COMMUNICATIVE & INTEGRATIVE BIOLOGY
2017, VOL. 10, NO. 4, e1325048 (3 pages)
https://doi.org/10.1080/19420889.2017.1325048

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ARTICLE ADDENDUM

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The case of *Darwinylus marcosi* (Insecta: Coleoptera: Oedemeridae): A Cretaceous shift from a gymnosperm to an angiosperm pollinator mutualism

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ABSTRACT
Abundant gymnosperm pollen grains associated with the oedemerid beetle *Darwinylus marcosi* Peris, 2016 were found in Early Cretaceous amber from Spain. This discovery provides confirmatory evidence for a pollination mutualism during the mid Mesozoic for the family Oedemeridae (Coleoptera), which today is known to pollinate only angiosperms. As a result, this new record documents a lateral host-plant transfer from an earlier gymnosperm to a later angiosperm, indicating that pollination of the latter is a derived condition within Oedemeridae. This new fossil record exemplifies one of the 4 ecological-evolutionary pollinator cohorts now known to have existed during the global shift from a gymnosperm to an angiosperm dominated global flora. Currently, all direct evidence for pollination during the 35 million-year interval of the mid Cretaceous gymnosperm-to-angiosperm transition entails recognition of gymnosperm pollen grains on insect mouthparts and other body contact surfaces, while analogous records involving angiosperms are lacking. The gathering evidence indicates that angiosperm pollination was preceded by at least 4 gymnosperm pollination modes that served as a functional and ecological prelude to the rise and expansion of angiosperms.

ARTICLE HISTORY
Received 10 April 2017
Revised 24 April 2017
Accepted 25 April 2017

KEYWORDS
beetle; Cretaceous; evolution; Fossil; gymnosperm; pollinator; Paleoecology; plant-insect interactions

Angiosperms currently are the most diverse and pervasive plant group, but their ecological dominance is relatively recent, extending to the mid Cretaceous but not in all biomes, such as modern coniferous forests. The earliest fossil evidence for angiosperms dates to about 130–125 million years ago;[1,2] soon thereafter, they explosively diversified to achieve dominance in most terrestrial habitats during the Late Cretaceous,[3] overtaking gymnosperms in the breadth of pollination mechanisms.[1] Nevertheless, the literature has been rife with inferences regarding the initial types of angiosperm pollination. Based on a variety of evidence, at least 6 modes of pollination have been suggested for Cretaceous angiosperms.[4] Some of these modes invoke a similarity with extant basal angiosperms, and accordingly almost all proposals advocate that ancestral flowering plants were insect pollinated.[5,6] However, the fossil record continues to withhold direct evidence of examples indicating pollination of angiosperms by insects during the Cretaceous, even though there is indirect evidence that provides for specialized pollination by insects such as flies[7] and bees.[8] By contrast, examples of gymnosperm pollination are becoming increasingly abundant, based on the direct evidence of identifiable gymnospermous pollen on insect mouthparts and other body regions. In addition, there is significant indirect evidence for pollination of gymnosperm plants.[9]

A recent publication by us illustrates the first case of pollination by a beetle in the fossil record.[9] This beetle, *Darwinylus marcosi* Peris, 2016 (Fig. 1), was discovered embedded within an amber piece from the Peñacerrada I locality in northern Spain. This new species corresponds to the oldest, definitive fossil described for this family, and was accommodated in a basal position within Oedemeridae after a phylogenetic analysis.[10] *Darwinylus marcosi* exhibits autapomorphies and many characters identified as primitive among extant oedemerid species, which were interpreted as uniquely optimized ecological

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Addendum to: Peris D, Pérez-de la Fuente R, Peñalver E, Delclòs X, Barrón E, Labandeira CC. False blister beetles and the expansion of gymnosperm-insect pollination modes before angiosperm dominance. Curr.Biol 2017; 27:897-904; https://doi.org/10.1016/j.cub.2017.02.009

Figure 1. A 3-dimensional reconstruction of *Darwinylus marcosi* Peris, 2016 with associated *Monosulcites* Cookson, 1947 ex Couper, 1953 pollen grains. Total length of the specimen almost 2 mm.

features or an indication of ancestral habits. After the amber piece was exhaustively studied, it revealed that the beetle possessed 126 associated and occasionally clumped pollen grains, 5 of which were still adherent to various parts of the insect's body.[9] A follow-up taphonomic study of the piece indicated that almost all pollen grains were initially attached to the oedemerid beetle, and the juxtaposition of pollen grains amid the beetle's body surface therefore represented direct evidence for a pollination mutualism.

The most parsimonious observation would have been that the pollen grains adhering to the beetle's body were from an angiosperm, particularly as all extant Oedemeridae feed exclusively on flowers.[11] However, this was not the case. Morphological and ultrastructural features of these pollen grains are attributable to the form-genus *Monosulcites* Cookson, 1947 ex Couper, 1953.[12] The specific taxonomic affinities of gymnospermous *Monosulcites* grains are not known for sure; nevertheless, the botanical affinity of *Monosulcites* grains from the Mesozoic unequivocally indicates attribution to the Ginkgoales, Cycadales and Bennettitales. Consequently, the present finding illustrates that Oedemeridae were pollinating gymnosperms during the Early Cretaceous at about 105 million years ago, whereas present day species are exclusively associated with flowering plants. An obvious conclusion is that within this beetle lineage there was a lateral transfer of hosts from gymnosperms in their basal forms to angiosperms as a derived condition.[9]

Direct evidence for pollination mutualisms are rare in the Mesozoic fossil record.[9] Mesozoic insect pollinators now have been shown to exhibit gymnosperm associations with ginkgoalean, cycad, conifer and bennettitalean plant hosts through the direct evidence of pollen clinging to the mouthparts, heads or other relevant body structures of insects. From Spanish amber alone, there are 4 distinct species among the 7 known examples that provide direct evidence for insect pollination. Reported from Spanish amber, these are: (i) the thrips *Gymnopollisthrips minor* Peñalver, Nel et Nel, 2012 and *G. maior* Peñalver, Nel et Nel, 2012;[13] (ii) the long-proboscid fly *Buccinatormyia magnifica* Arillo, Peñalver et Pérez-de la Fuente, 2015;[14,15] and (iii) the new pollinating beetle *Darwinylus marcosi*.[9,10] The 3 pollination modes associated with these 3 insect groups respectively represent the orders Thysanoptera (thrips), Diptera (true flies) and Coleoptera (beetles), each of which houses functionally very different mouthcone, long-proboscid and mandibulate mouthpart types that indicate very different modes of pollination.[9,16] This eclectic assemblage of insect pollinators points out the importance of amber for comprehending not only the nature of the fossil record, but also an understanding of the evolution of pollination mechanisms and their role in ancient ecosystems. Together with the amber record, a fourth pollination mode involves the sponging labellate mouthparts of *Paroikus* sp., a fluid-feeding brachyceran flies (order Diptera) known from a compression-impression deposit in Transbaikalian Russia.[4]

Amber deposits with bioinclusions from the Cretaceous were produced by gymnosperm source plants, such that arthropods found embedded as inclusions were likely more ecologically associated with then-contemporaneous gymnosperms than with angiosperms, thus displaying an entrapment bias.[17] Nevertheless, these data collectively indicate that 4 ecological-evolutionary cohorts of insect pollinators were present during the 35 million-year-long interval from 125 to 90 million years ago during the transition from a gymnosperm to an angiosperm dominated global flora.[9] These cohorts during the formative interval of host-plant and insect pollinator turnover were: (i) earlier pollinator lineages with gymnosperm hosts that became extinct; (ii) earlier pollinator lineages with gymnosperm hosts that survived; (iii) earlier pollinator lineages with gymnosperm hosts that successfully transitioned onto angiosperms (including *D. marcosi*); and (iv) pollinator lineages that originate solely with angiosperm hosts. The differential survival of these 4, distinctive cohorts, particularly the survival of cohorts (ii) and (iii), essentially structure the broad pattern of pollinator modes not only during the emergence of angiosperm lineages, but also explain the modern world of pollinators. Consequently, based on direct paleontological evidence, our conclusion is that insect pollination was an extensive activity among gymnosperm hosts during the Early Cretaceous, and it extended later into the Cretaceous at a time when flowering-plant lineages were proliferating. Additional exploration is needed to further determine the role that insect pollinator lineages had during the diversification of the most ecologically dominant plant group in our planet's recent history.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

Acknowledgments

We are grateful to all the people who allowed and supported our research on the fossil oedemerid *Darwinylus marcosi* and to Dr. Frantisek Baluska (Editor in chief of *Communicative & Integrative Biology*) for inviting us to submit this work. We thank José Antonio Peñas for reconstruction of the beetle.

Funding

This study is supported by the Spanish Ministry of Economy and Competitiveness Project CGL2014–52163. This is contribution 321 of the Evolution of Terrestrial Ecosystems consortium at the Natural Museum of Natural History, in Washington, DC.

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