

seed samples which originate from a dry temperate area (mean annual temperature 8.4 °C, and precipitation 580 mm).

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0014-4754/92/090904-03\$1.50 + 0.20/0
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Adhesive grass spikelet with mammalian hair in Dominican amber: First fossil evidence of epizoochory

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Received 31 January 1992; accepted 19 May 1992

Abstract. Discovery of a female spikelet of the grass genus *Pharus* (Gramineae: Bambusoideae: Phareae) in association with mammalian hair in Dominican Republic amber provides the first fossil evidence of epizoochory. Hooked macrohairs on the lemma of the spikelet show that morphological modifications in grasses for dispersal by attachment to the surface of animals were present in the Late Eocene. The fossil also represents 1) the second-oldest undoubted macrofossil record of the Gramineae, 2) the earliest record of a fossil grass that can be assigned to an extant genus, 3) the earliest undoubted record of a member of the bamboo subfamily and 4) the only known fossil of *Pharus*.

Key words. Fossil grass; *Pharus*; bamboo; Dominican amber.

Studies on the highly fossiliferous amber from the Dominican Republic have led to the discovery of many new taxa¹. The nature of the fossilization process can also result in the preservation of symbiotic associations that are rarely preserved otherwise^{2,3}. This study presents the first fossil evidence of epizoochory (dispersal by attachment to the surface of animals), by demonstrating a female spikelet of a representative of the monoecious grass genus *Pharus* R. Br. (Gramineae: Bambusoideae: Phareae) associated with mammalian hair (figs 1–3). The fossil specimen originated from the La Toca mine, located between Santiago and Puerto Plata in the Cordillera Septentrional of the northern portion of the Dominican Republic. This mine is in the Altimira facies of the El Mamey Formation (Late Eocene), which is shale-sandstone interspersed with a conglomerate of well-rounded pebbles⁴. Differences in the magnitudes of absorption peaks in nuclear magnetic resonance spectra of the exo-methylene group of amber⁵ from different mines in the Dominican Republic were used to calibrate the ages of the various mines, with the age of the Palo Alto mine (20 million to 23 million years, based on foraminifera counts) used as a standard⁶. The ages of various specimens of Dominican amber ranged from 15 million to 40 million years, with that from the La Toca mine being the oldest, some 35 million to 40 million years

old (Early Oligocene to Late Eocene). This age was corroborated by recently reported dating of the La Toca mine based on coccolith diversity which produced an age of 30 million to 45 million years⁷.

The amber containing the fossil has all the visual characteristics of natural Dominican amber. A series of chemical and physical tests⁸ performed on a small portion of the amber piece verified that it is authentic. The piece of orange amber containing the fossil weighs 7 g and is triangular in shape, measuring 37 mm longest length, 25 mm longest width and 15 mm thick. It is deposited in the Poinar collection of Dominican amber maintained at the University of California at Berkeley.

Results

Determination of the spikelet as belonging to *Pharus* was based on the distinctive combination of characters present in extant species⁹; these characters are 1) spikelet length, 2) spikelet with a single floret, 3) glumes shorter than lemma, 4) lemma 7-nerved, 5) lemma margins strongly inrolled, 6) lemma apically tapered to a beak, 7) lemma with uncinat (hooked) macrohairs and 8) lemma curved (in some) (figs 1–3). The fossil *Pharus* represents an extinct species that will be described elsewhere.

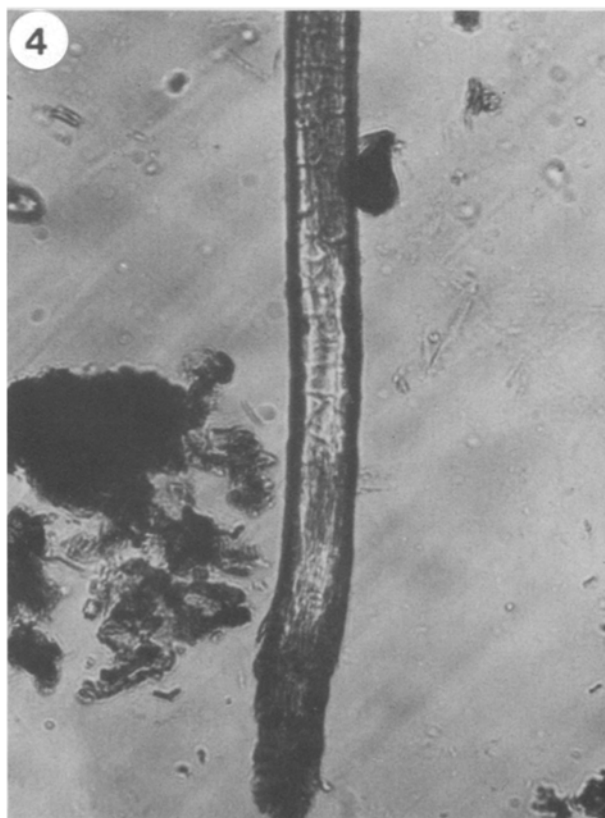
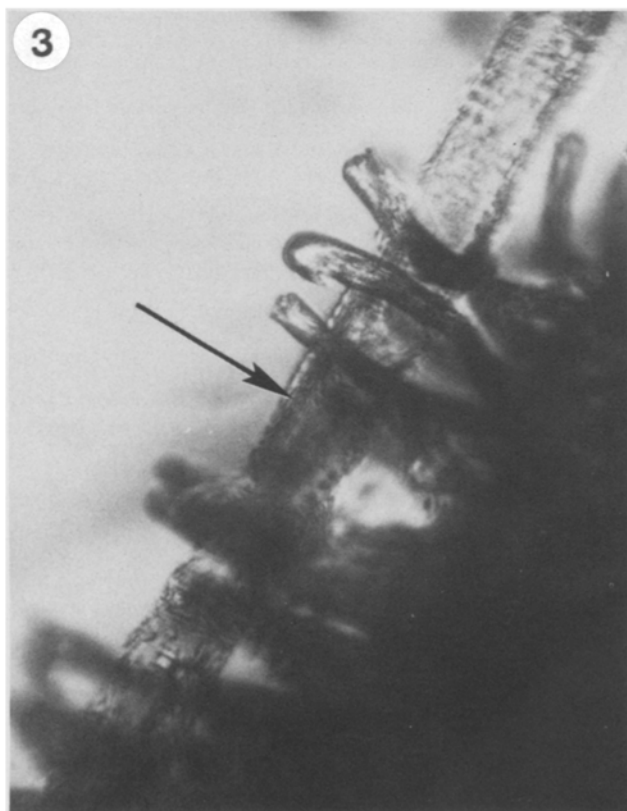
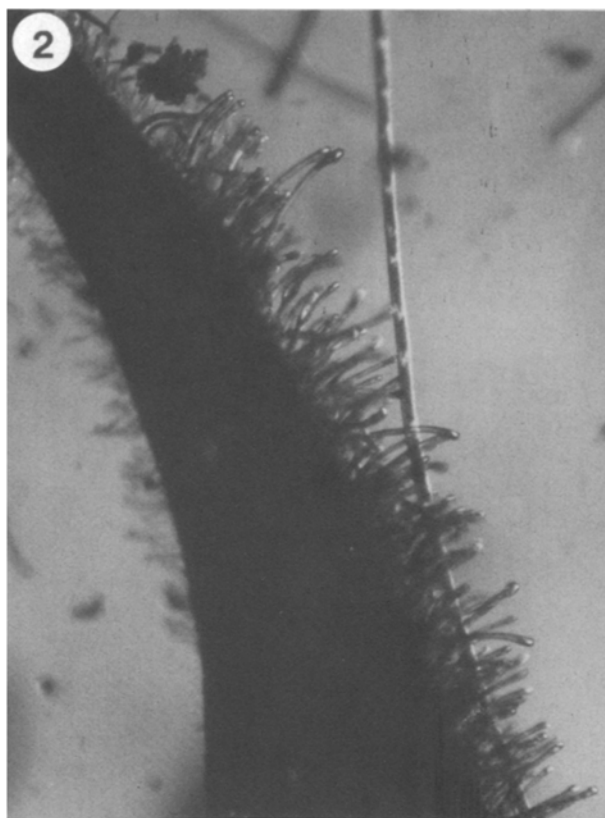


Figure 1. Female spikelet of *Pharus* in Dominican amber. Note strands of mammalian hair adjacent to the spikelet (length of spikelet is 10 mm).

Figure 3. Detail of hooked hairs on the lemma of a female spikelet of *Pharus* in Dominican amber. Note strand of mammalian hair in center (arrow).

Figure 2. Strand of mammalian hair running through the hooked hairs on the lemma of a female spikelet of *Pharus* in Dominican amber.

Figure 4. Basal region of a strand of mammalian hair in Dominican amber. Note root and irregular mosaic scale pattern.

Pharus exists today as a small genus (7 species) of New World broad-leaved herbaceous bamboos that occur in shaded tropical forest understories⁹. As in the fossil, the mature female lemmas of extant *Pharus* species are variously covered with uncinata hairs as an adaptation for external animal dispersal¹⁰. In the fossil *Pharus*, these hooked hairs occur on the apical and dorsal portions of the lemma (figs 1 and 2). Evidence that the fossil spikelet was carried to the sticky resin precursor of the present amber sample by a mammal is provided by a number (approximately 40) of mammalian hairs embedded adjacent to the spikelet. One strand of mammalian hair is still attached to the hooked hairs on the dorsal surface of the lemma (figs 2 and 3), suggesting how the spikelet was deposited in the sticky resin.

The mammalian hairs associated with the spikelet were interpreted to be guard hairs on the basis of their size and structure. The largest diameters in the lower shaft regions varied from 53 μ m to 73 μ m. The medulla comprised from 60% to 85% of the hair diameter in the shaft region and was sporadically interrupted (126–189 μ m long medulla segments were separated by 11–21 μ m long spaces). In the basal shaft region the scale pattern varied from double chevron to streaked wave and the scale margins were smooth and distant. Root portions of the hair were clearly visible (fig. 4). In the upper shaft region, the scale pattern was a rippled margin type with close margins. The only extant mammals with hair characters as described above are representatives of the Carnivora^{11,12}. These fossil hairs are distinctly different from the mammalian hair identified as Rodentia and reported earlier in Dominican amber¹³.

Epizoochory evolved as a means of dispersal that can account for the occurrence of many plant species on isolated islands. Approximately 10% of angiosperm families contain representatives with adhesive diaspores (units of dispersal)¹⁴. The most common methods of adhesion are hooked or barbed outgrowths. Advantages of epizoochory over anemochory (wind dispersal) are 1) the diaspore usually travels further and 2) the diaspore has a directed dispersal agent (nonrandomly dispersed to favorable habitats). Adhesive diaspores can be carried indefinitely by the dispersal animal; however, they are normally removed if they are detected or if they are irritating¹⁴. It is possible that the fossil *Pharus* spikelet was irritating to the dispersing mammal that rubbed itself against the trunk of a resin-bearing tree to rid itself of the nuisance. Spikelets of extant *Pharus latifolius* L. have been observed on tapirs and rodents in Panama¹⁵ and on jaguars in Ecuador⁹.

Boucot¹⁶ established a scale of reliability regarding evidence of behavioral characteristics of fossil organisms based on a functional analysis of external morphology. The presence of hooked macrohairs on the lemma of the fossil *Pharus* in association with mammalian hair would fall into Boucot's category 1, providing clear evidence of epizoochory.

Evidence indicates that long-distance dispersal is more frequent in adhesive fruits than with internally carried or wind dispersed fruits¹⁴. Wide dispersal is correlated with species survival since it allows seeds a greater chance to escape the vicinity of the parent ('Escape hypothesis') and a greater opportunity to take advantage of uncompetitive environments as they appear ('Colonization hypothesis')¹⁷.

Pharus possessed modifications for epizoochory some 35–40 million years ago which have survived to the present and may well account for its survival over that period of time.

Aside from representing the first fossil example of epizoochory, the present fossil represents 1) the second-oldest undoubted macrofossil record of the Gramineae, 2) the earliest record of a fossil grass that can be assigned to an extant genus, 3) the earliest undoubted record of a member of the subfamily Bambusoideae and 4) the only known fossil of *Pharus*^{18,19}.

Acknowledgments. The authors thank Richard Lis, Robert Ornduff and Alan Smith for critically reviewing the manuscript.

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