

hooked trichomes decreases as the leaf expands. This provides the greatest insect protection for the tender and succulent plant tissues.

Intraspecific variation in nymphal mortality was also accounted for by differences in trichome density. When nymphs were confined to upper leaf surfaces (low trichome density), total mortality for the two field bean cultivars was the same. This suggests that the two cultivars, excluding trichome effects, are equally suitable as leafhopper hosts. For nymphs confined to the lower leaf surface, however, capture mortality was approximately three times greater on the cultivar with the higher density of hooked trichomes.

Overall, nymphal capture and capture mortality are highly correlated ($r = .99$, $P < .01$) with hooked trichome density for the field bean cultivars (Fig. 2). Capture frequency increases rapidly with trichome density, but appears to level off beyond a density of 2000 trichomes per square centimeter. We suggest that the trichomes are so close together on terminal leaves that the nymphs are removed from most direct body contact with the leaf surface. Thus, very high densities of hooked trichomes could reduce capture and decrease the efficiency of this plant defense mechanism. Although removed from direct contact with the leaf surface, these nymphs could continue to feed, as their stylets are long enough to reach the leaf veins.

The percentage of caged leafhopper nymphs captured by the lima bean cultivar was much less than the percentage captured by either of the field bean cultivars (Table 1). This interspecific variation is not explained by differential trichome density, as lima bean leaves have moderately large densities of hooked trichomes. But the hooked hairs of *P. lunatus* are oriented at an angle of 10° to 30° (15) (Fig. 1d), whereas the hairs of *P. vulgaris* are relatively erect. Apparently these procumbent trichomes are oriented at such a small angle that the nymphs rarely come in contact with them. Thus the observed interspecific variability in nymphal capture for this cultivar is related to angle of trichome insertion rather than to density.

Clearly, hooked trichomes cause increased mortality of *E. fabae* on field beans. This reduction in nymphal infestation has dramatic implications for varietal plant resistance, as nymphal infestation density is generally correlated with the severity of leafhopper damage (8). Thus, hooked trichome density may be a valuable selection criterion in applied breeding programs for field beans, particu-

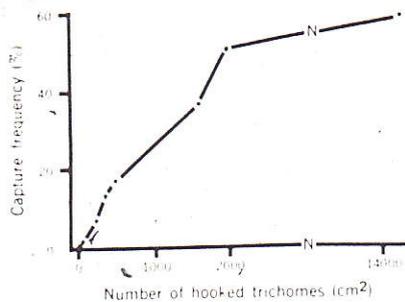


Fig. 2. Relationship between hooked trichome density and capture frequency of leafhoppers on field beans.

ularly if this defense mechanism can be combined with other plant factors mediating resistance to egg laying and growth of leafhoppers.

The role and importance of trichomes in resistance to crop pests has frequently been overlooked. In part, this may have been due to the inability of earlier workers to consistently correlate total plant pubescence with such general parameters as insect infestation level or crop yield. As our experience with *E. fabae* on field beans indicates, it is important to identify the biological impact on the pest of a specific trichome type. Other factors, including trichome density and angle of insertion, must also be considered. This knowledge should permit more effective selection of insect resistant cultivars.

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- We are indebted to S. Temple and D. H. Wallace for providing seed and to T. Eisner, P. P. Feeny, V. E. Gracen, and D. J. Paolillo for their critical reviews of the manuscript. This work was supported, in part, by a Rockefeller Foundation grant to D. H. Wallace. This is a publication of Cornell University Agricultural Experiment Station, New York State College of Agriculture and Life Sciences, a Statutory College of the State University of New York.

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Fog Catchment Sand Trenches Constructed by Tenebrionid Beetles, *Lepidochora*, from the Namib Desert

Abstract. *Three species of coastal Namib Desert tenebrionid beetles (Lepidochora) build trenches on desert sand dunes. Trenches are constructed perpendicular to fog winds and concentrate moisture during fogs. The beetles return along the ridges of the trenches extracting water from them. The water content of a population of these beetles increased by 13.9 percent during one fog.*

Field observations of three nocturnal beetle species, *Lepidochora discoidalis*, *L. porti*, and *L. kahani* were made during early summer (October 1975 through January 1976), in the coastal African Namib Desert dunes. These beetles establish trenches on the vegetationless surface of the sand dunes on mornings before and during advective fogs. Trenching creates two parallel sand ridges (Fig. 1). The usu-

al locomotory mode, however, is to walk over the surface without displacing sand (1). The ridges trap fog water, which is then taken up by the returning beetles.

During the early part of fogs, the beetles emerge on the barren sand dunes and move in a straight line, laying out trenches as long as a meter or more. The trenches become increasingly conspicuous as the parallel ridges trap blow-

ing fog moisture and darken. During this stage the beetles are found at the ends of the trenches, extending them. We were, however, unable to observe the actual trenching process because the beetles stopped moving when confronted with our lanterns. The water content (the weight ratio of water to dry sand in catchment ridges) was determined by collecting samples in vials with a scalpel and drying them. These samples contained more water than samples of the surrounding surface sand (Table 1). The absolute values varied with fog intensity, but the ratios of water in the ridge pushed by the trenching to the surrounding sand remained approximately constant (*L. discooidalis*, 2.85:1 and 2.08:1 for two fogs; *L. porti*, 2.80:1 for one fog; *L. kahani*, 4.06:1 and 5.88:1 for two fogs).

During the later stages of a fog, the beetles return along the ridges and flatten them as they apparently extract moisture. The mean water content of the ridges in front of five returning *L. discooidalis* was significantly greater than that behind them (Table 1). This value also varies with fog intensity and species. The ratio of water content in sand before processing by these beetles to processed sand is 1.93:1 for *L. discooidalis* and 1.81:1 for *L. kahani*. Ridges may be only partially broken down before dawn or when fog lifts and the ridges dry and crumble. On other occasions an entire ridge system may be flattened by the beetle occupant.

The trenches of these *Lepidochora* species are significantly oriented perpendicular to fog winds (Table 2). A beetle perfectly aligned perpendicular to the wind was considered to have zero deviation from the expected; random orientation would be 45° deviation. The actual deviation was for all three species oriented perpendicular to the wind. But, when the bearing of the fog is light, trenches are placed on the highest part of existing sand ripples regardless of wind directions. When the wind is strongly directional, the trenches are constructed perpendicular to the wind and can diverge markedly from the direction of ripples.

The location of these fog-catchment trenches on the dunes differs for each species. *Lepidochora discooidalis* concentrates on the dune slipfaces and especially the knife edges of the dune crests; *L. kahani* lives higher in the dunes than *L. porti* and makes its trenches on the almost level smooth or rippled sand near the dune slipface; *L. porti* builds its fog traps on nearly level sand.

Thus several characteristics of these trenches and the action of the beetles in them show that they are established to

Table 1. Water content (percentage) of sands from which two *Lepidochora* beetle species extract water during fog. Probability values are for within-species comparisons of water concentrations in sand. In one case the water content of the ridge is compared with that of the surrounding sand; in the other, the water content of a ridge is compared before and after the beetle extracts the water.

Species	N	Water content (%)	P
<i>Ridge versus surrounding sand</i>			
<i>L. discooidalis</i>	10		
Ridges		4.03	.001
Surround		1.53	
<i>L. kahani</i>	7		
Ridges		6.82	.001
Surround		1.68	
<i>Before versus after</i>			
<i>L. discooidalis</i>	6		
Before		2.80	.01
After		1.45	
<i>L. kahani</i>	3		
Before		2.82	.01
After		0.48	

trap fog water. The trenches are laid out only during or just before fog conditions prevail, they are oriented so that they maximize water entrapment, and the trapped water is depleted by the actions of the beetles.

Uptake of fog water was also established directly by determining the water content of a population of *L. discooidalis* before and after a fog. A mean water uptake of 13.88 percent of the field weight was found. These values were determined by collecting a sample of 20 speci-

mens in the field before and after a fog and drying them for 24 hours at 100°C. Control samples of the same size show no significant changes during similar intervals.

Observations of fog trapping have not been reported previously for any animal other than man. Numerous other desert arthropods in the Namib Desert visit detritus and plants to drink precipitated water droplets (2).

Lepidochora discooidalis is largely nocturnal but is also active in late afternoon, just before sunset (3). *Lepidochora porti* and *L. kahani* are strictly nocturnal. Wind-blown vegetal detritus, the trophic base of the diverse Namib fauna, is consumed by *Lepidochora* when the detritus has a low water content (\bar{X} = 1.93 percent, S.D. = 0.71, N = 5). Detritus is totally neglected during fogs, when it can reach a mean water content of 60.09 percent (S.D. = 20.38, N = 5, P = .001) and would thus represent a potentially far superior water source. The barren and often vegetationless sands where *Lepidochora* live limit the opportunity to collect water by eating living plants, and, when plants do grow in their habitats, they are not incorporated into the diets of these beetles.

These observations were made in the central Namib Desert dunes, 50 km inland from the South Atlantic Ocean. Adveective fogs arrive there between midnight and dawn and usually dissolve within 2 hours after sunrise (4). The principal

Table 2. Orientation of *Lepidochora* tracks during fogs.

Species	N	Observed	Orientation of track relative to wind direction			Orientation significance (P)
			Random	Range	S.D.	
<i>L. kahani</i>	15	7.4	45°	0.0 to 36.5	7.2	.001
<i>L. porti</i>	19	8.5	45°	0.5 to 42.5	9.9	.001
<i>L. discooidalis</i>	25	6.0	45°	0.0 to 42.5	7.1	.001

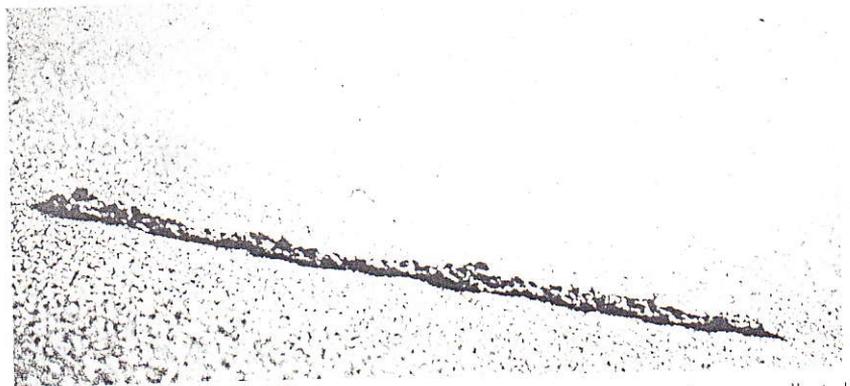


Fig. 1. A *Lepidochora kahani* returns along the ridge of a track, extracting the water collected there.

environmental conditions favoring the evolution of this fog-collecting behavior appear to be the vegetationless sand environment and the occurrence of advective fogs.

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Combustion Metamorphism in Southern California

Abstract. In several places in Southern California bituminous sediments of the Monterey Formation—siliceous shales, phosphatic rocks, dolomites, and arkoses—were affected during the Pleistocene and as late as the 19th century by spontaneous subsurface combustion of organic matter, during which temperatures up to 1600°C were reached. This oxidative heating (combustion metamorphism) affected rock complexes over areas of tens of square kilometers that tend to occur in clusters. As a result of these processes, the rocks recrystallized and partially melted to form pseudomagma which intruded the country rocks. The chemical compositions of these melts differ from those of igneous magmas. Acid and intermediate siliceous melts as well as phosphatic melts have formed. These two types are generally immiscible. The following high-temperature minerals were determined: α - and β -cristobalite, quartz, calcic plagioclase, diopside pyroxene, wollastonite, cordierite, graphite, fluorapatite, and fluorite; at lower temperature pyrite, gypsum, aragonite, calcite, jarosite, and hexahydrate crystallized.

During the last few years, several investigators have described the formation or mentioned the occurrence of rocks which burned spontaneously (1) and were, in consequence, affected by what might be termed combustion metamorphism. These rocks were originally sediments rich in organic matter, mainly bituminous carbonates, shales, or siliceous rocks, for example, diatomites. Under suitable conditions, the uppermost few hundred meters of these rocks undergo spontaneous combustion. The very high temperatures developed during this process frequently lead to partial melting of the mother rocks and the formation of pseudomagmas; the latter behave in a way very similar to the behavior of ordinary magmas and form small-scale intrusions such as dikes, sills, and laccoliths. In contrast to most magmatic occurrences, stages in the formation of the melts produced by combustion metamorphism can actually be studied in outcrops in situ. Almost any form of naturally occurring organic substance—bituminous matter, coal, or oil—can serve as fuel, but the most effective of these seems to be bituminous matter because of its intimate association with the inorganic constituents of the rocks. Occurrences of combustion metamorphic rocks are now known from Israel (2), Jordan, the

U.S.S.R. (3), Iran (4), India (5), Australia (6), and Canada (7). The occurrence studied in most detail is that of the Hatrurim Basin in Israel (2, 8), where not less than 130 minerals have been produced by this process (9). Combustion metamorphism in action was observed in the Kimmeridgean oil shales of Dorset by Cole in 1973 (10), and Cretaceous oil shales along a 65-km stretch on the northern coast of Canada ("Smoking Hills") are known to have undergone burning for at least the last 150 years (11). In contrast, combustion metamorphic rocks in the United States have rarely been studied, with the exception of the Clunker beds of Montana (12).

Recently we have undertaken an investigation of combustion metamorphic rocks at several places in California: the Grimes Canyon and Virgines Canyon areas, Ventura County, and three separate localities near Santa Maria, Santa Barbara County (13). In all these localities, combustion metamorphism has affected rocks of the Miocene Monterey Formation, where it is particularly rich in organic matter. Some of these places are located within producing oil fields; the participation of oil in the combustion process can therefore not be excluded. The rocks of the Monterey Formation represent a broad lithological spectrum,

and those affected by combustion metamorphism are correspondingly varied; they include diatomites, siliceous shales, dolomites, phosphatic rocks, and even arkoses.

The only locality we have thus far studied in some detail is Grimes Canyon (14), 5 km south of Fillmore. Here, the combustion metamorphic rocks form an almost uninterrupted belt 20 km long and 1 to 3 km wide. Within this belt, patches a few hundred meters long have occasionally escaped burning. Along some of the canyon walls, metamorphic rocks crop out over a vertical distance of about 400 m. Burning took place very recently, probably in the late 19th century, under the present topographical conditions; the depth below the surface affected by combustion is therefore not known. In the Hatrurim Basin, where burning occurred in the late Miocene, the metamorphic rock sequence is 260 m thick.

About 30 percent of the Grimes Canyon rocks are glasses, some vesicular and sluggy and others dense and closely resembling obsidian. The original melts were formed by selective melting of the parent rocks. Many Monterey rocks are finely laminated, phosphatic laminae alternating with others poor in P_2O_5 . During the combustion process, the phosphatic laminae became molten, whereas the more refractory ones recrystallized only by sintering. The result is a strongly laminated rock in which stony layers alternate with glassy ones (Fig. 1). Wherever only small amounts of melt were formed, the material solidified in situ, but, as the quantity of melt increased, it was mobilized and formed small intrusive bodies. Sills several hundred meters in length are abundant (Fig. 2). Veins and dikes, small stocks, and occasionally a laccolith also occur, very similar to those formed by igneous magmas. The central part of the sills and dikes is frequently highly vesicular, the vesicles being strongly elongated in the direction of flow. Chilled zones, dense and darker in color, occur on both sides. Melts, forming stocks, frequently continued moving after initial solidification and broke up into a blocky breccia, reminiscent of an aa lava field (lava with a blocky structure). They contain numerous metamorphosed xenoliths of the country rock. The country rock frequently collapsed, owing to volume contraction because of the dissociation of carbonates, the oxidation of organic matter, and the loss of much volatiles. Therefore, both collapse breccias and intrusion breccias occur (Fig. 3). The structure of the original rock sequence is generally preserved, however, and beds of