

AN EARLY MALPIGHIACEOUS PLANT-POLLINATOR RELATIONSHIP: EVIDENCE BY A GLAND-BEARING PETAL (OSMOPHORES) FROM THE EOCENE OF INDIA

Ashif Ali,* Rafael Felipe de Almeida,† Raman Patel,‡ Rajendra Singh Rana,‡ and Mahasin Ali Khan^{1,*}

*Palaeobotany, Palynology, and Plant Evolution Laboratory, Department of Botany, Sidho-Kanho-Birsha University, Ranchi Road, Purulia, India;

†University of the Witwatersrand, School of Animal, Plant, and Environmental Sciences, Life Sciences Museum, Johannesburg, South Africa;

and ‡Department of Geology, Hemvati Nandan Bahuguna Garhwal University, Srinagar, (Garhwal) Uttarakhand, India

Editor: Kathleen B. Pigg

Premise of research. Flowering plants have coevolved with their pollinator partners over millions of years, producing a fascinating and interesting diversity of floral tactics and pollinator adaptations. A fossilized malpighiaceae gland-bearing petal recovered from the Gurha lignite mine in Rajasthan, western India, from the early Eocene (~55–52 mya) helps to underscore the evolutionary significance of this angiosperm lineage in the Cenozoic history of India.

Methodology. We determine the fossilized gland-bearing petal's taxonomic position based on detailed macro-morphological traits and thoroughly compare them with the modern genera of the tribe Mcvaughieae.

Pivotal results. The Eocene specimen is an obovate to orbicular and symmetrical glabrous petal with four short and obovate glandular extensions or osmophores at the limb margin of the basal portion. The specimen is closely similar to the modern gland-bearing petal of the tropical South American genus *Mcvaughia* W.R. Anderson (Malpighiaceae).

Conclusions. As osmophores are oil-producing volatile glands used to signal pollinators (particularly anthophorid bees) the availability of floral resources, we suggest that such specific malpighiaceae plant–anthophorid bee relationships may have existed in the area during the time of deposition (early Eocene).

Keywords: early Eocene, Malpighiaceae, paleoecology, Rajasthan, taxonomy, western India.

Introduction

Malpighiaceae Juss. is one of the most varied flowering plant families and comprises about 75 genera and 1350 species in both the Old and New Worlds (Davis et al. 2001; Anderson 2004, 2014; Almeida et al. 2020, 2023). It is widely distributed in Africa, Australia, Asia, and North, South, and Central America (Raven and Axelrod 1974; Anderson et al. 2012). The petal glands of this family are confined to only three Brazilian genera, namely, *Mcvaughia* W. R. Anderson, *Burdachia* A. Juss., and *Glandonia* Griseb. (Anderson 1981; Guesdon et al. 2018). These three genera are now placed under the tribe Mcvaughieae with 12 species, including *Mcvaughia sergipana*, *Mcvaughia bahiana*, *Mcvaughia piauiensis*, *Burdachia atractoides*, *B. prismatocarpa*, *B. duckei*, *B. glandifera*, *B. loretoensis*, *B. williamsii*, *B. sphaerocarpa*, *Glandonia macrocarpa*, *Glandonia pranei*, and *Glandonia williamsii* (Anderson 1981; Reis e Silva 2007). The petal glands of the genus *Glandonia* are distinctive be-

cause they are conspicuous, short stalked, and positioned at the limb margin in the basal portion of the posterior petal (Guesdon et al. 2018).

Fossil records corresponding to reproductive structures of Malpighiaceae remain elusive. To date, only one malpighiaceae flower species, *Eoglandulosa warmanensis* Taylor and Crepet, was reported from Eocene deposits in the United States (Taylor and Crepet 1987), and winged fruits assigned to *Tetrapterys harpyiarum* Unger have been reported from the Oligocene of Hungary and Slovenia (Hably and Manchester 2000). In addition, winged fruits of the malpighiaceae genus *Dicella* are described from the latest Neogene (Pliocene) in Jharkhand, eastern India (Hazra et al. 2024). Here, we report and describe a fossilized malpighiaceae gland-bearing petal that is similar to *Mcvaughia* from the early Eocene (Palana Formation) sedimentary sequence of the Gurha lignite mine in Rajasthan, western India. It is interesting to note that no floral evidence associated with the petal gland has been hitherto found in the world's Cenozoic fossil history. Thus, our discovery of this unique fossilized gland-bearing petal is noteworthy for the evolution of the early-diverging Malpighiaceae lineage and concerns the evolution of a highly specific plant-pollinator relationship. The unexpected existence of the tropical South American genus in Rajasthan, western India, has important paleobiogeographical implications.

¹ Author for correspondence; email: khan.mahasinali@gmail.com.

Manuscript received October 2024; revised manuscript received January 2025; electronically published June 3, 2025.

Material and Methods

Age of the Material

The studied fossilized gland-bearing petal was recovered from the thin, laminated maroon shale beds of the Palana Formation, exposed in the Gurha opencast lignite mine (lat. 72.52269°E, long. 27.5229°N) in the Bikaner District, Rajasthan, western India (fig. 1). At first, the Palana Formation was assigned a Paleocene age based on stratigraphic correlation with the Ranikot beds in Sindh, Pakistan (Khosla 1971; Pareek 1984). At first, the Palana Formation was assigned as early Eocene in age (~55–52 mya) based on palynological evidence (Kumar 1996; Kumar et al. 2016). Singh and Kalia (1970) also suggested the early Eocene age based on the study of a palyno-assemblage (*Clavaperiporites clavatus*, *Dandotiaspora telonata*, *Triangulorites bellus*, *Tricolpites reticulatus*, *Lanagiopollis rugularis*, *Tricolporopollis rubra*, *Palmaepollenites eocenicus*, *Rhoipites kutchensis*, *Sastripollenites trilobatus*, *Ratariacolporites plicatus*, and *Kielmeyerapollenites eocenicus*), planktonic foraminifera (*Acarinina*, *Morozovella*, and *Subbotina*), and lower vertebrates (*Osteoglossidae* and *Lepisosteidae*; Kalia 1978a, 1978b).

Morphological Study

The morphology of an exquisitely preserved early Eocene gland-bearing petal (fig. 2A) was carefully observed in detail under a stereo zoom microscope (Leica s9i), photographed using a digital camera (Canon Power Shot A720IS), and edited with Photoshop software (ver. 19).

To confirm the identification of the specimen, we critically examined flower petals of several modern members of Malpighiaceae using digital herbarium catalogues, namely, the Kew herbarium catalogue (<https://apps.kew.org/herbcat/navigator.do>), e-flora of India (<https://sites.google.com/site/efloraofindia/home>), e-flora of China (<https://www.efloras.org>), and Global Biodiversity Information Facility (<https://www.gbif.org>). The detailed line drawing of the fossil flower specimen was made using CorelDRAW X7 software (figs. 2, 3). Cuticles are not well preserved for further study. The terminologies have been followed by Almeida et al. (2019) for the description of the morphology of the petal gland. The fossil specimen (SKBU/PPL/R/F/03) is housed in the Palaeobotany, Palynology, and Plant Evolution Laboratory, Department of Botany, at the Sidho-Kanho-Birsha University, in Purulia, West Bengal, India.

Results and Discussion

Systematic Paleobotany

Order—Malpighiales Juss. ex Bercht. & J. Presl

Family—Malpighiaceae Juss.

cf. *Mcvaughia* sp. (Fig. 2A)

Specimen number. SKBU/PPL/R/F/03.

Additional specimens. SKBU/PPL/R/F/05, SKBU/PPL/R/F/06.

Type horizon and age. Palana Formation, Early Eocene.



Fig. 1 A, Geological map of Rajasthan, showing the location of Gurha opencast lignite mine (red star) in Bikaner Rajasthan, India. B, Lithological log of the Palana Formation fossil-bearing succession of the fossil locality.

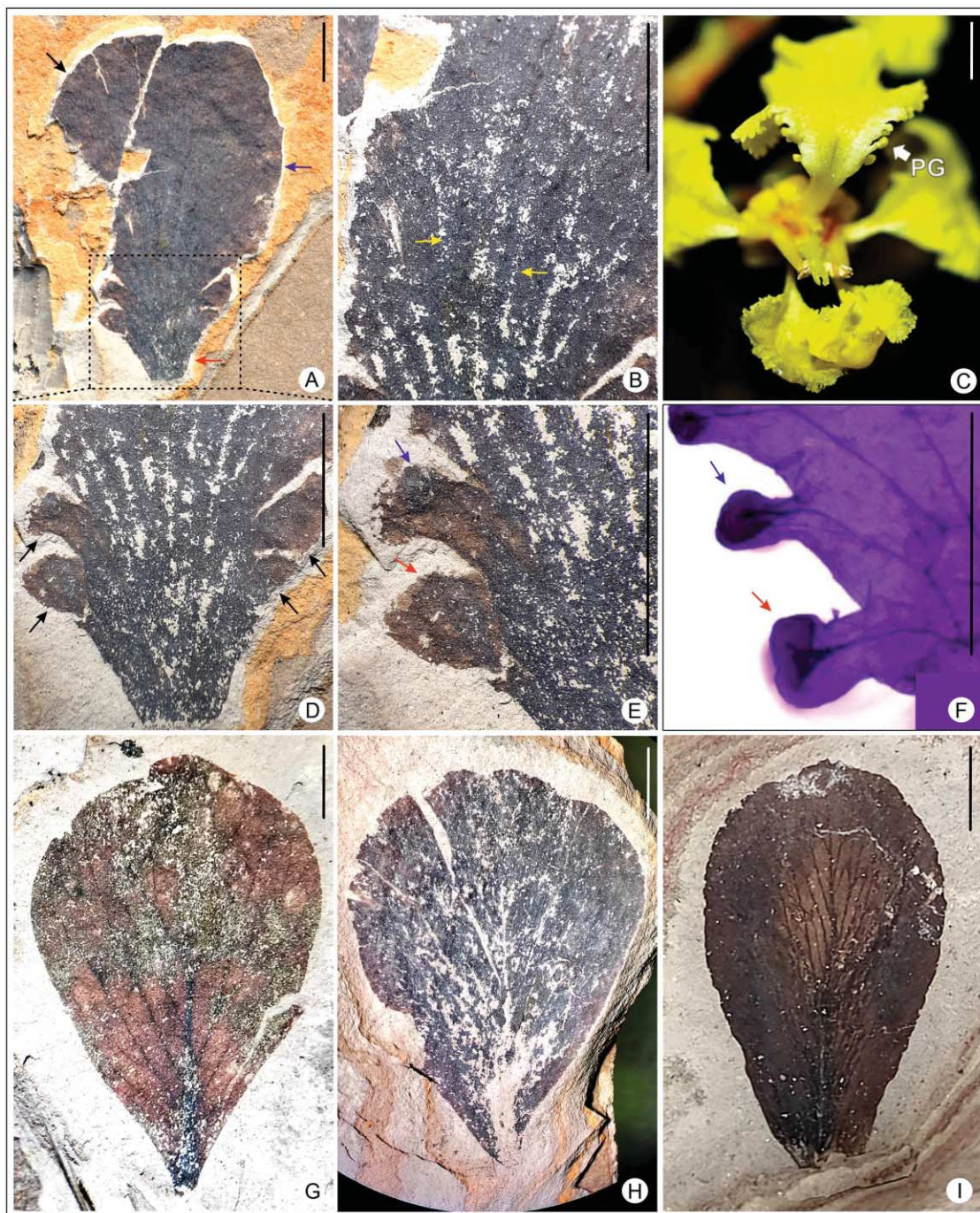


Fig. 2 Fossil and extant petal of Malpighiaceae. A, Fossil of cf. *Mcvaughia* sp. obovate to orbicular, entire (marked by blue arrow) to erose (marked by black arrow) margined; symmetrical petal with four short obovate glandular extensions or osmophores at the limb margin (marked by red arrow) of the basal portion (specimen SKBU/PPL/R/F/03). B, Enlarged view of A, showing numerous subparallel primary veins (marked by yellow arrows) at the central region proceeding from base to apex. C, Flower of an unidentified extant species of *Mcvaughia*, showing a prominent petal gland (PG) positioned at the margin of the posterior petal (reprinted from Almeida et al. 2019). D, Enlarged view of A, showing four oppositely arranged short obovate glands (marked by black arrows) at the limb margin of the petal basal portion. E, Enlarged view of D, showing two glands (marked by red arrow) with a terminal receptacle-like structure (marked by blue arrow). F, Modern *Mcvaughia sergipana*, showing similar petal glands. G–I, Additional malpighiaceaceous flower petals lacking obvious glands from the same fossil locality. G, Specimen SKBU/PPL/R/F/04. H, Specimen SKBU/PPL/R/F/05. I, Specimen SKBU/PPL/R/F/06. Scale bars = 5 mm.

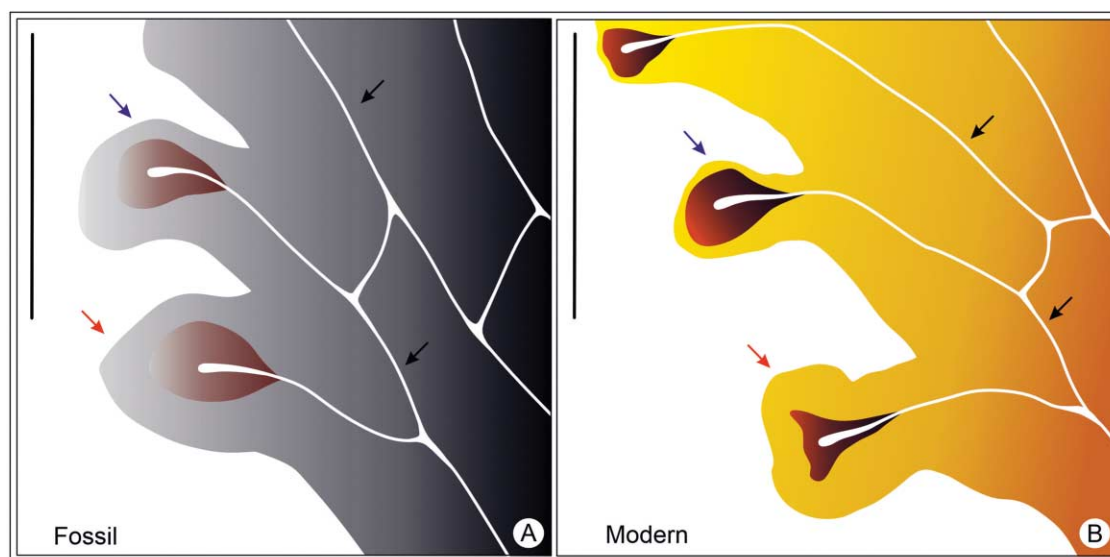


Fig. 3 A, Line drawing of petal-bearing glands of the fossil cf. *Mcvaughia* sp., showing two glands (marked by red arrow) with a terminal receptacle-like structure (marked by blue arrow) and subparallel primary veins (marked by black arrows). B, Line drawing of modern *Mcvaughia sergipana*, showing the nature of petal-bearing glands. Scale bars = 5 mm.

Type locality. Laminated maroon shale bed of Gurha open-cast lignite mine Bikaner (lat. 72.52269°E, long. 27.5229°N), Rajasthan, western India.

Repository. Palaeobotany, Palynology, and Plant Evolution Laboratory, Department of Botany, Sidho-Kanho-Birsha University, Purulia, West Bengal, India.

Description. Petal well preserved, obovate to orbicular, glabrous (fig. 2A); petal limb 4.5–5.6 mm × 4–6 mm; margin entire to erose (fig. 2A); apex rounded, glabrous, claws well preserved, 1.7–2.0 mm × 0.2–0.35 mm, glabrous, numerous primary veins subparallel at the central region proceeding from base to apex and forming slightly sinuous pattern to the apical one-third of the petal (fig. 2B), the distance between two prominent veins about 0.8–1.75 mm in the limb; petal glands well preserved, four, short, obovate to orbicular, oppositely arranged at the limb margin of the petal basal portion (fig. 2D), ca. 1.6–2.2 mm in length, with a single prominent vein and a terminal receptacle-like structure (fig. 2E), short stalked at the basal portion.

Taxonomic Assignment

Only three members of Malpighiaceae (*Mcvaughia*, *Burdachia*, and *Glandonia*) are widely known for their unique oil-secreting glandular petals (Guesdon et al. 2018; Almeida et al. 2023). In comparison to these genera, our specimen most closely resembles the genus *Mcvaughia*. This assignment is fully supported by glandular petal morphology (obovate to orbicular and symmetrical glabrous petal with four short and obovate glandular extensions or osmophores at the basal limb margin, prominent primary veins, and subparallel venation pattern). However, there is some variation in the petal glands of some species of *Mcvaughia*. In *M. sergipana*, two or three pairs of reniform glands are present throughout the limb margin of the posterior petal (fig. 2F). They are stalked in the basal portion and

sessile near the apex. In *M. bahiana*, three to five pairs of rounded glands are present at the base of the limb. *Mcvaughia piauiensis* exhibits two or three pairs of sessile to slightly subsessile reniform glands at the base of the limb. However, given that the fossil specimen dates to the early Eocene (approximately 55–52 mya), it might be a possible ancestor of the tribe Mcvaughieae.

Significance of the Fossil

Plant-pollinator relationship. Throughout evolutionary history, some Malpighiaceae lineages from the Neotropics and Paleotropics have lost their petal glands (Almeida et al. 2023). Neotropical Malpighiaceae are pollinated by different groups of solitary oil-collecting bees that are prevalent in this part of the world and completely absent from the Paleotropics (Simpson and Neff 1981). For this primary reason, it is suspected that Old World Malpighiaceae no longer possess petal glands, or if they do, the number of these glands is diminished and they exude nectar rather than oil (Davis et al. 2014). It is interesting to note that the floral morphology of Malpighiaceae species is related to the close association with a specific group of specialized pollinators (anthophorid bees; subfamily Anthophorinae). The floral morphology is suited to how species from three tribes of anthophorid bees gather rewards and pollinate flowers (Vogel 1974; Neff and Simpson 1981). These bees, belonging to the tribes Centridini, Exomalopsini, and Tetrapediini, possess unique behavior and organs for gathering oil (Vogel 1974; Neff and Simpson 1981). The bees typically grab a petal claw as they land in the flower's center. A single modified flag petal that aids pollinator orientation is frequently present on the flowers. Pollen sticks to the bees' ventral surfaces during oil collection, and pollination occurs later when the pollen is transferred onto the stigmas of other flowers the bees visit. No additional insects other than vespid wasps, pollen-gathering trigonid bees, and anthophorids have been

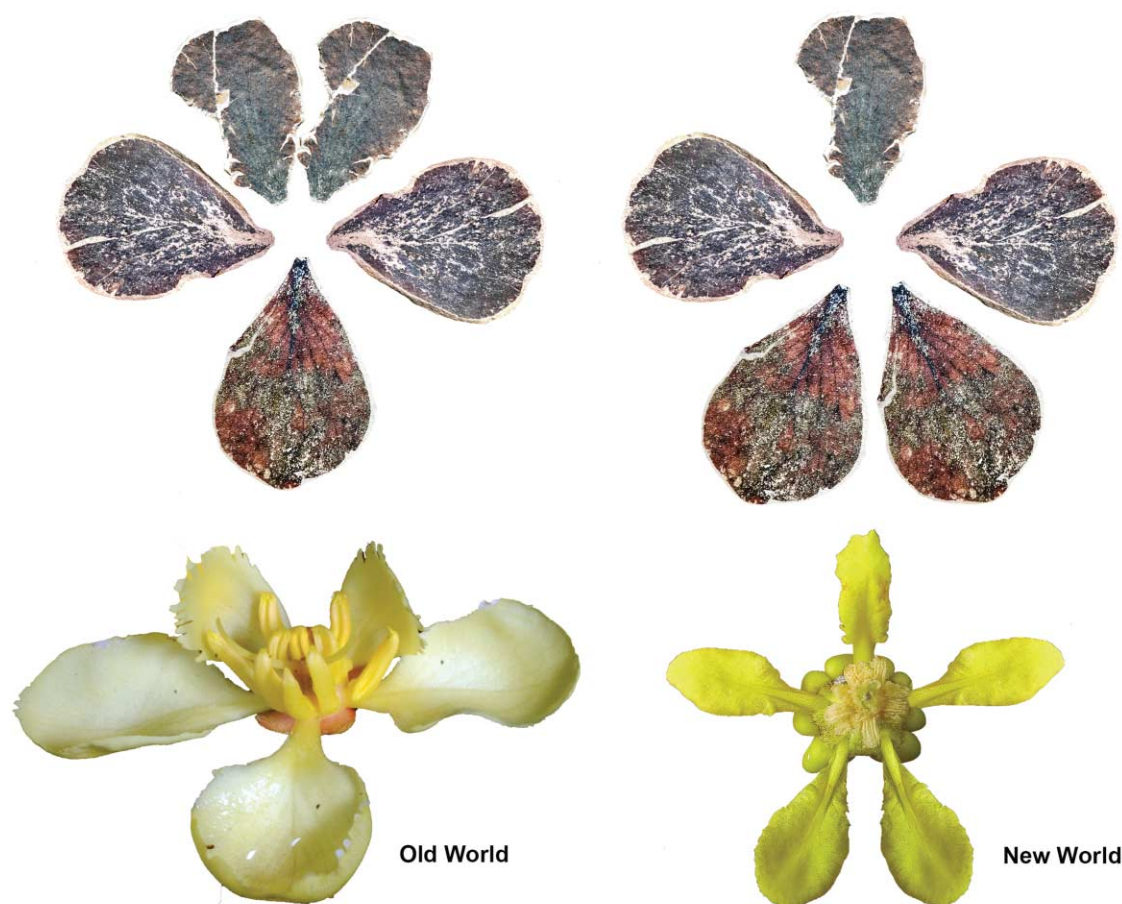


Fig. 4 Reconstruction of an independent type of floral morphology depicting Old World (*left*) and New World (*right*) Malpighiaceae flowers. The upper row shows images of the arrangement of the recovered fossil petals into hypothesized whole corolla, and the lower row's images depict extant flowers of *Acridocarpus staudtii* (Engl.) Engl. ex Hutch. & Dalziel. (photographed by E. Bidault) and *Dicella nucifera* Chodat (photographed by R. F. Almeida).

observed to visit the glandular blooms (Vogel 1974). The present evidence of a fossilized gland-bearing petal similar to *Mcvaughia* and other malpighiaceae petals (fig. 2G–2I) recovered from the early Eocene (Palana Formation) sedimentary sequence of Rajasthan, western India, suggests that the bees might have been important in the early Eocene radiation of Malpighiaceae. We also try to reconstruct the floral morphology of the recovered flowers as they would have appeared before fossilization (fig. 4). In addition, we also propose that such specific malpighiaceae plant–anthophorid bee associations might have existed in the area during the depositional period (early Eocene).

Acknowledgments

A. Ali and M. A. Kahn sincerely thank the Department of Science and Technology (DST), New Delhi, for its financial support (DST/INSPIRE/03/2022/005835, INSPIRE Code: IF220348). A. Ali, R. Patel, R. S. Rana, and M. A. Kahn are grateful to the authorities of the Gurha opencast lignite mine, in Bikaner, Rajasthan, India, for their kind permission and support during field investigation. A. Ali and M. A. Kahn also acknowledge the Department of Botany at the Sidho-Kanho-Birsha University for providing infrastructural facilities to accomplish this work.

Literature Cited

- Almeida RF, A Francener, C Pessoa, R Sebastiani, YR Oliveira, AMA Amorim, MCH Mamede 2020 Malpighiaceae: flora e funga do Brasil. Jardim Botânico do Rio de Janeiro. <https://floradobrasil.jbrj.gov.br/FB155>.
- Almeida RF, IR Guesdon, MR Pace, RMS Meira 2019 Taxonomic revision of *Mcvaughia* W.R. Anderson (Malpighiaceae): notes on vegetative and reproductive anatomy and the description of a new species. *Phytokeys* 117:45–72. <https://doi.org/10.3897/phytokeys.117.32207>.
- Almeida RF, GA Rodrigues, IL Morais, PC Gustavson 2023 Evolution of connective glands reveals a new synapomorphy for Malpighiaceae and the hidden potential of staminal glands for Malpighiales systematics. *Phytokeys* 232:109–131. <https://doi.org/10.3897/phytokeys.232.110162>.
- Anderson WR 2004 Malpighiaceae. Pages 229–232 in N Smith, ed. *Flowering plants of the Neotropics*. Princeton University Press, Princeton, NJ.

- 2014 Seven new species of Neotropical Malpighiaceae. *Acta Bot Mex* 109:23–43.
- Anderson WR, C Anderson, CC Davis 2012 Malpighiaceae. University of Michigan Herbarium. <http://herbarium.lsa.umich.edu/malpigh/index.html>.
- Anderson WR, B Gates 1981 *Barnebya*, a new genus of Malpighiaceae from Brazil. *Brittonia* 33:275–284.
- Davis CC, WR Anderson, MJ Donoghue 2001 Phylogeny of Malpighiaceae: evidence from chloroplast *ndbF* and *trnL-F* nucleotide sequences. *Am J Bot* 88:1830–1846. <https://doi.org/10.2307/3558360>.
- Davis CC, H Schaefer, Z Xi, DA Baum, MJ Donoghue, LJ Harmon 2014 Long-term morphological stasis maintained by a plant-pollinator mutualism. *Proc Natl Acad Sci USA* 111:5914–5919. <https://doi.org/10.1073/pnas.1403157111>.
- Guesdon IR, AMA Amorim, RMSA Meira 2018 The hydrochorous Amazonian genus *Glandonia* (Malpighiaceae): new records, morphoanatomy update, and taxonomic contributions. *Phytotaxa* 345:13–25. <https://doi.org/10.11646/phytotaxa.345.1.2>.
- Hably L, SR Manchester 2000 Fruits of *Tetrapteryx* (Malpighiaceae) from the Oligocene of Hungary and Slovenia. *Rev Palaeobot Palynol* 111:93–101.
- Hazra T, SR Manchester, M Khan 2024 First fossil record of the extant Neotropical genus *Dicella* Griseb. (Malpighiaceae) from India. *Int J Plant Sci* 185:503–570. <https://doi.org/10.1086/731323>.
- Kalia P 1978a Benthonic foraminiferal assemblage from the Kirthar Beds of Sri Kolayat ji, 267 India. *Micropaleontology* 16:76–82.
- 1978b Buliminids from the middle Eocene of Rajasthan, India. *J Palaeontol Soc India* 21–22:44–48.
- Khosla SC 1971 Classification of the lower tertiary beds of Rajasthan. *Bull Indian Geol Assoc* 4:54–60.
- Kumar M 1996 Palynostratigraphy and palaeoecology of early Eocene palynoflora of Rajpardi lignite, Bharuch district, Gujarat. *Palaeobotanist* 43:110–121.
- Kumar M, RA Spicer, TE Spicer, A Shukla, RC Mehrotra, P Monga 2016 Palynostratigraphy and palynofacies of the early Eocene Gurha lignite mine, Rajasthan, India. *Palaeogeogr Palaeoclimatol Palaeoecol* 461:98–108.
- Neff JL, B Simpson 1981 Oil-collecting structures in the Anthophoridae (*Hymenoptera*): morphology, function, and use in systematics. *J Kans Entomol Soc* 54:95–123.
- Pareek HS 1984 Prequaternary geology and mineral resources of northwestern Rajasthan. *Mem Geol Surv India* 115:1–114.
- Raven PH, DI Axelrod 1974 Angiosperm biogeography and past continental movements. *Ann Mo Bot Gard* 61:539–673.
- Reis e Silva I 2007 Taxonomia e análise cladística dos gêneros amazônicos *Burdachia* A. Juss. e *Glandonia* Griseb. (Malpighiaceae): inferências morfoanatômicas. MS thesis. Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
- Simpson BB, JL Neff 1981 Floral rewards: alternatives to pollen and nectar. *Ann Mo Bot Gard* 68:301–322. <https://doi.org/10.2307/2398800>.
- Singh SN, P Kalia 1970 A new planktonic foraminifer from the middle Eocene of south China and its biogeographic implications. *Front Plant Sci* 6:938.
- Taylor DW, WL Crepet 1987 Fossil floral evidence of Malpighiaceae and an early plant-pollinator relationship. *Am J Bot* 74:274–286.
- Vogel S 1974 Ölblumen und ölsammelnde bienen. *J Bot Taxon Geobot* 7:285–547.