

## GNETALEAN PLANTS FROM THE JURASSIC OF UST-BALEJ, EAST SIBERIA

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### Abstract

Krassilov, V.A. and Bugdaeva, E.V., 1988. Gnetalean plants in the Jurassic of Ust-Balej, East Siberia. *Rev. Palaeobot. Palynol.*, 53: 359–374.

The gnetalean affinity of the samaras described by Heer (1876) as *Ephedrites antiquus* is supported and a new generic name *Heerala* is proposed for them. They are conceived as borne axillary to the bracts of a new bract genus *Angarolepis*. The *Ephedra*-like leaves from the same locality, assigned to a new leaf genus *Cadmisega*, might belong to the same plant. Its supposed pollen organs have previously been described as *Kaidacarpum*, a monocot fruit, and *Equisetostachys*, a spore cone.

### Introduction

Rich fossiliferous shales on the right bank of the Angara River 60 km down from Irkutsk were discovered by Czekanowsky in 1869. Heer (1876) made this locality classical by describing the first mid-Jurassic Siberian flora conspicuously different from the then typical Yorkshire and Rajmahal assemblages. According to Heer, the Ust-Balej comprised a few ferns, horsetails and lycopods, together with abundant ginkgophytes ("salisbureans") and conifers, some of which have been subsequently transferred to the Czekanowskiales.

Conspicuous among these conventional Mesozoic plants were *Ephedrites antiquus* assigned to the gnetaleans and *Kaidacarpum sibiricum*, supposedly a pandalean fructification. In subsequent years these taxonomic assignments by Heer were viewed with suspicion, but despite a considerable interest in the geological history of both gnetaleans and monocots, they received surprisingly little attention.

The diagnosis of *Ephedrites antiquus* was given by Heer as "Eph. ramis articulatis, striatis, nuculis duabus semi-orbiculatis, apice acuminatis, bracteis 12–30 mill longis, ovato-oblongis, apice bilobis". He described under this name (1) slender longitudinally ribbed axial organs, (2) seeds, stones of which break readily into halves and (3) bilobed "bracts" bearing small elliptical bodies.

V.D. Prynada, in his monograph on the East Siberian Jurassic flora published posthumously in 1962, reconsidered Heer's material and concluded that "*E. antiquus*" was an assemblage of unrelated organs, namely (1) indeterminate shoots or roots, (2) a common-place *Carpolithes*, possibly produced by some ginkgoalean plant and (3) the cone scales of the conifer *Schizolepis*. We agree with Prynada's points (1) and (2), but not as to (3). The cone scales resemble *Schizolepis* only in the bilobed apex, whereas all the major characteristics are entirely different. Heer might be not wrong altogether.

*Kaidacarpum sibiricum* was diagnosed by Heer as a cone-like infructescence consisting of lignified fruits which showed hexagonal facets ("K. strobila ovali, centim 3–3.5 longo), fructibus lignosis, area apicalis hexagona, costis radiantibus 5–6"). It was compared with the extant Pandanaceae as well as the Jurassic *Kaidacarpum bucklandii*, *K. ooliticum* and *Mamillaria desnogensii*, once considered angiospermous fructifications but later recognised as araucarian cones. Prynada transferred *K. sibiricum* to *Equisetostachys*, a genus for equisetalean cones. As in the case of *Ephedrites* he declared trivial what Heer thought extraordinary.

Ust-Balej has yielded plant fossils for several generations of professional and amateur collectors. Most collections remained undescribed and only a few ginkgophyte leaf cuticles have been studied with light microscopy.

In the last years Ust-Balej was believed to be exhausted. However in the summer of 1985 it was possible to excavate from under debris two fossiliferous shale beds, one below and one above the thick cliff-forming coarse sandstone member. We found most plants favourably preserved as macerated compressions. The flora is taxonomically poor and our collection, though much larger than that studied by Heer, adds little to the originally revealed diversity. However, a considerable proportion of the flora is represented by reproductive organs, none of which is sufficiently understood, while most leaf taxa need redescription.

We open our revision of the Ust-Balej flora with two enigmatic plants described by Heer as *Ephedrites* and *Kaidacarpum*. Heer's taxonomic intuition, at least in the case of *Ephedrites* was correct, but unfortunately he chose generic names based on different organs. These have to be substituted by the new genera, *Heerala* and *Aegianthus*, supposedly the seed and pollen organs of a gnetalean plant. Two more genera, *Angarolepis* and *Cadmisega* are proposed for the hitherto underscribed bracts and leaves which might belong to the same plant.

***Angarolepis* Krassilov et Bugdaeva, gen. nov.**

*Name:* from the Angara River and *lepis* (Gr.): scale.

*Type species:* *Angarolepis odorata*, sp. nov.

*Diagnosis:* as for the type-species.

*Angarolepis odorata* Krassilov et Bugdaeva, sp. nov. (Plates I–IV).

*Name:* pertaining to secretory organs.

*Holotype:* Repository of the Institute of Biology and Pedology, Vladivostok (U.S.S.R.) N UB1-1, Plate I, 4.

*Diagnosis:* Bracts spatulate or oval, stalked to nearly sessile, convex to concave, about 15 × 8 mm. Base showing callous scar, apex acute or obtuse, margin fringed with a narrow membranous wing, median zone thick, showing dense longitudinally aligned resin bodies. Abaxial cuticle much thicker than the adaxial, epidermal cells mostly rectangular longitudinally filed on both sides. Stomata abaxial, sparse, longitudinal or oblique, with radially disposed subsidiary cells and a broad Florin's ring. Encircling cells in 1–2, occasionally up to 4 circles.

*Description:* Bract compressions are conspicuous by their thickness, convex to concave form and resin bodies. In the lower plant bed they are fairly numerous and show considerable morphological variation ranging from broadly spatulate tapering proximally into a more or less definite stalk-like extension, to the oval truncate at the base (Plate I, 1–3). Their dimensions range from 6.5 × 5 mm to 18 × 9 mm, average 15 × 8 mm. In the spatulate variety a stalk-like portion can be up to 5–6 mm long, about one third of a total length, but more often it is about 2 mm long or less. The apices are bluntly pointed in about two thirds of the specimens, acutely pointed in the rest.

Comparatively consistent characters are, first, a prominent callous scar at the base which is narrow elliptical, about 3 mm wide and also a thin marginal flange about 1 mm wide. Marginal and apical hairs were seen in a

few specimens (Plate I, 5). Venation is indistinct, probably consisting of two or more parallel veins in the median zone which is filled with abundant resin bodies. The resiniferous zone is constantly 2–2.5 mm wide. The resin bodies are fusiform or elliptical up to 3 mm long, but mostly 0.5–1.5 mm long, sometimes showing a longitudinal suture line (Plate IV, 3) possibly left by a collapsed epithelial sheath. A structureless membrane peels off the oxidised resin bodies when put in alkaline solution.

The abaxial (convex side) cuticle is fairly thick showing strongly marked longitudinally aligned cells. These are of two dominant shapes, quadrilateral, rectangular or trapezoidal about  $45\text{--}50 \times 25\text{--}30 \mu\text{m}$  and nearly square or irregularly polygonal, about  $30\text{--}37 \times 27\text{--}33 \mu\text{m}$ . They occur in different sectors of the cuticle or, less often, in alternating rows. At places a short row of isomorphic tabular cells, shorter than wide (about  $20 \times 30 \mu\text{m}$ ), results from anomalously frequent transverse divisions. The periclinal surface walls are convex, more or less prominently thickened in the middle.

The stomata are sparse, usually not more than 1 per  $\text{mm}^2$ , longitudinal or oblique to the cell rows. The stomatal pit is irregularly elliptical, about  $25\text{--}35 \mu\text{m}$  long. Florin's ring, when developed, appears flattened, about  $12 \mu\text{m}$  wide. The subsidiary cells, usually five or six, are radially disposed in a ring of uneven width. The encircling cells are not constant, forming more than one and occasionally up to four concentric rings but sometimes a single incomplete ring.

Cells of the marginal flange are rectangular somewhat smaller than in the median sector, about  $30\text{--}35 \times 20\text{--}25 \mu\text{m}$ .

The adaxial (concave side) cuticle is thin, showing cells as on the abaxial side. No stomata showed up but their absence could not be asserted with only small pieces of this cuticle available.

*Remarks:* These bracts are easily distinguishable from *Cycadolepis* and other fossil cataphyll genera by their narrow wing-like fringe and the median zone of resin bodies. They are

comparable to the cone bracts of the extant gnetalean genera *Ephedra* and *Welwitschia*, especially the latter on account of the convex to concave shape, membraneous wing and the basal callous scar where an axillar ovulate organ is attached. In *Welwitschia* a cone bract receives two vascular bundles which run along the thickened median zone while its membraneous wing is unvascularised as is almost certainly the case in *Angarolepis*.

Also in *Welwitschia* proximal cone bracts are acute while the more distal ones are bluntly pointed (Pearson, 1929) which may explain the analogous dimorphism of the fossil bracts. In herbarium ovulate cones we noticed occasional aborted bracts adnate to the normal ones. Similarly in a few specimens of *Angarolepis* small cordate scales attach near the base (Plate II, 4, 5). In their cuticular structure the latter do not differ from the normal bracts.

Though the median resiniferous zone of *Angarolepis* is without analogy in *Welwitschia*, some species of *Gnetum* have large mucilage ducts in the cone bracts (Pearson, 1929).

Another noteworthy feature of *Angarolepis* is a triangular mark on the adaxial side which was observed in a number of specimens (Plate II, 1, 2). It is up to 6.5 mm long, pointed, with parallel venation more distinct than in the bract. It appears as an axillar scale or rather a prophyll of an axillar shoot adnate to the subtending bract. We are not certain about the nature of this organ and can refer only to prophylls of the axillar female flowers observed as a rare anomaly in *Welwitschia* (Lignier and Tison, 1911).

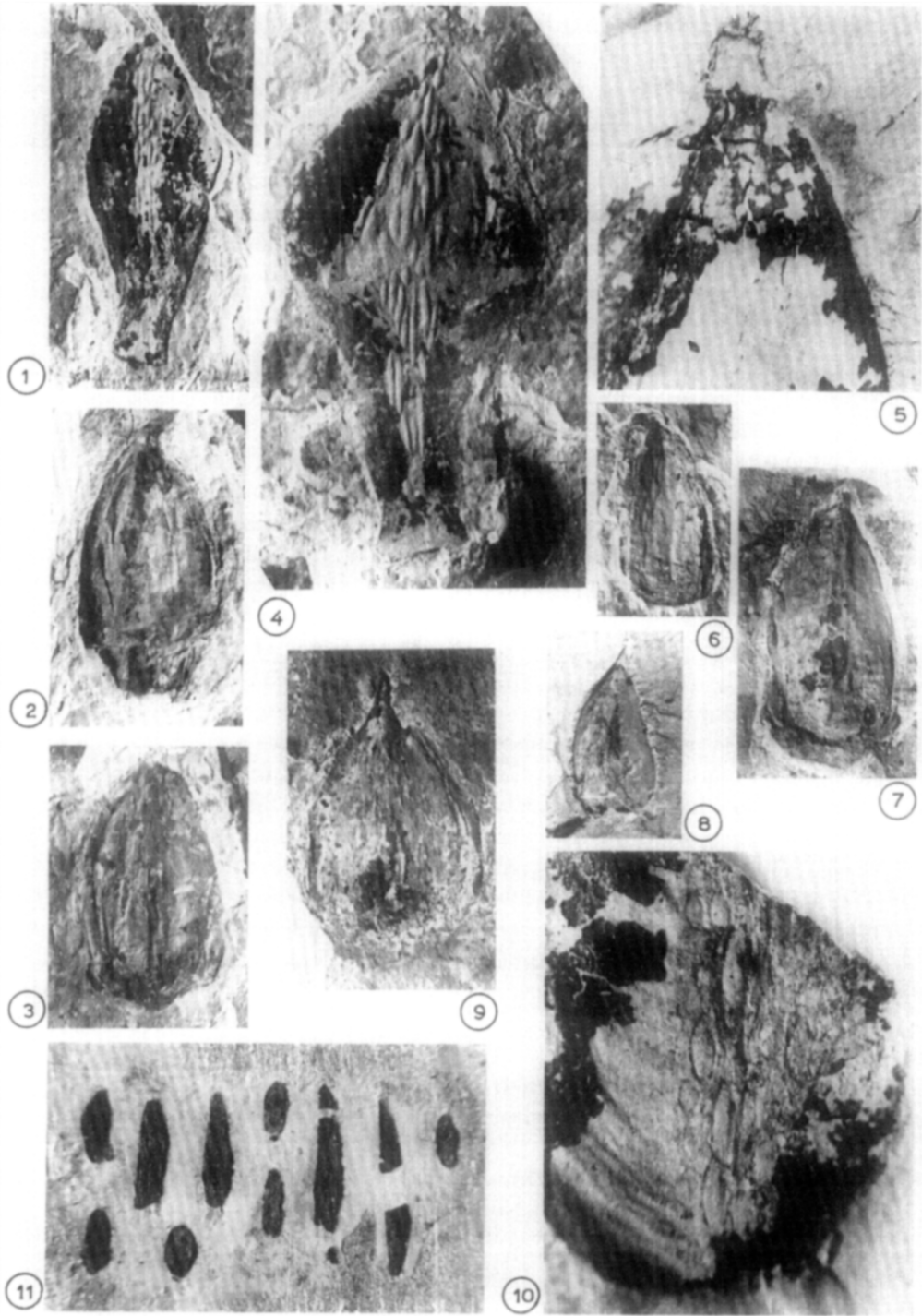
### ***Heerala* Krassilov, gen. nov.**

*Name:* after Oswald Heer and *ala* (Lat.): wing.

*Type species:* *Ephedrites antiquus* Heer (1876).

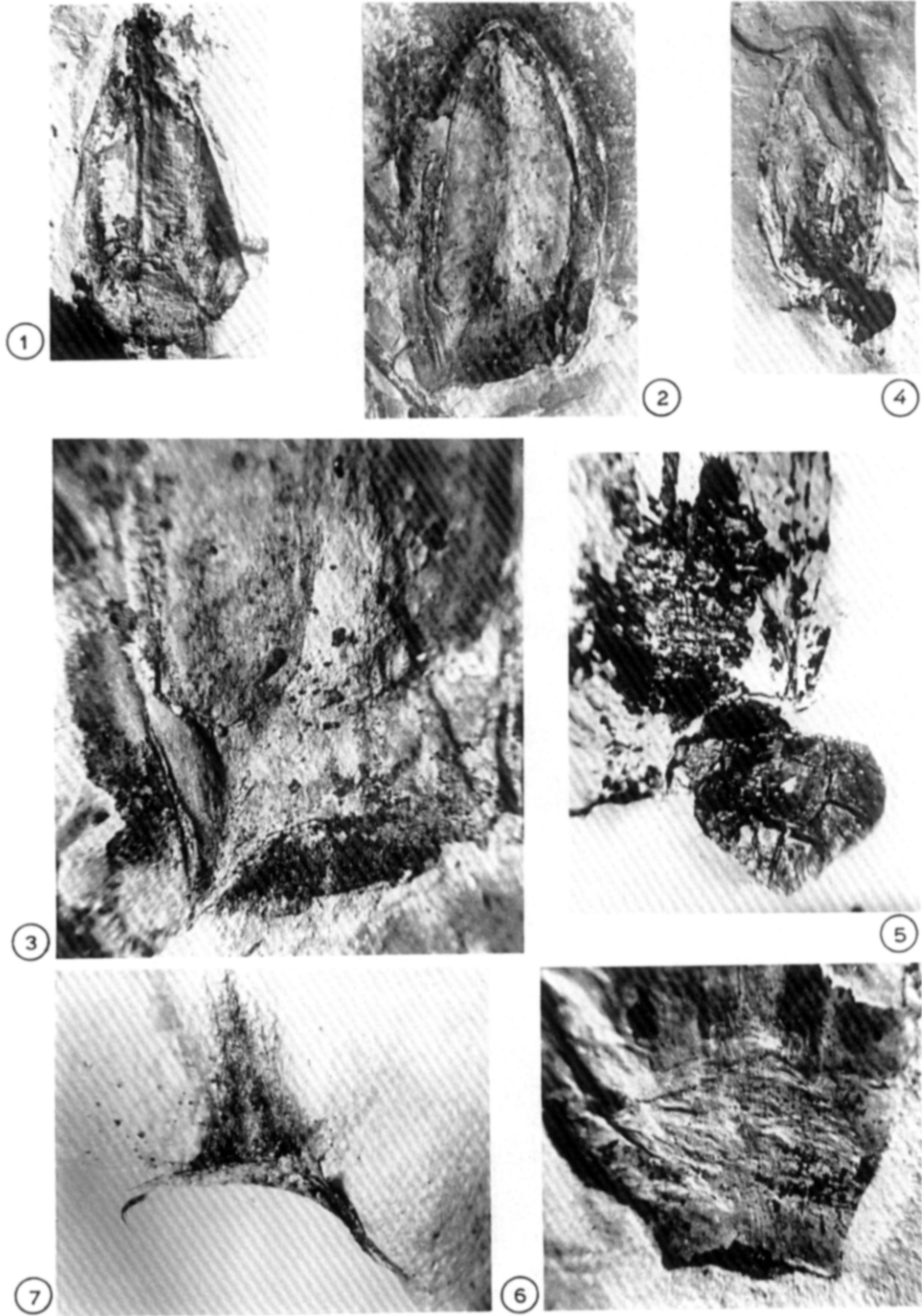
*Diagnosis:* Samaras large, with a fusiform central body surrounded by a membraneous wing except at the basal callous scar. Central body containing abundant secretory cavities, traversed by a median ridge. Wing with an apical notch or cleft not reaching central body.

PLATE I



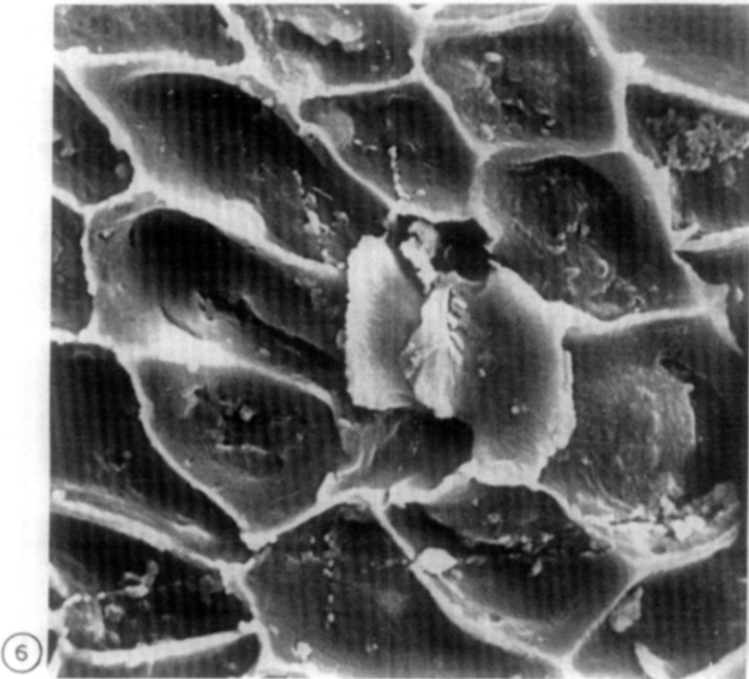
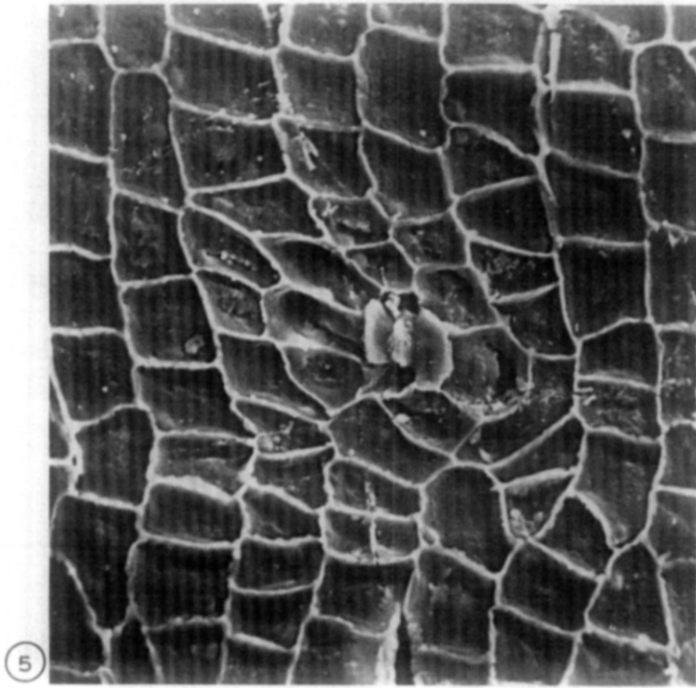
(for explanation see p.365)

PLATE II



(for explanation see p.365)

PLATE III



*Heerala antiqua* (Heer) Krassilov, comb. nov.  
(Plates V, VI)

*Basionym:* *Ephedrites antiquus* pro parte Heer, 1876, p. 82, plate XIV, 24–25.

*Schizolepis antiqua:* Prynada, 1962, p. 264, plate XVIII, 15–16.

*Description:* Samaras are elliptical or ovate, consisting of a solid central body surrounded by a membranous wing. The central body is fusiform, pointed at the micropylar end, rounded or truncate at the chalazal end, with a callous basal scar. The wing is symmetrical, interrupted at the basal scar, apically notched or cleft 1/10, to 1/5 its length but not as deep as the central body. A prominent median suture runs straight from the apical notch to the basal scar.

In the lower plant bed where these samaras are most common, they measure from 8 × 4 mm to 14 × 6 mm, average 12–13.5 × 6 mm. The central body is constantly 2.1–2.3 mm wide, the basal scar about 2 mm wide. A single samara from the upper plant bed is 16 × 5 mm, with a central body 12 × 2.7 mm.

The central body is densely pitted by elon-

gate-elliptical impressions of the longitudinally aligned resin bodies. Compressions, when preserved, yield abundant resin bodies and small fragments of a fairly delicate cuticle showing rectangular or trapezoidal longitudinally filed cells about 25–50 × 12.5–17, 55 μm under which there are much larger elongate-polygonal cells about 100–175 × 50–72 μm. The wing shows irregular folds and the fine striation diverging from the median suture. Large elongate-polygonal cells are often seen on the wing impressions under low magnification. In SEM such impressions reveal two superimposed layers of the larger and smaller cells (Plate VI, 5) as in the central body.

*Remarks:* These samaras have been described by Heer (1876) as bracts under *Ephedrites antiquus* which comprised also some featureless shoots and wingless seeds of the *Carpolithes* types. Of these fossils only the samaras were sufficiently distinctive to deserve a specific name, but for them *Ephedrites* based on shoots (Goeppert and Berendt in Berendt, 1845) was an inappropriate generic name.

These samaras are much larger than *Sa-*

PLATE I (see p.362)

*Angarolepis odorata*, sp. nov.

- 1–3. Bracts showing variable base shapes, × 4.
4. Spatulate bract, holotype, × 4.
5. Apical portion of a bract showing apical and marginal hairs, × 12.
- 6–9. Shapes of the apices, × 4.
10. Median resiniferous zone, × 8.
11. Resin bodies, × 12.

PLATE II (see p.363)

1–6. *Angarolepis odorata*, sp. nov.

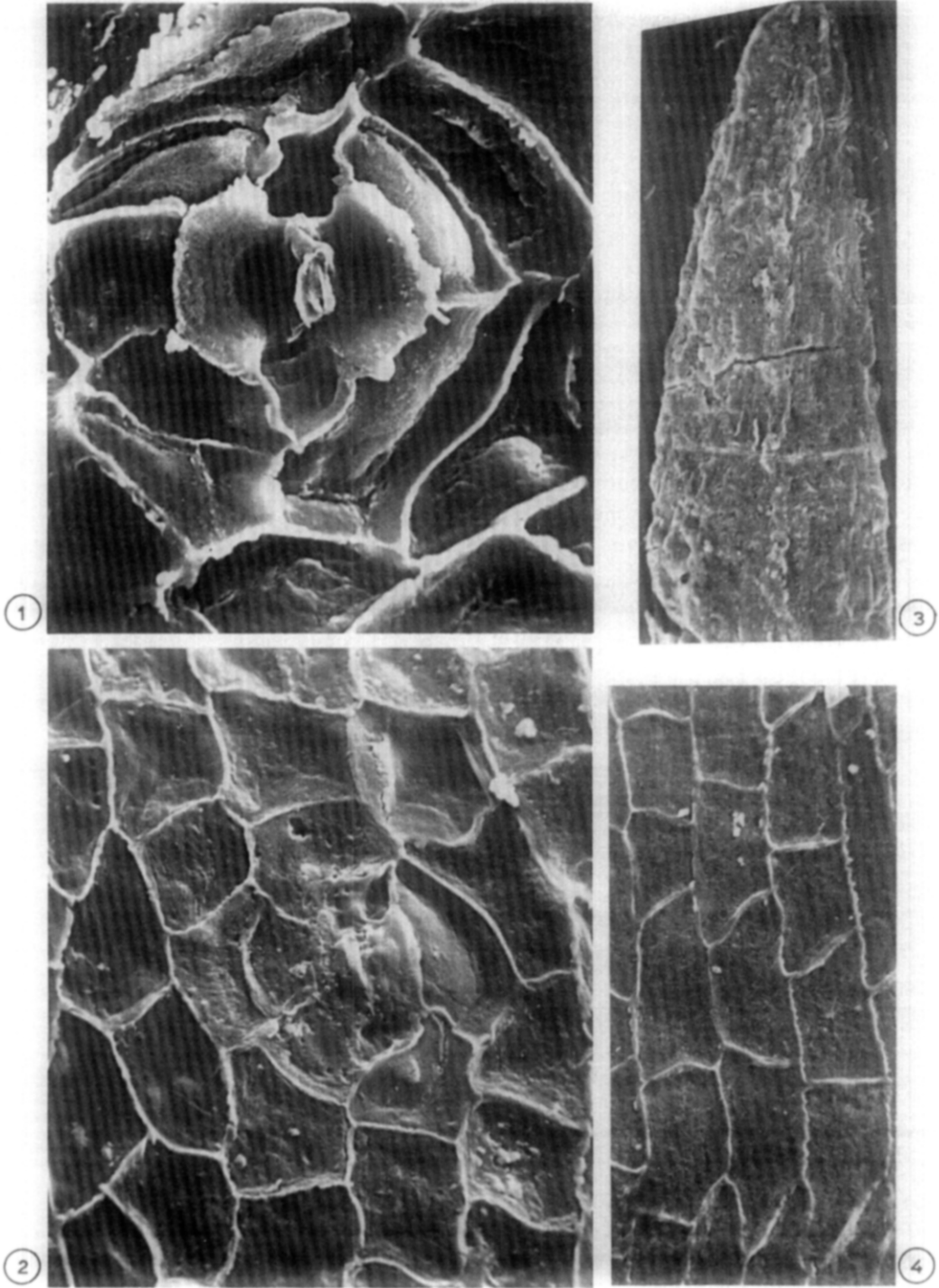
- 1, 2. Bracts showing impression of an axillary scale, × 3 and 4.
3. Part of 2 showing basal scar, × 8.
- 4, 5. Small aborted bract attached at the base of a normal one, × 4 and 8.
6. Scar at the base of a bract, × 8.
7. *Welwitschia mirabilis*, extant, basal scar of a samara, × 8.

PLATE III

*Angarolepis odorata*, sp. nov.

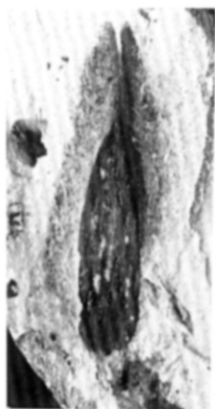
- 1–4. Various bract shapes, 1 showing impression of an axillary scale, × 4.
- 5, 6. Abaxial stoma with supernumerary subsidiary cells, SEM, × 600 and 1600.

PLATE IV



(for explanation see p.369)

PLATE V



1



4



6



2



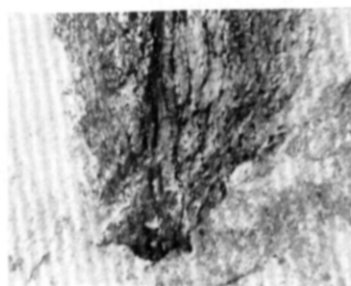
5



7



3



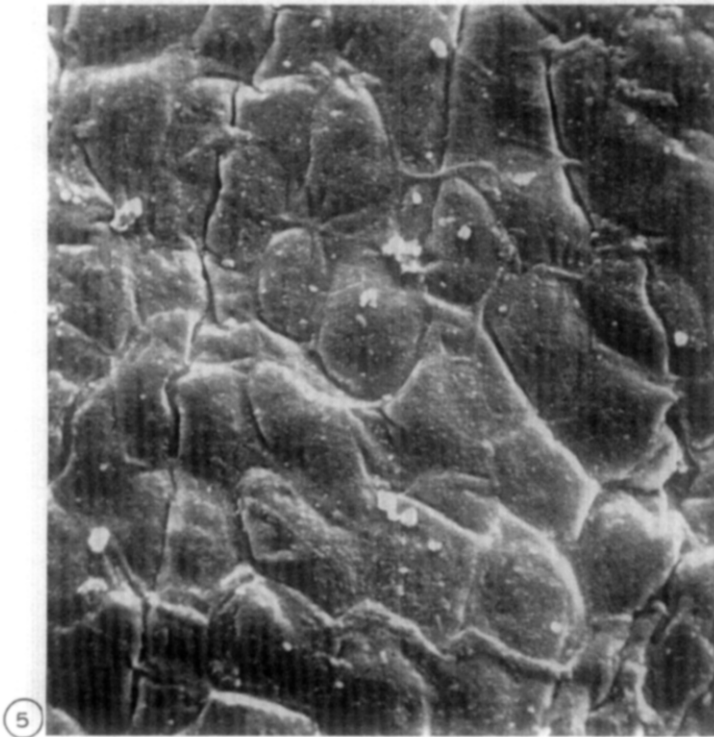
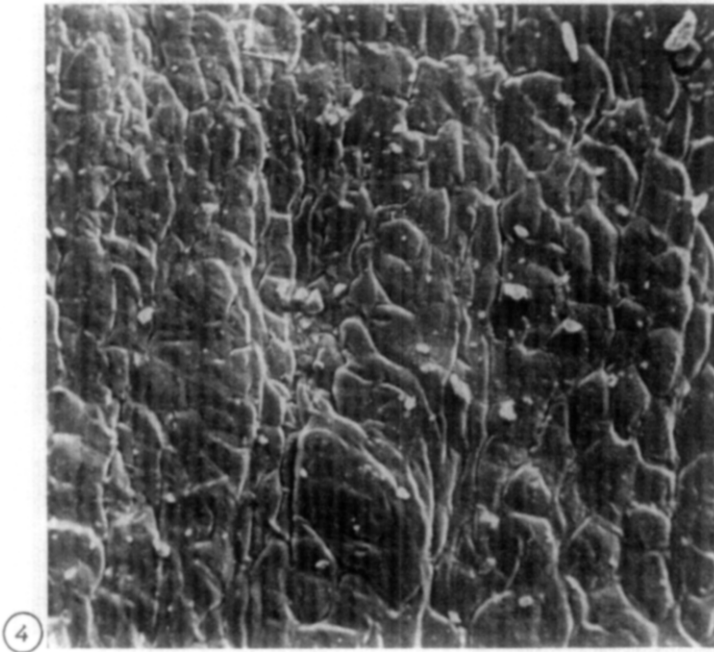
9



8

(for explanation see p.369)

PLATE VI



*maropsis* occurring in the same bed and differ from this and other winged desminules by the narrow apical cleft in the wing far not reaching the central body, the median suture, the basal callous scar and the conspicuous resin bodies. The latter are disposed exactly as in the *Angarolepis* bracts (above). Both organs show median resiniferous zones of equal width filled with densely packed resin bodies of the same shape and size ranges. Also the samaras and bracts are similar in general shape and dimensions and their basal callous scars match exactly. Added to the joint occurrence in comparable numbers — though the bracts are more abundant — these similarities obviously suggest connection, possibly of the kind of a subtending bract and its axillar ovulate organ. Both the bracts and samaras resemble the corresponding organs of *Welwitschia*, the samaras of which are bivalved one-seeded winged cupules joint to the bract at the base and left with a callous basal scar when detached. In *Heerala* the samaras are bitegmic and the median suture may indicate a bivalved outer coat, or cupule. They lack a protruding micropilar tube, as in *Welwitschia*, but this breaks off easily even in herbarium specimens.

***Aegianthus* Krassilov, gen. nov.**

*Name:* from *aegis* (gr.): shield and *anthus* (gr.): flower.

*Type species:* *Kaidacarpum sibiricum* Heer (1876).

*Diagnosis:* Pollen cones of many helically disposed peltate sporangiophores. Peltae polygonal, faceted, attached at the middle, bearing several sporangia submarginally under lateral facets. Pollen monosulcate.

*Aegianthus sibiricus* (Heer) Krassilov, comb. nov. (Plates VII–XI).

*Basionym:* *Kaidacarpum sibiricum*: Heer, 1876, p.84, plate XV, 10–12, 15–16.

*Equisetostachys sibiricus*: Prynada, 1962, p.147, plate XII, 5–10.

*Description:* Strobilar organs and their detached scales described by Heer as pandanaceous fruits, are among the most conspicuous and common Ust-Balej fossils. They are elliptical in general outline, from 20 × 10 mm to 50 × 22 mm, average 45 × 15 mm. Lateral organs are peltate, spirally disposed, adpressed or, in ripe cones, attached more loosely with a narrow space between them filled with rock matrix. Their

PLATE IV (see p.366)

*Angarolepis odorata*, sp. nov.

- 1, 2. Stomata, 1 showing Florin's ring from inside, SEM, × 1600.
3. Resin body showing a suture line, SEM, × 160.
4. Adaxial epidermal cells, SEM, × 600.

PLATE V (see p.367)

*Heerala antiqua* (Heer) comb. nov.

- 1–3. Samaras, × 3.
- 4, 5. Parts of 1 showing apical cleft and the resin bodies, × 10.
6. Wing impression showing large polygonal cells, × 10.
- 7–9. Base shapes with an attachment scar, × 8 and 10.

PLATE VI

*Heerala antiqua* (Heer) comb. nov.

- 1–3. Samaras with a shallow apical cleft or notch, × 4.
4. Impression of the outer coat cell pattern showing narrow cell rows alternating with the broader bands of polygonal cells, SEM, × 170.
5. Impression of two superimposed cell layers, SEM, × 400.

number varies from about 16 to 36 or more depending on the size of the cone. When split by cleavage the peltae appear as thick shiny coaly hexagons about 4.5–5 mm across, but under the coal they show a faceted impression of the adaxial surface, composed of a hexagonal or occasionally pentagonal central facet surrounded by lateral ones either polygonal or trapezoidal. All the facets are somewhat concave, separated by distinct ridges (Plate VII, 3–6).

The adaxial cuticle is fairly thick on the central facet, less so on the lateral facets, showing strongly marked polygonal cells about 30–42  $\mu\text{m}$  wide. Rectangular and trapezoidal cell shapes about 42–50  $\times$  20–25  $\mu\text{m}$  occasionally occur in the median sectors and more commonly toward the periphery of the facets. The surface cell walls are convex, thickened in the middle or even indistinctly papillate. The cell rows often arch around a topographic centre, either a stoma or undeveloped stomatal initial. There are usually no more than 2–3 fully developed stomata per central facet but on the lateral facets they can be more numerous, up to 15 per facet.

The stomatal pit is parallel or oblique to the cell rows, about 35–40  $\mu\text{m}$  long. There are normally six but occasionally eight radially disposed subsidiary cells forming an irregular ring. Florin's ring is rudimentary, sometimes as a thin dashed fold across the subsidiary

cells. The encircling cells are arranged in two or more concentric rings. When the stomata are sparse as in the central facets their effect as topographic centres can be seen through no less than five cell rows.

Sporangia are borne submarginally, one per lateral facet. In the apparently unripe peltae they address to the abaxial side radially facing the stalk. A few detached peltae with sporangia spreading from under the margin suggest that they became pendant when ripe. The marginal facets seem arched somewhat over adpressed sporangia but then became unfolded or spread more openly.

The individual sporangia are cigar-shaped, about 2.6 mm long, 0.7 mm wide, showing fine longitudinal striation. In one case a sporangium 3 mm long shows a rounded apical depression, while another sporangium from the same pelta is cleft at the apex (Plate VIII, 1). These features may indicate opening by an apical pore. At any rate, none of the sporangia shows longitudinal splitting. Under a thin membrane they are filled with a mass of no less than one thousand pollen grains.

The pollen grains are bilaterally symmetrical, monosulcate, elliptical in polar view, boat-shaped in longitudinal equatorial view, frequently folded, sometimes split into halves which may indicate equatorial zone of weakness. Longest equatorial axis 30–42.5  $\mu\text{m}$ , average 40  $\mu\text{m}$ , transverse equatorial axis 20–

#### PLATE VII

*Aegianthus sibiricus* (Heer) comb. nov.

1, 2. Larger and smaller cones,  $\times$  2.

3–6. Peltae showing facets,  $\times$  3 and 8.

7. Base of a cone showing bract-like lateral appendages,  $\times$  8.

#### PLATE VIII (see p.372)

*Aegianthus sibiricus* (Heer) comb. nov.

1–3. Peltae with pendant sporangia, in 1 showing apical pit or notch,  $\times$  10.

4. Pelta with sporangia facing the stalk,  $\times$  10.

5. Pollen grain, light micrograph, median focus,  $\times$  800.

6. Pollen grain, light micrograph, oblique distal view,  $\times$  800.

7, 8. Pollen grains, oblique distal views showing sulcus and exinal folds, SEM,  $\times$  2000.

PLATE VII

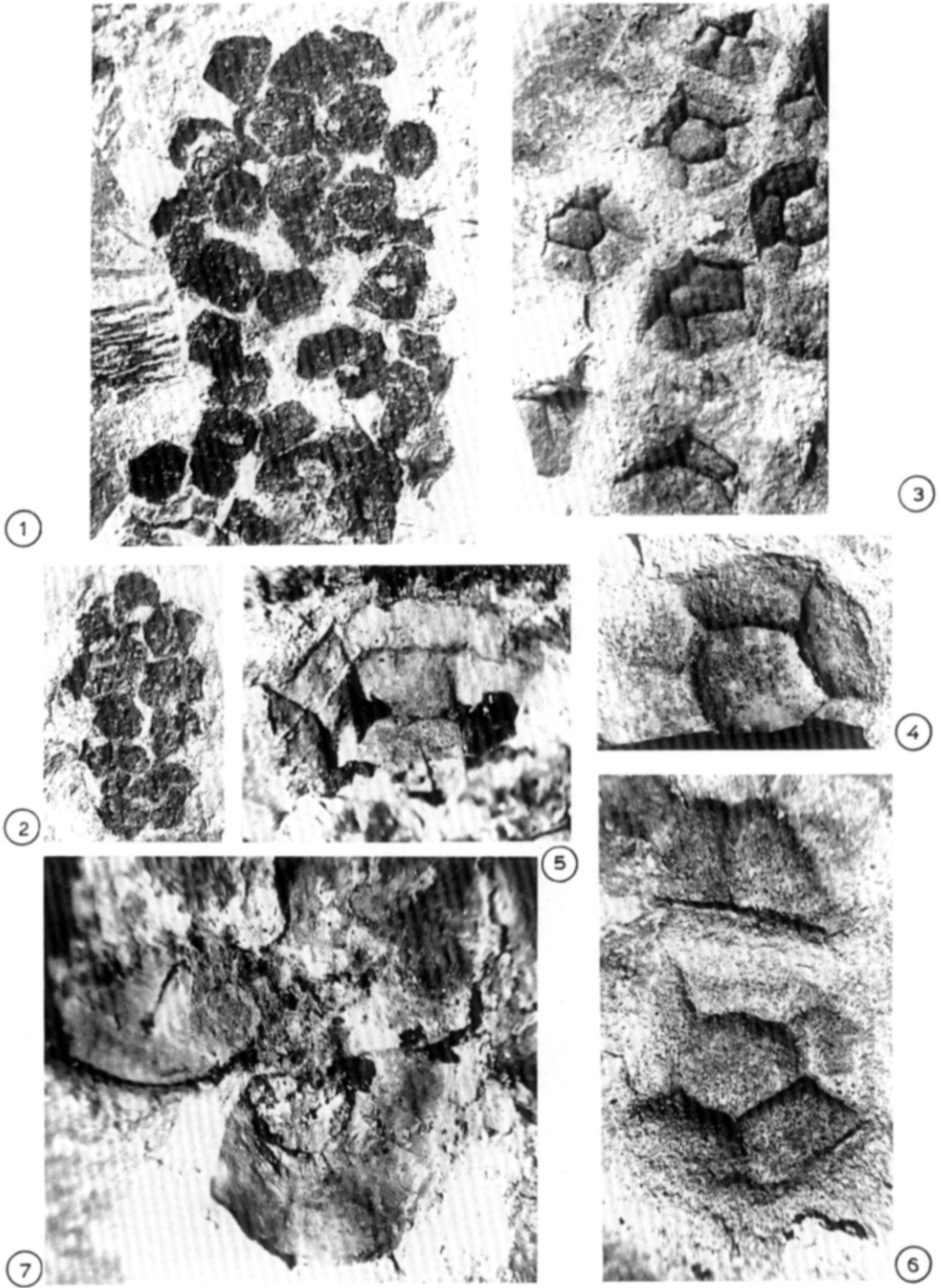
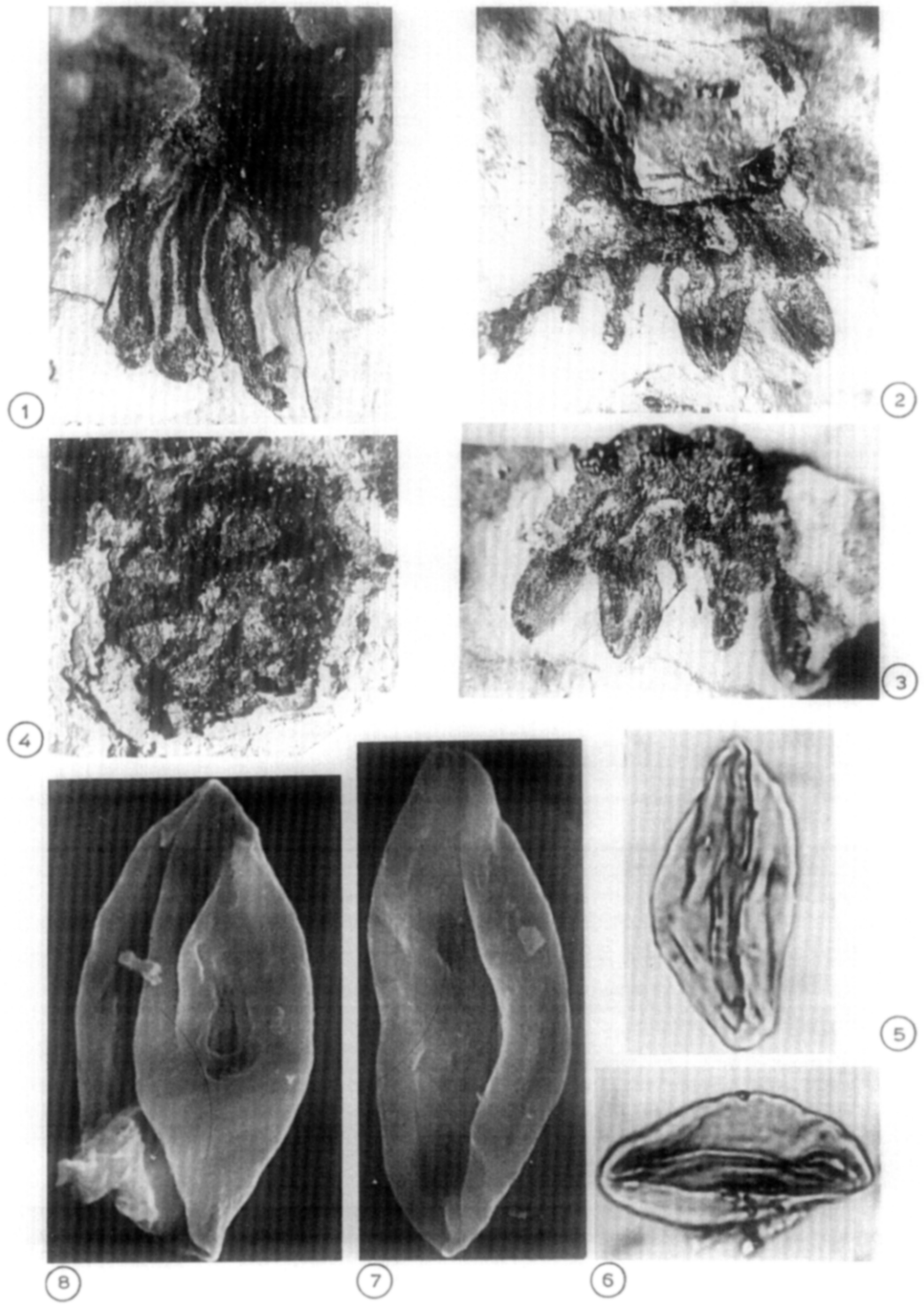
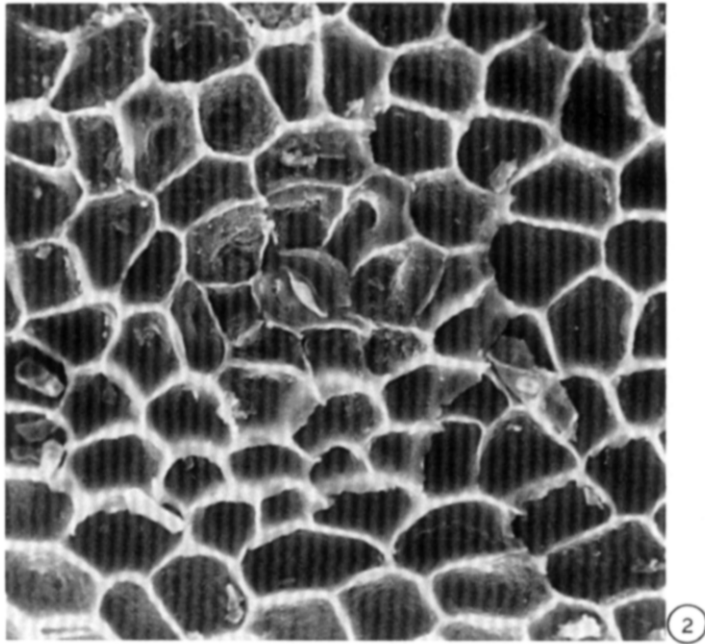
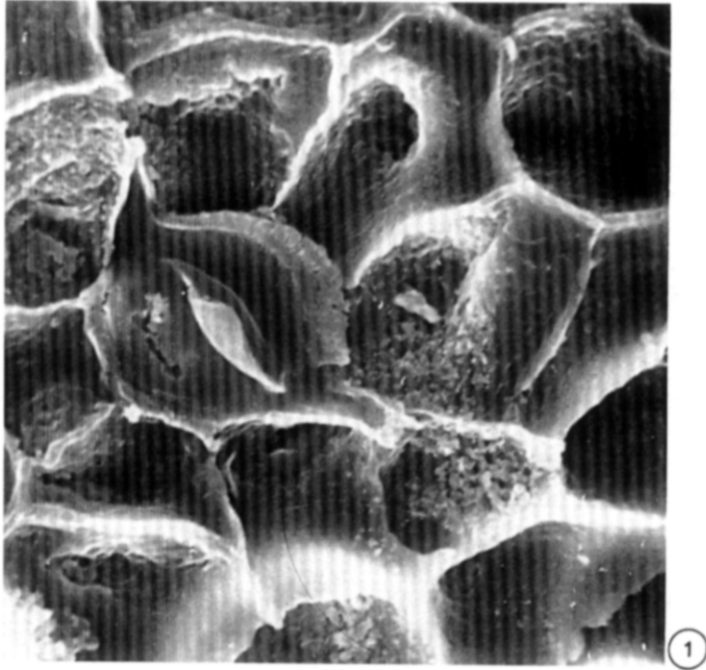


PLATE VIII



(for explanation see p.370)

## PLATE IX



1, 2. *Aegianthus sibiricus* (Heer) comb. nov., stoma, SEM,  $\times 600$  and 1600.

26  $\mu\text{m}$ , average 24  $\mu\text{m}$ . Sulcus extending the entire length of the grain, straight or slightly curved, mostly gaping in the middle or at one or both ends. Sulcus margins strongly folded. Additional exinal folds parallel to the sulcus may be present but do not seem a constant feature. Exine ca. 1.5  $\mu\text{m}$  thick, smooth in light microscope, minutely pitted in SEM. The pits are discernible with a magnification of ca. 10,000 $\times$ .

*Remarks:* Neither *Kaidacarpum* based on ovulate strobili (Carruthers, 1868) nor *Equisetostachys*, a spore cone genus are appropriate for these pollen cones. They are much larger than the pollen cones of most gymnosperms except the extant cycads and araucarian conifers. Microsporophylls are more or less distinctly peltate in the cycads, mesozoic pteridosperms, some conifers and *Classopollis* plants. The latter have similar sporangia (Barnard, 1968), but the peltae are not faceted. In some extant zamioid cycads the peltae can be faceted but less distinctly than in the fossil cones, while sporangia are in sori-like groups and dehisce by longitudinal slits. In pollen grain morphology *Aegianthus* resembles cycads as well as peltasperms. On account of the longitudinal exinal folds and finely pitted wall they are comparable with the *Praecolpatites*-*Marsupipollenites* group of dispersed pollen grains (Foster and Price, 1981).

It was noticed that in *Aegianthus* the lowermost peltae are bract-like flattened (Plate VII, 7). In cuticular characters they are not unlike *Angarolepis* bracts (above). Their stomata are nearly identical and though a prevailing cell shape is polygonal in the peltae while rectangular in the bracts, in certain sectors the cells are quite similar. Both fossils are equally common in the lower plant bed and, in the absence of other candidates, *Aegianthus* seems likely to be the pollen cone of the *Angarolepis* plant.

***Cadmisega* Krassilov et Bugdaeva, gen. nov.**

*Name:* from Cadmus who sowed dragon teeth, and *seges* (lat.): crop.

*Type species:* *Cadmisega ephedroides*, sp. nov.

*Diagnosis:* As for the type species.

*Cadmisega ephedroides* Krassilov et Bugdaeva, sp. nov. (Plate X).

*Holotype:* Depository of the Institute of Biology and Pedology, Vladivostok (U.S.S.R.) N UB1-90 (Plate X, 1).

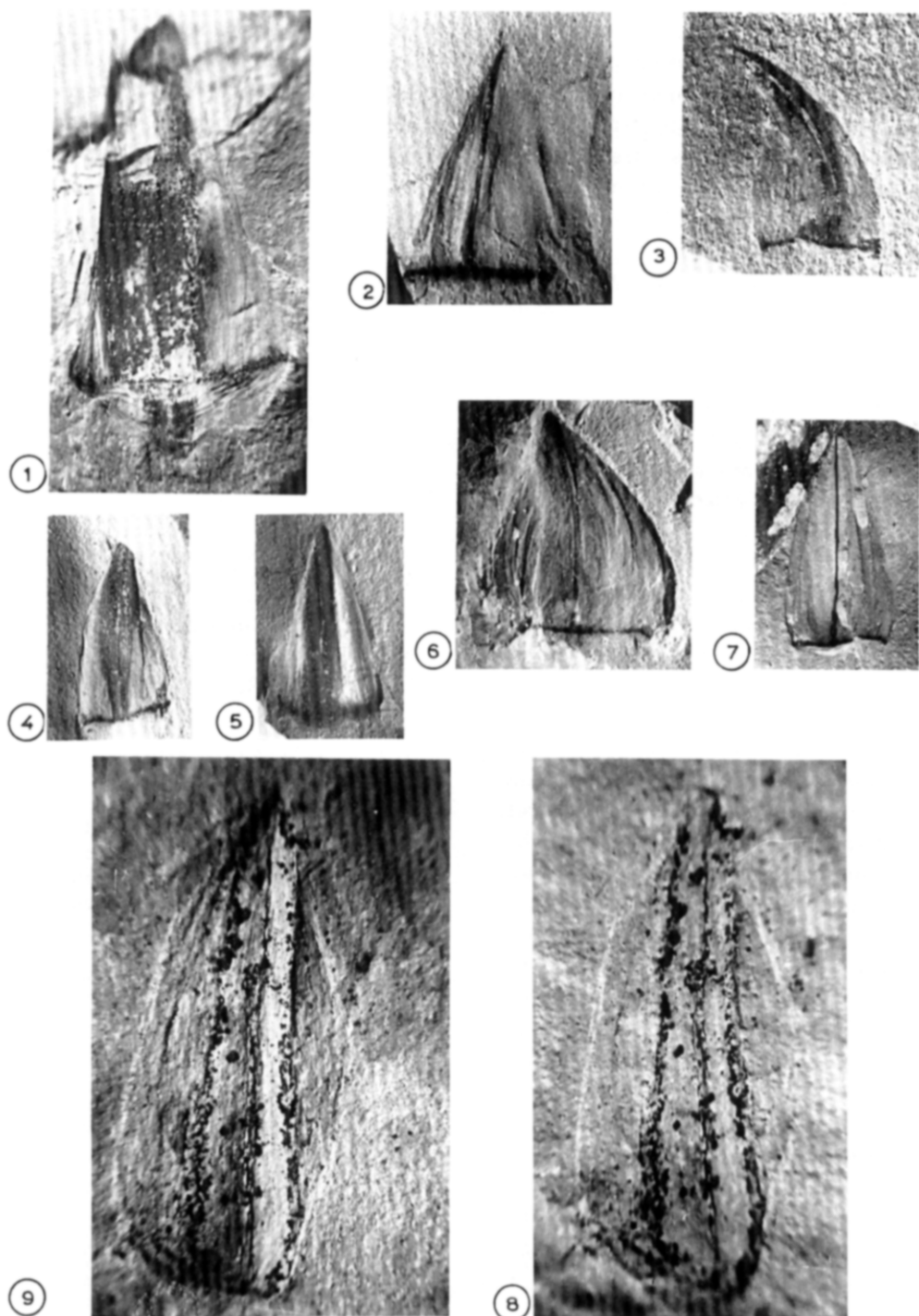
*Diagnosis:* Sheathing scale leaves, triangular, about 8–8.5  $\times$  5–6 mm, pointed, thickened in the middle and along the abscission line. The thickened median zone with one, two or three subparallel veins converging to the apex. Wings membranous unvascularised.

*Description:* Isolated dagger-shaped leaves are numerous in both lower and upper plant beds. The blade is straight or slightly falcate, pointed, up to 9  $\times$  7 mm, average 8.5  $\times$  5 mm. It is separated from the sheathing base by a straight or slightly curved abscission line. The sheath ("hilt") is preserved in a few specimens only. It is about 1.5 mm long (Plate X, 1).

The blade is conspicuously cross-thickened along median and abscission lines. The median thickened area is narrowly triangular, 1.5–2 mm wide at the base, filling the apex and proximally extending into the sheath. It is dark, coaly, sharply demarcated from the bleached membranous wings which are often irregularly folded. A transverse thickening along the abscission line is less dense, consisting of short vertical striae which suggest transfusion tissue. Venation is confined to the median thickened zone that can be traversed by a single median vein, or having in addition two flanking veins which converge to the apex; occasionally there are flanking veins only. The cuticle is exceedingly thin showing indistinct outlines of the elongate longitudinally aligned cells.

*Remarks:* Though detached scale leaves of various conifers and himmerelleans are common as fossils, none of them are closely comparable with the dagger-shaped leaves from Ust-Balej. These, more than any other Mesozoic plant fossils, resemble leaves of *Ephedra*. In this genus the leaves are connate

## PLATE X



*Cadmisega ephedroides* sp. nov.

1. Leaf, holotype, showing sheathing base, median thickened portion and the abscission line,  $\times 8$ .

2-7. Various blade shapes,  $\times 4$ .

8, 9. Leaf showing three veins, direct and oblique illumination,  $\times 10$ .

at the base, with the free tooth-like blades of varying and sometimes considerable length. They usually receive two vascular bundles, but in *E. chilensis* Foster and Gifford (1974) described both 2-veined and 3-veined leaves, often in the same shoot. The median zone between veins is filled with transfusion tissue and in cleared leaves stand out distinctly against the thinner and lighter wings, not unlike in the fossil leaves.

*Cadmisega* is common in both upper and lower plant beds which yielded the supposedly gnetalean reproductive organs described above. However, we obtained no evidence of connection with them; only a rather general resemblance to *Angarolepis* bracts also showing a markedly thickened median vascularised zone and membranous wings.

## Conclusion

Notable among the Ust-Balej fossil plants are the *Ephedra*-like leaves, the *Welwitschia*-like bracts and samaras and the peculiar pollen organs, supposedly belonging to the same plant but only remotely comparable with pollen organs of the extant gnetophytes. These findings suggest an extinct gnetalean genus considerably different from the living ones but combining some features of *Welwitschia* and *Ephedra*, probably more close to the latter in the life form. Thus, it may support the much disputed affinity between these living gnetalean genera. At the same time it may testify to a greater morphological diversity of Mesozoic gnetophytes which comprised forms with cycadoid pollen cones and monosulcate pollen grains.

The Ust-Balej flora thrived in rather harsh

environments of the mid-Jurassic East Siberian midcontinent and it was notably poor in thermophilous cycadophytes. The latter might have been replaced by the sturdier gnetophytes which, judging by the associated occurrence of different organs, grew near the deposition site, probably as riparian shrubs or weeds.

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