

# Flower use by late nineteenth-century orchid bees (*Eufriesea surinamensis*, Hymenoptera, Apidae) nesting in the Catedral Basílica Santa María la Antigua de Panamá

Paola Galgani-Barraza<sup>1</sup>, Jorge Enrique Moreno<sup>1</sup>, Sofia Lobo<sup>2</sup>,  
Wendy Tribaldos<sup>3,4</sup>, David W. Roubik<sup>1</sup>, William T. Wcislo<sup>1</sup>

**1** Smithsonian Tropical Research Institute (STRI), Panamá, Apartado 0843-03092, Balboa, Panamá  
**2** Dalmática Conservação e Restauro, Rua da zona Industrial de Covilhã, nº236 4620-276, Lustosa – Lou-  
sada, Portugal **3** Comité Arquidiocesano Amigos Iglesias Casco Antiguo, Panamá **4** Independent museologist,  
educator and journalist. Costa del Este, Avenida Centenario, Edificio PMG – Panama City, Panamá

Corresponding author: William T. Wcislo ([WcisloW@si.edu](mailto:WcisloW@si.edu))

Academic editor: J. Neff | Received 18 August 2019 | Accepted 24 November 2019 | Published 30 December 2019

<http://zoobank.org/2F25B41C-9797-4302-9A02-C9E923B24224>

**Citation:** Galgani-Barraza P, Moreno JE, Lobo S, Tribaldos W, Roubik DW, Wcislo WT (2019) Flower use by late nineteenth-century orchid bees (*Eufriesea surinamensis*, Hymenoptera, Apidae) nesting in the Catedral Basílica Santa María la Antigua de Panamá. Journal of Hymenoptera Research 74: 65–81. <https://doi.org/10.3897/jhr.74.39191>

## Abstract

A recent restoration of the Basilica Cathedral in Casco Viejo, Panamá, revealed that prior to 1871–1876 female orchid bees (*Eufriesea surinamensis*) built large nesting aggregations high above the main altar, based on physical evidence dating to a nineteenth-century restoration. Bees constructed cells in approximately 120 clusters in six different aggregations on the reredos (“altarpiece”). Palynological analyses of cell contents showed that bees visited 48 species of plants, representing 43 genera and 23 families. Contents of bee cells reflect elements of floristic diversity surrounding Panama City that are seen in historical contemporaneous photographs of the nesting site and environs.

## Resumen

Una restauración reciente de la Catedral Basílica en el Casco Viejo de la ciudad de Panamá reveló que las hembras de abejas solitarias (*Eufriesea surinamensis*) nidificaron en lo alto de su retablo mayor previo a 1871–1876, basada en evidencia física de una restauración del siglo XIX. Las abejas construyeron celdas en aproximadamente 120 grupos de seis agregaciones diferentes en este retablo. Un análisis de los granos de polen dentro de estos nidos demostró que las abejas visitaron 48 especies de plantas que representan 43 géneros y 23 familias. Los elementos de la diversidad florística en la ciudad de Panamá se pueden observar en fotografías históricas de esta época del sitio de anidación y sus alrededores.

## Keywords

Euglossini, pollination, floral utilization, nesting sites, historical reconstruction

## Introduction

The Euglossini is a diverse Neotropical taxon comprised of five genera and nearly 200 species of beautiful, often brilliantly colored and metallic bees (Dressler 1982; Ramírez et al. 2002; Cameron 2004; Roubik and Hanson 2004). Males are well-known for their behavior in collecting chemical fragrances, mainly from orchids and thereby pollinating them (Dressler 1982). Females are more secretive. Their nests generally are dispersed and difficult for us to locate (reviewed by Ramírez et al. 2002; Wcislo et al. 2012). Consequently, relatively little is known about females' behavior, including which plants they visit to collect floral resources for food (pollen and nectar) and nest-building materials (resin and wood fragments), and which plants they pollinate. Orchid bees tend to be denizens of natural forests and adjacent biomes (Dressler 1982; Roubik and Hanson 2004). Some species tolerate disturbances due to human activities (e.g., López-Uribe et al. 2008; Brosi 2009), and one species established itself in Florida USA, well outside its native range (Pemberton and Wheeler 2006). Based on limited information, females tend to gather pollen and nectar from many flowers, and do not specialize on specific host plant taxa (e.g., Cortopassi-Laurino et al. 2009; Villanueva-Gutierrez et al. 2013). For most euglossine species, however, there are no data on pollen preference and utilization.

The genus *Eufriesea* contains about 52 species of large bees (13–27 mm long), many of which are brilliantly metallic in color, while others have striking bands of yellow and black hairs (Michener 2007). They are mainly neotropical-forest-loving creatures, though species extend to southern Argentina and north to Sinaloa and Chihuahua, México (Kimsey 1982). *Eufriesea surinamensis* is widely distributed from central México to southern Brazil, occurring in forested, cultivated and disturbed habitats, up to 1100 m (Kimsey 1982; Roubik and Hanson 2004). Nests consist of exposed, adjacent brood cells (~13 × 22 mm) constructed of plant resin mixed with numerous small pieces of tree bark wood (Bennett 1972; Myers and Loveless 1976; Kimsey 1982). Isolated cells or aggregated clusters are situated on natural sheltered cavities and crevices, such as under overhanging rocky banks or in cliff caves, within rotten hollows in termite nests, under dead bark, or inside bamboo internodes (*op. cit.*). Females also

readily use sheltered human-built structures (e.g., under flooring, eaves, and trestles). A female constructs a cell, in which she places a cache of pollen mixed with nectar, lays an egg, and seals the cell. The larva feeds on the pollen and nectar, and later defecates the undigested pollen remains on an interior wall of the cell, coincident with the development of pupal features within the larval exoskeleton (Rozen 2018). Multiple females may build cells in close proximity to cells built by others, re-use the cells, and defend them from take-over, but they do not cooperate and are aggressive to neighbors (Myers and Loveless 1976). Nesting sites are likely re-used over a number of years by successive generations (Bennett 1972; Myers and Loveless 1976; Young 2012).

Floral resources used by *E. surinamensis* are little known, and we know of no published palynological studies of brood cell contents. Males are readily attracted by the scent vanillin in forested regions, and visit the orchids *Notylia*, *Pterostemma*, *Peristeria*, and *Sievekingia* (Orchidaceae) (Roubik and Hanson 2004). Based on specimen label data, Kimsey (1982) reports that females visited *Solanum* sp. (Solanaceae) and *Cassia* sp. (Fabaceae) for pollen, and also visited *Psidium guajava* (Myrtaceae), *Petastoma pateliferum* (Bignoniaceae), and *Argyria speciosa* (Convolvulaceae) for unknown purposes.

Here we provide an analysis of pollen grains recovered from old brood cells of *E. surinamensis* nesting in an urban setting in late nineteenth-century Panamá. The nesting sites were within the Basilica Cathedral, which was consecrated in 1796 (Calvo 1999). An extensive restoration was completed in 2018, in preparation for the consecration of a new altar by Pope Francis. While restoring the reredos (“altarpiece”; Fig. 3A), workers discovered large numbers of bee cell clusters in numerous locations; many cells were covered with gold leaf and other golden material applied during an earlier restoration more than a century ago. These golden bee cells reliably date the time of nest cell construction prior to the years 1871–1876, when restoration workers repaired damage from an 1870 fire (Calvo 1999; Lobo and Tribaldos unpublished MS).

In the face of changing environments, and recognizing that bees play key roles in most ecosystems as primary pollinators, we looked to the past to analyze historical data on pollen use by orchid bees, *E. surinamensis*, living in a human-modified environment. Our study provides a baseline for comparative studies with contemporary populations in natural environments. The unusual nesting site—within the first Cathedral on *tierra firme* in the Americas—helps call attention to Francis’ urgent plea in *Laudato Si* (2015, §42), for the need to increase investment in research to better understand the functions of natural ecosystems and their component species, and how these are being shaped by significant environmental modifications resulting from collective human behavior.

## Material and methods

Bee nests or cell clusters were discovered during restoration work of the Basilica Cathedral in Casco Viejo, Panama (8°57'N, 79°32'W) in 2018 by S. Lobo and other restorers working for Dalmática Conservação e Restauo. W. Tribaldos then brought

them to the attention of scientists at the Smithsonian Tropical Research Institute (STRI). These cells were carefully removed using chisels, spatulas and related restoration tools, and were sent to STRI. Twenty-seven brood cells were selected for analyses from the recovered cells.

Following chemical washes to isolate pollen grains at STRI's Center for Tropical Paleoecology & Archaeology (CTPA), we carried out standard palynological procedures (methods in Roubik and Moreno 1991). Subsequently, permanent microscope preparations were made using glycerin jelly as a mounting medium and paraffin as a sealant. Transects of all preparations were made at 40× magnification using a Nikon Eclipse-Ni binocular scope in order to identify all pollen types. Both biological bright light and differential interference contrast (DIC) microphotographs were obtained at 100× magnification using a Nikon DS-Ri1. The magnification of the camera lens of the Nikon scope was 0.7×, yielding a final magnification of 700 times unless indicated otherwise (Plates 1–5). Each photograph displays its own scale (in microns), but photographs in each plate are not to the same scale. Photographs are alphabetically sorted in families, genera and species. Palynology and pollen grain recognition was based on Moore et al. (1991) and Punt et al. (2007). Botanical names were established at the species level if possible, by comparisons with local and regional pollen atlases, STRI collections and botanical inventories (e.g., Croat 1978; Roubik and Moreno 1991; Moreno et al. 2014). The taxonomic status of botanical names was updated using the Tropicos on-line database (Missouri Botanical Garden 2019), following the new angiosperm phylogeny classification (APG IV 2016), and a new subfamily classification of the Leguminosae (LPWG 2017; Banks and Lewis 2018).

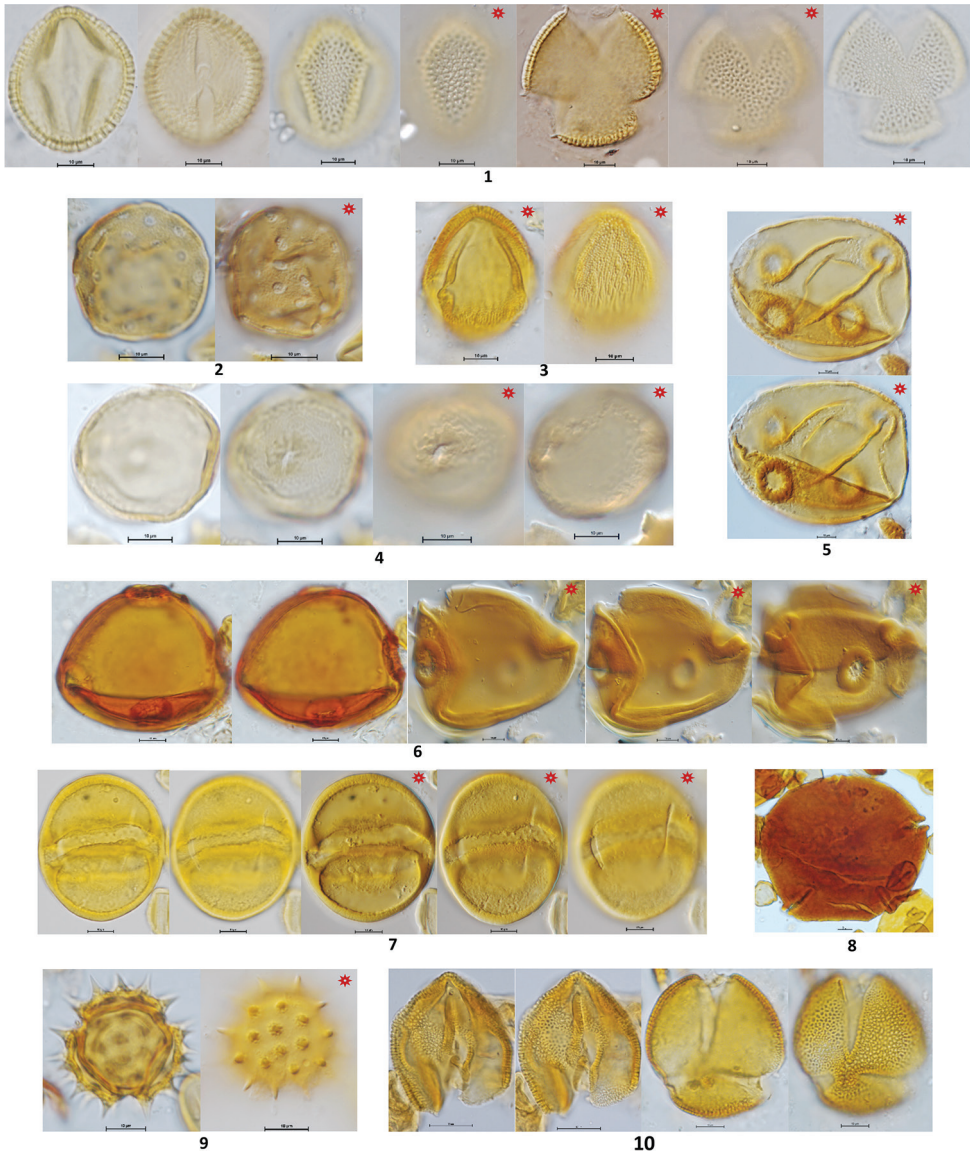
External fragments of nests, mainly small pieces of bark, were subjected to chemical analyses to obtain the siliceous fraction containing phytoliths for possible identification [methods from Piperno (2006) and using a reference collection at STRI's CTPA].

Voucher specimens of the bee cells and pupae are in the STRI Dry Reference Collection, which also houses the remaining unprocessed nest cells.

## Results

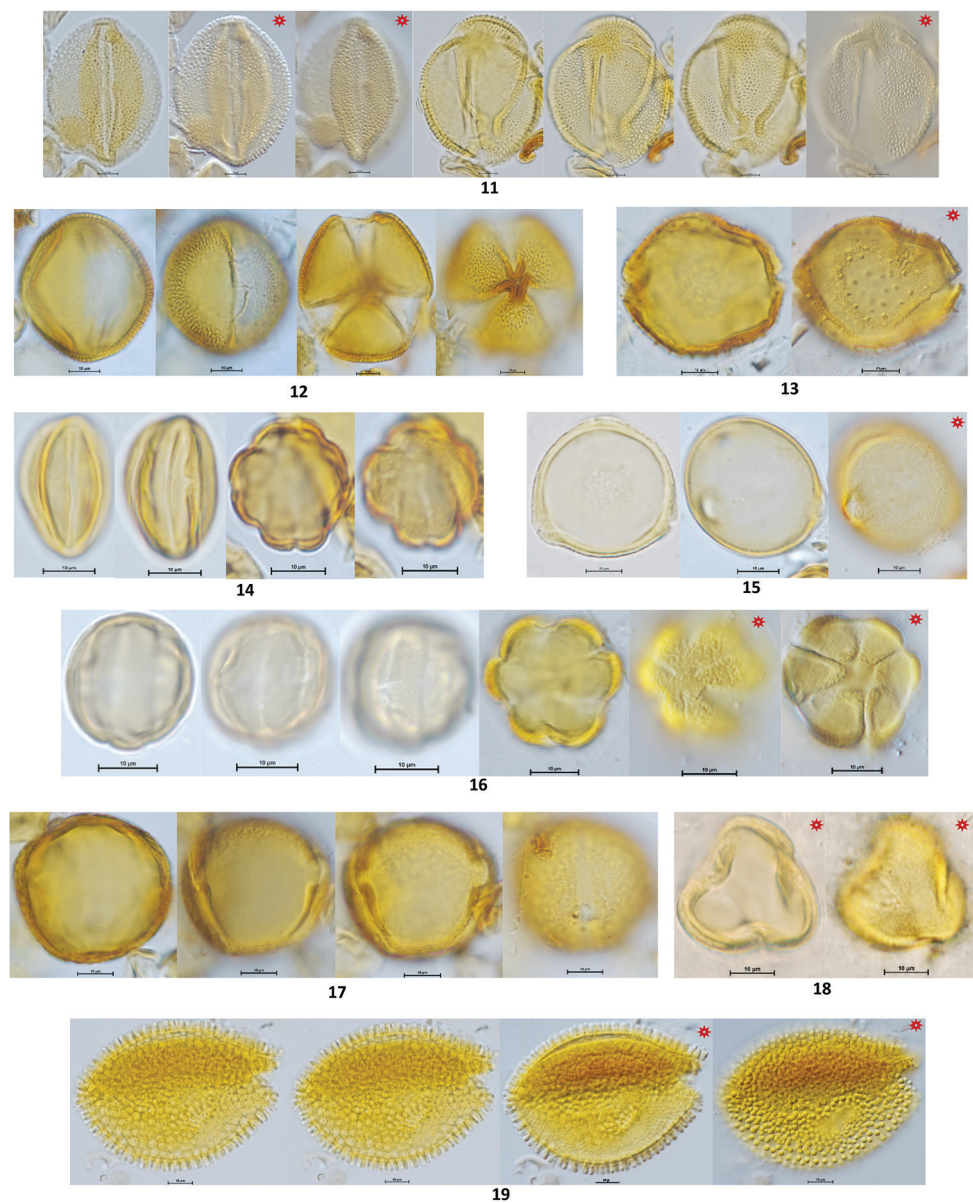
The nesting site was surrounded by a mosaic of disturbed forest and open land (Figs 1, 2). Brood cells ( $N = \sim 550$ ) of *Eufriesea surinamensis* were distributed among approximately 120 clusters or aggregations on the six capitals behind and above the altar (Fig. 3A), built in the crevices and scrolls of the capitals of the columns (Fig. 3B, C), at heights comparable to upper understory and lower canopy in adjacent natural forests. Nests were found in clusters (Fig. 4A, D) or in isolation. (Fig. 4E). Wood fragments were used extensively in nest construction (Fig. 4C, E); three different phytoliths were recovered from these fragments, but they are common to many species of woody plants, including *Vismia* (Hypericaceae) and could not be identified further (D. Piperno *in litt.* 2019). Nest cells must have been constructed prior to restoration work to repair fire damage (see Introduction). The nineteenth-century restorers left the bee





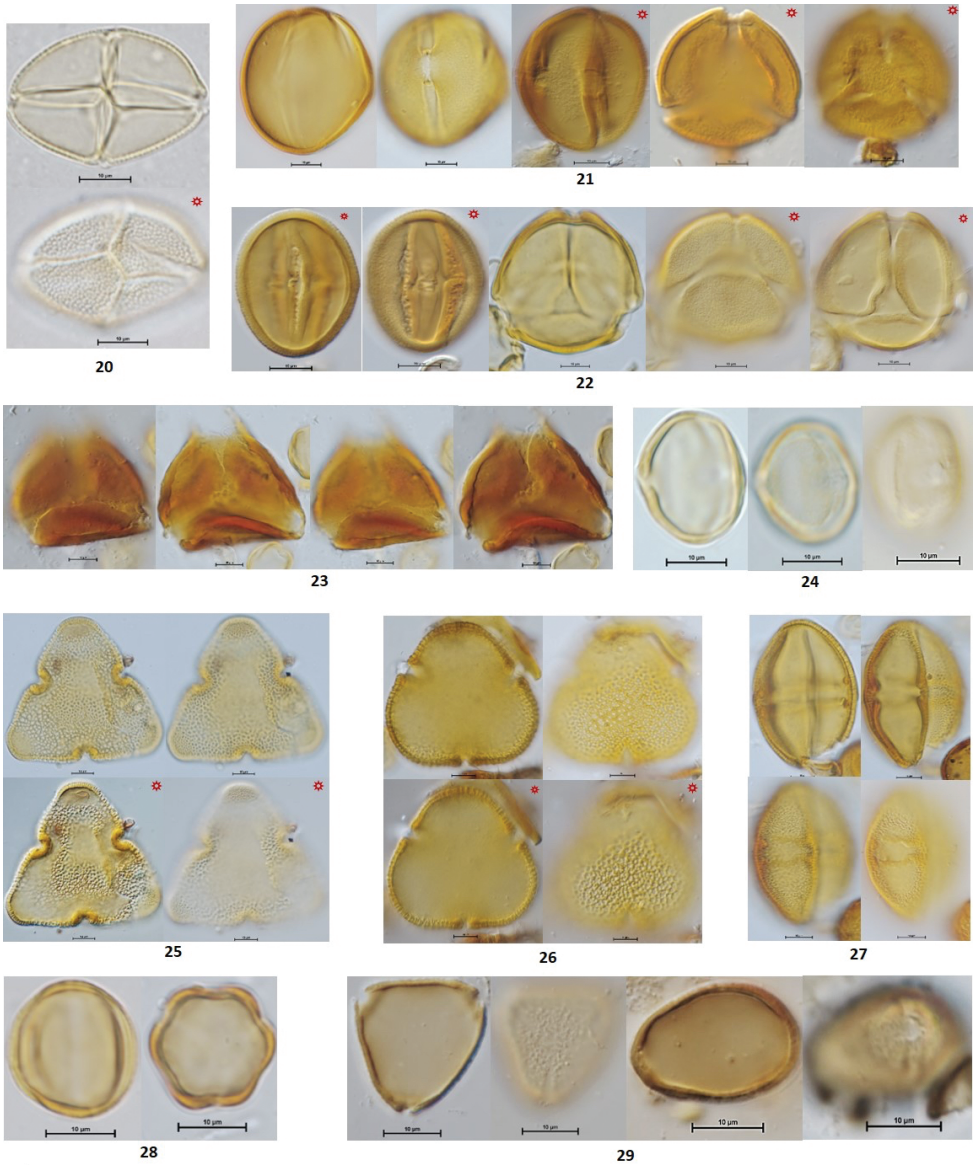
**Plate I.** Eudicots. Acanthaceae: *Avicennia germinans* (1) Amaranthaceae: aff. *Chenopodium* sp. (2) Anacardiaceae: *Spondias* sp. aff. *S. mombin* (3) Apocynaceae: *Malouetia guatemalensis* (4) *Mandevilla* sp. aff. *M. villosa* (5) *Prestonia* sp. (6) *Stemmadenia grandiflora* (7) *Thevetia abouai* (8) Asteraceae: undetermined (9) Bignoniaceae: *Arrabidaea* sp. (10) ( $\times 100$ ) (Red circle = DIC photo).

cells in place and covered them with gold leaf and golden paint (Figs 3C, 4). Pupal remains were found in seven cells (Fig. 5A), which allowed us to identify the bee species (Fig. 5B). Taxonomic identification of pollen grains showed that bees used 48 species of plants, representing 43 genera and 23 families (Table 1 and Plates 1–5).

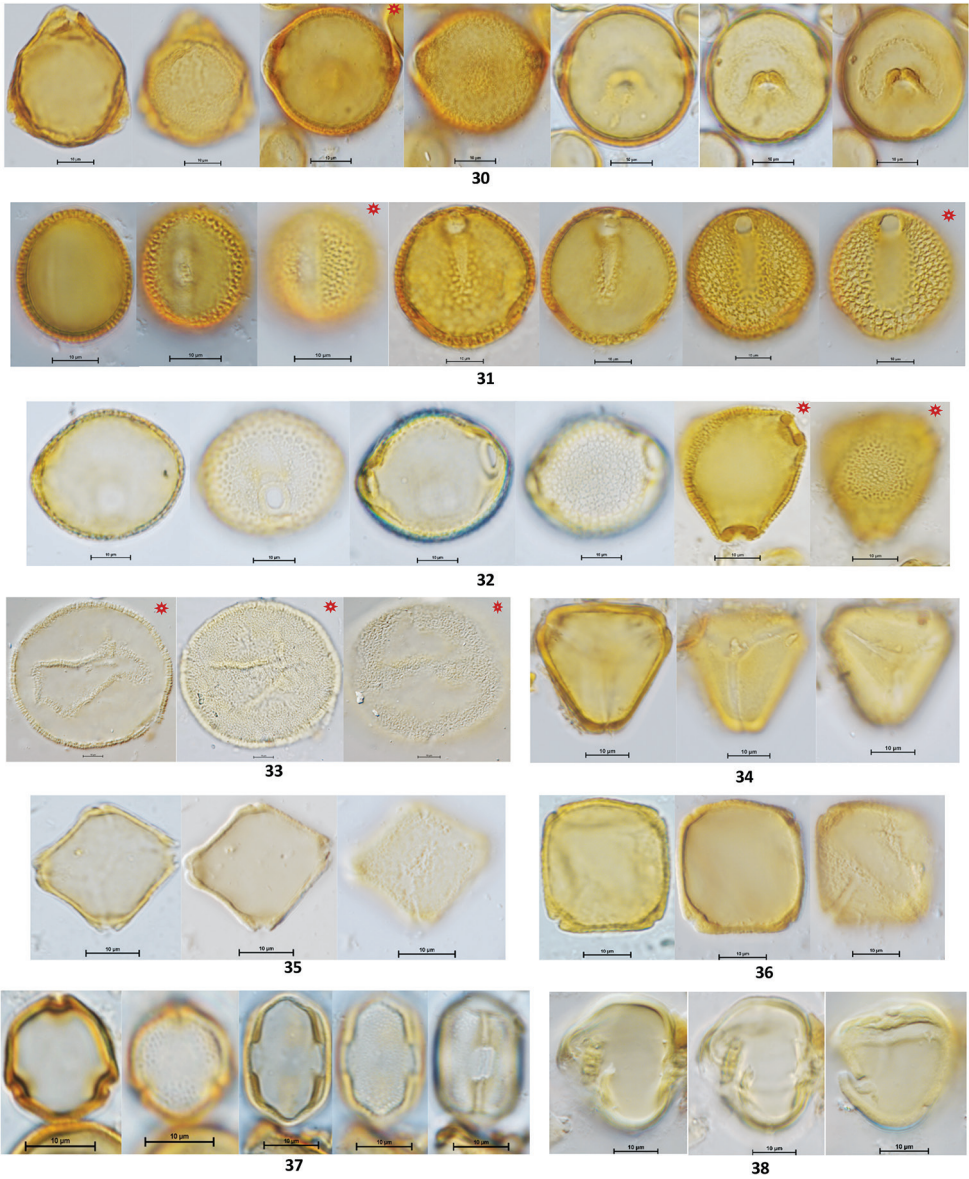


**Plate 2.** Bignonaceae: aff. *Ceratophytum tetragonolobum* (11) *Tabebuia* sp. (12) Boraginaceae: *Cordia* sp. aff. *C. spinescens* (13) *Heliotropium procumbens* (14) Cannabaceae: *Celtis* sp. (15) Combretaceae: *Conocarpus erectus* (16) *Laguncularia racemosa* (17) Euphorbiaceae: *Alchornea* sp. aff. *A. latifolia* (18) *Croton* sp. (19) (×100) (Red circle = DIC photo).



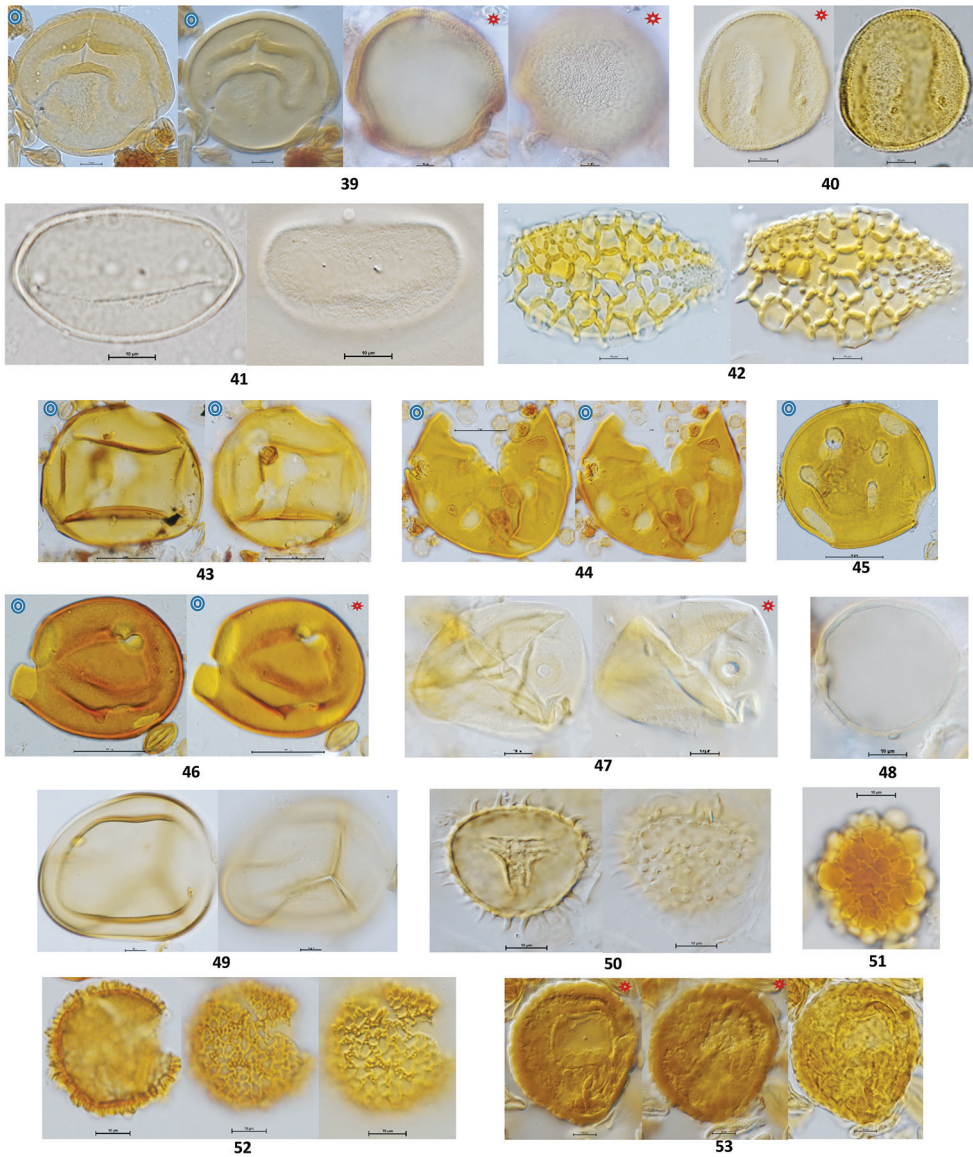


**Plate 3.** Fabaceae-Caesalpinioideae: *Mimosa* sp. (20) Fabaceae-Cercidoideae: *Bauhinia guianensis* (21) *Bauhinia reflexa* (22) Fabaceae-Papilionoideae: *Dioclea reflexa* (23) *Machaerium* sp. (24) Malvaceae-Bombacoideae: *Bombacopsis quinata* (25) *Pseudobombax septenatum* (26) Malvaceae-Grewioideae: aff. *Heliocarpus* sp. (27) Melastomataceae: *Miconia* sp. (28) Myrtaceae: *Eugenia* sp. (29) (×100) (Red circle = DIC photo).



**Plate 4.** Rubiaceae: aff. *Faramea* sp. (30) *Genipa americana* (31) *Macrocnemum glabrescens* (32) *Psychotria* sp. (33) Sapindaceae: *Cupania* sp. (34) *Serjania* sp.1 (35) *Serjania* sp.2 (36) Sapotaceae: *Pouteria* sp. (37) Solanaceae: *Solanum* sp. (38) (×100) (Red circle = DIC photo).





**Plate 5.** Tetrameristaceae: *Pelliciera rhizophorae* (39) Monocots. Arecaceae: Undetermined sp.1 (40) Undetermined sp.2 (41) Bromeliaceae: *Vriesea* sp. (42) Costaceae: *Costus* sp.1 (43) *Costus* sp.2 (44) *Costus* sp.3 (45) *Costus* sp.4 (46) Poaceae: aff. *Zea mays* (47) Undetermined sp. (48) FERN SPORES. Cyatheaaceae: *Cyathea* sp. (49) Selaginellaceae: *Selaginella* sp. (50) UNDETERMINED. Fungal sp.1 (51) Fungal sp.2 (52) Fungal sp.3 (53) (×100) (Blue circle = 60X) (Red circle = DIC photo)

**Table 1.** List of plants identified from pollen grains recovered of nest cells of *Eufriesea surinamensis* L. from Casco Viejo, Panamá, and subjective estimates of their relative occurrence.

Family	Genus/Species	Relative occurrence
<b>Eudicots</b>		
Acanthaceae	<i>Avicennia germinans</i>	Common
Amaranthaceae	aff. <i>Chenopodium</i> sp.	Rare
Anacardiaceae	<i>Spondias</i> sp. aff. <i>S. mombin</i>	Rare
Apocynaceae	<i>Malouetia guatemalensis</i>	Scarce
Apocynaceae	<i>Mandevilla</i> sp. aff. <i>M. villosa</i>	Scarce
Apocynaceae	<i>Prestonia</i> sp.	Common
Apocynaceae	<i>Stemmadenia grandiflora</i>	Rare
Apocynaceae	<i>Thevetia ahouai</i>	Rare
Asteraceae	Undetermined	Rare
Bignoniaceae	<i>Arrabidaea</i> sp.	Common
Bignoniaceae	aff. <i>Ceratophyllum tetragonolobum</i>	Common
Bignoniaceae	<i>Tabebuia</i> sp.	Common
Boraginaceae	<i>Cordia</i> sp. aff. <i>C. spinescens</i>	Scarce
Boraginaceae	<i>Heliotropium procumbens</i>	Common
Cannabaceae	<i>Celtis</i> sp.	Abundant
Combretaceae	<i>Conocarpus erectus</i>	Abundant
Combretaceae	<i>Laguncularia racemosa</i>	Scarce
Euphorbiaceae	<i>Alchornea</i> sp. aff. <i>A. latifolia</i>	Rare
Euphorbiaceae	<i>Croton</i> sp.	Rare
Fabaceae-Caesalpinioideae	<i>Mimosa</i> sp.	Rare
Fabaceae-Cercidoideae	<i>Bauhinia guianensis</i>	Common
Fabaceae-Cercidoideae	<i>Bauhinia reflexa</i>	Common
Fabaceae-Papilionoideae	<i>Dioclea reflexa</i>	Rare
Fabaceae-Papilionoideae	<i>Machaerium</i> sp.	Rare
Malvaceae-Bombacoideae	<i>Bombacopsis quinata</i>	Rare
Malvaceae-Bombacoideae	<i>Pseudobombax septenatum</i>	Rare
Malvaceae-Grewioideae	aff. <i>Heliocarpus</i> sp.	Rare
Melastomataceae	<i>Miconia</i> sp.	Frequent
Myrtaceae	<i>Eugenia</i> sp.	Frequent
Rubiaceae	<i>Faramea</i> sp.	Common
Rubiaceae	<i>Genipa americana</i>	Scarce
Rubiaceae	<i>Macrocnemum glabrescens</i>	Scarce
Rubiaceae	<i>Psychotria</i> sp.	Rare
Sapindaceae	<i>Cupania</i> sp.	Scarce
Sapindaceae	<i>Serjania</i> sp. 1	Common
Sapindaceae	<i>Serjania</i> sp. 2	Common
Sapotaceae	<i>Pouteria</i> sp.	Rare
Solanaceae	<i>Solanum</i> sp.	Rare
Tetrameristaceae	<i>Pelliciera rhizophorae</i>	Scarce
<b>Monocots</b>		
Arecaceae	Undetermined sp. 1	Rare
Arecaceae	Undetermined sp. 2	Rare
Bromeliaceae	aff. <i>Vriesea</i> sp.	Rare
Costaceae	<i>Costus</i> sp. 1	Common
Costaceae	<i>Costus</i> sp. 2	Common
Costaceae	<i>Costus</i> sp. 3	Common
Costaceae	<i>Costus</i> sp. 4	Common
Poaceae	aff. <i>Zea mays</i>	Rare
Poaceae	Undetermined	Rare
<b>Others</b>		
Cyatheaceae	<i>Polypodium</i> sp.	Contaminant
Selaginellaceae	<i>Selaginella</i> sp.	Contaminant
Fungal?	Undetermined 1	
Fungal?	Undetermined 2	
Fungal?	Undetermined 3	

## Discussion

*Eufriesea surinamensis* females nesting in a Cathedral in an urban area in nineteenth-century Panamá were catholic in their flower preferences, visiting a diverse array of flowering trees, shrubs and grasses to collect food and nest-building materials, consistent with the known behavior of other orchid bees. They visited more than twice the number of plant species used by related *Euglossa* in a present-day urban area of Brazil (Pinto et al. 2019), comparable to the 45 plant species used by two species of *Euglossa* in Yucatán, México (Villanueva-Gutierrez et al. 2013). The species composition of the collected pollen reflects a mixed-age Neotropical secondary forest, with a mosaic landscape of forest and open areas, as seen in Muybridge's landscape photographs (Figs 1, 2). The bees visited understory species such as *Costus* (Costaceae) that do well in full sunlight, such as gaps or along forested roads or openings, as well as canopy trees like *Pseudobombax* (Malvaceae-Bombacoideae) ("barrigón") that typically are found in more mature forests (Croat 1978).

Orchid bees are long-tongued bees (Michener 2007), a trait that facilitates the collection of nectar from flowers that have deep and fused corollas (Endress 1994), providing them with a rich nectar source (e.g., Apocynaceae of Table 1). Additionally, other flowers are structured such that the bee must grab the flower while buzzing to vibrate free the pollen (Buchmann 2015), which provide a rich protein source. Other important nectar flowers were likely *Avicennia germinans* (Acanthaceae), *Heliotropium procumbens*



**Figure 1.** Environs of the *Eufriesea surinamensis* nesting site in Casco Viejo, Panamá in 1875, as seen from the summit of Cerro Ancón. A white tower of the Cathedral where bees were nesting is visible in the distant background in the center of the peninsula. Photo by Eadweard Muybridge, courtesy of the Smithsonian American Art Museum; gift of Mitchell and Nancy Steir.



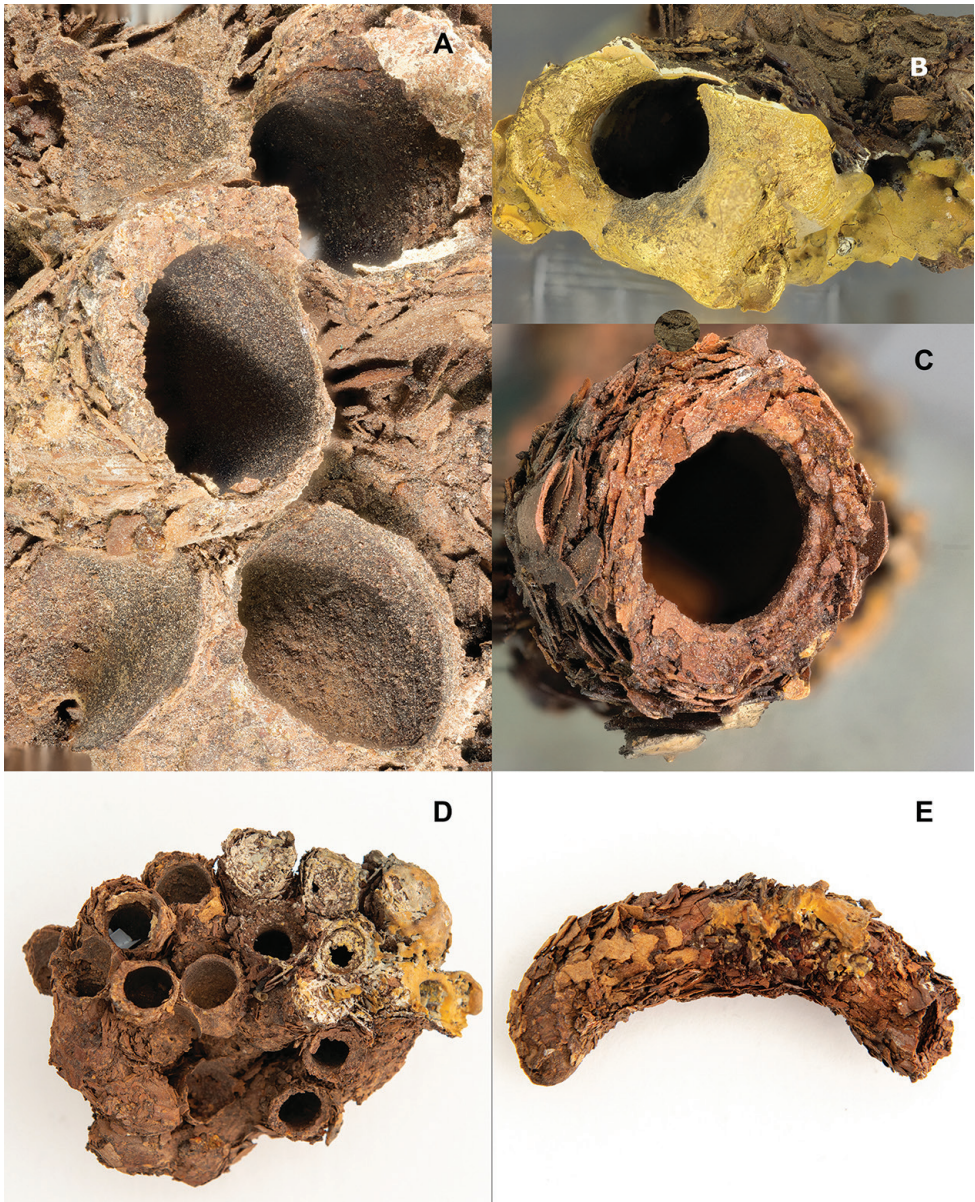


**Figure 2.** Panama City's waterfront and surrounding area as seen from the shoreline of Casco Viejo, Panamá in 1875. The large building in the left foreground is *La Casa de la Marina*, near *El Palacio de las Garzas* (Presidential Palace). The bees were nesting approximately 160 m in-land. The peak of Cerro Ancón is approximately 1.6 km distant. Photo by Eadweard Muybridge, courtesy of the Smithsonian American Art Museum; gift of Mitchell and Nancy Steir.



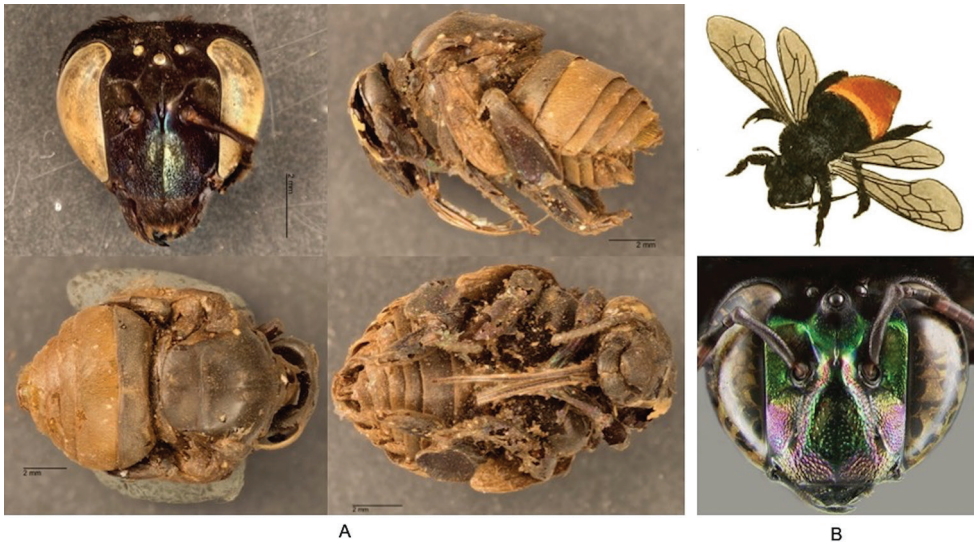
**Figure 3.** Locations of nest cell aggregations of *Eufriesea surinamensis* within the Cathedral in Casco Viejo, Panamá **A** restored reredos showing the capitals above the columns where the historical bee cells were found (black arrows) **B** a scroll removed during the contemporary restoration, showing bee cells within its crevices and golden material applied during the nineteenth-century restoration **C** close-up of scrolls on a capital showing painted bee cells from the prior restoration.





**Figure 4.** *Eufriesea surinamensis* cells painted during the nineteenth-century restoration **A** close-up of a cell cluster recovered from a capital **B** isolated cell entrance that was painted over **C** isolated cell entrance showing the abundance of bark fragments as a main resource for nest construction **D** cell cluster covered in golden paint **E** exterior view of an isolated cell, covered with golden leaf; the cell entrance faces right.

(Boraginaceae), *Bauhinia* spp. (Fabaceae- Cercidoideae), *Eugenia* sp. (Myrtaceae), *Farea* sp. (Rubiaceae) and *Serjania* spp. (Sapindaceae). Plants that were likely important protein sources include *Costus* (Costaceae), *Celtis* sp. (Cannabaceae), *Conocarpus erectus* (Combretaceae), *Miconia* sp. (Melastomataceae), and species of Bignoniaceae (Table 1).



**Figure 5.** *Eufriesea surinamensis* reared from cells **A** head, lateral, dorsal and ventral views of recovered bees **B** habitus drawing and head of exemplar (STRI-Portal; <https://www.stricollections.org/portal/taxa/index.php?taxon=48960>).

Together, these species comprise about half of the total taxa reported. Some of the species, though rare in this sample, likely contributed to the diet of *E. surinamensis*, while other species may be present from visits to plants collecting resin or nesting materials, or be contaminants (e.g., the two fern spores and fungal species reported). The pollen list also contains elements of a coastal forest with mangroves, including one species (*Pelliciera rhizophorae*, Tetrameristaceae) that today is extremely rare in central Panamá (Castillo-Cárdenas et al. 2016). The precise foraging range of these bees is unknown, but *E. surinamensis* females in Costa Rica's Osa Peninsula were capable of navigating home from distances as far as 23 km (Janzen 1971). Thus, the foraging range of the Cathedral bees likely extended far beyond Cerro Ancón (Fig. 2), approximately to present-day towns of Tocumen, La Chorrera, and Gamboa, depending on outbound flight direction.

Today in central Panamá, including the Panama City metropolitan region, these bees are confined to remote forested areas of the central isthmus (Roubik and Ackerman 1987), and there have been no detailed studies of female nesting biology. Accordingly, we now need to collect comparative data on the biology and distribution of contemporary populations of *E. surinamensis* in central Panama and elsewhere in the Neotropics, to better understand how these bees are responding to changing environments.

## Conclusions

Palynological studies of the contents of orchid bee brood cells indicate that late-nineteenth century Panama City was surrounded by a patchwork of tropical forests sufficient to sustain nesting populations of what today is a forest-dwelling species of bee.

## Acknowledgements

We are grateful to the entire group of collaborators from Dalmática Conservação e Restauro-represented here by Sofia Lobo-for their interest in understanding which biological agents cause damage to our cultural heritage. The staff of the Comité Arquidiocesano Amigos Iglesias Casco Antiguo and the Consorcio la Antigua helped in providing access to the samples and to the site. Current and former STRI colleagues contributed as follows: Jorge Ceballos helped with microscopy; Marleny Rivera and Jorge Aleman took photos of the bees and the nest cells, respectively; Carlos Jaramillo, Rick Condit, Stanley Heckadon, Joe Wright, and Jeff Hall provided helpful botanical or historical information; Dolores Piperno and Irene Holst analyzed phytoliths and provided related information; Lina Gonzalez helped with graphics; and Annette Aiello first recognized the recovered materials as hymenopteran nest cells, and brought them to the attention of WTW. We are especially grateful to our Smithsonian colleagues, John Jacob and Richard Sorensen of the Smithsonian American Art Museum, who promptly provided high-resolution copies of the original Muybridge photographs in their collection, and related information. Margarita López-Urbe, Santiago Ramírez, and Jack Neff provided many helpful and thoughtful comments, and corrections, which improved the manuscript.

## References

- Angiosperm Phylogeny Group IV (2016) An update of the angiosperm phylogeny group classification for orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1–20. <https://doi.org/10.1111/boj.12385>
- Banks H, Lewis G (2018) Phylogenetically informative pollen structures of “caesalpiniod” pollen (Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae and Duparquetioideae: Fabaceae). *Botanical Journal of the Linnean Society* 187: 59–86. <https://doi.org/10.1093/botlinnean/boy005>
- Bennett FD (1972) Observations on *Exaerete* spp. and their hosts *Eulaema terminata* and *Euplusia surinamensis* (Hymen., Apidae, Euglossine) in Trinidad. *Journal of the New York Entomological Society* 80: 118–124.
- Brosi B (2009) The effects of forest fragmentation on euglossine bee communities (Hymenoptera: Apidae: Euglossini). *Biological Conservation* 142: 414–423. <https://doi.org/10.1016/j.biocon.2008.11.003>
- Buchmann SL (2015) *The Reasons for Flowers: Their History, Culture, Biology, and How They Change our Lives*. Scribner, New York, 352 pp.
- Cameron SA (2004) Phylogeny and biology of neotropical orchid bees (Euglossini). *Annual Review of Entomology* 49: 377–404. <https://doi.org/10.1146/annurev.ento.49.072103.115855>
- Calvo AC (1999) *La Ciudad Imaginada: El Casco Viejo de Panamá*. Ministerio de la Presidencia, Panamá, 300 pp.
- Castillo-Cárdenas F, Sanjur O, Toro-Perea N (2016) Differences in sculpture and size of pollen grains: new morphological evidence of diversification in *Pelliciera rhizophorae*, an ancient



- Neotropical mangrove species. *Palynology* 40: 302–307. <https://doi.org/10.1080/01916122.2015.1045050>
- Cortopassi-Laurino M, Zillikens A, Steiner J (2009) Pollen sources of the orchid bee *Euglossa annectans* Dressler 1982 (Hymenoptera: Apidae, Euglossini) analyzed from larval provisions. *Genetics and Molecular Research* 8: 546–556. <https://doi.org/10.4238/vol8-2kerr013>
- Croat T (1978) *Flora of Barro Colorado Island*. Stanford University Press (Palo Alto), Stanford, 956 pp.
- Dressler RL (1982) Biology of the orchid bees (Euglossini). *Annual Review of Ecology & Systematics* 13: 373–394. <https://doi.org/10.1146/annurev.es.13.110182.002105>
- Endress PK (1994) *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge University Press, Cambridge, 420 pp.
- Francis P (2015) *Laudato Si*. The Vatican Press, Rome, 183 pp.
- Janzen DH (1971) Euglossine bees as long-distance pollinators of tropical plants. *Science* 171: 203–205. <https://doi.org/10.1126/science.171.3967.203>
- Kimsey LS (1982) Systematics of bees of the genus *Eufriesea*, University of California Publications in Entomology 95: 1–125.
- Legume Phylogeny Working Group (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66: 44–77. <https://doi.org/10.12705/661.3>
- López-Urbe MM, Oi CA, del Lama MA (2008) Nectar-foraging behavior of euglossine bees (Hymenoptera: Apidae) in urban areas. *Apidologie* 39: 410–418. <https://doi.org/10.1051/apido:2008023>
- Michener CD (2007) *The Bees of the World* (2<sup>nd</sup> ed.). The Johns Hopkins University Press, Baltimore, 953 pp.
- Missouri Botanical Garden (2019) Tropicos online database. <http://www.tropicos.org>
- Moore PD, Webb JA, Collinson ME (1991) *Pollen Analysis* (2<sup>nd</sup> ed.). Blackwell Scientific Publications, Oxford, 216 pp.
- Moreno JE, Vergara D, Jaramillo C (2014) Las colecciones palinológicas del Instituto Smithsonian de Investigaciones Tropicales (STRI), Panamá. *Boletín de la Asociación Latinoamericana de Paleobotánica y Palinología (ALPP)* 14: 207–222.
- Myers J, Loveless MD (1976) Nesting aggregations of the euglossine bee *Euplusia surinamensis* (Hymenoptera: Apidae): individual interactions and the advantage of living together. *The Canadian Entomologist* 108: 1–6. <https://doi.org/10.4039/Ent1081-1>
- Pemberton RW, Wheeler GS (2006) Orchid bees don't need orchids: evidence from the naturalization of an orchid bee in Florida. *Ecology* 87: 1995–2001. [https://doi.org/10.1890/0012-9658\(2006\)87\[1995:OBDNOE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1995:OBDNOE]2.0.CO;2)
- Pinto RS, Silva AG, Rêgo MMC, Albuquerque PMC (2019) Pollen analysis of the post-emergence residue of *Euglossa* bees (Apidae: Euglossini) nesting in an urban fragment. *Sociobiology* 66: 88–96. <https://doi.org/10.13102/sociobiology.v66i1.3434>
- Piperno DR (2006) *Phytoliths*. Altamira Press, Oxford, 238 pp.
- Punt W, Hoen PP, Blackmore S, Nilsson S, Le Thomas A (2007) Glossary of pollen and spore terminology. *Review of Paleobotany and Palynology* 143: 1–81. <https://doi.org/10.1016/j.revpalbo.2006.06.008>

- Ramírez S, Dressler RL, Ospina M (2002) Abejas euglosinas (Hymenoptera: Apidae) de la Región Neotropical: Listado de especies con notas sobre su biología,” *Biota Colombiana* 3: 7–118.
- Roubik DW, Ackerman JD (1987) Long-term ecology of euglossine orchid-bees (Apidae: Euglossini) in Panama. *Oecologia* 73: 321–333. <https://doi.org/10.1007/BF00385247>
- Roubik DW, Hanson PA (2004) Abejas de Orquideas de la America Tropical / Orchid Bees of Tropical America. Inbio, Costa Rica, 370 pp.
- Roubik DW, Moreno JE (1991) Pollen and spores of Barro Colorado Island. Missouri Botanical Garden, Monographs in Systematic Botany 36: 1–268.
- Rozen Jr JG (2018) On egg eclosion and larval development in euglossine bees. *American Museum Novitates* 3910: 1–15. <https://doi.org/10.1206/3910.1>
- Villanueva-Gutierrez R, Quezada-Euan J, Eltz T (2013) Pollen diets of two sibling orchid bee species, *Euglossa*, in Yucatán, southern Mexico. *Apidologie* 44: 440–446. <https://doi.org/10.1007/s13592-013-0194-9>
- Wcislo DO, Vargas G, Ihle KE, Wcislo WT (2012) Nest construction behavior by the orchid bee *Euglossa hyacinthina*. *Journal of Hymenoptera Research* 29: 15–20. <https://doi.org/10.3897/jhr.29.4067>
- Young AM (2012) Notes on emergence of orchid bees, *Eufriesea surinamensis* (L.) Apidae: Euglossinae in Costa Rican nest cell aggregations. *Journal of the Kansas Entomological Society* 85: 378–379. <https://doi.org/10.2317/0022-8567-85.4.378>