Heliyon 10 (2024) e40794

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Research article

The first macrofossil record of parasitic plant flowers from an Eocene Baltic amber

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A R T I C L E I N F O

Keywords:
Flower
Corolla
Schoepfiaceae
Amber
Eocene
Kaliningrad
Russia

A B S T R A C T

Parasitic plants left little trace in the macrofossil record, making their evolutionary history mysterious. Baltic amber and other fossil lagerstätts have provided plenty of angiosperm fossils, there are only three reports of fossil leaves (cf. *Schoepfia republicensis* and *Schoepfia* sp. 1) related to Schoepfiaceae until now, making many hypotheses related to its evolution untested. Here we report a fossil corolla and stamens of a probable schoepfiaceous flower (Schoepfiaceae, Santalales) from late Eocene (37.8–33.9 Ma ago) of Kaliningrad, Russia. Unlike previously reported flowers, the new fossil is characterized by its five fused petals bearing adnate stamens. This character assemblage points to an affinity of Schoepfiaceae. This is the debut of schoepfiaceous flower in the macrofossil record, shedding a new light on the evolution of this poorly understood family. Its unexpected occurrence in Russia adds information to the discussion on the history of Schoepfiaceae.

Although early angiosperms have been abundantly documented [1–17], there are still many lacunae in our understanding of angiosperm evolution. For example, due to their special habit, parasitic plants (especially their flowers) are rarely reported in the fossil record. Schoepfiaceae, a family now restricted to the Neotropical (20 species) [18] and southeast Asia (4 species) [18,19], have very limited macrofossil record: only 9 pieces of leaves from the Eocene (38–55.8 Ma) of Northwest USA (cf. *Schoepfia republicensis*) [20,21] and 1 piece of leaf (*Schoepfia* sp. 1) from the Miocene-Pliocene (5.3–11.6 Ma) of Southwest China [22] have been reported until now, while their flowers are completely lacking in the fossil record. Such a lack of macrofossil data makes the evolution and history of Schoepfiaceae elusive. Here we report a new fossil taxon, *Schoepfioides kaliningradensis* gen. et sp. nov (including corolla and adnate stamens), from the late Eocene (37.8–33.9 Ma ago) of Kaliningrad, Russia. The unique morphology of *Schoepfioides* compares itself best with *Schoepfia*, a genus in the parasitic family Schoepfiaceae (Santalales). Thus it can be determined that our fossil represents the debut of schoepfiaceous flower in the current macrofossil record, and will add much to our understanding of this poorly understood family.

The fossil material was uncovered from an outcrop of the Blue Earth near Yantarny Village, Samland Peninsula, Kaliningrad, Russia (54°52′22″N, 19°56′26″E) in 2015. The studied specimen was preserved three dimensionally in a brownish amber. Various works [23–30] suggest a late Eocene age (37.8–33.9 Ma) for the amber enclosing the fossil. It was observed and photographed using a Nikon SMZ1500 stereomicroscope with a DS-Fi1 digital camera housed at the Nanjing Institute of Geology and Palaeontology, Nanjing,

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https://doi.org/10.1016/j.heliyon.2024.e40794
Received 25 July 2024; Received in revised form 24 November 2024; Accepted 27 November 2024
Available online 28 November 2024
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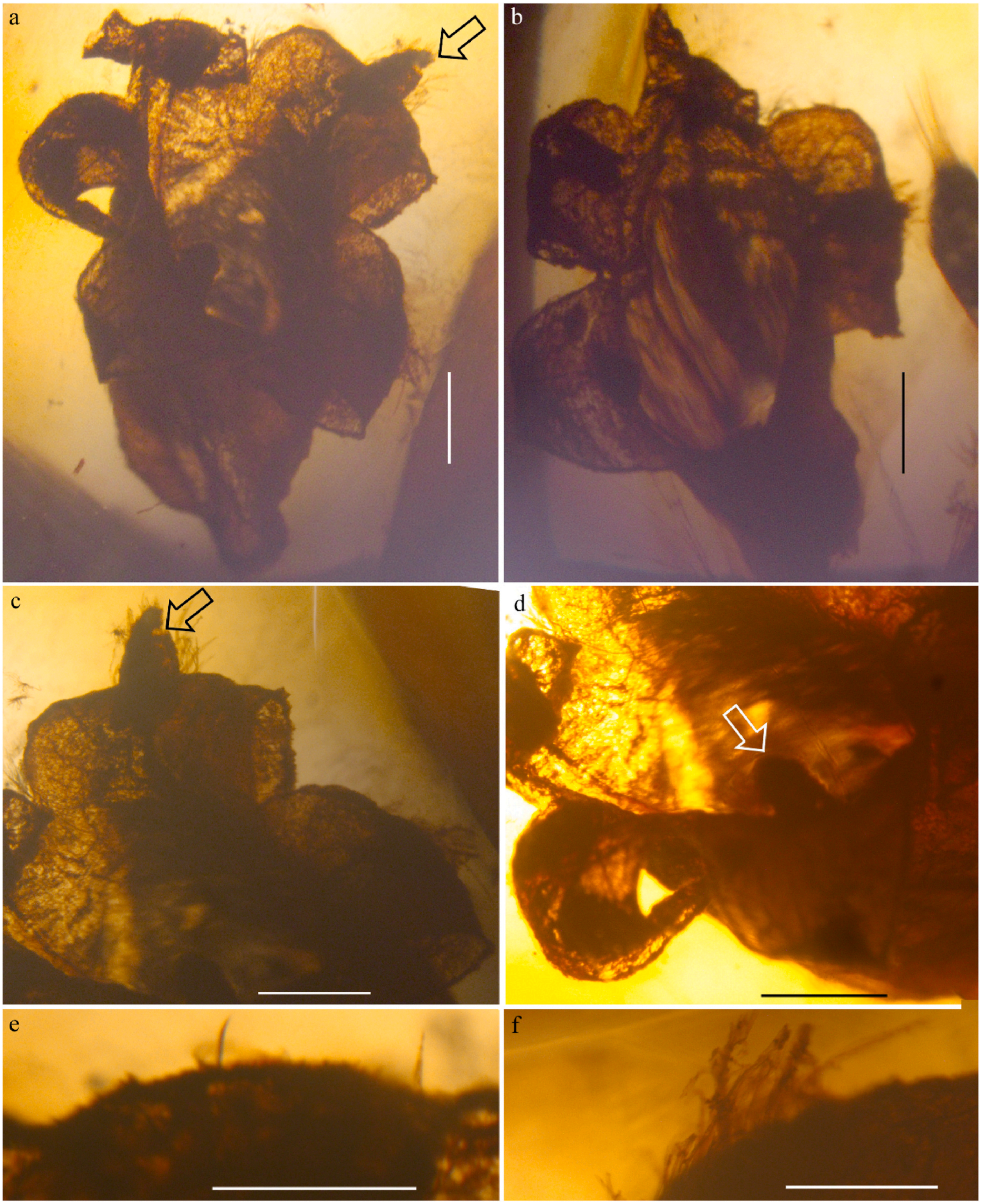

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Fig. 1. General view and details of *Schoepfioides kaliningradensis* gen. et sp. nov.
a. Top view of the corolla. Note one (arrow) of the stamens. Scale bar = 1 mm
b. An oblique top view of the corolla, showing five relfexing lobes. Scale bar = 1 mm.
c. Adaxial view of a petal and its epipetalous stamen (arrow). Note the post-staminal hair tuft. Scale bar = 1 mm
d. A reflexing lobe and its epipetalous stamen (arrow). Scale bar = 1 mm.
e. Acuicular epidermal trichomes on a petal surface. Scale bar = 0.5 mm.
f. A hair tuft associated with a stamen (fallen off). Scale bar = 0.5 mm.

China. Micro-CT observation was performed using a Zeiss Xradia 520 versa X-ray microscope housed at the Nanjing Institute of Geology and Palaeontology, Nanjing, China. The three dimensional reconstruction and virtual sections were generated using VG Studio MAX 3.0. All figures were organized for publication using a Photoshop 7.0.

Eudicots

Santalales

Schoepfiaceae

***Schoepfioides* gen. nov**

Diagnosis: Corolla tubular, campanulate, with 5 triangular reflexing lobes. Five epipetalous stamens, dorsifixed, bilocular, with a hair tuft between stame and petal, adnated to the middle of the petals. Filament short.

Type species: *Schoepfioides kaliningradensis* gen. et sp. nov.

Etymology: *Schoepfioides*-for its close resmblance to extant plant *Schoepfia*.

Type horizon: The Priabonian, late Eocene (37.8–33.9 Ma).

Type locality: Yantarny Village, Samland Peninsula, Kaliningrad, Russia (54°52′22″N, 19°56′26″E).

***Schoepfioides kaliningradensis* gen. et sp. nov**
(Figs. 1 and 2)

Diagnosis: the same as the genus.

Description: A single flower corolla is preserved (Fig. 1a–b, 2a-b). The corolla is campanulate in form, 5.7 mm long (Fig. 1a–b, 2a-b). Oval in cross view, 4.5 mm × 4 mm (Fig. 2b–i). There are five triangular lobes on the top of the corolla tube (Fig. 1a–d, 2g-h, k). The lobes are triangular in shape, reflexing, measuring 2.6 mm long and 1.7 mm wide at the base (Fig. 1a–b, 2a-b). On the middle of each lobe there is an epipetalous stamen, behind which is a tuft of hairs (Fig. 1a–d, 2a-b, g-h, l-m). Each stamen has a 0.17 mm-long filament, two locules, and a pointed connective (Fig. 1a–d, 2a-h, l-m). Each anther is 1.4 mm long, 0.48 mm wide, 0.37 mm thick, and the connective is about 0.2 mm long (Fig. 1a–b, 2c-f, l-m).

Etymology: *kaliningradensis* for the fossil locality Kaliningrad, Russia.

Holotype: BMM5586.

Depository: the Blue Miracle Museum Science Research Studio, Guangzhou, China.

Remarks: Corolla with epipetalous stamens, especially those with a post-staminal hair tuft, are present in families of Santalales. For example, stamens adnate to the corolla base in Loranthaceae [31]. However, stamens in Loranthaceae lack an associated hair tuft, adnate to the base (rather than top) of the corolla, and have basifixed anther [31]. These constitute a strong contrast against Schoepfiaceae, stamens of which have an associated tuft of hairs, adnate to the top (rather than base) of the corolla, and have dorsalifixed anther [31]. These characters support the identification of the fossil flower as an extinct member of Schoepfiaceae.

Discussion

Comparison of *Schoepfioides kaliningradensis* with extant species of *Schoepfia* The Schoepfiaceae (Santalales) is a small family of parasitic angiosperms, consisting of about 50 species endemic to South America and Asia, living in moist habitat such as high elevation cloud forests [18,19]. This family was named after Dr. David Schoepf, a German botanist. This small family is a sister of two more diverse, widespread, parasitic families, Misodendraceae and Loranthaceae [31–33]. Flowers in Misodendraceae have apetalous or 3 petals, while flowers of Loranthaceae have a connate perianth of 3 or 5 lobes with adnate slender-filamented anthers [31,32], and thus both are distinct from Schoepfiaceae, in which the flowers have 5-lobeed perianth with adnate stout-filamented stamens opposite to petals. As a parasitic family, plants in Schoepfiaceae rely on other plants to obtain nutrients, thus having little potential to be fossilized. Until now there are only three reports of total ten pieces of leaves related to Schoepfiaceae [20–22], making the evolution and history of Schoepfiaceae poorly understood.

The post-staminal hair tuft in *Schoepfioides kaliningradensis* (Fig. 1c) is a feature never seen in the fossil record. The occurrence of this feature appears to be very informative as hairs behind the anthers are commonly considered a feature characteristic of Santalaceae, although they occur elsewhere infrequently [32]. According to the diagnosis of Schoepfiaceae, “petals (4)5(6), united for most of their length to form a cylindrical to subcampanulate corolla, the limbs spreading or recurved at anthesis; stamens as many as the petals and connate with them at the latter’s middle, opposite the petals, each associated with a post-staminal hair tuft; filaments as long as the ovoid, dorsifixed, biloculate anthers that are placed at the flower’s mouth” [32], and they can be verified in extant *Schoepfia*

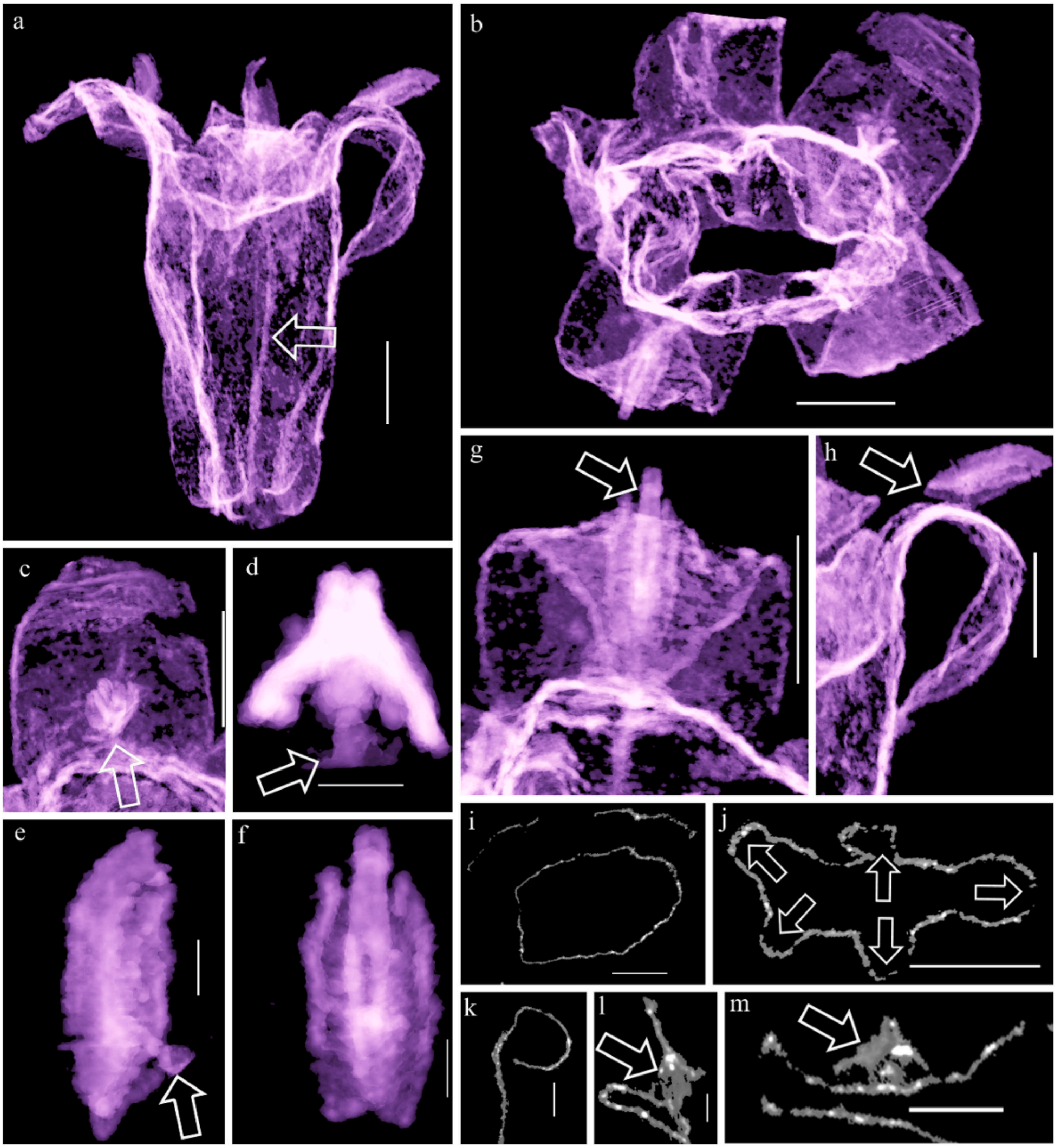

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Fig. 2. Micro-CT virtual sections of the corolla.
a. Side view of the corolla, showing four preserved epipetalous stamens, each of which is supported by a vein running through the whole length of the petal (arrow). Scale bar = 1 mm
b. Bottom view of the corolla, showing the deployment of five petal lobes and an elongated oval hole (central) at the corolla bottom. Scale bar = 1 mm.
c. Adaxial view of petal lobe and its epipetalous stamen (arrow). Scale bar = 1 mm
d. Cross view of the epipetalous stamen in Fig. 2e–f, showing its dorsal short filament (arrow) and two locules. Scale bar = 0.2 mm.
e. Side view of the epipetalous stamen in Fig. 2h, showing its short dorsal filament (arrow). Scale bar = 1 mm.
f. Adaixal view of the stamen shown in Fig. 2h, showing its apical connective and two locules. Scale bar = 1 mm
g. Adaxial view of petal and its epipetalous stamen (arrow). Scale bar = 0.2 mm
h. Side view of a petal, showing reflexing lobe and its epipetalous stamen (arrow). Scale bar = 0.2 mm.
i. Oval cross view of the corolla (near the top), showing fused petals and two reflexing petal lobes (top). Scale bar = 1 mm.
j. Cross view of the corolla (near the bottom), showing five fused petals (arrows). Scale bar = 1 mm
k. A reflexed petal tip. Scale bar = 0.5 mm
l. Side view of a petal lobe, showing reflexed tip and epipetalous stamen (arrow). Scale bar = 0.2 mm
m. Cross view of a petal, showing epipetaous stamen (arrow) adnated to the petal. Scale bar = 0.5 mm.

Fig. 3. Flowers of *Schoepfia jasminodora* Sieb. & Zucc. and their details.
a. Several flowers of various developmental stages in an infructescence.
b. Side view of a flower showing connate petals and reflexing lobes.
c. Oblique top view of a flower showing five stamens (dark dots) adnate to the petals and a hair tuft (black triangle) asscoaited with a stamen.

flowers (Fig. 3a–c). Almost all these features occur in the fossil specimen of *Schoepfioides kaliningradensis* (Fig. 1a–d, 2a-m). This observation suggests that *Schoepfioides kaliningradensis* represents a flower of Schoepfiaceae, which has never been seen in the macrofossil record so far, especially at this early age (late Eocene). Although there are two other genera (*Arjona* and *Quinchamalium*), frequently placed in the Schoepfiaceae, these two genera distinguish themselves from the fossil flower by their different corolla forms and longer petal lobes [18,33].

Palaeogeography and Evolution Extant Schoepfiaceae is a poorly understood family restricted to America (20 species in Mesoamerica, Caribbean, Argentina, Bolivia, and Peru) and Asia (4 species in India, Malesia, China) (Fig. 4) [18,19,32,34]. The family is frequently regarded as related to Misodendroaceae and Loranthaceae [31–33]. Although there are some fossil of Santalales, most of them are restricted to pollen records the significance of which is "compromised by intrageneric polymorphism and convergence" [33]. Fortunately, some macrofossil records are found related to *Schoepfia*, leaves from the Eocene (38–55.8 Ma) of Northwest USA [20,21] and from the Miocene-Pliocene of Southwest China [22] (Fig. 4). Such extant and past geographical distributions are debatable topics for botanists: While extant center of diversity (Fig. 4) appears to suggest a southern hemisphere origin for the family, which was also favored by molecular analysis [33], the present reported occurrence of flower corolla and stamens indicate that Schoepfiaceae have existed in Kaliningrad, Russia by the late Eocene. It is possible Schoepfiaceae may migrate from their Eocene center of diversity in North America and west Europe, to their extant diversity center in South America and Asia (the latter has their Miocene fossil record [22] and a few extant species). Although we have limited fossils of Schoepfiaceae currently, it appears that the Southern hemisphere origin of Schoepfiaceae suggested previously [33] should be reconsidered, especially when more fossil information is available in the future.

Origin of Parasitism The occurrence of *Schoepfioides kaliningradensis* raises new questions concerning the origin and evolution of parasitism. Haustorial parasitism occurs in 270 genera (>4500 species) of angiosperms [33]. Extant Schoepfiaceae is known to be root parasitic [33]. However, it is unknown when they became parasitic, before or after the age of *Schoepfioides kaliningradensis*, which we now compare with Schoepfiaceae. Considering the relatively longer history of Schoepfiaceae among Santatales [33], it is possible that *Schoepfioides kaliningradensis* was not parasitic yet. If really so, then parasitism in Schoepfiaceae should occur after the age of *Schoepfioides kaliningradensis* (late Eocene), but one question rises, exactly when it occurred. In the meanwhile, if *Schoepfioides*

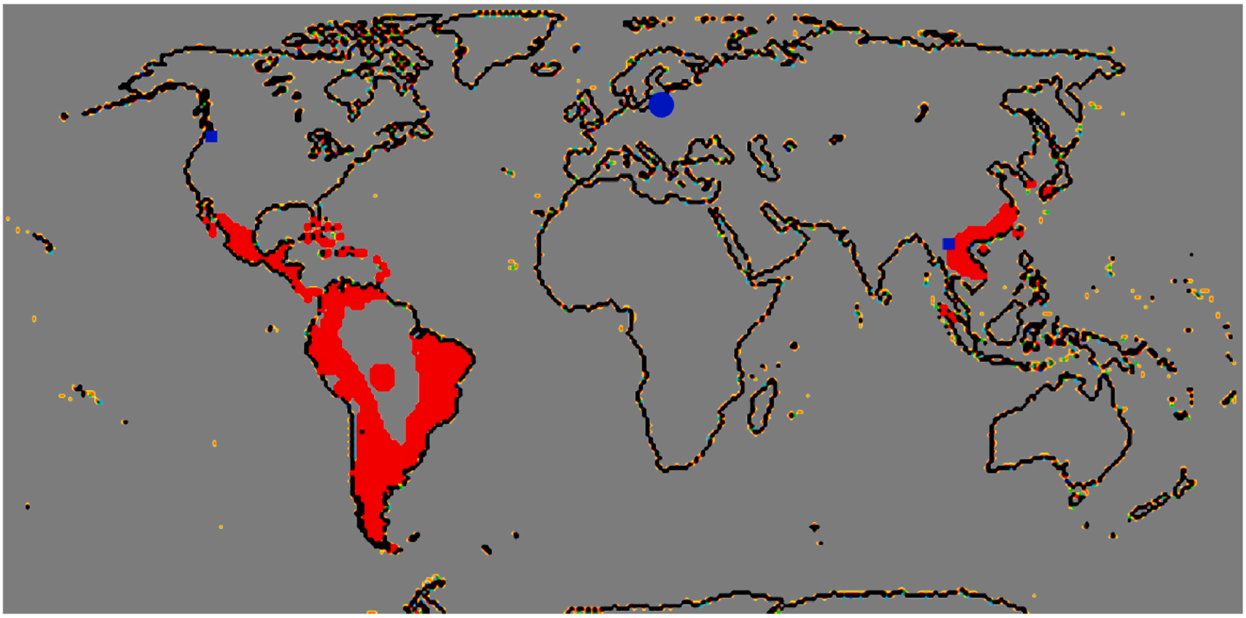

Fig. 4. Global distribution of *Schoepfia* (red) and the fossil locality of *Schoepfioides kaliningradensis* gen. et sp. nov. in Kaliningrad, Russia (blue dot), two previous fossil localities in NW USA and SW China (blue squares).

kaliningradensis were parasitic, then parasitism in Schoepfiaceae should have occurred before the age of *Schoepfioides kaliningradensis* (late Eocene), and again we will face exactly the same question. We hope future fossil discoveries will help to answer this question.

CRediT authorship contribution statement

Weijia Huang: Writing – review & editing, Writing – original draft. **Wenzhe Liu:** Writing – review & editing, Writing – original draft. **Xin Wang:** Writing – review & editing, Writing – original draft.

Data availability

Data included in article is referenced in the article.

Ethics declaration

Review and approval by an ethics committee or informed consent was not required for this study because it did not involve human subjects or laboratory experiments.

Funding

This research was supported by the National Natural Science Foundation of China (42288201).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Mr. Suping Wu for her help with Micro-CT.

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