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A unique flower in Miocene amber sheds new light on the evolution of flowers

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Abstract

The evolution of flowers is among the foremost topics in evolutionary science. The question for botanists of how flowers evolved exists mainly due to lack of relevant fossil evidence, especially of well-preserved flowers. Dominican amber has yielded abundant fossils (including those of flowers) and thus opens a unique window on flower evolution. Here we report a unique flower preserved in mid-Miocene Dominican amber, *Dinganthus pentamera* **gen. et sp. nov.** The flower is actinomorphic, pentamerous, bisexual flower including two bracts, five tepals, 10 stamens, and gynoecium. The stamens are dorsifixed, filamentous, and latrorse. The gynoecium in the centre comprises three portions, namely, a basal gynophore, multiple ovaries in the middle, and an apical style. Supplementing to the developmental and genetic evidence, the unique morphology of *Dinganthus* suggests that a flower is a condensed shoot with lateral appendages, a long-held belief in botany.

Keywords: flower, Miocence, amber, eudicots, Dominica, *Dinganthus*

Introduction

Flowers bring beauty to the world and they are cherished by many. How flowers have evolved is among the 125 top science questions listed by *Science* (Kennedy & Norman, 2005). A long-held belief dated back to the Linnean age is that a flower is a condensed shoot with lateral appendages. Although developmental and genetic studies support it (Wang *et al*., 2011; Zhang, 2019), almost none of fossil flowers (Poinar & Chambers, 2005; Poinar *et al*., 2007, 2008a, b, 2016; Poinar, 2017; Poinar & Rasmussen, 2017; Fu *et al*., 2018; Liu *et al*., 2018; Manchester *et al*., 2018; Wang, 2018) favors this belief. Dominican amber (15–20 Ma, mid-Miocene) is famous for its diverse fossil inclusions, including some of flowers (Iturralde-Vinent & MacPhee, 1996; Iturralde-Vinent, 2001; Sherwin, 2006; Poinar, 2010, 2016a, b; Ayala *et al*., 2017; Ross, 2019). Here we report a new fossil flower, *Dinganthus* **gen. nov.**, in an amber uncovered from eastern Dominican Republic (Fig. 1). The flower is actinomorphic, bisexual, including two bracts, five tepals, 10 filamentous stamens, and a gynoecium. Its unique morphology resembles that of a shoot with various lateral appendages, favoring the above long-held botanical belief.

Material and methods

The specimen was collected from the Comatillo Mine, eastern Dominican Republic (18.750°N, 69.635°W) (Fig. 1). The holotype (FAI-D-p00057) is deposited in the collection of the Fushun Amber Institute, Fushun, China.

Observations and photographs were made with a Nikon SMZ1500 stereomicroscope. Micro-CT was performed using a Zeiss Xradia 520 versa X-ray microscope. The 3D reconstruction and virtual sections were generated using VG Studio MAX 3.0. All figures were organized for publication using Photoshop 7.0.

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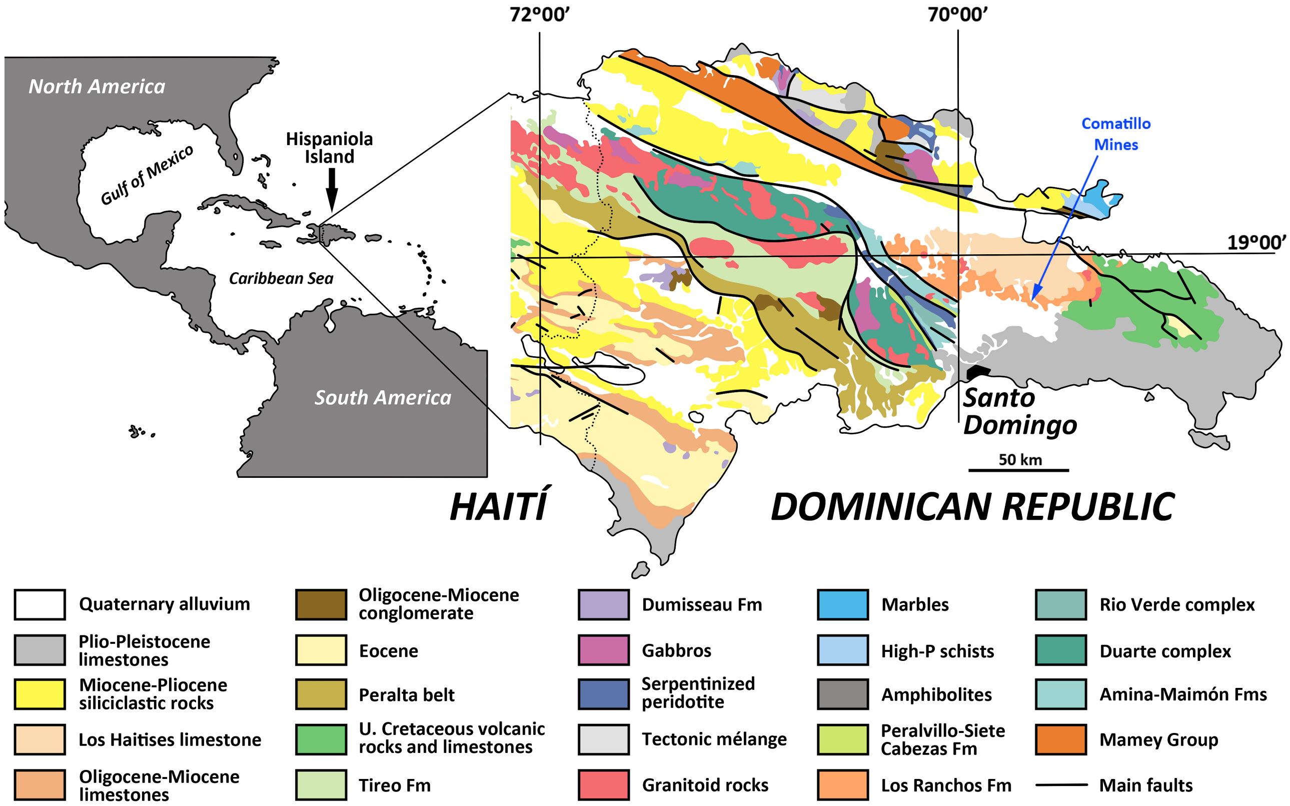

FIGURE 1. Dominican Republic geological map (modified from Ayala *et al.* (2017)) showing the location of the fossil site of *Dinganthus pentamera* **gen. et sp. nov.**, the Comatillo Mine in eastern Dominican Republic.

Systematic palaeontology

Angiospermae
Eudicots
Family *Incertae sedis*

Dinganthus gen. nov.

Type species. *Dinganthus pentamera* **sp. nov.**

Etymology. *Ding*-, dedicated to the former president of the Peking University and famous mathematician, Dr. Shisun Ding (September 5, 1927–October 12, 2019; Fig. 2C); "*anthus*", for the Greek "*anthos*" (flower).

Diagnosis. Flower actinomorphic, bisexual, with two subopposite bracts, a whorl of five tepals, a whorl of ten stamens, and gynoecium. Tepals and stamens arising on a hypanthium. Tepals distinct, oval, entire-margined. Stamens filamentous, dorsifixed, latrorse. Gynoecium comprising multiple (probably eight) fused carpels arranged in a whorl, with a basal gynophore and an apical elongated style.

Dinganthus pentamera gen. et sp. nov.

(Figs 2–3)

Holotype. FAI-D-p00057, deposited in Fushun Amber Institute, Fushun, China.

Etymology. The specific epithet *pentamera* is for the pentamerous symmetry of the flower.

Type locality and age. The Comatillo mine, eastern Dominican Republic (18.798˚N, 69.595˚W) (Fig. 1). The late Early Miocene−early Middle Miocene (15−20 Ma) (Iturralde-Vinent & MacPhee, 1996).

Description. The flower (including the stalk) is 4 mm long and 3.3 mm in diameter (Figs 2A, B, 3C). The flower includes a stalk, two bracts, five tepals, ten stamens, and a gynoecium (Figs 2A, B, 3C). The stalk is terete, 0.37 mm in diameter and 1.6 mm long (Figs 2A, B, E, 3C). Two bracts are subopposite at the base, distanced from the tepals, each about 0.65 mm long and 0.33–0.49 mm wide (Figs 2E, 3C). Five tepals are distinct, in a whorl, each 1.8 mm long and 1.3–2 mm wide, with a round tip and recurved fringes, imbricate, sessile on the outer margin of the hypanthium (Figs 2F, 3C, H). Ten distinct stamens are in a whorl, arranged on the inner margin of the hypanthium, each includes a slender filament and a dorsifixed, latrorse, probably tetrasporangiate anther (Figs 2F–I, 3A, B, G–I). The filament is approximately 0.15 mm wide basally, slightly tapering to only 66 μm wide distally, up to 2.4 mm long (Figs 2F–H, 3A, B). The anther is 0.61 mm long, 0.3–0.37 mm thick, and 0.33 mm wide, opens by two lateral longitudinal slits 234–310 μm wide, with a ridge in each half of the opened

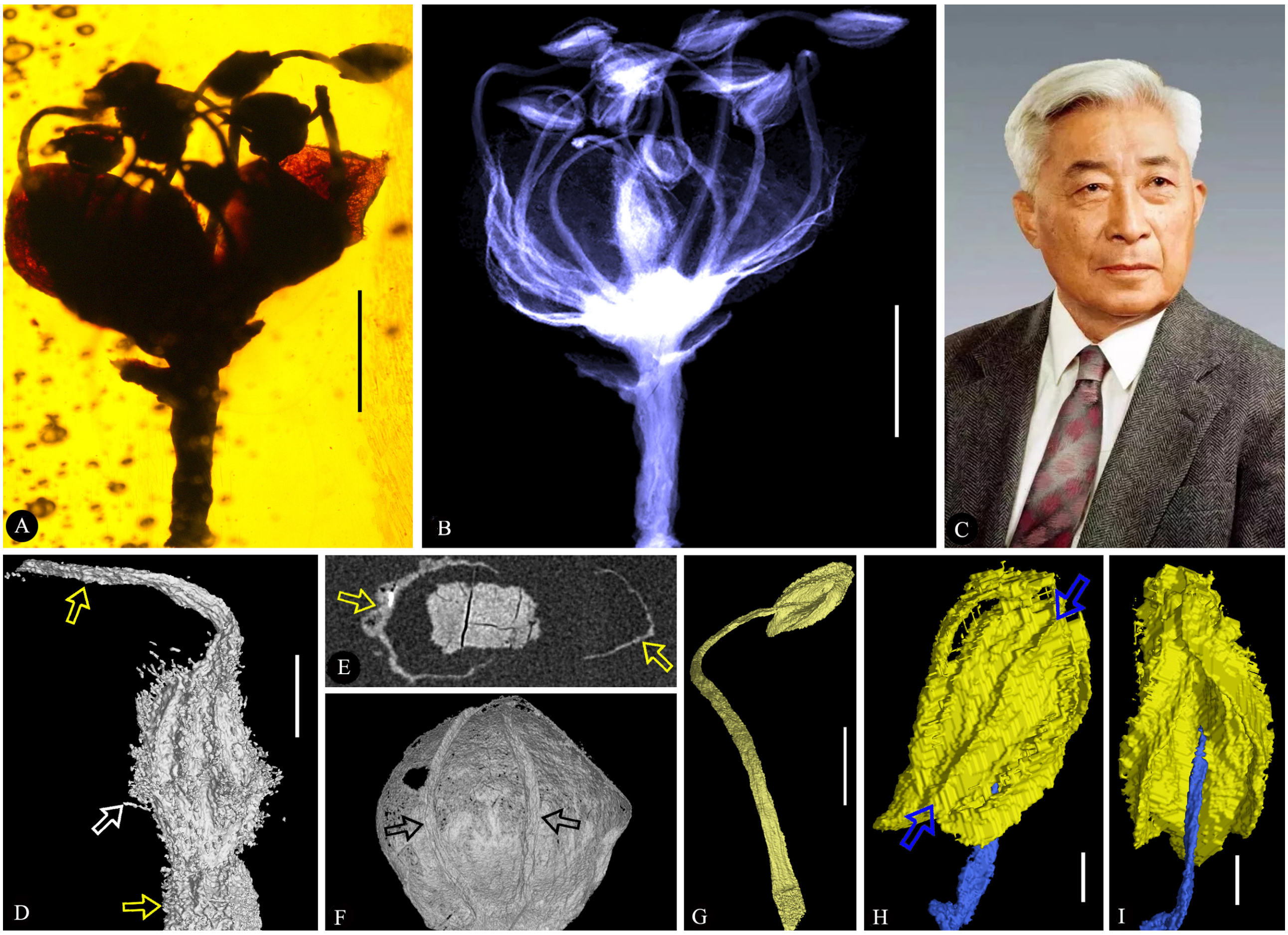

FIGURE 2. *Dinganthus pentamera* **gen. et sp. nov.** in a Dominican amber and its details. **A**, The specimen is three dimensionally preserved in amber. Scale bar = 1 mm. **B**, Micro-CT rendering of the flower. Scale bar = 1 mm. **C**, Dr. Shisun Ding (1927−2019), former president of Peking University and leading mathematician. **D**, Micro-CT view of the gynoecium, showing the basal gynophore (lower yellow arrow), middle hirsute fertile portion (white arrow), and apical style (upper yellow arrow). Scale bar = 0.3 mm. **E**, Transverse view showing two subopposite bracts (yellow arrows) on either side of the stalk. Scale bar = 0.2 mm. **F**, Adaxial view of a tepal with two corresponding filaments (arrows) on its adaxial. Scale bar = 0.5 mm. **G**, One of the stamens, with a curving filament. Scale bar = 0.5 mm. **H** and **I**, Lateral (**H**) and abaxial (**I**) views of the anther in **G**, showing spatial relationship between the filament (blue) and the dorsifixed anther. Note a ridge (between two blue arrows in H) inside each half of the opened anther. Scale bars = 0.1 mm.

anther suggesting each half of the anther is result of the fusion between two formerly separated pollen sacs (Figs 2G–I, 3A, B). The gynoecium is situated centrally above a discoid structure, including a basal gynophore, several ovaries in middle, and an apical curved style (Figs 2D, 3C–E). The gynophore is 0.43 mm in diameter, about 0.4 mm long (Figs 2D, 3C, D). The middle portion has eight longitudinal hirsute ridges, 0.52 mm in diameter, 0.6 mm long (Figs 2B, D, 3C, D, J). The carpels (suggested by the longitudinal ridges) are in a whorl, each with void locule and covered with hairs arranged in longitudinal files (Figs 2D, 3C–E, J). The apical elongated style is curved, about 1 mm long, 89 μm wide basally, tapering to only 49 μm apically (Fig. 2D).

Remarks. There is uncertainty over our interpretation of the gynoecium. Currently, we interpret it as multiple (probably eight) syncarpous carpels sharing a single style, due to eight obvious longitudinal hirsute ridges on the gynoecium surface (Fig. 2D). It appears possible that these carpels are plurilocular (Figs 3C–E), but this could not be confirmed as definitely true since Micro-CT cannot differentiate ovules/seeds from other plant tissues (such as septa) within carpels. We prefer to leave this question open for future investigations.

Discussion

Affinity

Angiosperms are distinguished from gymnosperms by their ovules enclosed before pollination (Tomlinson &

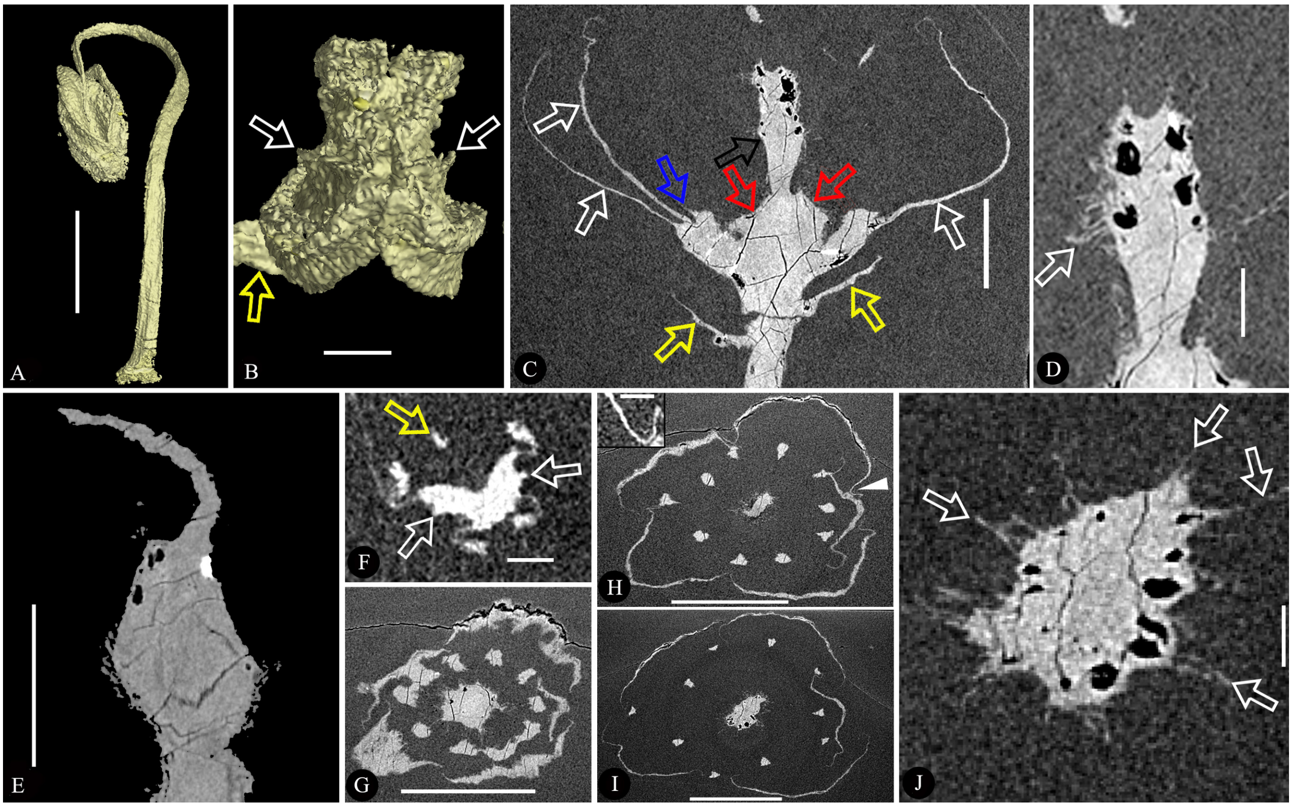

FIGURE 3. Micro-CT renderings and views of *Dinganthus pentamera* **gen. et sp. nov. A**, Rendering of a stamen including an elongated curving filament and dorsifixed anther. Scale bar = 0.5 mm. **B**, Apical view of the anther in **A**, showing the filament (yellow arrow) and a ridge (white arrows) inside each half of the opened anther. Scale bar = 0.1 mm. **C**, Longitudinal section of the flower, showing bracts (yellow arrows), tepals (white arrows) and stub of a filament (blue arrow) on the hypanthium, discoid structure (red arrows), and gynoecium (black arrow). Scale bar = 0.5 mm. **D**, Detailed longitudinal section of the gynoecium, showing hairs (white arrow) and carpels with void locules (black regions) arranged at different levels. Scale bar = 0.2 mm. **E**, A longitudinal section of the gynoecium, showing the hairy periphery and apical style. Scale bar = 0.5 mm. **F**, Transverse section of a stamen, showing the filament (yellow arrow) and a ridge (white arrows) in each half of the anther. Scale bar = 0.1 mm. **G** and **I**, Two transverse sections of the flower at different levels. Note five tepals, 10 filaments, and gynoecium in the center. Scale bars = 1 mm. **H**, Transverse section of the flower, showing five tepals, 10 filaments, and gynoecium in the center. Inset shows recurved tepal fringe marked by triangle in the main figure, rotated by 90 degrees. Inset scale bar = 0.1 mm. Scale bar = 1 mm. **J**, Detailed transverse section of the fertile portion of gynoecium showing void locule in the ovary and hairs (arrows) on the surface. Scale bar = 0.1 mm.

Takaso, 2002; Wang, 2010, 2018). The dark regions in longitudinal and transverse Micro-CT views of *Dinganthus* gynoecium are conspicuous (Figs 3C–E, J) due to the presence of secluded void locule. If they were not fully secluded, these ovarian locules should have been filled with the amber, when it was a fluid resin originally. The presence of void ovarian locules in these views indicates that the ovaries are closed in *Dinganthus*, namely, ovules in *Dinganthus* are enclosed. This feature, in addition to its flower-like general morphology, pins down the *bona fide* angiospermous affinity for *Dinganthus*.

Among angiosperms, *Dinganthus* resembles eudicots in pentamery, whorled arrangement of tepals, stamens, and carpels. Core Eudicots usually are characterized by their well-differentiated sepals and petals, pentamerous perianth, pentamerous androecium, and shared style, as seen in, for example, *Wimmeria*, *Salacia* (Celastraceae), *Telephium* (Molluginaceae), and *Cyrilla* (Cyrillaceae) (Tab. 1). The carpels in *Dinganthus* are more or less arranged in a whorl (Fig. 2D). The multitude of carpels and shared apical style are features frequently seen in typical Eudicots. The pentamerous perianth and stamens also suggest an affinity of Eudicots. But the possibly octamerous gynoecium makes *Dinganthus* unique and different from all known Eudicots.

Many flowers have been reported from amber (Poinar & Chambers, 2005, 2015, 2017; Poinar *et al*., 2007, 2008a, b, 2013, 2016; Ross *et al*., 2010; Chambers & Poinar, 2012a, b, 2014a, b, 2016; Chambers *et al*., 2010, 2012; Poinar & Struwe, 2016; Liu *et al*., 2018), including *Treptostemon*, *Brevitrimaris*, *Trochanthera*, *Distigouania*, *Ticodendron*, *Strychnos*, *Trichilia*, *Swietenia*, and *Dasylarynx* from

TABLE 1. Comparison between *Dinganthus* and some living flowers.

	Dinganthus	*Wimmeria* (Celastraceae)	*Salacia* (Celastraceae)	*Telephium* (Molluginaceae)	*Cyrilla* (Cyrillaceae)
#Sepal/bract	2	5	5	5	5–7
#Tepal/petal	5	5	5	5	5–7
#Stamen	10	5	2–4	5	5
Stamen fixing	dorsal	dorsal-basal	basal	dorsal-basal	dorsal
#Pollen cells	4	2	2	4	4
Stamen orientation	latrorse	introrse	extrorse/apical	introrse	introrse
Anther dehiscence	slit	slit	longitudinal / transverse	slit	pore/slit
Pollen	?	3-colporate	3-colporate, 3-porate	3-colpate	3,4-colporate
Nectar disk	present?	present	present	lacking	lacking
#Carpel	8?	3	3	3	2
#Style	1	1	1	lacking?	1
Placentation	?	axile	axile	axile	axile

FIGURE 4. Reconstruction of *Dinganthus pentamera* **gen. et sp. nov. A**, Oblique side view. **B**, Top view. **C**, Side view. **D**, Bottom view.

Dominican amber. The history of Eudicots can be dated back to the mid-Cretaceous (Liu *et al*., 2018; Manchester *et al*., 2018). Some of the comparable representatives of Eudicot fossils, including *Lijinganthus*, *Dakotanthus*, *Lachnociona*, *Tropidogyne*, *Eoèpigynia*, *Trochanthera*, *Distigouania*, *Ticodendron*, *Strychnos*, *Trichilia* and *Swietenia* are compared with *Dinganthus* in Table 2.

Different from flowers typical of Eudicots in which all three or four whorls of organs are highly concentrated to the same point (receptacle) or very limited range of the flower axis, *Dinganthus* has an obvious gynophore. A gynophore similar to *Dinganthus* has been seen in some angiosperms, *e.g*., Magnoliales (*Michelia* (Magnoliaceae)) (Zhang *et al*., 2017), Malpighiales (*Passiflora* (Passifloraceae)) (Judd *et al*., 1999), Brassicales (Cleomaceae, Capparaceae, Brassicaceae) (Endress, 2010), Sapindales (*Boenninghausenia* (Rutaceae) (Endress, 2010)). Compared with typical flowers in core Eudicots, *Dinganthus* with its gynophore and distantly spaced flower parts demonstrates a great resemblance to that of a shoot with various lateral appendages.

Theoretical implications

A long-held botanical belief is that a flower is a metamorphosed shoot. This idea can be dated at least back to 1751 when Carl Linnaeus published his monograph *Philosophia Botanica*. Although supported by developmental and evo-devo genetic evidence (Wang *et al*., 2011; Zhang, 2019), this hypothesis remains unfounded by fossil evidence hitherto. Considering this hypothesis is a premise for many botanical speculations, fossil evidence favoring it helps to consolidate the foundation of botanical mansion. *Dinganthus* seems to be the badly wanted fossil evidence in this term.

It is conceivable that, in ancestral flowers, an elongated shoot with various vegetative and reproductive lateral appendages becomes increasingly telescoped, leading to morphology typical of extant eudicot flowers, namely, all their organs are concentrated to very limited range along the flower axis (called receptacle now). If this inference is correct, future search for ancestors of flower should focus on some fossil taxa with shoots bearing distanced fertile

TABLE 2. Comparison between *Dinganthus* and some fossil flowers.

	Symmetry	Bisexual	Sepal/bract	Petal/Tepal	Stamen	Filament	Pollen sacs	Pollen grain	Floral cup	Ovary	Carpel	Style	Preservation media	Locality	Reference
Dinganthus pentamera	actinomorphic	yes	2, free	5, free, recurved	10, dorsifixed, latrorse, slit	slender	4	?	hypanthium	superior	8?, fused	1, curved	amber	Dominica	This study
Lijinganthus revoluta	actinomorphic	yes	5, free	5, free, revolute	8 (10?), dorsifixed, introrse, slit	slender	2	tricolpate	none	superior	3, fused	no	amber	Burma	Liu *et al.*, 2018
Dakotanthus cordiformis	actinomorphic	yes	5, free	5, free, spatulate	10?, dorsifixed, slit	stout	4	triaperturate	none	superior	5, fused	divergent	siltstone	USA	Manchester *et al.*, 2018
Lachnociona terriae	actinomorphic	no	5, free	none	10?	slender	?	?	present	superior, half-inferior	5, fused or not	connivent	amber	Burma	Poinar *et al.*, 2008b
Cascolaurus burmitis	actinomorphic	no	none	6	9, basifixed, introrse/ extrorse, valve	short	4	?	?	?	?	?	amber	Burma	Poinar, 2017
Tropidogyne	actinomorphic	yes	5, slightly fused	0	10, basifixed/dorsifixed, introrse?, slit	short, slender	?	?	present	inferior	2–3, fused	2–3, divergent	amber	Burma	Chambers *et al.*, 2010; Poinar & Chambers, 2017
Eoëpigynia burmensis	actinomorphic	yes	4, fused	4, free, valvate	4, dorsifixed, introse	slender	?	tricolporate?	present	inferior	fused	?	amber	Burma	Poinar *et al.*, 2007
Palaeoanhtella huangii	actinomorphic	no	none	8, fused	8, basifixed	short	4	inaperturate	none	?	?	?	amber	Burma	Poinar & Chambers., 2005
Micropetasos burmensis	actinomorphic	yes	5, basally connate	0	numerous	slender	2	triaperturate	none	superior	1	1, curved	amber	Burma	Poinar *et al.*, 2013
Trochanthera lepidota	actinomorphic	no	peltate	perianth	3–4, extrorse	short	2	spherical	none	?	?	?	amber	Hispaniola	Poinar *et al.*, 2008a

......*continued on the next page*

TABLE 2 (Continued)

	Symmetry	Bisexual	Sepal/bract	Petal/Tepal	Stamen	Filament	Pollen sacs	Pollen grain	Floral cup	Ovary	Carpel	Style	Preservation media	Locality	Reference
Trichillia	actinomorphic	yes?	?	5, free	4–10	short	?	?	none	?	?	?	amber	Hispaniola	Chambers & Poinar, 2012a
Treptostemon domingensis	actinomorphic	no	?	6, free	9, extrorse, pores	short	?	?	none	?	?	?	amber	Hispaniola	Chambers *et al.*, 2012
Brevitrimaris arcuatus	actinomorphic	yes	3	3, free	3, latrorse	short	4	monosulcate	none	?	1	1, short	amber	Hispaniola	Chambers & Poinar, 2016
Ticodendron palaios	actinomorphic?	no	3	0	?	?	?	?	none	inferior	?	2	amber	Hispaniola	Chambers & Poinar, 2014b
Distigouania irregularis	zygomorphic	no	5	4+1	4+1	slender	2	?	Hypanthial disc	?	?	2	amber	Hispaniola	Chambers & Poinar, 2014a
Swietenia dominicensis	actinomorphic	no?	?, basally fused	5, free	10	?	?	?	none	?	?	1	amber	Hispaniola	Chambers & Poinar, 2012b
Strychnos electri	actinomorphic	yes	?	5, fused	5, introrse, slit	sessile	2	spherical	?	?	?	1	amber	Hispaniola	Poinar & Struwe, 2016
Gouania miocenica	actinomorphic	yes	5	5	5, basifixed	slender?	2	?	hypanthium	inferior	3, fused	1, trifid	amber	Mexico	Hernández-Hernández & Castañeda-Posadas, 2018

and sterile lateral parts. This inference also helps botanists to understand the perplexing flower morphology in early fossil angiosperms, including *Archaefructus* (Sun *et al*., 1998) and *Yuhania* (Liu and Wang, 2017).

Conclusion

The unique morphology of *Dinganthus* suggests that a flower is a condensed shoot with various lateral appendages, strengthening the long-cherished condensing interpretation of flower origin.

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