

CLASSOPOLLIS IN THE GUTS OF JURASSIC INSECTS

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ABSTRACT. The gut contents of two specimens of fossil insects from the Upper Jurassic of the Karatau Range, Kazakhstan include clumps of *Classopollis* pollen grains. The insects are assigned to different species of *Aboilus* (Hagloidea, Ensifera, Orthoptera) resembling the larger extant grasshoppers. The pollen grains show the conventional *Classopollis* external features, columellate-regulate infrastructure and exinal filaments of the proximal Y-mark as well as a microporous membrane of the distal pore-like structure. Pollinivory may explain excessive *Classopollis* pollen production, while the intricate harmomegathic structures are compatible with the pollen transfer being by large, short distance fliers.

POLLEN in the guts of fossil insects was first reported by Krassilov and Rasnitsyn (1982). They described well-preserved bisaccate and monosaccate grains extracted from two early Cretaceous Xyelidae species found in the fossil plant-insect locality Baisa, Vitim River Valley, Trans-Baikal Region. Later, a third species from the same locality yielded a different type of bisaccate grain. Subsequently, we scanned a rich collection of fossil insects deposited in the Palaeontological Institute of the Russian Academy of Science, Moscow, in search of appropriately preserved material. Our recent findings include striate pollen grains obtained from three species of Permian Hypoperlidae and Grylloblatidae (Krassilov and Rasnitsyn 1997), and *Classopollis* from two species of Jurassic hagloids (Hagloidea), a semi-extinct superfamily of orthopterid insects related to extant grasshoppers and katydids (Tettigonoidea). The latter finding is of interest not only for the reconstruction of insect feeding habits but also for palynology and plant palaeoecology. *Classopollis* is a characteristic type of Mesozoic pollen showing some angiospermoid (although not necessarily related to angiosperm ancestry) characters (Hughes 1994) and having some palaeoclimatological significance (Vakhrameev 1981; Alvin 1982; Francis 1983; Pocock *et al.* 1990).

MATERIALS AND METHODS

The material came from the Late Jurassic lacustrine marls of Mikhailovka in the Karatau Range, Southern Kazakhstan. The Mikhailovka locality is well-known for its exceptionally rich flora and fauna, the latter including insects, fish and pterosaurs. Its stratigraphy and palaeoecology are described by Hecker (1948) in his monographic study of the Jurassic Karatau Lake. The flora consists of diverse ferns, bennettites and conifers (Doludenko and Orlovskaya 1976) and a few peculiar, achene-like diaspores with pappus (Krassilov 1973). The insect fauna includes abundant orthopterans, of which the genus *Aboilus* Martynov (Prophalangopsidae, Hagloidea, Ensifera) with 12 described, and additional unnamed, species forms a conspicuous element. These large insects are preserved as light brown to yellowish ferruginous impressions with a species-specific pattern of darker bands and spots on the wings, and with the guts often filled with a coaly organic matter.

The gut contents were sampled on several occasions. Small pieces of organic matter were detached with entomological needles, cleaned successively in hydrochloric and hydrofluoric acids, and processed through the Schulze's mixture and potassium hydroxide (strong oxidation was found

necessary for separating the pollen grains from the amorphous organic matter; more gentle treatment gave less satisfactory results). Pollen clumps and other resistant residues were then mounted for SEM examination.

The material is deposited in the Palaeontological Institute, Russian Academy of Sciences.

INSECTS

Pollen was extracted from two female specimens of *Aboilus*, evidently belonging to different species. In the Karatau material large insects are represented mostly by isolated wings, but there is also a few intact specimens with the intestines well preserved and conspicuous by their coaly infilling.

Since the taxonomy of fossil Hagloidea is based mainly on male stridulatory organs (Gorochoy 1995), there are some problems in the taxonomic assignment of females at the specific and even generic level. However, *Aboilus* from the Mikhailovka locality often show well preserved species-specific patterns of dark spots and transverse bands on the forewings, that allow conspecific female and male specimens to be recognized.

Specimen No 2997/317 (Pl. 1, fig. 1) can be assigned provisionally to *A. amplus* Gorochoy, one of the largest representatives of the genus, on the basis of its dimensions (forewing about 75 mm long) and the presence of six irregularly arched moderately broad and occasionally interrupted transverse bands, as well as the fairly large additional spots along both costal and anal margins of the forewings. The field between the radial and the median veins near the point of the anterior median vein second branch departure is narrowed, as is also characteristic of *A. amplus* (Gorochoy 1995).

The second specimen, No 2904/1675 (Pl. 1, fig. 2) is similar to *A. dilutus* Gorochoy in the forewing pattern, with only three incomplete dark bands in the apical half of the wing near the costal margin and numerous irregular spots behind the radial anterior vein. However, our specimen is much larger than the type and only known specimens of *A. dilutus* (with forewing length 65 mm against 48.5 mm in the latter) and may represent a new species. A more precise assignment has to await the discovery of a male specimen with a similar wing pattern.

In both specimens the organic infilling of the guts contained abundant *Classopollis* grains in large clumps (Pl. 1, fig. 5). No other types of pollen or any other distinctive plant remains were found.

POLLEN GRAINS

Pollen grains found in the intestines of *Aboilus amplus* and *A. cf. dilutus* do not show any consistent differences and are assumed to belong in a single species of *Classopollis*. The grains are disc-shaped with a central body bordered by an annular equatorial girdle distally marked off with subequatorial groove, or rimula (Pl. 1, figs 3–4) and showing the proximal Y-mark and the distal pore-like depression (pseudopore in Reyre 1970; cryptopore in Taylor and Alvin 1984) typical of the genus (see Couper 1958; Boltenhagen 1968; Reyre 1970; Traverse *et al.* 1975; Pocock *et al.* 1990 for a discussion of the diagnostic features and related nomenclatural problems).

EXPLANATION OF PLATE 1

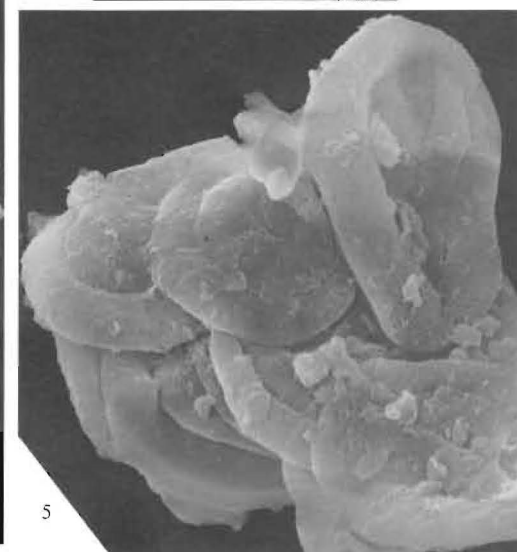
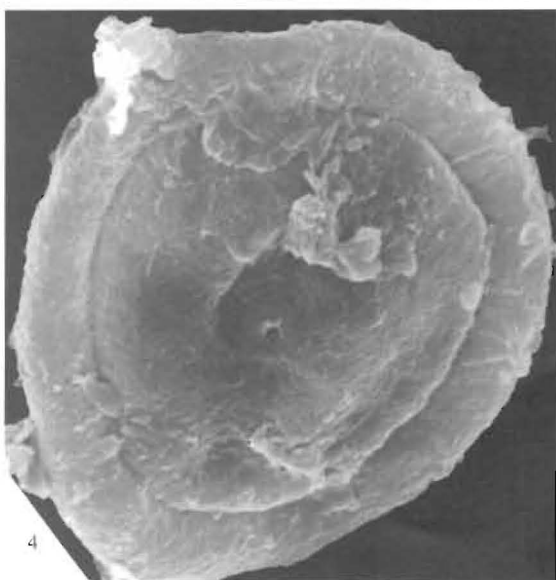
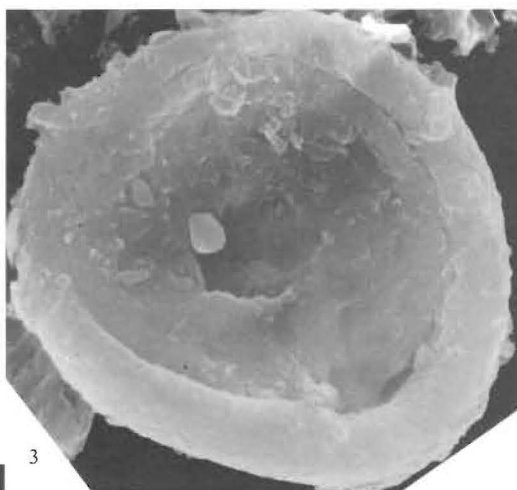
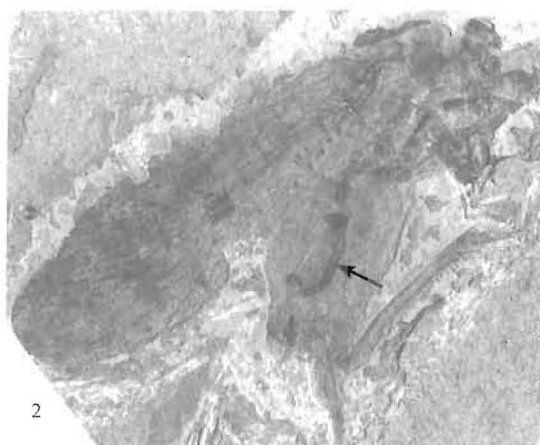
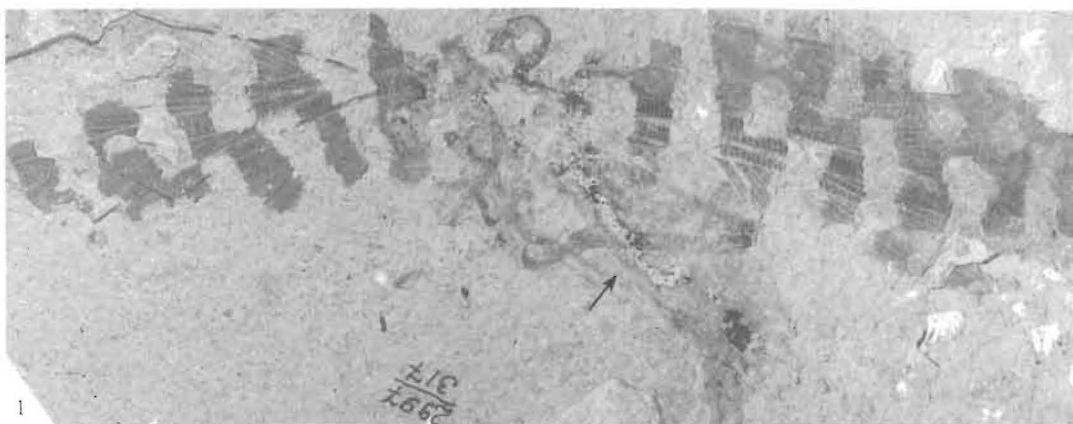
Fig. 1. *Aboilus amplus* Gorochoy; PINRAN 2997/317; insect compression with organically preserved gut content (arrow); $\times 1$.

Fig. 2. *Aboilus cf. dilutus* Gorochoy; PINRAN 2904/1675; insect compression with organically preserved gut content (arrow); $\times 1$.

Fig. 3. *Classopollis* grain from gut of *A. amplus* (fig. 1); distal view (SEM); $\times 3000$.

Figs 4–5. *Classopollis* grains from gut of *A. cf. dilutus* (fig. 2); SEMs. 4, distal view; $\times 3000$. 5, clumped grains; $\times 1700$.

All specimens from Mikhailovka, Karatau range, Kazakhstan; Upper Jurassic.



The fully developed grains are of a rather uniform size, with the long equatorial axis ranging from 22 μm to 25.5 μm (30 specimens). The smaller grains, 15–20 μm , with a less distinct rimula and distal pore, are considered immature. The equatorial outline is irregular-elliptical, with one end of the ellipse broader than the other, occasionally almost triangular. The girdle is of uniform width, about 3.5 μm . Endostriation normally does not show up on the surface but is occasionally visible in the partly digested grains. The proximal triradiate mark is a triangular area of variable width, 5–9.5 μm . As a rule, a plexus of interconnecting exinal filaments or their remnants protrudes from the Y-mark (Pl. 2, fig. 2). However, in a few specimens the triangular area shows an apparently delicate membrane with small scattered granules (Pl. 2, fig. 3). The rimula is a narrow, occasionally gaping, slit between the central body and equatorial girdle. The distal pore-like structure is a somewhat irregular ellipsoidal depression about 4–5 μm wide, occasionally showing a porous membrane perforated by the dense hexagonal microtubes or micropores (Pl. 2, fig. 1). The grain surface is smooth or minutely scabrate, occasionally showing a rugulate-verrucate pattern, here interpreted as a reflection of infrastructure.

The infrastructure, as seen in fractures of the tectum, consists of conical or clavate columellae, about 1 μm high, distinct or fused and forming a rugulate pattern (Pl. 2, fig. 5). In the grains eroded by intestinal exudates one can see transitions from fully exposed infrastructure to infrastructural elements protruding through the worn-out tectum. The infrastructure is uniformly developed over the central body and the girdle, vanishing in the rimula. Infrastructure of the girdle is traversed by subparallel ridges seen in fractured grains (Pl. 2, fig. 4).

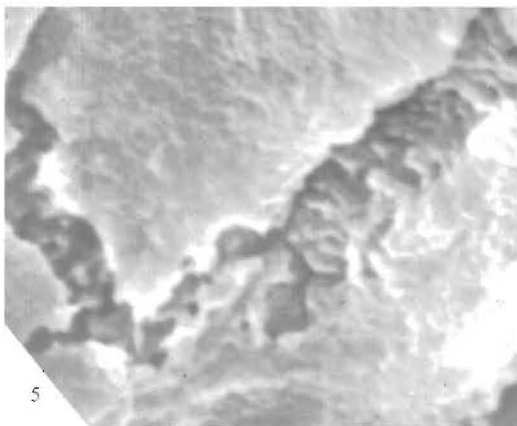
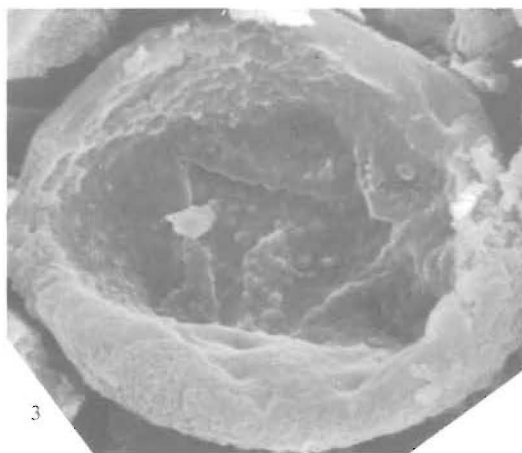
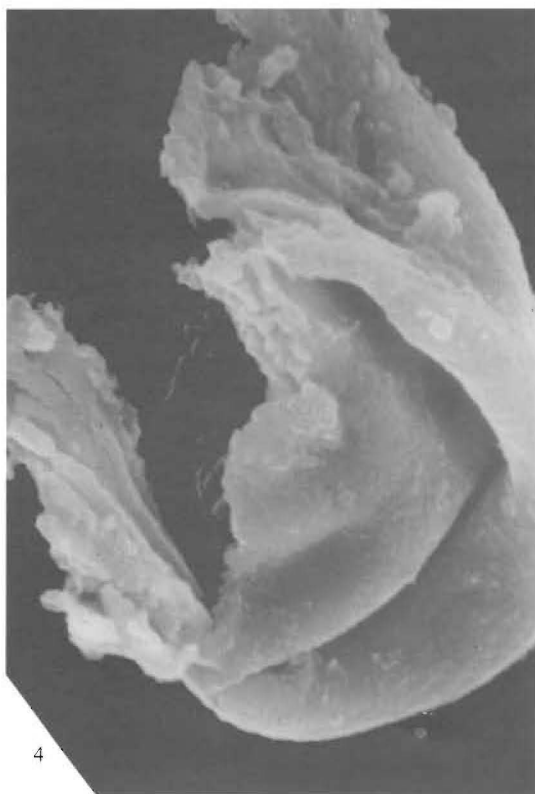
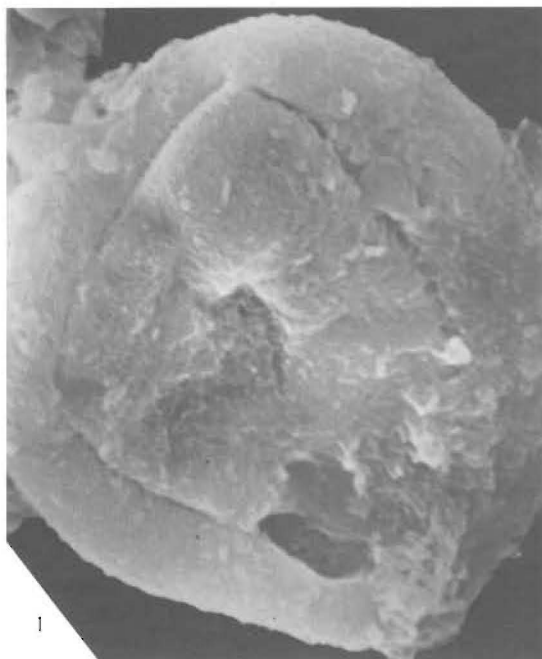
COMMENTS ON THE POLLEN GRAIN MORPHOLOGY

In our material, infrastructure is essentially the same as seen in sectioned *Classopollis* grains (Pettitt and Chaloner 1964; Medus 1977; Taylor and Alvin 1984; Rowley and Srivastava 1986) showing gradations from distinct columellae to a irregular rugulate pattern. Exinal filaments protruding from the proximal Y-mark are a constant feature related to dispersal of intact tetrads or diads (Trevisan 1973; Scheuring 1976; Courtinat 1980). However, neither of these aggregate structures are preserved in the guts. The granular Y-mark membrane is a feature not hitherto reported in *Classopollis*, whereas the microporate membrane of the distal pore favours its interpretation as a germinal aperture.

In contrast with the diverse vegetative morphology of *Classopollis*-producing plants (Watson 1982; Clement-Westerhof and van Konijnenburg-van Cittert 1991; Srinivasan 1995; Zhou 1995), the pollen morphology itself is fairly constant, the variations in the prominence of rimula, distal pore and striation of the girdle being related to the maturity of the grains. Reyre (1970) used surface ornamentation for distinguishing species of dispersed *Classopollis* grains, defining three major structural types as rugulate-verrucate, spinulate (echinulate) and mixed. A comparison of our specimens which show infrastructure with Reyre's examples of rugulate-verrucate and mixed sculptures suggests that the latter might actually reflect infrastructure protruding through the tectum. Our species is comparable to *C. chateaunovii* Reyre, *C. bussonii* Reyre and *C. noeli* Reyre as well as the pollen grains from the cones associated with *Cupressinocladus valdensis* (Seward) Seward (Francis 1983).

EXPLANATION OF PLATE 2

Figs 1–5. *Classopollis* grains from gut of *A. amplus* (Pl. 1, fig. 1); SEMs; Mikhailovka, Karatau Range, Kazakhstan; Upper Jurassic. 1, microporous membrane of distal pore; $\times 3700$. 2, exinal filaments in the proximal Y-mark area; $\times 3300$. 3, proximal view showing Y-mark membrane with granules; $\times 3000$. 4, fractured grain showing endostriation of girdle; $\times 4000$. 5, fractured grain showing infrastructure; $\times 5300$.



DISCUSSION

Our findings cast some light on the trophic adaptations of *Aboilus*, the type genus of the extinct subfamily Aboilinae which was widespread in the Jurassic and early Cretaceous. Aboilinae is considered as ancestral to grasshoppers, with the Tettigonioidae (Gorochoff 1995) first appearing in the early Cretaceous but remaining rare until the Paleogene. *Aboilus* is similar to the larger extant grasshoppers of the subfamily Cyphoderrinae living in trees or shrubs. However, representatives of the latter are mostly nocturnal whilst *Aboilus* shows a variegated wing pattern more typical of species active in the daylight. Grinfeld (1962), in his extensive studies of insect feeding habits, found that in grasshoppers pollinivory is fairly common. He suggested that pollinivorous adaptations are primary for the family, already appearing in ancestral forms, and that Ensifera, rather than beetles, could have been the most ancient unspecialized pollinators. These suggestions are now receiving some factual support.

That these large insects fed exclusively on *Classopollis* pollen can be taken as evidence of *Classopollis*-producing plants being if not the only then the most abundant pollen source in their habitats. There is little doubt that these habitats were close to the site of deposition, for insects of this size can hardly be transported intact over a considerable distance, either by wind or by water. There is ample evidence (discussed in Francis 1983) of *Classopollis* producers growing in littoral environments. We suggest that the xeromorphic vegetative characters of the *Classopollis*-producing plants are due to littoral adaptations rather than to an arid regional climate. *Classopollis* occurs in both finely laminated marly sediments with gypsum, indicative of seasonal droughts, and coal-bearing polymictic deposits typical of a humid climate (e.g. in the paralic coal basins of Far East Russia and the adjacent Sea of Japan Basin, where these pollen grains constitute up to 80 per cent. of the Lower Cretaceous spore-pollen assemblages). The equatorial girdle and rimula have been interpreted as harmomegathic structures developed in an arid climate (Pocock *et al.* 1990). Alternatively they may have mitigated the effects of long exposure of the pollen when being transferred in larger masses by the slow short distance fliers such as *Aboilus*.

Although pollinivory does not necessarily associate with entomophily, our evidence may strengthen the idea of an animal pollen vector, which has been suggested previously because of the distinctive *Classopollis* morphology (e.g. Pocock *et al.* 1990). Abundance of dispersed *Classopollis* grains may seem more consistent with anemophily than entomophily (Taylor and Alvin 1984). However, entomophilous plants pollinated by pollinivorous insects are known to produce extra pollen for attraction (Faegri and van der Pijl 1966). The same factor might favour the inclosure of ovules and extraovular germination of pollen grains (Krassilov 1982).

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REFERENCES

- ALVIN, K. L. 1982. Cheirolepidiaceae: biology, structure and palaeoecology. *Review of Palaeobotany and Palynology*, **37**, 71–98.
- BOLTENHAGEN, B. 1968. Revision du genre *Classopollis* Pflug. *Review of Micropaleontology*, **11**, 29–44.
- CLEMENT-WESTERHOF, J. A. and KONIJNENBURG-van CITTERT, J. H. A. van 1991. *Hirmeriella muensteri*: new data on the fertile organs leading to a revised concept of the Cheirolepidiaceae. *Review of Palaeobotany and Palynology*, **68**, 147–179.
- COUPER, R. A. 1958. British Mesozoic microspores and pollen grains. *Palaeontographica, Abteilung B*, **103**, 75–179.
- COURTINAT, B. 1980. Structure d'adhérence des grains de pollen en tétrade du genre *Classopollis* Pflug, 1953, de l'Hettangien de Saint-Fromont, Manche (France). *Geobios*, **13**, 209–229.
- DOLUDENKO, M. P. and ORLOVSKAYA, E. R. 1976. [*Jurassic flora of Karatau*.] Nauka, Moscow, 262 pp. [In Russian].
- FAEGRI, K. and PIJL, L. van der 1966. *The principles of pollination ecology*. Pergamon Press, Toronto, 248 pp.

- FRANCIS, J. E. 1983. The dominant conifer of the Jurassic Purbeck Formation, England. *Palaeontology*, **26**, 277–294.
- GOROCHOV, A. V. 1995. [System and evolution of orthopteroid order Ensifera (Orthoptera).] *Transactions of Zoological Institute, Russian Academy of Science, St-Petersburg*, **260**, 1–224. [In Russian].
- GRINFELD, E. K. 1962. [The origins of anthophily in insects.] University Press, Leningrad, 186 pp. [In Russian].
- HECKER, R. F. 1948. [Karatau locality of fauna and flora of the Jurassic age.] *Transactions of Palaeontological Institute, USSR Academy of Science, Moscow*, **15**. [In Russian].
- HUGHES, N. F. 1994. *The enigma of angiosperm origins*. Cambridge University Press, Cambridge, 303 pp.
- KRASSILOV, V. A. 1973. The Jurassic disseminules with pappus and their bearing on the problem of angiosperm ancestry. *Geophytology*, **3**, 1–4.
- 1982. On the ovuliferous organ of *Hirmerella*. *Phyta, D. D. Pant Commemorative Volume*, 141–144.
- and RASNITSYN, A. P. 1982. [Unique finding: pollen in the guts of the early Cretaceous xyelotomid insects.] *Palaeontologicheskii Zhurnal*, **4**, 83–96. [In Russian].
- 1997. Pollen in the guts of Permian insects: first evidence of pollinivory and its evolutionary significance. *Lethaia*, **29**, 369–372.
- MEDUS, J. 1977. The ultrastructure of some *Circumpolles*. *Grana*, **16**, 23–28.
- PETTIT, J. M. and CHALONER, W. G. 1964. The ultrastructure of Mesozoic pollen *Classopollis*. *Pollen et Spores*, **6**, 611–620.
- POCOCK, S. A. J., VASANTHY, G. and VENKATACHALA, B. S. 1990. Pollen of *Circumpolles* – an enigma of morphotrends showing evolutionary adaptation. *Review of Palaeobotany and Palynology*, **65**, 179–193.
- REYRE, R. 1970. Stereoscan observations on the genus *Classopollis* Pflug, 1953. *Palaeontology*, **13**, 302–322.
- ROWLEY, J. R. and SRIVASTAVA, S. K. 1986. Fine structure of *Classopollis* exines. *Canadian Journal of Botany*, **64**, 3059–3074.
- SCHEURING, B. W. 1976. Proximal exine filaments, a widespread feature among Triassic *Protosaccites* and *Circumpolles* to secure the dispersal of entire tetrads. *Pollen et Spores*, **18**, 611–639.
- SRINIVASAN, V. 1995. Conifers from the Puddledock locality (Potomac Group, early Cretaceous) in eastern North America. *Review of Palaeobotany and Palynology*, **89**, 257–286.
- TAYLOR, T. N. and ALVIN, K. L. 1984. Ultrastructure and development of Mesozoic pollen *Classopollis*. *American Journal of Botany*, **71**, 575–587.
- TRAVERSE, A., CORNET, B. and AMES, H. T. 1975. A new look at the 'Classopollis–Circulina' taxonomic–nomenclatural problem. *Geoscience and Man*, **11**, 159–160.
- TREVISAN, F. 1973. Peculiar structures connecting fossil pollen grains in pairs (Lower Cretaceous sediments of Southern Tuscany, Italy). *Proceedings of the 3rd International Palynological Conference, Novosibirsk*, 28–30.
- VAKHRAMEEV, V. A. 1981. Pollen of *Classopollis*: indicator of Jurassic and Cretaceous climates. *Palaeobotanist*, **28/29**, 301–307.
- WATSON, J. 1982. The Cheirolepidiaceae: a short review. *Phyta, D. D. Pant Commemorative Volume*, 265–273.
- ZHOU ZHIYAN (CHOW TSIYAN) 1995. On some Cretaceous pseudofrenelopsids with a brief review of cheirolepidiaceae conifers in China. *Review of Palaeobotany and Palynology*, **84**, 419–438.

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