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Revised morphological descriptions of *Otatea nayeeri* and *O. transvolcanica* (Poaceae: Bambusoideae: Guaduinae) and a reproductive key to *Otatea*

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Abstract

Otatea, with 12 described species, is the second most diverse genus in the subtribe Guaduinae. Eleven species of *Otatea* occur in Mexico, of which 10 are endemic. The Mexican *Otatea* species grow in tropical dry forest, the ecotone between tropical dry forest and oak forest, cloud forest, humid oak-pine forest, and xerophilous scrubs. Here, we describe the synflorescence and flowers of *Otatea nayeeri* and *O. transvolcanica*, based on newly collected specimens and review of existing herbarium material. We present a key based on the flowering characters of the Mexican *Otatea* species, and provide expanded morphological descriptions and illustrations of *O. nayeeri* and *O. transvolcanica*. *Otatea nayeeri* and *O. transvolcanica* do not exhibit the gregarious monocarpic flowering pattern that has been recorded for other *Otatea* species. A flowering individual of *O. transvolcanica* was observed being visited by a *Lasiosiglossum (Dialictus)* sp. (Halictidae) bee. This is the first record for *Otatea* being visited by bees. The geographical distribution of *O. nayeeri* is extended northwards to the state of Durango in Mexico.

Keywords: Durango, flower, Mexico, Nayarit, synflorescence

Introduction

With 12 described species, *Otatea* (McClure & E.W. Sm. in McClure (1973: 116)) Calderón & Soderstrom (1980: 21) is monophyletic and the second most diverse of the six genera that belong to subtribe Guaduinae (Bambuseae) (Clark *et al.* 2015, Ruiz-Sánchez & Sosa 2015, Wysocki *et al.* 2015, Tyrrell *et al.* 2018). *Otatea* species range from northern Colombia, El Salvador and Honduras in Central America to northwestern (Sonora) and northeastern (Querétaro) Mexico (Soderstrom in McVaugh 1983, Clark & Cortés 2004, Ruiz-Sánchez *et al.* 2011, Ruiz-Sánchez 2012, 2015, Ruiz-Sánchez & Castro-Castro 2016, Ruiz-Sánchez & Londoño 2017).

Eleven of the 12 *Otatea* species are present in Mexico, and 10 of them are endemic (Ruiz-Sánchez *et al.* 2015, 2019, Ruiz-Sánchez & Castro-Castro 2016, Ruiz-Sánchez & Londoño 2017, Ruiz-Sánchez 2019). The Mexican *Otatea* species grow in tropical dry forest, the ecotone between tropical dry forest and oak forest, cloud forest, humid oak-pine forest and xerophilous scrubs (Ruiz-Sánchez *et al.* 2011, Ruiz-Sánchez 2012, 2015, Ruiz-Sánchez & Castro-Castro 2016).

The species of *Otatea* are monocarpic, with flowering periods every 20–30 years. This has made it difficult to obtain information on reproductive traits for many species. For example, *Otatea ramirezii* Ruiz-Sánchez (2012: 25) was described from vegetative material, as were *O. carrilloi* Ruiz-Sánchez, Sosa & Mejía-Saulés in Ruiz-Sánchez *et al.* (2011: 324), *O. nayeeri* Ruiz-Sánchez in Ruiz-Sánchez & Castro-Castro (2016: 213), *O. transvolcanica* Ruiz-Sánchez & L.G. Clark in Ruiz-Sánchez *et al.* (2011: 330), and *O. victoriae* Ruiz-Sánchez (2015: 267). In 2012, after *O. ramirezii* was published, the taxon was found flowering in the Mexican National Living Bamboo Collection in the Francisco Javier Clavijero Botanical Garden in Xalapa, Veracruz and at the type locality. Those flowering records allowed us to describe the synflorescences and flowers of the species (Ruiz-Sánchez 2013).

Based on a recent review of material in the United States National herbarium (US), we were able to confirm the determination of a specimen, in a reproductive stage, of *Otatea nayeeri* deposited there previously identified as *O. acuminata* (Munro 1868: 25) Calderón & Soderstrom (1980: 21). A living collection of *O. nayeeri* began flowering in September 2018 in the Mexican National Living Bamboo Collection in the Francisco Javier Clavijero Botanical Garden, which allowed us to obtain additional reproductive material of this species. Furthermore, during recent fieldwork (November 2017 and April 2018) in the Mexican state of Jalisco, we found a small population (fewer than five individuals) of *O. transvolcanica* that was flowering. The *O. transvolcanica* specimen growing in the Mexican National Living Bamboo Collection in the Francisco Javier Clavijero Botanical Garden, collected from the type locality in the Estado de Mexico, was also flowering. We here present a key based on the reproductive characters to the *Otatea* species, and revised morphological descriptions and illustrations for the synflorescence and flowers of *O. nayeeri* (Figs. 1–2) and *O. transvolcanica* (Figs. 3–4).

Key to the *Otatea* species based on reproductive characters

1. Synflorescences with 30–125 spikelets 2
- Synflorescences with 2–15 spikelets 6
2. Synflorescences 9–28 cm long 3
- Synflorescences 5–10 cm long 5
3. Synflorescences 17.5–28 cm long; glume II 9–13 mm long (including the awn), glabrescent *O. transvolcanica*
- Synflorescences 9–15 cm long; glume II 5–9.5 mm long (including the awn), scabrous to sparsely pubescent to the apical third 4
4. Glumes sparsely pubescent to the apical third; lemmas 9–9.5 mm long including the awn, abaxially sparsely pubescent *O. nayeeri*
- Glumes scabrous; lemmas 10–13 mm long including the awn, abaxially scabrous *O. fimbriata* Soderstrom in McVaugh (1983: 280)
5. Lemmas pubescent; paleas keels pubescent; lodicules glabrous with ciliate margins *O. acuminata*
- Lemmas scabrous; paleas keels glabrous; lodicules and margin pubescent at the upper third *O. ramirezae*
6. Glumes glabrous 7
- Glumes scabrous, scabrous-pubescent or pubescent 8
7. Lemmas slightly scabrous, 10–13 mm long; paleas 7.5–8.5 mm long *O. rzedowskiorum* Ruiz-Sánchez (2015: 265)
- Lemmas scabrous-pubescent, 14.5–21 mm long; paleas 14–15.4 mm long *O. glauca* Clark & Cortés (2004: 3)
8. Spikelets purple-blue *O. ximenae* Ruiz-Sánchez & Clark in Ruiz-Sánchez *et al.* (2011: 330)
- Spikelets green 9
9. Lemmas scabrous 14.3–18 mm long *O. reynosoana* Ruiz-Sánchez & Clark in Ruiz-Sánchez *et al.* (2011: 328)
- Lemmas pubescent on the lower half 19–24 mm long *O. colombiana* Ruiz-Sánchez & Londoño (2017: 2017)

Revised morphological descriptions

Otatea nayeeri Ruiz-Sánchez (Figs. 1, 2).

Type:—MEXICO. Nayarit: Acaponeta, road from Casas Coloradas to San Diego de Alcalá at 500 m approx. from the intersection of the tres caminos, 770 m, 22°26'37.99"N, 105°10'37.59"W, 27 November 2014, E. Ruiz-Sánchez & A. Castro-Castro 493 (holotype IBUG!, isotypes ISC!, MEXU!, MO!, US!).

Description:—Rhizomes pachymorph with necks 35–74 cm long. Culms 3–6 m tall, 1–5 cm in basal diameter, erect; internodes 8–24 cm long, terete, glabrous, green and pruinose when young, culms with some internode solid and some hollow on the same culm, when hollow then thick-walled. Culm leaves 28.5–63.5 cm long, rectangular, overlapping, deciduous, thin-papery; sheaths 26–41.5 cm long, 5.8–8 cm wide at the base, rectangular, abaxially sparsely pubescent with thick brown-copper hairs, hairs deciduous, margins minutely ciliate, the leaf blades polymorphic in size, the basal leaf blades 2.5–9.5 cm long, triangular, erect, persistent, shorter than the sheaths, abaxially and adaxially glabrous, the margins minutely ciliate, the apex acuminate; the mid-culm leaf blades 10.5–22 cm long, triangular, reflexed, deciduous, shorter than to half the length of the sheath, abaxially glabrous, adaxially pubescent, margins minutely ciliate, apex acuminate; inner ligule, coriaceous 0.5–2 mm long, truncate and glabrous; oral setae absent; fimbriae at the summit of the sheath present on both sides, 7–8 mm long, ca. 0.2 mm wide, flat, deciduous, curly. Branching intravaginal; three main branches produced per node, 57–92 cm long, diverging from the main culm at 45°, and rebranching in second order developing one branch per bud; supranodal ridge pronounced; nodal line horizontal. Foliage leaves 2–4 per complement; sheaths pubescent, rounded on the back with a sheath summit extension on both

sides; outer ligule an irregular glabrous rim up to 0.2 mm long with two lobes at the apex, these 0.5–1.5 mm long, 1–1.5 mm wide; inner ligule 0.5–1.5 mm long, truncate, irregular, glabrous; oral setae 3–8 mm long, basally free, flattened, abaxially scabrous, free from the inner ligule, in living specimens the base purple with white tips; fimbriae absent; pseudopetioles ca. 3 mm long, pulvinate at the base, purplish; blades 14.5–23.5 cm long, 1.3–2.1 cm wide, lanceolate, adaxially glabrous, glaucous, abaxially pubescent, green, not tessellate, with a very dense patch of white cilia at the base extending along both sides of the midrib for more than 10 mm, the base attenuate, the apex attenuate-subulate, the margins serrulate. Synflorescences 9–14 cm long, paniculate, 50–65 spikelets, the rachis angular, scabrous; pedicels 5–15 mm long, angular, scabrous. Spikelets 1.5–2 cm long, green, with 3–4 florets, upper floret sometimes sterile; rachilla joints 4–5 mm long, scabrous and pubescent at the apex of each joint; glume narrowly triangular and navicular, abaxially sparsely pubescent to the apical third; glume I 4.5–5 mm long including the awn, 5-nerved, the awn 1 mm long; glume II 5–5.5 mm long including the awn, 7-nerved, the awn 1 mm long; lemmas 9–9.5 mm long including the awn, narrowly triangular and navicular, abaxially sparsely pubescent 7-nerved, the awn 1.5–2 mm long, antorseously scabrous; paleas 8 mm long, the keels scabrous-pubescent, the sulcus pubescent, wing scabrous-pubescent, apex rounded and pubescent. Lodicules 3, abaxially glabrous, margins ciliate, dark brown, the anterior pair 1.2–1.5 mm long, the posterior one 1–1.2 mm long. Caryopsis 5.5–6 mm long, dark amber.

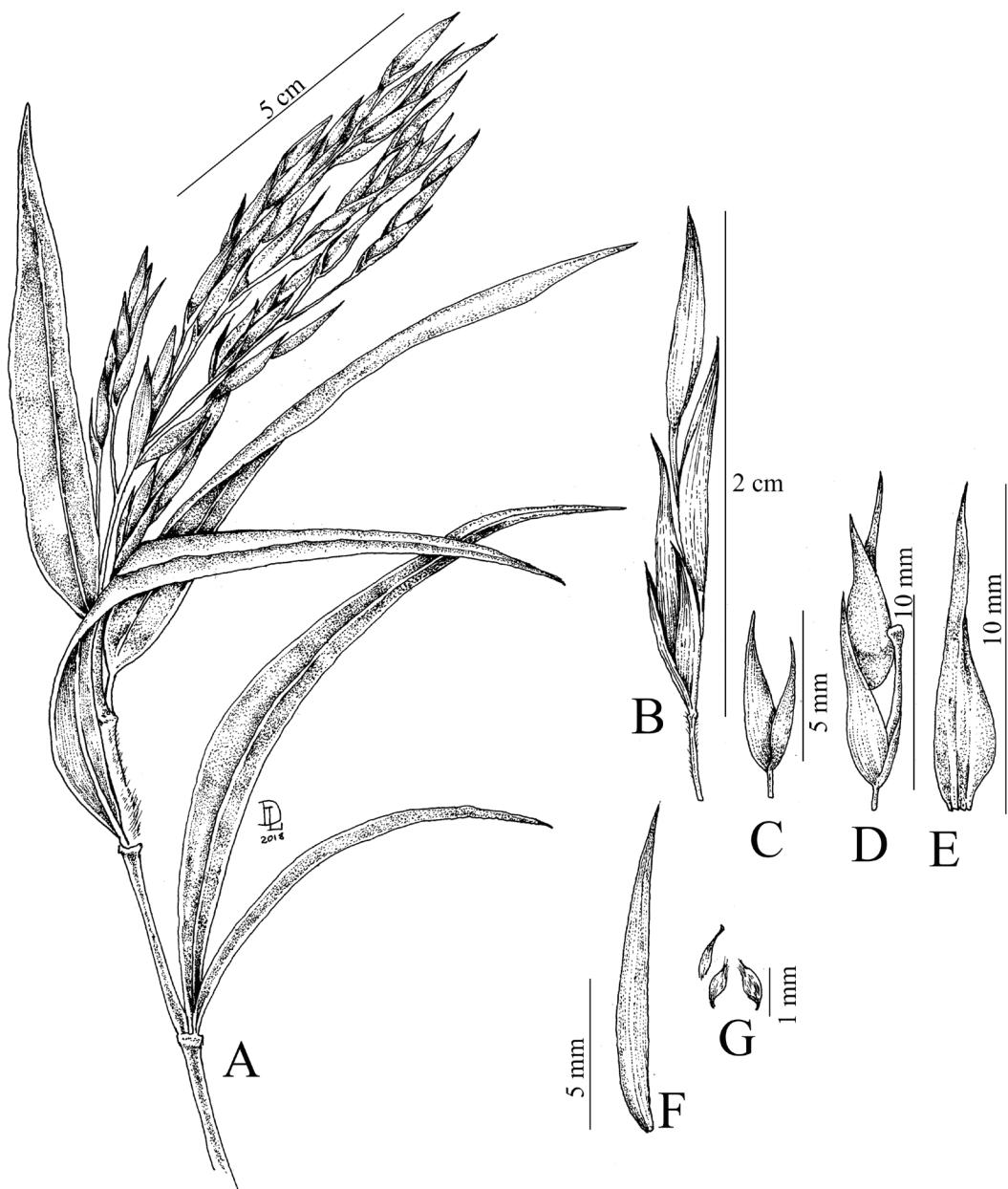


FIGURE 1. *Otakea nayeeri*. A. Flowering branch, with synflorescence. B. Spikelet. C. Glumes. D. Floret, showing glumes and rachilla joint. E. Lemma ventral view. F. Lemma lateral view. G. Lodicules. Based on R. Macías s.n. (IBUG). Illustrated by Daniel Barba.



FIGURE 2. *Otakea nayeeri*. Flowering branch, with synflorescence. Photo by Phil Brewster.

Specimens Examined:—MEXICO. Durango: Tamazula, La Bajada, 460 m, 25°3'8"N, 106°46'40"W, November 1921, J. González Ortega 4341 (CIIDIR, MEXU, US); La Bajada, November 1922, J. González Ortega 571 (MEXU). Veracruz: Xalapa, Mexican National Living Bamboo Collection, Francisco Javier Clavijero Botanical Garden (cultivated), 6 September 2018, R. Macías s.n (IBUG).

Otakea nayeeri was previously documented only from the state of Nayarit (Ruiz-Sánchez and Castro-Castro 2016). Through review of additional herbarium specimens (CIIDIR, MEXU, US), we found specimens of the species from Durango (J. González Ortega 4341 (CIIDIR, MEXU, US), J. González Ortega 571 (MEXU)) that were previously identified as *O. acuminata* by Ruiz-Sánchez *et al.* (2011). The geographical distribution of this species now extends northwards to the state of Durango in Mexico.

Otakea transvolcanica Ruiz-Sánchez & L.G. Clark (Figs. 3–4).

Type:—MEXICO. Estado de México: municipio de Temascaltepec, Puente Río Verde a 4.5 km de Temascaltepec por la carretera rumbo a Toluca, creciendo en la cañada a orilla del Río Verde, 1840 m, 4 Sep. 2007, E. Ruiz-Sánchez, D. Ángulo & E. Gándara 179 (holotype XAL!; isotypes IBUG!, ISC!, MEXU!, MO!, NY!, US!).

Description:—Rhizome with necks 30–45 cm long. Culms 3–8 m tall, 1–6 cm in basal diameter, erect to apically arched; internodes 24–27 cm long, terete, glabrous, light green when young and yellow when old, pruinose, basal internodes solid, the apical hollow, the walls 2.8–4 mm thick, the lacuna occupying ≥ 50% of the total diameter. Culm leaves 36–46 cm long, overlapping, persistent; sheaths 24–29.5 cm long, 7–11 cm wide at the base, 1.3–3.2 times as long as the blades, ± rectangular, abaxially hispid for the upper 1/2–2/3, the shoulders rounded and sometimes with a small sheath summit extension 2–3 mm long, the margins glabrous; inner ligule 0.9–2.2 mm long, truncate, glabrous; oral setae 10–15 mm long, deciduous, present only in young shoots, green; fimbriae absent; blades 9–20 cm long, triangular, reflexed, deciduous, adaxially and abaxially glabrous, apex subulate. Branching extravaginal; one or two main, unequal branches per node, if three then the central 2 times wider than the lateral, 110–130 cm long, diverging from the main culm at 45°; supranodal ridge pronounced; nodal line more or less horizontal. Foliage leaves 6–10 per complement; sheaths glabrous, rounded on the back, sheath summit extension absent; outer ligule an irregular glabrous rim to 0.3–0.7 mm long with two lobes at apex, these 3–11 mm long, 1.9–4.5 wide; inner ligule

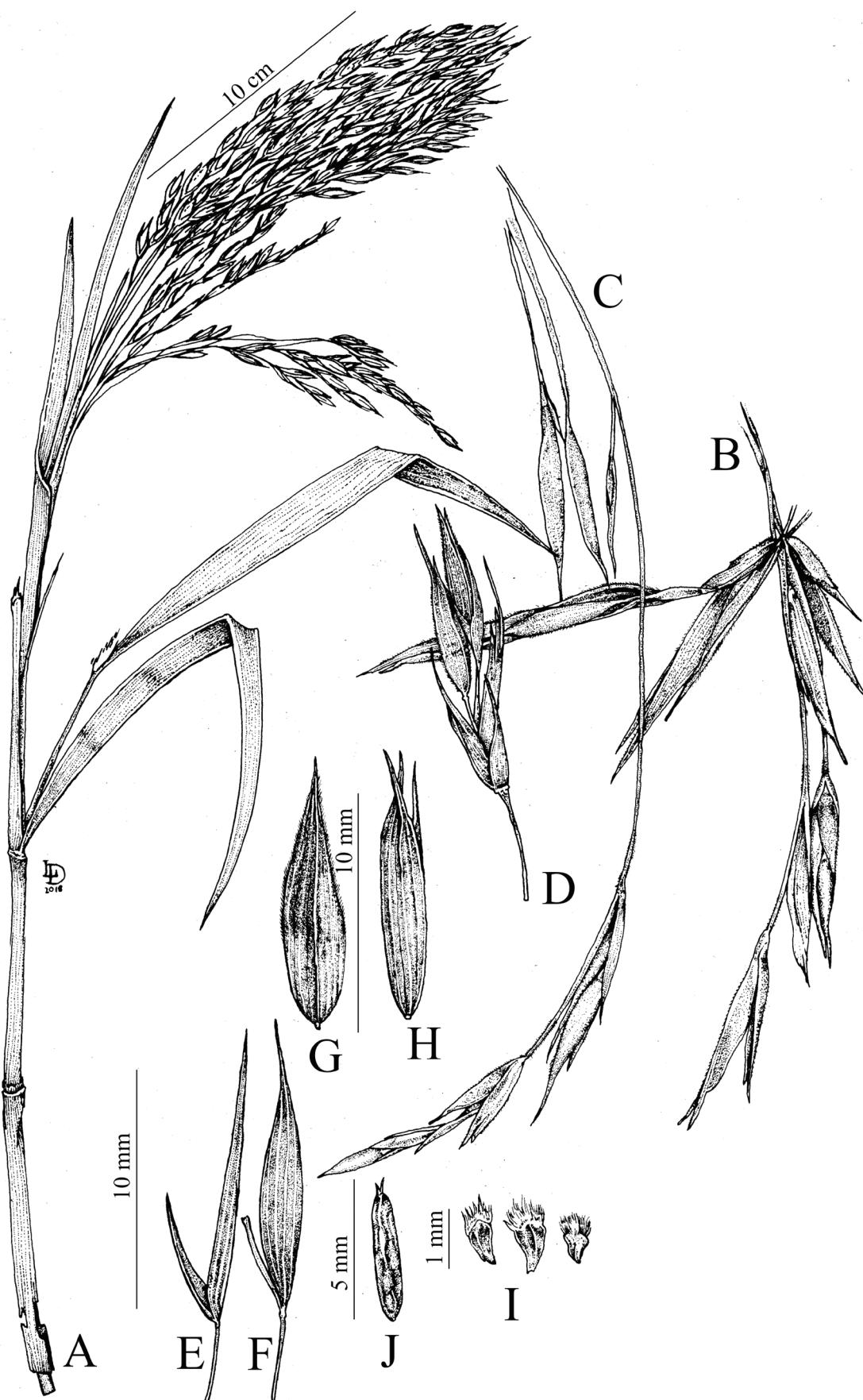


FIGURE 3. *Otakea transvolcanica*. A. Flowering branch, with synflorescence. B, C. Synflorescence branches showing spikelets. D. Spikelet. E. Glumes, lateral view. F. Floret, showing lemma and rachilla joint. G. Lemma ventral view. H. Lemma lateral view and palea. I. Lodicules. J. Caryopsis. Based on E. Ruiz-Sánchez & J.P. Ortíz-Brunel 576 (IBUG). Illustrated by Daniel Barba.

0.1–0.2 mm long, truncate; oral setae 13–21.5 mm long, basally connate for 1/3 or more of their length, splitting into narrower segments above, flattened, glabrous, free from the inner ligule, in living specimens purple with green apices; fimbriae on both sides of the blade at the apex, 5–15 mm long, 0.05–0.1 mm in diameter, slightly flattened, curly, glabrous and deciduous; pseudopetioles ca. 3 mm long, yellowish, pulvinate at the base; blades 34–60 cm long, 2.5–6 cm wide, lanceolate, adaxially glabrous, glaucous, abaxially scabrous, green, not tessellate, with a very dense patch of yellow cilia at the base extending along both sides of the midrib for 12.5–26.1 mm, the base attenuate, the apex attenuate-subulate, the margins serrulate. Synflorescences 17.5–28 cm long, paniculate, 55–125 spikelets, rachis angular, glabrous; pedicels 4–18 mm long, angular, glabrous. Spikelets 2–3 cm long, green, with 2–4 florets, upper floret sometimes sterile; rachilla joints 5–6 mm long, sparsely pubescent; glume narrowly triangular and navicular, abaxially glabrescent; glume I 4–8 mm long including the awn, 3-nerved, the awn 1–4 mm long; glume II 9–13 mm long including the awn, 3-nerved, the awn 3–5 mm long, some spikelets lack glume I or it is developed in an internode below the glume II; lemmas 11–15 mm long including the awn, narrowly triangular and navicular, abaxially scabrous 8–9-nerved, the awn 3–5 mm long, antrorsely scabrous; paleas 9–10 mm long, the keels scabrous, the sulcus pubescent, wing glabrescent, the apex rounded, and acute. Lodicules 3, abaxially glabrous, margins ciliate, with translucent cilia, the anterior pair 1 mm long, the posterior one 0.8 mm long, dark brown. Caryopsis 5.5–6 mm long, dark amber.



FIGURE 4. *Otatea transvolcanica*. A. Flowering branch, with synflorescence. B. Detail of spikelet. White arrow indicates *Lasioglossum (Dialictus)* sp. (Halictidae) bee removing pollen. C. White arrow indicates *Lasioglossum (Dialictus)* sp. bee removing pollen at the anther. Photos by Eduardo Ruiz-Sánchez.

Specimens Examined:—MEXICO. Jalisco: Tecalitlán, km 13 road from Tecalitlán to Jilotlán, 1646 m a.s.l., 8 November 2017, E. Ruiz-Sánchez & J.P. Ortíz-Brunel 576 (IBUG); *ibid*, 15 April 2018, E. Ruiz-Sánchez & J.P. Ortíz-Brunel 582 (IBUG).

Discussion

With the revised synflorescence and flower descriptions for *Otatea nayeeri* and *O. transvolcanica* presented here, we have increased to 10 the number of species of *Otatea* known from Mexico for which complete descriptions are available. There are other two species (*Otatea carilloi* and *O. victoriae*) that have never been observed flowering nor collected with flowers. These two species are in cultivation at the Francisco Javier Clavijero Botanical Garden, where they are being monitored for flowering.

The woody bamboo species present four different flowering patterns: (1) a small percentage of clumps flower the year (or two) before and after the main flowering event; (2) gregarious flowering occurs in patches in successive years; (3) variation in periodicity between populations leads to diffuse temporality within a species; and (4) “sporadic flowering”, which may imply random or other non-gregarious patterns (Janzen 1976, Franklin 2004). *Otatea nayeeri* and *O. transvolcanica* do not exhibit the gregarious monocarpic flowering pattern (Janzen 1976) that has been recorded for other *Otatea* species (e.g. *O. fimbriata*, *O. ramirezii*, *O. rzedowskiorum*) (Ruiz-Sánchez *et al.* 2011, Ruiz-Sánchez 2013, 2015). For *O. nayeeri* we found only a single branch flowering in the Mexican National Living Bamboo Collection at the Francisco Javier Clavijero Botanical Garden, and the complete clump flowered some months later. The sporadic flowering pattern was also observed for *O. glauca* (Ruiz-Sánchez 2013).

In contrast to flowering observed in *Otatea nayeeri*, we found two individuals of *O. transvolcanica* from a single population in the state of Jalisco flowering and the single individual growing in the Francisco Javier Clavijero Botanical Garden that came from the type locality at Estado de México was also flowering at the same time. We visited two different populations of this species in Jalisco, and only one of them was flowering. This flowering pattern corresponds to the variation in periodicity between populations and leads to diffuse temporality within species (Franklin 2004).

The flowering individual of *O. transvolcanica* living in the Mexican National Bamboo Collection was observed being visited by a *Lasioglossum (Dialictus)* sp. (Halictidae) bee, which was removing pollen (Fig. 4B,C). This is the first record for any *Otatea* species being visited by bees. Bees have been recorded collecting pollen from other Mexican woody bamboo species [*Guadua inermis* Ruprecht ex Fournier (1886: 129) and *G. paniculata* Munro (1868: 65)] (Ruiz-Sánchez *et al.* 2017). This is also the first record of a *Lasioglossum (Dialictus)* sp. bee visiting any bamboo flowers (Ruiz-Sánchez *et al.* 2017).

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