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Pollen cones and in situ pollen of *Aegianthus* Krassilov from the Middle Jurassic of East Siberia, Russia

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ABSTRACT

The paper documents in detail the morphological and epidermal characters of the pollen cones and in situ pollen of *Aegianthus* based on the study of specimens from the Prisayan Formation (Middle Jurassic) in the Irkutsk Basin (Siberia, Russia). An emended diagnosis is provided and a lectotype is selected for the type species, *A. sibiricus*, since a holotype/lectotype was not indicated in the previous publications of this species. Resin bodies are found in sporangiophores of *A. sibiricus* for the first time. The number of sporangia is specified as 10–12 per sporangiophore. This species differs from other *Aegianthus* species in smooth periclinal cell walls and lacking papillae on the subsidiary cells of the stomata in the abaxial epidermis of the peltate head. A new species, *A. irkutensis*, is described from the same Prisayan Formation of the Idan locality in the Irkutsk Basin. Unlike *A. sibiricus*, the cells of the outer epidermis of *A. irkutensis* are strongly papillate. *A. irkutensis* differs from other *Aegianthus* species by smaller resin bodies, numerous and longer sporangia. Pollen cones of both *A. sibiricus* and *A. irkutensis* were found in association with leaves of *Sphenobaiera*. The pollen of *A. irkutensis* are similar to those of *A. sibiricus* in morphology and ultrastructure. Pollen grains are boat-shaped, monosulcate. The exine surface is psilate or scabrate in the light microscope, and scabrate to granulate in SEM; the infratectum consists of large granules or columella-like elements. The exine ultrastructure of the *Aegianthus* pollen under study implies a ginkgoalean or gnetophytalean affinity.

1. Introduction

The genus *Aegianthus* Krassilov with the type species *Aegianthus sibiricus* (Heer) Krassilov (in Krassilov and Bugdaeva, 1988) was established for pollen cones from the Middle Jurassic of the Ust'-Baley locality (Irkutsk Coal Basin, East Siberia, Russia). First, these cones were described by Heer (1876, 1878) as fructifications of Pandanaceae and named as *Kaidacarpum sibiricum* Heer. Later, Prynada (1962) assigned them to the equisetalean spore cone genus *Equisetostachys* Halle, *Equisetostachys sibiricus* (Heer) Prynada, based on morphology of their peltate sporangiophores. Krassilov and Bugdaeva (1988) suggested a gnetophytalean affinity of those cones based on the studied epidermal features of the peltate sporangiophore head and extracted pollen grains.

The cones possess helically arranged sporangiophores. The sporangiophore consists of a thin central stalk terminating in a pentagonal or hexagonal thickly cutinized peltate head (apex). Sporangia are born on the adaxial side of the peltate head. They contain medium-sized monosulcate pollen grains.

Determining the systematic affinities of *Aegianthus, Loricanthus* Krassilov et Bugdaeva (1999), and *Solaranthus* Zheng et Wang (2010), Deng et al. (2014) supposed that two last genera are younger synonyms of *Aegianthus.*

We have studied pollen cones of *Aegianthus* from three occurrences in the Irkutsk Coal Basin and their in situ pollen grains. Besides Ust'-Baley, pollen cones of *A. sibiricus* were found in the Tolstiy Mys locality. We designate a lectotype of *A. sibiricus*, since a holotype/lectotype was not indicated in the previous publications of this species (Heer, 1876, 1880; Prynada, 1962; Krassilov and Bugdaeva, 1988; Deng et al., 2014). An emended diagnosis is provided for this species.

A new species, *A. irkutensis* sp. nov., is described here based on the unique morphological and epidermal features of pollen cones from a third occurrence, the Idan locality (Irkutsk Basin).

Previously, the exine ultrastructure of in situ pollen grains from *Aegianthus* was studied only for the Ust'-Baley material (Tekleva et al., 2006). We obtained additional information on the morphology and exine ultrastructure of in situ pollen grains of the studied *Aegianthus*

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specimens, and compared the pollen grains under study with those of other *Aegianthus* species as well as with other similar pollen.

2. Material and methods

The material comes from three localities: Ust'-Baley (52°37′47″ N, 103°59′1″ E), Idan (2 km upstream the Ust'-Kuda settlement, near the mouth of the Idan creek valley, 52.438036°N, 104.149345°E), and Tolstiy Mys (52.773595°N, 103.729140°E, near the Usolye-Sibirskoye stream crossing), Irkutsk Coal Basin, Irkutsk oblast', south-west of East Siberia, Russia (Fig. 1).

The collections from the Irkutsk Coal Basin are kept at the Laboratory of Palaeobotany of the Komarov Botanical Institute of the Russian Academy of Sciences (BIN RAS, Saint Petersburg, Russia, collections BIN 6, 6a, and 1434) and at the Geological Institute of the Russian Academy of Sciences (GIN RAS, Moscow, Russia, collection GIN 165).

The plant-bearing sediments are outcrops of massive grayish yellow block sandstones with intercalating lenses of siltstones, carbonaceous mudstone, sandstones, and coal beds. These deposits are regarded as the lower part of the Prisayan Formation, which is dated as Aalenian based on the comparison between its plant assemblages and those from deposits of West Siberia, which are dated by the marine fauna (Kiritchkova et al., 2005, 2017).

The material studied in this paper consists of fragmentary pollen cones of *Aegianthus* and dispersed sporangiophores. In layers with fragments of *Aegianthus*, the following plant remains have been found: leaves of *Ginkgoites sibirica* (Heer) Seward, *Sphenobaiera czekanowskiana* (Heer) Florin, *Czekanowskia* sp., and samaras of *Heerala antiqua* (Heer) Krassilov in the Ust'-Baley locality; leaves of *G. celebris* (Kiritchkova) Kiritchkova, *G. sibirica*, *S. angarensis* Kiritchkova, Kostina et Nosova, *S. czekanowskiana*, *S. irkutensis* Kiritchkova, Kostina et Nosova, samaras of *H. antiqua*, and microstrobili of *Ixostrobus heeri* Prynada in the Tolstiy Mys locality; leaves of *G. heeri* Doludenko et Rasskazova, *S. vigentis* Kiritchkova et Batjaeva, pollen cones of *Schidolepium gracile* Heer, female reproductive structures of *Karkenia irkutensis* Nosova, and seeds of *Allicospermum* sp. in the Idan locality (Kiritchkova et al., 2020; Nosova et al., 2017, 2021).

Ten specimens (BIN 6/2, BIN 6/4, BIN 6a/9, BIN 1434/455, BIN 1434/520, BIN 1434/641, GIN 165/66, GIN 165/111, GIN 165/124) from Ust'-Baley, four specimens (BIN 1434/20a-49, BIN 1434/21-49, BIN 1434/22-49, BIN 1434/23-49) from Tolstiy Mys, and eight specimens (BIN 1434/801, BIN 1434/860-2, BIN 1434/862-1, BIN 1434/863-1, BIN 1434/864-2b, BIN 1434/869k, BIN 1434/891, BIN 1434/903-5) from Idan were studied. Pollen grains were extracted from the specimens BIN 1434/520, BIN 1434/22-49, BIN 1434/23-49, BIN 1434/860-2, BIN 1434/862-1, and BIN 1434/864-2b. Pollen grains from spec. BIN1434/864-2b were studied using scanning electron microscopy (SEM), and from specs. BIN 1434/520, BIN 1434/862-1, and BIN 1434/2249 using transmitted light (LM), SEM and the transmission electron (TEM) microscopy. More than 50 pollen grains were studied under LM and SEM, from which 13 – under TEM, from the Ust'-Baley locality. Four pollen grains were studied under LM and SEM, two – under TEM from the Tolstiy Mys locality. Twenty pollen grains were studied in LM, 18 – in SEM, 9 – in TEM from the Idan locality.

The samples were cleaned with HF for about one day, followed by maceration in Schulze's reagent (HNO_3 catalyzed with $KClO_3$) for about 1 h. Then the material was rinsed with water, and then treated in 10% solution of KOH for a few minutes.

Hand specimens were photographed with a Canon EOS-60D digital camera. Details were taken using a Stemi 2000-CS stereomicroscope equipped with a Lomo Microsystems MC-16 camera. The prepared

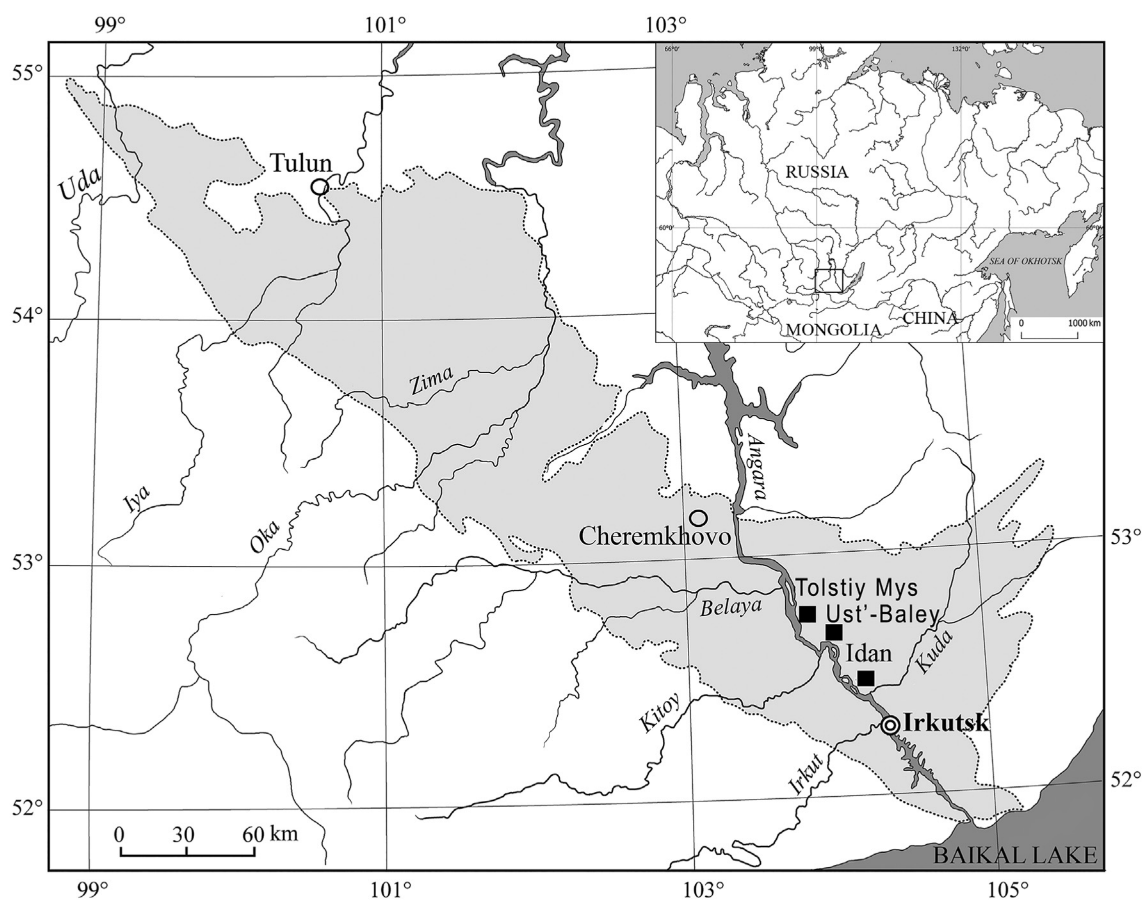


Fig. 1. Map of the Irkutsk Coal Basin (East Siberia) showing the Idan, Ust'-Baley, and Tolstiy Mys localities.

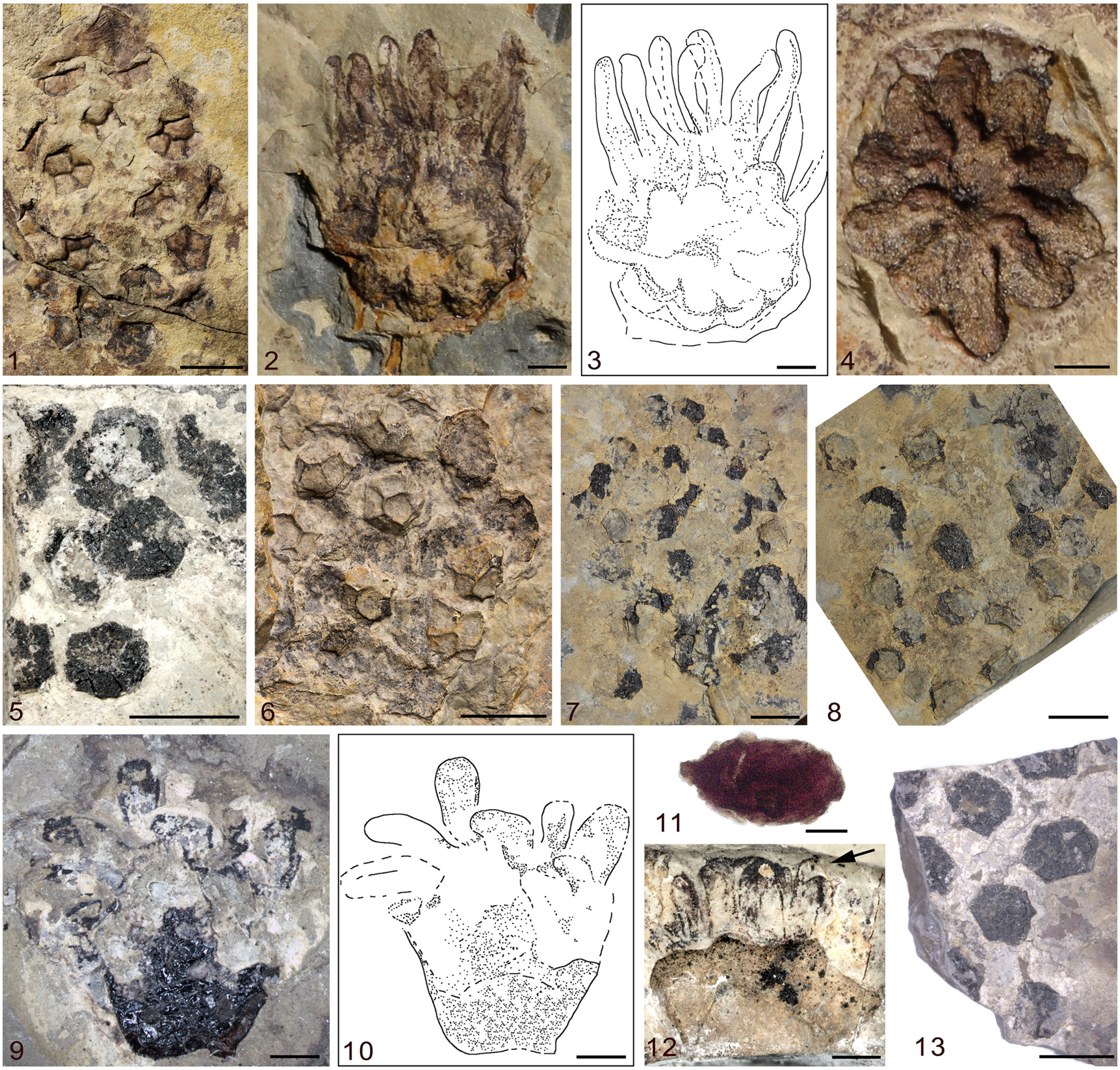


Plate I. *Aegianthus sibiricus* (Heer) Krassilov from the Middle Jurassic of the Irkutsk Coal Basin (1–6, 12, 13 – Ust'-Baley locality; 7–11 – Tolstiy Mys locality), East Siberia, Russia:
1 – pollen cone; 2, 3 – sporangiophore with pending sporangia and their line drawing; 4 – sporangiophore with sporangia facing to the center of the peltate head; 5–8, 13 – fragments of the pollen cones; 9, 10 – sporangiophore with sporangia and their line drawing; 11 – resin body; 12 – sporangiophore with partially broken sporangia (arrow)
Specimen numbers: 1 – spec. GIN 165/66 (lectotype); 2, 3 – spec. GIN 165/124; 4 – spec. GIN 165/111; 5, 11 – spec. BIN 1434/641; 6 – spec. BIN 6/4; 7 – spec. BIN 1434/21–49; 8 – spec. BIN 1434/23–49; 9, 10 – spec. BIN 1434/22–49; 12 – spec. BIN 6a/9; 13 – spec. BIN 1434/520.
Scale bars: 1, 5–8, 13–5 mm, 2–4, 9, 10, 12–1 mm; 11–50 μm.
Photos on the figs. 1, 2 and 4 by Elena Kostina (GIN RAS).

cuticles were examined and photographed using Carl Zeiss Axio Scope A1 light microscope equipped with a Lomo Microsystems MC-16 camera, a Jeol JSM–6390LA scanning electron microscope at the Core Facility Center "Cell and Molecular Technologies in Plant Science" at the BIN RAS (Saint Petersburg, Russia).

Glycerine slides of individual pollen grains were prepared and the pollen grains were photographed with a Carl Zeiss Axioplan-2 light microscope equipped with a 100× oil immersion objective and with a 40× objective and an AxioCam 105 digital camera at the A.A. Borissiak Paleontological Institute, Russian Academy of Sciences (PIN RAS). Pollen grains from Ust'-Baley were examined and images were taken using a Nikon Eclipse Ci (Nikon, Tokyo, Japan) microscope equipped with a Nikon DS-Vi1 digital camera at Lomonosov Moscow State University.

Individual pollen grains and pollen clumps were washed in hot water and ethanol and transferred to a piece of photographic film for SEM studies. The film was mounted on an aluminum stub (glued with nail polish) and sputter coated with gold and palladium mixture or with gold mixture for 6 or 8 min. The pollen grains were observed and photographed under a Tescan Vega-III XMU SEM with an accelerating voltage of 10, 20 and 30 kV at PIN RAS.

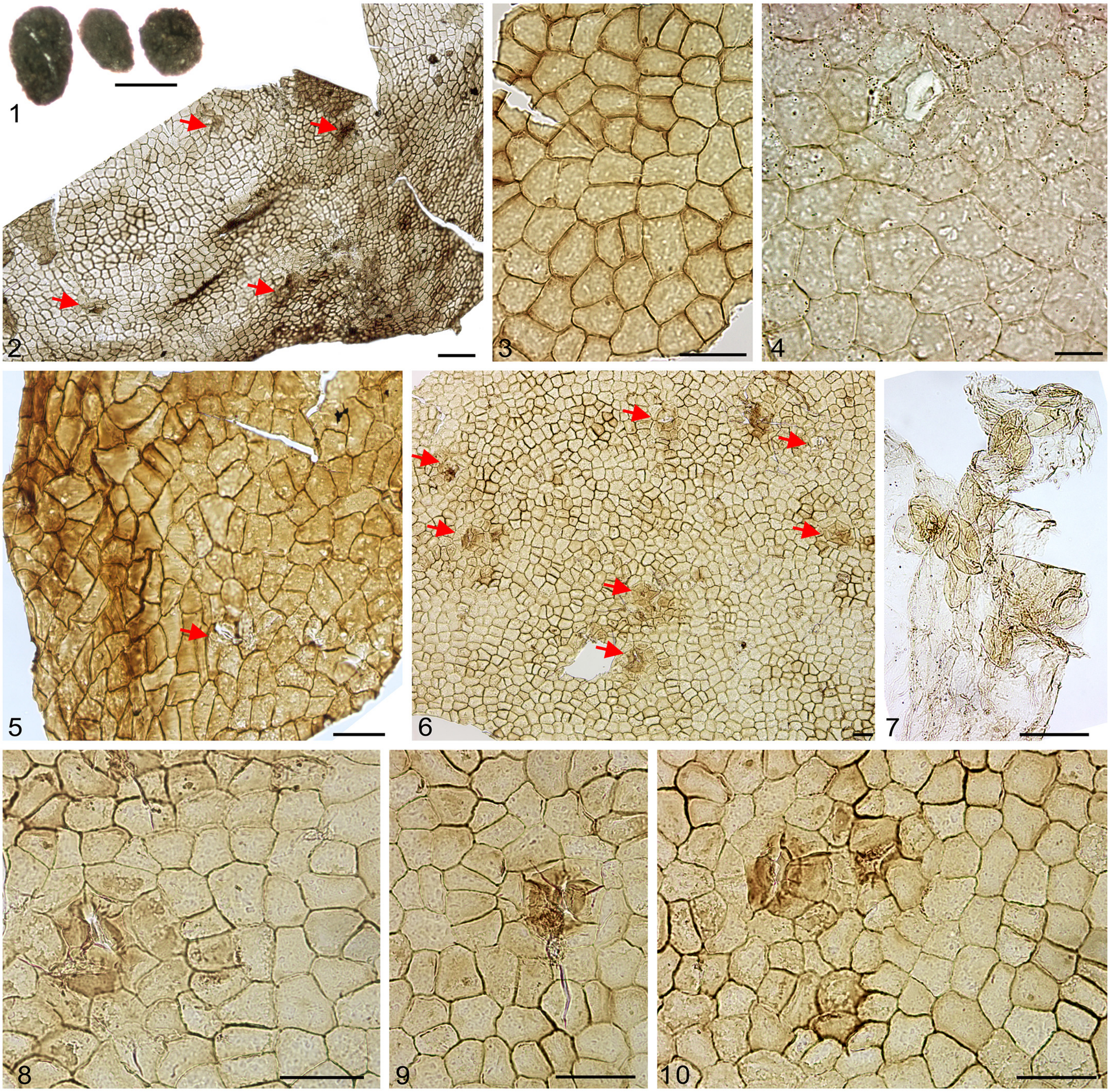


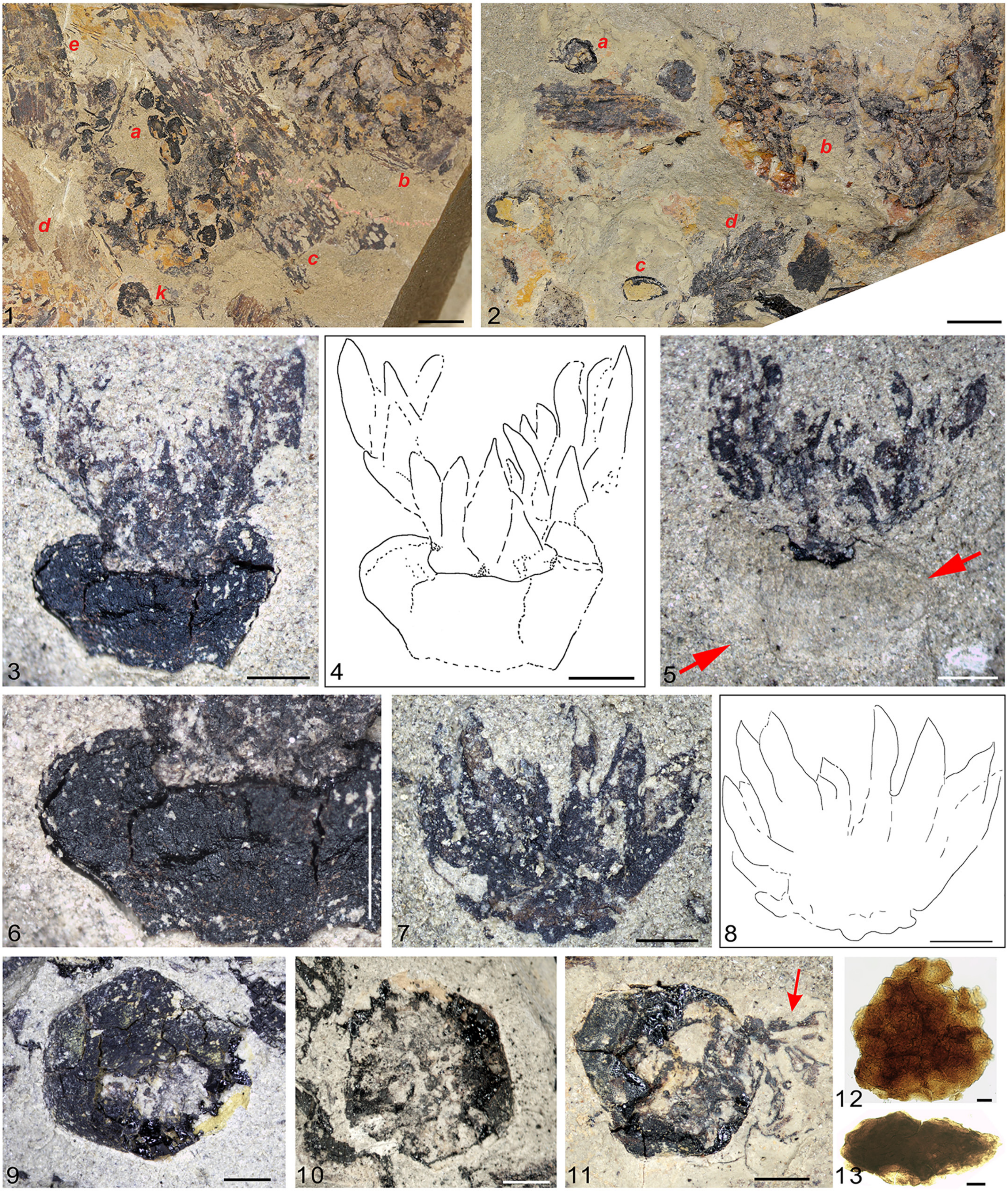
Plate II. *Aegianthus sibiricus* (Heer) Krassilov from the Middle Jurassic of the Irkutsk Coal Basin (1, 4–10 – Tolstiy Mys locality; 2, 3 – Ust'-Baley locality), East Siberia, Russia: 1 – resin bodies; 2–6, 8–10 – cells and stomata (arrows at figs. 2, 5, 6) of the outer epidermis; 7 – pollen grains and sporangia cuticle
Specimen numbers: 1, 6–10 – spec. BIN 1434/23–49; 2 – spec. BIN 1434/520; 3 – spec. BIN 1434/641; 4 – spec. BIN 1434/21–49; 5 – spec. BIN 1434/22–49.
Scale bars: 1–500 μm; 2–100 μm; 3–10 – 50 μm.

For TEM analyses, pollen grains were embedded in epoxy resin as described by Zavialova et al. (2018). The pollen grains were sectioned with a Leica EMUC6 ultramicrotome equipped with a diamond knife in 70-nm ultrathin sections. The ultrathin sections were examined under a Jeol 100B and Jeol 1011 TEM with an accelerating voltage of 80 kV at the Laboratory of Electron Microscopy, Biological Faculty, Lomonosov Moscow State University. The Jeol 1011 TEM was equipped with a side-mounted Orius SC1000W digital camera (11 megapixels, effective 8.5 megapixels); Digital Micrograph v. 2.0 (Gatan) software was used for image processing.

3. Systematic descriptions

3.1. Pollen cones

Genus: **Aegianthus** Krassilov, in Krassilov and Bugdaeva, 1988
Species: Aegianthus sibiricus (Heer) Krassilov, in Krassilov and Bugdaeva, 1988, here emended.
Plates I; II; V, figs. 1–10, 13–15; VI; VIII; IX, figs. 1, 2
Synonymy and selected references: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1876 *Kaidacarpum sibiricum* Heer – Heer, p. 84, pl. XV, figs. 10–12, 14–16.

1878 *Kaidacarpum sibiricum* Heer – Heer, p. 92, pl. XV, figs. 10–12, 14–16.

1876 *Kaidacarpum stellatum* Heer – Heer, p. 85, pl. XV, fig. 19.

1878 *Kaidacarpum sibiricum* Heer – Heer, p. 94, pl. XV, figs. 10–12, 14–16.

1880 *Kaidacarpum sibiricum* Heer – Heer, p. 29, pl. I, fig. 4b; pl. IX, figs. 6a, c.

1962 *Equisetostachys sibiricus* (Heer) Prynada – Prynada, p. 147, pl. XII, figs. 5–8.

1988 *Aegianthus sibiricus* (Heer) Krassilov – Krassilov and Bugdaeva, p. 369, pl. VII–IX.

2006 *Aegianthus sibiricus* (Heer) Krassilov – Tekleva, Krassilov, Kvacek, van Konijnenburg-van Cittert, p. 139, pl. III, figs. 1–5.

2014 *Aegianthus sibiricus* (Heer) Krassilov – Deng, Hilton, Glasspool, and Dejax, p. 1012.

Lectotype: Coll. GIN 165, spec. 66, Heer, 1876, p. 84, pl. XV, fig. 10; Plate I, fig. 1 designated here.

Type locality and age: Ust'-Baley locality, Irkutsk Coal Basin, East Siberia, Russia; lower part of the Prisayan Formation, Aalenian, Middle Jurassic.

Other locality and strata: Tolstiy Mys locality, Irkutsk Coal Basin, East Siberia, Russia; lower part of the Prisayan Formation, Aalenian, Middle Jurassic.

Material studied: Coll. GIN 165, specs. 66 (lectotype), 111, 124; coll. BIN 6, specs. 2, 4; coll. BIN 6a, spec. 9; coll. BIN 1434, specs. 455, 520, 641, 20a-49, 21–49, 22–49, 23–49.

Emended diagnosis: Cone elliptical in outline. Sporangiophores helically arranged, each with a peltate head (apex). Peltate head pentagonal to hexagonal in outline, and comprises a pentagonal to hexagonal central facet surrounded by 5–6 polygonal to trapezoidal lateral facets, separated by prominent ridges. Sporangiophores containing ellipsoid resin bodies. Outer epidermal cells of the peltate head polygonal, with smooth periclinal walls. Stomatal complexes with 6–8 subsidiary cells lacking papillae. 10–12 sporangia born on adaxial side of the peltate head. Sporangia elongated, with rounded apex. Pollen medium-sized, boat-shaped, monosulcate, with psilate to scabrate surface.

Description: see Krassilov and Bugdaeva, p. 369.

Remarks. We provide the emended diagnosis based on the previously emended diagnosis by Deng et al., (2014) and taking into account the results of our study of material from the type locality (Plate I, 1–6, 11, 12). Also, we have designated *Aegianthus sibiricus* from the Tolstiy Mys locality (Plate I, 7–10).

Maceration of the sporangiophores from both Ust'-Baley type locality and Tolstiy Mys locality yields small resin bodies (Plate I, 11; Plate II, 1). The resin bodies are ellipsoid, 330–800 μm long and 290–480 μm wide. Previously, *Aegianthus sibiricus* was described lacking any resin bodies (Krassilov and Bugdaeva, 1988).

Peltate heads of the sporangiophores consist of a pentagonal to hexagonal central facet surrounded by lateral facets (Plate I, 1, 6). We observe a small oval depression in the center of the peltate sporangiophore head and assume that it may represent a place (attachment scar) where the stalk was attached (Plate I, 2, 4).

Sporangia are born on the adaxial side of the peltate head and surround the stalk. According to Krassilov there is one sporangium per a lateral facet (Krassilov and Bugdaeva, 1988). In Ust'-Baley, we have found nine pendant sporangia in one sporangiophore (Plate I, 2) and ten sporangia facing to the center of the peltate head and adpressing to its adaxial surface in another sporangiophore (Plate I, 4). Based on this, we assume that there are two sporangia per a lateral facet and that means there are 10–12 sporangia per sporangiophore. The dimensions of the visible part of sporangia are 0.6–0.9 mm wide and 2–3 mm long. This length of the sporangia is equal to or less than the height of the lateral facets (Plate I, 2, 9). The sporangia have a rounded apex.

All studied specimens are characterized by smooth periclinal epidermal cell walls lacking any papillae (Plate II, 2–6, 8–10). According to the first description of *A. sibiricus*, periclinal cell walls of the outer epidermis are "thickened in the middle or even indistinctly papillate" (Krassilov and Bugdaeva, 1988). We did not find any thickenings or papillae at the epidermal cells, as well as at the figures of *A. sibiricus* in Krassilov and Bugdaeva (1988). Subsidiary cells of the stomata also lack papillae (Plate II, 4, 8–10). According to Krassilov and Bugdaeva (1988), the central facet has no more than 2–3 stomata, but we discovered more numerous stomata in this facet in some samples (Plate II, 6).

Pollen grains were extracted from *A. sibiricus* both from Ust'-Baley and Tolstiy Mys localities (Plate II, 7; Plate V, 1–10, 13–15; Plates VI, VIII; Plate IX, 1, 2). A description of the pollen grains is given in the chapter *3.2. Pollen grains*.

Species: Aegianthus irkutensis Nosova, sp. nov.

Plates III; IV; V, figs. 11, 12; VII; IX, figs. 3–6

Etymology: From the Irkut River.

Holotype: Coll. BIN 1434, spec. 862-1; Plate III, 3 designated here.

Type locality and age: Idan locality, Irkutsk Coal Basin, East Siberia, Russia; lower part of the Prisayan Formation, Aalenian, Middle Jurassic.

Material studied: Coll. BIN 1434, specs. 801, 860-2, 862-1 (holotype), 863-1, 864-2b, 869k, 891, 903-5.

Diagnosis: Sporangiophores with a peltate head comprised a hexagonal to pentagonal central facet surrounded by trapezoidal concave lateral facets. Sporangiophores containing ellipsoid resin bodies. Outer (abaxial) cuticle of the peltate sporangiophore head thick, inner (adaxial) cuticle thin. Outer epidermal cells square to polygonal, papillate; inner epidermal cells large, polygonal. Subsidiary cells of the stomatal complexes with papillae. Sporangia (>12) born on adaxial side of the peltate head, assembled in a sheaf. Sporangia elongated, two times longer than lateral facets, with acute apex. Pollen boat-shaped, monosulcate, with psilate to scabrate surface.

Description: The studied material includes detached sporangiophores preserved in different positions: (1) revealing only the abaxial features of the peltate sporangiophore head (Plate III, 1, 9, 10), (2) an oblique view of the peltate head (Plate III, 2, 11), (3) sporangia and lateral facets of the peltate head are visible (Plate III, 3–6). The peltate

Plate III. *Aegianthus irkutensis* Nosova, sp. nov. from the Middle Jurassic of the Idan locality in the Irkutsk Coal Basin, East Siberia, Russia:
1 – peltate sporangiophore of *A. irkutensis* (k), two partially broken ovule-bearing structures of *Karkenia irkutensis* Nosova (a, b) and leaf fragments of *Sphenobaiera vigentis* Kiritchkova et Batjaeva (c, d);
2 – peltate sporangiophore of *A. irkutensis* (a), partially broken ovule-bearing structure of *Karkenia irkutensis* (b), seed of *Allicospermum* sp. (c) and pollen cone of *Schidolepium gracile* Heer (d);
3, 4 – sporangiophore with elongated sporangia and their line drawing;
5 – counterpart of the sporangiophore from fig. 3 showing elongated sporangia and fuzzy imprint of the microsporangiate head (red arrows);
6 – detail of lateral facets of the microsporangiate head enlarged from fig. 3;
7, 8 – sheaf of sporangia with line drawing;
9, 10 – peltate sporangiophores;
11 – peltate sporangiophore with partially preserved sporangia (arrow) enlarged from fig. 2a
12, 13 – resin bodies.
Specimen numbers: 1 – spec. BIN 1434/869; 2, 11 – spec. BIN 1434/903 (2a and 11 – spec. BIN 1434/903–5); 3, 4, 6, 12 – spec. BIN 1434/862–1 (holotype); 5 – spec. BIN 1434/863–1 (counterpart of spec. BIN 1434/862–1); 7, 8 – spec. BIN 1434/864-2b; 9, 10, 13 – spec. BIN 1434/891.
Scale bars: 1, 2–5 mm; 3–11 – 1 mm; 12, 13–50 μm.

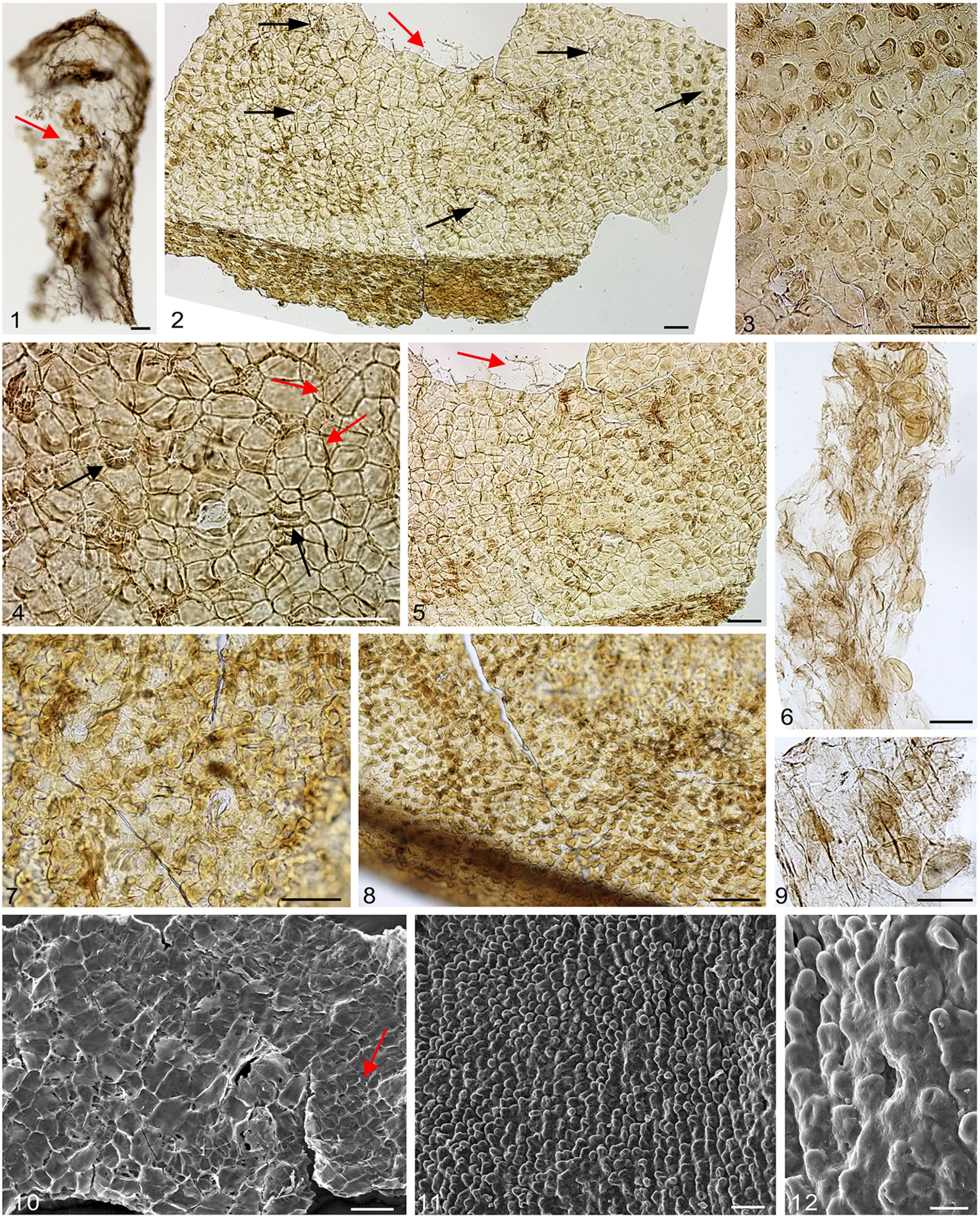

Plate IV. *Aegianthus irkutensis* Nosova, sp. nov. from the Middle Jurassic of the Idan locality in the Irkutsk Coal Basin, East Siberia, Russia:
1 – sporangia cuticle with pollen grains (arrow); 2 – outer and inner (red arrow) cuticles of the lateral facet and stomata (black arrows); 3, 7, 8 – cells and stomata of the outer epidermis; 4 – cells (red arrows) of the inner epidermis, and cells, idioblasts (black arrows) and stoma of the outer epidermis, 5 – cells and stoma of the outer epidermis and cells (arrow) of the inner epidermis; 6, 9 – pollen grains and sporangia cuticle; 10 – internal view of the inner (left side) and outer (arrow) cuticles, SEM; 11 – external view of the outer cuticle, SEM; 12 – external view of stoma, SEM
Specimen numbers: 1 – spec. BIN 1434/864-2b; 2–5 – spec. BIN 1434/903–5; 6, 7 – spec. BIN 1434/862–1 (holotype); 8–12 – spec. BIN 1434/891.
Scale bars: 1–11 – 50 μm; 12–20 μm.

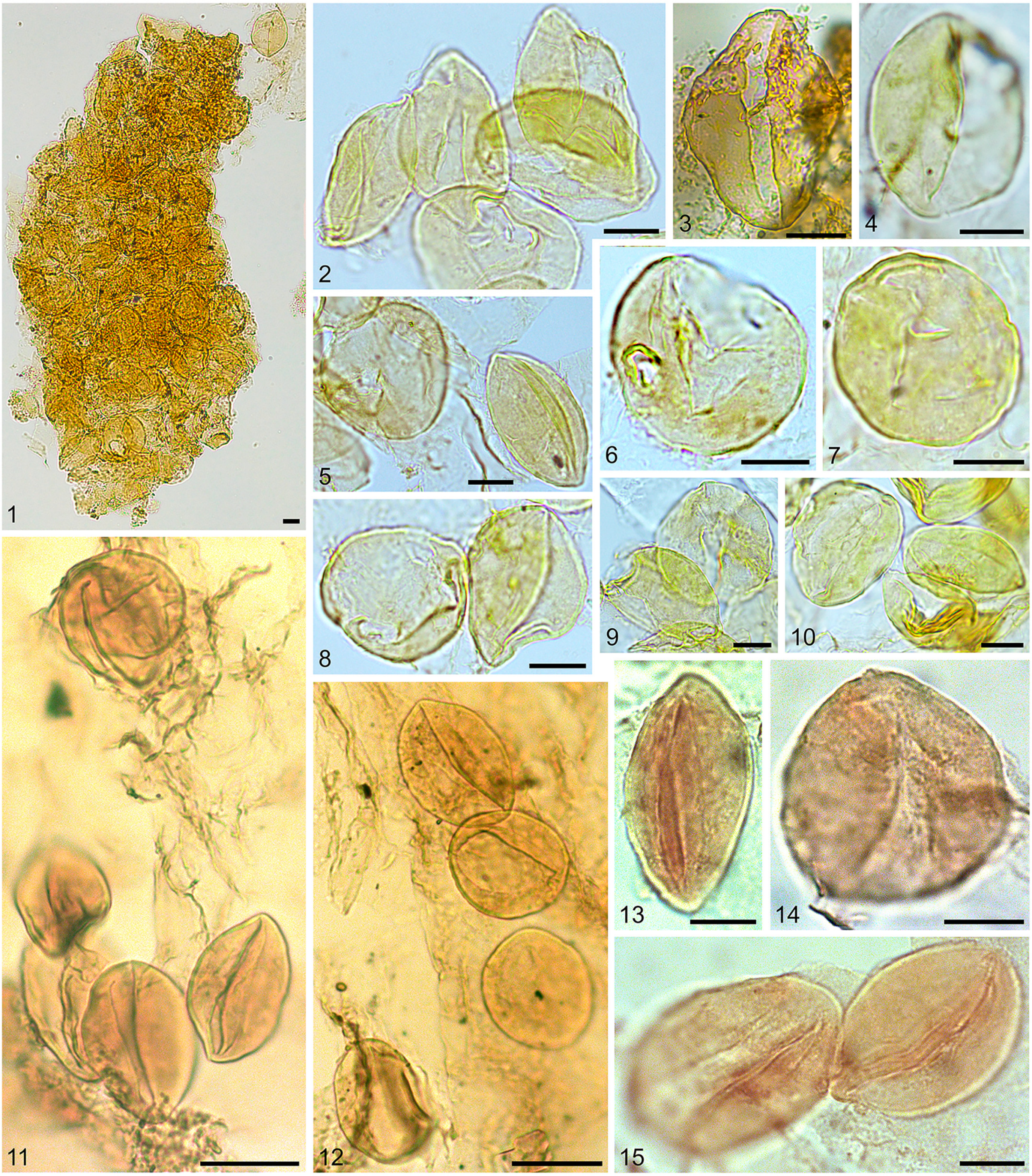

Plate V. *Aegianthus sibiricus* (Heer) Krassilov from the Middle Jurassic of the Irkutsk Coal Basin (1–10 – Ust'-Baley locality; 13–15 – Tolstiy Mys locality), and *A. irkutensis* Nosova, sp. nov. from the Middle Jurassic of the Idan locality (11, 12) in the Irkutsk Coal Basin, East Siberia, Russia, LM:
1, 2, 5, 8–12, 15 – cluster of pollen grains in a sporangial cuticle; 3, 4, 13, 14 – individual pollen grains, distal view; 6, 7 – individual pollen grains, lateral view.
Specimen numbers: 1–10 – spec. BIN 1434/520; 11, 12 – spec. BIN 1434/862-1; 13–15 – spec. BIN 1434/22-49.
Scale bars: 1–10, 13–15 – 10 μm; 11, 12–20 μm.

Table 1
Comparison between the species of *Aegianthus.*

	A. phialophora	*A. daohugouensis*	*A. sibiricus*	*A. irkutensis* sp. nov.	*A. hailarensis*	*A. resinifer*
Size of pollen cone (in mm)	70 long	22 × 57	10–22 × 20–50	?	30–40 × 50	20 × 50
Outer diameter of peltate head (in mm)	2	4–4.5	4–5.5	3.5–4	4–5	7
Sporangia number	numerous	>12 (after the photo)	10–12	>12	?	10
Sporangia size (in mm)	0.4 × 1.5	0.6–0.9 × 1.5–2.7	0.6–0.9 × 2–3	0.4–0.6 × 3–4.5	?	0.3 × 3
Size of resin bodies (in μm)	400–1000	350–880 × 500–1400	350–480 × 470–800	126–457 × 197–510	300–500	600–800
Papillae on the epidermal cells	+	+	–	+	+, some adjacent papillae unite to form tuberculate or verrucate papillae	+
Stomatal complexes	With papillae	?	Lack papillae	With papillae	With papillae	With small papillae
Pollen size (in μm)	40 × 25–30	23–38 × 13–23	25–43 × 15–33	25–44 × 15–29	25–30 × 15–20	17–19.5 in diameter
Associated leaves	*Sphenobaiera spectabilis*	?	*Sphenobaiera czekanowskiana*	*Sphenobaiera vigentis*	*Sphenobaiera longifolia*	*Sphenobaiera vitimica*
Age	Early Jurassic	Middle Jurassic	Middle Jurassic	Middle Jurassic	Early Cretaceous	Early Cretaceous
Locality	Greenland	Daohugou locality, Inner Mongolia, China	Ust'-Baley and Tolstiy Mys localities, Irkutsk Basin, Russia	Idan locality, Irkutsk Basin, Russia	Hailar Basin, Inner Mongolia, China	Transbaikalia, Russia
Reference(s)	Harris, 1935; van Konijnenburg-van Cittert, 1993; Deng et al., 2014	Zheng and Wang, 2010; Deng et al., 2014	Krassilov and Bugdaeva, 1988; Tekleva et al., 2006; Deng et al., 2014; present paper	Present paper	Deng et al., 2014	Krassilov and Bugdaeva, 1999; Tekleva and Krassilov, 2004; Tekleva et al., 2006; Deng et al., 2014

heads comprise a pentagonal to hexagonal central facet surrounded by 5–6 trapezoidal concave lateral facets (Plate III, 3, 4, 6, 9–11). The peltate heads are 3.5–4 mm in diameter; the lateral facets are 1.5 × 1.7 × 2.5 mm. Maceration of the sporangiophore yields ellipsoid resin bodies, 126–457 × 197–510 μm (Plate III, 12, 13).

The outer (abaxial) cuticle of the sporangiophore head is thick, the inner (adaxial) cuticle is thin. The cells of the outer epidermis are short, tetra- to polygonal, measuring e.g., 10 × 25 μm, 18 × 30 μm, and 20 × 37 μm. Most cells have hollow papillae, 12–18 μm in diameter (Plate IV, 2–5, 7–8, 11, 12). The anticlinal cell walls are straight. Stomata are not numerous (Plate IV, 2). Stomatal complexes are with 5–7 subsidiary cells having proximal papillae (Plate IV, 3–5, 7, 12). Several idioblasts occur in the outer epidermis (Plate IV, 4). The cells of the inner epidermis are polygonal, much larger than the cells of the outer epidermis, measuring e.g., 35 × 84 μm, 47 × 54 μm, and 55 × 80 μm (Plate IV, 2, 4, 5, 10). Their anticlinal cell walls are straight, the periclinal walls are smooth.

Sporangia are born on the adaxial side of the peltate sporangiophore head, assembled in a sheaf (>12, up to 18?), but the mode of their attachment to the microsporophyll is unclear (Plate III, 3–5, 7, 8). Sporangia are elongated, with an acute apex. They are two times longer than lateral facets. The dimensions of the visible part of the sporangia are 0.4–0.6 × 3–4.5 μm.

Maceration yields a thin cuticle of the sporangia and clumps of pollen grains (Plate IV, 1, 6, 9; Plate V, 11, 12). A description of the pollen grains is given in the chapter *3.2. Pollen grains*.

Comparison: Five species were placed in the genus *Aegianthus* by Deng et al., 2014 (Table 1): *A. sibiricus, A. resinifer* (Krassilov et Bugdaeva) Hilton, Glasspool, Deng et Dejax (=*Loricanthus resinifer* Krassilov and Bugdaeva, 1999), *A. phialophora* (Harris) Hilton, Glasspool, Deng et Dejax (=*Bernettia phialophora* Harris, 1935), *A. hailarensis* (Deng, Ren et Chen) Deng, Glasspool, Hilton et Dejax (=*Ixostrobus hailarensis* Deng et al., 1997), and *A. daohugouensis* (Zheng et Wang) Hilton, Glasspool, Deng et Dejax (=*Solaranthus daohugouensis* Zheng and Wang, 2010).

Sporangiophores of the new species differ from those of *A. sibiricus* from the same Prisayan Formation in having more numerous, longer and narrower sporangia with an acute apex. Unlike *A. sibiricus,* the cells of the outer epidermis of *A. irkutensis* are strongly papillate. The pollen grains of *A. irkutensis* are similar to those of *A. sibiricus* in the morphology and ultrastructure (see *3.2. Pollen grains*).

Besides *A. sibiricus,* all other species of *Aegianthus* are characterized by papillate cells of the outer epidermis of the peltate head (Table 1). *A. irkutensis* differs from other species of *Aegianthus* by smaller resin bodies, numerous and longer sporangia. Comparison of the pollen grains is given in the chapter **4. Discussion**.

3.2. Pollen grains

Here we brought a generalized description of the pollen grains from three localities as they are almost indistinguishable from each other. Pollen grains are boat-shaped, monosulcate, with a long and often widely open sulcus (Plate V, 2–12). In the light microscope (LM) the exine surface is psilate or scabrate (Plate V), in SEM the exine surface is scabrate to granulate, with rare perforations (Plates VI, VII). The polar axis varies from 15.2 to 32.9 μm in LM, from 15.8–32.1 μm in SEM, the equatorial diameter – from 25.7 to 44 μm in LM and from 24.7 to 42.5 μm in SEM (Table 2). The sulcus length is from 21.4 to 38.8 μm in LM and from 22.1 to 37.4 μm in SEM. The aperture membrane is smooth with perforations and sometimes with rugulae/folds (Plate VI, 2, 4, 8, 9, Plate VII, 1).

In the non-apertural region the ectexine is from 0.34 to 0.97 μm thick, but mostly about 0.5–0.7 μm as seen under TEM; the thickness of the ectexine is irregularly non-uniform throughout the pollen perimeter (Plate VIII, 1–3, Plate IX, 1–3). The tectum is from 0.17 to 0.46 μm thick, often is hardly

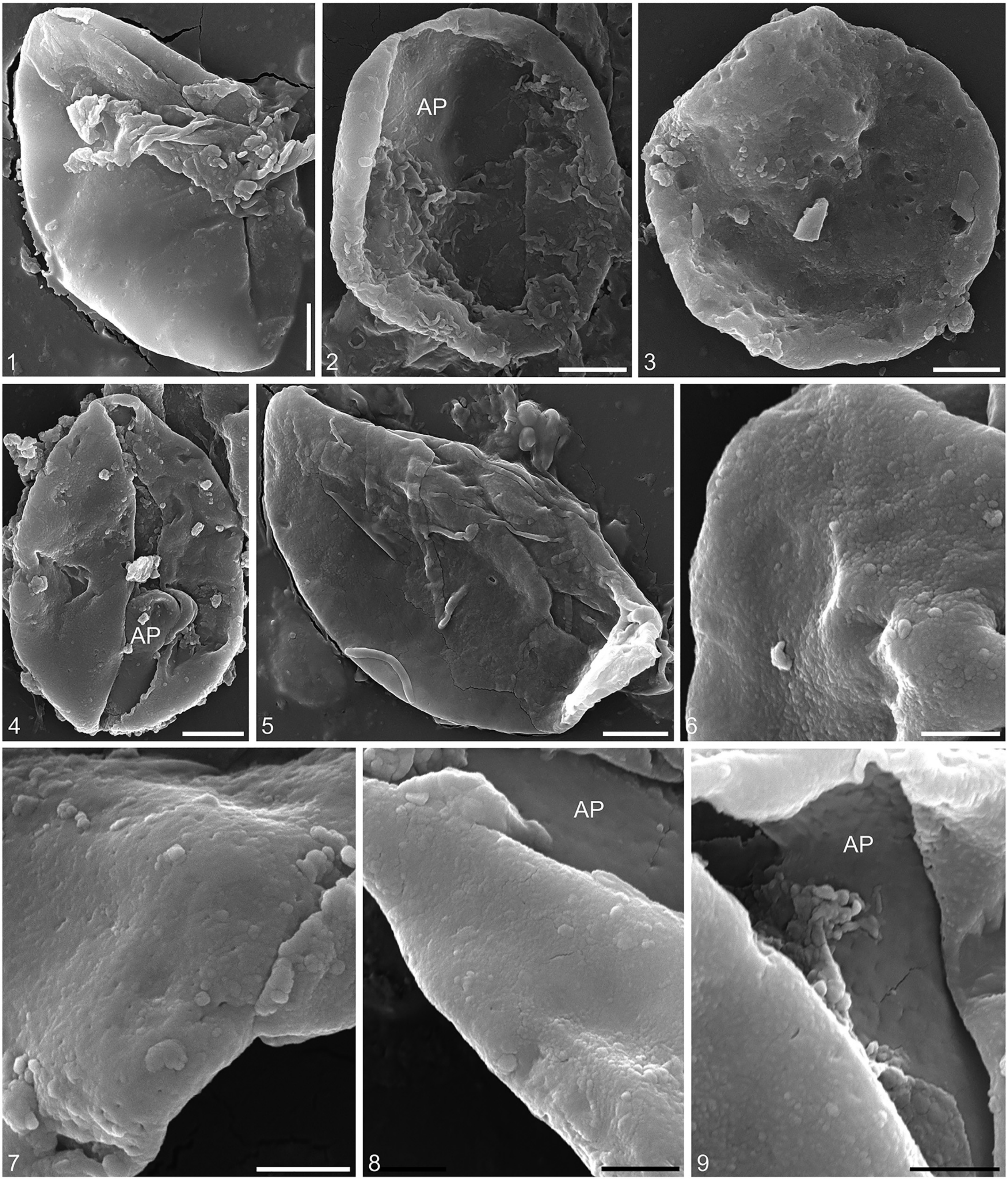

Plate VI. *Aegianthus sibiricus* (Heer) Krassilov from the Middle Jurassic of the Ust'-Baley locality in the Irkutsk Coal Basin, East Siberia, Russia, SEM:
1, 2, 4, 5 – pollen grain, distal view; 3 – pollen grain, proximal view; 6, 7 – close-up of a pollen; 8, 9 – details of apertural membrane.
AP – apertural region where sculpture of the apertural membrane is seen.
Specimen number: BIN 1434/520.
Scale bars: 1–5 – 5 μm; 6–9 – 2 μm.

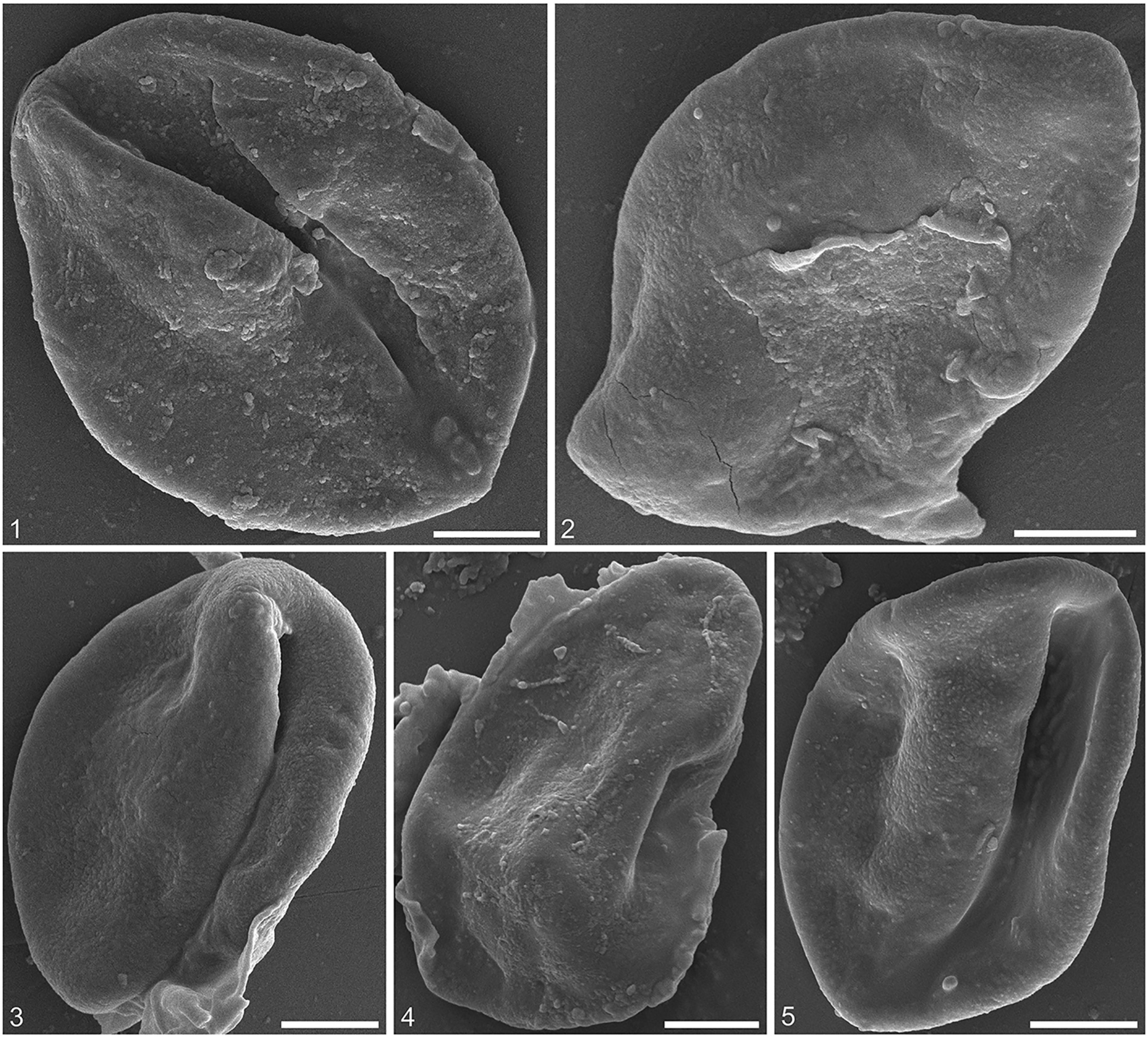

Plate VII. *Aegianthus irkutensis* Nosova, sp. nov. from the Middle Jurassic of the Idan locality in the Irkutsk Coal Basin, East Siberia, Russia, SEM:
1, 3, 5 – pollen grain, distal view; 2, 4 – pollen grain, proximal view.
Specimen number: spec. BIN 1434/862–1.
Scale bars 5 μm.

distinguishable from the infratectum (Plate VIII, 4–8, Plate IX, 4–7). The infratectum consists of large granules disposed in one or two rows or columella-like elements (Plate VIII, 4–8, Plate IX, 4–7); the infratectal elements are about 0.1–0.56 × 0.16–0.52 μm high. The foot layer is discontinuous, from 0.01 to 0.14 μm. The endexine is less electron dense, from 0.01 to 0.13 (rare to 0.21) μm, homogeneous, most probably its structure is destroyed due to the fossilization. Toward the apertural region, the ectexine sharply reduces and in the apertural region the exine is represented by a thin ectexine layer and endexine (Plate VIII, 1–4, 7, Plate IX, 1–4, 6); the endexine does not thicken toward and in the apertural region.

4. Discussion

Including *Aegianthus irkutensis*, there are six species of *Aegianthus* described so far (Table 1). All these species have more or less similar gross morphology. Key features for the reliable delimitation of them appear to be a combination of the dimensions of the peltate sporangiophore heads; epidermal features; shape, size and number of sporangia; and an exine structure of in situ pollen grains.

4.1. Comparison of pollen morphology and ultrastructure of the studied Aegianthus species and similar pollen

The studied pollen grains of *Aegianthus sibiricus* from the Ust'-Baley and Tolstiy Mys localities and *A. irkutensis* from the Idan locality in the Irkutsk Coal Basin show quite similar morphology and ultrastructure (Table 2). There are some minor differences between individual pollen grains observed due to the abundance of the in situ material from Ust'-Baley. Also, there are some differences due to the preservation which appears slightly better from Tolstiy Mys. The endexine structure

Table 2
Pollen measurements in LM, SEM, and TEM of *Aegianthus sibiricus*, *A. irkutensis* sp. nov., and *A. resinifer*.

Species	*A. sibiricus*				*A. irkutensis* sp. nov.		*A. resinifer*
Region	Irkutsk Coal Basin, Siberia						Transbaikalia
Localities	Tolstiy Mys		Ust'-Baley		Idan		Baisa
Specimens	BIN 1434/22–49	BIN 1434/23–49	BIN 1434/520	–	BIN 1434/862–1	BIN 1434/864-2b	–
LM, polar axis, µm	19.5–26.7	16.7–27.7	18.3–32.9	20–26	15.2–25.2	21.3–24.1	–
LM, equatorial diameter, µm	29–37.6	29–43	31.3–42.9	30–42.5	25.7–36.2	30–44	–
LM, sulcus length, µm	24.3–31.9	–	25.4–38.8	–	21.4–32.4	–	–
SEM, polar axis, µm	19.2–25	–	16.4–32.1	20–26	15.8–22.7	19–29	17–19.5
SEM, equatorial diameter, µm	34.5–38.5	–	26.3–39.6	30–42.5	24.7–29.5	25.6–39.7	17–19.5
SEM, sulcus length, µm	31.1	–	23.3–37.4	–	22.1–27	19–36	–
Ectecxine, µm	0.5–0.97	–	0.5–0.82	0.7	0.34–0.89	–	0.8–1.2
Tectum, µm	0.21–0.46	–	0.17–0.21	0.26	0.22–0.37	–	0.2
Infratectum, µm	0.17–0.48 × 0.34–0.48	–	0.24–0.44 × 0.16–0.24	0.2–0.6 × 0.2–0.25	0.1–0.56 × 0.2–0.52	–	0.2–0.5 × 0.2–0.3
Foot layer, µm	0, 0.06–0.13	–	0, 0.01–0.14	Thin, discontinuous	0, 0.03–0.11	–	0.04–0.07, rare up to 0.17
Endexine, µm	0.07–0.11	–	0.01–0.03	0.06	0.03–0.13 (rare 0.21)	–	Lamellate, of five lamellae, 0.03 µm each
Reference(s)	Present paper	Present paper	Present paper	Krassilov and Bugdaeva, 1988; Tekleva et al., 2006	Present paper	Present paper	Krassilov and Bugdaeva, 1999; Tekleva and Krassilov, 2004; Tekleva et al., 2006

is similar in the studied pollen, however, its preservation is worse in pollen grains from Ust'-Baley. The exine thickness and its unevenness are the same in pollen grains from all three localities; however, in pollen grains from Tolstiy Mys the foot layer appears more distinct than that of the pollen grains in the other two localities. Pollen grains of *A. sibiricus* from Ust'-Baley, studied by Tekleva et al. (2006) are also of the same morphology and ultrastructure; the reported pollen size is slightly larger but this difference is inconsiderable.

Among other *Aegianthus* species (sensu Deng et al., 2014) pollen grains of *A. resinifer*, *A. daohugouensis,* and *A. hailarensis* were studied using LM and SEM, and the first two species were studied additionally with TEM. The morphology in LM and SEM and pollen size of these species are similar to the studied pollen. Zheng and Wang (2010) showed two small photos of exine parts for *A. daohugouensis* which are difficult to interpret; the indicated exine thickness is unbelievably small. The infratectum of elongated alveolae in one row might be assumed for this species, differing from the infratectum of the pollen under study. Pollen grains of *A. resinifer* show similar tectum thickness and infratectal structure, although the infratectal elements appear somewhat larger than those in the pollen under study. The foot layer in *A. resinifer* is similarly thin but uniform in thickness and continuous in contrast to our pollen. The endexine in *A. resinifer* is well preserved, rather thick and lamellated (Tekleva and Krassilov, 2004). The exine ultrastructure of other *Aegianthus* species was not studied so far.

The pollen grains under study show an infratectum composed of large granules and columella-like elements. Such an ultrastructure is found in ginkgoalean and some gnetophytalean pollen (Friis and Pedersen, 1996; Tekleva et al., 2006; Tekleva and Krassilov, 2009; Zavialova and Nosova, 2019). In contrast, cycadalean pollen grains are characterized by an infratectum with an elongated thin alveolae and relatively thin tectum (Tekleva et al., 2007; Zavialova and van Konijnenburg-van Cittert, 2012, 2016).

Asaccate pollen grains with an infratectum of large granules or columella-like elements are known from several taxa, supposedly related to gnetophytes (at least, by some authors). Among those, dispersed pollen of two *Eucommiidites* Erdtman species from the Early Cretaceous of Italy and Jurassic of England (Trevisan, 1980; Zavada, 1984) and in situ pollen of *Eucommiitheca hirsuta* Friis et Pedersen from the Early Cretaceous of Portugal (Friis and Pedersen, 1996), *Aegianthus resinifer*, and *A. sibiricus* (Krassilov and Bugdaeva, 1988, 1999; Tekleva et al., 2006). Pollen grains of *Eucommiitheca hirsuta* differ from those under study in smaller, trisulcate pollen with thinner ectexine; the tectum portion in the ectexine is larger, and the infratectal elements are smaller in comparison to *A. sibiricus*/*A. irkutensis*. The infratectum structure of our material is somewhat similar to that in dispersed *Eucommiidites* sp. 1 by Trevisan (1980) and *Eucommiidites* sp. by Zavada (1984), but the pollen grains of these taxa differ from *A. sibiricus* in trisulcate aperture condition, and *Eucommiidites* sp. described by Zavada (1984) additionally differs in a thick endexine and supratectal layer.

Ultrastructural studies on pollen grains related to ginkgoaleans are few (Zavialova et al., 2011, 2014, 2016; Nosova et al., 2018; Zavialova and Nosova, 2019, 2021). In situ pollen grains are known from a pollen cone with unclear morphological features (Zavialova and Nosova, 2019) and from *Sorosaccus sibiricus* Prynada (Nosova et al., 2018; Zavialova and Nosova, in preparation) both from the Middle Jurassic of the Irkutsk Coal Basin, Russia. Pollen grains associated with ginkgoalean or supposedly ginkgoalean remains (seeds, leaves) were studied with LM, SEM, and TEM from the Middle Jurassic and the Early Cretaceous of Russia (Zavialova et al., 2011, 2014, 2016; Zavialova and Nosova, 2021). Most of those findings are similar to the pollen under study in the general morphology, pollen size, exine sculpture, and exine thickness. However, all those pollen grains differ from our material in a considerably larger proportion of the tectum and smaller proportion of the infratectum in the ectexine; the only exception is a pollen grain associated with *Ginkgo gomolitzkyana* Nosova (Zavialova et al., 2016) with an ultrastructure similar to that of *Aegianthus sibiricus*. Pollen grains from *Sorosaccus sibiricus* (Zavialova and Nosova, in preparation) differ both from our material and all supposedly ginkgoalean pollen studied ultrastructurally in the exine sculpture and sporoderm ultrastructure.

Pollen grains from the pollen organs of *Sahnia laxiphora* Drinnan et Chambers (Osborn et al., 1991) from the Early Cretaceous of Australia are similar or slightly smaller in the size, exine sculpture and thickness than those of *Aegianthus* from the Irkutsk Basin. The sporoderm differs from our material in a thicker tectum and thinner infratectum with smaller granules.

Three dispersed *Chasmatosporites* Nilsson species, *C. apertus* Nilsson, *C. hians* Nilsson, and *C. major* Nilsson, from the Early Jurassic of Denmark were studied with LM and TEM (Batten and Dutta, 1997) and show,

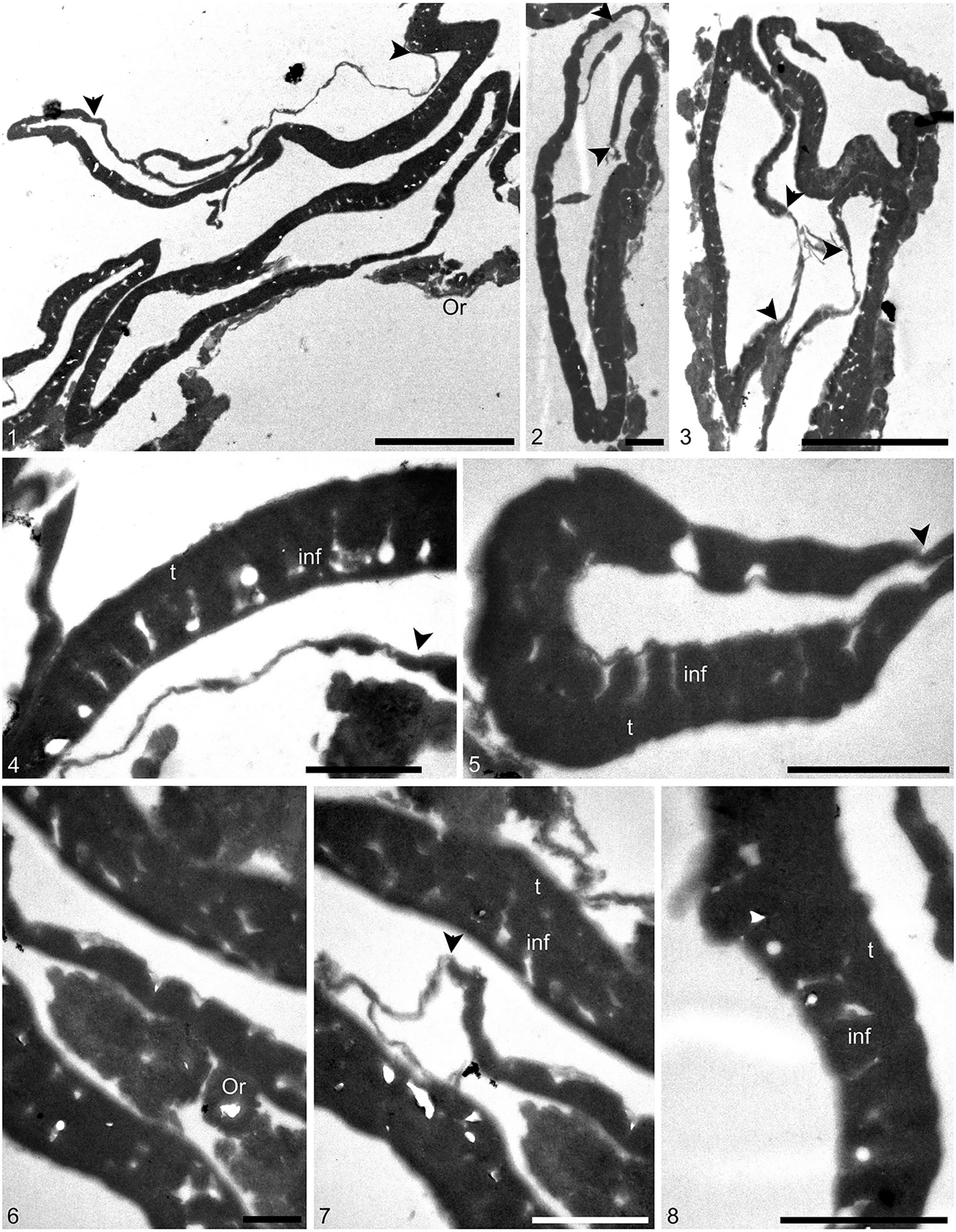

Plate VIII. *Aegianthus sibiricus* (Heer) Krassilov from the Middle Jurassic of the Ust'-Baley locality in the Irkutsk Coal Basin, East Siberia, Russia, TEM: 1–3 – pollen grains, whole sections; 4–8 – parts of non-apertural and apertural sporoderm regions showing granular/columella-like infratectum. Arrowheads indicate borders of the apertural region; arrow indicates foot layer; Or – orbicule, t – tectum, inf – infratectum, end – endexine.
Specimen number: spec. BIN 1434/520.
Scale bars: 1, 3–5 μm; 2, 4, 5, 7, 8–1 μm; 6–0.5 μm.

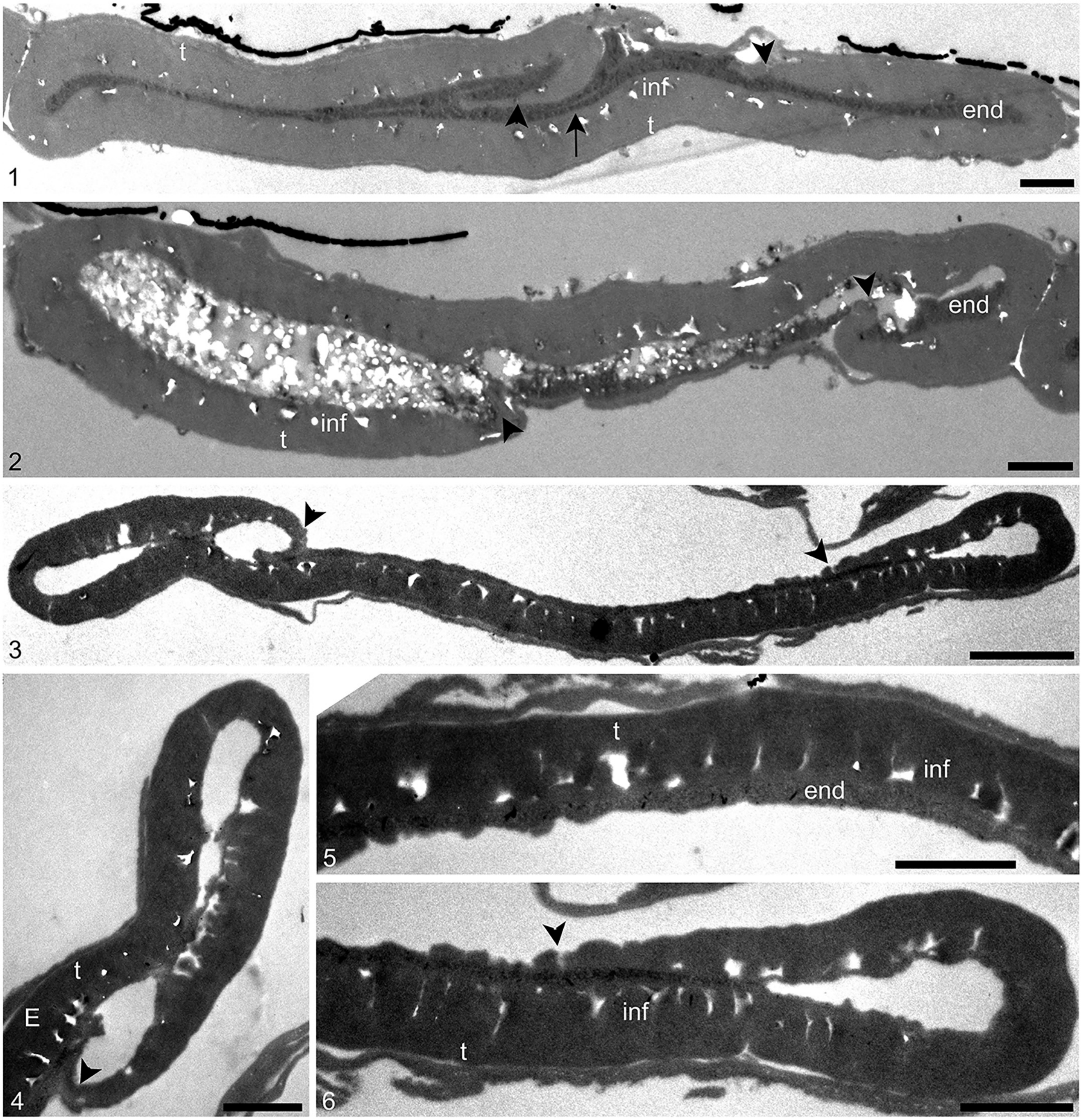

Plate IX. *Aegianthus sibiricus* (Heer) Krassilov from the Middle Jurassic of the Tolstiy Mys locality (1, 2) in the Irkutsk Coal Basin and *A. irkutensis* Nosova, sp. nov. from the Middle Jurassic of the Idan locality (3–6) in the Irkutsk Coal Basin, East Siberia, Russia, TEM:
1–3 – pollen grains, whole sections; 4–6 – parts of non-apertural and apertural sporoderm regions showing granular/columella-like infratectum.
Arrowheads indicate borders of the apertural region; arrow indicates foot layer; t – tectum, inf – infratectum, end – endexine.
Specimen numbers: 1, 2 – spec. BIN 1434/22–49; 3–6 – spec. BIN 1434/862–1.
Scale bars: 1, 2, 4–6 – 1 μm; 3–2 μm.

compared to our material, similar aperture condition, pollen size, and ectexine and endexine structure; the exine thickness is however reported to be twice as thick. In general, the ultrastructure of the *Chasmatosporites* species studied with TEM suggests their possible ginkgoalean affinity. Batten and Dutta (1997) also reported columella-like infratectum for dispersed *Spheripollenites psilatus* Couper, but a smaller size, aperture condition, regular pattern of the columella-like infratectal elements, and supratectal layer clearly distinguished this pollen type from the pollen under study. *S. scabratus* Couper studied from the Early Jurassic of Hungary by Kedves and Párdutz (1973) and illustrated also in Kedves (1990, 1994) has principally the same ultrastructure as *S. psilatus*.

4.2. Possible affinities of the pollen cones of Aegianthus

Krassilov and Bugdaeva (1988) suggested a relationship of *Aegianthus* with Gnetales sensu *lato* on account of its association with *Welwitschia*-like seed scales *Heerala* Krassilov. However, remains of *Heerala* are unknown in the other occurrences of *Aegianthus,* including the Idan locality of the Irkutsk Basin. The arrangement of the sporangia in *Aegianthus* on peltate sporangiophore heads is distinctly different from that in the Gnetales.

One of the main characters of *Aegianthus* pollen cones is the attachment of sporangia to the adaxial side of the peltate head where they surround the stalk of the sporangiophore. Sporangia are preserved facing to the center of the peltate head and adpressing to its adaxial surface or freely pendant. We agree with the opinion of Krassilov and Bugdaeva (1988) that a sporangiophore with such adpressed sporangia indicates to its unripe stage.

Similar structures of the sporangiophores are known in different plant groups, such as *Equisetum* L. (Equisetales), some Taxaceae (Coniferales), and the extinct Erdtmanithecales (Friis and Pedersen, 1996). However, unlike *Aegianthus,* the sporangiophore heads in those taxa lack lateral facets, and the sporangiophore stalk is quite thick. Besides this, the peltate sporangiophore heads of *Eucommiitheca* Pedersen, Crane et Friis (Erdtmanithecales) differ from those of *Aegianthus* by their smaller size (about 1.5 mm in diameter) and arrangement of sporangia in two whorls around the distal part of the stalk (Pedersen et al., 1989). According to Friis and Pedersen (1996), the sporangiophores in *Erdtmanitheca* Pedersen, Crane et Friis (Erdtmanithecales) have a central stalk and free sporangia borne on the peltate head in whorls around the distal part of the stalk in an arrangement similar to *Eucommiitheca*. Sporangiophore heads in *Erdtmanitheca* are smaller (0.6–1.1 mm in diameter) than in *Aegianthus* (Table 1). Unlike *Aegianthus, Erdtmanitheca* and *Eucommitheca* produced trisulcate pollen (Pedersen et al., 1989; Friis and Pedersen, 1996; see the chapter *4.1.*).

Deng et al. (2014) supposed a cycad affinity of *Aegianthus.* However, at the same time, they registered co-occurrence of *Aegianthus hailarensis* and ginkgoalean leaves of *Sphenobaiera longifolia* (Pomel) Florin in the same samples from the Hailar Basin (China) and similarities of their epidermal features. Besides the Hailar Basin, pollen cones of *Aegianthus* and their fragments were found in association with leaves of *Sphenobaiera* Florin in the majority of other known occurrences (Table 1). At first, *Sphenobaiera* leaves were not recorded in the plant assemblage of the Baisa locality (Zaza Formation, Barremian–Aptian) in Transbaikalia (Russia) where remains of *A. resinifer* (=*Loricanthus resinifer)* were found (Krassilov and Bugdaeva, 1999). Later, Bugdaeva (2010) described leaves of *Sphenobaiera vitimica* Bugdaeva from the same locality and strata.

In the Ust'-Baley locality, the remains of *Aegianthus sibiricus* and leaf fragments of *Sphenobaiera* were found in the same samples. Doludenko and Rasskazova (1972) studied the epidermal features of all *Sphenobaiera* leaves from this locality kept in the Heer's collection GIN 165 (Moscow, Russia). They discovered that all leaves have similar epidermal characters and assigned them to *Sphenobaiera czekanowskiana.* Later, leaves of this species were described from the Tolstiy Mys locality too (Kirichkova et al., 2016) where we have found remains of *A. sibiricus*.

Recently, we have studied in detail the ovule-bearing structures of *Karkenia irkutensis* (Ginkgoales) from the Idan locality (Nosova et al., 2021). Based on their co-occurrence with leaves of *Sphenobaiera vigentis* in the same samples, we suggested that these remains were most likely produced by the same kind of plant. The microsporophylls of *Aegianthus irkutensis* occur in association with leaves of *S. vigentis* and structures of *K. irkutensis* in many specimens from Idan (Plate III, 1, 2). Characters of the epidermal cells and stomatal complexes of all these taxa are comparable. Important epidermal features of *S. vigentis*, such as the papillate ordinary epidermal cells and proximal papillae on the subsidiary cells (Nosova et al., 2021, pl. X), similar to the features of the outer epidermis of *A. irkutensis*. An interesting fact is that we have found monosulcate pollen grains attached to a nucellar cuticle of *K. irkutensis* (Nosova et al., 2021, pl. III, figs. 5, 7, 12) similar in shape and size (23–33 × 14–20 μm) to in situ pollen grains of *A. irkutensis.* We are planning to study an exine ultrastructure of the pollen grains attached to a nucellar cuticle of *K. irkutensis* and compare it with in situ pollen grains of *A. irkutensis.* We hope this will allow us to determine the systematic affinities of these taxa.

5. Conclusions

New features of the pollen cones of *Aegianthus sibiricus* were revealed based on the detailed study of specimens from the lower part of the Prisayan Formation (Aalenian) in two localities: Ust'-Baley (type locality) and Tolstiy Mys in the Irkutsk Coal Basin (East Siberia, Russia). In the sporangiophores of *A. sibiricus*, resin bodies were found for the first time. The number of sporangia is specified as 10–12 per sporangiophore. This species differs from other *Aegianthus* in smooth periclinal cell walls and in lacking papillae on the subsidiary cells of the stomata in the abaxial epidermis of the peltate head.

Aegianthus irkutensis Nosova sp. nov., is described from the lower part of the Prisayan Formation of the Idan locality in the Irkutsk Basin based on a unique combination of the gross morphology of sporangiophores, epidermal patterns and in situ pollen. The new species is characterized by numerous and long sporangia with an acute apex, strongly papillate cells of the outer epidermis, and the presence of papillae on the subsidiary cells of the stomata.

The pollen grains of *A. irkutensis* are similar to those of *A. sibiricus* in the morphology and ultrastructure. They are boat-shaped, monosulcate, with a long and often widely open sulcus. The exine surface is psilate or scabrate in LM, and scabrate to granulate in SEM; the infratectum consists of large granules or columella-like elements. Among *Aegianthus* species with studied sporoderm ultrastructure, *A. daohugouensis* differs in thinner elongated infratectal elements implying a possible cycadalean affinity of such pollen, while *A. resinifer* shows an infratectum of large granules and columella-like elements similarly to the pollen grains under study. However, the quality of the photos of the exine ultrastructure in *A. daohugouensis* is insufficient to make a reliable comparison.

While pollen size, shape, and morphology of the studied *Aegianthus* species are characteristic both for cycadalean and ginkgoalean pollen, the exine ultrastructure unequivocally excludes a relationship to cycads. An infratectum of large granules and columella-like elements implies ginkgoalean or previously supposed gnetophytalean affinity.

Remains of *A. irkutensis* have been found in association with leaves of *Sphenobaiera vigentis* different from the leaves of *S. czekanowskiana* associated with *A. sibiricus.* Pollen cones of *Aegianthus* occur in association with leaves of *Sphenobaiera* in most occurrences suggesting that these remains may have been produced by the same kind of plant. But more evidence is needed to clarify this assumption.

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.

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Microscopy of Lomonosov Moscow State University, and Microscopy lab at PIN RAS.

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