

Evidence of temporary mining in the Cretaceous fossil mine assemblage of Negev, Israel

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Abstract Temporary mining is a peculiar behavioral trait in leaf parasites requiring adaptations of consecutive larval stages to the endophytic and ectophytic life. The first fossil evidence for the origin of the trait comes from the Cretaceous (Turonian) plant–insect locality of the Negev Desert containing rich trace assemblages of leaf parasites, including blotch mines with leaf pieces cut out for case construction, as well as attached larval cases. The host plants are deciduous broadleaves or aquatic angiosperms with emergent leaves, suggesting that initial acquisition of the habit might have been related to leaf abscission and the risk for the larva being choked in the mine during floods. Unlike tracks of permanent miners, temporary mines never co-occur on leaves with other type mines, which attests to their effect of enhancing plant resistance. Mine predation appears to have been widespread in the Cretaceous biotic community, suggesting a possibility of top-down regulation of mining habits at this early stage of their evolutionary development.

Key words behavior evolution, Cretaceous, early angiosperms, fossil mines, plant–insect interaction

Introduction

In distinction from permanent mining through the entire larval life from hatching until pupation, temporary mining is restricted to certain (early, with few exceptions) developmental stages, after which the larva lives openly or under the shelter of a folded leaf margin or else in leaf cases constructed for this purpose. Temporary mining is commonly considered as a less specialized feeding habit than permanent mining (Hering, 1951). However, temporary mining is a complex behavior, including larval adaptations to both endophytic and ectophytic environments, with grades of specialization in both.

Generally, the mining habit is advantageous for herbivorous insects in terms of food availability and protection, but

like other parasitic habits, it incapacitates an active defense response, making the larva most vulnerable to both internally and externally induced changes of foliar environments, such as suppression by plant defense, ageing of leaf tissues, leaf abscission, predation, and parasitoid attacks. Temporary mining opens a way out of this controversy, sheltering young larvae at their most sensitive stage and bypassing the adverse effects of later protracted mining.

For the host plant, temporary mining is less damaging than permanent mining and can even be beneficial by alerting the plant's defense mechanisms. Current knowledge of plant defense strategies (Zhu-Salzman *et al.*, 2005) may suggest that pre-emptive stimulation by a short-term injurious impact increases resistance to persistent parasite attacks. In this sense, temporary mining can be seen as a co-adaptive plant–insect interaction.

Temporary mining is far less common than permanent mining, typically occurring in the Lepidoptera. Even in this order of specialized miners, it is confined only to a few families. The origin of permanent mining from temporary mining is as problematic as the other way round. Few

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intermediate cases, in which the caterpillar of a temporary miner (*Parornix*) occasionally continues mining until pupation (Hering, 1951) are ambiguous in respect of historical precedence. Such pending problems in evolution of behavior require direct paleontological information.

Paleontological evidence of mining was for a long time neglected or underrated. Recent advances in the study of insect associations on fossil plants (reviewed in Labandeira, 2002a, b and elsewhere) prove the habit to be minimally as ancient as the Triassic, but evolution of mining behavior through times is far from being firmly grounded in the fossil record. In this paper I report on the first fossil record of temporary mining and larval case construction coming from the Cretaceous of the southern Negev Desert, Israel.

Material and methods

Cretaceous shales with fossil plants and insects represent episodic inputs of terrestrial material in the predominantly marine carbonate sequence of the Negev Desert, southern Israel. The terrestrial assemblages are well dated, because their age assignments are based on ammonite records that provide chronostratigraphic markers for the Cretaceous stages. Fossil plant assemblages of the mid-Cretaceous interval, from the Aptian to Turonian, document the rise of angiosperms to dominant position in the terrestrial plant world. Outcrops of the Turonian Ora Shales (about 90 million years old) at the mouths of Gerofit and Qetura wadies on the western slope of Arava Rift Valley (Fig. 1) contain the richest plant localities in the Mediterranean region. About 50 angiosperm morphotypes are recognized, both dicotyledons of the orders Ranunculales, Nymphaeales, Nelumbonales, Trochodendrales, Hamamelidales, Juglandales, Rosales, Myrtales, and Sapindales and monocotyledons of the orders Najadales, Pontederiales, Arales, Cycolanthales, Arecales, and Typhales (Krassilov *et al.*, 2005).

In comparison with the preceding Albian and Cenomanian angiosperm records (Krassilov & Bacchia, 2000; Silantieva & Krassilov, 2006), the Turonian flora of Gerofit is much more diverse and modern looking, indicating that the rise of morphological diversity was accompanied by a rapid ecological differentiation. A shoreline to inland sequence of mangroves, marshes, back-mangrove freshwater macrophytes and dryland broadleafed forests or woodlands was reconstructed on the basis of quantitative representation, preservation and sedimentary facies containing the fossil plant remains (Krassilov *et al.*, 2005; Silantieva & Krassilov, 2006).

Traces of mining and galling activity are exceptionally abundant and well preserved. In the collection of more than 1 000 specimens of terrestrial and aquatic angiosperms,

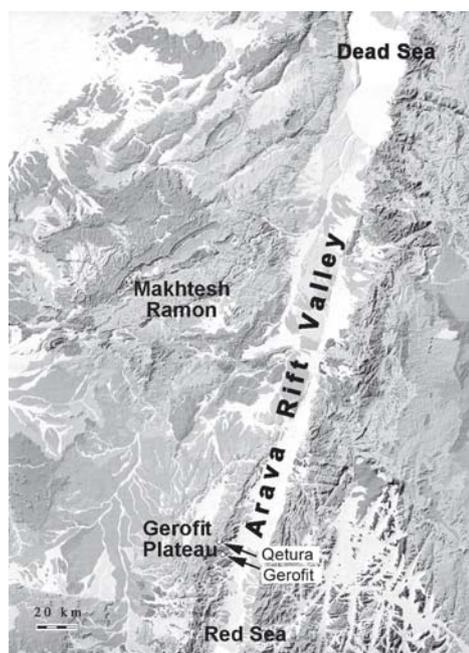


Fig. 1 Map of southern Israel showing plant and insect localities in the Arava Valley (arrows).

almost all the leaves are parasitized. The foliar material is preserved as ferruginous mineral films deposited on leaf surfaces and beneath the cuticles. In the process of fossilization, mineral solutions were driven by chemical gradients between the organic matter of the mine, its surrounding callus, and unaffected leaf tissues. Differential precipitation of mineral films over these gradients ensured that mine tracks became distinctly visible on fossil leaves. Changes in the configuration and color of the mine tracks or blotches were registered as evidence for developmental events affecting the lateral extent and depth of larval feeding, as well as frass deposition inside or outside the mine.

Mined leaves were collected in the field using a magnification glass and were further studied and photographed under a LEICA MZ6 stereomicroscope and a LEICA DFC320 digital camera. The collection is deposited in the Institute of Evolution, University of Haifa, Israel, depositary number IG1. The terminology of mine configurations is after Hering (1951).

Results

A repeated occurrence of small helices or minute superficial blotches lacking pupal chambers may indicate temporary mining, but they also may be evidence of occasional interruption of mine construction. Likewise, finds of at-

tached larval cases are not entirely convincing as evidence of temporary mining, because they could be made not only by the Lepidoptera, but also by the case-bearing beetles that are not miners at all. On the other hand, the imprints of mines with leaf pieces excised at a certain developmental stage are unequivocal evidence of temporary mining.

The best specimen of this type mines in the Gerofit collection, IG1-107 (Fig. 2a), represents the lower surface of peltate leaf belonging to *Nelumbites aravensis* Krassilov (Nelumbonaceae). The leaf is extensively marked with rounded-polygonal blotches that are occasionally paired or contiguous. The blotches are conspicuous owing to their deeper yellow and brown hues and the presence of dark masses of frass pellets. These blotches tend to avoid primary veins and their stronger branches, but are often delineated and occasionally crossed by tertiary veins that are distinctly marked around the mined area.

Although the blotches vary in size and the extent of frass accumulations, they undoubtedly are the work of one and the same mining species. The smaller blotches over the central part of leaf blade are irregular, 4–5 mm

wide, smooth or minutely cogged over their margins, with abundant frass grains scattered over the mine or occasionally concentrated in the folded peripheral zone (Fig. 2b). All such mines are accompanied by a curvilinear sharply outlined excision on the edge, occasionally in the middle. Usually the excised leaf pieces are minimally four times smaller than the blotches, but occasionally they are equal to, or even larger than, their diminutive blotches.

The larger blotches over the periphery are 5–7 mm wide, rounded-polygonal, consisting of a broad elliptical or somewhat angular central cell encircled by an incomplete ring of smaller meshes marked by a deeply impressed higher order venation (Fig. 2c). The central part of the mine is flat, smooth, and devoid of frass, which is collected along the marginal fringe. Fine radial striae over the peripheral meshes apparently represent spun silk threads, as in the present-day tentiform mines.

A comparison with mining habits in extant *Coleophora* (Lepidoptera: Gelechioidea: Coleophoridae) implies that the first type of blotches were constructed by young larvae analogous to the first instar larva in *Coleophora* that cuts

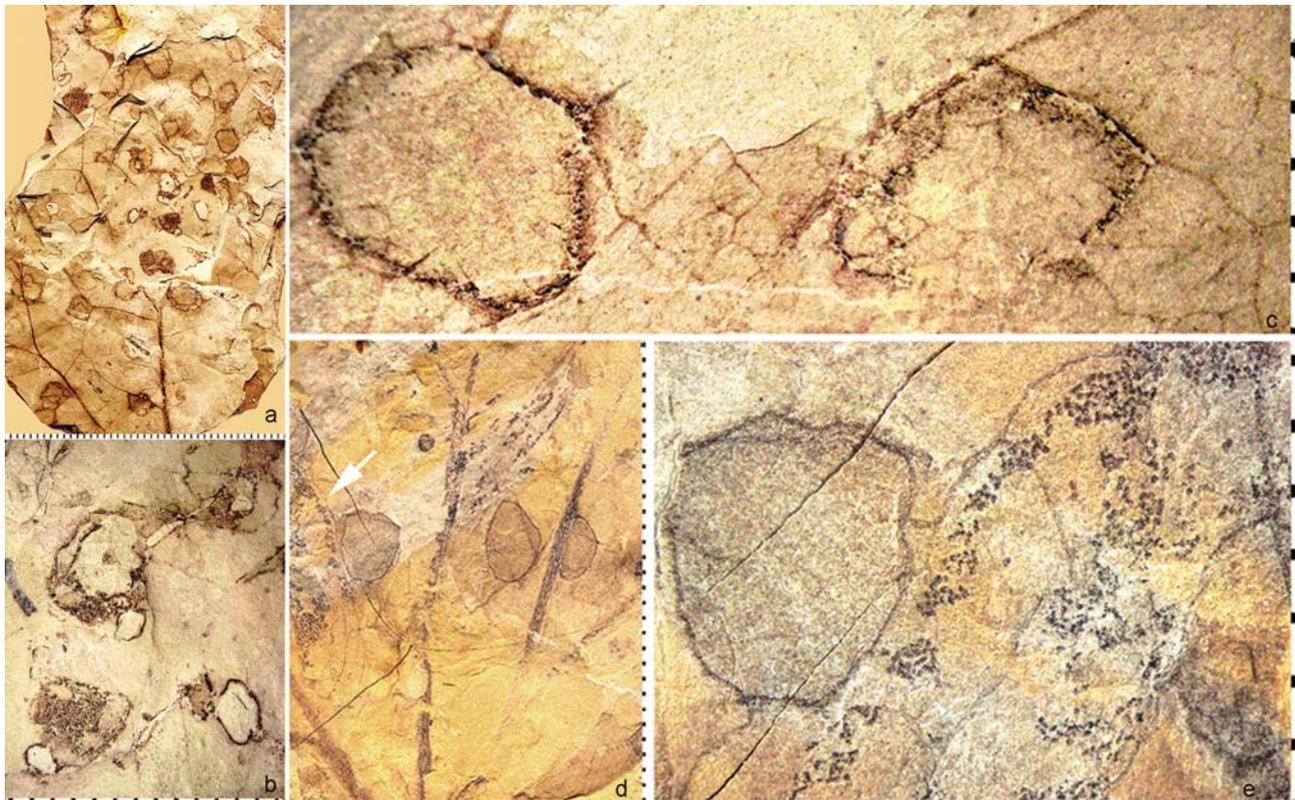


Fig. 2 Traces of temporary mining on emergent leaves of an aquatic plant, *Nelumbites aravensis* Krassilov from the Cretaceous of Gerofit, Israel: a, mined leaf, IG1-107, cut-outs for case construction in the central region of the leaf blade; b, early mines with cut-outs magnified; c, late mines magnified; d, leaf IG1-676, with polygonal structures (larval cases) plot out; e, larval case magnified. Scale division = 1 mm.

their first case out of the mine. As in *Coleophora*, the early cut-outs occur in the central part of the leaf blade (Needham *et al.*, 1928). The larva then emerges from the mine, but later in development it resorts to mining, producing larger blotches (devoid of frass in *Coleophora*) around the previously mined area and plotting its second case. In our material, the larger peripheral blotches, with a strongly marked central cell, may correspond to this stage.

Another peltate leaf of *Nelumbites negevensis*, IG1-676 (Fig. 2d) bears three isometric blotches in line across the leaf blade and parallel to the primary veins, one slightly overlapping an adjacent vein. The larger blotch is angular-ovate, 17 mm long, somewhat darker than the leaf impression, showing faint venation traces, marked out by a thin thread-like borderline with staple-like dents at the angles. The other cases are angular-ovate, likewise staple-

like indented, with few threads extending across the contoured area. These structures resemble early cases of *Paraclemensia* (Lepidoptera: Incurvarioidea: Incurvariidae) that are fixed on leaves allowing the larva to feed under the cover of the leaf disk (Needham *et al.*, 1928). They are preserved together with masses of small globular eggs that may belong to the same or different species of Lepidoptera (Fig. 2e).

Gregarious case-constructing miners produce excisions, the configurations of which are sometimes typical of an insect genus or family. The orthogonal blotches on the leaves of *Eocercidiphyllites glandulosus* Krassilov, IG1-200 perforated by numerous elliptical holes delineated by minutely dentate borderlines (Fig. 3b,d), appear exactly as the mines with excisions plotted out for case construction by extant *Antispilina* (Lepidoptera:

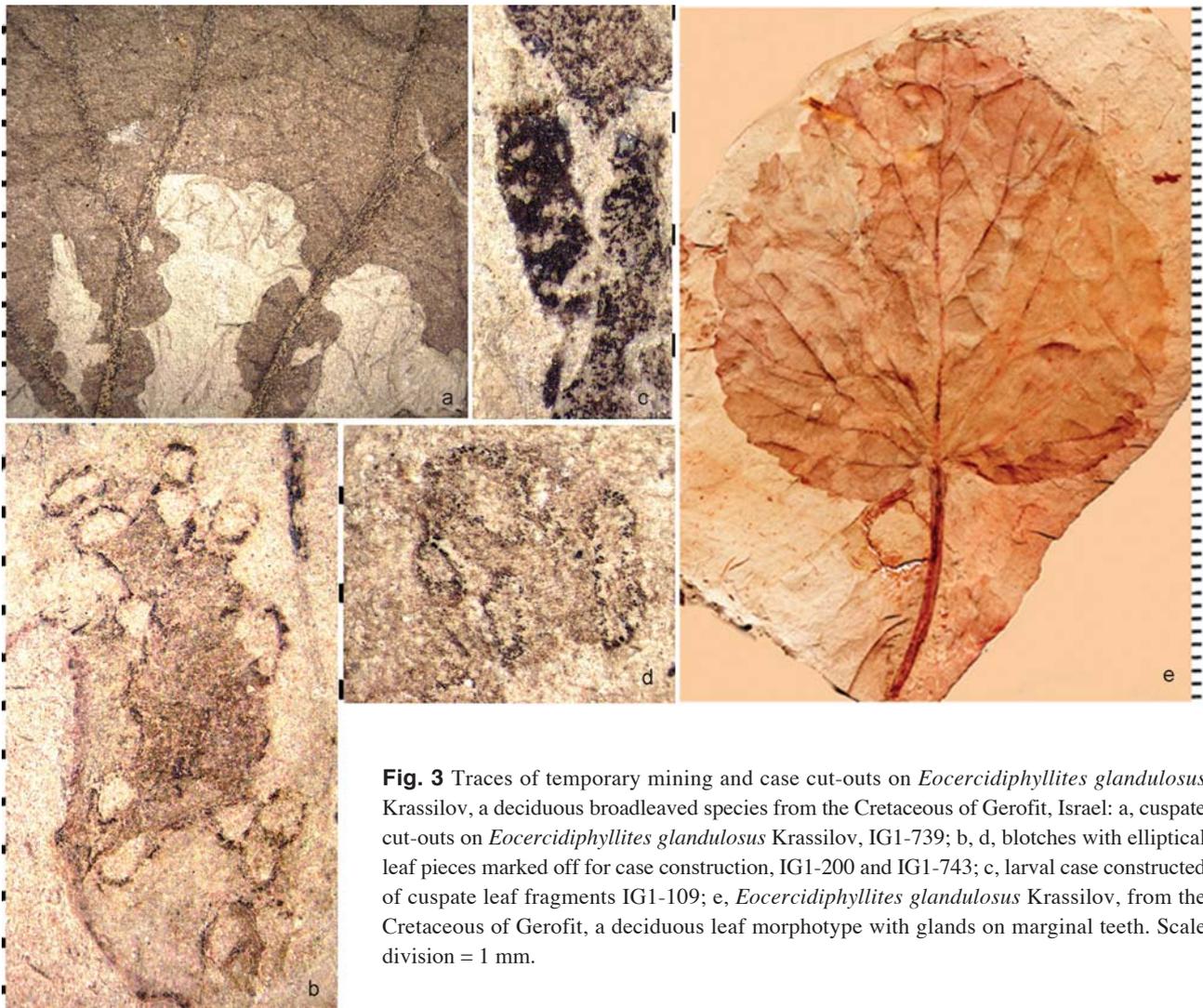


Fig. 3 Traces of temporary mining and case cut-outs on *Eocercidiphyllites glandulosus* Krassilov, a deciduous broadleaved species from the Cretaceous of Gerofit, Israel: a, cusped cut-outs on *Eocercidiphyllites glandulosus* Krassilov, IG1-739; b, d, blotches with elliptical leaf pieces marked off for case construction, IG1-200 and IG1-743; c, larval case constructed of cusped leaf fragments IG1-109; e, *Eocercidiphyllites glandulosus* Krassilov, from the Cretaceous of Gerofit, a deciduous leaf morphotype with glands on marginal teeth. Scale division = 1 mm.

Incurvarioidea: Heliozelidae) on broadleaved plants (Hering, 1957). Another type of case construction by incurvarioid larvae are the curvilinear crenulate-cusate cut-outs with borders of callus. Fossil example of such structures on leaves of *Eocercidiphyllites glandulosus* is shown in Fig. 3a.

Larval cases attached to mine-bearing leaves also are found in the Gerofit collection. Remarkably, one case is constructed of cusate leaf stripes like those cut out from the abovementioned specimen of *Eocercidiphyllites glandulosus* (Fig. 3c). The case is cylindrical; attached at about 30°, which implies that its mouth plane was inclined at about 15° to the leaf margin (“mouth type II”: Hering, 1951). The stripes are constructed of leaf fragments about 0.2 mm wide, loosely coiled and criss-crossed at about 45°. Gaps between the coils are traversed by delicate striae presumably left by silk threads. A short mucronate appendage at the hind end may represent a primordial case. In its shape and attachment the case is comparable to the “pupa type” coleophorid cases (Hering, 1951, 1957), but with no known close equivalents among the living species as far as the arrangement of the leaf pieces is concerned.

Discussion

The present-day case-constructing temporary leaf miners mostly belong to the Incurvariidae, Heliozelidae, Gelechiidae, Coleophoridae, and minor incurvarioid families. The trait is far more common in the temperate than tropical realms (Hering, 1951). Few fossil traces attributable to temporary miners are illustrated in Labandeira *et al.* (2002) and Wilf *et al.* (2006) from the latest Cretaceous and Paleocene of North America. In the mid-Cretaceous Gerofit assemblage, traces of case construction on mines constitute about 10% of all feeding traces and 20% of all mines constructed by the Lepidoptera (lepidopteronomes), thus attesting to a considerable diversity of temporary miners.

Although the taxonomic affinities of leaf parasites remain uncertain, their behavioral traits appear quite modern. In particular, the lepidopteronomes associated with excisions for foliar case construction on *Nelumbites* type leaves represent two consecutive developmental stages, quite similar to those of extant coleophorids. The attached cases are closely comparable with those produced by these moths as well, whereas the crenulate–cusate cut-outs on *Eocercidiphyllites* resemble those made by extant incurvarioid temporary miners on birch leaves (Needham *et al.*, 1928; Hering, 1951, 1957). In fact, extant behavioral equivalents can be found for all types of temporary mining

and case construction on Cretaceous leaves from the Gerofit locality, indicating that evolution of the trait essentially was accomplished during the mid-Cretaceous and remained unchanged afterwards. Remarkably, the traces of temporary mining occur on leaves of modern aspect, assignable to extant families Nelumbonaceae, Cercidiphyllaceae and Platanaceae, while being conspicuously absent from extinct plants of obscure familial affinities. These observations imply a considerable evolutionary conservatism of plant–insect communities, in which a temporary mining habit was of high adaptive value.

As one of the leaf parasite strategies in terrestrial ecosystems, temporary mining is regulated up the trophic cascade, by host–plant defense, and down the trophic cascade, by predators and parasitoids. Our data indicate that both types of regulation might have exercised their roles in the origin of the habit.

The choice of host plants by Cretaceous temporary miners may bear on the origin of the habit. Traces of case construction occur on *Eocercidiphyllites glandulosus* Krassilov (Cercidiphyllaceae), an extinct species akin to *Cercidiphyllum japonicum* Ziebold et Zuccarini, a deciduous tree of temperate montane forests in central-eastern China and Japan, descending to sea level in Hokkaido (Endress, 1993). As in the extant species, the leaves of *Eocercidiphyllites glandulosus*, long-petiolate, with an entire shield-like blade are typical of deciduous trees (Fig. 3e). *Platanervia integrifolia* Krassilov (Platanaceae) is a relatively small platanoid leaf type, likewise common in deciduous riparian trees. *Nelumbites aravensis* Krassilov (Nelumbonaceae), like extant *Nelumbo*, had leaves of two types, floating and emergent. The latter are thick, funnel-shaped, and used for foraging and reproduction by various terrestrial insects (Krassilov *et al.*, 2005; Krassilov, 2007).

These plant species represent two ecological groups: (i) broadleaved plants of deciduous leaf aspects (*Eocercidiphyllites*, *Plataneria*) inhabiting inland sites back of the more abundantly represented coastal vegetation, the leaf remains of which are heavily mined, and yet providing no evidence of temporary mining, and (ii) aquatic plants with emergent leaves (*Nelumbites*). These habitats seem potentially favorable (although for different reasons) for acquisition of the short-time mining habit. Such life habits might have acquired an adaptive value in respect of: (i) rapid leaf ageing in deciduous plants (making the leaf tissues hard and less palatable for a miner operating over a restricted area of a single leaf); and (ii) high larval mortality from flooding and excessive leaf surface moisture in wetland plants. Early leaf shedding may cause mass mortality of miners (reviewed in Hespenheide, 1991) conceivably conferring a selection pressure for abbreviation of mining stages.

It has to be noted that, unlike other insect damage on

leaves in our collection, temporary mines are never accompanied by traces of other parasitic species. This implies that plant defense reaction to temporary mining effectively deterred other parasites.

Predation likewise introduces selection pressure in favor of a shorter mining life. This is because early mines are less conspicuous for predators and their construction is completed before the peak of mine predation by ants and birds, which in temperate regions increases during the fall, when other trophic resources are depleted. Leaves of *Eocercidiphyllites glandulosus* are endowed with conspicuous mammiliform marginal glands, like in the ant-attracting plants. Indeed, a number of leaf mines from Gerofit bear traces of mine predation, suggesting that this factor might have come into play already, but no such traces were found in association with temporary mining.

Although paleoclimatic inference based on modern analogues are inevitably biased by distinctions brought about by evolution rather than climate, such criteria as the relative abundances of temporary miners seem instructive, being directly correlated with climate seasonality and deciduousness. In the Gerofit assemblage, temporary mining is associated with temperate floristic elements, thus strengthening the conclusions based on paleofloristic evidence alone (Krassilov *et al.*, 2005; Silantieva & Krassilov, 2006).

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