

Reproductive structures associated with *Cobbania*, a floating monocot from the Late Cretaceous of the Amur Region, Russian Far East

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ABSTRACT. *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & Johnson, an aquatic plant previously known from the Late Cretaceous of North America is found in the roughly coeval deposits of Amur Province, Russian Far East. It is associated with fruits and dispersed seeds assigned to *Cobbanicarpites amurensis* Krassilov & Kodrul gen. et sp. nov. The fruit emerged from a spatulate bract and was detached at maturity, with persistent laminar appendages and ovoid (olfactory?) bodies. The fruit interior shows a central prominence and low radial ridges. The seeds are numerous, radially disposed in a continuous girdle along the inner fruit wall. Cleared seed compressions show an operculate micropylar cap in line with a chalazal cap or the latter is displaced toward the ventral side and at a variable distance from the hilum. The seed coat consists of two cell layers composed of different, transversely elongated and polygonal papillose cells, with fibres in the inner layer. Comparable spatulate fruits or coenocarps are known in the extant Arales and Alismatales. Similar features of seed morphology occur in the Hydrocharitaceae and other alismatalean families. Paleogeology of *Cobbania* plant is discussed on account of its stratigraphic proximity to dinosaur localities.

KEY WORDS: aquatic plants, monocots, Alismatales, Arales, dinosaur feeding, Late Cretaceous, Amur Province, Russia

INTRODUCTION

The Cretaceous and Paleogene aquatic monocots of aroid–alismatoid affinities have recently attracted much attention as a group of considerable phylogenetic and paleoecological significance. Prominent among them is *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & Johnson, an easily recognizable aquatic plant previously known as *Pistia corrugata* Lesquereux from the Campanian of Wyoming, U.S.A. and recently described under new generic name from the coeval deposits of Dinosaur Provincial Park in southern Alberta (Stockey et al. 2007).

Cobbania corrugata was based on stems with roots and leaf rosettes. No reproductive

remains have been ever found attached to the vegetative parts and their purported assignment to the Araceae was based on the leaf morphological comparisons with *Pistia stratiotes* L. and the other extant representatives of the family, as well as *Limnobiophyllum scutatum* (Dawson) Krassilov that was originally assigned to the Arales on the basis of stomatographic characters (Krassilov 1973). Two fruits and dispersed “smooth seeds” associated with *Cobbania* in the Canadian locality were briefly mentioned as of unknown affinities (Stockey et al. 2007, p. 614).

Even before formal validation of the genus, the Asiatic *Cobbania* was recognized by Kirk

Johnson from photographs of specimens found in the Kundur Locality of the Amur Province, Russian Far East (Fig. 1). The associated fruits and seeds appear identical with those found in the Canadian locality making their assign-

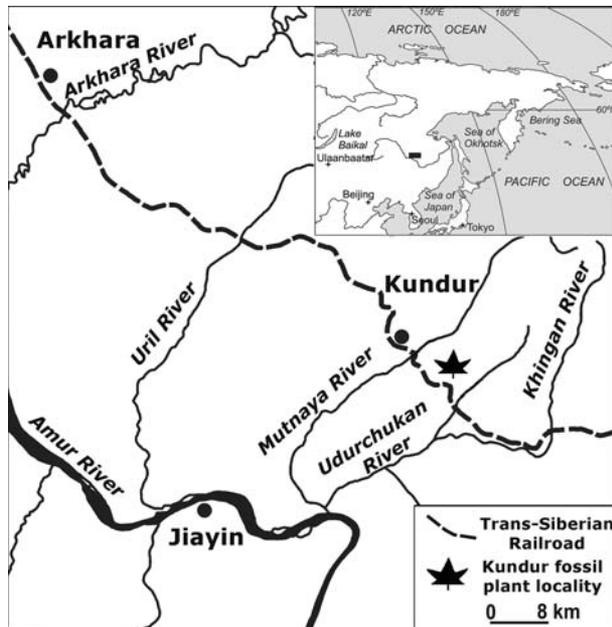


Fig. 1. Kundur fossil plant and dinosaur locality in the Amur Province, Russian Far East

ment to *Cobbania* plant fairly probable. Yet because these reproductive structures are not organically connected to the vegetative parts they are here described under separate name as a new morphotaxon. Seeds are studied in detail and compared with different groups of extant monocots.

MATERIAL AND METHODS

The material was collected from the Kundur Formation exposed in a road cut of the Federal Highway Chita – Khabarovsk (Fig. 1) 10 km southeast of Kundur Village and about 2.5 km east of the Trans-Siberian Railway (GIS coordinates 49°03'46.7"N, 130°52'18.2"E). The Kundur Formation is represented by cross-bedded sandstones alternating with siltstones and lenticular clay shales with a slender coal seam (detailed description in Bugdaeva et al. 2001, van Itterbeek et al. 2005). It is assigned to the Campanian on the basis of palynological data (Markevich et al. 2005a, b). The macrofossil assemblage includes ferns, ginkgophytes, taxodiaceous conifers, platanoid leaves, *Trochodendroides*, and diverse aquatic plants. Prominent among the latter are heterosporous aquatic ferns and a floating angiosperm *Quereuxia*. A rich dinosaur locality occurs in coarse sandstones upsection.

Cobbania was found in the ferruginous yellowish brown clay lenses interpreted as oxbow lake deposits.

Its abundant stems, roots, leaf rosettes and detached leaves sometimes form monodominant or single-species accumulations (mats) covering the bedding planes.

Fruits and seeds found with *Cobbania* occur in slab associations with, or impressed upon, the leaves. While the leaf remains are all impressions, the dispersed seeds are weathered compressions and those inside the fruit locules are well-preserved compressions. Conceivably, the exceptional preservation of the intact seeds is due to anoxic conditions inside the fruit locule filled with a rapidly degrading organic material, such as mucilage.

The plant fossils were studied and photographed under the stereomicroscope Leica MZ16 equipped with the digital camera Nikon Coolpix 4200. A few seed compressions were removed from the locule and cleared by a brief exposure to nitric acid followed by dilute potassium hydrate. The transparent compressions were studied under the light microscope Nikon Eclipse 801

The collection is deposited in the Geological Institute, Russian Academy of Sciences, Moscow (GIN 4867-K16).

SYSTEMATIC DESCRIPTION

Genus *Cobbanicarpites* Krassilov & Kodrul, gen. nov.

Type species. *Cobbanicarpites amurensis* Krassilov & Kodrul sp. nov., designated here.

Etymology. From *Cobbania*, a fossil leaf genus and *carpos*, fruit.

Diagnosis. As for the type species.

Species content. Type species only.

Cobbanicarpites amurensis Krassilov & Kodrul, sp. nov.

Pl. 1 figs 1–5, Pl. 2 figs 1–4, Pl. 3 figs 1–6, Pl. 4 figs 1, 2

Holotype. GIN 4867-K16/3-54 and slides GIN 4867-K16/3-54 a-c (Pl. 1 figs 4, 5, Pl. 2 figs 1–4, Pl. 3 figs 1–6, Pl. 4 figs 1, 2), designated here.

Type locality and stratum. The Kundur locality 9 km southeast of the Kundur Village, Amur Region, Russian Far East (49°03'46.7"N, 130°52'18.2"E); a lenticular clayey horizon of the Kundur Formation, Campanian, Late Cretaceous.

Etymology. From the Amur River.

Diagnosis. Fruit globose, subtended by a funnel-shaped spatulate bract, emergent

and detachable at maturity, with a persistent whorl of numerous (about 24) short laminar appendages and ovoid bodies (nectaries?). Fruit interior with a central prominence and low radial ridges. Seeds numerous (about 30), radially disposed in a continuous girdle along the inner fruit wall. Seed shapes elliptical or obovate, 1.4–1.8 mm long, straight or slightly bent, with small-celled caps on both ends. Micropylar cap operculate, in line with chalazal cap or the latter ventrally displaced and at a variable distance from a knob-like hilar scar. Seed coat of two cell layers composed of, transversely elongated and polygonal papillose cells, with fibres in the inner layer.

Description. The holotype is a detached fruit selected on account of well-preserved seed compressions. It is a compressed rounded body 6 mm in diameter. The interior is partly exposed at broken wall, showing a central knob (Pl. 1, fig. 4, C) and a few feebly marked ridges radiating from it. Small polygonal cells are locally discernible on fragments of fruit wall. Eight overlapping seeds are disposed in a continuous arch that is not interrupted by the ridges. When removed they reveal a lower tier of seeds tightly appressed to the upper one. Some seeds appear to be attached to the inner fruit wall by minute funicles that are occasionally well marked (Pl. 1, fig. 5 arrows). A few persistent tepal-like appendages are seen at the top of the fruit body (Pl. 1, fig. 4, A), but these are better preserved in a specimen described as a paratype below.

Paratype no. 4867-K16/3-55 (Pl. 1, figs 1–3) appears to represent an earlier stage of fruit development from a radially symmetrical floral structure 8 mm in diameter emerging from a spatulate bract (Pl. 1, fig. 1, S). Seeds (or maybe ovules) are elongate-ovate, radially disposed (Pl. 1, fig. 3). About 15 seeds are fully exposed, but more are immersed in the rock matrix, with only apices protruding beneath the upper tier. Their complete set must have been no less than thirty, perhaps as many as forty.

A circle of short laminar appendages (Pl. 1, fig. 1, A) is impressed at a somewhat higher level than the central part that is filled with overlapping seeds or ovules. About 12 appendages are preserved over one half of the perimeter; their complete set must be no less than 24. They are irregular lingulate or trapezoid,

flat or slightly reflexed, about 1 mm long, truncate or notched with swollen apices.

The spatulate bract is 6.6 mm long, 2.5 mm wide, preservationally truncate at base, expanded to 5.5 mm and flared at the mouth.

Three cleared seed compressions removed from the holotype are shown in Plates 2–4. They are ovate to obovate, straight or slightly curved, 1.4–1.8 mm long, 0.9–1.2 mm wide, showing no evidence of a raphe (dark marginal band in Pl. 3, fig. 1 represents a compression fold), with nearly symmetrical small-celled caps at both ends. The micropylar pole is recognized as one with a flared integumental extension (crown or collar) of small cells encircling the micropyle. The crown (part of it) is detachable as an operculum leaving a circular scar. The chalazal pole has a thick cap of concentrically disposed small cells. It can be in line with the micropylar cap or displaced towards the ventral side. The hilar scar appears as a small knob that can be displaced at a variable distance from the chalazal cap.

The seeds seem to represent somewhat different developmental stages. A smaller one, GIN 4867-K16/3-54c, with a more conspicuous nucellar beak may represent a very early development from the ovule (Pl. 3, figs 3–5, Pl. 4, fig. 1). It is straight, obovate, 1.4 × 0.9 mm, with the crown shed exposing a conical nucellar beak (epistase), erect in the median plane and in line with chalaza that is thickened, but not furnished with a concentric cap. The epistase is composed of small thick-walled longitudinally striated cells protruding as minute dents over the slopes and continuous over the summit (Pl. 3, fig. 5). It is surrounded by a concave operculum scar, with the seed coat layers extended as raised shoulders on both flanks of it.

Seed GIN 4867-K16/3-54a (Pl. 2, figs 1–4) is ovate, 1.7 × 1.2 mm, with a short apical protuberance filled with dark matter at the pointed end representing a micropylar tube. It is surrounded by a circular scar with irregularly raised borders (Pl. 1, fig. 2, arrow) marking the position of a shed operculum. A knob-like prominence of a hilum scar (Pl. 2, fig. 1, Hi) occurs at the opposite end of the seed body, which is broadly truncate. The chalazal concentric cap of thick small tabloid cells (Pl. 2, fig. 3, Ch) is displaced sideways in the median plane. It is partly covered with the outer cuticle.

Seed GIN 4867-K16/3-54b (Pl. 3, figs 1, 2, 6) is oblong, 1.8×1 mm, dorsally slightly arched, with a thin-walled micropylar tube oblique to the median line, surrounded by a massive collar of radially disposed small tabloid cells (Pl. 3, fig. 1, Mi). The top of the crown is shed exposing the micropylar tube. At the opposite end, hilar scar is seen as a longitudinally orientated conical protuberance (Pl. 3, fig. 6, Hi) on the margin of the chalazal cap of small concentric cells (C") similar to cells of the apical cap. However, the chalazal cap is displaced to the ventral side and turned obliquely to the median line of seed body.

In transmitted light, the seed coat reveals two cell layers covering seed body between the apical and basal caps. The outer layer is expanded toward the hilum at the basal end and wedges out at the shoulders of the crown at the apical end. The layers are formed of dimorphic cells, the inner of which is covered with cuticular papillae. In optical section (Pl. 4, fig. 1 Ol), the outer layer is composed of thin feebly cutinized cells. The inner layer (Il) is much thicker and apparently fibrous. Small lenticular thickenings between them are the cuticular papillae in side view.

In surface view, cells of the outer layer are elongate, transversely stretched, strongly marked, about 100×35 μm , wedge-shaped and interlocked or obliquely truncate at lateral ends (Pl. 5, figs 2, 4). This layer is responsible for the transverse striation of seed body seen at low magnification. The inner layer seen at a lower focus is composed of polyhedral cells about 50×40 – 50 μm , their angular flanks forming longitudinal zigzag lines over the seed body (Pl. 5, fig. 2).

Long pointed fusiform sclerenchymous fibres extend from the base of the crown down the seed body (Pl. 4, fig. 2, F). They are difficult to assign a definite position in the seed coat, supposedly in the inner layer. Scattered over the outer layer are small solid spinules with a dark content arising from an expanded base with cuticular folds radiating from it (Pl. 4, fig. 2, Sp). Cells of the inner layer bear large hollow papillae on the outer periclinal wall. The papillae are dome-shaped, pointed or truncate, in the latter case appearing as annular thickenings in surface view (Pl. 2, fig. 4, P; Pl. 5, fig. 1).

Interpretation and comparison. *Cobbanicarpites* appear to be a many-seeded

fruit emerging from a spathe. The disposition of seeds suggests derivation from a unilocular ovary with parietal placentation. However, the fruit interior shows a central prominence (carpophore intruding the fruit interior?) and radial ridges. Although these features are not very well expressed in the fossil, they must be taken into account as indicating a possibility of a coenocarpous nature of the fruit. The epigynous appendages form a perianth-like whorl of many parts. They are short laminae associated with large glandular bodies and are comparable to staminodal appendages in a number of both monocot and dicot families, including the Hydrocharitaceae and Nymphaeaceae.

The seeds are peculiar in having well developed and nearly symmetrical micropylar and chalazal caps. Their polarity suggest derivation from an orthotropous ovule. Plate 3, figures 3–5 may represent such an ovule at a very early stage of seed development, lacking a chalazal cap, but showing a well developed epistase that usually degrades later in development. Further stages are characterized by a tendency to acquire a hemitropous polarity (Maheshwari 1950) by the seed body turning at an angle to the funicle, with the hilar scar shifting away from the chalaza.

A well-developed chalazal cap is a feature related to seed dormancy in several angiosperm families, including the Convolvulaceae, Geraniaceae, Fabaceae, and Malvaceae (Werker 1980/1981, Baskin & Baskin 1998). It is formed of chalazal subpalisade cells preventing water uptake until the cap is ruptured prior to germination (Werker op. cit., Baskin & Baskin op.cit).

The seed coat is distinctly bilayered. In terms of testa/tegmen differentiation (Corner 1976), it consists of a thin one-layered exotesta formed of the outer integument of the ovule) and a thicker fibrous tegmen formed of the inner integument. This interpretation is supported by the outer cells stretched across the longitudinal fibres, as is often the case in bitegmic ovules. Both layers are traceable from the basal cap to the base of the micropylar cap. Their separating papillose cuticle may correspond to a joint cuticle of endotesta and exotegmen that are often fused in seeds with a thin seed coat (examples in Briggs et al. 2005). The patchily developed, perhaps incipient fibrous layer (Pl. 4, fig. 2, F) is certainly substetal and apparently endotegmic.

The presence of a spathe suggests morphological affinities with the Arales or Alismatales. Typical of the aroids are pseudanthial inflorescences (spadices), the female part of which produces a cylindrical infructescence of tightly packed, but distinct small fruits (berries). A comparison with typical aroids does not account for the shape of the fruit and the laminar appendages of *Cobbanicarpites*. The seed compressions are tightly appressed to each other and difficult to separate, with no intervening fruit wall tissue.

However, in *Cobbanicarpites*, the fruit interior shows a central prominence (a carpophore scar?) and radial ridges. Although these features are not very well expressed in the fossil, they must be taken into account as indicating a possibility of a coenocarpous nature of the fruit. In the Araceae, only two genera of more than one hundred, *Syngonium* and *Cryptocoryne*, have coenocarpia, a highly aberrant feature in the family (Mayo et al. 1998).

At the same time, an aquatic genus *Pistia* (Pistiae) has inflorescence of a solitary pistillate flower in a spathe (topped by a cluster of staminate flowers). The ovary is unilocular with many parietal ovules. In fruit, the seeds are seen through a thin transparent pericarp. A similar situation in *Cobbanicarpites* suggests a likewise thin and brittle fruit wall, through which seeds are imprinted, and liberation of seeds through decay of pericarp. The seeds are operculate. The analogy can be extended to the epigynous whorl of short laminar appendages that may correspond to reduced staminate flowers, although the shapes and dimensions of these organs are very different in *Pistia* and *Cobbanicarpites*.

Spathes with solitary flowers occur in alismatoid monocots as well. In particular, the Hydrocharitaceae comprises genera with epigynous flowers on a stout hypanthial pedicel as in *Hydrocharis* (Cook & Lüönd 1982), *Elodea* (Catling & Wojtas 1986), and *Blyxa* (Rangasamy 1941). In *Elodea*, the female flower breaks through the apex of the spathe and is carried to the water surface on an elongate hypanthium (Cook & Urmi-König 1985), a condition that can be assumed for *Cobbanicarpites* as well. Fruits with rudimentary partitions and numerous seeds developing from parietal ovules are rather typical of the Hydrocharitaceae, whereas the perianth-like appendages of *Cobbanicarpites* are more similar to those in the Posidoniaceae and some other Najadales sensu

Dahlgren et al. (1985), purportedly staminodal in this group. The ovate bodies associated with the laminar appendages (Pl. 1, fig. 4, arrows) is another feature encouraging comparison with the Hydrocharitaceae and allied families of alismatalean (s.l.) affinities, in which such nectaries develop from a distal (antepetalous) whorl of staminodes (Cook & Lüönd 1982).

Seeds present the most distinctive characters, of which the general shape and the presence of a detachable micropylar cap prompt a comparison with both the alismatoid and aroid monocots, as well as with the Nymphaeaceae. In distinction of the latter, the seeds of *Cobbanicarpites* are interpreted as basically orthotropous with symmetrically developed micropylar crown and chalazal cap composed of nearly identical cells. On account of a well-developed epistase beneath the crown they are similar to the Eocene *Keratosperma allenbyense* Cevallos-Ferriz & Stockey assigned to the Araceae (Cevallos-Ferriz & Stockey 1988, Smith & Stockey 2003). However, the latter are anatropous with a funnel-shaped crown and a prominent hypostase. Similar Late Cretaceous seeds are compared with those of the Araceae or Lemnaceae possibly representing an allied extinct group (Krassilov & Makulbekov 1995, Estrada-Ruiz & Cevallos-Ferriz 2007). The Late Campanian *Operculifructus lopezii* Estrada-Ruiz & Cevallos-Ferriz and *O. lotomatensis* by the same authors are described as developing from orthotropous ovules, with operculum intruding the funnel-shaped apical extension of the outer integument and with a thickened chalazal zone of rectangular or polyhedral cells. Four integumental zones are distinguished in *Operculifructus lopezii*, whereas *O. lotomatensis* is bitegmic (Estrada-Ruiz & Cevallos-Ferriz 2007).

In *Cobbanicarpites*, the chalazal cap is displaced from the strictly orthotropous position betraying a tendency to hemitropous polarity. The position of hilum relative to chalazal cap varies from adjacent to distinctly separate. A similar inter- and intraspecific variability, with hilum ranging from subbasal to subapical is described in anatropous seeds of extant and fossil *Stratiotes*, the Hydrocharitaceae (Palamarev 1979, Cook & Urmi-König 1983). Bitegmic condition with two-layered integuments becoming the one-layered seed coat components is typical of the Hydrocharitaceae (Lakshmanan 1963, Birch 1981).

Unlike most of the aroid and alismatoid seeds those of *Cobbanicarpites* are scantily ornamented with small spinulose trichomes and on account of this character can be confused with seeds of some aquatic and even terrestrial dicots.

Yet, while ornamentation of the seed surface widely varies in both Araceae and Hydrocharitaceae, the papillose inner integument is a rare feature found so far in the Hydrocharitaceae alone (Lakshmanan 1963).

ASSOCIATED LEAVES

In the Kundur locality, *Cobbanicarpites* is found in close association with *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & Johnson, often occurring on the same slabs and even imprinted upon the leaf impressions. Other plants are rare in the *Cobbania* beds and *Cobbanicarpites* is not assignable to any of them. Fruits and seeds reported from the Canadian locality of *Cobbania corrugata* (Stockey et al. 2007) are quite similar, although not studied in detail. We therefore assume that *Cobbanicarpites* belongs to the *Cobbania* plant.

Cobbania corrugata (Lesquereux)
Stockey, Rothwell & Johnson, 2007

Pl. 5, figs 1–4; Fig. 2

Syn. *Cobbania corrugata* Stockey, Rothwell & Johnson 2007; full synonymy in this work.

Description. Specimen GIN 4867-K16/3-23 (Pl. 5, fig. 1) is a rosette of small, perhaps juvenile leaves attached to a corm-like stem. The leaves are orbicular, about 2 cm wide, with a broad slightly undulate, rim, proximally constricted into a not clearly demarcated petiole-like base. Minute scars at the base of the leaves are suggestive of stipules, but this feature is not unequivocally represented in the material.

Seven distinct parallel veins run through the basal part and diverge in the blade as its primary veins, branching at about 45° at a variable distance from the base. The branches join into a thin collective vein interstitial between the primaries. Lateral primaries and their branches enter the rim forming three acrodromous intramarginal veins traversed by a series of cross-veins. In the central part of the blade, the tertiary venation is reticulate, forming

irregular-polygonal areoles that are filled with the likewise irregular higher order areoles.

Another specimen GIN 4867-K16/3-53 (Pl. 5, fig. 2) is a rosette of larger leaves, 2–3 cm wide. Here the leaves are more distinctly petulate than in the juvenile rosette, with a sharp hinge line between the orbicular blade and the petiole-like base. A larger leaf in Pl. 5, fig. 2 is impressed their adaxial face up showing indistinct venation. The smaller leaf of the rosette and a number of detached leaves (Fig. 2) show their abaxial face with a pad of aerenchyma in the central part of the blade bordered by the acrodromous primaries with festoon-like outer branches. The blades are pitted with trichome bases, several per a higher order areole in the central part, but denser over the rim (Pl. 5, fig. 4).

The larger detached leaves attain up to 4.5 mm in diameters. Disintegrated fruits and shed seeds are often superposed upon the leaf impressions (Pl. 5, figs 3, 4).

Comparison. Asiatic *Cobbania* is similar in all the taxonomically significant features and is here considered to be conspecific with American *C. corrugata*. The distinctions seem mostly interpretational. Thus, we failed to observe a division of the primary veins into adaxial and abaxial series as inferred by Stockey et al. (2007). The leaves are not three-dimensional,

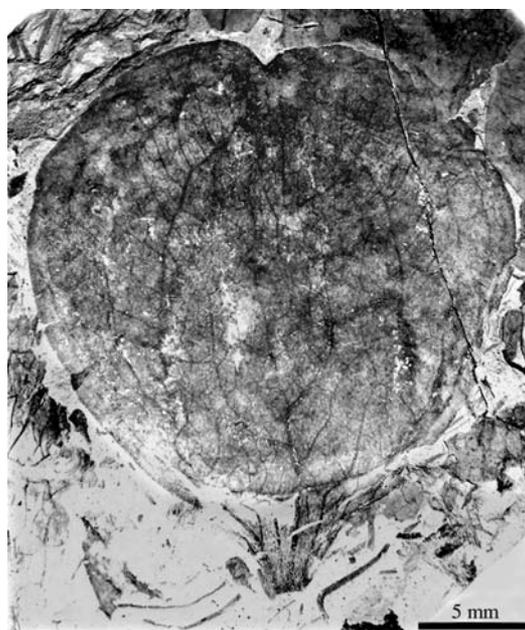


Fig. 2. *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & Johnson, leaf showing a central pad appearing as aerenchyma of floating leaves in *Hydrocharis dubia* (Cook & Lüönd 1982)

but they have air pads, on which venation is well engraved.

Cobbania was assigned to the Araceae mostly on account of the vein pattern (Stockey et al. 2007). Yet in the Araceae, the sympodial collective veins (e.g., in the Anthurieae) commonly associate with pinnate, rather than acrodromous venation (Bunting 1986, Mayo et al. 1998). Although areolate venation occurs in the aroids, its hierarchical 4-order structure in *Cobbania* is unique among the present day aquatic monocots.

None of the present day aroids is comparable with *Cobbania* in the life form. Even *Pistia stratioides* L., an aberrant member of the family, conspicuously differs in having acaulescent floating rosettes of emergent leaves, which are flabellate, rather than orbicular, with digitate venation.

On the other hand, quite similar growth forms with contracted and stoloniferous stems, adventitious roots, floating leaf rosettes of orbicular leaves with acrodromous venation and the analogously positioned abaxial pads of aerenchyma occur in the Hydrocharitaceae (e.g., *Hydrocharis dubia*; Cook & Lüönd 1982).

DISCUSSION

Palaeobotanical data on monocots of the aroid – alismatoid affinities are highly controversial. A possibility of modern families being represented in the Cretaceous already depends on how old the group can be. The Early Cretaceous age is claimed for the Araceae on evidence of striate pollen grains *Mayoa portugalica* (Friis et al. 2004) compared with those of *Spathiphyllum* and allegedly different from *Welwitschia* and extinct gnetophytes in being inaperturate rather than monocolpate. In fact, monocolpate pollen morphology occurs in *Spathiphyllum* as well (Hesse et al. 2000, Tarasvitch 2002), whereas the morphologically and ultrastructurally similar proangiospermous Triassic pollen grains of *Equisetosporites chinleana* – *Cornetipollis reticulata* group include inaperturate forms (Pocock et al. 1990, Vasanthi et al. 2004). In view of these findings, an araceous and even angiospermous affinities of *Mayoa* seem highly questionable. Such pollen morphotypes do not prove the Araceae as a family of early angiosperms.

A number of Late Cretaceous leaves and a few fructifications have been recently assigned to the Araceae (Bogner et al. 2005, 2007). However, the better studied of them are not unequivocal members of this family, perhaps representing an ancestral “synthetic” alismatoid – aroid group sensu Estrada-Ruiz & Cevallos-Ferriz (2007) that might survived well into the Tertiary.

Cobbania plant is remotely comparable to *Pistia*, an aberrant and somewhat questionable member of the Araceae. It was also compared to *Limnobiophyllum*, supposedly a link between the Araceae and Lemnaceae (Kvaček 1995). At the same time, it shares some critical features, both vegetative and reproductive, with the Alismatales s.l., in particular, the hydrocharitoid – najadoid group. Among the latter, the Hydrocharitaceae has a sparse fossil record since the Eocene, with some dubious Late Cretaceous occurrences (*Thalassiocharis* Debey in Miquel 1853). Systematic position of the family is controversial: it is most commonly placed in the Alismatales s.l. (Mayo et al. 1998) or Alismatales s.s., with the najadoid families excluded (Dahlgren et al. 1985) or is separated in a monotypic order Hydrocharitales (Cronquist 1981).

In growth habit, *Cobbania* plant is close to *Hydrocharis*, which includes both bottom-rooted and free-floating forms with rosettes of reniform to orbicular leaves with aerenchymous pads and acrodromous venation. However the network of minor veins is more complex in *Cobbania*, comparable to some present day aroids and dicots. The fruit morphology is here interpreted as combining features aberrant in the Arales (coenocarps in *Cryptocoryne*; solitary gynoecia in *Pistia*), but commonly occurring in the Najadales (spathe with solitary flowers, epigynous staminodal appendages). The seeds exhibit certain characteristic features of the Hydrocharitaceae, such as a flexible location of hilum relative to chalaza and papillose inner integument (exotegmen of seed coat). Orthotropous condition is thought to be plesiomorphic in the basal monocots (Igersheim et al. 2001). The plant is therefore “synthetic”, sharing characters of at least two and probably more recent groups of aquatic plants.

The taphonomy of *Cobbania* from Kundur locality suggests a rapid prolific growth developing a considerable leaf mat biomass, as in the present day *Elodea* or *Egeria*, the prolific

aquatic weeds significant as a food resource for various animals (Catling & Wojtas 1986). Cook & Urmi-König (1985) indicate standing crop of 52 200 tones dry weight for *Elodea potamogeton* in Lake Huinamarca, where this species occupies about 22 km², 16% of water surface.

Like these aquatics, *Cobbania* plants might have proliferated in warm climate, which explains its bloom in the Campanian, the warmest Late Cretaceous age (Krassilov 1975), followed by a decline in the Maastrichtian. The Amurian dinosaurs are found above the *Cobbania* beds at Kundur. A possibility of dinosaur foraging upon leaf mats of aquatic macrophytes is discussed in Krassilov and Makulbekov (1995) on account of abundant lemnooid seeds in the Maastrichtian dinosaur localities of Mongolia and by Stockey et al. (2007) in connection with *Cobbania* from the Dinosaur Park Formation of Alberta.

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PLATES

Plate 1

Cobbanicarpites amurensis gen. et sp. nov.

1. Paratype GIN 4867-K16/3-55, pistillate structure emerging from spathe (**S**), surrounded with laminar appendages (**A**)
2. Same, laminar appendages
3. Same, seeds
4. Holotype GIN 4867-K16/3-54, fruit interior with seed compressions and with ovate bodies (nectaries?) over the periphery (arrows). Interior space free of seeds shows a central knob (**C**) with radial ridges
5. Same, seeds magnified, some attached by minute funicles

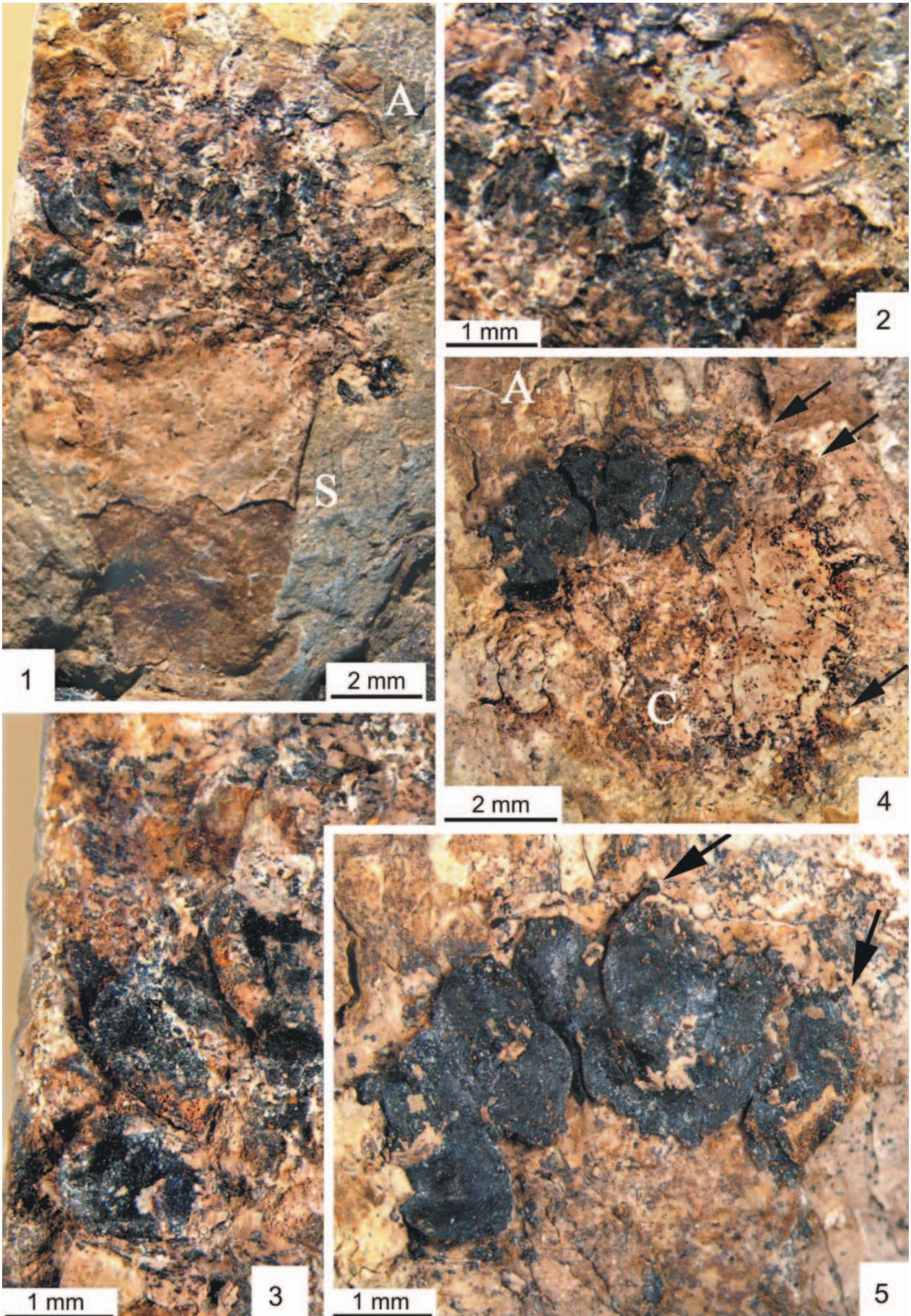


Plate 2

Cobbanicarpites amurensis gen. et sp. nov.

1. Holotype, slide GIN 4867-K16/3-54a, cleared seed removed from the fruit (**Ch** – chalazal cap, **Hi** – hilum, **Mi** – micropyle)
2. Same, micropyle surrounded by a circular scar of operculum (arrow)
3. Same, basal pole with hilum (**Hi**) and with chalazal cap (**Ch**) displaced to the ventral side
4. Same, layers of seed coat, focus on the inner layer with hollow papillae seen as annular thickenings

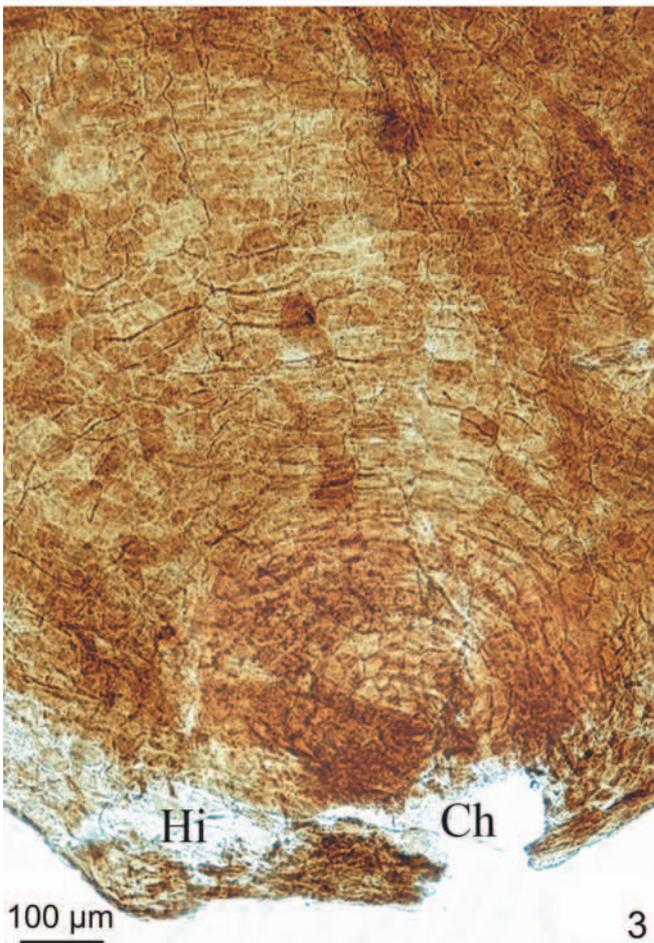
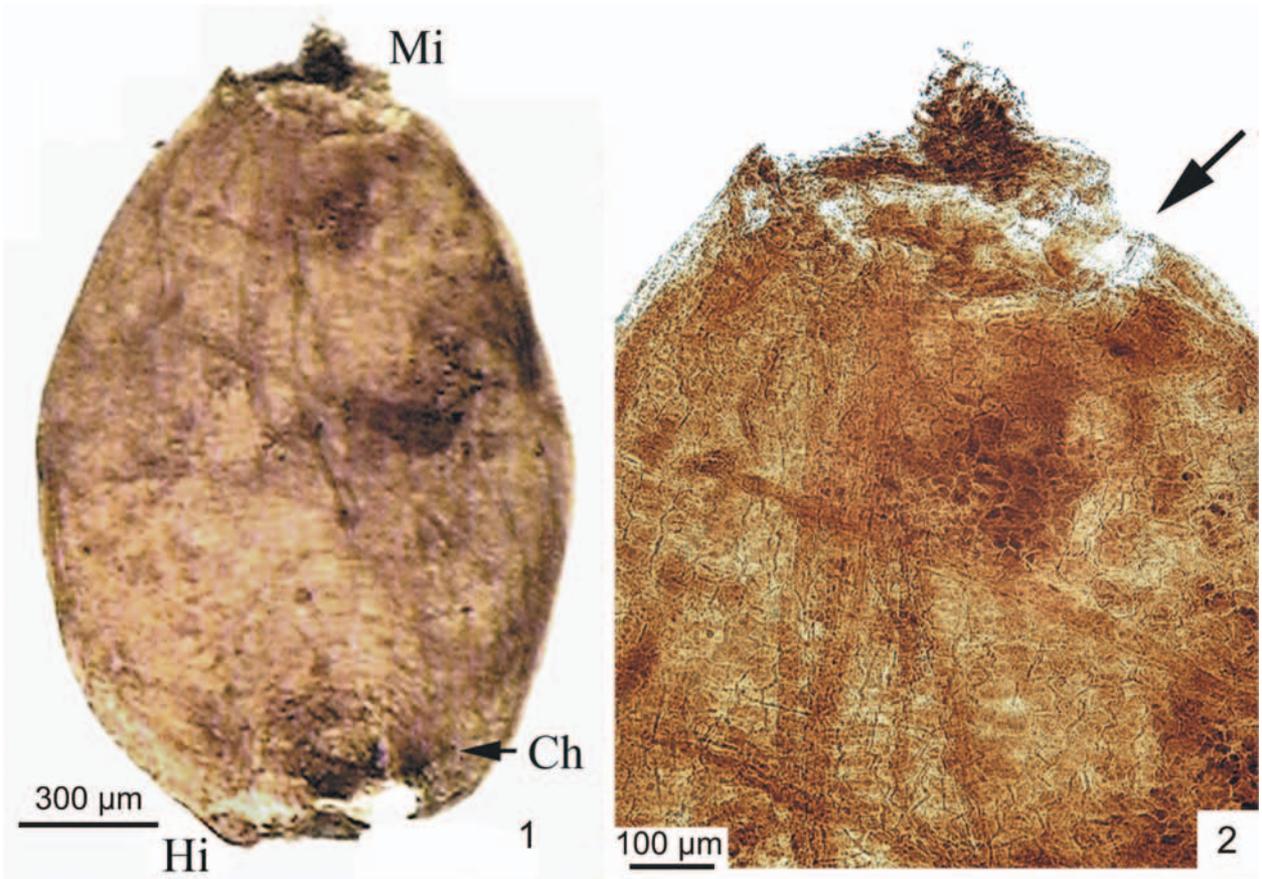


Plate 3

Cobbanicarpites amurensis gen. et sp. nov.

1. Holotype, slide GIN 4867-K16/3-54b, cleared seed removed from the fruit (**Ch** – chalazal cap, **Hi** – hilum, **Cr** – crown, **Mi** – micropyle)
2. Same, micropyle surrounded by the crown cells
3. Holotype, slide GIN 4867-K16/3-54c, cleared seed removed from the fruit (**Nb** –nucellar beak)
4. Same, nucellar beak and shoulders of operculum
5. Same, nucellar beak showing small protruding cells
6. Same seed as in fig. 1, basal pole with hilum (**Hi**) as a conical protuberance and with chalazal cap (**Ch**) displaced to the ventral side

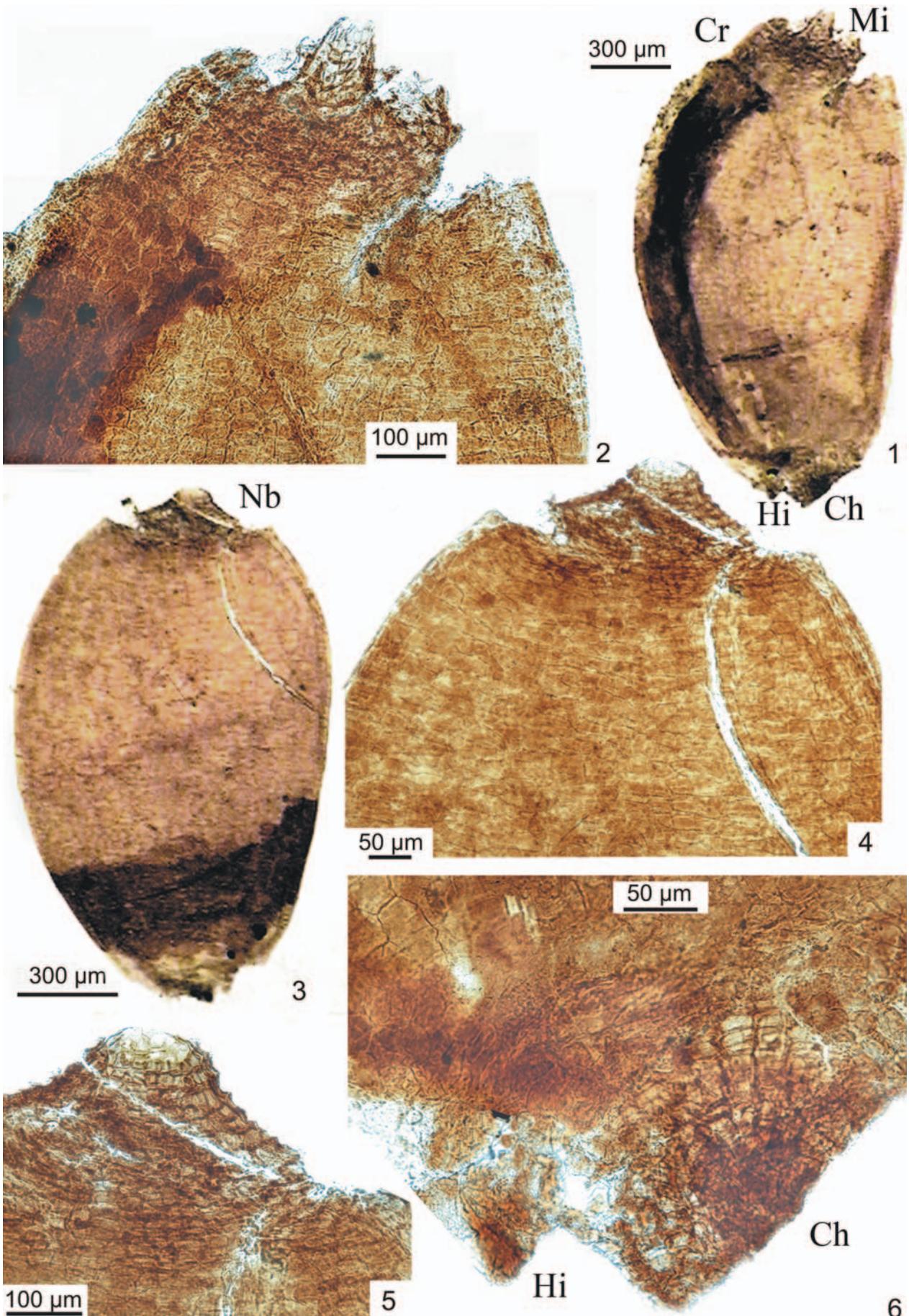


Plate 4

Cobbanicarpites amurensis gen. et sp. nov.

1. Holotype, slide GIN 4867-K16/-54c, cleared seed (Pl. 3, fig. 3), seed coat layers in optical section. **OI** – outer layer (exotesta formed of the outer integument), **II** – inner layer (tegmen formed of the inner integument) with papillae in side view appearing as a series of lenticular thickenings
2. Holotype, slide GIN 4867-K16/3-54b, cleared seed (same as in Pl. 3, fig. 1), focus on the outer layer showing transverse cell rows and spinules (**Sp**). Cells of the inner layer are seen as longitudinal zigzag lines. **F** – longitudinal fibres of the inner layer

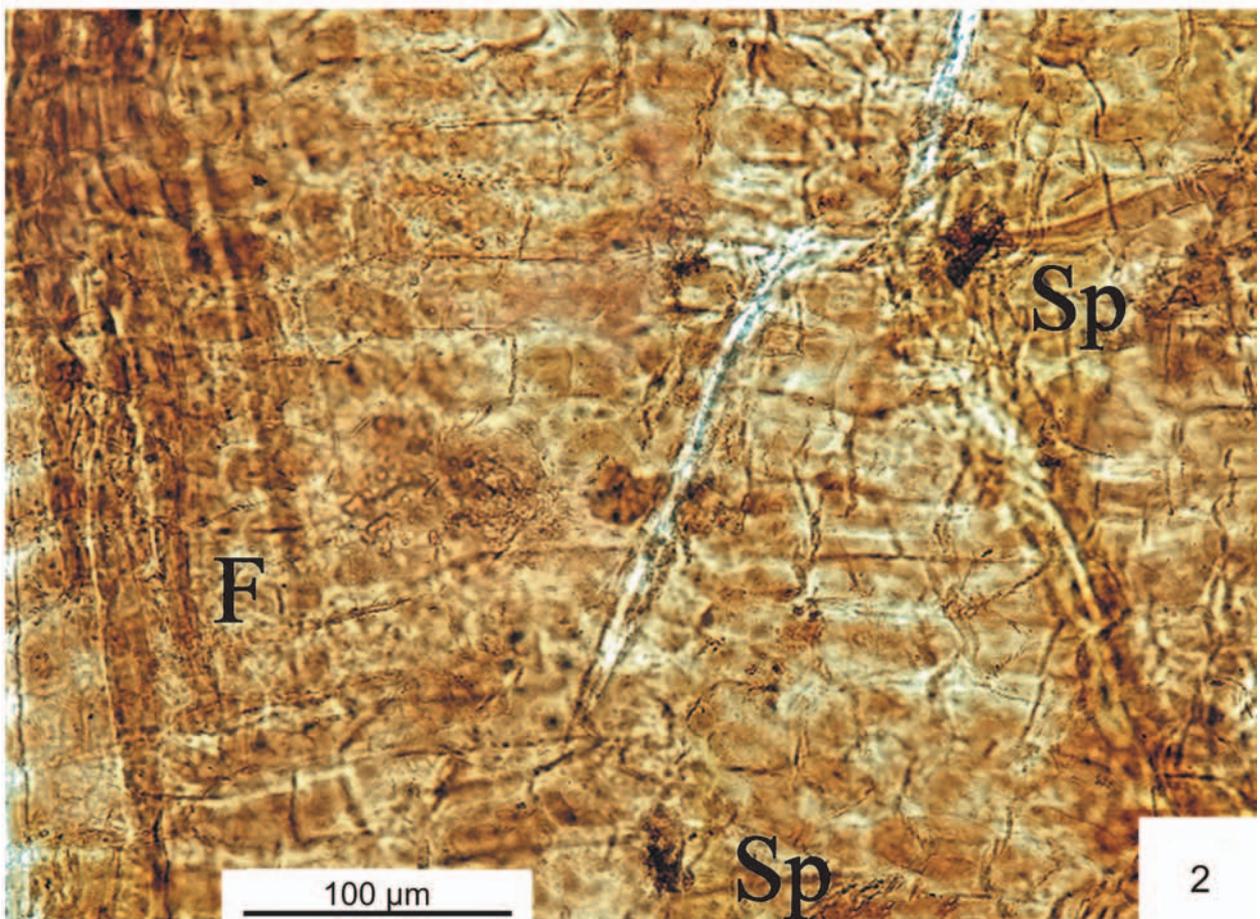
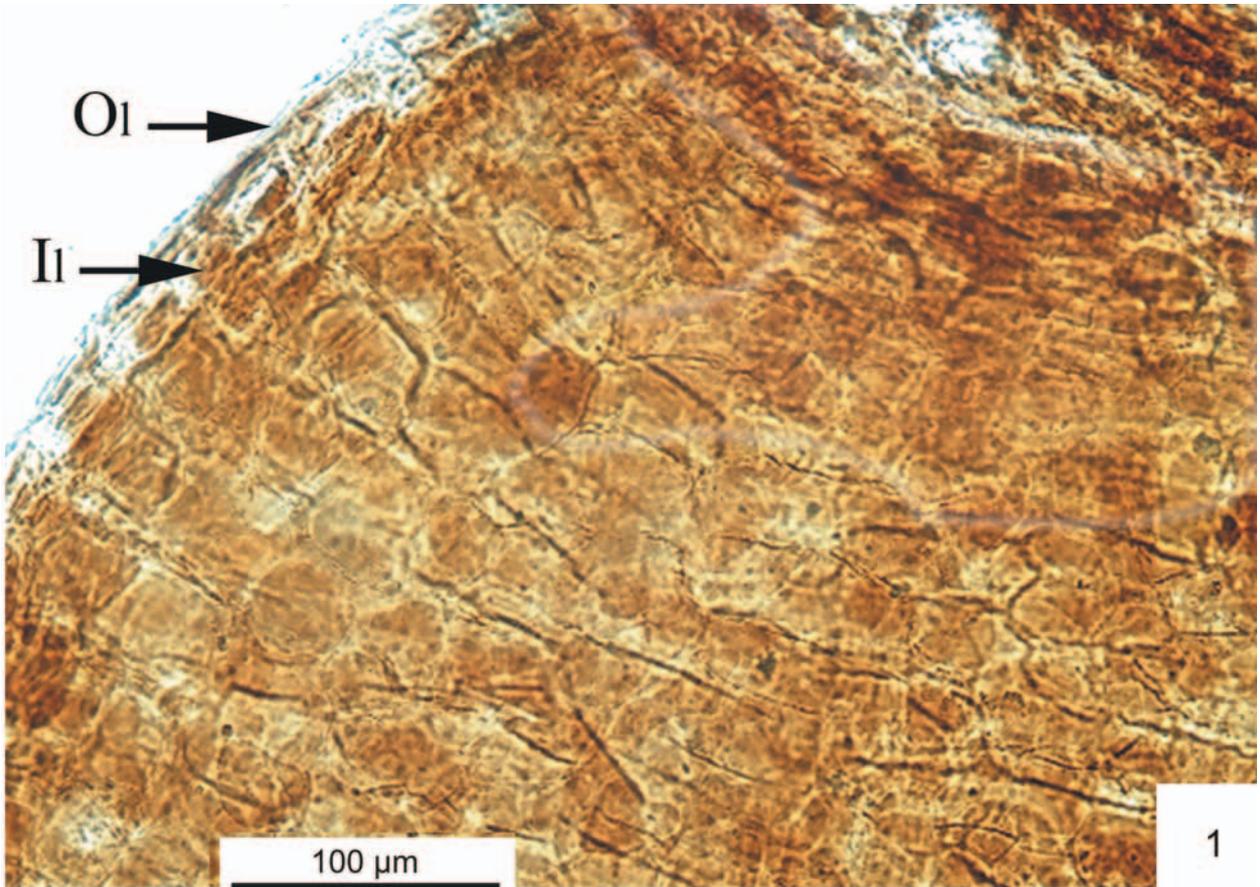


Plate 5

Cobbania corrugata (Lesquereux) Stockey, Rothwell & Johnson

1. Specimen GIN 4867-K16/3-23, stem with a rosette of small leaves
2. Specimen GIN 4867-K16/3-53 , rosette of larger leaves
3. Specimen GIN 4867-K16/6-1, impression of a leaf folded over disintegrated fruit
4. Specimen GIN 4867-K16/6-2, leaf impression showing trichome bases, with seeds adhered to the surface

