

Mine and gall predation as top down regulation in the plant–insect systems from the Cretaceous of Negev, Israel

Valentin Krassilov *

*Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel
Paleontological Institute, 123 Profsoyusnaya Street, Moscow 117997, Russia*

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Abstract

Fossil evidence of predation on leaf mines and galls opens the way to analyzing regulatory circuits in plant–insect interaction systems and assessing their evolutionary advancement. In the Cretaceous (mid-Turonian) flora of Negev, Israel, predation traces vary from the entire gall or mine excisions to minute punctures and slits over the mine tracks. Bite marks on the borders of predation holes representing different mouthpart morphologies may show how diverse the predators were. The efficiency of predation as a top down regulation force is attested on the basis of the gall and mine abundance, gall morphologies, mine configurations, co-occurrence of different mine types on leaves, and temporary mining. In turn, the regulation efficiency is considered as a criterion of evolutionary advancement of the plant–insect community as a whole. It is suggested that the coeval Cretaceous coastal and inland communities differed in the relative significance of top-down regulation.

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1. Introduction

Fossil leaf mines and galls are distinctive structures imposed by parasitic organisms on their host plants. Paleontological record of mine and gall structures provides for an evolutionary approach toward understanding this kind of specialized parasitic behavior and its impact on both plant and parasite evolution (Labandeira et al., 1994; Labandeira, 2002a,b; Labandeira et al., 2002; Wilf et al., 2005, 2006). Moreover, as this paper endeavors to show, fossil evidence places these processes in the broader context of ecosystem evolution, highlighting the systemic regulation circuits and their significance for morphological diversity.

Gall production, or cecidogenesis, interferes with the plant host's developmental program inducing various malformations

of plant tissues and organs (the histoid and organoid galls), as well as the special structures for endophytic larval habitation (the prosoplasmatic galls). Both types of malformations are features of systemic gall etiology that can leave their traces on fossil plants. Galls can be produced by various parasitic organisms, with the highest diversities of gall inducers among the mites and insects. In contrast, mining is a parasitic behavior known in insects mainly (on possibility of mite mining see Walter and Proctor, 1999), in which the larvae penetrate plant tissues leaving the cuticles intact except at the entrance and exit holes. Plant responses to mining are wound reactions, typically along the mine borders, although their effects may spread over considerable parts of leaf causing cell death or even morphological deformities at a distance from the mine (Hering, 1951). Mining insects occur in the orders Lepidoptera, Coleoptera, Hymenoptera, and Diptera. Mined plants include pteridophytes, gymnosperms and angiosperms, predominantly the latter. The diversity of mining strategies range from permanent to temporary, from epidermal to whole depth, and from linear to blotch configurations, with variations.

* Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel. Fax: +972 4 8246554.

E-mail address: vkrassilov@gmail.com.

The plant–parasite interaction is a two-level trophic system superimposed by the third level of mine predators and parasitoids. Mine predators are ants and birds mainly, but also mites, lacewings, wasps, bugs, and beetles. The system is regulated from the bottom up, by plant responses, and from the top down, by predation of the mining and gall dwelling larvae. Predators seem to affect the parasites in different ways, by reducing their densities on leaves, enhancing their developmental rates and encouraging the use of leaf prominences, such as leaf margins, midribs or strong lateral venation for concealing the parasitic structures from visual detection (reviewed in [Hering, 1951](#); [Mani, 1964](#); [Hespenheide, 1991](#)).

Despite their considerable economic and theoretical significance, the effects of regulatory circuits upon the endophytic parasite behavior are insufficiently understood, their evolutionary dimensions being scarcely explored at all. Plant galls are recorded from the Carboniferous ([Van Amerom, 1973](#)), but may

be as ancient as the terrestrial plants themselves ([Boucot, 1990](#); [Scott et al., 1994](#)), whereas mining traces are known since the Triassic ([Labandeira, 2002a,b](#)), with some preliminary studied finds in the Permian. Both of these types of endoparasitic structures increased in abundance and diversity with the rise of angiosperms, providing albeit indirect evidence of behavioral adaptations and allowing certain inferences on the origins and evolution of the plant–parasite interactions. Here, I describe unequivocal evidence of gall and mine predation in the Cretaceous and discuss implications for the evolution of endophytic parasite communities during the time of the basal angiosperm radiation. Conclusions of this regional study has to be considered as preliminary to be verified and extended by comparison with the rapidly accumulating evidence on Cretaceous and Paleogene mines and galls from other regions, some of which may represent similar forms of plant–insect interaction ([Brooks, 1955](#); [Labandeira et al., 2002](#); [Wilf et al., 2005, 2006](#)).

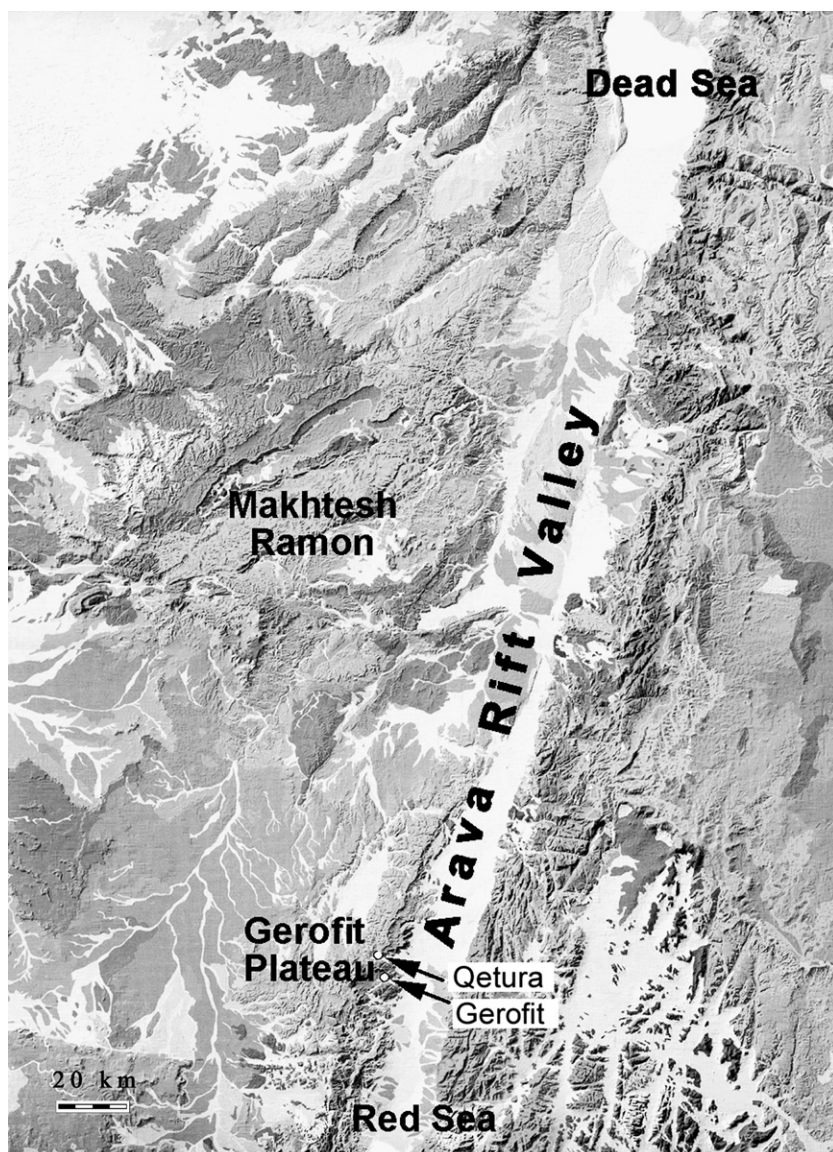


Fig. 1. Map of the Negev, with the Turonian Gerofit and Qetura localities marked by arrows.

2. Material and methods

The Gerofit fossil plant locality of the Arava Valley, the southern Negev, described in Krassilov et al. (2005), contains abundant traces of leaf galls and mines (Krassilov, 2007). Here the plant bearing Upper Shale Member of the Ora Formation consists of cross-bedded sands and laminated greenish-gray clays with freshwater gastropods in the lower part, grading upsection into variegate gypsiferous clays and dolomites of a hypersaline lagoon. The age assignment is based on the mid-Turonian ammonite records from the normal marine carbonate sequences below and above the Upper Shale Member (Freund and Raab, 1969; Bartov et al., 1972; Lewy, 1989). The floristic assemblages comprise transported remains of (1) the broad-leaved inland vegetation (the *Eocercidiphyllum*–*Platanervia*–*Platydebeya* assemblage) and (2) the freshwater aquatic plants (the *Nelumbites*–*Typhacites* assemblage), abundantly represented in the lower part of the section, and (3) a coastal wetland, probably mangrove, narrow-leaved community (the *Dewalquea*–*Eudebeya* assemblage) from the overlying red clay with extensive root beds (Krassilov et al., 2005; Silantieva and Krassilov, 2006). An analogous succession of plant horizons was sampled in the Qetura locality several kilometers to the north (Fig. 1).

In the collection of about 1500 specimens of terrestrial and aquatic angiosperms, most of the leaves are parasitized. The fossil leaves are preserved as reddish ferruginous mineral films deposited on the leaf surface and beneath the cuticle. The galls and mines are conspicuous on fossil leaves due to their usually brighter coloration and the darker hues of the surrounding callus.

Parasitic structures on fossil leaves were studied and photographed under a LEICA MZ6 stereomicroscope and a LEICA DFC320 digital camera. The collection is deposited at the Institute of Evolution, University of Haifa, Israel, under the depository number IG1.

3. Results

The collection contains abundant leaf mines of linear, blotch and digitate types referred to as ophionomes, stigmatonomes, and asteronomes, respectively, of the morphologic classification by Hering (1951). The mines are mainly produced by the larvae of Lepidoptera and Diptera. The leaf galls are less diverse and mostly organoid (causing conspicuous deformations of plant organs), less spectacular in their external (prosoplomatic) expression, although several types of cephaloneon (head-like) and ceratoneon (horn-like) structures are present (such purely

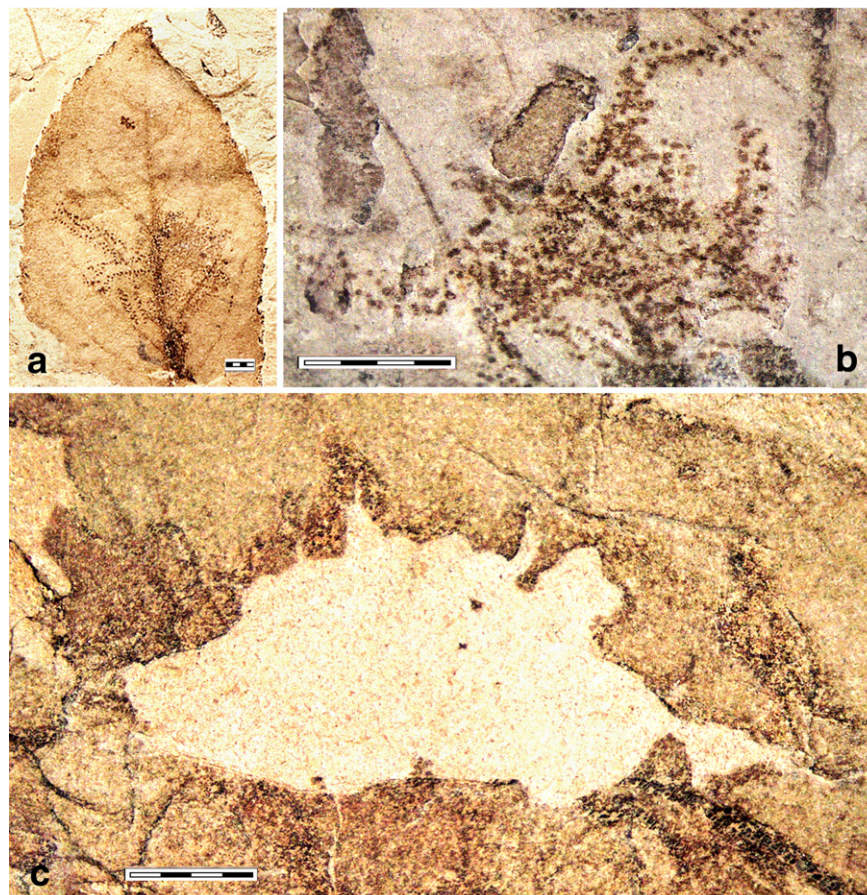


Fig. 2. Predation of asteronome-type mine: a, an asteronome on *Platydebeya papiloinacea* Krassilov, IG1-138; b, an asteronome of the same type showing double rows of small rounded frass pellets, co-occurring with other type blotch mines, IG1-128; c, asteronome of the same type cut out in the central area and over the rays, the tips of which, with characteristic frass pellets, are left on the leaf, IG1-1150. Scale bar=2 mm.

morphological designations have been widely applied and are still used for extant galls of uncertain origin, see Küster, 1911; Ross, 1932; Meyer, 1987).

Most prominent among the leaf mines are asteronomes with double rows of frass pellets similar to those produced by agromyzid flies (Diptera: Agromyzidae). Modern examples of such mines, most closely resembling the asteronomes on the Cretaceous leaves, can be found in Hering (1957) and Spencer (1976, 1990). They vary in the configurations of radial arms and the shape and size of their frass pellets. The most widespread type is a “spidery” mine on compound trifoliate leaves of *Platydebeya papilionacea* Krassilov, asymmetrically expanded on both sides of the midrib in the middle of the leaflets (Fig. 2a, b). The arms are radially spreading and recurved, of unequal length, with frass deposited in double rows of minute rounded pellets. Similar mines are produced by an extant European species *Chromatomyia periclymeni* and *C. chamaemetabola* on *Lonicera*, Caprifoliaceae (Hering, 1957, fig. 376; Spencer, 1990, fig. 909).

Mines of this kind seem to have been especially attractive for predators of the mining larvae, because about half of them are entirely cut out or else perforated by predation holes detectable by the bite marks along their margins. In specimen IG1-138 (Fig. 2c), an irregularly lobed hole retains configuration of the

mine, taking out the entire central part and extending to the arms, the tips of which, with characteristic arrangement of frass pellets, are left on the leaf. The lobes over the arms vary from low arches to broad wedges tapered into narrow slits. The predator might have worked from the central area into the arms, failing, however, to cut them out as precisely as the extant mine predators, ants or birds, would do when excavating the entire mine.

Another specimen, IG1-600, also on *Platydebeya papilionacea*, shows a bunch of digitate arms with frass pellets, the rest of the mine being cut out leaving an irregularly lobed hole between lateral veins (Fig. 3c, d). Similar holes on the opposite side of the midrib are also cut into the mined area bordered by the thickened (hypertrophied) lateral veins. The borders of excised areas between the veins are sinuous, representing a series of arcuate bites about 1 mm long and 0.2 mm deep.

A larger radial asteronome, with elongate frass pellets, evidently produced by a different species of agromyzid or anthomyid flies, occurs on a peltate leaf of *Nelumbites arvensis* Krassilov, specimen IG1-868 (Fig. 4c). It is cut in the middle by a large nearly circular hole with a microcrenulate borderline of the kind produced by a predator with hooked mandibles. Three smaller holes mark additional cut outs over the radial arms indicating that there were several larvae in the mine, such

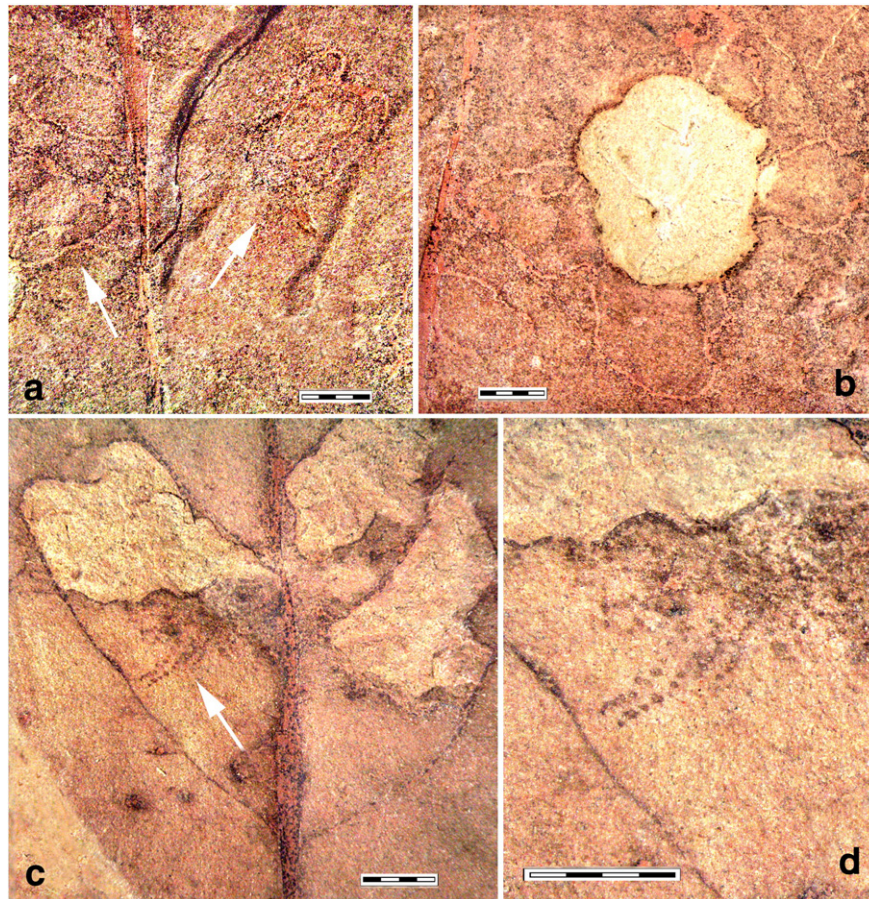


Fig. 3. Predation holes on mines: a, concentrically coiled mines (arrows) on *Dewalquea geroftica* (Dobruskina) Krassilov, IG1-1001; b, the same type mine cut out in the central area, with petal-like looping tracks; c, crenulate excisions on asteronome mines, one of which (arrow) is partly preserved, IG1-600.; d, the same region of asteronome enlarged to show the rows of small, rounded frass pellets. Scale bar=2 mm.

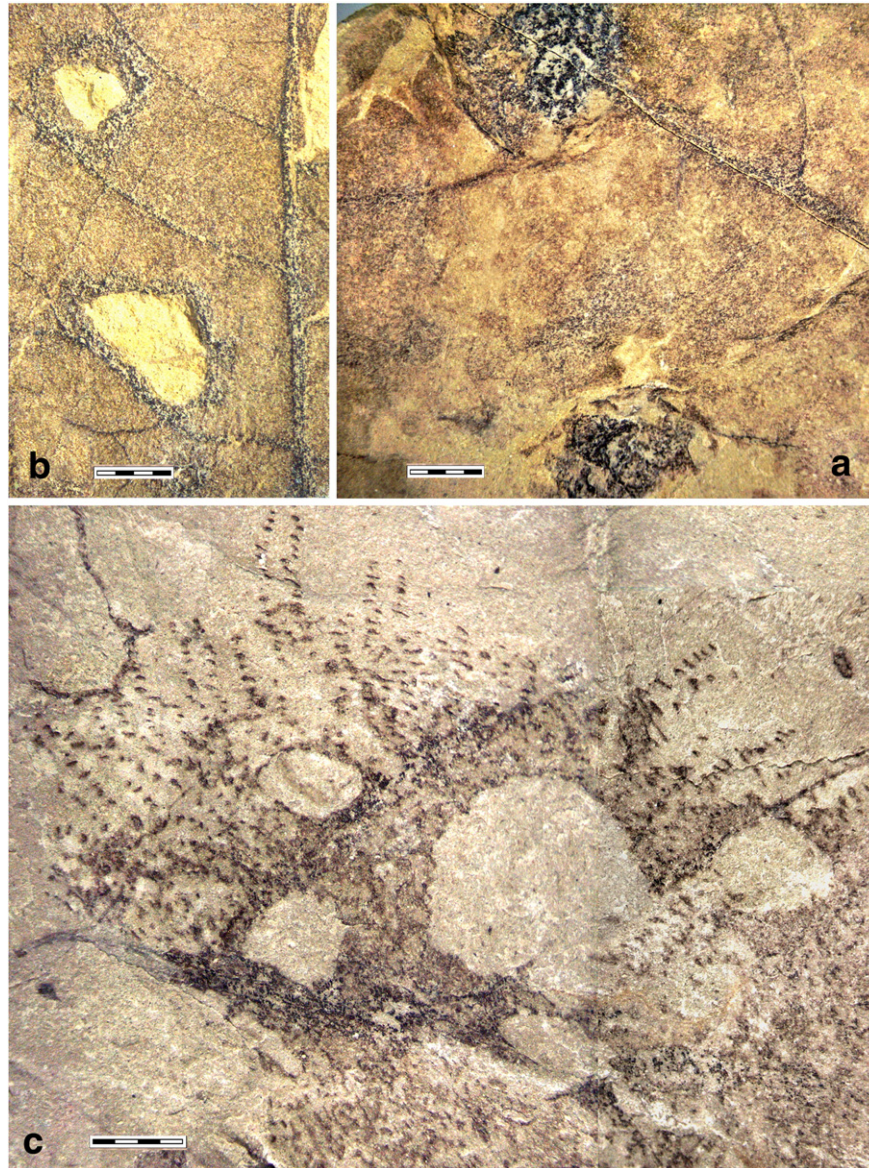


Fig. 4. Predation holes on galls and mines: a, cephaloneon-type scaly gall on the branches of strong lateral veins of *Menispermites cuspidentatus* Krassilov, IG1-403; b, predation holes on the same type galls, IG1-753; c, an asteronome-type mine with elongate frass pellets showing a large crenulate hole in the middle and the symmetrically arranged smaller cut-outs over the periphery. Scale bar=2 mm.

as in the extant communal mines of Diptera: Anthomyiidae (Needham et al., 1928) or Agromyzidae, such as *Chromatomyia gregaria* (Spencer, 1990, fig. 908). Evidently, the predator was large enough to detect and pick out all the larvae in the mine.

The angular holes on a broad subpeltate leaf of *Menispermites cuspidentatus* Krassilov, specimen IG1-753 (Fig. 4b) mark the sites of cut-out cephaloneon galls occurring on many specimens of such leaves (Fig. 4a). These galls are hemispherical, consisting of many imbricate scaly chambers that disintegrate into a bunch of scales at maturity, comparable to the scaly galls of extant aphids (Aphidoidea: Adelgidae). They occur on strong lateral veins at their forking point or on their distal branches and are surrounded by the dark pitted fringes of callus showing large hypertrophied cells. The fringes remain intact around the holes when the body of the gall is taken out.

A linear type mine (ophionome) attacked by mine predators is a small erratically coiled *Stigmella*-type track (Lepidoptera: Nepticulidae) on compound leaves of *Dewalquea gerofitica* (Dobruskina) Krassilov, a dominant species of the coastal plant assemblage. This mine has its middle part removed, leaving a rounded elliptical hole surrounded by the radial festoons of looping filiform tracks (Fig. 3a, b). The borders of the central hole are broad cuspules, about 2 mm long, 0.2 mm wide, divided by shallow notches, and with minute crenulations on the callus fringe.

A different kind of predation activity is represented by small rounded or elliptical holes over the winding linear mines on *Platydebeya papilionacea*, IG1-192a (Fig. 5a). The mine tracks are sinuous, marked by discontinuous frass lines of variable width. The holes are solitary, rather evenly spaced over the track

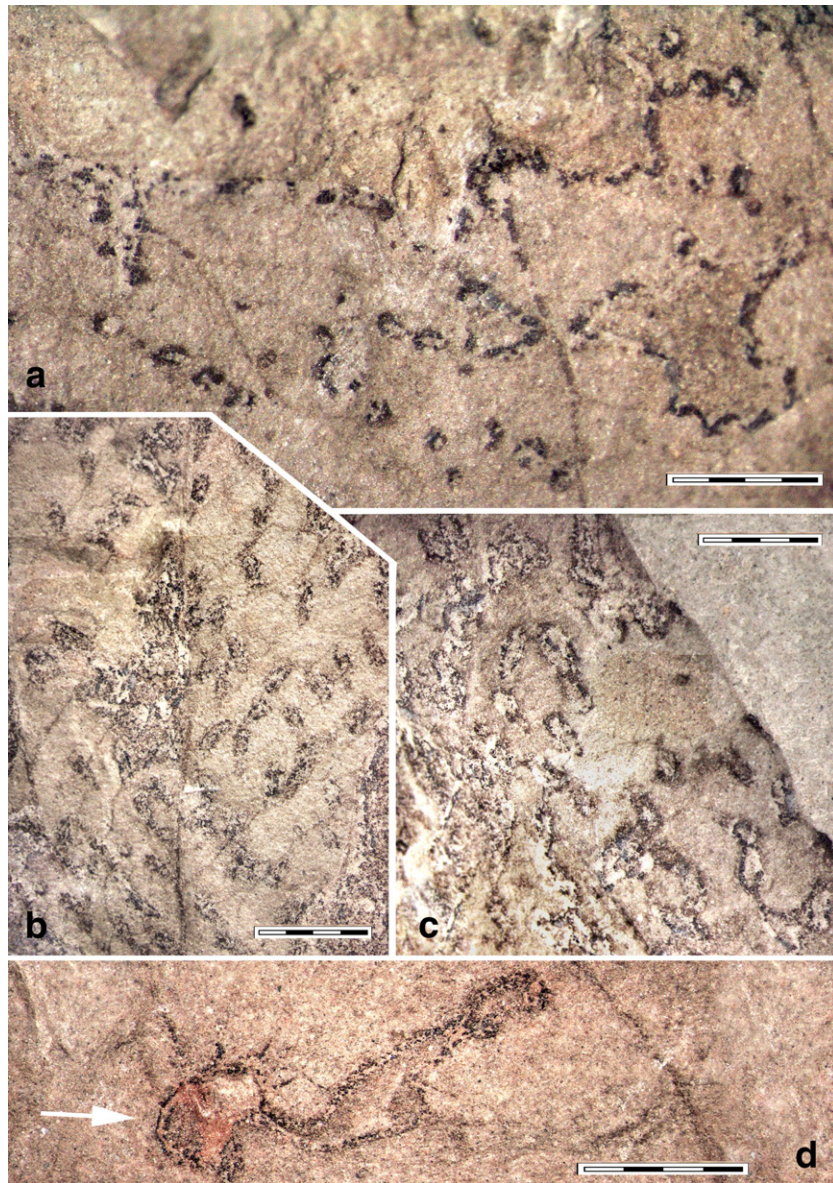


Fig. 5. a–c, punctures on winding tracks, IG1-192; d, mine track transecting a truncate pouch gall, IG1-160. Scale bar=2 mm.

coils, or paired, occasionally contiguous, about 0.4 mm in diameter, with thick patchy borders. Another leaf on the same hand specimen is mined over the nearly entire surface by tortuously coiled tracks that are more densely pecked or punctured. The holes are mostly elliptical, oblique to the mine, concatenate or contiguous, cutting arcuate slits over the loops of the track (Fig. 5b, c).

4. Discussion

Mines are opened by predators in search of larvae mainly (sometimes also by free living phytophagous larvae, although mined leaf tissue is nutritionally inferior to the leaf itself), whereas galls can be taken out also for the sake of their nutritive tissue. Galls of Gerofit assemblage are mostly organoid, attesting to a low grade of co-evolution in the plant–cecidozoan

systems. It is commonly surmised on account of gall etiology, that bottom up regulation in the plant–cecidozoan systems impels a restriction of the gall systemic effects (Ananthakrishnan, 1984; Wool, 1984; Meyer, 1987), ideally localized in the prosoplasmatic gall body itself. The logic of interaction dictates that, with its co-evolutionary advancement, the gall's prosoplasmatic prominence would increase at the expense of the gall's organoid effects. As a consequence of enhanced conspicuousness of the gall body, the top-down regulation by predators would gain in importance.

Organoid galls strongly prevail in the Cretaceous Gerofit assemblage, attesting to its primitive status over the general trend of co-evolutionary advancement as defined above. Accordingly, gall predation should be rare, which is the case. An exception is the morphologically most advanced type of the few prosoplasmatic galls, the scaly cephaloneon on the

broadleaved *Menispermites cuspidentatus*, which is regularly predated (Fig. 4a, b). The only evidence of possible predation upon the ceratoneon-type pouch galls of the narrow leaved coastal assemblage is a mine track passing through the gall that appears truncate, as if partly eaten by the mining larva (Fig. 5d).

In contrast, the proportion of mines bearing unequivocal predation traces, about 7%, is by no means insignificant. Both blotches and linear tracks are predated with a notable preference of the former (in extant mines, the adaptive advantages of blotch vs. linear configurations are uncertain).

The most frequently attacked among the Gerofit mines are the asteronemes that are fairly conspicuous owing to the spatial extent of their digitate arms that are speckled with frass pellets. That such mines were preferred indicates a predator with predominantly visual detection. The spidery mines with small frass pellets (Fig. 2a–c) are excised in the central part and at various extents over the arms, but with no more than a narrow slit reaching to the tips, leaving the narrow marginal fringe intact. Ants and birds are currently the most widespread mine predators, taking out the entire mine with the larva(e) in it. Yet extant ants would more precisely follow the perimeter of a mine, whereas in the fossil asteronemes, the slits over the arms appear as thrust and shear cuttings with a beak. Such an interpretation may not seem compatible with our ideas of bird feeding during the Cretaceous, but this is what the cut-outs seem to suggest.

The symmetrical disposition of predation holes on a large communal mine (Fig. 4c), presumably constructed by several larvae simultaneously at work, likewise testifies to visual orientation of a predator. Bite marks preserved as crenulations at the border of such cut-outs are of different shapes and dimensions indicating more than one predatory species differing from each other in their mouthpart morphologies.

Among the linear mines, only those winding over large leaf areas are predated, perhaps on account of their conspicuousness to visual detection from flight. The mines were pecked, punctured or thrust open by miniature beaks, stylets or rostra (Fig. 5a–c). The relative rarity of these mines indicates that predation selection for particular mine track configurations might have been at work already. All the cases are from the broadleaved inland assemblages.

Predation traces attest to top-down regulation in the system of plant–insect interactions, but only indirect evidence is available for a provisional assessment of its relative effectiveness vis-à-vis the bottom-up regulation. The following features of the Turonian mine trace assemblages are potentially informative in this respect.

- (1) In the plant collection of about 1500 specimens, about 80% bear traces of incipient to advance mine construction. In present-day biotic communities, such abundance of mined leaves would represent a pest outbreak that can be experimentally induced by an elimination of mine predators (Hickley, 1963). Since mine predators were there in the Turonian assemblages, we infer that their efficiency as top-down regulators was inferior to that of

today. Additionally, the frequencies of mine traces are considerably higher in the coastal narrow leaved *Dewalquea–Eudebeya* assemblage than in the inland broadleaved *Eocercidiphyllum–Platanervia–Platydebeya* assemblage, thus being negatively correlated with the occurrences of predation marks in these assemblages.

- (2) Leaf morphological evidence of predatory insect (ant) attraction, such as marginal glands, occur in the inland broadleaved assemblage, such as the fairly prominent marginal glands in *Eocercidiphyllites glandulosus* (Cercidiphyllaceae) and *Platydebeya papilionacea* (Figs. 2a, 6), but hitherto has not been recorded in the coastal assemblage.
- (3) Mine morphological evidence of protection against visual detection involves a restriction of the mined area, in particular, by tight helical coiling of the mine track, which ubiquitously occurs in extant mining insects, but is rare in the Turonian. Small size of the mines is another mode of avoidance, which may explain, why small blotch mines prevail in the inland broadleaved community. At the same time, the coastal assemblage provides examples of large whole leaf (leaflet) blotches with abundant frass deposits making the mine conspicuous when most of the leaf tissue is excavated.
- (4) Foliar topography of mines is suggestive of a cryptic behavior when their visual detection is reduced by proximity of the leaf margin, midrib and stronger veins. Midribs are impediments for the majority of invertebrate



Fig. 6. *Eocercidiphyllum glandulosum* Krassilov, IG1-999, a deciduous leaf morphotype with marginal glands. Scale bar=2 mm.

predators (but not for *Chrysopa*: Hering, 1951). Midrib miners are scarcely protected from acoustic detection guided by the sounds of feeding (Sugimoto et al., 1988), unless the larva resided to the midrib when not feeding. It may be significant in this respect that the proportion of midrib miners in the Gerofit assemblage, about 30% of all mine types, is exceptionally high by present-day standards.

- (5) Synecological evidence for top-down predation effects includes the co-occurrence of different mine types on leaf, as well as temporary mining. These synecological features are regulated in a complex way, including both top-down and bottom-up, as well as horizontal (competition of larvae) circuits. Crowded mines are more conspicuous for predators than solitary mines. Yet crowding of different mine types may confer protection for a specifically targeted mine type. Co-occurrence of two or more mines on the leaf is quite common in the Gerofit assemblage as a whole, being more frequent in the coastal assemblage than in the inland assemblage. Notably, the most frequently targeted arachnoid asteronomes may escape predation when they are entangled among the other type mines on the leaf (Fig. 2b). At the same time, plant resistance either increases or decreases with crowding, in the latter case, known as “weakness parasitism”, encouraging more parasites to join. “Weakness parasitism” might have been responsible for the ubiquitous co-occurrence of different mine types in the coastal assemblage. Crowding increases competition between the simultaneously mining larvae and between them and the co-occurring surface feeders (Hespenheide, 1991) that tend to avoid mined leaves on account of their decreased palatability. This latter phenomenon is obvious in the Gerofit assemblage, where the copiously mined leaves seldom show the otherwise abundant traces of surface feeding, such as punctures, feeding holes, scratches, skeletonization, etc.

- (6) Temporary mining through early development, after which the larva escapes to the surface is likewise a complexly regulated trait. The top-down regulation by predators confers selection for smaller size and shorter mining period if the risk of predation increases with the mine size or, in the case of bird predation, to the end of summer when other prey is scarce (Hering, 1951). In the Gerofit assemblage, traces of temporal mining followed by case construction occur either on leaves of a typically deciduous aspect, such as *Eocercidiphyllites glandulosus* and *Platanervia integrifolia*, or on emergent leaves of aquatic angiosperm, *Nelumbites arvensis*, Nelumonaceae (Fig. 7). The origin of the habit is presumably related to the leaf longevity (deciduousness) or instability of the habitat, as on the emergent leaves where the larvae encounter a high risk of being choked in the mine with the rise of water level. However, the relative frequency of temporary mining traces in the inland and coastal assemblages, 20% and 5% respectively, is positively correlated with the

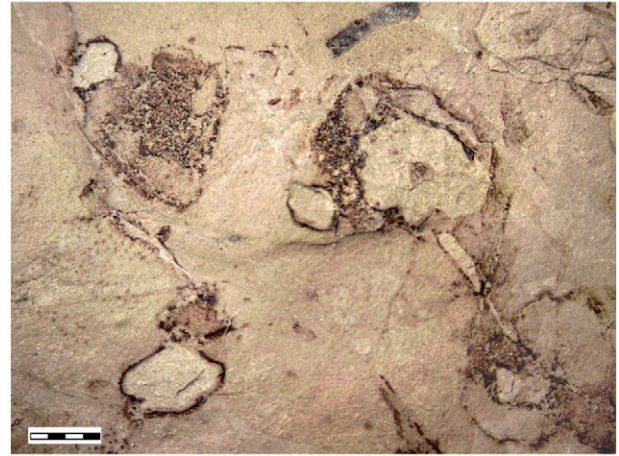


Fig. 7. Blotches of a temperate miner with leaf pieces cut out for case construction, IG1-107. Scale bar=2 mm.

frequencies of predation marks, indicating a contribution of top-down regulation.

Deciduousness as a factor in bottom-up regulation implies seasonal climate. In fact, the leading groups of the Turonian gall-makers (aphids and gall midges) and miners (agromyzid flies) of the Negev are largely temperate in their present day distribution (Hering, 1951; Skuhravá et al., 1984; Wool, 1984; Meyer, 1987; Hespenheide, 1991).

5. Conclusions

The fossil record of gall and mine predation is analyzable in terms of top-down and bottom-up regulation of the three interacting trophic levels: the host plant, the mining or gall inducing insect and the predator of the endophytically feeding larvae. Evidence of top-down regulation pertains to the selective occurrence of predation marks on galls and mines. Its efficiency can be assessed by the overall mine and gall abundance (decreasing with predation), as well as by their prominence and location in respect of the leaf topography (on or near the leaf margin or stronger veins, concealing such structures from visual detection).

The effects of top down regulation are superimposed upon bottom-up regulation by plant defenses and horizontal regulation by competition of larvae. Such synecological features as co-occurrence of different mine types on leaves (typically reduced by predation and competition, but enhanced in the case of “weakness parasitism”) and temporary mining are regulated in a complex way, the different regulation effects jointly contributing to evolutionary advancement of the system of plant–insect interaction.

The insect induced damage to the leaf typically decreases, whereas the host specialization (monophagy) increases with evolutionary advancement. Differences in efficiency of top-down regulation are highlighted by comparison of predation marks and related synecological features recorded from the Cretaceous coastal and inland communities, the latter being relatively advanced in terms of plant–insect interaction.

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