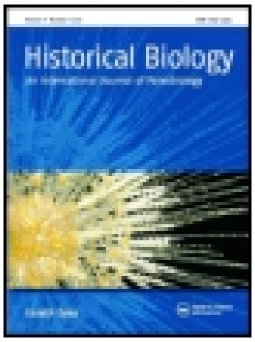

Taylor & Francis
Taylor & Francis Group

Historical Biology

An International Journal of Paleobiology

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: http://www.tandfonline.com/loi/ghbi20

The antiquity of floral secretory tissues that provide today's fragrances

George Poinar & Greg Poinar

To cite this article: George Poinar & Greg Poinar (2018): The antiquity of floral secretory tissues that provide today's fragrances, Historical Biology

To link to this article: https://doi.org/10.1080/08912963.2018.1502288

Published online: 25 Jul 2018.

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2018.1502288

ARTICLE

The antiquity of floral secretory tissues that provide today's fragrances

George Poinar[a] and Greg Poinar[b]

[a]Department of Integrative Biology, Oregon State University, Corvallis, OR, USA; [b]Portland, OR, USA

ABSTRACT
It is well known that flowers use scents to attract pollinators and that these fragrances are composed of a mixture of different chemical compounds, many of which form the basis of perfumes and colognes we use today. An examination of fossil flowers in mid-Cretaceous Burmese amber and mid-Tertiary Dominican amber revealed a range of secretory tissues in the form of nectaries, glandular trichomes, eliaphores and osmophores. These tissues most certainly secreted liquids and volatiles to attract pollinators, just as they do in modern flowers. The morphological similarities of secretory tissues found on fossil flowers dating back to 100 mya to those of their present day descendants suggests that ancient and modern flowers may have produced similar essences, including those used in the production of today's perfumes and colognes.

ARTICLE HISTORY
Received 26 June 2018
Accepted 16 July 2018

KEYWORDS
Floral secretory tissues; Burmese amber; Dominican amber; perfumes

Introduction

Floral scents have been used by humans for ages, with some of the earliest records of fragrances dating back to the Bronze Age some 4000 years ago (Arctander 1960). Today we still rely on the appeal of perfumes and colognes to make us attractive and irresistible. But floral scents did not develop for human use. They originated in primitive Early Cretaceous flowers as a means to attract pollinators. When angiosperms were diversifying some 100 million years ago, most flowers lacked petals. Since colors, one of the other methods flowers use to attract pollinators, are typically associated with petals, these early flowers would have depended mostly on scents and nectar to attract potential pollinators.

Floral scents are produced in a number of diverse secretory compartments, including nectaries, glandular trichomes, eliaphores and osmophores (Rehman et al. 2016). Nectaries are glands that produce fragrances and sweet deposits that are very attractive to insects. Glandular trichomes are hairs with cells that produce and emit specific scented secretory products. Eliaphores are stalked aromatic oil glands and osmophores, or floral fragrance glands, are cell clusters that specialize in scent emission. These secretory tissues can occur on all parts of flowers (Arctander 1960). While it is not possible to detect scents or analyze the chemical components of fossil flowers, it is feasible to locate scent-producing glands, showing that floral scents played an important role in attracting pollinators millions of years ago.

The present study demonstrates the presence of secretory tissues, some of which are in the process of emitting compounds, in extinct flowers in mid- Cretaceous amber from Burma (Myanmar) and mid- Tertiary amber from the Dominican Republic. The secretory tissues of these ancient flowers are compared with those of related descendants that produce secretory products used in the production of perfumes and colognes.

Materials and methods

The Burmese amber flowers, *Cascolaurus burmensis* (Lauraceae) and *Tropidogyne pentaptera* (Cunoniaceae) originated from amber mines excavated in the Hukawng Valley in Kachin State in Myanmar. Based on paleontological evidence, this site was dated to the late Albian of the Early Cretaceous (Cruickshank and Ko 2003), placing the age at 97 to 110 Ma. A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Ma or at the Albian/Cenomanian boundary (Shi et al. 2012).

The Dominican amber flowers, *Discoflorus neotropicus* (Apocynaceae) and *Senegalia eocaribbeansis* (Fabaceae) were obtained from mines located in the Cordillera Septentrional of The Dominican Republic. Estimated ages range from 15–20 Ma (Iturralde-Vincent and MacPhee 1996) to 45–30 mya based on coccoliths (Cepek in Schlee 1990). All of the fossil flowers are deposited in the Poinar amber collection maintained at Oregon State University. Examination and photographs were made with a Nikon stereoscopic microscope SMA-10-R at 80× and a Nikon Optiphot microscope at 800 × .

Results

The Glandular laurel flower (*Cascolaurus burmensis*: Lauraceae) (Poinar 2017A) in Burmese amber (Figure 1) lacked petals but attracted pollinators by forming very large nectaries that were completely exposed on the top of the flowers (Figure 2).

The Veined Star flower (*Tropidogyne pentaptera*: Cunoniaceae) (Poinar and Chambers 2017) in Burmese

CONTACT George Poinar poinarg@science.oregonstate.edu

Published online 25 Jul 2018

Figure 1. Glandular laurel flower (*Cascolaurus burmensis*: Lauraceae) in Burmese amber. Arrow shows position of the nectary. Scale bar = 1.1 mm.

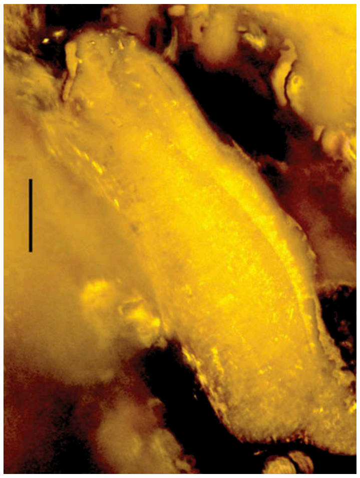

Figure 2. Nectary of Glandular laurel flower (*Cascolaurus burmensis*: Lauraceae) in Burmese amber. Scale bar = 74 µm.

amber also lacks petals but has 5 outstretched sepals that contain two types of secretory glands (Figure 3). Along the edge of the sepals are small multicellular glandular trichomes with branched hairs at their tips (Figure 4). On the surface of the sepals are eliaphores secreting oil droplets (Figure 5).

By the time Dominican amber was formed in the mid-Tertiary, flowers with petals were much more common. The Ten-lobed milkweed flower (*Discoflorus neotropicus*: Apocynaceae)(Poinar 2017B) in Dominican amber has 5 large outstretched petals, as well as a set of 5 short sepals and a ten-lobed stigmatic disk (Figure 6). The petals bear short, clustered osmophores in the shape of fleshy pillars (Figure 7) and extended glandular trichomes (Figure 8).

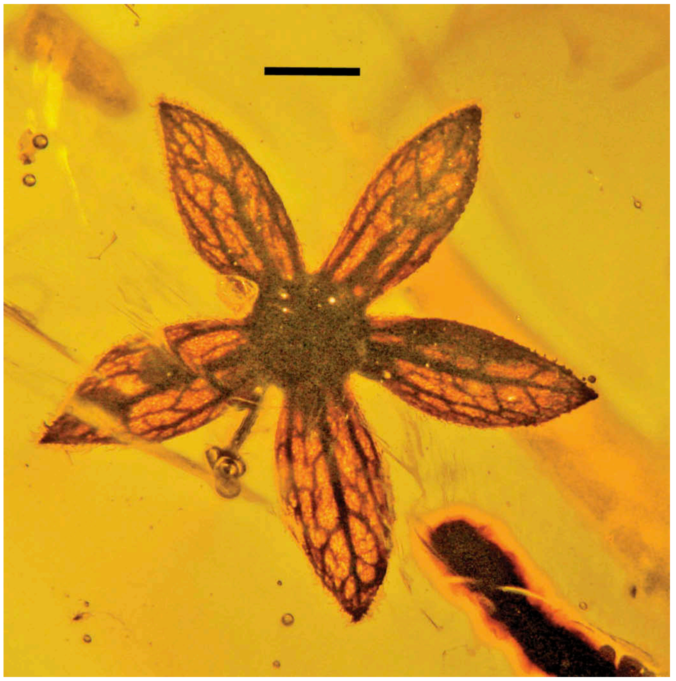

Figure 3. Veined star flower (*Tropidogyne pentaptera*: Cunoniaceae) in Burmese amber. Scale bar = 1.2 mm.

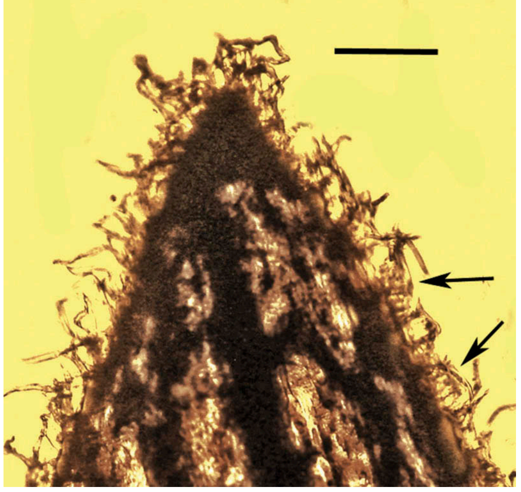

Figure 4. Glandular trichomes (arrows) attached to the margin of a sepal of veined star flower (*Tropidogyne pentaptera*: Cunoniaceae) in Burmese amber. Scale bar = 0.1 mm.

Also in Dominican amber are flowers of the Multiple Stamen acacia (*Senegalia eocaribbeansis*: Fabaceae) (Poinar and Chambers 2016). These flowers are quite spectacular with their numerous interwoven stamens that completely conceal the female floral parts (Figure 11). Especially interesting are the anthers that support small stalked nectaries (Figure 11, 12).

Discussion

An examination of nectaries and secretory tissues on extinct flowers in amber shows that floral essences, which today are the most common source of perfume aromatics, were being produced some 100 million years ago.

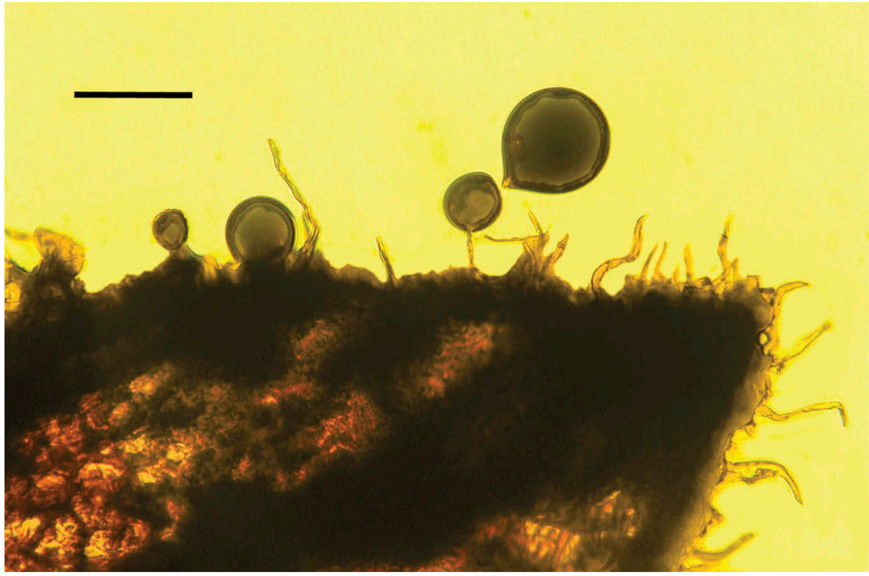

Figure 5. Glands secreting oil droplets on sepals of veined star flower (*Tropidogyne pentaptera*: Cunoniaceae) in Burmese amber. Scale bar = 70 µm.

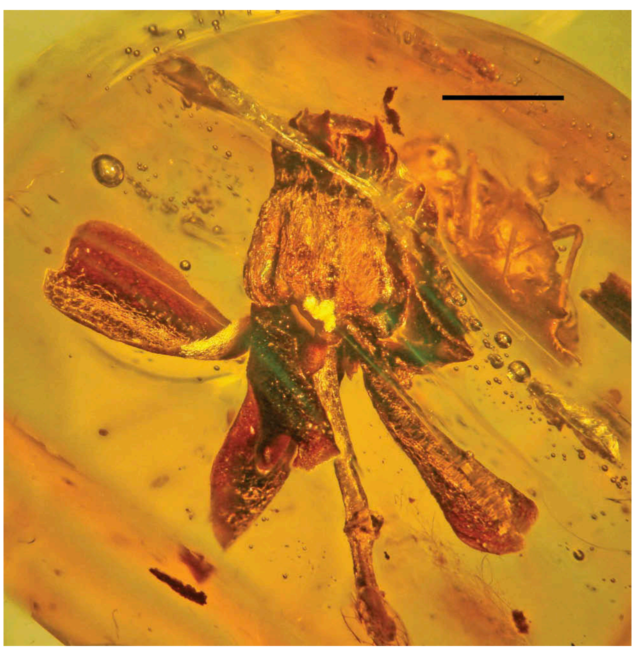

Figure 6. Ten-lobed milkweed flower (*Discoflorus neotropicus*: Apocynaceae) in Dominican amber. Scale bar = 1.8 mm.

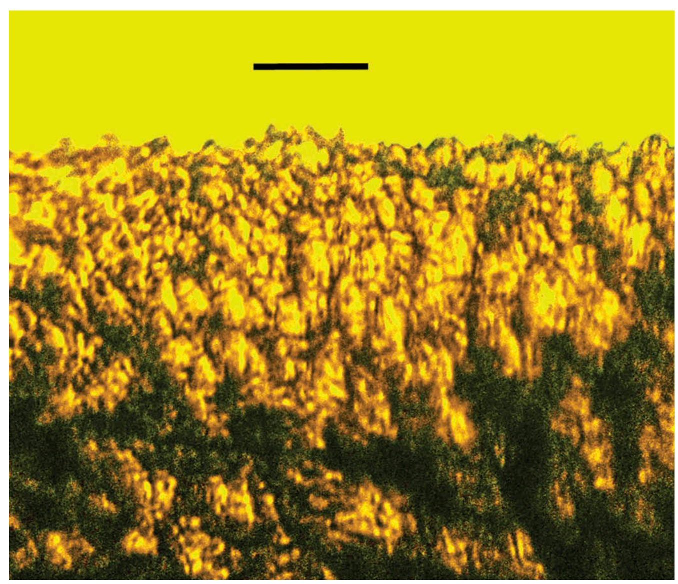

Figure 7. Osmophores on surface of petal of ten-lobed milkweed flower (*Discoflorus neotropicus*: Apocynaceae) in Dominican amber. Scale bar = 38 µm.

By producing attractive scents as well as sweet deposits, nectaries are one of the main floral features that attract pollinators. Many present day members of the family Lauraceae produce nectaries at the base of the inner whorl of stamens (Rohwer 2009), similar to those of The Glandular laurel flower in Burmese amber (Figure 2). These nectaries secrete a variety of essential oils used in perfumes today, including eugenol, camphor and benzyl benzoate (Salleh et al. 2016). Extant members of the genus *Laurus* release floral scents dominated by terpenoids, which are attractive to bees (Dobson 2006). Small bees that inhabited the forests containing Glandular laurel could have been attracted to such floral scents (Danforth and Poinar 2011).

The Veined Star flower in Burmese amber is related to members of the present day Australian genus *Ceratopetalum*. Coumarin, a fragrant organic compound used in perfumes, has been isolated from the flowers of coachwood (*Ceratopetalum apetalum*) (Maiden 1890) and Hornpetal trees (*Ceratopetalum* spp.) (Arctander 1960). Related

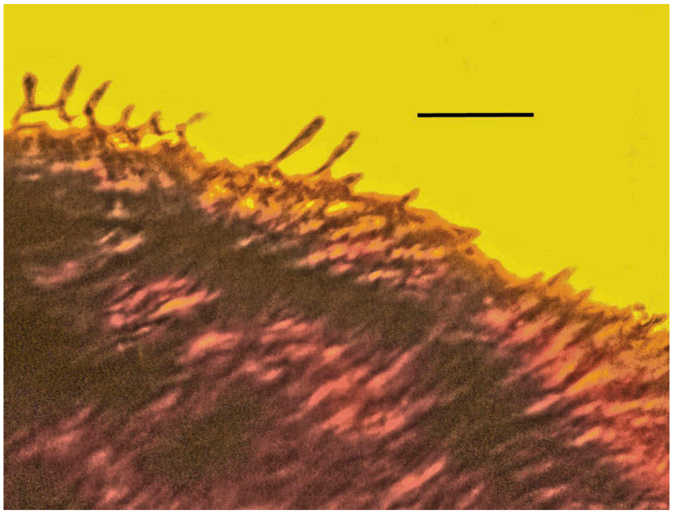

Figure 8. Extended glandular trichomes on petal of ten-lobed milkweed flower (*Discoflorus neotropicus*: Apocynaceae) in Dominican amber. Scale bar = 40 µm.

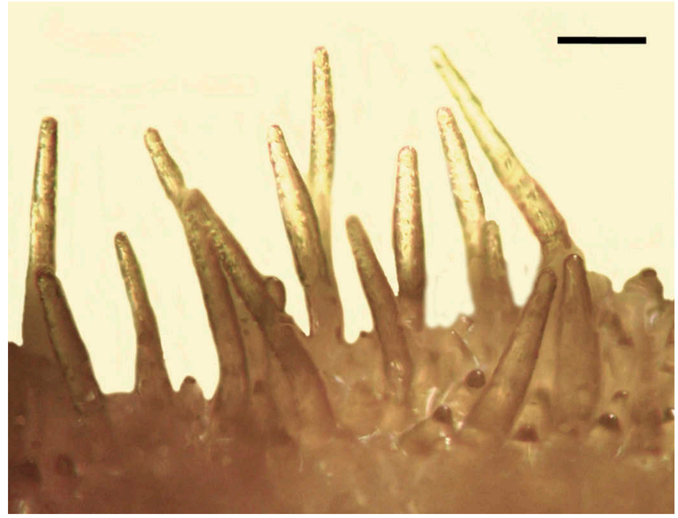

Figure 10. Glandular papillose cells at the base of a petal of showy milkweed flower (*Asclepias speciosa*: Apocynaceae). Scale bar = 40 µm.

Figure 9. Flower of extant showy milkweed (*Asclepias speciosa*: Apocynaceae). Scale bar = 3.0 mm.

compounds could have been present in the eliaphores of Veined Star flowers. Such secretions would have been especially attractive to oil seeking insects.

Glandular papillose cells similar to those found on the Ten-lobed milkweed flower in Dominican amber occur on the inner surface of petals of the extant Showy Milkweed, (*Asclepias speciosa*) (Figure 9, 10). Such secreting/emitting cells arise from the epidermal cell layer of the glandular epithelium and resemble non-secreting decorative cells. Glandular papillose cells also occur on the petals and along the margins of the extant related genus *Periploca* (Vogel 1990; Heneidak and Naidoo 2015). Various fruit scents such as benzyl alcohol, benzaldehyde and phenylacetaldehyde, as well as floral essential oils used in perfumes, are produced by extant members of the Apocynaceae (Formisano et al. 2009). The sweetly scented flowers of various species of *Plumeria*, including the well known American Red Frangipani and Australian Pink Frangipani, produce various citrus, berry and other fruit scents used in perfumes (Arctander 1960).

Anther nectaries similar to those on the Multiple Stamen acacia flowers (Figure 11, 12) occur on many present day species of *Acacia* and *Senegalia* (Seigler and Ebinger 2017). Their attractiveness to bees possibly accounts for the presence of an extinct stingless bee (*Proplebeia dominicana*: Apidae) enmeshed in the stamens of Multiple Stamen acacia flowers in Dominican amber (Figure 13). Honeybees (*Apis mellifera*: Apidae) presently are drawn to flowers of the related White Thorn acacia (*Acacia constricta*: Fabaceae) (Figure 14). Mimosoid floral secretions have sweet-woody to deep floral odors and the prepared perfumes are often sweet and frequently used with other perfume bases (Arctander 1960).

Even amber, the fossilized resin that contains these ancient flowers, is used in the manufacture of perfumes. Dry distillates of Baltic amber yield succinol, a crude amber oil with an odor of tanned leather that blends well with other perfume ingredients used in the production of men's cologne and after-shaves (Arctander 1960). The source of Dominican amber was the extinct algarrobo tree (*Hymenaea protera*: Fabaceae) that produced scents from resin glands on the inner surface of its petals (Poinar 1991). Oleoresins similar to copal balsam are produced by trees of the closely related genus *Copaifera* (Fabaceae: Caesalpinioideae). The copal is burnt for incense but also contains essential oils with woody, spicy- peppery odors that are valued for their fixative properties when combined with other perfumery products (Arctander 1960).

Floral scents would have attracted a wide variety of potential pollinators in the mid-Cretaceous, many of which would have been beetles and flies searching not just for nectar and food but for oviposition sites. While some of these insect visitors may have been 'blossom vandals' and 'nectar thieves', early insect-floral associations are difficult to understand (Bernhardt 1999). Dependable cross pollination by insects became established with the diversification of bees in the mid to late Cretaceous. By visiting a series of flowers to collect pollen for raising their young, bees greatly assisted cross pollination. It probably was

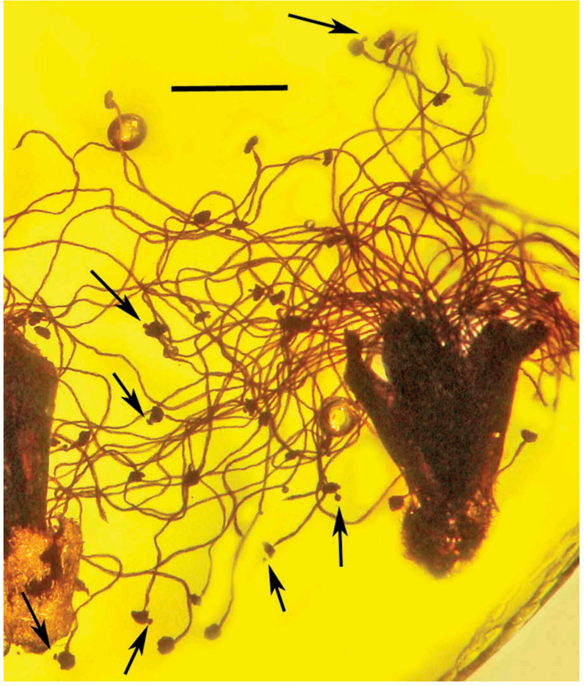

Figure 11. Multiple stamen acacia florets (*Senegalia eocaribbeansis*: Fabaceae) in Dominican amber. Arrows show anthers with apical nectaries. Scale bar = 0.7 mm.

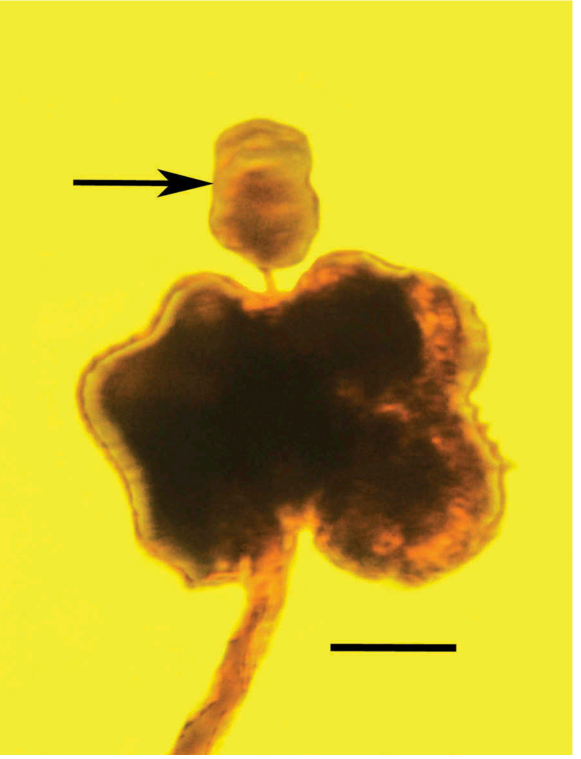

Figure 12. Anther nectary (arrow) of a multiple stamen acacia flower (*Senegalia eocaribbeansis*: Fabaceae) in Dominican amber. Scale bar = 42 µm.

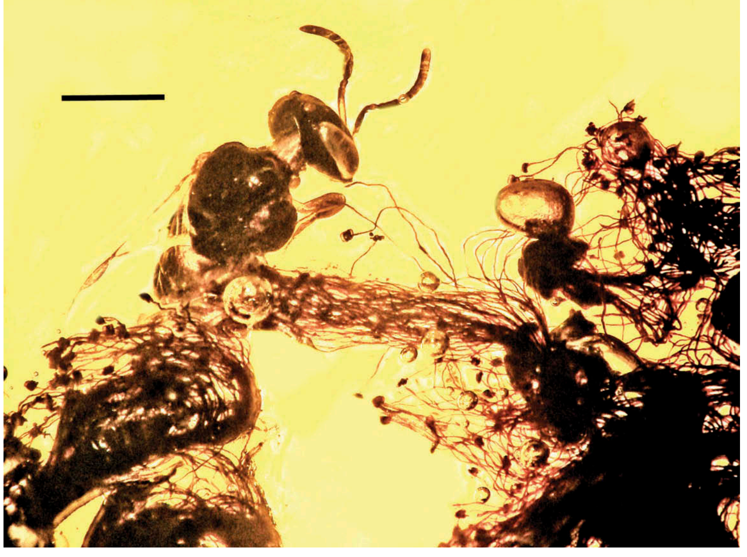

Figure 13. Stingless bee (*Proplebeia dominicana*: Apidae) adjacent to anthers of a multiple stamen acacia flower (*Senegalia eocaribbeansis*: Fabaceae) in Dominican amber. Scale bar = 1.8 mm.

only after bees and other dependable pollinators became more steadfast that flowers produced colored petals with additional secretory tissues for greater appeal.

It is obvious that flowers were producing aromatic scents to make them more attractive to pollinators long before humans began using perfumes to make themselves more appealing to others. And it is likely that some of these ancient scents were similar to those we use today in our cosmetics. While humans enjoy flowers for their variety of artistic designs and striking colors, certainly one of the most profitable uses of flowers involves their tantalizing scents. From these essences can be extracted a multitude of chemical compounds, many of which are used in the preparation of perfumes and colognes (Arctander 1960).

Figure 14. Honey bee (*Apis mellifera*: Apidae) visiting flowers of the white thorne acacia (*Acacia constricta*) bearing anther nectaries. Scale bar = 9.0 mm.

Acknowledgments

The authors thank Roberta Poinar for discussions on the subject of floral essences, John and Martha Nygaard for the use of Figure 14, and two anonymous reviewers who provided information and comments that improved the paper.

Disclosure statement

No potential conflict of interest was reported by the author.

References

Arctander S. 1960. Perfume and flavor materials of natural origin. Elizabeth (New Jersey); Createspace Independent Publishing Platform: p. 437.

Bernhardt P. 1999. The rose's kiss. a natural history of flowers. Chicago: University of Chicago Press; p. 267.

Cruickshank RD, Ko K. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. J Asian Earth Sci. 21:441–455.

Danforth BD, Poinar GO Jr. 2011. Morphology, classification, and antiquity of *Melittosphex burmensis* (Apoiodea: Melittosphecidae) and implications for early bee evolution. J Paleontology. 85:882–891.

Dobson HEM. 2006. Relationships between floral fragrance composition and type of pollinator. In: Dudareva N, Pichersky E, eds. Biology of floral scent. Boca Raton: CRC Press; p. 147–198.

Formisano C, Senatore F, Della Porta G, Scognamiglio M, Bruno M, Maggio A, Rosselli S, Zito P, Sajeva M. 2009. Headspace volatile composition of the flowers of *Caralluma europaea* N.E.Br. (Apocynaceae). Molecules. 14:4597–4613.

Heneidak S, Naidoo Y. 2015. Floral function in relation to floral structure in two *Periploca* species (Periplocoideae) Apocynaceae. Turkish J Botany. 39. doi:10.3906/bot-1403-43

Iturralde-Vincent MA, MacPhee RDE. 1996. Age and paleographic origin of Dominican amber. Science. 273:1850–1852.

Maiden JH. 1890. Notes on Australian economic botany, No. 1. Vol. 5. New South Wales: Proc Linnaean Soc; p. 273–279.

Poinar GO Jr. 1991. *Hymenaea protera* sp. n. (Leguminosae, Caesalpinioideae) from Dominican amber has African affinities. Experientia. 47:1057–1082.

Poinar GO Jr., Chambers KL. 2016. Mimosoideae (Fabaceae) diversity and associates in mid-tertiary Dominican amber. J Bot Res Inst Texas. 10:121–136.

Poinar GO Jr., Chambers KL. 2017. *Tropidogyne pentaptera*, sp. nov., a new mid-Cretaceous fossil angiosperm flower in Burmese amber. Palaeodiversity. 10:135–140.

Poinar GO Jr. 2017A. A mid-Cretaceous Lauraceae flower, *Cascolaurus burmitis* gen. et sp. nov., in Myanmar amber. Cretaceous Res. 71:96–101.

Poinar GO Jr. 2017B. Ancient termite pollinators of milkweed flowers in Dominican amber. Am Entomologist. 63:52–56.

Rehman R, Hanif MS, Mushtaq Z, Al-Sadi AM. 2016. Biosynthesis of essential oils in aromatic plants. Food Rev Int. 32:117–160.

Rohwer JG. 2009. The timing of nectar secretion in staminal and staminodial glands in Lauraceae. Plant Biol. 11:490–492.

Salleh WMNHW, Ahmad F, Yen KH, Zulkifli RM. 2016. Essential oil compositions of Malaysian Lauraceae: a mini review. Pharm Sci. 22:60–67.

Schlee D. 1990. Das Bernstein-Kabinett. Stuttgarter Beitr Naturk. C 28:1–100.

Seigler DS, Ebinger JE. 2017. A new *Senegalia*, (*S. alexae*, Fabaceae: Mimosoideae) from Panama, Brazil, and Peru. Phytologia. 99:221–225.

Shi G, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang M, Lei W, Li Q, Li X. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Res. 37:155–163.

Vogel S. 1990. The role of scent glands in pollination: on the structure and function of osmophores. New Delhi: Model Press Ltd; p. 202.