

ACHENE-LIKE FOSSILS FROM THE LOWER CRETACEOUS OF THE LAKE BAIKAL AREA

V.A. KRASSILOV and E.V. BUGDAEVA

Institute of Biology and Pedology, 690022, Vladivostok-22 (U.S.S.R.)

(Received May 5, 1981; revised version accepted November 13, 1981)

ABSTRACT

Krassilov, V.A. and Bugdaeva, E.V., 1982. Achene-like fossils from the Lower Cretaceous of the Lake Baikal area. *Rev. Palaeobot. Palynol.*, 36: 279–295.

Achene-like disseminules with a pappus of hypogynous hairs are described from the Lower Cretaceous lacustrine deposits of the Vitim River, Lake Baikal area. They are interpreted as uniovulate cupules with persistent receptacles bearing clusters of very long hairs. The receptacles can be occasionally detached from the cupules. Stone cells and tracheids of the cupule and the seed cuticles are described. In a single specimen, pollen grains are preserved at the top of the nucellus. They are monosulcate, showing alveolar exinal structure. These fossils are compared with bennettitalean strobili and cyperaceous achenes. The accompanying plants are mostly gymnosperms common in the Early Cretaceous Siberian province.

INTRODUCTION

Recent years were marked by a renewed interest in the problem of angiosperm origin. Important finds of proangiospermous plants and early angiosperms in southern Siberia, Mongolia, Kazakhstan, and Iran (Krassilov, 1977; Schweitzer, 1977; Vachrameev and Krassilov, 1979) show that this broad area has prospects for further search. East of the Lake Baikal, there are many small sedimentary basins filled with lacustrine deposits of Late Jurassic—Early Cretaceous age. They contain abundant fresh-water mollusk and ostracod shells, aquatic and terrestrial insects, fishes and fossil plants. Guide fossils for the lower horizons of the Lower Cretaceous are *Lycoptera* among fishes, the aquatic beetle larva *Coptoclava* and the ephemeral larva *Ephemeroptopsis* (Zherikhin, 1978). Plants belong mostly in the ginkgoalean, czekanowskian and conifer genera common in the Siberian (*Phoenicopsis*) realm. A single, supposedly angiosperm macrofossil was found by palaeoentomologists in the upper reaches of the Vitim River — a small narrow-lanceolate leaf or leaflet with comptodromous lateral veins described by Vachrameev (1973; Vachrameev and Kotova, 1977) as *Dicotylophyllum pusillum*. It was accompanied by characteristic Neocomian ostracods, insects and plant macrofossils, but the *Asteropolis*-type pollen grains suggested a younger age. A compro-

mise age assignment by Vachrameev and Kotova (1977) was Barremian—Aptian. In 1979 a party including the palaeontologists V. Zherikhin, N. Zherikhina, I. Dobrokhotova and palaeobotanists V. Krassilov, E. Bugdaeva and L. Sokur worked at the same locality, known as Baisa. They found that the most abundant, though previously neglected fossils in the locality were the achene-like disseminules bearing long trusses of hairs, nicknamed the Venus hair.

LOCALITY

About 600 m of Lower Cretaceous beds crop out on the left bank of the Vitim River near the mouth of its tributary, the Nakhlanda Creek, or Baisa (Fig.1). At the base of the section, there are thick conglomerates lying on granites. The fine-grained sequence above the conglomerates consists of twelve cyclothems each of which comprises sandstones, aleurolitic shales, black paper-shales and a top marl bed. While the fish skeletons are found mostly in the sandstones and paper shales, the insect and plant fossils concentrate in marls. They yielded also a few bird feathers. The entomofauna remains constant through the twelve cyclothems, except that the dragonfly larvae are more abundant in the lower marls whereas *Ephemeropsis* predominates above. Among the plants, the conifers *Podozamites*, *Elatides*, *Schizolepis* and *Pseudolarix* (twigs, brachyblasts, pollen cones, ovuliferous scales, samaras) constitute a dominant group. The czekanowskian genera *Phoenicopsis* and *Czekanowskia* are next in abundance. The ginkgoalean leaves *Baiera* and *Sphenobaiera* are common in the lower horizons. These plants are typical representatives of the temperate Jurassic—Early Cretaceous forests. A few bennettitalean leaves and *Brachyphyllum*-type conifer shoots are found in the middle cyclothems, suggesting a warmer climate. *Dicotylophyllum pusillum* came from the penultimate cyclothem. "Venus hair" — *Baisia* achenes are abundant in all marl beds.

Baiera manchurica Yabe et Oishi and *Czekanowskia rigida* Heer are stratigraphically important species indicating a Neocomian rather than Aptian age (Krassilov, 1972).

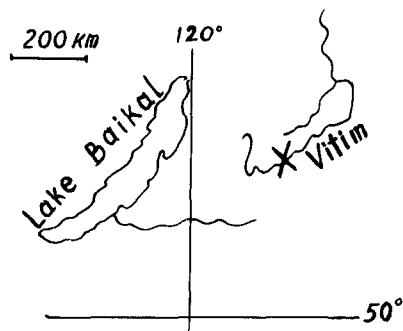


Fig.1. Location of the fossil plant beds (X).

SYSTEMATICS

Genus *Baisia* Krassilov, gen. nov.

Name: After locality.

Type species: *Baisia hirsuta* Krassilov, sp. nov.

Diagnosis: Achene-like disseminules, narrow ovate or flask-shaped, about 4–5 mm long, consisting of a cupule with persistent receptacle bearing fascicles of unicellular hairs much longer than the body. Apical portion demarcated as a low corona showing irregular pits. Receptacle rounded—triangular, slightly cordate, occasionally detached from the achene. Cupule wall soft, with a thin fibrous layer and much thicker stone tissue. Outer epidermal cells tabular, scarcely cutinized. Stone cells elongate, minutely and/or coarsely pitted. Inner epidermal cells tabular, papillate. Vascular bundles consisting mostly of spiral tracheids. Ovule single, orthotropous. Integumental cuticle thick, showing two superimposed layers of polygonal and elongate cells. Nucellus free to the base. Nucellar cuticle moderately thick at the chalazal end, thin above, granular, showing large irregular-polygonal cells.

Baisia hirsuta Krassilov, sp. nov. (Plate I, 1–6; Plate II, 1–10; Plate III, 1–7; Plate IV, 1–3; Plate V, 1, 2; Plate VI, 1–6; Plate VII, 1–5; Plate VIII, 1–4).

Holotype: Institute of Biology and Pedology repository, N 31/321 (Plate I, 1).

Diagnosis: As for the genus.

Description: The achene-like disseminules are frequent in all plant beds and commonly there are several of them on a hand specimen (Plate VII, 5). Most disseminules are preserved as compressions incrustated with a thin layer of carbonaceous material. They are narrow ovate or flask-shaped, bluntly pointed. The apical portion about 0.5 mm long is rather sharply demarcated by a transverse groove. This apical “corona” is irregularly pitted.

The body appears soft and shows rather large tabular cells arranged in longitudinal rows. These cells are distinctly marked on compressions and can be seen under low magnification. At the base there is a persistent receptacle which is delimited from the body by transverse folds.

The receptacle in a side-view is slightly cordate, about 1 mm high, with more or less prominent corner lobes (Plate I, 1). Sometimes an achene is twisted so that a proximal face of the receptacle is exposed on the bedding plane (Plate II, 7). There are also numerous detached receptacles showing rounded (Plate I, 5) or rounded—triangular (Plate I, 6) outlines with a central scar. They are covered with transverse scars arranged in a low spiral and, in adequately preserved specimens, show festoons of laminar appendages which occasionally appear as lanceolate bracts (Plate V, 1, 2) but more often are reduced to short rounded lobes (Plate I, 2, Plate IV, 3).

Plate descriptions

PLATE I (p. 283)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River.

1. Achene showing a thick receptacle and epidermal cells, holotype, $\times 12$.
2. Achene with a stylopodium-like apex (an apical corona) and conspicuous laminar appendages on the receptacle, $\times 12$.
3. Split achene showing nucellar cuticle, $\times 12$.
4. Achene with the looping hair fascicles, $\times 12$.
- 5, 6. Detached receptacles, $\times 12$.

(*ac* = apical corona; *b* = bracts; *c* = cupule; *n* = nucellus; *r* = receptacle).

PLATE II (p. 284)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River.

- 1, 2, 5. Uncompressed achenes showing ovules, $\times 12$.
3. Ovule from the achene shown in fig. 2, $\times 15$.
- 4, 6. Split achenes showing nucellar cuticles, $\times 12$.
7. Achene with a receptacle turned to the foreground, $\times 12$.
8. Achene with a shrunken ovule, $\times 12$.
9. Same, different illumination.
10. Achene showing cordate receptacle, $\times 12$.

(*o* = ovule, *n* = nucellus, *r* = receptacle).

PLATE III (p. 285)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River.

1. Ovule from the achene shown in Plate II, 8, $\times 12$.
2. Nucellus from the achene shown in Plate II, 6 $\times 12$.
3. Nucellar cuticle, $\times 170$.
4. Double cuticle of the coat, narrow elongate cells in focus, $\times 170$.
5. Same, polygonal cells in focus, $\times 170$.
- 6, 7. Inner epidermal cells of the integument, $\times 300$ and 500 .

PLATE IV (p. 286)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River, SEM.

1. Upper part of the cupule broken at the base of the corona, $\times 140$.
2. Epidermal cells of the cupule, $\times 400$.
3. Receptacle showing short laminar appendages, $\times 180$.

PLATE V (p. 287)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River, SEM.

1. Lower portion of the achene showing receptacle, $\times 60$.
2. Same receptacle with the bract-like appendages (*b*), $\times 140$.

PLATE VI (p. 288)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River.

- 1, 3. Spiral tracheids, $\times 300$ and 600 .
- 2, 4–6. Stone cells of the cupule showing various pitting, $\times 600$.

PLATE I

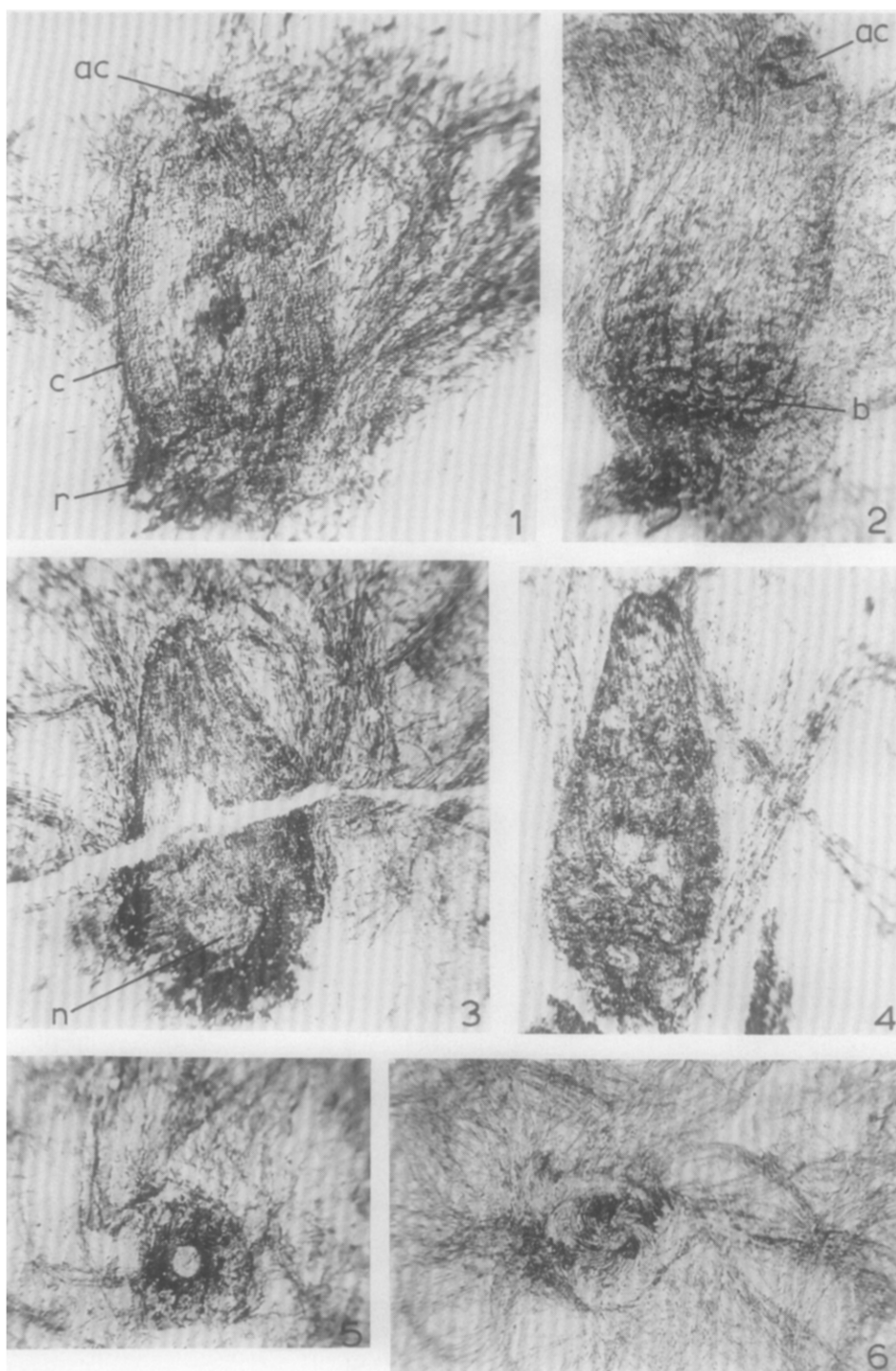


PLATE II (Description on p. 282)

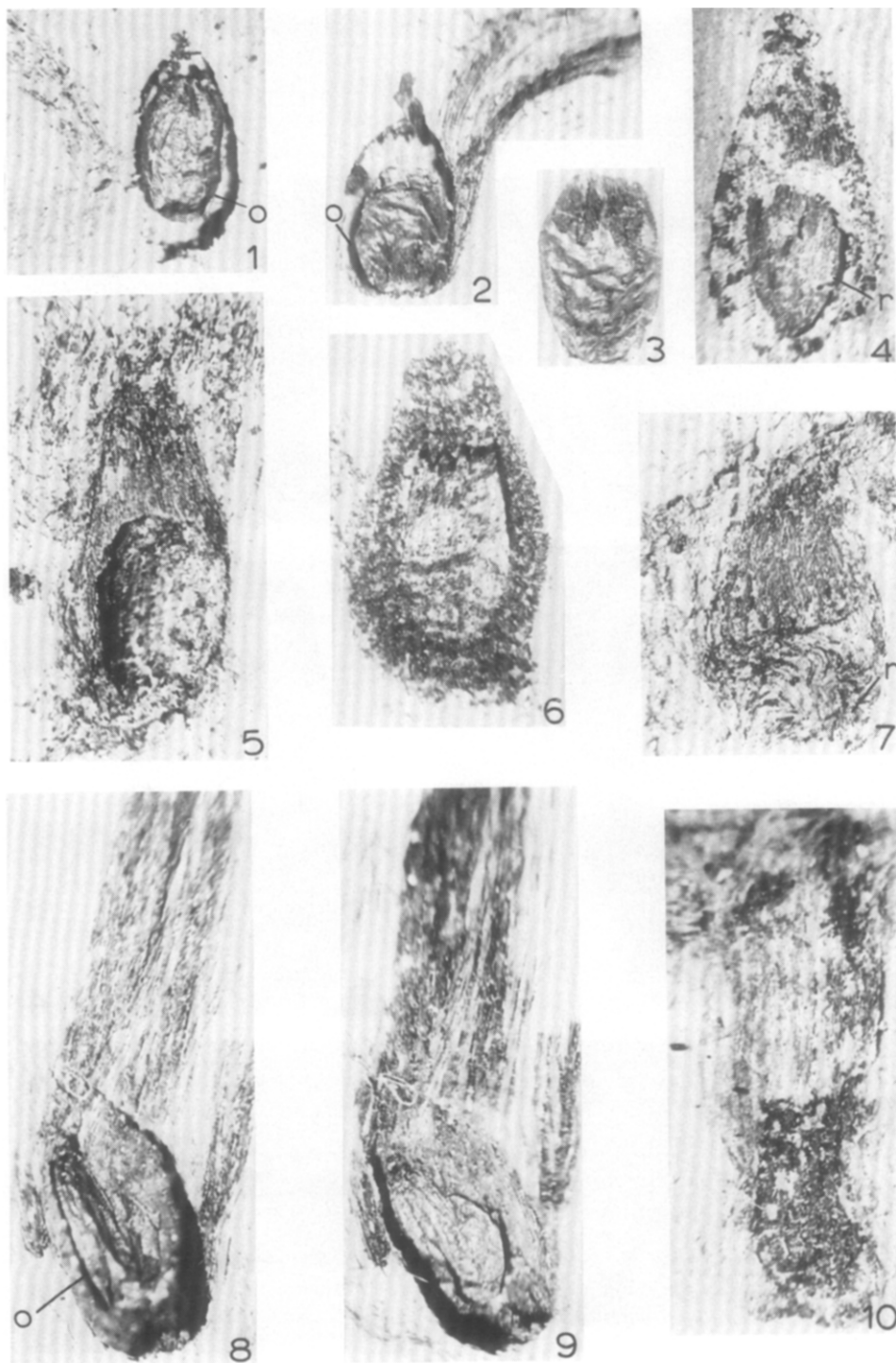


PLATE III (Description on p. 282)

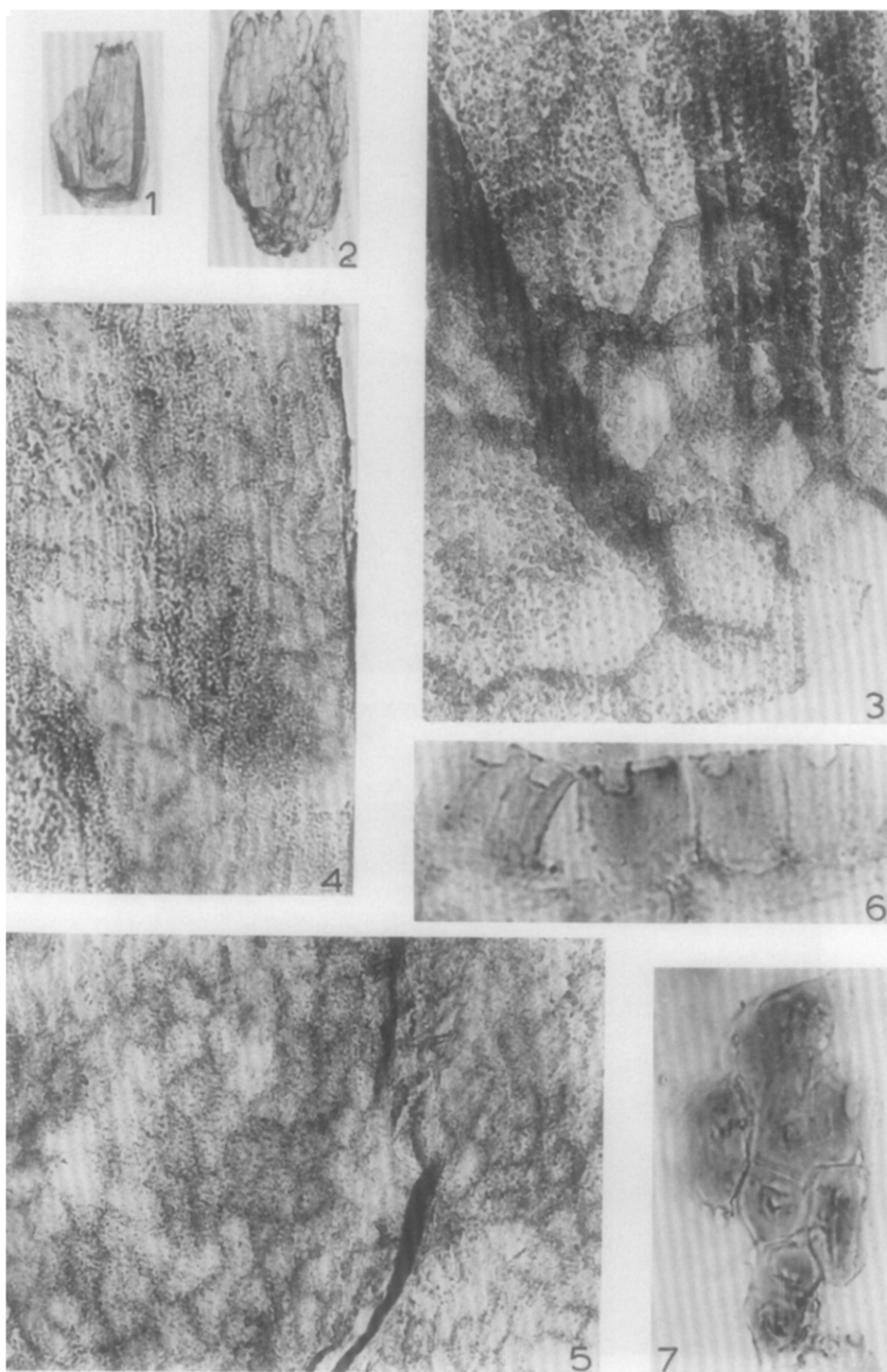


PLATE IV (Description on p. 282)

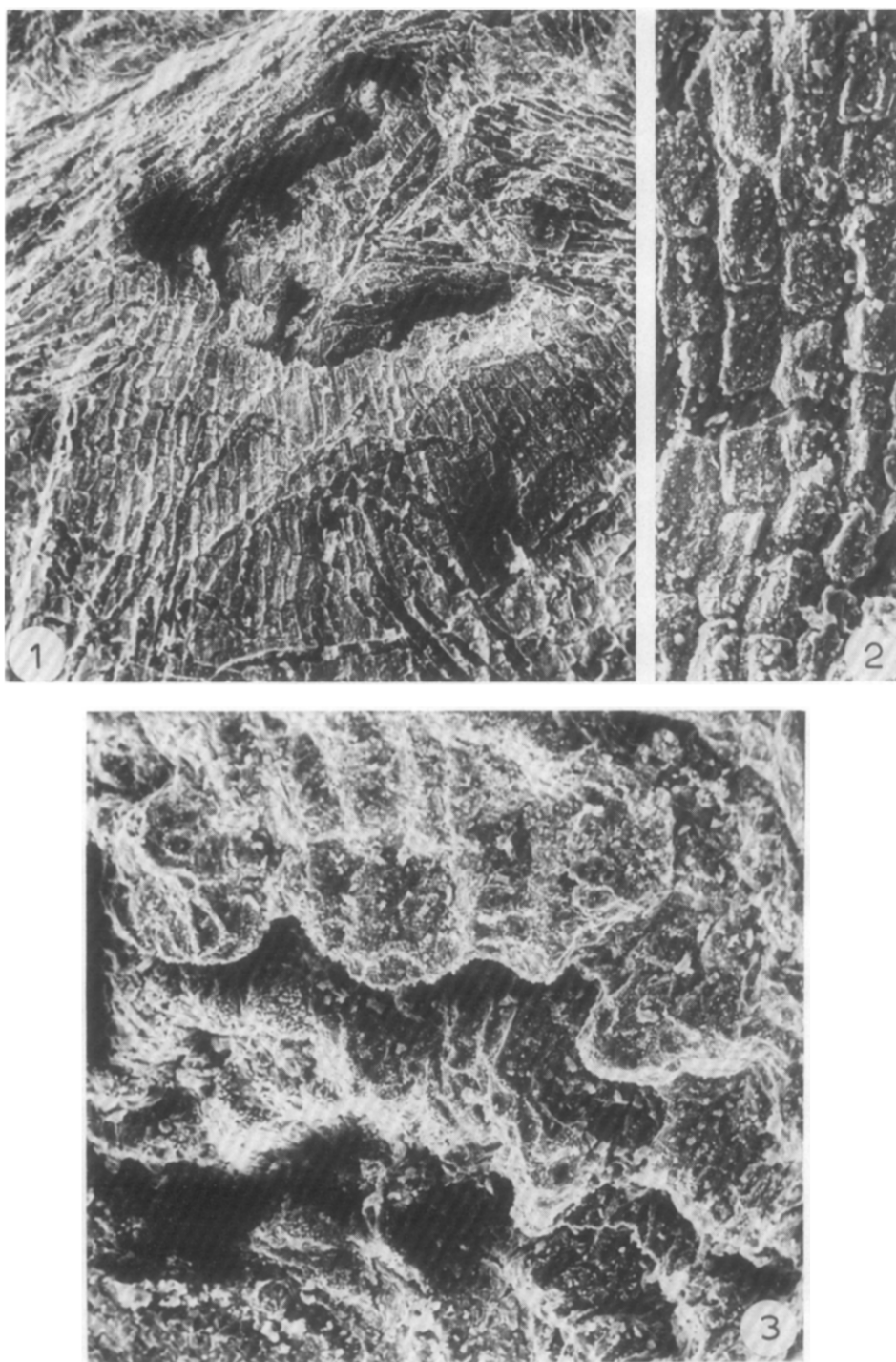


PLATE V (Description on p. 282)

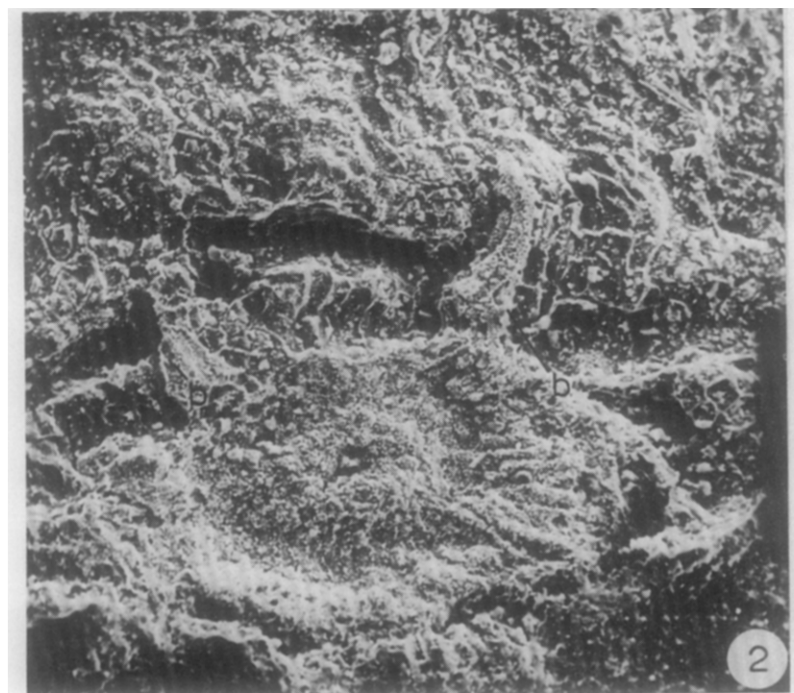


PLATE VI (Description on p. 282)

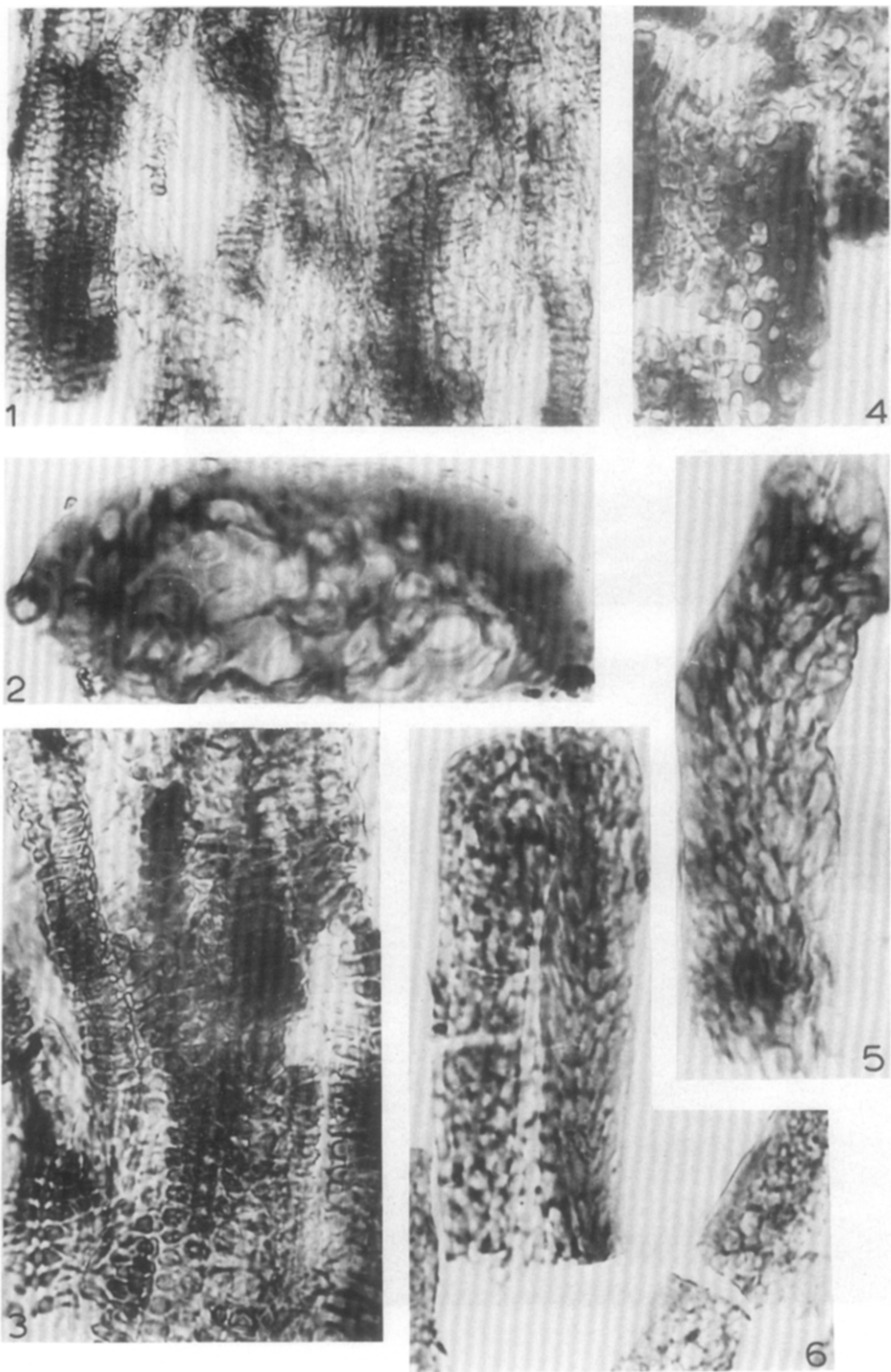


PLATE VII (Description on p. 291)

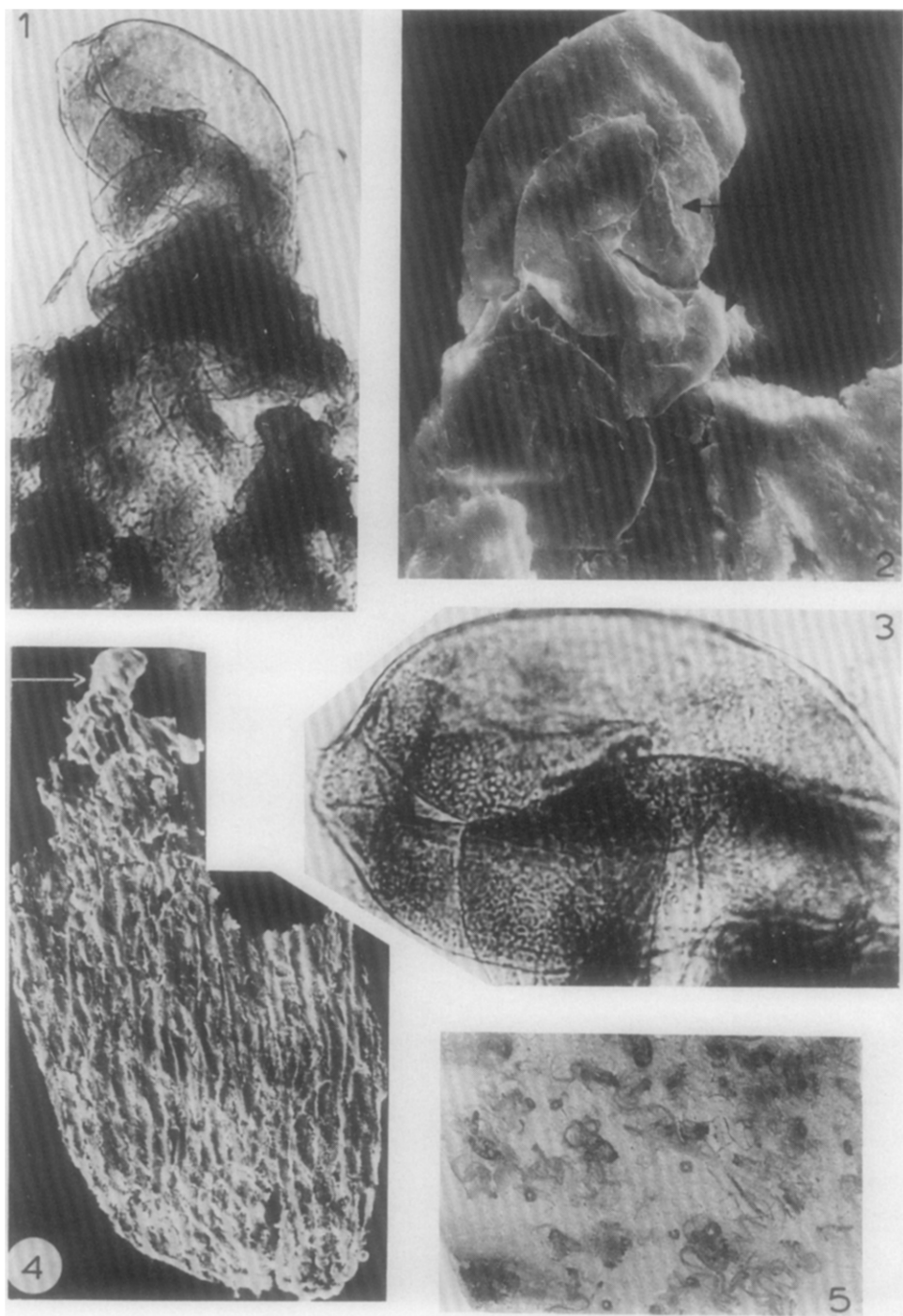


PLATE VIII (Description on p. 291)

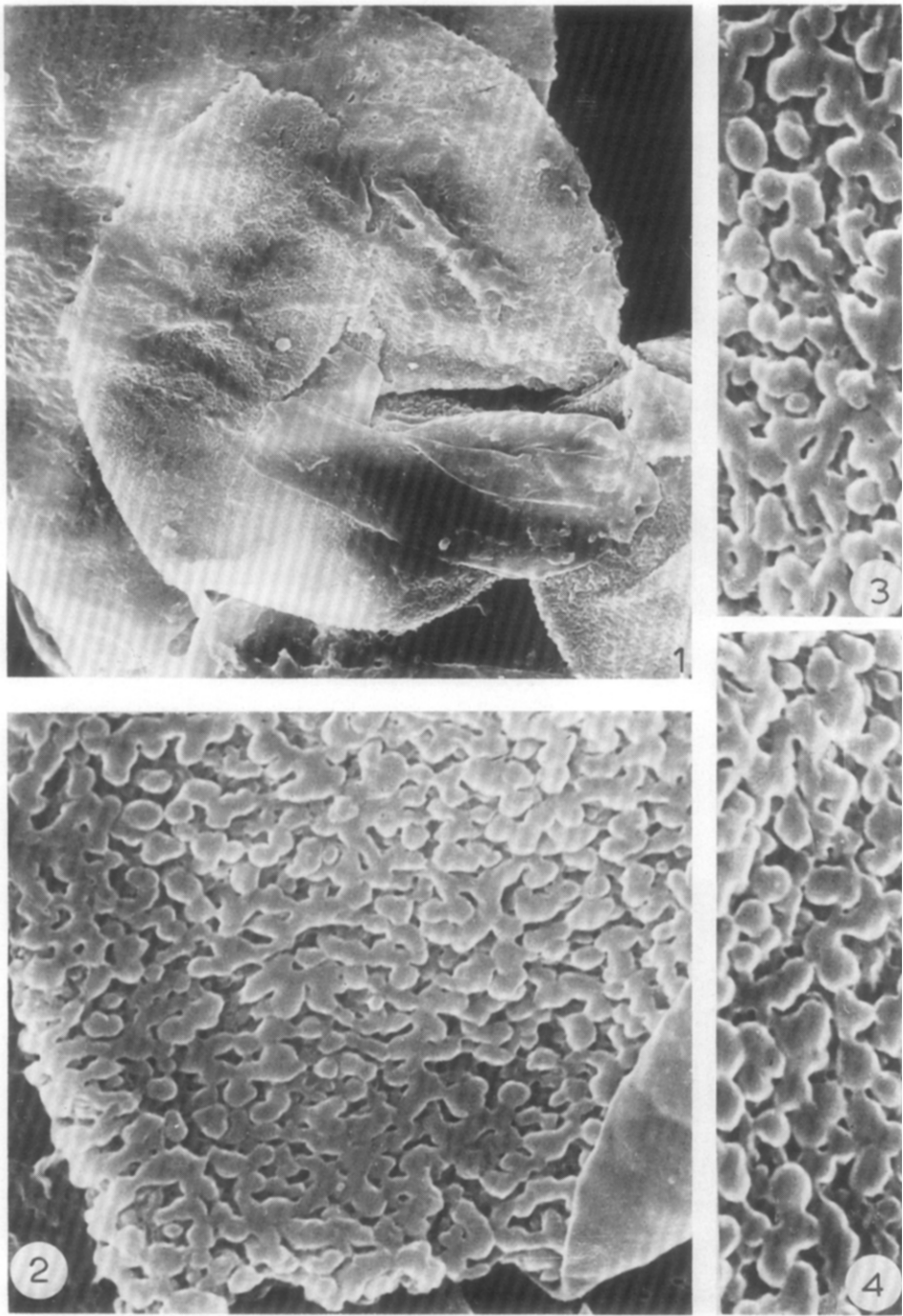


PLATE VII (p. 289)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River.

- 1, 2. Pollen grains at the top of a nucellus, light microscope, $\times 300$, and SEM, $\times 400$ (arrow on pollen grains showing infratectal structures).
3. Top pollen grain from the cluster showing a sulcus gaping to the right end and the infratectal exinal structure, $\times 600$.
4. Nucellus with pollen grains at the top (arrow) $\times 60$.
5. Achenes and detached receptacles on a marl slab, $\times 1$.

PLATE VIII (p. 290)

Baisia hirsuta sp. nov. from the Lower Cretaceous of the Vitim River, SEM.

1. Pollen grain from a cluster shown in Plate VII, 2 with the infratectal structure exposed, $\times 1600$.
2. Clavate-rugulate structure below the tectum a fragment of which is seen in the bottom right corner, $\times 10000$.
- 3, 4. Infratectal clavate-rugulate pattern, $\times 15000$.

Dense tufts of hairs surround the receptacles. On closer inspection the hairs appear to arise in fascicles from the outgrowths (vestigial bracts) of the receptacles. They are several times longer than the body, often looped (Plate I, 4, 6).

The morphology of the achenes remains constant through successive plant beds while their size increases from the average 4×2 mm ($3.5-5.5 \times 1.2-3$ mm) in the lower bed N 31 to 4.4×2.2 mm ($4-5.5 \times 1.9-2.8$ mm) in the middle bed N 15.

A few almost uncompressed specimens show a locule which contains a single ovule or seed. In one case the ovule, apparently shrunken, occupies about $2/3$ of the locule. This achene was photographed intact (Plate II, 2) after which the ovule was extracted and photographed separately (Plate II, 3). It is elliptical, broadly rounded at the chalazal end, bluntly pointed at the apex, with inconspicuous micropyle. The coat is thick, transversely wrinkled. This ovule was then macerated for integumental cuticles (Plate III, 1, 4, 5). In another specimen (Plate II, 1) the ovule almost fills the locule leaving a narrow air-space only (apparently due to shrinkage). The ovule was left in place for documentation. It is somewhat more pointed, with the micropylar end reaching the apical corona of the cupule.

Some compressions are cleaved longitudinally, exposing either the ovule or the inner, supposedly nucellar cuticle (Plate I, 3; Plate II, 6).

The compressions were removed from the rock by HCl. Maceration procedure included a 15 min exposure to dilute HNO_3 , followed by dilute KOH. I failed to obtain an outer cuticle. It appears that the outer epidermis was scarcely cutinized at all. Outer epidermal cells, as seen in SEM (Plate IV, 2), are polygonal, about $100 \mu\text{m}$ wide, but in some specimens they are nearly twice as small. Hairs are unicellular, at least no partitions were observed in transfer preparations.

Epidermis is underlain by a thin fibrous layer below which there is a much thicker stone tissue. The stone yielded two kinds of cells: the long tubulate cells with minute pits and somewhat shorter cells with coarser pits (Plate VI, 2, 4–6). Inner epidermis of the cupule consists of the thin-walled tabular cells showing a prominent median papilla or pit (Plate III, 6, 7). Vascular bundles, occasionally attached to the seed coat, consist of long tracheids with spiral thickenings (Plate VI, 1, 3).

Seed coat cuticle is fairly thick, almost smooth, on closer inspection showing two superimposed layers of different cells: isodiametric polygonal, 30–40 μm wide and narrow elongate, 12–15 μm wide (Plate III, 4, 5). These layers are interpreted as corresponding to the outer and the inner integumental cuticles.

Nucellar cuticle is thickened in the basal region which in most cases is the only obtainable portion. The most complete nucellus (Plate III, 2) is elongate-elliptical, constricted at the base into a vestigial chalazal platform, torn above the middle into triangular teeth (the teeth are cut naturally, not in the course of preparation). The cuticle is granular, showing large polygonal and trapezoidal cells, about $230 \times 65 \mu\text{m}$.

In one case a cluster of pollen grains is preserved at the top of a nucellus. This nucellus was photographed under light microscope (Plate VII, 1) and then transferred for SEM (Plate VII, 2). There are five elliptical pollen grains of unequal size. The largest and most conspicuous grain is 140 μm long and shows a sulcus gaping toward one end (Plate VII, 3). Under the light microscope the exine appears microreticulate while it is smooth under SEM. Of the smaller pollen grains two are smooth while the other two, near the centre of the cluster (arrow in Plate VII, 2), show clavate–rugulate surface pattern (Plate VIII, 1–4). It is evident, however, that this pattern is infratectal, because there are fragments of the outer smooth layer (Plate VIII, 2). The exinal structure can, therefore, be described as alveolar. The tectum might have been partially dissolved by a pollen chamber exudate.

DISCUSSION

These fossils are unlike any of the Mesozoic diaspores. Another achene-like diaspore, *Problematospermum ovale* Ketova from the late Jurassic of Kazakhstan, has a short stalk and bears a long style-like apical tube crowned by a tuft of hairs. Though resembling a dandelion achene, *Problematospermum* has shown some bennettitalean cuticular features (Krassilov, 1973).

In the case of *Baisia*, the persistent receptacle suggests comparison with bennettitalean flowers (or strobili) which have rather similar receptacles bearing bracts, interseminal scales and ovules. The bracts are often hairy and can easily be transformed into the *Baisia*-type fascicles of hairs on vestigial laminar appendages. It is conceivable also that a bennettitalean gynaecium was reduced to a single ovule while a few remaining interseminal scales formed the cupule (Fig. 2). In *Williamsonia*, the tips of interseminal scales are united into a “corona” of which the apex of the *Baisia* cupule can

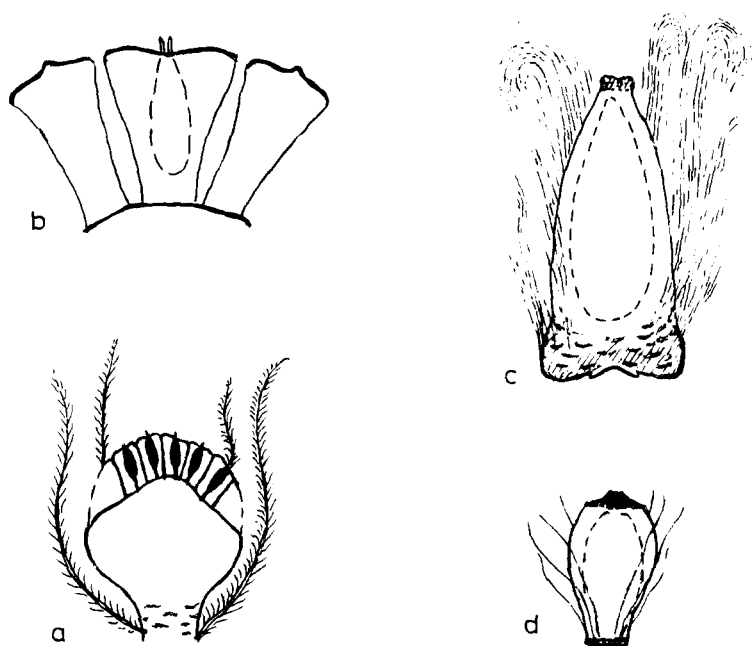


Fig. 2. Sketch-drawings of a, bennettitalean receptacle with a few hairy bracts, ovules and interseminal scales; b, bennettitalean ovule enclosed by fused interseminal scales as is apparently the case in *Bennetticarpus crossospermus* Harris; c, *Baisia* achene; and d, cyperaceous achene (*Eleocharis* sp.).

be a vestige. Free cutinized nucelli and rather large monosulcate pollen grains are also characteristic bennettitalean features.

On the other hand, *Baisia* resembles achenes of some extant cyperaceous monocotyledons, especially those which, like *Eriophorum*, *Carpha*, and several species of *Rhynchospora*, have numerous hypogynous bristles. In *Eriophorum vaginatum* L., the bristles or hairs arise in fascicles from the conical receptacle. There are five fascicles in this species, but a more common number of bristles is six and they are conventionally interpreted as reduced perianth lobes. In *Rhynchospora*, there are usually two series of three bristles each, but some species have as many as twenty bristles. In *Dulichium arundinaceum*, three abaxial bristles are above the stamens supporting a pseudanthial theory of the cyperaceous flower (Schultze-Motel, 1959).

The apical corona of the *Baisia* cupule resembles a persistent style-base (stylopodium) characteristic of many sedge species. Further points of resemblance are the shape and dimensions of achenes and their epidermal cells. Large, tabular, distinctly marked epidermal cells of *Baisia* are exactly like those of many cyperaceous achenes.

The outer coat of the cyperaceous achenes is variously interpreted as (1) an utricle or perigynium — presumably a prophyll-derived membranaceous bladder persistent in the ripe achene (in *Carex* and allied genera); (2) a cupule formed by hypanthial growth of the receptacle in *Scleria* and *Dipla-*

crum; (3) an utricle-like pericarp separated by an air space from the endocarp (in *Coleochloa* and other Lagenocarpeae). The coat characters are related to the floating adaptations and they can be convergently similar despite a supposedly nonhomologous derivation (Gilly, 1943; Haines and Lye, 1972, 1973; Eiten, 1976).

The outer coat of *Baisia* is comparable with the utricle-like pericarp of Lagenocarpeae and with the *Scleria*-type cupule. At the same time, *Baisia* was gymnospermous as to the mode of pollination and retained some vestigial characters suggesting a bennettitalean ancestry. We believe that *Baisia* represents an important evolutionary stage within a gymnosperm—angiosperm transition. It may rule out a textbook notion of bennettites as a blind alley. It may also influence evolutionary thinking in cyperology and related fields of botany. It is no longer compulsory to derive Cyperaceae from Magnoliaceae or any other angiosperm group of entirely different morphology.

One can suggest that all the above-mentioned similarities between *Baisia* and cyperaceous achenes are convergent, thus providing no ground for phylogenetic speculations, especially those which contradict traditional concepts of the angiosperm evolutionary morphology. However, current interpretations of the cyperaceous flower and achene are so ambiguous that any new idea, even so precocious as the derivation of sedges from bennettites via *Baisia*, cannot be easily dismissed.

In the Vitim plant beds, abundant achene-like fossils are not accompanied by adequate record of leaves assignable to the same plant. Bennettitalean leaf fragments are too rare. It is conceivable that in the *Baisia* lineage not only the reproductive structures but also leaves have considerably deviated from the bennettitalean archetype. The plant bearing *Baisia* achenes may have been a marsh herb of a sedge habit with reduced leaves, of which only floating achenes have reached the lake.

REFERENCES

- Eiten, L.T., 1976. Inflorescence units in the Cyperaceae. *Ann. Mo. Bot. Gard.*, 63: 81—112.
- Gilly, Ch.L., 1943. An Afro—South-American Cyperaceous complex. *Brittonia*, 5(1): 1—20.
- Haines, R.W. and Lye, K.A., 1972. Studies in African Cyperaceae. 8. Panicle morphology and possible relationships in *Sclerieae* and *Cariceae*. *Bot. Not.*, 125: 331—343.
- Haines, R.W. and Lye, K.A., 1973. The morphology of *Coleochloa* Gilly and *Afrotrilepis* J. Rayn. *Bot. Not.*, 126: 330—339.
- Krassilov, V.A., 1972. Mesozoic flora of the Bureja River. Nauka, Moscow, 150 pp. (in Russian).
- Krassilov, V.A., 1973. The Jurassic disseminules with pappus and their bearing on the problem of angiosperm ancestry. *Geophytology*, 3: 1—4.
- Krassilov, V.A., 1977. The origin of angiosperms. *Bot. Rev.*, 43(1): 143—176.
- Schultze-Motel, W., 1959. Entwicklungsgeschichtliche und vergleichend-morphologische Untersuchungen im Blütenbereich der Cyperaceae. *Bot. Jahrb.*, 78(2): 129—170.
- Schweitzer, H.-J., 1977. Die Rätö—Jurassischen Floren des Iran und Afghanistans. 4. Die Rätische Zwitterblüte, *Irania hermaphroditica* nov. spec. und ihre Bedeutung für die Phylogenie der Angiospermen. *Palaeontographica*, 161 B (1—4): 98—145.

- Vachrameev, V.A., 1973. Angiosperms and the Early—Late Cretaceous boundary. In: *Palynology of the Mesophyte*. Nauka, Moscow, 131—135 (in Russian).
- Vachrameev, V.A. and Kotova, I.Z., 1977. Earliest angiosperms and associated plants from the Lower Cretaceous of Transbaikalia. *Palaeontol. Zh.*, 4: 101—109 (in Russian).
- Vachrameev, V.A. and Krassilov, V.A., 1979. Reproductive structures of angiosperms from the Albian of Kazakhstan. *Palaeontol. Zh.*, 1: 121—128 (in Russian).
- Zherikhin, V.V., 1978. *Development and Replacement of the Cretaceous and Cenozoic Faunistic Assemblages*. Nauka, Moscow, 198 pp. (in Russian).