minute columellae, which may fuse into a wavy membranous structure, extend along the colpus margins (Fig. 11D).

Hygroscopic features. — Dehiscence was triggered by placing a drop of water on the tip of a mature capsule (specimen *Greuter & al. 27118*). As the surface is water

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Table 1. A summary of diagnostic features of the four species treated.

Character	***Dyschoriste bayatensis***	***Apassalus cubensis* and *A. parvulus****	***Hygrophila urquiolae***	***Ruellia shaferiana***
Habit	erect (or straggling climber), to > 1 m tall	decumbent for most of its length, often rooting at nodes	erect, to > 1 m tall; base decumbent, rooting at nodes	ascending, to 40 cm tall; base decumbent, rooting at nodes
Calyx segments	united in lower 1/3–1/2, linear-lanceolate, apex setaceous	united for c. 1/3, linear-lanceolate, apex setaceous	united to at least 2/3, triangular, acuminate	free to the base, narrowly linear, apex setaceous
segment margins	membranous proximally	narrowly membranous at base	narrowly membranous at base	herbaceous
indumentum	homomorphic, eglandular, antrorse	none or eglandular-scabrid, segments ciliolate	none, but segments ciliolate	patent, of long gland-tipped and short eglandular hairs
inside	appressed-setulose	appressed-setulose	densely appressed-setulose	normally glabrous
Corolla	c. 14 mm long, limb almost regular, expanded	[5–6]* / 9–10 mm long, limb subregular	16–18 mm long, limb strongly bilabiate	c. 14 mm long, limb regular, expanded
tube	3–4 mm long, slightly shorter than limb	[c. 2.5]* / c. 4 mm long, slightly shorter than limb	c. 6 mm long, shorter than limb	c. 7 mm long, equalling limb
limb outside	densely eglandular-pubescent all over except at base	minutely eglandular-pubescent	densely glandular-pubescent all over except at base	glandular- and eglandular-pubescent mainly on lobes and along veins
Anther thecae	awned at base	rounded at base, lacking awn	rounded at base, lacking awn	rounded at base, lacking awn
Style	strigulose-hairy	subglabrous, scabrid at base	glandular- and eglandular-pubescent	glabrous
Stigma	lacking dorsal branch	dorsal branch obsolete	lacking dorsal branch	with ± well developed dorsal tooth or branch
Seeds, no. per capsule	(3–)4	(2–)4	(28–)32	(6–)8
wing	absent	absent	absent	membranous
hairs	on whole surface	on whole surface	on whole surface	only along margin
Pollen grain shape	subprolate	subprolate*	spheroidal to suboblate	spheroidal
apertures	3-colporate, with atrium formation	3-colporate, with atrium formation*	4-colporate, without atrium formation	3-colporate
exine structures	∞ longitudinal ribs (“Rippenpollen”)	∞ longitudinal ribs (“Rippenpollen”)*	∞ longitudinal ribs (“Rippenpollen”)	reticulate muri (“Wabenpollen”)

repellent, the imbibing process took considerable time (c. 15 min), but then the capsule exploded forcefully, projecting some of the seeds to a distance of over 30 cm. In this species, too, the calyx shows hygroscopic properties, even though they are scarcely noticeable. After the shedding of the capsule, articulated at the base, the formerly erect calyx segments spread from the very base, then curve upward to an upright distal portion. In water the bend is completely straightened out, but upon renewed drying it is recovered and more pronounced than before. The hygroscopic portion is limited to the proximal fifth of the calyx.

Pollination-relevant aspects. — When, in the field, we found only a few withered flowers but plentiful buds and fruits, we decided to monitor the flowering rhythm of freshly cut material. We had to wake early to do so: unfolding of the corolla started before dawn, at 5 a.m., and was complete by sunrise. By noon the corollas, which from bright blue had turned pale burgundy, were withering and being shed. The flowers are scentless and lack nectar, so that colour is the only attractant and pollen the only possible reward. Indeed the white pollen, partly sticking to the thecae and partly scattered in clusters around the mouth of the corolla throat (Fig. 10B), enhances colour attraction, but its small quantity makes it improbable that it could serve as a reward for pollen harvesting pollinators. Are we, then, facing a case of pollination by deceit? Self-pollination may also play a role, but only at the end, when the corolla is falling off; before that time, we did not observe any pollen deposited on the stigma, in spite of its being placed in close proximity to the anthers.

Discussion and conclusions

Seeds. — Seed number, in the species studied, ranges from 4 to 32 and is species-specific, allowing for slight downward variation due to abortion. All seeds are strongly lenticular-compressed. As already noted by Oehm (1932: fig. 9–11), outline shape varies in function of the space available during maturation, which differs depending on the position of each seed within the capsule. By consequence, seed shape is not suitable as a taxonomic character.

As soon as their hairs unfold in water, a smeary cloud of mucilaginous matter forms around the seeds (Fig. 2B, 2D, F, H). That cloud appears almost instantaneously, and surrounds the hairs in the first place. Kippist (1842: 69) reports that the mucilage "may be seen to flow from the extremity of the tube", or "from a terminal pore", and that the hairs "are frequently detached from the testa by the rapid expansion of the fluid within, and numbers of them may be seen floating about loose". Schaffnit (1906: 459) gives a detailed description based principally on *Hygrophila salicifolia* (Vahl) Nees. According to him, the hairs are initially filled with cellulose mucilage, which at maturity is seen as a vitreous, crumpled gelatine strand. Upon wetting, the hairs tear off at the base and are carried upward by the unfolding mucilage string, which is up to 8 times as long and twice the diameter of the hair itself. Our own observations do not bear out any such scenario. We are unconvinced of the hypothesis that the mucilage comes from within the hairs and rather doubt that the hairs have any content of note. A much more logical assumption, that would better explain the observed phenomena, is that the glue or lacquer that initially fastens down the hairs and the mucilage released in water are one and the same substance.

The main function of the mucilage, which dries out as a sticky film well visible in SEM images (e.g. in Fig. 3C, D), is to attach the seed firmly to the substrate so as to provide a hold during germination. Only exceptionally, when the substrate happens to be the claws or plumage of waterfowl, this may be an effective way of long-distance dispersal. The hairs themselves serve as the seed's anchor in the glue, which holds them fast thanks to their annular or spiral surface pattern, and for this to function they must of course remain firmly attached to the seed coat. Indeed, we never observed loose hairs floating about after immersion.

Mucilaginous seed hairs of the kind here described (and presumably homologous mucilage cells mentioned above under *Ruellia*) are arguably a so far neglected synapomorphy for the subtribe *Ruelliinae*. True, exceptions apparently exist. Seeds with hairs lacking mucilage have been reported for a few representatives of *Ruelliinae,* including *Eranthemum* and at least two species of *Strobilanthes* Blume, *S. fimbriata* Nees and *S. wallichii* Nees (Kippist 1842); the seeds of *Bravaisia* are described as glabrous, smooth and shiny (Daniel 1988). Conversely, mucilaginous seed hairs or papillae exist in *Acanthaceae,* outside of *Ruelliinae,* at least in *Blepharis* (incl. *Acanthodium* Delile), where they are of a different type: fasciculate, compound of many concrescent cells with a free, filiform distal portion resembling ruelliinid single hairs (Kippist 1842: fig. 1–5, Schaffnit 1906: 462–463). *Barleria* and *Crabbea (Barleriinae)* were said by Stopp (1958) to have mucilaginous, sticky seed hairs, but Kippist (1842: 71) stated that no mucilage is secreted in the 9 *Barleria* species he studied, and Schaffnit (1906: 462) confirmed this for *B. cristata* L. We suggest that a comparative study of seed hair types of *Acanthaceae* and of their distribution in a modern, phylogenetically based classification of the family would be a rewarding subject for future research.

From a practical point of view, we suggest that the substance initially holding together the ruelliinid seed hairs, whether or not it be the same as the sticky mucilage released in water, may present properties interesting in the context of bionics. Adhesiveness coupled with instant water solubility might be useful in structures to be set free, and processes to be triggered, upon contact with water. The mucilage may also present useful if less spectacular qualities as a fast and extremely elastic glue.

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Pollen morphology. — The pollen of *Dyschoriste bayatensis, Hygrophila urquiolae* and *Ruellia shaferiana* fits perfectly within the general pollen morphological pattern characterising their respective genera and confirms that the current generic placement of these species, based on gross morphology, is correct. *Apassalus parvulus* has pollen of the *Dyschoriste* type, and its study has not produced support for the maintenance of *Apassalus* as a separate genus.

Hygroscopic features. — In all four species examined, the capsules are hygrochastic. One is initially tempted to see a contradiction between this result and the fact that during the drying of fruiting specimens for the herbarium several capsules open and disperse their seeds. The explanation is easy: in the early stages of drying, especially when some heat is used, moisture accumulates within the plant press and can trigger the release. In Cuba, the explosive capsules of *Ruellia tuberosa* and its congeners are well known among local people, as documented by the vernacular names "saltaperico", "dinamita", "fulminante" and "triquitraque" (Roig y Mesa 1963). It is a popular pastime to wet a capsule in the mouth and watch it explode.

Sell (1969) reports that only one fifth of the *Acanthaceae* species he studied (5 out of 25) have hygrochastic capsules. This figure is surprisingly low. In a group such as the *Ruelliinae,* where the seeds must be wet for their adhesive mechanisms to function, one might have expected hygrochasy to be favoured (as it indeed is on Cuba). But then, there may be no cogent reason why the seeds should become fixed immediately upon release, as long as it is ensured that fixation precedes germination. At any rate, the *Acanthaceae* appear to be playing a dual game, as exemplified by *Crossandra nilotica* Oliv., in which half of the capsules open xerochastically and the other half hygrochastically, depending on whether the initial tension that builds up in drying suffices to break the apical clamp or whether it must be weakened by moisture (Sell 1969: 434–435). If, as in this case, there is a subtle balance between both strategies, that is tilted by slight quantitative, non-structural changes, it is safe to assume that the evolutionary step from xerochasy to hygrochasy and back is an easy one that may frequently happen.

The hygroscopic movements of the calyx segments that we have observed in three of our species are less easily interpreted. They appear to be associated with a hardening of certain (proximal or medial) portions of the calyx segments at the end of the maturation process, and can be observed once the void capsules have been shed. There is an abscission layer at the base of the capsules, from where they disarticulate (Fig. 6C), apparently a general though little noticed feature in these genera. We can see no conceivable functional advantage in the hygroscopic movements of the segments of the empty old calyces. The most likely interpretation, to us, is that these movements are the by-product of pressure building up in the calyx segments at maturation, aimed at keeping together the capsule halves at their base. Without such a firm hold the capsule, clamped together by the beak and with tension building up along its valves, risks to implode before the explosion can be triggered. We have indeed observed imploded capsules (with the valves still united at the tip but spreading basally) in herbarium specimens of *Apassalus cubensis* and *Ruellia shaferiana*. In *Hygrophila urquiolae,* where the calyx is not hygroscopic, its long tubular portion is firm enough to prevent implosion, but not in the other three species. Whereas hygroscopic movements of bracts are well documented in the family (reported by Sell 1969 for *Barleria, Blepharis* and *Crabbea* species) and their function is easily explained (exposure of the capsules to rain), we have found no published mention of the calyx movements here described.

Dyschoriste and Apassalus. — As we mentioned initially, opinions are currently split on the question whether these two genera should be maintained or better merged. The single difference of presence versus absence of a basal mucro in the anther thecae is unconvincing, even more so as this character varies within *Hygrophila* (Wasshausen 2005). Throughout our study we have therefore been looking for additional differences supporting the segregation of *Apassalus,* but failed to find any. On the contrary: we observed that the calyx of *A. cubensis* is very similar to that of *D. bayatensis,* not only in morphology but also in its hygroscopic properties. We therefore come to the conclusion that the merger of *Dyschoriste* and *Apassalus* is unavoidable.

The distinctness of the plants described as *Apassalus parvulus* became questionable when material subsequently collected close to its locus classicus was studied, which in general aspect, indumentum, and the dimensions of its vegetative parts was indistinguishable from *A. cubensis*. However, the two E Cuban gatherings share some features that can be used to distinguish them from the Central and W Cuban populations: the short calyx (5–6 versus 6–9 mm), corolla (5–6 versus 9–10 mm), and capsule (c. 5 versus 7–8 mm), and moreover, the hygroscopic incurving of the old calyx segments, much more pronounced in *A. parvulus* than in *A. cubensis*. In view of the discontinuous variation and geographical isolation, we opt for maintaining *A. parvulus* as a separate species, for which, when placed in *Dyschoriste,* a new combination is required. The correct names of the two Cuban species formerly placed in *Apassalus* as follows:

Dyschoriste cubensis Urb., Symb. Antill. 7: 381. 1912 ≡ *Apassalus cubensis* (Urb.) Kobuski in Ann. Missouri Bot. Gard. 15: 2. 1928.

Dyschoriste parvula (Alain & Leonard) Greuter & R. Rankin, **comb. nov.** ≡ *Apassalus parvulus* Alain & Leonard in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 15: 20. 1956.

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