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Alarista succina gen. et sp. nov. (Poaceae: Bambusoideae) in Dominican amber

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Alarista succina **gen.** et **sp. nov.** (Poaceae) is described from a single floret preserved in amber of Tertiary age originating from the Dominican Republic. The new genus is characterised by (1) a narrow-winged lemma awn, (2) numerous (as many as 17) lemma nerves, (3) a lengthy rachilla internode (implying a lax spikelet), (4) sinuous-margined long cells, (5) silica cells arranged transversely, (6) stomatal subsidiaries low domed and (7) papillae. The epidermal features are characteristic of the abaxial leaf blade surface of members of the Bambusoideae and the fossil is placed in this group.

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Keywords: Tertiary grass; Greater Antilles; Hispaniola; fossilised resin

Introduction

Amber has remarkable preservative qualities for both plant and animal fossils (Poinar 1992). A number of identifiable angiosperm remains occur in Tertiary and Cretaceous amber (Chambers et al. 2010, 2011a, 2011b; Chambers and Poinar 2012; Poinar and Poinar 1999), including those of the extinct resin-producing tree, *Hymenaea protera* (Poinar, 1991) (Fabaceae: Caesalpinioideae). Dominican amber not only provides us with ages and past distributions of Greater Antillean fauna, but also insights into character evolution of extinct lineages. This study describes a new grass genus in Dominican amber.

Material and methods

The piece of amber containing the fossil is roughly rectangular in shape, measuring 22 mm in length by 12 mm in width and 7 mm in depth. The specimen was obtained from mines in the Cordillera Septentrional of the Dominican Republic. Dating of Dominican amber is controversial with the latest proposed age of 20–15 mya based on Foraminifera (Iturralde-Vincent and MacPhee 1996) and the earliest of 45–30 mya based on coccoliths (Cêpek in Schlee 1990). A range of ages may be likely, since the amber fossils are associated with turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994). Dominican amber is secondarily deposited in sedimentary rocks, which makes a definite age determination difficult (Poinar and Mastalerz 2000). Observations and photographs were made with a Nikon stereoscopic microscope SMZ-10 R and Nikon Optiphot TM at magnifications up to 1060 ×.

Description

The fossil, comprising a lemma, palea and rachilla internode, is readily assigned to the Poaceae. The floret is complete except for the callus and possibly a distal portion of the awn (Figure 1). A narrow transparent wing (membrane) on the awn (Figures 2, 4, 7, 8) is positioned sufficiently close to the surface of the amber to be examined with a compound microscope, allowing detailed features of the epidermis to be observed.

Order Poales

Family Poaceae

Subfamily Bambusoideae

Alarista *Poinar & Columbus, gen. nov. (Figures 1–10)*

Type species: A. succina *Poinar & Columbus, sp. nov.*

Diagnosis: Complete spikelet with awn 13 mm in length; lemma narrowly lanceolate, semiterete in cross section on lower half, laterally compressed and keeled on upper; nerves numerous (11 +), awn narrowly winged; palea slightly shorter than lemma, ciliate apically, contains two principal nerves, positioned on two keels; long rachilla internode (7.5 mm); awn winged; long cells sinuous-margined, silica

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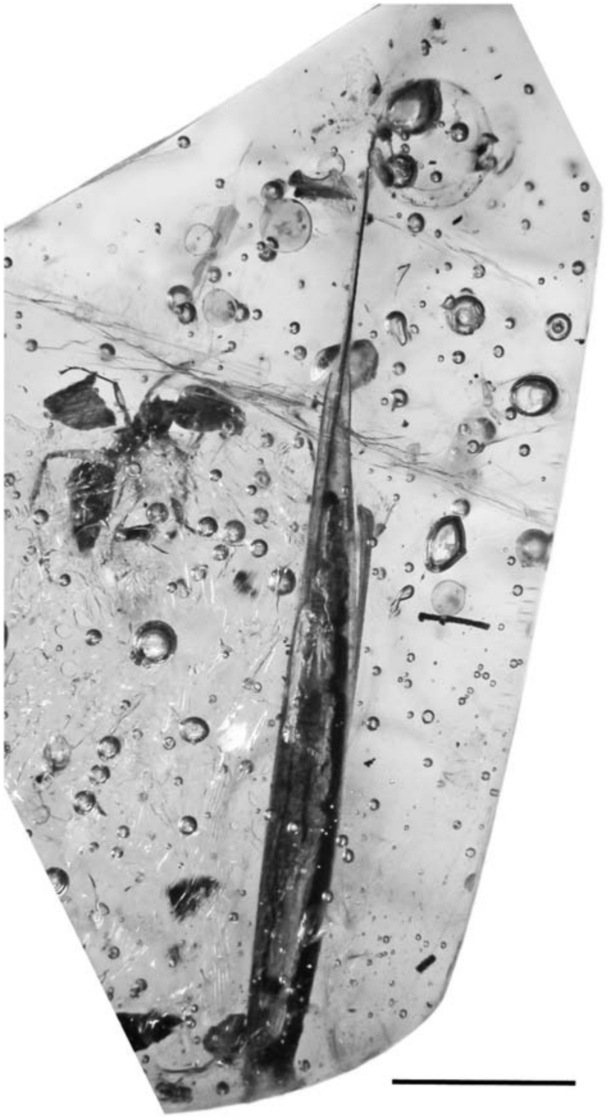


Figure 1. Holotype of *A. succina* in Dominican amber adjacent to a worker *Dolichoderus* ant (Hymenoptera: Formicidae). Bar = 2.4 mm.

cells arranged transversely, stomatal subsidiaries low domed, papillae and bicellular microhair present.

Etymology: *Alarista* is a compound of the Latin *ala* (wing) and *arista* (awn).

Alarista succina ***Poinar & Columbus, sp. nov.***

Description: With characters listed in the generic diagnosis.

Lemma: Length, 10 mm (excluding awn and missing basal callus region); greatest width, 1.2 mm; narrowly lanceolate; acute at apex; semiterete in cross section on lower half; laterally compressed and keeled on upper half; apical 1 mm of keel with narrow membranous wing continuing on awn; surface antrorsely scabrous; 11–17 nerves with 7–9 principal nerves (more conspicuous; includes midnerve) interspaced by 4–8 secondary (fainter) nerves; all nerves converging at apex; midnerve and two lateral nerves extending full length of lemma; awn terminal, 3 mm long, possibly broken apically, with narrow translucent abaxial wing (membrane) (30–40 μm wide) extending length of awn and gradually narrowing distally (Figures 2, 7, 8); awn antrorsely scabrous, twisted 180° on terminal 0.5 mm.

Palea: Length, 8.7 mm, rounded and ciliate (at least) apically, with two conspicuous keeled nerves separated by several fainter nerves.

Rachilla: Internode 7.5 mm long, slender, bowed slightly away from anthecium, three nerved and/or angled, antrorsely scabrous, apically oblique, thickened and cupped; cup fringed with one-celled hairs of varying lengths, reaching 0.2 mm.

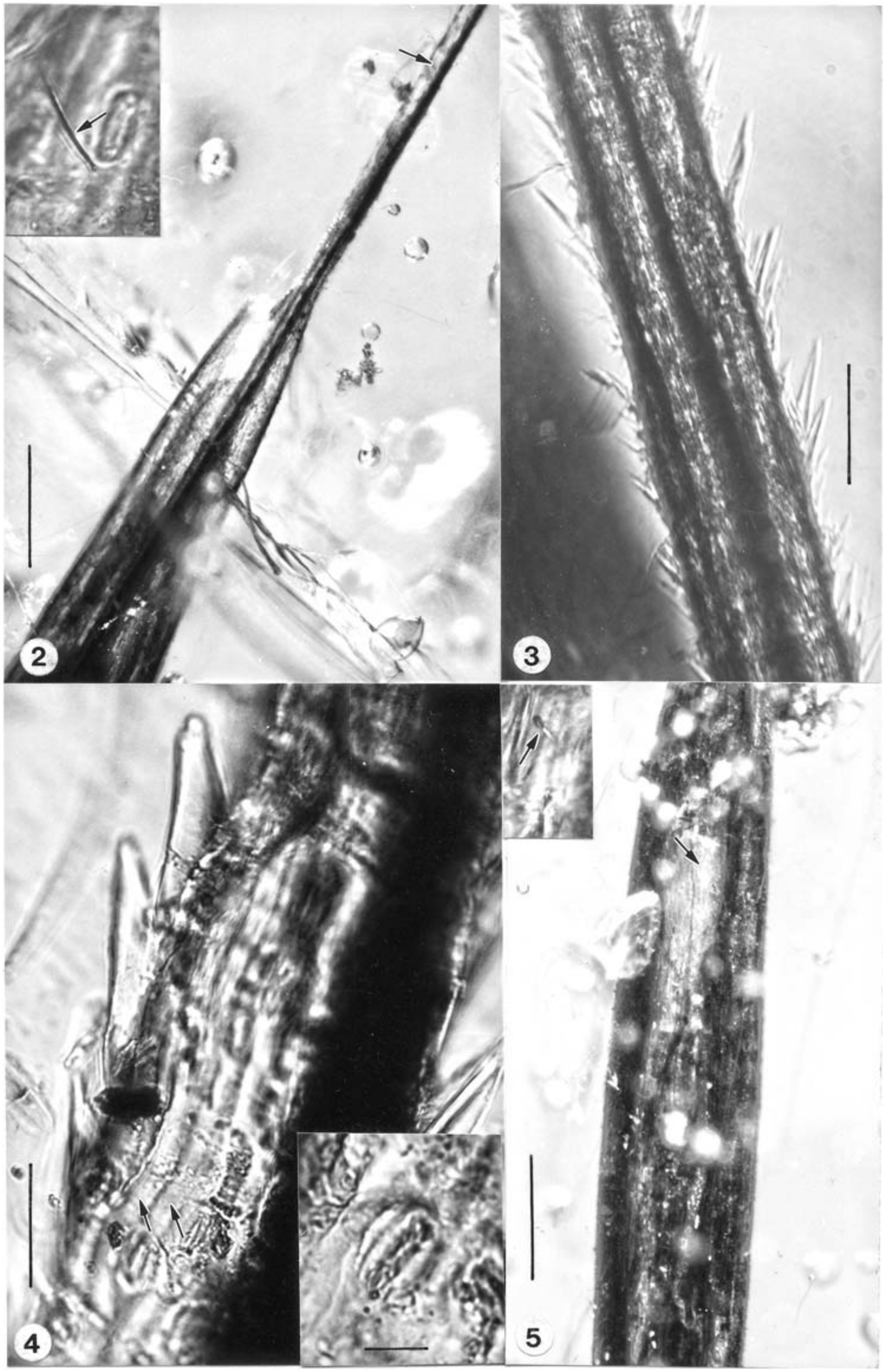
Awn wing epidermis: Cells arranged in at least five longitudinal (parallel to vascular bundle and margin) files (rows); stomata present in at least three consecutive files, those of adjacent files in proximity to one another but not side by side, subsidiary cells low dome shaped; longitudinally elongate cells present, some slightly curved, at least some anticlinal; side (longitudinal) walls sinuous; interstomatal anticlinal (end) (transverse) walls flared and concave where abutting stomates and subsidiary cells; one long cell uniquely shorter and having unequivocally markedly sinuous long walls; two short silica cells, one associated with sinuous-walled long cell; two types of papillae evident on long cells, one type globose, thick walled, second type bordering stomatal apparati, thin walled; bicellular microhair (Figure 5, inset), 9 μm long; prickles on margin common, antrorsely oriented; one thin macrohair, 36 μm long, at end of interstomatal long cell adjacent to stomate and subsidiary cells (Figure 2, inset).

Etymology: The specific epithet is from the Latin *succinus* (of amber).

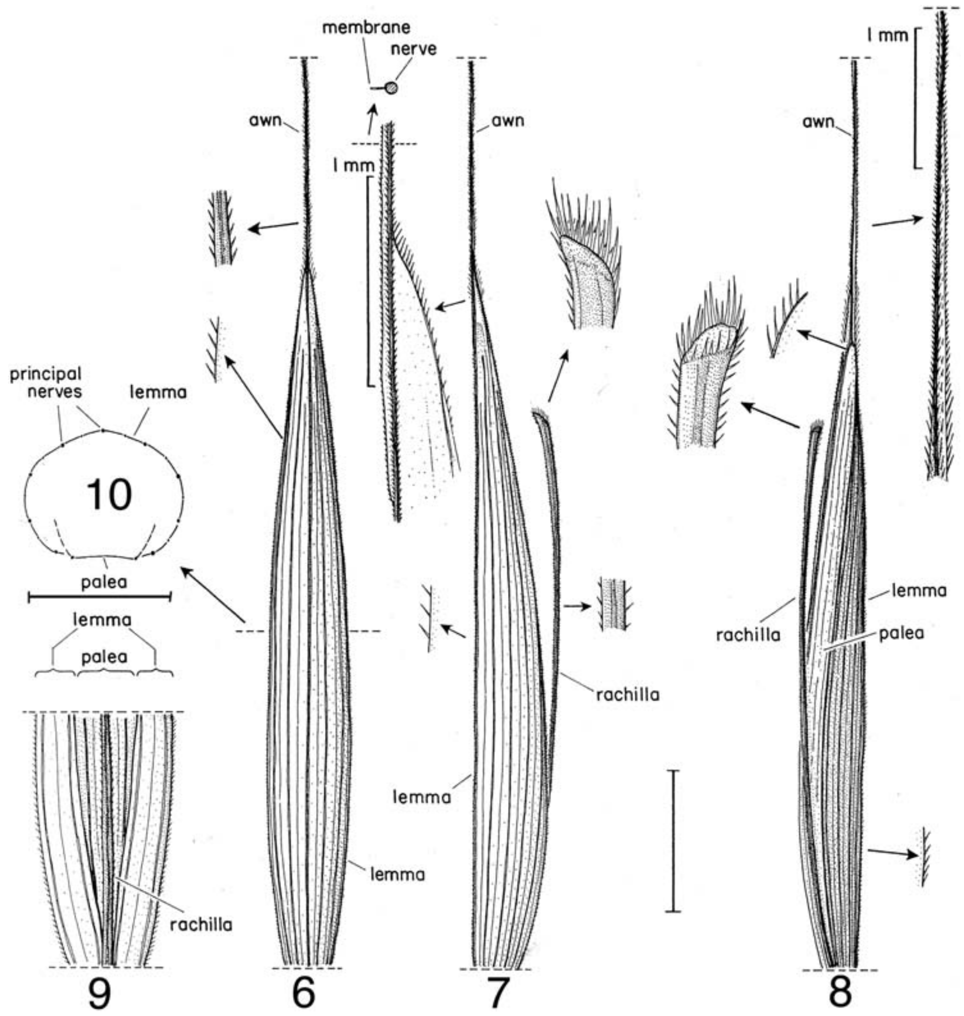
Holotype: Accession number Sd-9-17 (Dominican amber), Poinar amber collection maintained at Oregon State University, Corvallis, Oregon, USA.

Type locality: Dominican Republic, Cordillera Septentrional, unspecified amber mine.

Comments: Although a total of 11 nerves can be seen on the lemma, there may actually be 17 since some nerves appear to be uncertain due to degraded patches on the lemma surface and obscurities in the amber. The cupped apex of the rachilla internode suggests that the spikelet possessed at least two florets. The length of the internode implies a lax, linear spikelet. Disarticulation was evidently at the base of the floret, above the glumes and between the florets.



Figures 2–5. *A. succina.* (2) Upper portion of floret showing membrane portion of awn (arrow). Bar = 400 μm. Inset shows a thin macrohair (36 μm long) (arrow) adjacent to a stomatal complex on the awn membrane. (3) Detail of the antrorsely scabrous rachilla. Bar = 83 μm. (4) Epidermal features on the membrane (wing) portion of the antrorsely scabrous awn. Note periclinally elongate, curved long cells (arrows). Bar = 26 μm. Inset shows a stomata on the awn membrane. Bar = 25 μm. (5) Adaxial view of floret showing palea (arrow). Bar = 845 μm. Inset shows a bicellular microhair (9 μm long) (arrow) on the awn membrane.



Figures 6–10. *A. succina*. (6) Abaxial view of floret. (7) Lateral view of floret. (8) Lateral-adaxial view of floret. (9) Adaxial view of base of floret. (10) Cross section of floret showing principal nerves. Vertical bar on right for (6)–(8) = 2 mm. Horizontal bar on left for (9) and (10) = 1.1 mm.

Discussion

Although *A. succina* bears a resemblance to some members of Pooideae (e.g. species in *Elymus* and *Festuca*), it is best placed in the Bambusoideae. The many-nerved lemma, low-domed stomatal subsidiary cells and papillae are characters of the Bambusoideae (Melcalfe 1960; Calderón and Soderstrom 1980; Clayton and Renvoize 1986; Ellis 1987; Soderstrom and Ellis 1987; Watson and Dallwitz 1994; Grass Phylogeny Working Group [GPWG] 2001). Likewise consistent with this placement are the size and shape of the anthecium; the lemma; the lengthy, several-nerved palea; sinuous-walled long cells; the lengthy rachilla internode with a cupped apex, suggesting multiple florets per spikelet, disarticulation between the florets, a lax, linear spikelet, a bicellular microhair and transversely elongate silica cells. The number of awns and attachment are also consistent, although awns are infrequent in Bambusoideae (Calderón and Soderstrom 1980; Clayton and Renvoize 1986). Bicellular microhairs are common in Bambusoideae, but rare in Pooideae (restricted to two genera) (Clayton and Renvoize 1986; GPWG 2001). However, the cells forming microhairs in Bambusoideae are usually more or less equal in length (Tateoka et al. 1959; Melcalfe 1960), whereas in *A. succina* the apical cell is decidedly shorter than the basal cell. It should be noted that the epidermal features of the subfamilies presented in the literature, including the papers cited here, derive from studies of the leaf blade (principally the abaxial surface). A dearth of micromorphological studies of bambusoid anthecia makes it impossible at present to know the level of similarity in epidermal features between the anthecial and foliar surfaces.

The affinities of other organisms preserved in amber from the Dominican Republic provide indirect support for the placement of *A. succina* in Bambusoideae. The great majority of the Dominican amber taxa are related to extant Neotropical groups, and the amber forest was concluded to be most similar to a present day Neotropical moist forest (Poinar and Poinar 1999). Pooideae, however, are 'virtually limited' to the temperate zones (Clayton and Renvoize 1986).

Within the Bambusoideae, *A. succina* bears a strong resemblance to members of the Bambuseae, the woody bamboos. In Bambuseae, the position of *Alarista* is uncertain. We have not encountered in the literature or through the examination of herbarium specimens a bamboo having the narrowly winged awn of *Alarista*. Two genera of woody bamboos are native to the West Indies, including the Dominican Republic; namely *Arthrostylidium* Rupr. and *Chusquea* Kunth (Hitchcock 1936; Judziewicz et al. 1999). *Chusquea*, like Olyreae with one floret per spikelet and no rachilla extension, also differs from *Alarista* by its rarely entire palea apex (McClure 1973; Clayton and Renvoize 1986; Watson and Dallwitz 1994). However, within *Arthrostylidium* and other genera in subtribe Arthrostylidiinae, there are species with lax, linear spikelets or pseudospikelets containing florets and long rachillar internodes similar to *Alarista*. The lemma of some species also bears a terminal awn. Further narrowing becomes difficult, but the Neotropical Arthrostylidiinae is a logical candidate (L.G. Clark and R.W. Pohl, pers. comm.). Several of the genera of the Arthrostylidiinae have florets remarkably similar to that of *A. succina*. Most notable include species of *Aulonemia* Goudot, *Rhipidocladum* McClure (L.G. Clark and R.W. Pohl, pers. comm.) and *Arthrostylidium* Rupr., which have long rachillar internodes with hairs at the summit and ciliate paleas (Watson and Dallwitz 1994). *A. succina* was placed in a new genus because of its possession of an apparently unique character, a winged awn. Also there were not enough other characters (e.g. habit, organisation of the inflorescence) known to confidently assign it to any specific genus. Perhaps closest to the fossil is *Arthrostylidium*, a genus composed of some 20–30 species of scandant to climbing bamboos ranging from Mexico and the West Indies to Bolivia and Central Brazil at elevations from 0 to 3000 m (Watson and Dallwitz 1994; Judziewicz et al. 1999).

Diversification of the angiosperms in the American tropics during the Tertiary was probably quite extensive and extinctions of various clades obviously occurred, probably due to climatic factors that occurred in the Pliocene and Pleistocene (Poinar and Poinar 1999). Although the oldest Poaceae fossil is the Early Cretaceous *Programinis laminatus* Poinar based on morphological leaf characteristics and silica cell morphology (Poinar 2004, 2011), Upper Cretaceous grasses were obviously diverse. Phytoliths from dinosaur coprolites in India showed that at least five taxa of extant grass subclades were present by the Late Cretaceous (Prasad et al. 2005). Tertiary grass fossils are more abundant. Daghlian (1981) considered 11 reported macrofossils as true fossil grasses but remarked that assigning fossil pollen grains to the Poaceae is difficult since other members of the Poales have similar pollen types. Thomasson (1987) cited 11 published reports of fossil grasses from the tropics, but determined just three of these to be undoubted representatives of the Poaceae.

A. succina is the second grass fossil from Dominican amber. The first was *Pharus primuncinatus* Poinar & Judziewicz. The latter fossil was represented by a spikelet apparently carried into the resin by a carnivore, based on an analysis of mammalian hairs associated with the spikelet that was uniquely structured for epizoochory (Poinar and Columbus 1992; Poinar and Judziewicz 2005).

How *A. succina* arrived in the amber is unknown. A worker ant, *Dolichoderus caribbaea* (Wilson), adjacent to the spikelet raises the possibility that it was carrying the floret back to its nest since extant species of *Dolichoderus* are known to carry seeds (Youngstead et al. 2009). Another possibility is that *A. succina* had scandant habits, possibly climbing up the trunk or even branches of the amber tree, which brought it into contact with resin deposits.

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