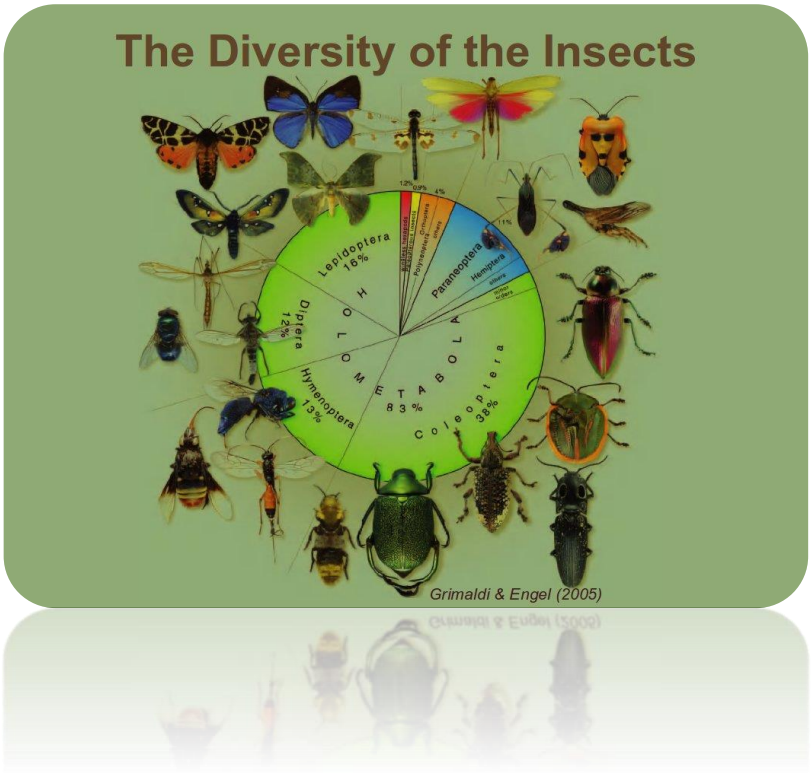
Beetles as floral visitors in the Magnoliaceae: an evolutionary perspective

Gerardo Hernández-Vera

Beetle diversity

- More than 380,000 described species.
- Constitute nearly the 40% of all described insect species.
- Approximately 30% of all animal species.

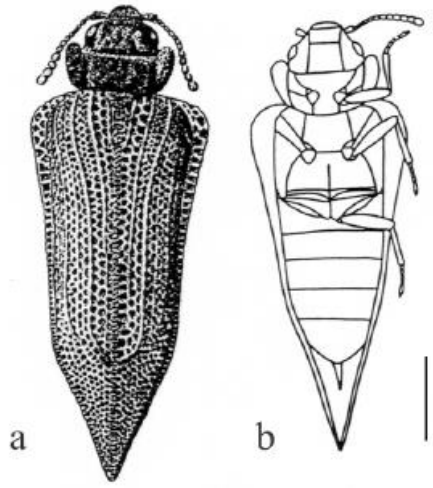


(Grimaldi & Engel 2005, Zhang 2013, Stork 2018)

Origin of Coleoptera

- The oldest known fossils are described from the earliest Permian (ca. 296 Ma) and assigned to the family Tshekardocoleidae (Ponomarenko 2003, Kirejtshuk *et al*. 2013).

- Similar to modern representatives within Cupedidae.



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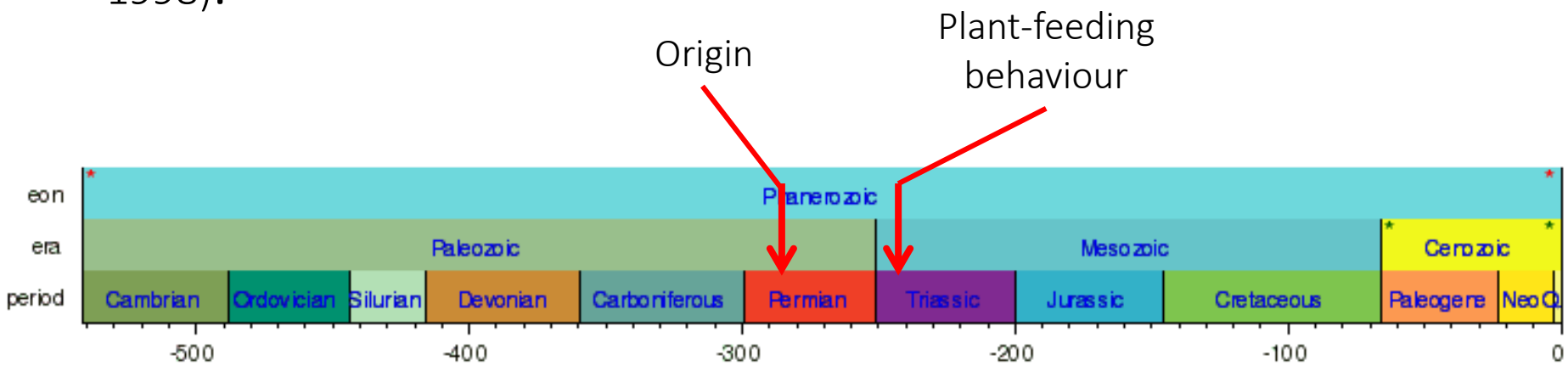
Origin of Coleoptera

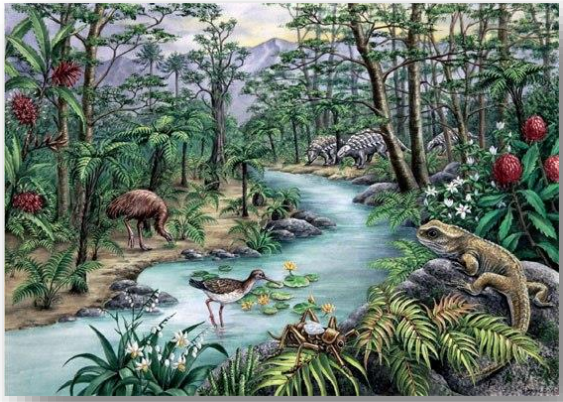
- From molecular data: ca. 269 Ma (95% C.I. 293–246) (Misof *et al*. 2014).

- Plant-feeding behaviour evolved in the Triassic ca. 50 Ma after their origin in the Permian (Carpenter 1992, Farrell 1998).



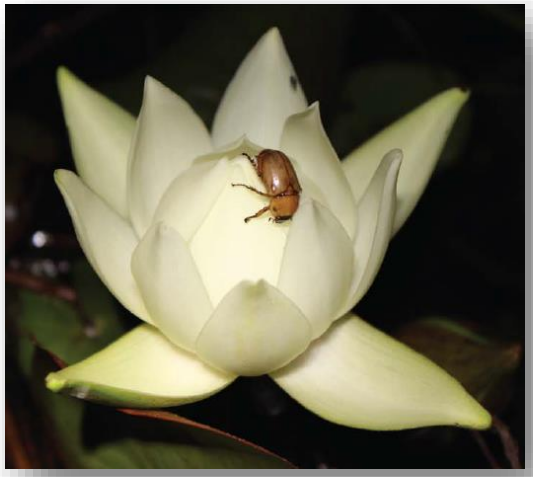
Beetles as floral visitors to first angiosperms on Earth

- Ancient origin in the Permian.



- High proportion of beetle-pollinated taxa within extant basal angiosperm lineages.

- Beetles were among the first floral visitors to proto-angiosperms on Earth.



(Thien 1980, Bernhardt 2000, Friis *et al*. 2006, Wang *et al*. 2013).

Origin of Magnoliaceae

- Based on DNA sequence data and molecular dating methods.
- Origin of Magnoliidae: ca. 135–130 Ma (early Cretaceous).
- Origin of Magnoliaceae: ca. 112–104 Ma.

(Magallón *et al*. 2015)

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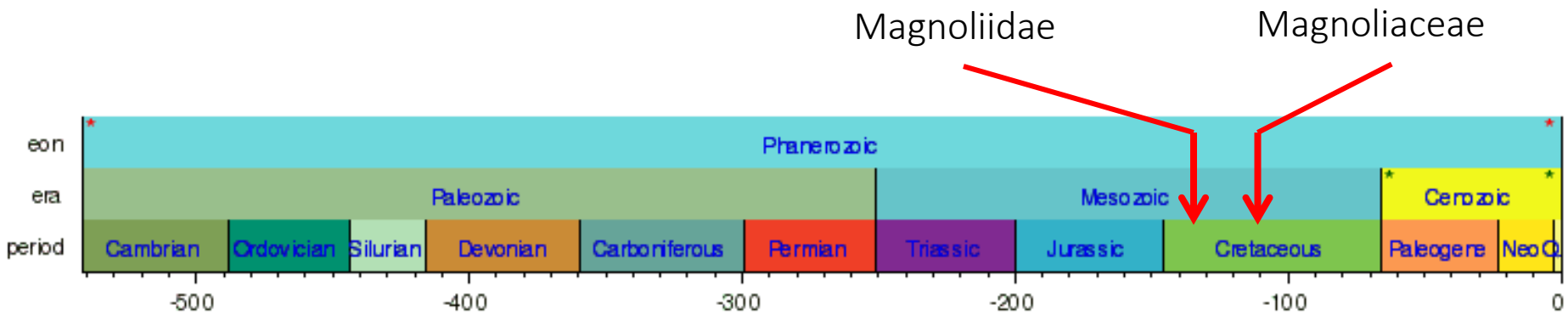
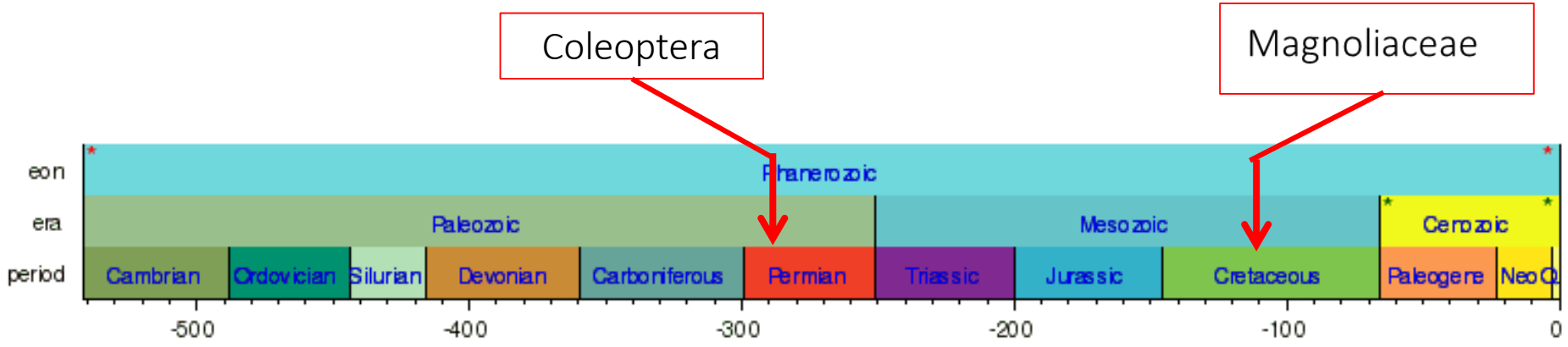


Possible origin of beetle-Magnoliaceae interaction

- Most modern families of Coleoptera had already originated.

- Including all the families with known taxa associated to Magnoliaceae.

(Hunt *et al*. 2007, McKenna et al. 2015, Zhang *et al*. 2018)



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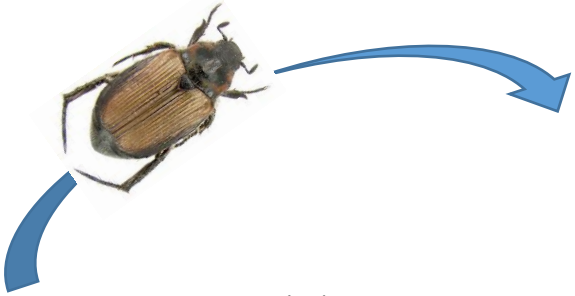
Possible origin of beetle-Magnoliaceae interaction

- Ecological opportunity.
- Beetles gradually colonized the newly opened ecological niche.
- Shifted from either other basal angiosperms or non-angiosperm hosts.



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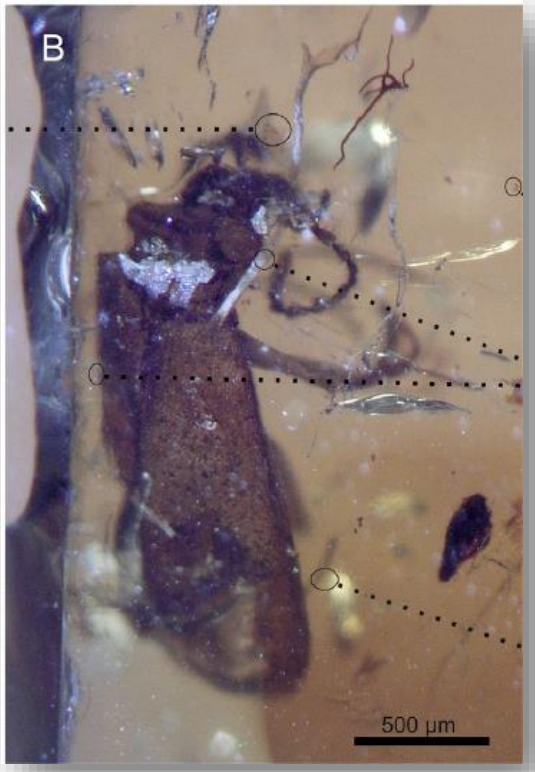
Possible origin of beetle-Magnoliaceae interaction

- Fossilized beetle from the late Albian (105 Ma). Amber from Burgos, Spain.
- Based on phylogenetic analyses assigned to the family Oedemeridae.
- Extant members known to pollinate or be associated only with angiosperms.

(Peris et al. 2017, Peris 2017)



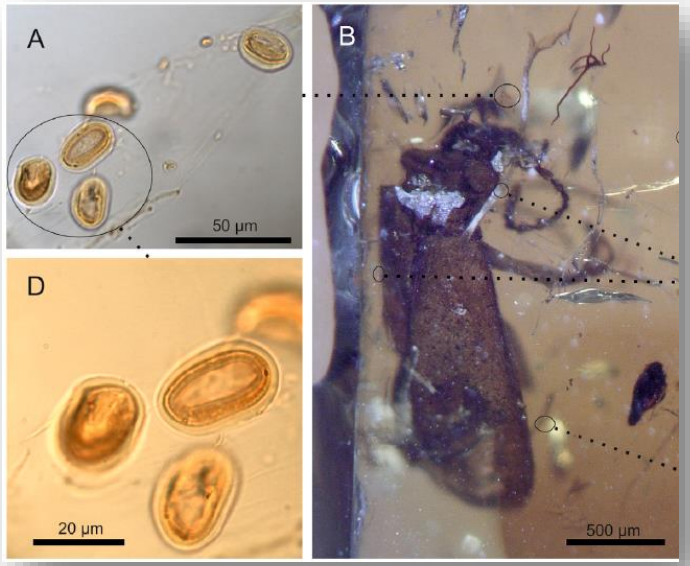
Darwinylus marcosi

Possible origin of beetle-Magnoliaceae interaction

- Abundant gymnosperm pollen grains (cycad) attached to its body.

- Direct evidence of a beetle pollinator associated with gymnosperms later transitioning onto angiosperm hosts.

(Peris *et al.* 2017, Peris 2017)



Darwinylus marcosi

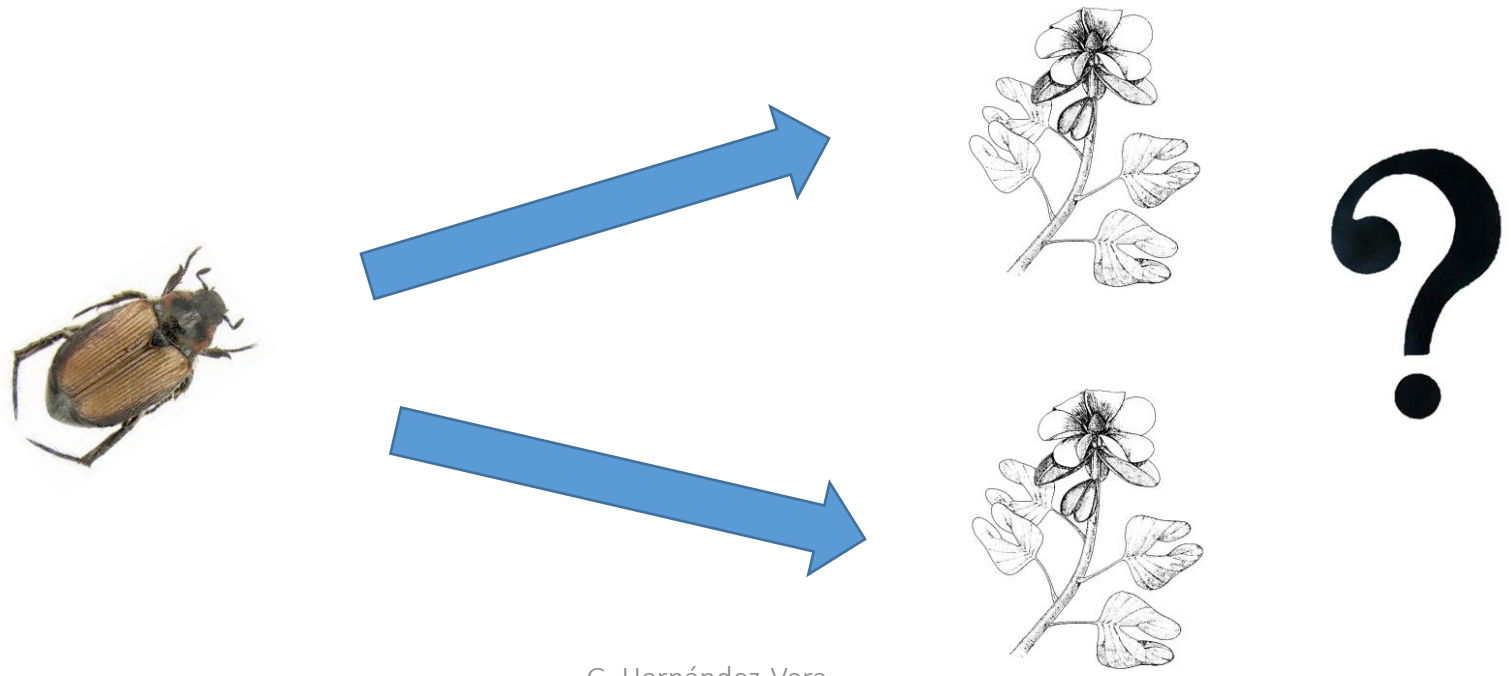
Possible origin of beetle-Magnoliaceae interaction

- Consumption of pollen, spores, pollination drop rewards.
- Pre-angiosmperm lineages: ferns, cycads, conifers.
- Ecological and evolutionary preamble to early angiosperm pollination.

(Labandeira 2000, Labandeira *et al*. 2007).

Possible origin of beetle-Magnoliaceae interaction

Any good candidates as ancestral host plants for beetles within Magnoliaceae or a closely related lineage?



Possible origin of beetle-Magnoliaceae interaction

- *Endressinia brasiliana*
- *Schenkeriphyllum glanduliferum*
- From the Aptian Crato Formation in Brazil (125–113 Ma).
- Representatives of extinct lineages inferred to be sister groups and a sister clade to Magnoliaceae.

(Mohr & Bernardes-de-Oliveira 2004, Mohr *et al*. 2013).

Possible origin of beetle-Magnoliaceae interaction

- Presence of staminodes (rudimentary stamens).
- Multiple floral parts spirally arranged.
- Floral traits common in several groups of Magnoliales and inferred to be related to beetle pollination.

(Endress 1984, Bernhardt 2000)

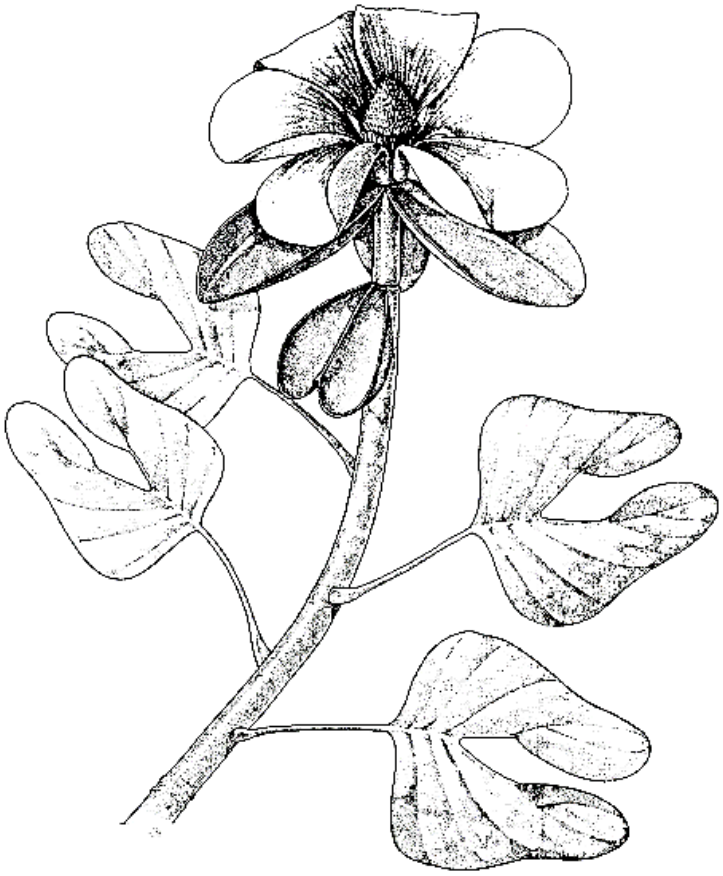
Possible origin of beetle-Magnoliaceae interaction

- Genus ***Archaeanthus***
- The earliest known plant inferred to be the stem-group of Magnoliaceae (Doyle & Endress 2010).
- A fossil described from the mid-Cretaceous Dakota Formation in central Kansas (Dilcher & Crane 1984).
- Uppermost Albian-mid-Cenomanian (ca. 105–97 Mya).

Archaeanthus linnenbergeri

Possible origin of beetle-Magnoliaceae interaction

- Multiple floral parts spirally arranged.
- Bisexual flowers visually conspicuous.
- Dilcher & Crane (1984) suggest that it was probably beetle-pollinated.

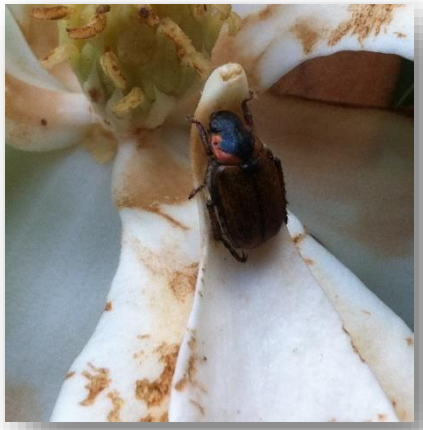


Archaeanthus linnenbergeri

Evolutionary adaptations to beetle pollination in Magnoliaceae

- Beetles not only feed, but also mate and shelter in flowers of the Magnoliaceae.

- ¿What floral traits could have evolved in response to these activities?



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Evolutionary adaptations to beetle pollination in Magnoliaceae

- **PROTOGYNY:**

➢ Temporal isolation of female and male functions in plants (dichogamy) ⇒ primarily a **mechanism to avoid self-fertilization** (Bertin & Newman 1993).

➢ Development or maturation of floral female structures before the male ones (protogyny) is **characteristic of beetle-pollinated plants; particularly of basal angiosperms** (Faegri & Van der Pijl 1979).

➢ Nearly 90% of beetle-pollinated plants are protogynous (Bertin & Newman 1993, Thien *et al*. 2000).

Evolutionary adaptations to beetle pollination in Magnoliaceae

- THERMOGENESIS:

➢ Production of heat by plant reproductive structures as a result of biochemical reactions.

➢ Not an uncommon feature among the extant basal angiosperms (e.g. Nymphaeaceae, Illiciaceae and Annonaceae).

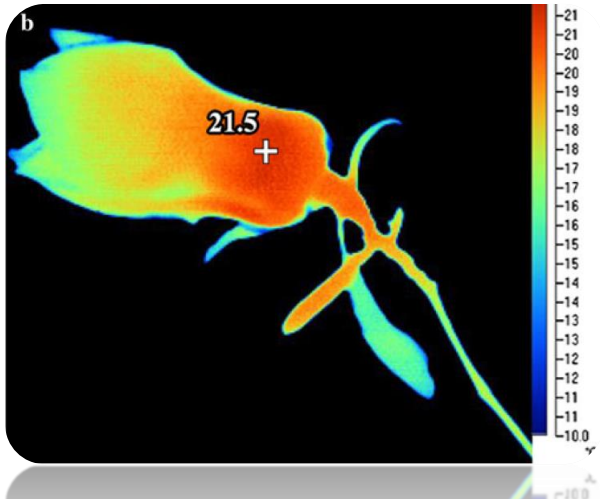
➢ Estimated to occur in at least 900 species in tropical forests.

(Endress 1994, Bernhardt 2000, Thien *et al*. 2000)

Evolutionary adaptations to beetle pollination in Magnoliaceae

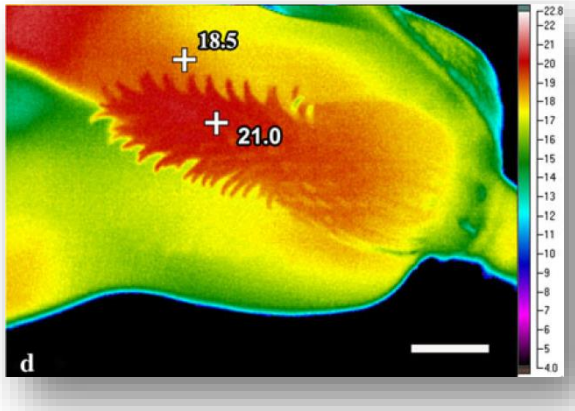
- <u>THERMOGENESIS</u>:

➢ Documented for several *Magnolia* species, including: *M. tamaulipana* (Dieringer *et al*. 1999), *M. ovata* (Gottsberger *et al*. 2012), *M. sprengeri* (Wang *et al*. 2014) and *M. denudata* (Wang *et al*. 2013).



Evolutionary adaptations to beetle pollination in Magnoliaceae

- <u>THERMOGENESIS</u>:



➢ Inferred to be an adaptation to beetle pollination because heat represents an **energy reward for beetles.**

➢ Allows them to save energy; enhancing feeding and mating in the flowers, thus increasing the odds of pollination.

(Seymour *et al*. 2003, Seymour *et al*. 2009, Gottsberger *et al.* 2012)

Evolutionary adaptations to beetle pollination in Magnoliaceae

- FLORAL ODORS:

➢ Approximately 76 volatile compounds have been identified in the floral scents produced by Magnoliaceae plants.

➢ Initially evolved from insect-feeding chemical deterrents (terpenoids found in floral scents are also produced in damaged leaves).

➢ Later on they evolved as chemical cues for food and mating sites for insects.

(Pellmyr & Thien 1986, Pellmyr *et al*. 1991, Azuma *et al*. 1997)

Evolutionary adaptations to beetle pollination in Magnoliaceae

- FLORAL MOVEMENTS:

➢In several species flowering occurs in a 2-day period.

➢Petals open partially during the female phase and then close afterwards to open again in the male phase.

(Thien 1974, Thien 1976, Ishida 1996, Gottsberger *et al*. 2012)

Evolutionary adaptations to beetle pollination in Magnoliaceae

DAY 1
Female phase
(Stigmas are receptive)

- Petals open partially during the female phase. Beetles enter the flower.
- Petals close. Floral chamber where beetles feed and mate.

DAY 2
Male phase
(Pollen is shed)

- Petals open completely.
- Stamens dehisce.

Evolutionary adaptations to beetle pollination in Magnoliaceae

- FLORAL MOVEMENTS:

➢ Presumably, the closed petals preserve nectar, pollen and stigma tissue exclusively for beetles.

➢ Prevent other types of insects from gaining access to these resources.

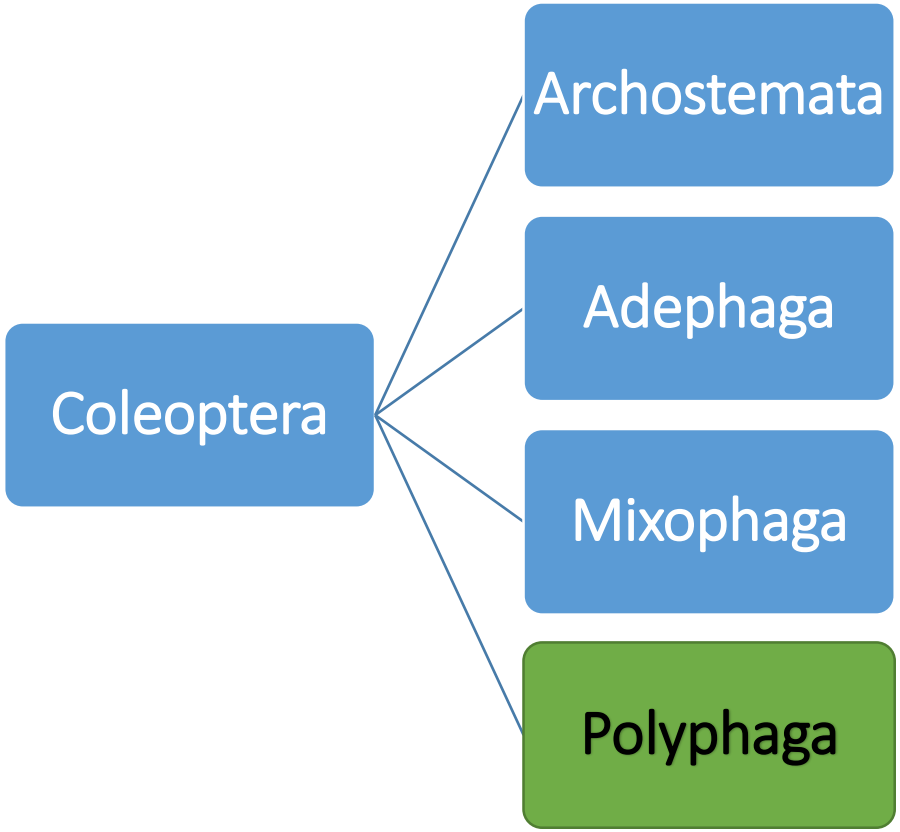
(Thien 1974, Thien 1976, Ishida 1996, Gottsberger *et al*. 2012)

Extant groups of Coleoptera reported as floral visitors to Magnoliaceae

- All extant beetles known to be associated with Magnoliaceae belong to Polyphaga.

- The largest and most diverse suborder of Coleoptera with approximately 350,000 species (ca. 90% of the total number of beetle species).

(Slipinski *et al*. 2011, Gullan & Cranston 2014)

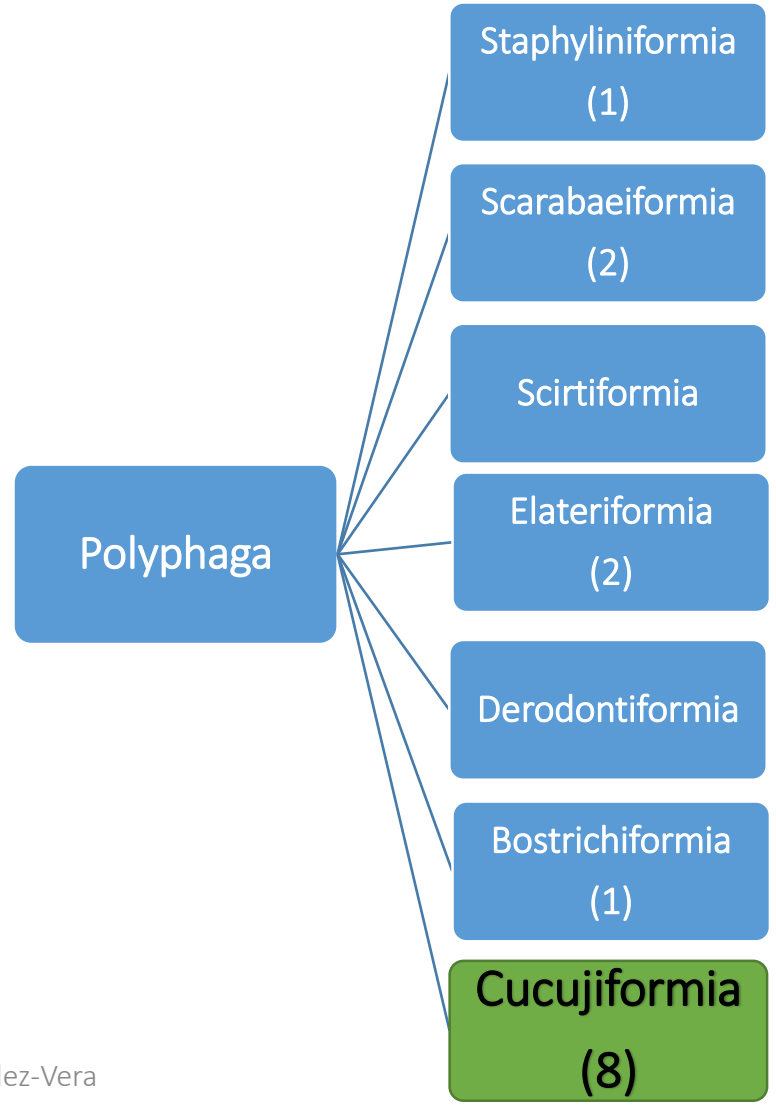


Extant groups of Coleoptera reported as floral visitors to Magnoliaceae

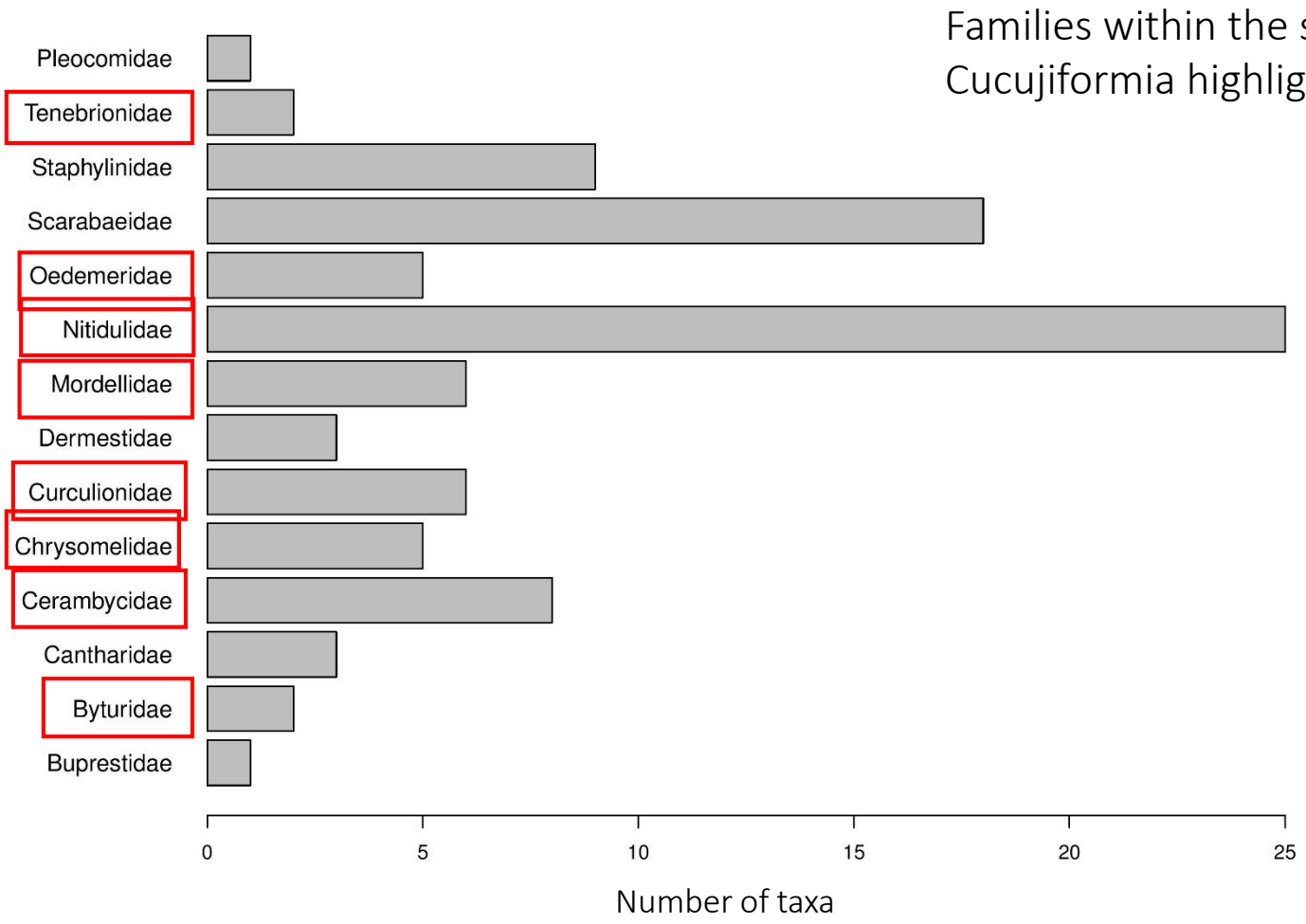
- 8 of 14 beetle families within the series Cucujiformia.

- A clade which comprises the vast majority of plant-feeding beetles

(Hunt *et al*. 2007, Gullan & Cranston 2014).



Extant groups of Coleoptera reported as floral visitors to Magnoliaceae



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Scarabaeidae

- Cetoniinae

- Melolonthinae

- Dynastinae

- Rutelinae

Flower-feeding lineages; appeared ca. 62–56 Ma (Paleocene)

Magnoliaceae started to diversify ca. 54.8–42 Ma (Eocene)

Assess their possible role on diversification processes of Magnoliaceae

Concluding remarks, Prospects & Challenges

- When it first appeared on Earth, the family Magnoliaceae most likely represented a newly opened ecological niche that beetles gradually colonized and exploited, possibly shifting from gymnosperm hosts.

- By feeding, mating and sheltering in their flower structures, beetles have played a major role in shaping the floral biology and morphology of Magnoliaceae.

Concluding remarks, Prospects & Challenges

- Since we do not know with certainty the degree of dependence upon beetles as pollinating agents, conservation strategies for Magnoliaceae should not neglect this ecological interaction.

- There is still little knowledge on floral insect visitors and the floral biology of most of *Magnolia* species. More field observations are required that can contribute for a better comprehension of the ecological and evolutionary processes that have shaped the diversity of one of the earliest extant lineages of flowering plants.

Picture: R. Domínguez