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A New Species of *Tarigidia* (Poaceae, Panicoideae, Paniceae) from Puerto Rico and Additional Evidence for a Hybrid Origin of the Genus

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Abstract—A new species of *Tarigidia* from Puerto Rico is described and illustrated. Additional micromorphological characters of the inflorescence and spikelets are included. This species constitutes the first report of the genus *Tarigidia* in the New World. *Tarigidia axelrodii* grows together with *Antheophora hermaphrodita* and *Digitaria bicornis*, showing intermediate characters. This species gives additional evidence to support Loxton's hypothesis that *Tarigidia* is derived from hybridization between *Antheophora* and *Digitaria* and also supports the phylogenetic hypothesis showing close relationships between *Antheophora* and *Digitaria*.

Resumen—Se describe e ilustra una nueva especie de *Tarigidia* en Puerto Rico. Se incluyen caracteres adicionales de la inflorescencia y espiguillas. Esta especie constituye el primer registro del género *Tarigidia* en América. *Tarigidia axelrodii* crece junto a *Antheophora hermaphrodita* y *Digitaria bicornis*, mostrando caracteres intermedios. Esta especie provee evidencia adicional apoyando la hipótesis de Loxton sobre el origen híbrido de *Tarigidia* a partir de *Antheophora* y *Digitaria* y, al mismo tiempo, sustenta la hipótesis filogenética donde se sugieren estrechas relaciones entre *Antheophora* y *Digitaria*.

Keywords—*Antheophora*, *Digitaria*, hybrid origin, phylogeny, *Tarigidia*.

The genus *Tarigidia* Stent (1932), an anagram of *Digitaria* Haller emend. A. S. Vega & Rúgolo (Vega and Rúgolo de Agrasar 2001), comprises only one species distributed in Namibia and South Africa (Gibbs Russell et al. 1990). According to Clayton and Renvoize (1986), who place both genera in subtribe Digitariinae Butzin, *Tarigidia* combines the characters of *Digitaria* and certain genera of subtribe Cenchrinae Dumort. Cenchrinae is characterized by the presence of bristles or scales subtending the spikelet and deciduous with it.

Loxton (1974) suggested that *Tarigidia* arose by hybridization between the genera *Digitaria* and *Antheophora* Schreb., without providing any plausible evidence. Until now, *Tarigidia* has been considered monotypic. The single species *T. aequiglumis* (Gooss.) Stent, is a perennial and possible intergeneric hybrid between *Antheophora pubescens* Nees and an unidentified species of *Digitaria* sect. *Erianthae* Henrard (Loxton 1974). Hybridization between these genera is considered a rare phenomenon that occurs under natural conditions and caryopsis production of *T. aequiglumis* has never been reported (Goossens 1932; Stent 1932; Loxton 1974; Watson and Dallwitz 1992).

According to Chippindall (1955), in general appearance *Tarigidia* looks like a species of *Antheophora*, but in the latter genus the spike-like panicle is not branched. In *T. aequiglumis* the inflorescence is variable, with a woolly spike or a contracted panicle. Spikelets of *Tarigidia* are similar to *Digitaria*, but differ from it in having the lower glumes well developed.

The aim of the present paper is to report a new species of *Tarigidia*, *T. axelrodii* A. S. Vega & Rúgolo, whose parents possibly may be *Digitaria bicornis* (Lam.) Roem. & Schult. and *Antheophora hermaphrodita* (L.) Kuntze. This species constitutes the first report of the genus *Tarigidia* in the New World and provides additional information both for the hybrid origin of the genus and for the hypothesis of a phylogenetic alliance between *Digitaria* and *Antheophora*.

MATERIALS AND METHODS

Morphology—The description is based primarily on living and herbarium material deposited at BAA, MO, NY, SI, UPRRP, and US (acronyms after Holmgren et al. 1990).

Micromorphology—Micromorphological observations were based on herbarium material. The main axis of the inflorescences, spikelets and their bracts, as well as the caryopses, were selected and cleaned in xylene for 1 hr with an ultrasonic cleaner (Cleanson, model CS 1106, Argentina). The material was air-dried, mounted and coated with a gold-palladium (40% - 60%) alloy by a Thermo VGScientific and then observed using a Phillips XL 30 (Phillips, The Netherlands) Scanning Electron Microscope (SEM) at the Museo Bernardino Rivadavia, Argentina.

TAXONOMIC TREATMENT

Tarigidia axelrodii A. S. Vega & Rúgolo, sp. nov.—TYPE: PUERTO RICO. Cabo Rojo: Bo. Boquerón, Rt 301, km 11, behind information center opposite salinas, at end of nature trail, salt flats, 17°57.53' N, 67°11.93' W, ca. 1 m, 9 Nov 2008, F. Axelrod & R. Thomas 14068 (holotype: US!; isotypes: BAA!, MO!, NY!, SI!, UPRRP!).

A *Tarigidia* *aequiglume* differt habitu annuo statura minore, usque ad 50 cm alto; axe inflorescentiae quadrangulari, scabroso, racemis (4 vel) 5–8, divergentibus, deciduis, alternis; spiculis binis, inaequaliter subsessilibus, heteromorphis, cleistogamis; spiculae inferiores glumis dissimilis, gluma inferiore (0.5–)1–1.5(–2.5) mm longa, cartilaginea, 1–3-nervata, glabra vel margine piloso; gluma superiore 3–3.5 mm longa, 3-nervata, pilosa; lemmate sterili cum pilis filiformibus ad marginem; lemmate fertili cartilagineo, margine membranaceo; staminibus 3, antheris 1.8–1.9 mm longis; caryopside oblonga, 2.2–2.4 mm longa. Spiculae superiores lemmate sterili in dorso pilis filiformibus, setaceis, rigidis munita.

Annual plants ca. 50 cm tall. Culms 1–2.3 mm diam., terete, decumbent, rooting at the lower nodes, glabrous. Nodes compressed, conspicuous, brown, glabrous. Leaf sheaths 3.5–6 cm long, hirsute, the hairs with a swollen base. Ligules 2–2.7 mm long, membranous, truncate, the margin erose. Base of the

leaf-blade (behind the ligule) hirsute. Leaf blades 6.3–8.5 cm long, 5.5–7 mm wide, lanceolate, flat, papyraceous, the apex acuminate, the adaxial surface scabrous, the abaxial surface scabrous and the midrib is sparsely hirsute with hairs that have a swollen base. Peduncle 35 cm long, glabrous. Panicle (3.2–) 4–7.5 cm long, (0.8–)1–2 cm wide, with (4–)5–8 alternate racemes on an axis (1–)3–4.5 cm long, quadrangular, scabrous, sinuous. Racemes ending in a spikelet, rigid, divergent, deciduous. Rachis 0.6–1 mm wide, winged, the wings reduced toward the apex of the racemes, the margin scabrous. Pedicels 0.3–1 mm long, scarcely developed, scabrous. Spikelets 4.5–5 mm long, 1.2–1.3 mm wide, paired, heteromorphous, cleistogamous, with purplish tints at maturity. Lower spikelets of the racemes scarcely pilose, with 5 nerves visible on the back, the back glabrous, pilose on the margins. Pedicellate spikelets with 3 or 5 nerves visible on the sterile lemma backs, with both sericeous and long hirsute hairs, these setiform, whitish, spreading at maturity. Subsessile spikelets with 3 nerves on the sterile lemma backs, the indumentum composed of sericeous hairs. Lower glume (0.5–)1–1.5 (–2.5) mm long, 1–3-nerved, narrow-triangular, the apex acuminate, the margin scabrous, glabrous, occasionally pilose, in this case the hairs largely exceeding its length. Upper glume 3–3.5 mm long, 3-nerved, lanceolate, pilose in internerve and marginal zones, the hairs exceeding its length. Lower sterile floret reduced to a lemma as long as the spikelet, the apex acute, 7-nerved, the nerves prominent, smooth, the midnerve distant from contiguous lateral and marginal nerves, glabrous on both sides of midnerve and alternately pilose and glabrous on the remaining zones, the indumentum not exceeding the length of the lower lemma. Upper fertile floret ca. 4 mm long, 1 mm wide, cartilaginous with membranous margins, striate, narrowly-lanceolate, apiculate, the apex scabrous, stramineous with purplish tints at maturity. Upper lemma 3-nerved, the midnerve distant from marginal nerves, without a germination flap. Upper palea 2-nerved. Lodicules 2, truncate. Stamens 3; anthers 1.8–1.9 mm long, yellow with purplish tints. Ovary glabrous; stigmas plumose, purplish. Caryopsis 2.2–2.4 mm long, 1–1.3 mm wide, ellipsoid; embryo 1.4 mm long; hilum 0.3 mm diam, circular, brown. Figures 1–3.

Etymology—The specific epithet is dedicated to Dr. Franklin S. Axelrod, collector of the type of this new species, specialist in the vascular plants of Puerto Rico and Herbarium Collections Manager at UPRRP.

Additional Specimens Examined—PUERTO RICO. Cabo Rojo: Bo. Boquerón, Rt 301, km 11, behind information center opposite salinas, salt flats, 17°57.53' N, 67°11.93' W, ca. 1 m, 12 Nov 2007, F. Axelrod & J. Turnquist 13906 (BAA, UPRRP).

Associated Species—*Tarigidia axelrodii* (Axelrod & Thomas 14068) was found in a population of *Antheophora hermaphrodita* in a large patch in an open area in sand flats near the sea. *Digitaria bicornis* was growing about a kilometer away. Vouchers for these associated species are: *Antheophora hermaphrodita* - PUERTO RICO. Mpio. Cabo Rojo: Bo. Boquerón, Rt. 301, km 11, nature trail though salt flats behind information center and opposite salinas, open area at edge of salt flats, 17°57.53' N 67°11.93' W, 1 m, 9 Nov 2008, F. Axelrod & A. Axelrod 14069 (UPRRP). *Digitaria bicornis* - PUERTO RICO. Mpio. Cabo Rojo: on the hill E of the lighthouse at Cabo Rojo, dry thickets in salt spray, 0–30 m, 3 Dec 1989, C. M. Taylor 9705 (UPRRP).

Distribution and Morphological Features in Species of *Tarigidia*—So far as is known *Tarigidia* is composed of only

two species: *T. aequiglumis* and *T. axelrodii*. In Table 1 the morphological characters of *T. aequiglumis* (derived from Goossens 1932; Chippindall 1955; Clayton et al. 2006 onwards) are compared with those of *T. axelrodii*.

Tarigidia* and Relationships with *Digitaria* and *Antheophora—*Tarigidia axelrodii* shows characters intermediate between *Digitaria bicornis* and *Antheophora hermaphrodita*, the possible parents. Cytogenetics and molecular studies are being undertaken to confirm this hypothesis (Vega et al. in prep.). The existence of *Tarigidia aequiglumis* and *T. axelrodii*, both proposed on the hypothesis of hybridization between *Digitaria* and *Antheophora*, supports the phylogenetic hypothesis that includes *Digitaria*, *Antheophora*, and two other small genera [*Chaetopoa* C. E. Hubb. and *Chlorocalymma* Clayton (L. Aagesen pers. comm.)] in the same well supported clade (Morrone et al. in press). Taxa in this clade share a 24 bp deletion within the plastid *ndhF* sequences (Morrone et al. in press).

Digitaria bicornis and *A. hermaphrodita* were observed growing in or near the same site where this new species was found. In November 2007 and 2008 two collections were made of *T. axelrodii*. Caryopses collected from this population were seeded and the resulting plants have been successfully maintained under cultivation at the Jardín Botánico Lucien Hauman, Facultad de Agronomía, Universidad de Buenos Aires (Argentina).

At the end of December 2008, the dry season began in the southwest corner of Puerto Rico. The populations of *T. axelrodii* and *A. hermaphrodita* had died back and only a handful of old inflorescences with caryopses persisted. *Digitaria bicornis* was not to be seen, although it is generally widespread within about a kilometer or so of the site in Cabo Rojo. *Digitaria bicornis* has also been collected in Fajardo, Juana Díaz, Lajas, Loíza, Mayagüez, Río Grande, Anegada, Guana Island, and Great Camano Island, at 1–550 m, flowering and fruiting in June through April (Vega & Rúgolo de Agrasar unpubl.).

Antheophora is mainly distributed in Africa and temperate Asia. Only one species, *A. hermaphrodita*, is extensive in the neotropics (Clayton et al. 2006 onwards). *Digitaria* is a genus of worldwide distribution in tropical, subtropical, and temperate areas (Watson and Dallwitz 1992). In particular, *D. bicornis* (sect. *Biformes* Henrard) is a weed introduced into the New World from the Old World and grows from sea level to 1,500 m in disturbed areas, in dry riverbeds, on eroded slopes with bare soil, and in semideciduous forests. This species is characterized by the presence of heteromorphous spikelets and this character is also shared by *T. axelrodii*. *Digitaria bicornis* differs from *T. axelrodii* in having the following characters: panicle digitate or subdigitate, 6–17 cm long, with 2–7 nondeciduous racemes, on an axis 0.3–0.9 cm long; rachis triquetrous (3-angled), narrowly winged, straight; pedicels unequal in length; subsessile spikelets 2.7–2.8 mm long, 0.8–0.9 mm wide; pedicellate spikelets 3–3.3 (–3.6) mm long, 0.9–1 mm wide; lower glumes 0.3–0.5 mm long, nerveless, triangular, apex obtuse; upper glumes 2–2.5 mm long; anthers 0.7–0.8 mm long.

Species of *Digitaria* can be recognized by their cartilaginous upper florets, with fertile lemmas having a germination flap and noninrolled membranous margins, scarcely exposing the fertile palea. The cartilaginous and striate upper floret of *T. axelrodii* is similar to that in *D. bicornis*. Margins of the upper lemma are membranous, flat, and noninrolled (Fig. 2G).

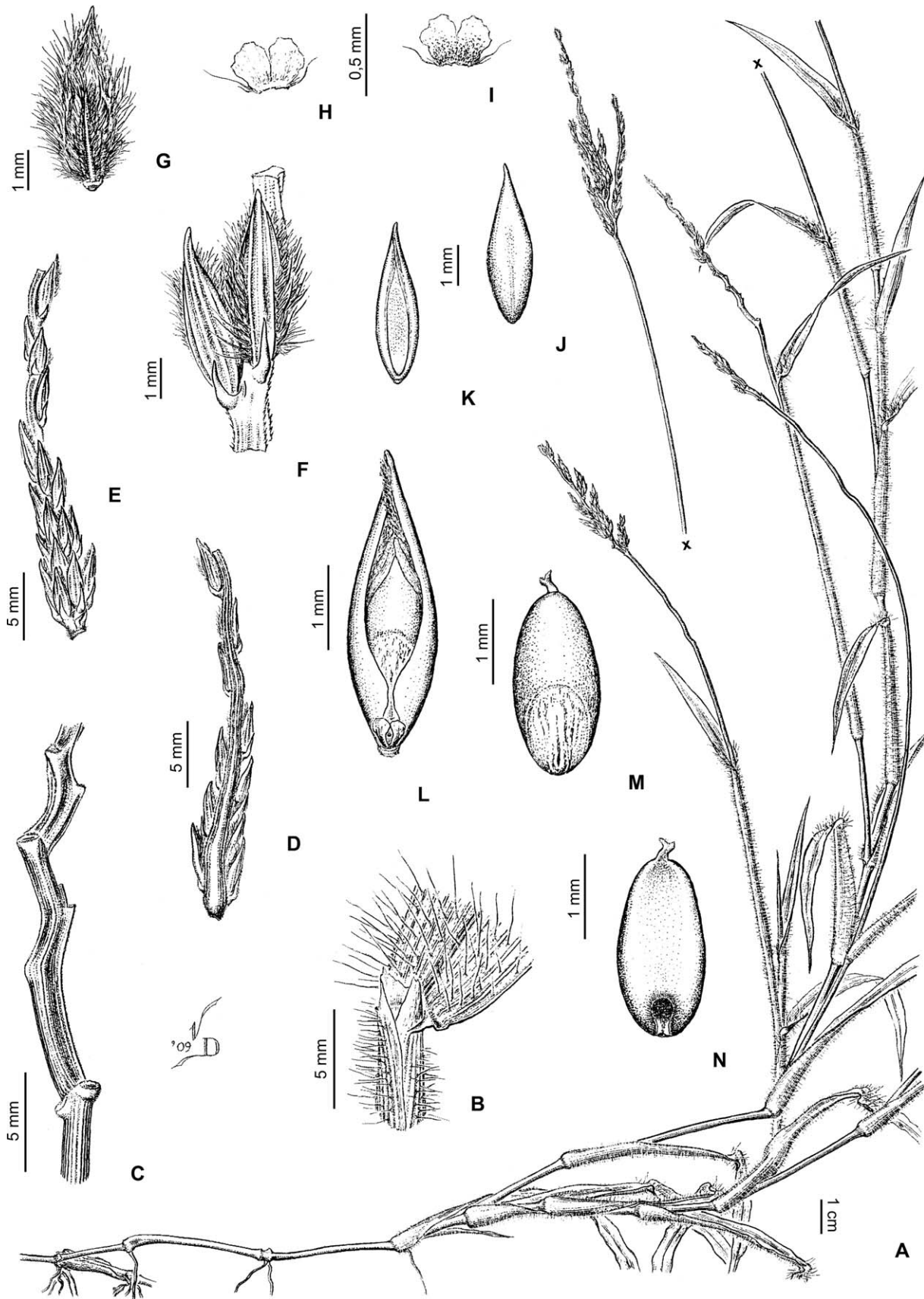


FIG. 1. *Tarigidia axelrodii* (Axelrod & Thomas 14068, US). A. Habit. B. Ligule. C. Main axis after raceme dispersal. D. Raceme, view from the back of the rachis. E. Raceme, view from the upper glume. F. Heteromorphic paired spikelets: subsessile (left) and shortly pedicelled (right). G. Spikelet, view from the back of the upper glume. H-I. Lodicules of the lower flower, dorsal and ventral view. J. Upper floret, view from the back of the upper lemma. K. Upper floret, view from the back of the upper palea. L. Upper palea, lodicules, caryopsis, and the remains of anthers and stigmas. M. Caryopsis, scutellar view. N. Caryopsis, hilar view.

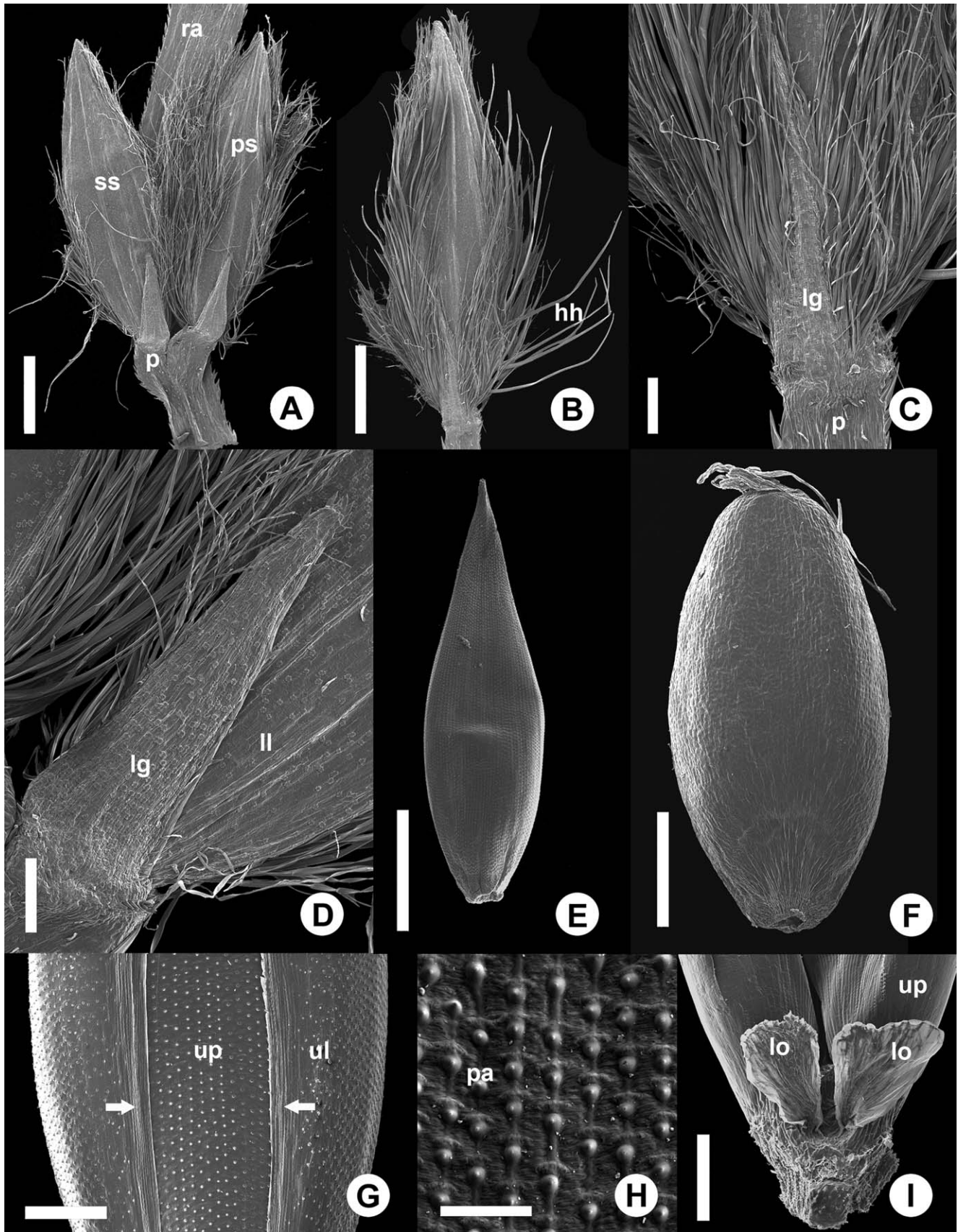


FIG. 2. SEM photographs of *Tarigidia axelrodii* spikelets. A. Rachis fragment with a pair of spikelets. B. Terminal spikelet of a raceme. C. Back of the occasionally pilose lower glume in a terminal spikelet of a raceme. D. Back of the lower glume. E. Upper floret (not containing a mature caryopsis). F. Caryopsis, hilar view. G. Middle portion of the upper floret view from the back of the palea. Note flat and membranous margins of the upper lemma (arrow). H. Striate upper lemma in dorsal view. I. Lodicules of the upper flower. Abbreviations: hh. hirsute hairs; lg. lower glume; ll. lower lemma; lo. lodicule; p. pedicel; pa. papilla; ps. shortly pedicelled spikelet; ra. rachis; ss. sessile spikelet; ul. upper lemma; up. upper palea.

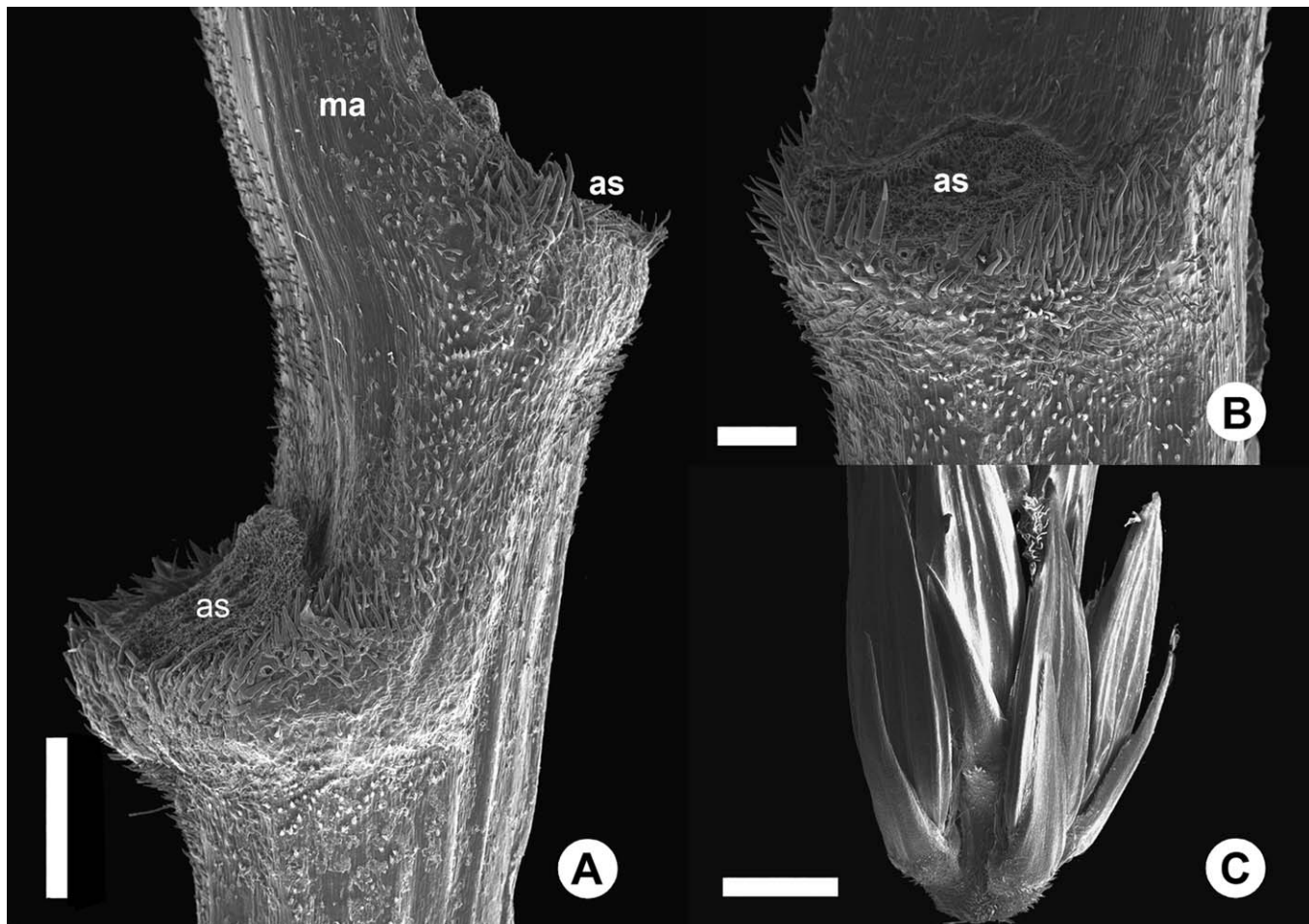


FIG. 3. Main axis and racemes of *Tarigidia axelrodii*. A. Fragment of the main axis in a mature inflorescence showing abscission scars after raceme dispersal. B. Detail of an abscission scar, frontal view. C. Base of a raceme showing congested clusters of spikelets. Abbreviations: as, abscission scars; ma, main axis.

Epidermal cells of upper lemma and palea are 1-papillate and this papilla occupies an eccentric position (Fig. 2H).

In relation to caryopsis dispersal in *D. bicornis*, as well as in most species of the genus, the unit of dispersal is the spikelet. Another dispersal mechanism is exhibited by species with

“tumbleweed” inflorescences and marks a well supported morphology-based clade that is composed of members of *Digitaria* sections *Parvoiglumae* Henrard and *Pennatae* (Stapf) Henrard, and *D.* subg. *Leptoloma* (Chase) Henrard (Vega et al. 2009). The pedicellate spikelets of *Digitaria bicornis* are the first

TABLE 1. Comparative diagnostic characters between *T. axelrodii* and *T. aequiglumis*.

	<i>T. axelrodii</i>	<i>T. aequiglumis</i>
Life cycle duration	annuals	perennials
Height (cm)	ca. 50	80–120
Blade length (mm)	5.5–7	3–4
Inflorescence length (cm)	(3.2–)4–7.5	5–12
Raceme length (cm)	2–4.2	0.5–3
Inflorescence type	panicle with divergent racemes at maturity	contracted panicle, spike-like, or sometimes with long branches not closely appressed to the main axis
Spikelet length (mm)	4.5–5	4–4.5
Spikelet paired (appearance)	heteromorphous	homomorphous
Length relation between lower and upper glumes	unequal	equal or subequal
Lower glume length (mm)	(0.5–)1–1.5(–2.5) (1/4–1/3 of the spikelet)	ca. 2.7–3 (2/3 of the spikelet)
Lower glume nerves and indumentum	1–3 glabrous, rarely pilose, in this case largely exceeding its length	1 glabrous or densely villous, shortly ciliate on the margins
Upper glume length (mm)	3–3.5 (2/3–3/4 of the spikelet)	ca. 2.7–3 (2/3 of the spikelet)
Lower lemma nerves and indumentum	7 glabrous on both sides of midnerve and alternately pilose and glabrous on the remaining zones	5–7 villous between the nerves and near the margins
Upper floret	cartilaginous with membranous margins	not indurated
Caryopsis length (mm) × width (mm)	2.2–2.4 × 1–1.3	unknown
Geographical distribution	Puerto Rico (America)	Namibia and South Africa (Africa)

to disarticulate, followed by the subsessile spikelets. The rachis of the racemes of digitate or subdigitate panicles is persistent after diaspore dispersal (i.e. the panicles persist on the plant).

Tarigidia shows a type of dispersal not observed in *Digitaria*. In *T. axelrodii* the branches of the inflorescences provided with spikelets constitute the units of dispersal; they are rigid, straight, and disarticulate easily at the base. The denuded

main axis persists showing circular abscission scars after the racemes disperse (Fig. 3A-B).

Another characteristic not observed in *Digitaria* is the disposition of the spikelets: due to the poor development of pedicels and internodes between them along the rachis, the spikelets form dense clusters at the base and congested pairs toward the apex of the racemes (Fig. 3C).

KEY TO THE GENERA *ANTHEPHORA*, *TARIGIDIA*, AND *DIGITARIA*

1. Racemes persistent; diaspores formed either by the spikelets or complete inflorescences; spikelets solitary, paired or in groups of 3 or more, each one disarticulating from the pedicels, not surrounded by an involucre of stiffly coriaceous narrowly elliptic several-nerved bracts; lower glumes reduced to a membranous margin or developed, nerveless, rarely 1-nerved, not joined to those of other spikelets, glabrous; upper lemma with a germination flap *Digitaria*
1. Racemes deciduous, constituting the units of dispersal; spikelets grouped in clusters, not disarticulating from the pedicels, surrounded or not by an involucre of stiffly coriaceous narrowly elliptic several-nerved bracts; lower glumes coriaceous, 1–3-nerved, joined or not to those of other spikelets, glabrous or pilose; upper lemma without a germination flap 2
2. Racemes 0.35–1.1 cm long, composed of 2–10 fertile spikelets, surrounded by an involucre of 2–10 sterile spikelets represented by stiffly coriaceous, narrowly elliptic several-nerved bracts, free or connate in lower third; lower glumes joined or not to those of other spikelets *Antheophora*
2. Racemes 0.7–4.2 cm long, composed of 2–21 fertile spikelets, not surrounded by an involucre of bracts; lower glumes not joined to those of other spikelets *Tarigidia*

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