A minute mid-Cretaceous flower from Siberia and implications for the problem of basal angiosperms

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Krassilov V. A. & Golovneva L. B. 2004. — A minute mid-Cretaceous flower from Siberia and implications for the problem of basal angiosperms. *Geodiversitas* 26 (1) : 5-15.

ABSTRACT
A new taxon of fossil angiosperms, *Callicrypta chlamydea* n. gen., n. sp., is established for a minute pistillate flower less than 2 mm wide from the mid-Cretaceous (Cenomanian) of East Siberia. It is preserved as compression, showing under SEM a calyx of six sepals, a biserrate corolla and an apocarpous gynoecium. Pollen grains adhering to the perianth are like in *Freyantha*, a staminate flower from contemporaneous deposits. These floral structures are compared with the Amborellaceae and Menispermaceae suggesting a possible link between these families, with implications for the current concept of basal angiosperms.

KEY WORDS
Plant morphology,
flower,
basal angiosperms,
ranunculids,
pollination ecology,
Cretaceous,
Cenomanian,
Siberia,
new genus,
new species.

RÉSUMÉ
Découverte d'une petite fleur dans le Crétacé moyen de Sibérie et ses implications dans le problème des angiospermes basaux.
Un nouveau taxon d'angiosperme fossile, *Callicrypta chlamydea* n. gen., n. sp., du Crétacé moyen de Sibérie orientale, est décrit. Le matériel qui lui est rapporté se compose d'une petite fleur carpellaire de moins de 2 mm de largeur. L'examen au SEM montre un calice à six sépales, une double corolle et un gynécée apocarpe. Des grains de pollen sont également conservés et associés à la fleur carpellaire, une disposition qui est déjà connue chez *Freyantha*. Ces fleurs sont comparées avec celles des Amborellaceae et des Menispermaceae, elles partagent certaines caractéristiques qui indiqueraient une parenté possible avec ces familles. Le concept d'angiosperme basal est discuté.

MOTS CLÉS
Morphologie végétale,
fleur,
angiospermes basaux,
ranunculides,
écologie de la pollinisation,
Crétacé,
Cénomanien,
Sibérie,
nouveau genre,
nouvelle espèce.

INTRODUCTION

We describe a new fossil flower that is the smallest of the hitherto found, yet showing a high degree of morphological accomplishment of its miniature parts and having a certain bearing on the problem of "basal angiosperms" (Mathews & Donoghue 1999; Qiu *et al.* 1999; Sampson 2000; Endress 2001; Hesse 2001). This find supports our earlier view that small size and dicliny are primitive whereas large perfect flowers are derived (Krassilov 1984, 1997). It contributes to a diversity of early ranunculids comprising forms related to the present-day Ranunculaceae, Menispermaceae, Sargentodoxaceae and even Paeoniaceae as a link to the Dilleniales, hence fairly differentiated in the mid-Cretaceous already (Vakhrameev & Krassilov 1979; Krassilov *et al.* 1983; Krassilov 1984; Krassilov & Golovneva 2001).

MATERIAL AND METHODS

The material was obtained by bulk maceration of a slab from the plant-bearing clay horizon in the lower part of Timerdyakhskaya Formation (Cenomanian) in the middle reaches of the Tyung River about 200 km upstream of its confluence with the Vilyuy River, eastern Siberia. The locality has been described in Vakhrameev (1958) and the recent finds of hamamelid remains are reported in Maslova & Golovneva (2000). The flower was picked from among the mesofossil debris, cleaned from the remaining rock matrix with hydrofluoric acid, cleansed in distilled water, photographed with stereomicroscope, mounted on SEM stub and coated with gold. No parts were removed. The pollen grains sticking to the perianth and carpels were noticed when scanning the flower with CAMSCAN.

MORPHOLOGICAL DESCRIPTION

The flower is preserved as a compression with parts radially spreading in four overlapping whorls (Figs 1A; 2). It appears somewhat zygomorphic, the longer axis 1.8 mm, shorter axis 1.4 mm. However the original symmetry might have been distorted by a slightly oblique compression. Hence the flower is described later on as actinomorphic or slightly zygomorphic. The receptacle is not preserved, leaving a hole 0.4 mm wide in the center. Since it is rather large in comparison with the carpels it might have been expanded with divergence of the latter.

The flower shows three cycles of perianth and an incomplete apocarpous gynoecium inside. The outermost perianth members are thin membranous sepals, apparently in a single whorl of six, of which five are preserved and the sixth one (bottom right in Fig. 1) is required by the symmetry. They are *c.* 0.6 mm long, elliptical, apically smoothly rounded, flat, apparently brittle, with a conspicuous epidermis cell pattern.

The next perianth cycle is turned about 25° clockwise against the calyx, its members alternating with the sepals and readily distinguishable by being shorter, 0.55 mm long, thicker, ovate in outline, proximally concave, with involute margins and narrow blunt apex. They are slightly imbricate basally, but apparently distinct (Figs 1C; 2).

The innermost perianth segments are clasped by the outer petals, although they appear slightly displaced clockwise (Fig. 1C). The inner petals are considerably smaller than the outer ones, 0.35-0.40 mm long, membranous, rounded ovate, flat or only slightly concave, notched at the apex. A better preserved inner petal shows a papillate body at the apical notch that can be a nectary (Fig. 1E). The body is thick with distinct borders, of irregular outline, 87 µm long, covered with dense relatively large hollow papillae that are elongate, apically depressed, leaving elliptical scars when detached.

One of the outer petals (bottom left in Fig. 1A) clasps a tubular appendage 0.24 mm long, 0.08 mm thick that appears as a filament of a staminode the distal part of which is squashed (Fig. 1D). Two pollen grains were found sticking among the fragments of the distal part,

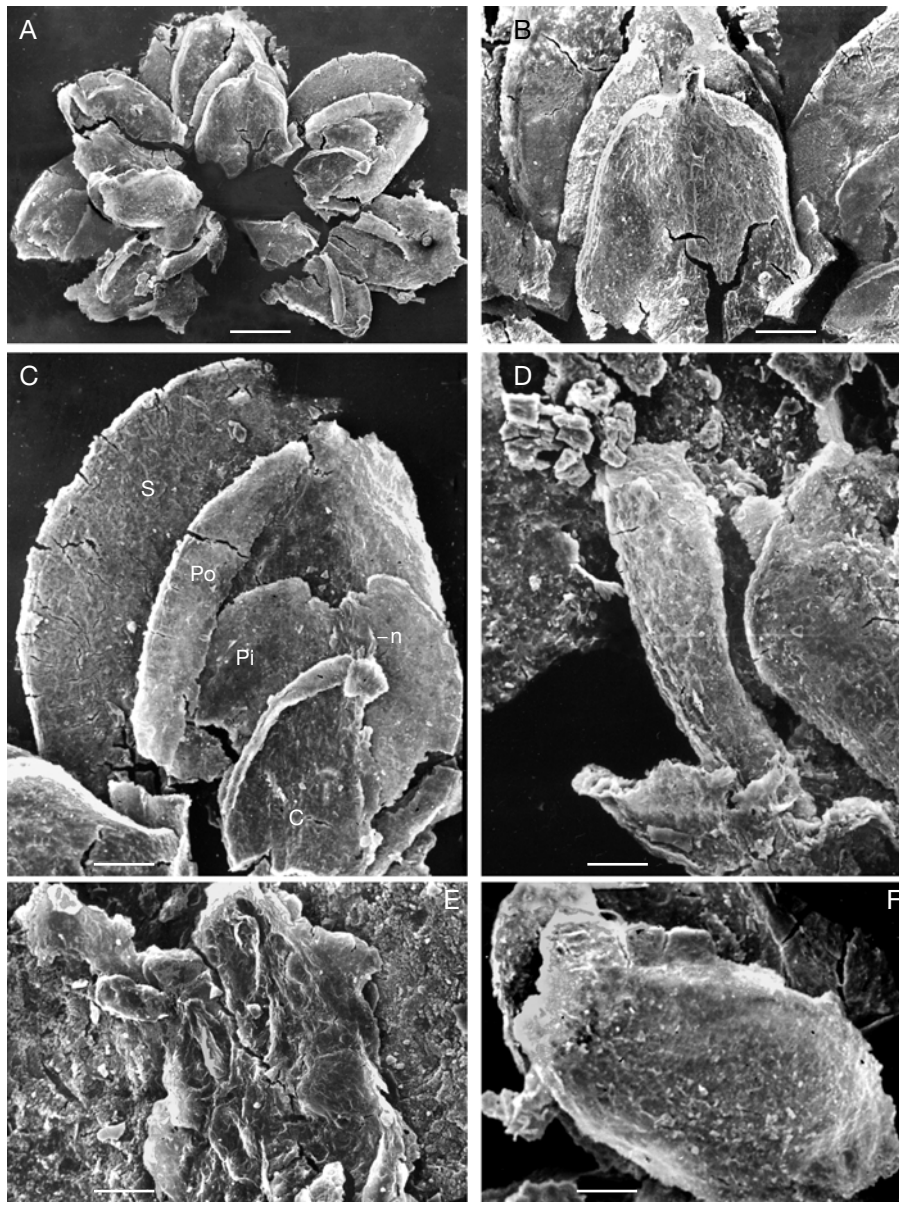

FIG. 1. — *Callicrypta chlamydea* n. gen., n. sp. from the Cenomanian of Vilyuy Basin, Siberia, SEM photographs; **A**, holotype, a pistillate flower with a calyx, biseriate corolla, and apocarpous gynoecium (see Fig. 2 for interpretation); **B**, carpel with a short style, abaxial aspect; **C**, radial sequence of sepal (**S**), outer petal (**Po**), inner petal (**Pi**) and carpel (**C**), the carpel is split in the median plane showing the locule, the position of papillate gland on the inner petal is marked as **n**; **D**, tubular structure (staminode?) clasped at base by the inner petal; **E**, papillate gland (nectary?) below the apical notch of an inner petal (see **n**); **F**, carpel, lateral view, style missing. Scale bars: A, 300 µm; B, 120 µm; C, 90 µm; D, 40 µm; E, 21 µm; F, 70 µm.

FIG. 2. — *Callicrypta chlamydea* n. gen., n. sp., a flower from the Cenomanian of Vilyuy Basin, Siberia, outline of the holotype (see Fig. 1A) showing interpretation of the floral parts. Abbreviations: **C**, carpel; **Pi**, inner petal; **Po**, outer petal; **S**, sepal; **St** , staminode?. Scale bar: 150 µm.

which can be a mere coincidence, although staminodes sometimes produce some amount of sterile pollen.

The carpels facing the observer are in a single whorl, widely separated, opposite to the inner petals or only slightly displaced against them. A carpel in posterior view (Fig. 1B) is ovate with a broad base, broadly rounded distally, 0.4 mm long, with a single style 50 µm long. It shows a median keel and thin striation corresponding to longitudinal rows of large epidermal cells. The style is filled with a spongy tissue, distally slightly expanded and notched, perhaps at the base of stigma that is not preserved. A carpel in lateral view (Fig. 1F) is gibbose, with an apical notch where the style was broken off. It appears incompletely sealed near the apex, but this may be owing to lateral compression. Still another carpel (Fig. 1C) is split, showing a single locule. Ovules are not preserved.

The surface of sepals appears granular owing to the slightly bulging polygonal epidermal cells disposed in longitudinal files. The outer petals are smooth, with a faint longitudinal striation over the margins. The inner petals are marked by irregularly scattered rounded pits. The carpels are abaxially pubescent, with dense hair bases and occasionally preserved unicellular hairs *c.* 10-15 µm long.

The pollen grains found sticking to the petals and carpels are all of the same morphotype, slightly oblate, tricolpate, reticulate, equatorial aspect rounded-elliptical, polar aspect trilobate, with deeply incised lobes, equatorial diameter 18-20 µm, polar axis 16-18 µm. The colpi are slit-like, slightly invaginate, long, nearly reaching the poles. The surface reticulum is polygonal, scarcely differentiated on the colpi margins, with thick muri and relatively narrow lumina of rounded, elliptical, triangular, elongate, arcuate or irregular shapes (Fig. 3).

SYSTEMATICS

Our material is fairly different from all hitherto described fossil flowers in combining very small size with dicliny, hexamerous structure, well differentiated perianth and apocarpous gynoecium of many carpels. Most early (mid-Cretaceous) flowers are considerably larger, pentamerous with bracteate perianth of undifferentiated tepals and variously connate carpels (reviewed in Friis & Crepet 1987; Krassilov 1997). The comparisons based on surveys of angiosperm families (Hutchinson 1926; Takhtajan 1966; Heywood 1978; Cronquist 1981; Goldberg 1986; Zomlefer 1994) have revealed the closest affinities with the Menispermaceae, in which the flowers are minute diclinous, with staminodes in the pistillate ones, hypogynous and basically trimerous, with a calyx of typically six sepals and a biseriate to triseriate corolla of distinct (rarely connate) petals. The petals are smaller than sepals (indistinguishable in the tribes Coscineae and Anomospermae) and often valvate, without nectaries in this family but nectariferous in the closely allied Sargentodoxaceae and Lardizabalaceae. The gynoecium is apocarpous of six (rarely more) free carpels in a single whorl. The carpels are ascidiform, gibbose, with a short style or sessile stigmas, unilocular, producing two ovules initially, but uniovulate at maturity (Imkhanitskaya 1980; Thanikaimoni 1986). Most features are shared also with the Sargentodoxaceae in which, however, the carpels are spiral and more numerous.

The monotypic Amborellaceae is similar in having minute pistillate flowers only 3-5 mm in diameter, with five or six gibbose pubescent unilocular carpels and often with a solitary staminode, yet the floral organs appear more distinctly spiral in mature flowers (Endress 2001).

Kingdonia, a ranunculoid genus included in the Circaeasteraceae or sometimes considered as representing a monotypic family Kingdoniaceae (Foster 1961; Cronquist 1981), is similar in the general aspect of flowers, morphology of gynoecium and petaloid sepals. The nectariferous staminodes of *Kingdonia* are perhaps homologous to nectariferous petals of the fossil flower, yet the

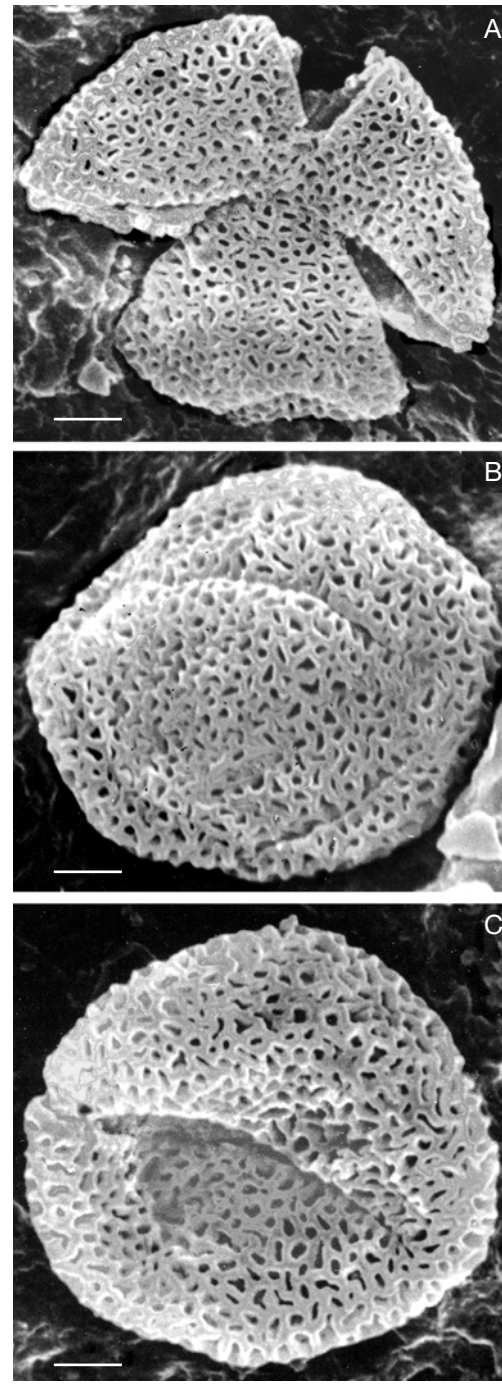

FIG. 3. — Pollen grains adhering to the petals and carpels of *Callicrypta* n. gen., n. sp., a pistillate flower from the Cenomanian of Vilyuy Basin, Siberia; **A**, polar aspect; **B**, oblique equatoriopolar aspect; **C**, lateral aspect. Scale bars: 3 µm.

petals are formally lacking in the former genus and the flowers are monoclinous. The tricolpate pollen grains of *Kingdonia* are like those found adhering to the fossil flower (Nowicke & Skvarla 1982; Savitsky 1982).

The adhering pollen grains are too numerous to be just occasional. They might come from the same plant (or adjacent plant with staminate flowers, if dioecious). Remarkably, the pollen grains are similar to those produced by staminate flowers *Freyantha sibirica* Krassilov et Golovneva (2001) in the shape and dimensions, as well as in configuration of the surface reticulum and the long slit-like invaginate colpi nearly reaching the poles. *Freyantha sibirica* came from approximately the same stratigraphic horizon, but from a different sedimentary basin within the broad geographic region. It is represented by a racemose inflorescence with minute prophylls bearing the shortly pedicellate staminate flowers of five or six hemispiral (transitional from spiral to circular: Weberling 1989) stamens the anterior of which constantly forms a basally connate group of three, subtended by three calyptrate bracts with prominent abaxial glands (Figure 4 gives a better idea of the structure than the original black and white illustrations).

The affinities of *Freyantha* have been sought with the Menispermaceae and Sargentodoxaceae, thus it might have been actually related to the new form, which explains the similarity of pollen grains. The flowers are minute in both, but at least twice larger in *Freyantha* than in the new form. In the Menispermaceae, the staminate flowers are sometimes larger than the pistillate ones, yet the distinctions in the perianth structures, bracteate in *Freyantha* vs. differentiated into calyx and corolla in the new form, indicates that they belonged to different genera within the group.

Fossil menisperms are represented by peltate leaves (*Menispermites*) that are not easily distinguishable from those of the Nymphaeaceae, Piperaceae (*Peperomia*), Platanaceae, etc., therefore not reliable as evidence of the family. The fairly distinctive curved and sculptured endocarps of menisperms have not been found until the Palaeocene. A peculiar extinct genus *Nordenskioldia* is based on the pistillate inflorescences bearing flowers with a calyptrate perianth of connate bracts and an apocarpous gynoecium. *Nordenskioldia* has been traditionally assigned to the Trochodendraceae (Kryshtofovich 1958; Crane *et al*. 1991; Pigg *et al*. 2001) although it better complies with the Menispermaceae on account of perianth and the apocarpy (in *Trochodendron* the carpels are proximally connate to about half their length) and to the Illiciaceae on account of floral axis protruding beyond the gynoecium (Krassilov *in* Krassilov & Fotyanova 1995). It is readily distinguishable from the new form in the perianth structure and the more numerous carpels.

Other supposed ranunculids include *Caspiocarpus* with small unicarpellate flowers (Vakhrameev & Krassilov 1979; Krassilov 1984) and *Hyrcantha* with relatively large monoclinous pentamerous flowers of an inconspicuous undifferentiated perianth and the urn-shaped carpels topped by the broad sessile stigmas (Krassilov *et al*. 1983). Neither of these genera is matching the new form at the generic level. It is therefore considered here as representing a new genus.

Genus *Callicrypta* n. gen.

TYPE AND ONLY SPECIES. — *Callicrypta chlamydea* n. sp.

ETYMOLOGY. — From *kallos* (Greek) = beauty, and *krypte* (Greek) = to hide.

DIAGNOSIS. — Pistillate flower minute actinomorphic or slightly zygomorphic, hypogynous, with a calyx of six sepals, a biseriate corolla and an apocarpous gynoecium of six carpels. A single or few staminodes might have been present. The sepals are membranous, brittle, larger than petals. The outer petals are relatively thick, valvate. The inner petals are much smaller, with apical glands, supposedly nectariferous. The carpels are ascidiform, unilocular, with a short style, densely pubescent.

Callicrypta chlamydea n. sp.
(Figs 1-3)

HOLOTYPE. — Komarov Botanical Institute, St. Petersburg, No. 1181-3-585(1), a flower from the Cenomanian (Timerdyakhskaya Formation) of the

TABLE 1. — Morphological comparison of Cretaceous ranunculids with the Amborellaceae, Menispermaceae and allied families.

Characters	Amborellaceae	Menispermaceae and related families	*Freyantha* ♂ *Callicrypta* n. gen. ♀
Growth habit	Small scrambling tree or shrub	Diverse, commonly small scrambling trees or shrubs as is also the monotypic Sargentodoxaceae	Unknown, yet a slender axis and minute prophylls of *Freyantha* suggest a diminutive habit
Leaves	Alternate, entire or rarely lobed	Alternate, entire or rarely lobed, occasionally peltate	In *Freyantha* lobbed of *Liriodendropsis* type
Sex allocation	Dioecious	Commonly dioecious	Unknown, probably dioecious since ♂ and ♀ came from different localities
Inflorescence	Axillary cyme	Axillary or supra-axillary cymes or racemes	Supra-axillary raceme in *Freyantha*
Prophylls	Small scales on peduncle	Occasionally conspicuous in Menispermaceae (*Cissampelos*), scaly in Lardizabalaceae and *Sargentodoxa*	Small scales on peduncle in (*Freyantha*)
Flower symmetry	Actinomorphic, hypogynous or slightly perigynous	Actinomorphic, or somewhat zygomorphic hypogynous	Actinomorphic or slightly zygomorphic, hypogynous
Flower morphology	Minute, 3-5 mm in diameter functionally diclinous, with 1-2 staminodes in pistillate flower	Minute, diclinous with rudimentary organs of opposite sex	Minute, diclinous with a single staminode in pistillate flower
Perianth	Of variable numbers of distinct tepals, sepals and petals indistinguishable	Of variable number, commonly 6, distinct, occasionally connate sepals and smaller valvate biseriate petals (indistinguishable in the tribes Coscineae and Anomospermae), nectariferous in Sargentodoxaceae and Lardizabalaceae	Perygonal of bracteate, calyptral nectariferous tepals in *Freyantha*, heterochlamydeous of distinct mebranous sepals and valvate biseriate nectariferous petals in *Callicrypta* n. gen.
Floral receptacle	Expanded, cuplike in bud	Somewhat expanded in Menispermaceae, elongate in Sargentodoxaceae	Elongate in *Freyantha*, broad relative to carpels, apparently expanded in *Callicrypta* n. gen.
Floral phyllotaxis	Spiral in mature flowers, at early stages indistinguishable	Bi- to multiseriate, in Sargentodoxaceae hemicyclic (transitional from spiral to cyclic)	Transitional from spiral to cyclic in *Freyantha*, cyclic (petals bicyclic) in *Callicrypta* n. gen.
Pollination	Mixed anemo- or entomophilous	Anemo- or entomophilous	Supposedly entomophilous
Staminate flowers	With 9-11 tepals and a more numerous, 12-21, stamens in several cycles, bearing a rudimentary gynophore	With 6, rarely fewer or more numerous biseriate stamens mostly opposite the petals	With 3 bracteate tepals and 6 stamens, hemicyclic, indistinctly biseriate

Characters	Amborellaceae	Menispermaceae and related families	*Freyantha* ♂ *Callicrypta* n. gen. ♀
Stamens	Basally adnate to inner tepals, with a short filament, connective protruding, anthers bithecate introrse	Free to variously connate, connective occasionally inflated, sometimes protruding (*Chondrodendron*), anthers bithecate, mostly introrse, with a short filament and a broad protruding connective in Sargentodoxaceae, some Lardizabalaceae (*Decaisnea*) and Berberidaceae (*Nandina*)	Free or the anterior slightly connate, with a short filament and protruding connective, anthers bithecate, apparently introrse
Anther opening	By longitudinal slit	By longitudinal slit	By longitudinal slit
Pollen grains	Monoporate operculate or inaperturate	Of diverse apertural types more commonly tricolpate, tricolporate, porate or inaperturate. Tricolpate irregularly reticulate with long slit-like invaginate colpi in Sargentodoxaceae	Tricolpate irregularly reticulate with long slit-like invaginate colpi in *Freyantha* and dispersed adhering to *Callicrypta* n. gen.
Pistillate flowers	Smaller than the staminate, with 1-2 staminodes	Commonly with staminodes	Smaller than *Freyantha*, with a single staminode
Gynoecium	Apocarpous	Apocarpous, often on a gynophore, with carpels widely diverging in the Lardizabalaceae	Apocarpous, with widely diverging carpels
Carpels	In a single whorl, mostly 5-6, minute, gibbose, ascidiform, shortly stipitate, unilocular	Commonly 6 (1-3 to 30) in one or more cycles, gibbose, unilocular, unsealed in Lardizabalaceae	6 in a single whorl, minute, distinct, sessile, gibbose, incompletely sealed, unilocular
Stigma	Sessile, bilobed, with multicellular papillae	Sessile or on a very short style	On a short style
Ovule	In mature carpels solitary, hemitropous (or described as orthotropous curved at base), bitegmic	Initially 2, but in mature carpels single, mostly bitegmic. In *Sargentodoxa* solitary hemianatropous	Unknown
Endosperm	Abundant	Scanty in Menispermaceae, yet abundant in Sargentodoxaceae and Lardizabalaceae	Unknown
Fruit	Drupaceous	Aggregates of drupes or nutlets	Aggregates of nutlets in association with *Freyantha*

FIG. 4. — *Freyantha sibirica* Krassilov et Golovneva (2001), from the Cenomanian of Tschulymo-Yenisey Basin, Siberia, inflorescence of staminate flowers subtended by calyptrate bracts with a prominent nectar gland (**n**). Scale bar: 1.5 mm.

middle reaches of Tyung River about 200 km upstream of its confluence with the Vilyuy River, eastern Siberia.

ETYMOLOGY. — Chlamidea (from Greek) with a mantle (perianth).

DIAGNOSIS. — As for the genus.

DISCUSSION

Callicrypta chlamydea n. gen., n. sp. is similar to Amborellaceae in general aspect of the minute diclinous oligomerous flowers of free parts, with one or few staminodes and with a single whorl of five or six gibbose ascidiform carpels. At the same time, it shares with the Menispermaceae and/or the allied ranunculid families Sargentodoxaceae, Lardizabalaceae and Kingdoniaceae such diagnostic features of floral morphology as the calyx of petaloid sepals, corolla of more numerous biseriate nectariferous petals which are smaller than sepals, imbricate and valvate, clasping the staminodes, and the apocarpous gynoecium of six carpels with a short style. *Callicrypta chlamydea* n. gen., n. sp., thus, indicates an affinity between the Amborellaceae and Menispermaceae, which can be reinforced by involving in the comparison the staminate flowers of the Cretaceous ranunculid *Freyantha sibirica* which produced pollen of the same type as found attached to *Callicrypta chlamydea* n. gen., n. sp.

The morphological comparison (Table 1) places both these Cretaceous species in the plexus of archaic ranunculids the present day survivors of which form the monotypic families Sargentodoxaceae, Kingdoniaceae, Circaeasteraceae, Glaucidiaceae and the closely allied Amborellaceae. A traditional assignment of *Amborella* to the Laurales (Monimiaceae) is based mainly on a single feature in common, the inflated floral receptacle (Cronquist 1981) that occurs, although in a less conspicuous form, in the Menispermaceae also. A recently advocated link to the Nymphaeales (Mathews & Donoghue 1999; Qiu *et al.* 1999), an order of aquatic angiosperms, is scarcely justified by a few homoplastic features in common, such as the porose vessels (Schneider & Carlquist 1996) or a spiral floral phyllotaxis,

widely scattered among the angiosperm orders. The tracheary elements in *Amborella* with small pores in pit membranes or altogether lacking pit membranes are unlike those in Nymphaeaceae with large pores (Field *et al.* 2000). The more strictly diagnostic features of the flower topology, gynoecium, ovules, fruit, pollen grains, etc., are so disparate that a detailed comparison does not make much sense. Basic nymphaeaceous floral structure has been fairly distinct in the mid-Cretaceous already (Krassilov & Bacchia 2000).

We emphasize the extreme diminution of the flower in *Callicrypta* n. gen. not only because it counters once popular idea of primitiveness, but also because dimensions are important in pollination ecology. Our studies of gut contents of fossil insects have revealed a widespread Palaeozoic and Mesozoic pollen feeding by various relatively large insects, such as hypoperlids, booklice, katydids and xyelids (Krassilov & Rasnitsyn 1998). Floral organs of proangiosperms might have been visited for pollen primarily, as in the case of *Preflosella*, an Early Cretaceous pre-flower foraged by two xyelid species (Krassilov & Rasnitsyn 1998). Co-adaptation of plants and pollinivorous insects implied a certain robustness of floral organs.

A miniaturization of floral parts accompanied by a development of secreting structures (glands on the bracteate tepals in *Freyantha sibirica* and on the inner petals in *Callicrypta chlamidea* n. gen., n. sp.) suggests a major innovation in pollination ecology involving new groups of insects coming for nectar and capable of gently handling the flower. This line of co-evolution might have led to a diversification of forms related to the present-day ranunculids. The finds of such forms in the mid-Cretaceous of Siberia and northern Kazakhstan (*Caspiocarpus*: Vakhrameev & Krassilov 1979; Krassilov 1984; *Hyrcantha*: Krassilov *et al.* 1983) suggest a diversification center in the northern temperate realm.

Acknowledgements

We thank the reviewers, W. L. Crepet and an anonymous one, for their valuable comments. This work was supported by the Russian Foundation of Basic Research, grant 03-05-64794.

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Submitted on 14 November 2002;
accepted on 2 June 2003.