

New pollen morphotype from gut compression of a Cretaceous insect, and its bearing on palynomorphological evolution and palaeoecology

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Accepted 21 February 2003

Dedicated to our co-author and good friend Nona Meyer-Melikyan

Abstract

Plant remains from gut compressions of fossil insects are evidence of plant-insect interaction with implications for plant evolution and functional palynomorphology. We obtained pollen grains from compressed intestines of five xyelid species from the Lower Cretaceous Baisa locality, Transbaikalia, each with a single pollen morphotype in the pollen load. Among them, *Ceroxyela dolichocera* Rasnitsyn was loaded with the bilobed, monosaccate pollen grains *Vitimipollis edulis* Krassilov. A recently found specimen of the same species yielded a new pollen morphotype, *Cryptosacciferites pabularis* gen. et sp. nov., with ultrastructural evidence of a residual saccus, demonstrating a transition from saccate to asaccate morphologies. It is also unusual in having a well-developed lamellate apertural endexine as in some basal angiosperms. Although two individuals of *Ceroxyela dolichocera* studied for pollen load visited different plants, neither of them had mixed loads, which may suggest consecutive, rather than simultaneous, flowering of the source plants.

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Keywords: Cretaceous; Palynomorphology; Plant-insect co-evolution; Plant palaeoecology; Proangiosperms

1. Introduction

Our search for structurally preserved plant material in gut compressions of fossil insects has revealed widespread pollen-feeding (pollinivory) in the Permian and during the Mesozoic (summarized in Krassilov & Rasnitsyn, 1998). Implications of these findings for plant-insect co-evolution and palynomorphology are discussed in Krassilov (2000). Our Cretaceous material came from the Baisa locality, which is situated in the upper reaches of the Vitim River, Transbaikalia. The locality is rich in fishes and aquatic invertebrates, as well as terrestrial plants and insects, preserved in a lacustrine black shale-marl sequence, which has been

dated on the basis of fossil plants and ostracods as late Hauterivian–Barremian (Krassilov & Bugdaeva, 2000), possibly extending to the Aptian (Vakhrameev & Kotova, 1977). The plant assemblage contains diverse gnetophytes and other proangiospermous plants (Krassilov, 1986; Krassilov & Bugdaeva, 1982, 1999, 2000). Pollen grains were extracted from compressed intestines of five xyelid species, each with a single-species pollen load (Krassilov & Rasnitsyn, 1982, 1998).

Among the previously described material, a xyelid species, *Ceroxyela dolichocera* Rasnitsyn, contained pollen grains of a bilobed-monosaccate morphotype *Vitimipollis edulis* Krassilov. This morphotype has been found *in situ* in sporangia of a flower-like structure, *Preflosella nathania* (Krassilov & Bugdaeva, 1999). A recently found specimen of *Ceroxyela dolichocera* (Fig. 1) has yielded a different type of pollen grain which is assigned here to *Cryptosacciferites pabularis* gen. et sp.

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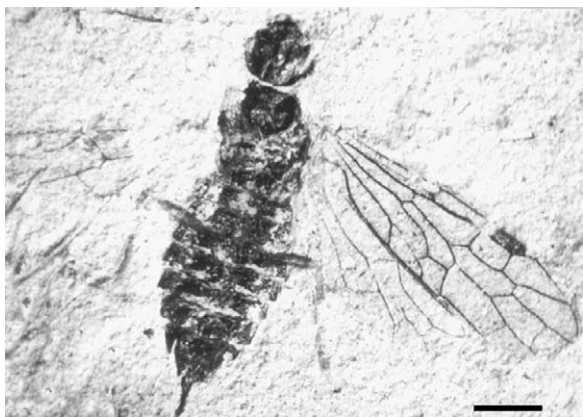


Fig. 1. *Ceroxyela dolichocera* Rasnitsyn, a xyelid from the Lower Cretaceous of Baisa, Transbaikalia, 4210/7084; scale bar represents 2 mm.

nov. The significance of this find for palynomorphology and palaeoecology is discussed below.

2. Material and methods

Ceroxyela dolichocera is preserved as a coaly compression on the bedding plane of a thinly laminated fossiliferous marl bed. Pollen grains are discernible all over the gut area under the comparatively low magnifications of a stereomicroscope. They fill the intestine and are scattered where the latter is squashed. Larger concentrations of pollen grains are confined to the oesophagus (fore-gut) and the hind end. The counterpart of the specimen, shown in Fig. 1, was mounted on a scanning electron microscope (SEM) stub and covered with gold. Figs. 2 and 3 show the abdomen with pollen clumped close to the anus. Most pollen grains are crumpled, but a few are well preserved. Individual grains were extracted at several points along the gut and prepared for examination under a light microscope (LM), SEM and transmission electron microscope (TEM). Exinal ultrastructures were observed under the TEM and, in broken or partly digested grains, also in the SEM.

The material is deposited in the Palaeontological Institute, Moscow, catalogue numbers 4210/7084 (impression of *Ceroxyela dolichocera*), 4210/7084 (ST1), counterpart of the same specimen attached to SEM stub; 4210/7084 (SL1–4), slides with pollen grains from the gut; and 4210/7084 (TEM), sectioned pollen grain.

3. Systematics of the pollen morphotype

Cryptosacciferites Krassilov & Tekleva, gen. nov.

3.1. Derivation of name

From cryptic and *saccifer*, bearing bladders.



Fig. 2. *Ceroxyela dolichocera* Rasnitsyn, 4210/7084 (ST1), counterpart of specimen shown in Fig. 1, with pollen grains scattered over the gut and amassed at the hind end of the abdomen, SEM; scale bar represents 300 µm.

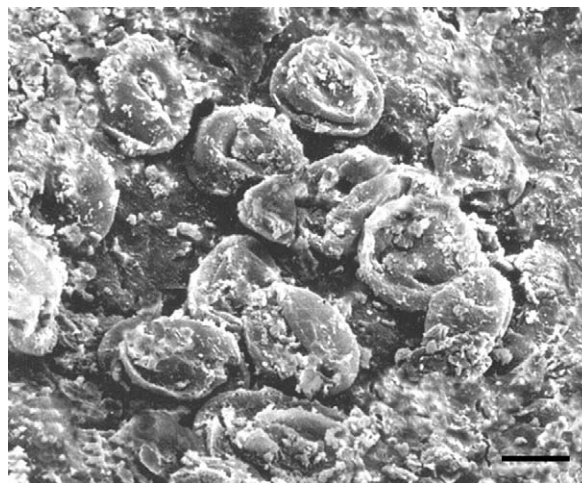


Fig. 3. Pollen mass of *Cryptosacciferites pabularis* gen. et sp. nov. at the hind end of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia, 4210/7084 (ST1), SEM; scale bar represents 30 µm.

3.2. Type species

Cryptosacciferites pabularis Krassilov & Tekleva, sp. nov.

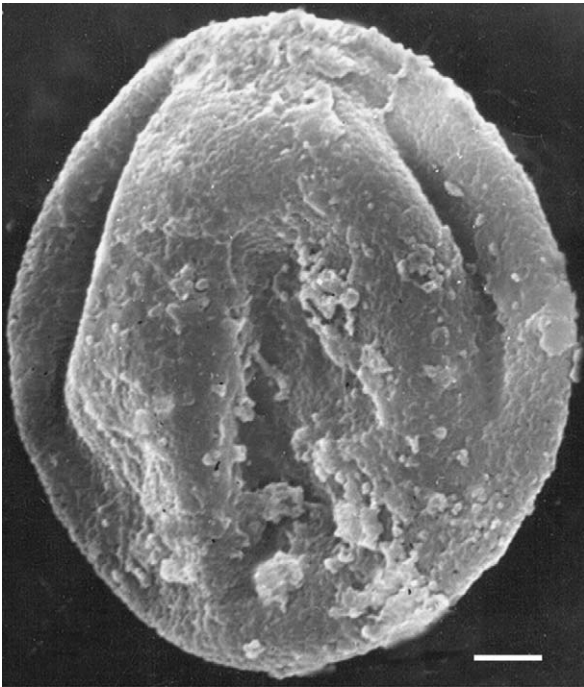


Fig. 4. *Cryptosacciferites pabularis*, pollen grain from the gut of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia, distal view, holotype, 4210/7084 (ST1), SEM; scale bar represents 7 μm .

3.3. Diagnosis

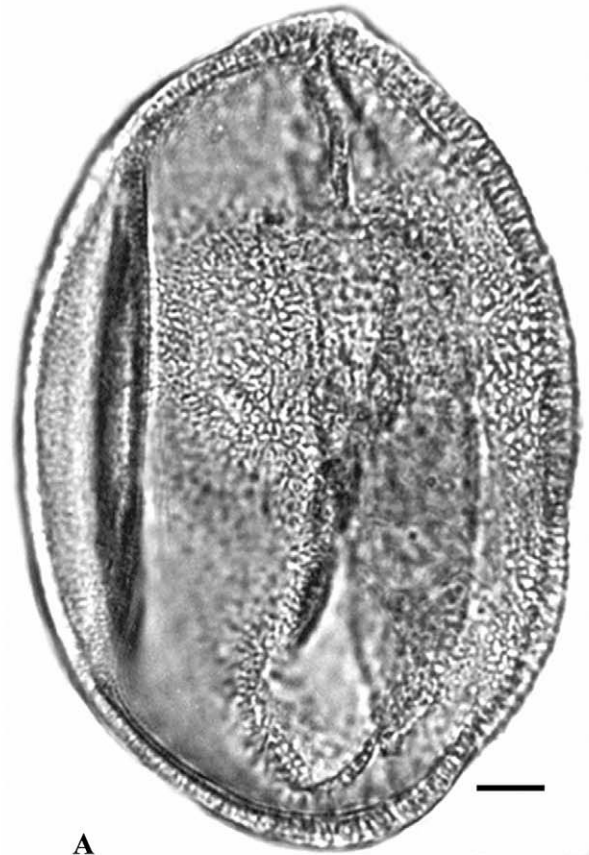
Pollen grains elliptical, about $70 \times 55 \mu\text{m}$, with a thickened equatorial flange. The apertural (supposedly the distal) face with a broad median sulcus and two symmetrically disposed crescent-shaped lateral furrows that are considerably longer than the sulcus. The tectum is undulating, with an indistinctly granular surface sculpture, minutely perforate, relatively thin over the apertural face, lacking over the furrows. The infratectum is proximally alveolar, expanded, with longer radial brochi over the equatorial flange, granular over the apertural area, reduced in the lateral furrows. The nexine is formed by a dense homogeneous foot layer in nonapertural regions; it is differentiated into a crumpled foot layer and a thicker lamellate endexine over the median aperture. The orbicules are solid or hollow, with a thick dense coat.

Cryptosacciferites pabularis Krassilov & Tekleva, sp. nov.

Figs. 2–10

3.4. Derivation of name

L. pabularis, feeding.



A



B

Fig. 5. *Cryptosacciferites pabularis*, pollen grain from the gut of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia, LM. A, oblique distal view, paratype, 4210/7084 (SL1). B, nearly circular end view of a grain compressed over the long axis, paratype, 4210/7084(SL2); scale bar represents 6 μm .

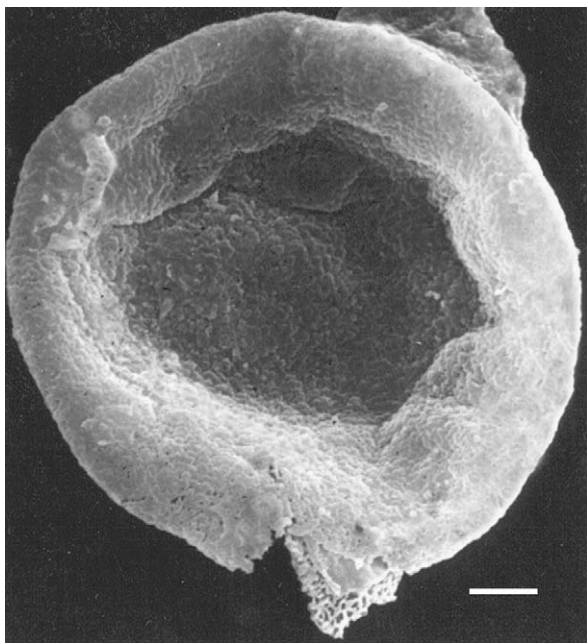


Fig. 6. *Cryptosacciferites pabularis*, pollen grain from the gut of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia, compressed proximal view, showing ultrastructure of the ruptured marginal flange (bottom), paratype, 4210/7084 (ST1), SEM; scale bar represents 7 μ m.

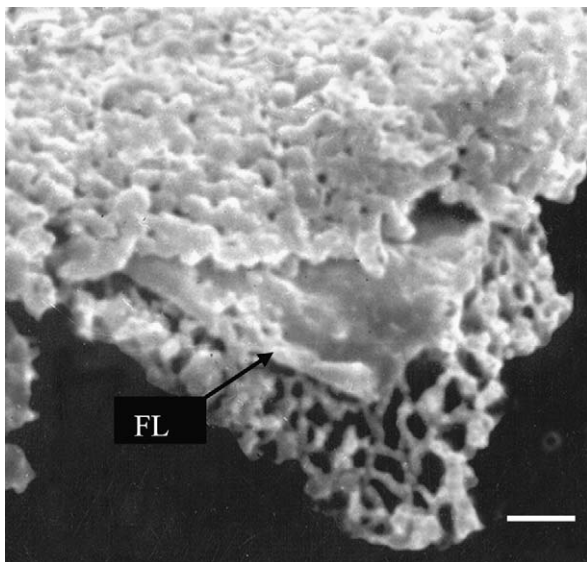


Fig. 7. *Cryptosacciferites pabularis*, pollen grain from the gut of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia, enlarged from Fig. 6, showing reticulate infrastructure and membranous foot layer (FL) of a ruptured marginal flange, paratype, 4210/7084 (ST1), SEM; scale bar represents 2 μ m.

3.5. Holotype

Palaeontological Institute, Moscow, catalogue no. 4210/7084 (ST2), a pollen grain extracted from the

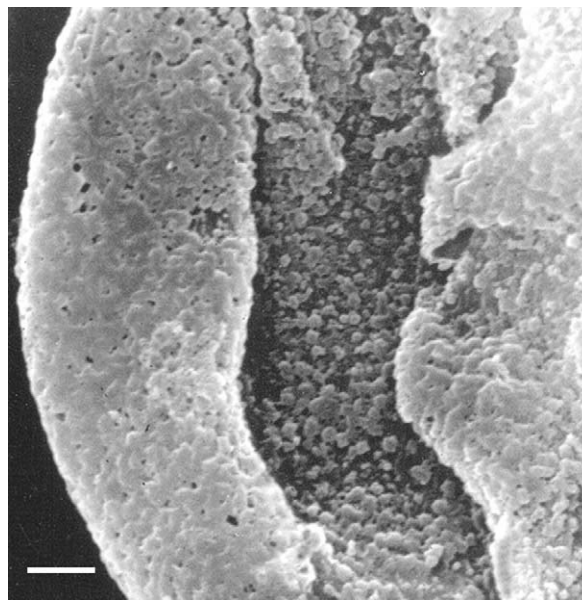


Fig. 8. *Cryptosacciferites pabularis*, pollen grain from the gut of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia, showing granular infrastructure of marginal furrow, paratype, 4210/7084 (ST1), SEM; scale bar represents 4 μ m.

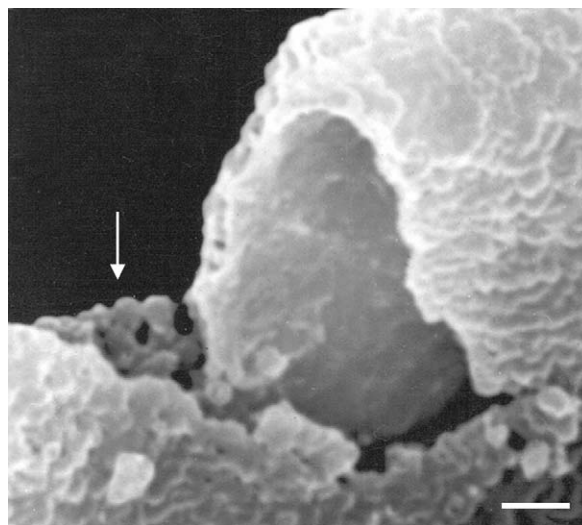


Fig. 9. *Cryptosacciferites pabularis*, pollen grain from the gut of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia, showing granular infrastructure at a rupture of distal exine, paratype, 4210/7084 (ST1), SEM; scale bar represents 2 μ m.

gut compression of *Ceroxyela dolichocera* Rasnitsyn (Fig. 4). Baisa, Vitim River, Transbaikalia, Lower Cretaceous.

3.6. Diagnosis

As for the genus.

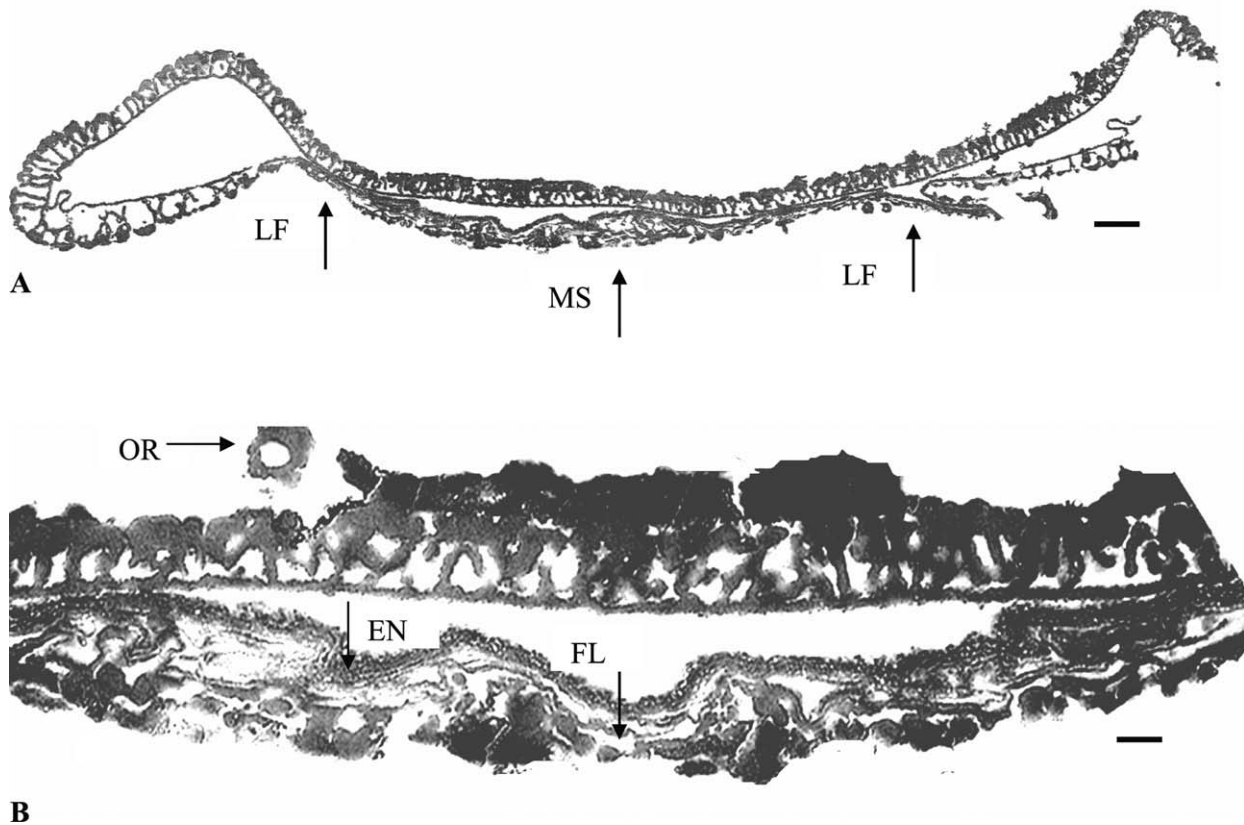


Fig. 10. *Crytosacciferites pabularis*, pollen grain from the gut of *Ceroxyela dolichocera* Rasnitsyn, Lower Cretaceous of Baisa, Transbaikalia. A, oblique transverse section, distal face down; LF, lateral furrow; MS, median sulcus. B, apertural area enlarged to show crumpled foot layer (FL), expanded lamellate endexine (EN), and an orbicule (OR), paratype, 4210/7084 (TEM); scale bars represent 3 μm and 0.7 μm .

3.7. Description

The pollen grains are elliptical with rounded ends (Figs. 4 and 5A), long axis c. 70 μm , short axis c. 55 μm (ten grains measured). The grains compressed over the long axis are nearly circular in end view, with concentric peripheral folds and occasionally with a median compression slit (Fig. 5B). The apertural, supposedly distal, face shows a slightly protruding central part with a median sulcus, laterally bordered by two symmetrical crescent-shaped furrows. The sulcus appears as a deep median depression about one-half of the grain length, 10 μm wide, of irregular elliptical outline with meandering margins (Fig. 4). The lateral furrows are well marked over the central part where they are c. 2 μm wide, attenuating to the ends. The proximal face is moderately convex, devoid of any haptotypic marks, in compressed grains with a marginal flange marked off by concentric folds (Fig. 6).

Under the LM the exine is granular in surface view, radially striated in optical section, resembling baculate infrastructure, with the tectum and foot layer appearing as distinct dark lines (Fig. 5A, B).

Under the SEM, the tectum is indistinctly granular or scabrate, with minute, irregularly scattered pits (Figs. 7 and 8). Orbicules and irregular bodies of tapetal origin are occasionally preserved. The tectum is reduced over the furrows, exposing infrastructure (Fig. 8). The infrastructural elements, as seen in the furrows and over eroded areas, are dense, spherical granules about 0.5 μm in diameter or short clavae of two confluent granules (Fig. 9). A ruptured marginal zone reveals a residual honeycomb infrastructure, with the foot layer appearing as a thin, smooth membrane (Fig. 7).

Under the TEM, the exine is c. 1 μm thick over the central area, increasing to c. 2 μm over the marginal flange (Fig. 10A). Proximally, the tectum is relatively massive, up to 0.53 μm thick, irregular, undulating, the thickenings protruding as rounded tubercles or granules. It is pierced by narrow channels. The infratectum is about the same maximum thickness as the tectum, with alveoli in a single layer or in two, occasionally three, tiers. In the marginal flange the infratectum is expanded, with the alveoli radially stretched and resembling brochi of protosaccate bladders. The inner layer appears to consist of the foot layer alone over the proximal face and marginal flanges. It is dense, uniformly c. 0.1 μm thick.

Distally the tectum is less than 0.26 μm thick, reduced over the furrows. The infratectum is irregularly alveolate or granular, with granules decreasing in the furrows. The inner layer is considerably thickened and lamellate over the central apertural region. Here the foot layer appears as a discontinuous (crumpled) undulating lamella 0.05 μm thick, separated from the somewhat less electronically dense endexine showing 3–5 more or less distinct lamellae (Fig. 10B).

Amorphous tapetal deposits appear denser than the tectum. The orbicules are nearly spherical, somewhat angular in cross section, solid or hollow, with a small circular lumen and a thick dense coat.

3.8. Comparison

The pollen grains are of *Eucommiidites* morphology, with a sulcus and two lateral furrows (sometimes described as colpi, but this term should be reserved for transequatorial apertures typical of angiosperms) on the supposedly distal face of the grain. This morphotype was established for dispersed Early Jurassic pollen grains originally described as tricolpate and assigned to angiosperms (Erdtman, 1948). However, their symmetry suggested a gymnospermous affinity (Couper, 1956), and this was confirmed by finds of similar pollen grains in pollen chambers of fossil ovules (Hughes, 1961; Reymanówna, 1968) as well as *in situ* in pollen organs ranging from Late Triassic to Late Cretaceous in age (Pedersen et al., 1989; Friis & Pedersen, 1996; Kvacek & Pacltová, 2001). At Baisa, the pollen organ *Loricanthus resinifer* yielded small, circular pollen grains comparable to *Eucommiidites*, but differing in a less consistent development of lateral furrows (Krassilov & Bugdaeva, 1999).

Eucommiidites, which is defined by two lateral furrows running parallel to the sulcus, has a long stratigraphic range and includes pollen grains that differ widely in shape, dimensions and relative development of the lateral furrows. The lateral furrows might not have been homologous in the Jurassic and Cretaceous species (compare Hughes, 1961, 1976 with Pedersen et al., 1989). In particular, in the type species, *E. troedssonii*, as interpreted by Hughes (1976), the furrows appear to be derived from a rimula of a *Classopollis*-type pollen grain. Pollen grains of *Eucommiidites* morphology have been found in different types of reproductive structures.

The pollen grains extracted from the gut compression of *Ceroxyela dolichocera* are much larger than typical *Eucommiidites* (Erdtman, 1948; Couper, 1956, 1958) and differ in the relative development of their apertures, with median laesura being much shorter than the lateral furrows, which show vestigial sexual elements and are, therefore, leptomatic. The exine is thickened over the equatorial flange, which appears as a reduced

protosaccate structure. The infrastructure is alveolar proximally and over the marginal flange, but essentially granular over the distal face. In contrast, the ultrastructure of Late Cretaceous *Eucommiidites* is described as indistinctly granular all over the body (Friis & Pedersen, 1996). The apertural endexine is not known in *Eucommiidites*. Therefore, it does not seem appropriate to extend *Eucommiidites*, a composite genus already, to include also such forms as extracted from the gut compression of *Ceroxyela*.

In both *Eucommiidites* and *Cryptosaccites*, pollen grains compressed over the long axis appear rounded in end view (compare our Fig. 5B with pl. 37, fig. 4 in Hughes, 1961), and because the infrastructure is pseudo-baculate, such grains can be confused with the early angiospermous pollen *Clavatipollenites*. However, the identity of micromorphological features convinces us that they are preservation forms of the less crumpled elliptical morphotypes.

Parvisaccites radiatus Couper, 1958 is close in having reduced bladders, yet these are better developed than in the Baisian morphotype, with more regularly branched brochi. Moreover, in *Parvisaccites* the tectum is imperforate and the infratectum is alveolate throughout except over the aperture (Kedves, 1994).

Thus the morphology of the pollen grains under consideration are sufficiently distinctive to justify their assignment to a new pollen genus.

4. Discussion

The pollen grains from a gut compression of an Early Cretaceous xyelid, *Ceroxyela dolichocera*, present several points of interest for studies of the morphological evolution of pollen grains, as well as for palaeoecology. Differentiation of the apertural exine in *Cryptosacciferites* is unusual for Mesozoic gymnosperms, in most of which the electronically dense inner layer corresponding to the foot layer or incorporating the endexine, is continuous all over the grain. In archaic (basal) angiosperms, the foot layer is interrupted in the apertural region, while the endexine is expanded, as in *Amborella* (Hesse, 2001). In this latter genus the endexine is homogeneous, but in other archaic genera it is more often lamellate (Endress & Honegger, 1980; Walker & Walker, 1984; Zavada, 1984).

With respect to the vestigial protosaccate structure of the equatorial flange, *Cryptosacciferites* can be considered as transitional from saccate to asaccate morphologies. Since saccate morphotypes are widespread among gymnosperms (even the pollen grains of cycads and *Ginkgo* occasionally show rudimentary bladders; Herzfeld, 1927), the typically asaccate condition of angiosperm pollen grains can be considered derived. If so, then there should have been intermediate forms

at the time of early angiosperm evolution, and *Cryptosacciferites* might have been one of them. It is linked on the one hand to asaccate *Eucommiidites*, and on the other, to such forms as *Parvisaccites* with reduced, but morphologically distinct bladders (Couper, 1958; Kedves, 1994).

This latter morphotype is in turn morphologically related to the monosaccate, bilobed forms common in Late Palaeozoic and Mesozoic gymnosperms, e.g., the *Vesicaspora*-like forms produced by the Permian peltasperms (Krassilov et al., 1999). A slightly modified *Vesicaspora*-like morphotype (*Vitimipollis*) persisted in the proangiospermous *Preflosella* from the Lower Cretaceous of Baisa (Krassilov & Bugdaeva, 1999).

Although fairly distinct at the time of their co-occurrence in the Baisian biotic community, *Vitimipollis* and *Cryptosacciferites* represent various stages of a saccate–asaccate series. The fact that both of these pollen types were found in the pollen load of a single species of pollinivorous insects may suggest that an affinity between them might not have been purely morphological. The Baisian assemblage contains a high proportion of plants with intermediate gymnospermous/angiospermous character states of proangiosperm grade supposedly belonging to different lineages of parallel evolution (Krassilov, 1986; Krassilov & Bugdaeva, 1982, 1999, 2000). The plant producing *Cryptosacciferites* is not yet known, but *Ceroxyela dolichocera* might have distinguished it as allied to its other forage species, *Preflosella nathania*.

Sawflies (Xyelidae, Hymenoptera) are a relatively small group of scarcely more than 50 species, mostly confined, since the late Mesozoic at least, to the temperate zone of the Northern Hemisphere (Rasnitsyn, 1971, 1995). Their Triassic ranges extended much wider, to Australia and South Africa (Riek, 1955; Schlüter, 2000). In extant sawflies, the early larval stages develop endophytically in shoots and cones of conifers, less frequently on the leaves of broadleaved deciduous trees (Smith, 1967; Smith et al., 1977). In *Xyela*, the most successful genus of the family, the larvae feed on unripe pine pollen (with the exception of a single shoot-boring species; see Rasnitsyn, 1971, 1995).

Adult sawflies are spring insects active mainly in April and May, the only exception being *Xyelecia*, which is active in June–July. *Macroxyela* and *Megaxyela* eat leaf primordia through holes in the bud scales (Smith & Schiff, 1998); the rest are pollinivorous. Unlike immature forms, which often show strict feeding specialisation, adult Xyelidae usually forage a wide range of conifers and broadleaved species (Rasnitsyn, 1971).

In contrast, none of the Early Cretaceous species studied hitherto had a mixed pollen load. This may be a result of either strict feeding preferences or a short and non-synchronous pollen presentation in the forage plant

species. For *Ceroxyela dolichocera* there is evidence of at least two forage species, yet here also the individual pollen loads are monospecific. If the pollen grains were presented simultaneously, such a situation would have been unlikely. It is more consistent with consecutive ephemeral pollen production during a short spring season of adult sawfly activity.

Acknowledgements

We are grateful to David Batten and an anonymous reviewer for their comments and editorial work. This study was supported by the Russian Foundation of Basic Research, grant 03-05-64794.

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