

Singpuria, a new genus of Eudicot flower from the latest Cretaceous Deccan Intertrappean Beds of India

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ABSTRACT. A new bisexual flower, *Singpuria kapgatei*, gen. et sp. nov., is described from chert of latest Cretaceous age from the Deccan Intertrappean Beds at Singpur, Madhya Pradesh, in central India. The hypogynous, actinomorphic flower is ~1.6 mm wide, with distinct sepals and petals. The androecium consists of 18 tetrasporangiate, dithecal, basifixed anthers borne in radial pairs on nine bifurcate filaments. The gynoecium is superior and syncarpous, with pentagonal symmetry. Pollen from the stamens is tricolporate and microreticulate. The combined morphological features of this flower indicate that *Singpuria* is a eudicot with affinities in the Pentapetalae, but we have been unable to make a more precise assignment. Nevertheless, we consider it useful to place this rare fossil flower on record as an exemplary extinct member of the Deccan biota. *Singpuria* may represent a clade that was isolated on the Indian subcontinent and became extinct in response to environmental changes at the K/Pg boundary, or later in the Cenozoic as the land mass moved northward through new climate zones and collided with Eurasia.

KEYWORDS: Deccan chert, Singpur, paleobotany, bifurcate stamens, tricolporate microreticulate pollen

INTRODUCTION

Fossil plants preserved in the Deccan Intertrappean Beds of central India provide insights into the biota that inhabited the Indian subcontinent when it was isolated from other major land masses in the late Cretaceous and early Cenozoic. The late Maastrichtian to Paleocene flora of the Deccan Intertrappean Beds is rich in silicified woods, fruits and seeds (reviewed, Kapgate, 2005; Smith et al., 2015; Wheeler et al., 2017) but the flowers that have been recovered are low in diversity. The myrtalean

flower *Sahnianthus* Shukla (1944; syn. *Chital-eypushpam* Paradkar, *Deccananthus* Chitaley et Kate, *Floshfemina* Kar, Ambwani, A. Sahni et Sharma, *Lythraceopushpam* Narkhede, Bhowal et Meshram, *Raoanthus* Chitaley et Patel) is an exception, being common at several (at least seven) localities and in various states of maturation. Very small flowers (1.0 to 1.5 mm diameter) include those described as *Chenopodianthus* VD Kapgate, DK Kapgate et Sheikh (2006), *Tetraplasandranthus* VD Kapgate, DK Kapgate et Sheikh (2009) and *Floshvirulus* Kar, Ambwani, A. Sahni et

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Sharma (2003) from the classic locality of Mohgaonkalan. Here we recognize a new kind of flower with intact stamens and pollen from a site near Singpur, northeast of Nagpur in central India.

The late Maastrichtian Singpur locality is well known for its flora preserved in chert, including pollen and spores (Samant et al., 2008) and fruits and seeds, such as *Baccato-carpon* Bhowal et Sheikh (2004; Manchester et al., 2019), *Drupaceocarpon* Nandeshwar et Narkhede (2016), *Pantocarpon* Kapgate, Patil, Ilamkar et Ramteke (Kapgate et al., 2007; Manchester et al., 2020; syn. *Verbenaceocarpon* Dhabarde, Sheikh, et Kolhe), *Phyllanthocarpon* Mistri, Kapgate et Sheikh ex Kapgate et Manchester (Kapgate et al., 2017), *Ramakonospermus* Matin et Juneja (Sheikh and Bhowal, 2003), *Singhpurospermum* Nandeshwar et Narkhede (2017) and *Viracarpon* Sahni (Matsunaga et al., 2018). In addition, we have recognized specimens of *Enigmocarpon* Sahni and *Graminocarpon* Chitaley et Sheikh in collections from this site, supplementary to the original occurrence reports of these taxa from Mohgaonkalan (Sahni, 1943; Chitaley and Sheikh, 1971), a paleobotanically rich site 64 km northeast of Singpur.

The new permineralized flower presented here adds to the diversity of angiosperms known from the Deccan Intertrappean Beds. Analysis of successive serial peels facilitated three-dimensional (3-D) conceptualization of the specimen, and an examination of pollen within the anthers by light and scanning electron microscopy yielded additional characters. Here we document the morphology and consider its systematic placement among eudicot angiosperms.

MATERIAL AND METHODS

The flower was discovered in a piece of black chert collected from the edge of a farming field near Singpur (alternate spelling Singhpur), ~65 km NNW of Nagpur in Chhindwara District, Madhya Pradesh, India (21°36.958'N, 78°43.827'E). The Singpur locality is interpreted to be latest Maastrichtian, based on stratigraphic correlations of pollen (Samant et al., 2008) and megafossils (Smith et al., 2015).

The flower was exposed in a natural fracture of the chert and was serially sectioned by the acetate peel method. Successive cellulose acetate peels were prepared by etching first with hydrofluoric acid, washing in water, squirting acetone across the etched surface,

and carefully applying an acetate sheet to bond with the etched surface. When dry, the peels were detached, cut with scissors, mounted on glass slides and covered by a glass coverslip affixed with Canada balsam. The peels were photographed on a Nikon Labophot microscope and imported to Avizo 9.0 Lite (FEI Visualization Science Group, Bordeaux, France) for alignment and 3-D reconstruction. Successive peel images and a slice movie of the holotype are accessible at Morpho-source.org (key word = Singpuria).

Pollen was studied and photographed by transmitted light microscopy of the peels with a Nikon Eclipse compound microscope. In addition, one of the peels was cleaned in hydrofluoric acid, mounted on an aluminum stub (etched surface upward) and analyzed with a Hitachi SU5000 field-emission scanning electron microscope (SEM) at the Interdisciplinary Center for Biotechnology Research at the University of Florida.

The floral diagram was generated with automatic rendering from http://kvetnidiagram.su.cz/index_en.php (Kebert, 2014–2020). In attempting to place the flower systematically, we entered morphological characters of the fossil into the web-based key, *The Families of Angiosperms* (Watson and Dallwitz, 1992 onwards), to obtain lists of extant families conforming to those characters, and considered each of those results in light of additional characters not available in the key program. Additional floral features were investigated with reference to those described in the *The Families and Genera of Flowering Plants* (e.g. Bayer, 2003; Bayer and Kubitzki, 2003; Anderberg, 2004; Fritsch, 2004; Stevens, 2004; Stevens et al., 2004a,b; Horn, 2007; Daly et al., 2011; Kubitzki et al., 2011; Pell et al., 2011) and other literature. Pollen was compared with that of extant taxa treated in systematic literature as cited, and with reference to the SEM survey of Li et al. (2010). Terminology for pollen follows Halbritter et al. (2018).

SYSTEMATICS

Clade. Pentapetalae

Family. *Incertae Sedis*

Genus. *Singpuria*

Ramteke, Manchester, et Nagrale **gen. nov.**

Pls. 1, 2

Etymology. The generic name refers to the town of Singpur (also known as Singhpur), close to the location where this fossil was collected.

Type species. *Singpuria kapgatei* Ramteke, Manchester et Nagrale sp. nov.

Plant Fossil Names Registry.PFN001778 (for new genus).

Species: *Singpuria kapgatei* Ramteke,
Manchester et Nagrale **sp. nov.**

Etymology. The specific epithet honors Prof. Dashrath K. Kapgate, whose research and mentorship have greatly improved our knowledge of the Deccan Intertrappean flora.

Holotype. UF19278-62141.

Repository. Paleobotanical Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

Type locality. Singpur, Madhya Pradesh, India; Late Maastrichtian.

Plant Fossil Names Registry. PFN001779 (for new species).

Generic and specific diagnosis. Flower bisexual, actinomorphic, perianth in two whorls, petals imbricate, merosity estimated at 5, imbricate, sepals imbricate. Androecium of 9 stamens with basally bifurcate filaments and 18 anthers. Anthers tetrasporangiate, dithecal, basifixed, opening by longitudinal slits. Each anther of outer whorl connected by bifurcate filament to an anther of inner whorl. Pollen tricolporate, prolate, psilate by LM, finely punctate by SEM. Gynoecium pentacarpellate; style pentagonal in cross section, ovary circular in cross section, with 10 radial ribs in upper half.

Description. The flower is actinomorphic, hermaphroditic, and is ~1.6 mm in diameter at the level of style and stamens. The perianth is not completely preserved, but enough is present to establish that there are two whorls (Pl. 1, figs 4, 6). The inner perianth whorl is represented by portions of three adjacent petals that have their edges overlapping in an imbricate organization (Pl. 1, figs 12, 13). Although the apical extremities of the petals are not known, at the level of style and anthers they are 0.1 mm thick and 1.0 mm wide. From the geometry, five petals can be inferred. Only one sepal is clearly preserved, but its size (0.6 mm wide, 0.19 mm thick) and shape indicate that there were likely five sepals, although this remains uncertain. The anthers are arranged in two whorls of nine each (Pl. 1, figs 1–5). The stamens are in a distinctive paired arrangement with only nine filaments at the base, each of which bifurcates dorsiventrally (Pl. 1, figs 5, 6) to connect with a radial pair of anthers, one

in the outer whorl and the other in the inner whorl. Thus, while there are 18 anthers in total, each dorsiventral pair shares a common filament. The anthers are 0.3 mm wide and 1.9 mm deep, with four pollen sacs dehiscing by longitudinal slits, attached to a connective that is 0.12 to 0.15 mm in diameter (Pl. 1, figs 13, 14; Pl. 2 figs 1, 2). Successive serial peels reveal that the anthers are basifixed (Pl. 1, figs 4, 5). The pollen grains are prolate, elongate, 32–35 μm long, 19–23 μm in equatorial diameter, tapered at the poles, and tricolporate (Pl. 2, figs 2–5). They are psilate by LM (Pl. 2, fig. 2), with microreticulate ornamentation visible at higher magnification by SEM (Pl. 2, fig. 5). The style is ~0.2 mm in diameter and pentagonal in cross section (Pl. 1, figs 13, 14), suggesting a pentamerous gynoecium. The apical-most part of the flower is missing, so we were unable to observe whether there is a single stigma or more. The ovary is circular in cross section and ~0.52 mm in diameter. The apical portion of the ovary has ten equally spaced vertical ribs (Pl. 1, figs 6, 7) but the lower portion is smooth (Pl. 1, figs 8, 9). The ovary content is not well preserved; hence the number of locules, placentation type and ovule condition are unknown.

DISCUSSION

The arrangement of the perianth, androecium and gynoecium for *Singpuria kapgatei* is summarized in the floral diagram (Fig. 1). Although the perianth is incompletely preserved, enough is present to establish that there clearly are two whorls, and from the symmetry of those petals and sepals that are present we infer five per cycle. The edges of the petals overlap, indicating imbricate rather than valvate aestivation. The androecium, with 18 anthers joined in radial pairs on nine bifurcate filaments, is distinctive. This arrangement is seen by studying the positions of each radial pair of anthers and their filaments through successive transverse peels (Pl. 1, figs 1–6). Because only one specimen is available, we do not know if the number of stamens was fixed or variable in the species. The gynoecium is syncarpous, and is inferred to be pentamerous because the style base is pentagonal. However, the upper part of the ovary has ten equally prominent radial ribs, so

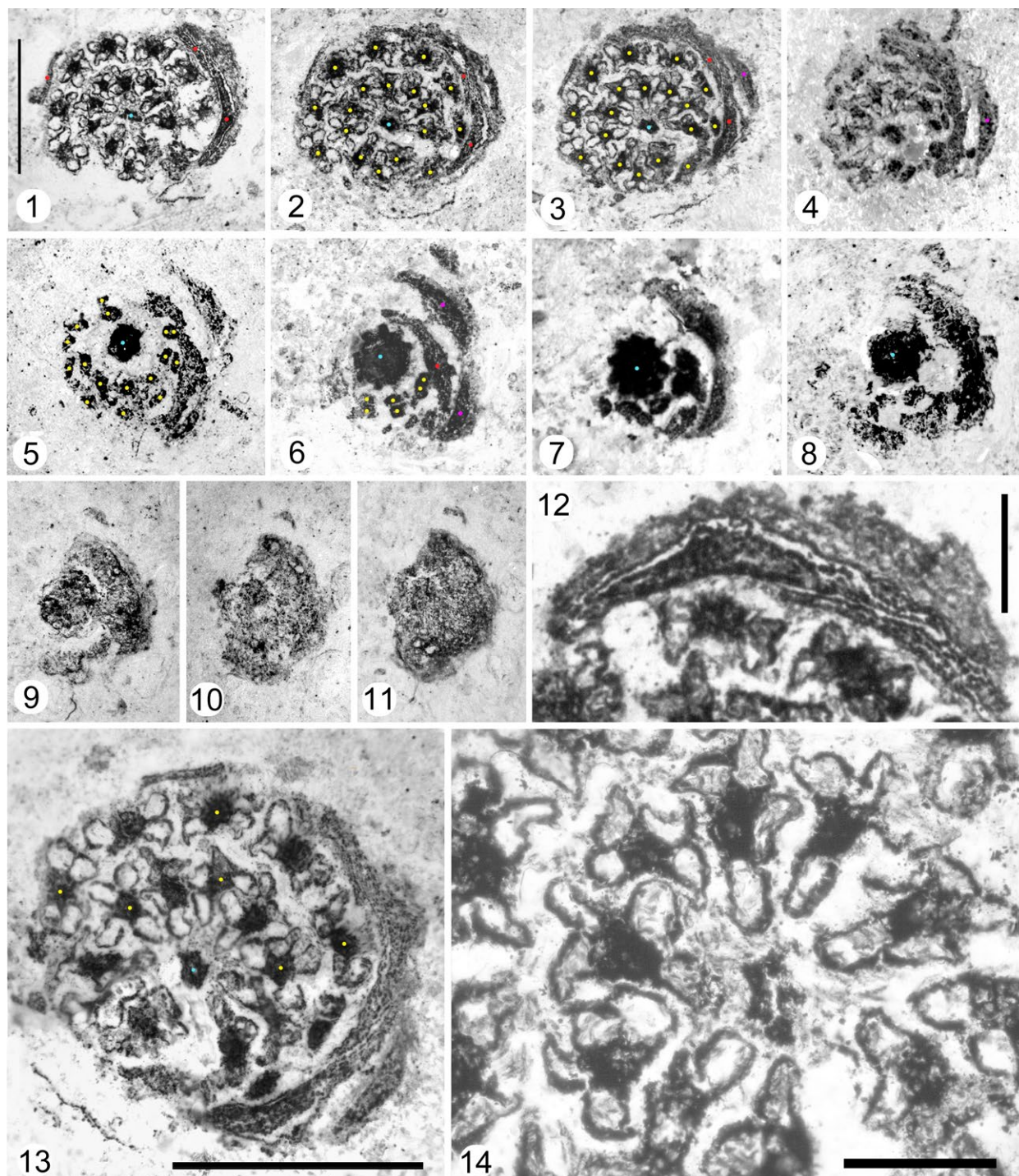


Plate 1. Floral morphology of *Singpuria kaggatei* gen. et sp. nov. Holotype, UF19278-62141. 1–11. descending serial sections of the flower. Colored dots indicate different floral parts: blue = gynoecium, yellow = anthers, red = corolla, violet = calyx; 1–4. sections showing remnants of perianth and 18 anthers in two whorls surrounding a single style; 5. section at level showing bifurcate stamen filaments (paired filaments above the bifurcation, single filaments below the bifurcation), and widened base of the style; 6, 7. dorsiventral pairs of stamen filaments coalescing; apical part of ovary with ten ribs; 8–11. successive sections of lower part of flower, showing base of perianth and receptacle; 12. enlargement from fig. 1, showing imbricate perianth members; 13. enlargement showing the anthers, with alternate pairs of anthers color-coded, with yellow dots showing their radial arrangement. Style indicated by blue dot; 14. detail of inner whorl of anthers and central pentagonal style. Scale bars: 1 (applies also to 2–11) and 13 = 1 mm; 12, 14 = 0.25 mm

there is an alternate possibility that the flower bore ten carpels. The internal structure of the gynoecium is unknown because the base is not fully preserved. Hence the ovary content and the placentation type are unknown.

Affinities. Pollen recovered from the anthers of *Singpuria* differ from the dispersed pollen types so far recorded from Singpur (Samant et al., 2008). Also, we were unable to link this flower directly with any of the

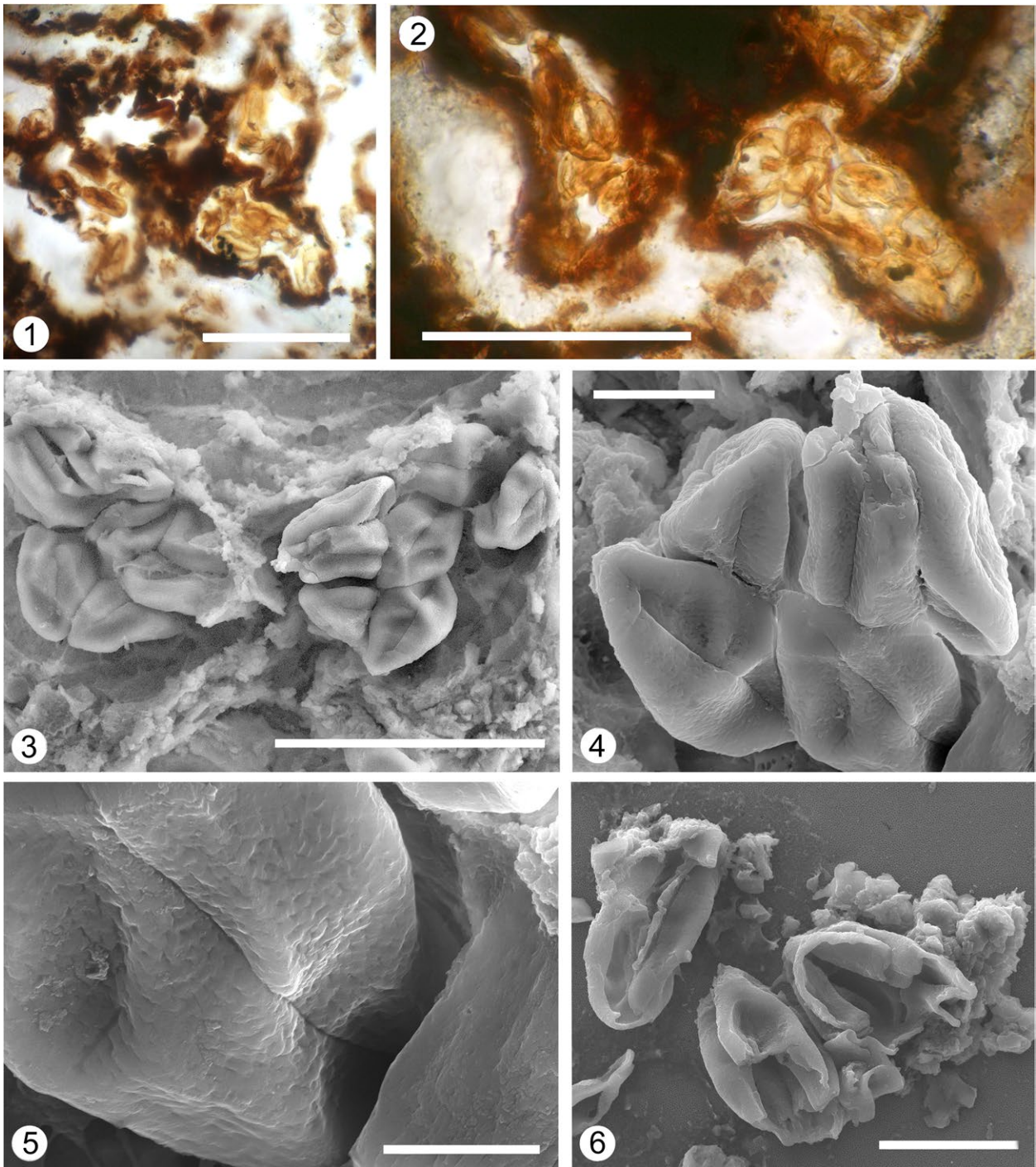


Plate 2. *Singpuria kapgatei* androecium and pollen. **1, 2.** anther in transverse section, showing in situ prolate tricolporate pollen grains; **3–5.** clumps of tricolporate pollen in situ, SEM; **6.** broken pollen grains, showing endoaperture and thin exine; Scale bars: 1, 2 = 0.1 mm; 3 = 50 μ m; 4 = 10 μ m; 5 = 5 μ m; 6 = 2 μ m

fruits known from Singpur or other Deccan Intertrappean Beds. The presence of ten ribs on the apical part of the gynoeceium (Pl. 1, fig. 7) leads us to hypothesize that the fruit that developed from this species of flower may have been ten-carpellate. The extinct fruit genus *Daberocarpon* Chitale et Sheikh (Malvaceae: Malvoideae) has ten-loculed capsules (Chitale and Sheikh, 1973) but it would be expected to associate be associated with spiny

porate pollen characteristic of Malvoideae rather than with the smooth tricolporate pollen produced by *Singpuria*.

The perianth of *Singpuria*, differentiated into sepals and petals, and the tricolporate pollen, are features diagnostic of eudicots (Ronse de Craene, 2010). We attempted to key out this flower to the family level by seeking those taxa possessing the following suite of characters available in the database of Watson and

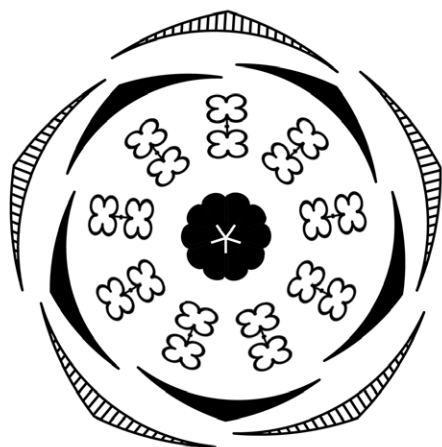


Fig. 1. Floral diagram for *Singpuria*, showing two imbricate whorls of perianth, 18 anthers, and 10-ribbed ovary

Dallwitz (1992 onwards): flowers actinomorphic, corolla five-lobed, imbricate, stamens nine, filantherous, anthers basifixed, dehiscing via longitudinal slits, pollen shed as single grains, tricolporate, gynoecium superior, syncarpous, composed of five carpels, and having a single style. A second keying attempt used the same features, with the exception of carpel number being indicated as ten rather than five, because it is uncertain whether the ten ribs on the upper part of the ovary each were distributed one or two per carpel. As an alternative to the specification of nine stamens (interpreting each filament base as one stamen), we also entered 18 stamens (the number of anthers). The 27 resulting families (26 when Tiliaceae and Malvaceae s.s. are treated together as Malvaceae s.l.) from these keying runs, shown in Table 1, all belong to the Pentapetalae (Chanderbali et al., 2017; Judd et al. 2016).

Based on characters included in the keying exercise summarized above, *Singpuria* has similarities with the core eudicot family Dilleniaceae (sensu Soltis et al., 2018) as well as 25 families of Rosids and Asterids (Tab. 1). The fossil differs from Dilleniaceae by its syncarpy, however, contrasting with the apocarpous to hemisyncarpous condition characteristic of that family (Horn, 2007). The Rosid families retrieved in the keying exercise included Anacardiaceae, Burseraceae, Cistaceae, Guttiferae, Humiriaceae, Irvingiaceae, Malvaceae, Muntingiaceae, Ochnaceae, Paracryphiaceae, Pentadiplandraceae, Rutaceae, Salicaceae, Sapindaceae and Zygophyllaceae. Ten Asterid families were recovered, including Aizoaceae, Aquifoliaceae, Ericaceae, Lennoaceae (Boraginaceae), Marcgraviaceae, Primulaceae,

Sarraceniaceae, Sapotaceae, Scytopetalaceae (Lecythidiaceae), Styracaceae and Theaceae. Each of these families differs in a number of traits from the fossil (Tab. 1).

Some pollen features not included in the Watson and Dallwitz (1992 onwards) key, such as shape and ornamentation, rule out affinities of *Singpuria* with these families (Tab. 1). The monad pollen of *Singpuria* is clearly distinct from the permanent tetrads typical of Ericaceae (Stevens et al., 2004b; Hofmann, 2018) and from Sarraceniaceae, which is usually four-colpate or more (Oswald et al., 2011; Thanikaimoni and Vasanthi, 1972). We can also rule out affinities with Aizoaceae, Aquifoliaceae and Malvaceae subf. Malvoideae by their ornamentation being scabrate, clavate and spinulate, respectively, rather than microreticulate as in *Singpuria* (see references in Tab. 1). Most of the other families listed in Table 1 include taxa with pollen that, at least in some genera, is tricolporate and microreticulate like *Singpuria*. However, whereas the colpus membrane of *Singpuria* is smooth (Pl. 2, fig. 4), it is granular in Dilleniaceae, Burseraceae, Clusiaceae, Humiriaceae, Marcgraviaceae and Sapindaceae. The pollen grains of *Singpuria* are markedly narrowed toward each pole, rather than smoothly rounded as in Sapotaceae, Burseraceae and most Malvaceae. The unique structure of the androecium of *Singpuria* with its bifurcate stamens and radial alignment of the two whorls of anthers distinguishes the fossil from extant genera in all of these families.

Conclusion. Recognition of this new kind of flower increases the diversity of taxa known from the Deccan Intertrappean cherts. After comprehensive comparative work, it might seem frustrating that the well-preserved features of this flower do not lead us to a precise systematic assignment with respect to modern angiosperm families. However, we cannot expect late Cretaceous plants always to conform to extant families. We conclude that *Singpuria kaggatei* likely represents an extinct family, but with only one specimen available, and lacking additional details of the gynoecium, we refrain from proposing a new family name. If *Singpuria* represents a clade that was isolated on the Indian subcontinent, it could have become extinct in response to the Deccan volcanism and environmental changes at the K/Pg boundary (e.g. Sprain et al., 2019), or later as the land mass

Table 1. List of families compared with *Singpuria*, based on results from *The Families of Angiosperms* key (Watson and Dallwitz, 1992 onwards)

	Affinity	Carpel number	Stamen number	Pollen ornamentation	Morphological differences
<i>Singpuria</i> gen. nov.	Pentapetalae	10 (or 5?)	18 anthers; 9 filaments	Microreticulate, colpus membrane smooth	–
Dilleniaceae	Dilleniales	(1–)2–7(–20)	1–10 (rarely) or 15–150	Punctate to reticulate, colpus membrane granular (Dickison et al., 1982)	Apocarpous to hemisyncarpous gynoecium (Horn, 2007); Colpus membrane granular
Anacardiaceae	Rosids Sapindales	1–12	(1–)5–10(–12)	Striate to microreticulate to reticulate (Ibe and Leis, 1979)	(Pell et al., 2011)
Burseraceae	Rosids Sapindales	2–5(6–12)	4–5 or 8–10	Diverse ornamentation types, echinate when microreticulate (Harley et al., 2005)	Sepals usually valvate (Daly et al., 2011); Colpus membrane granular
Cistaceae	Rosids Malvales	(2)3–5(6–numerous)	(3–)15–many	Reticulate to finely reticulate (Ukrainitseva, 1993; Civeyrel et al., 2011)	Stamens usu. numerous (Arrington and Kubitzki, 2003)
Clusiaceae	Rosids Malpighiales	(1–)3 carpelled, or 5(–13)	3–4 (rarely), or 20–many	Variable incl. microreticulate (Seetharam and Maheshwari, 1986)	Colpus membrane granular
Humiriaceae	Rosids Malpighiales	(4–)5(–8)	10–100	Microreticulate (Bove and Melhem, 2000)	Colpus membrane granular; grains suboblate to subprolate
Irvingiaceae	Rosids	(4–)5, or 2	9–10	Microreticulate to striate; subglobose (Satabié, 1974)	Intrastaminal nectary disk
Malvoid Malvaceae	Rosids Malvales	6–14	5–15–50 (–100)	Spheroidal, echinate (Christensen, 1986)	Spheroidal, echinate exine, usually polyporate; calyx gamosepalous, valvate
Tilioid Malvaceae	Rosids Malvales	2–100	(8–)15–100	Reticulate to micro-reticulate (Perveen et al., 2004)	Stamens numerous, sometimes fascicles of 5.
Muntingiaceae	Rosids Malvales	5, or 6–7	11–15–100 ('many')	Microreticulate (Bayer, 2003)	Petals thin, crumpled in bud; stamens numerous
Ochnaceae	Rosids Malpighiales	2–15	5 or 10 or 11–100	Striate (Ferreira de Sousa et al., 2020)	Style gynobasic (Bayer, 2003)
Paracryphiaceae	Asterids Paracryphiales	8–15	8–11	Reticulate (Dickison and Baas, 1977)	Only 4 tepals, triplosteminous
Pentadiplandraceae	Rosids Brassicales	3–5	9–13	Reticulate, spheroidal to oblate	Pollen shape (Bayer and Appel, 2003)
Rutaceae	Rosids Sapindales	(1–3) or 4–5 (–100)	2–5 or 8 or 10 or 20–60	Reticulate to micro-reticulate (Fernanda Vitorete and Custódio Gasparino, 2018)	Obdiplosteminous (Kubitzki et al., 2011)
Sapindaceae	Rosids Sapindales	(2–)3(–8)	4–5(–6) (rarely) or 8 or 10 or 11–100	Verrucate, striate, microreticulate, granular colpus membrane (Muller and Leenhouts, 1976).	Carpels usually 3 or 2; granular colpus membrane
Salicaceae	Rosids Malpighiales	2–10	1–2–30–60	Reticulate to microreticulate (Keating, 1973)	Stamens usually many
Aizoaceae	Asterids Caryophyllales	1–5 –many	(3–) 4–5 or 8–10 or 15–200	Pollen scabrate (Perveen and Qaiser 2000)	Pollen ornamentation
Aquifoliaceae	Asterids	(2–)4–6(–24)	4 or 7–8(–12)	Clavate (Lobreau, 1969)	Stamens alternate with petals; Pollen ornamentation
Ericaceae	Asterids Ericales	(2–)4–5(–10)	5 (rarely) or 8–10	Microrugulate, fossulate to sometimes perforate (Hoffman, 2018)	Corolla usually synpetalous; pollen shed in tetrads (Stevens et al., 2004b)
Lecythidaceae [Scytopetalaceae]	Asterids Ericales	3–8	(10–)20–240	Microreticulate with duplibaculate muri (Appel, 1996)	Calyx synsepalous, colpus membrane granular; pollen suboblate to spheroidal

Table 1. Continued

	Affinity	Carpel number	Stamen number	Pollen ornamentation	Morphological differences
Lennoaceae [alternately placed in Boraginaceae]	Asterids	6–14	5–10	Microreticulate or punctate (Yatskievych and Zavada, 1984)	Pollen obovate; stamens epipetalous (Yatskievych and Mason, 1986)
Marcgraviaceae	Asterids Ericales	2–8	3–40	Microreticulate to reticulate (Lens et al., 2005)	Colpus membrane granulate
Primulaceae	Asterids Ericales	5	(3–)5(–9)	Reticulate to microreticulate (Nowicke and Skvarla, 1976)	Corolla sympetalous (Anderberg, 2004)
Sapotaceae	Asterids Ericales	(2–)4–14(–30)	4–15	Psilate to microreticulate (Harley, 1991)	Androecial sympetalous; pollen prolate, rounded at poles
Sarraceniaceae	Asterids Ericales	3 or 5	(10–)50–100	(Thanikaimoni and Vasanthi, 1972)	(3–) to 9-colpate rather than colpate
Styracaceae	Asterids Ericales	(5–)8–10(–20)	(5–)8–10(–20)	Rugulate to micro-reticulate (Morton and Dickison, 1992)	Stamens usu. twice or equal the corolla lobes (Fritsch, 2004)
Theaceae	Asterids Ericales	(2–)3–5(–10)	5 or 10 or 15 or 16–100	Microreticulate (Li et al., 2010)	Styles usually as many as carpels; stamens 20+ (Stevens et al., 2004a)

moved northward through new climate zones and collided with Eurasia (e.g. Ding et al., 2017; Klaus et al., 2016), facilitating new competition from the introduction of Laurasian taxa. Additional collections leading to future recognition of *Singpuria*-type flowers in the Deccan cherts (or elsewhere) should provide the additional data needed to test our hypotheses about this flower's affinities and evolutionary history.

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