Reinterpretation of the flower, *Kapgateanthus intertrappea* P.A. Paliwal, from the Deccan Intertrappean Beds (latest Cretaceous) of Mohgaonkalan, Madhya Pradesh, India

Steven R. Manchester^{1*}, Walter S. Judd² and Pratibha A. Paliwal³

^{1*}Florida Museum of Natural History, University of Florida, Gainesville FL., 32611 U.S.A. E-mail: steven@flmnh.ufl.edu
²Bell Museum Herbarium, University of Minnesota, 1445 Gortner Ave., Saint Paul, MN, 55108-0215 U.S.A. E-mail: lyonia@ufl.edu
³J.M. Patel College, Bhandara–441904, India. E-mail: paliwalpratibha.paliwal7@gmail.com
*Corresponding author

> Manuscript received: 14 July 2024 Accepted for publication: 06 August 2024

ABSTRACT

Manchester S.R., Judd W.S. & Paliwal P.A. 2024. Reinterpretation of the flower, *Kapgateanthus intertrappea* P.A. Paliwal, from the Deccan Intertrappean Beds (latest Cretaceous) of Mohgaonkalan, Madhya Pradesh, India. Geophytology 54(2): 145–150.

Kapgateanthus intertrappea P.A. Paliwal was recently established as a new genus and species based on an anatomically preserved silicified flower from the latest Cretaceous Deccan Intertrappean beds. Reexamination of the holotype, along with a new specimen of the same kind, leads to a revised interpretation of the morphology and systematic relationships. The flowers are actinomorphic and pentamerous with a whorl of five stamens or staminodes surrounding a pentalocular ovary with a single style with five radiating branches/stigmatic arms and two ovules per locule. Perianth is missing from these specimens. Available characters, including five stamens in a single whorl, rather than numerous, and a syncarpous, rather than apocarpous, gynoecium indicate that the fossil is distinct from *Amborellaceae* and instead represents a member of the *Pentapetalae*.

Keywords: *Kapgateanthus intertrappea*, *Pentapetalae*, Maastrichtian, not *Ambrellaceae*, Deccan Intertrappean Beds, Latest Cretaceous, Mohgaonkalan, Madhya Pradesh, India.

INTRODUCTION

The flora of the Deccan intertrappean beds at the classic locality of Mohgaonkalan in Chhindwara, NP, is well known from a diversity of fruit, seed and wood taxa, but flowers are relatively rare. Most of the recovered flowers represent one species of the extinct myrtalean genus *Sahnianthus* Shukla 1944 with distinctive hypanthium, stipitate 5–9 loculed ovary axile placentation and a variable number of stamens with psilate, triaperturate pollen (Synonyms: *Chitaleypushpam* Paradkar 1971, *Deccananthus* Chitaley & Kate 1972, *Raoanthus* Chitaley & M.Z. Patel 1975, *Flosfemina* R.K. Kar et al. 2003, *Menispermaceopushpam* Narkhede & G.V. Patil 2006, *Liliaceopushpam* Narkhede & G.V. Patil 2006, *Lythraceopushpam* Narkhede et al. 2010 and *Surangepushpam* Lanjewar et al. 2015). Aside from *Sahnianthus parijai*, only a few distinct flowers have been observed from Mohgaonkalan including the likely monocot, *Sahnipushpam* (known both from fruits and flowers, e.g. Kapgate et al. 2011), and eudicots such as the bicarpellate flowers of uncertain affinity named *Chenopodianthus mohgaoense* V.D. Kapgate et al. 2006 (in situ pollen is unlike *Chenopodiaceae*; Kapgate et al. 2006), and *Tetraplasandranthus deccanii* V.D. Kapgate et al. (Kapgate et al. 2009). From other exposures of the Deccan intertrappean chert, two additional flower types are known, including a representative of *Burseraceae* (*Debursera indica* Kumar et al. 2023) and a distinctive unplaced eudicot, *Singpuria kapgatei* Ramteke et al. 2022).

Paliwal (2020) described a distinctive new genus, *Kapgateanthus*, based on a fossil flower with a pentamerous gynoecium from the Deccan Intertrappean beds at Mohgaonkalan. Although it was suggested to be related to extant *Amborella*, the fossil differs in many definitive morphological characters. We here provide evidence that the fossil conforms to the Eudicots, as a member of the *Pentapetalae*.

MATERIAL AND METHODS

Kapgateanthus is currently known from two specimens, the holotype from Mohgaonkalan, and a new specimen from nearby Paladaun (Figure 1). Both were found by breaking fossiliferous cherts with a hammer, etching with hydrofluoric acid, washing in water, and examining the exposed surfaces with a hand lens. Once located, the specimens were studied by preparing more than 90 successive transverse sections using the acetate peel method. Images of successive peels were prepared with combined reflected and transmitted



Figure 1. Map updated from Sahni and Rode (1937) showing the location of sites where *Kapgateanthus* is known including the type locality of Mohgaonkalan. Inset map shows location in relation to the Deccan Traps, shaded gray. The flowers of *Kapgatianthus* were recovered from cherts at Mohgaonkalan (site 1) and Paladaun (site 2).

light, using a Keyence digital microscope.

For systematic placement of the flower, we referred to morphological characters as distributed among extant clades recognized in the angiosperm phylogeny classification (APG IV 2016). Cited specimens are in the paleobotanical collection of the Florida Museum of Natural History, Gainesville, Florida, USA (UF).

DESCRIPTION

Genus: Kapgateanthus P.A. Paliwal 2020

Kapgateanthus intertrappea P.A. Paliwal emend. Manchester, Judd & P.A. Paliwal **emend. nov.**

Figures 2, 3

Emended Description: Flowers ca. 2.1–2.3 mm in diameter, actinomorphic and rounded-pentangular in transverse outline. Perianth

Figure 2. 1–12. Successive transverse peels of flower from near equator with pentalocular ovary moving toward apex with five styles. Duplicate slides from Holotype, UF 18311-53554. 13–20. Successive transverse peels from additional flower approaching the apex, UF 19506-70456. Scale bar in 1 = 1 mm, applies to all.



Figure 2

unknown. Five petaloid and apically appendaged stamens or staminodes arranged in a whorl and alternating with the carpels. Gynoecium syncarpous and pentalocular, 0.9 to 1.0 in diameter. Style short, giving rise distally to five equal branches. Ovary rounded-pentagonal in outline, with a longitudinal groove corresponding to each septum. Septa thin, each locule containing two ovules in apparent axile placentation. Ovary wall with a thin inner layer of isodiametric sclereids surrounded by anticlinally oriented sclereids and showing planes of loculicidal dehiscence, indicating it would have developed into a loculicidal capsule, probably with two seeds per locule.

Specimens: The holotype from Mohgaonkalan, Madhya Pradesh, was specified as PAP/Ang/ Dflr-1, deposited at Botany Department, J.M. Patel College, Bhandara, Maharashtra, India (Paliwal 2020). In addition, 72 duplicate peel slides of the holotype, donated by D.K Kapgate, are housed at the Florida Museum of Natural History under the designation, UF18311-53554 (Figures 2.1–12, 3.1–2). An additional specimen from Paladaun, near Mohgaonkalan, was investigated, UF19506-



Figure 3. 1. Transverse peel section of ovary showing five 2–ovuled locules, thin septa and wall composed of anticlinally oriented fibers. **2.** Peel adjacent to 1, enlarged showing the ovules and ovary wall. Note plane of loculicidal dehiscence (at top of figure). **3.** Staminodes showing parenchymatous filling of locule. **4.** Staminode locule occluded with parenchyma. Scale bars 500 μ m in 1, 200 μ m in 2; 100 μ m in 3, 4.

70456, represented by a chert sample and 46 transverse peel slides (e.g. Figure 2.13–20).

DISCUSSION

Both specimens preserve only the androecium and gynoecium. The whorl of appendages surrounding the ovary was interpreted by Paliwal (2020) as five tepals; however, they are organized alternate with the carpels, and have the shape of stamens or staminodes, rather than petals or sepals. Although sepals and petals are not observed, we agree that the flower was probably hypogynous, because if it were epigynous, we would expect to observe adjacent remnants of surrounding perianth or hypanthium. In the holotype, stamens resemble dehisced anthers, but no pollen was observed in or around them. In the other specimen, anther locules also lack pollen and are occluded with parenchyma tissue (Figure 3.3-4) indicating that they are likely staminodial. This suggests that the plant bore functionally unisexual flowers and these were the functionally pistillate flowers. The ovary wall is composed mainly of anticlinally oriented fibers (Figure 3.1) and shows planes of loculicidal dehiscence (Figure 3.2), indicating it would likely have developed into a loculicidal capsule, probably with two seeds per locule. As yet, we are not aware of any mature fruits of this kind among the numerous angiosperm fruit remains present in the Deccan Intertrappean beds.

The successive peels of both flowers extend from approximately the middle portion of the ovary through the apical regions, but the lower portion that likely would have included the pedicel and perianth are missing. These parts would have extended into the adjacent fragment of chert that was not recovered when the flowers were discovered. Fortunately, the available sections extend through morphologically informative regions of the flower, including part of the ovary showing the five carpels and two ovules within each locule (Figures 2.1-3, 3.1-2), the base of the style (Figure 2.6, 16), and the divergence of five style arms (Figures 2.7–1.11). Through this same sequence of sections, the staminodal anthers show a transition in shape from their midlevel toward the apex. At mid-level transverse sections each anther shows a central thickened horizontal band, bordered by a pair of C-shaped, inwardly concave extensions resembling open pollen locules. Closer to the apex, the central band bends to a U- or V-shape (Figures 2.9-12, 19-20), indicating a simple apical termination.

SYSTEMATIC PLACEMENT

We reconstruct the 3-dimensional morphology of the preserved structures as diagrammed in Figure 4. Although the flowers are distinctive in appearance, the lack of characters for perianth and pollen limits our ability to place them in a



Figure 4. Diagram showing inferred three-dimensional morphology of the gynoecium (A) and a staminodal anther in dorsal (E) and ventral (F) views inferred from the transverse sections of the gynoecium (B–D and staminode (G–J).

particular extant family. However, contrary to the initial interpretation (Paliwal 2020), they are readily distinguished from *Amborella* by the syncarpous, rather than apocarpous, gynoecium, five stamens/staminodia rather than numerous stamens, and two ovules per carpel rather than one per carpel (Endress & Igersheim 2000). It can be distinguished from magnoliids (*Magnolidae*) by these characters and by stamens in a whorl (and alternating with the carpels) rather than in a spiral organization.

Based on the possession of 5-merous gynoecium and androecium, it is reasonable to conclude that Kapgateanthus belongs in the Pentapetalae clade, which includes rosids and asterids (e.g. Judd et al. 2018). As yet, we do not have sufficient characters to narrow the affinities to a particular extant order and family. Features of pollen morphology would be helpful, but the preserved staminodal anthers do not contain pollen. Among the various angiosperm fruits known from the Deccan intertrappean beds, we have not found mature pentacarpellate capsular fruits of the kind expected to develop from these flowers. Thus, our knowledge of Kapgateanthus augments the biodiversity known from the latest Cretaceous of India.

ACKNOWLEDGEMENTS

We thank Professor D.K Kapgate for providing the slides used in this study. Laboratory facilities were provided by the Florida Museum at University of Florida.

REFERENCES

- APG IV (Angiosperm Phylogeny Group). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV, Botanical Journal of the Linnaean Society 181(1): 1–20. doi:10.1111/boj.12385
- Chitaley S.D. & Kate U.R. 1972. *Deccananthus savitrii*, a new petrified flower from the Deccan Intertrappean Beds of India. The Palaeobotanist 21(3): 317–320.

- Chitaley S.D. & Patel M.Z. 1975. *Raoanthus intertrappea*, a new petrified flower from India. Palaeontographica, Abt. B, 153: 141–149.
- Endress P.K. & Igersheim A. 2000. The reproductive structures of the basal angiosperm *Amborella trichopoda (Amborellaceae)*. International Journal of Plant Sciences 161(S6): S237–S248.
- Judd W.S., Campbell C.S., Kellogg E.A., Stevens P.F. & Donoghue M.J. 2018. Plant Systematics: A Phylogenetic Approach (4th ed.). Sinauer Associates.
- Kapgate D.K., Awasthi N, Manchester S.R. & Chitaley S.D. 2011. Inflorescences and flowers of *Sahnipushpam* Shukla from the Deccan Intertrappean beds of India. Acta Palaeobotanica 51(2): 207–227.
- Kapgate V.D., Kapgate D.K. & Sheikh M.T. 2006. *Chenopodianthus*, a fossil flower genus from the Deccan Intertrappean Beds of India. Geophytology 36(1): 27–34.
- Kapgate V.D., Kapgate D.K. & Sheikh M.T. 2009. Araliaceous fossil flower from the Deccan Intertrappean beds of Madhya Pradesh, India. The Palaeobotanist 58(1–3): 67–74.
- Kar R.K., Ambwani K., Sahni A., & Sharma P. 2003. Unisexual flowers from the Deccan Intertrappean Bed of Madhya Pradesh, India. The Palaeobotanist 52(1–3): 73–79.
- Kumar S., Manchester S.R., Judd W.S. & Khan M.A. 2023. Earliest fossil record of *Burseraceae* from the Deccan Intertrappean Beds of Central India and its biogeographic implications. International Journal of Plant Sciences 184 (9): 696–714.
- Lanjewar S.G., Puranik S.D., & Sakundarwar R.S. 2015. A fossil flower, *Surangepushpam deccanii* gen. et sp. nov. from the Deccan Intertrappean of Mohgaonkalan, M.P., India. International Journal of Researches in Biosciences, Agriculture and Technology 2(7): 328–332
- Narkhede S.D., Bhowal M. & Meshram S.M. 2010. A petrified flower from the Deccan intertrappean beds of India. Vidarbha Journal of Science 5(3–4): 1–7.
- Narkhede S.D. & Patil G.V. 2006. A petrified flower from the Deccan Intertrappean beds of Mohgaonkalan, Madhya Pradesh, India. Geophytology 36(1&2): 17–22.
- Paliwal P.A. 2020. A new petrified pentacarpellary flower "Kapgateanthus intertrappea" from the Deccan Intertrappean Beds of Mohgaonkalan, M.P., India. International Research Journal of Engineering and Technology 7(10): 1031–1039.
- Paradkar S.A. 1971. *Chitaleypushpam mohgaoense* gen. et sp. nov. from the Deccan Intertrappean beds of India. The Palaeobotanist 20(1–3): 334–338.
- Ramteke D., Smith S.Y., Kapgate D.K., Stanley E.L. & Manchester S.R. 2022. Angiosperm affinities of *Surangea* from the late Cretaceous Deccan Intertrappean Beds of central India. Acta Palaeobotanica 62(2): 196–204.
- Shukla V.B. 1944. On *Sahnianthus*, a new genus of petrified flowers from the Intertrappean Beds at Mohgaonkalan and its relation with fruit *Enigmocarpon parijaii* Sahni from the same locality. Proceedings of the National Academy of Sciences India 14: 1–39.