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Wettability and Contaminability of Insect Wings as a Function of Their Surface Sculptures

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Abstract

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The wing surfaces of 97 insect species from virtually all relevant major groups were examined by high resolution scanning-electron-microscopy, in order to identify the relationships between the wing microstructures, their wettability with water and their behaviour under the influence of contamination.

Isolated wings with contact angles between 31.6° and 155.5° were artificially contaminated with silicate dusts and subsequently fogged until drops of water ("dew") formed and rolled off. The remaining particles were counted via a digital image analysis system. Remaining particle values between 0.41% and 103% were determined in comparison with unfogged controls. Some insects with very unwettable wings show a highly significant "self-cleaning" effect under the influence of rain or dew.

Detailed analysis revealed that there is a correlation between the wettability and the "SM Index" (quotient of wing surface/(body mass)$^{0.67}$) with values ranging from 2.42 to 57.0. Furthermore, there is a correlation between the "self-cleaning" effect and the SM Index, meaning that taxa with a high SM Index, e.g. "large-winged" Ephemeroptera, Odonata, Planipennia, and many Lepidoptera, have very unwettable wings and show high particle removal due to dripping water drops. The "small-winged" insects, such as Diptera and Hymenoptera, and insects with elytra, such as Blattariae, Saltatoria, Heteroptera and Coleoptera, show completely opposite effects. This is clearly a result of the fact that species with a high SM Index are, in principle, more restricted in flight by contamination than species with a low SM Index which can also actively clean their own wings. The wings primarily serve a protection function in insects with elytra, so that the effects of contamination are probably of minor importance in these insects. Copyright © 1996 The Royal Swedish Academy of Sciences. Published by Elsevier Science Ltd.

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Introduction

Until now, the wettability of the surfaces of insects has only been investigated in species with special adaptations, e.g. fresh water bugs, such as *Aphelocheirus aestivus* (Thorpe & Crisp 1947) or species living on the water surface, such as *Podura aquatica* (Noble-Nesbitt 1963a) or *Paulinia acuminata* (Barthlott *et al.* 1994). Applied entomology investigates methods to enhance the wettability of the cuticle using suitable additives in order to increase the efficiency of insecticides (Pal 1950; Noble-Nesbitt 1970; Gilby 1984; Croghan & Noble-Nesbitt 1989).

Micro-morphological studies of insect surfaces are primarily descriptive, e.g. in Collembola with their complex microsculpture (Massoud 1969). This is also the case for the Diplopods *Polyxenus* spec. (Seifert 1966) and *Polyzonium* spec. (Wegensteiner 1982), and the Isopods *Porcellionides* spec. (Hadley & Hendricks 1984). Diffraction gratings in beetles were investigated by Hinton (1969, 1976). Butterfly scales have been the subject of particular interest since the comprehensive studies of Süffert (1925). The introduction of the Scanning Electron Microscope (SEM) led to more intense investigation of the scale structure, especially with regard to systematics. Roonwal (1985) used microsculptures on termite wings in studies of the phylogenetic relationship between individual subgroups of Isoptera. This phylogenetic–taxonomic aspect is also occasionally applied to other groups, particularly for identifying subordinate taxa (Schawaller 1987).

In botany, the ultrastructure of cuticular surfaces (e.g. epicuticular waxes) has been recognized as a valuable systematic feature (Barthlott & Wollenweber 1981; Barthlott 1990). It was shown that reduced wettability depends on the hydrophobic nature of the surface in connection with a sculpturing in microscopic dimensions (Holloway 1970). Water repellency in most cases was investigated in relation to gas exchange (Smith & McClean 1989) or as a problem in spray application (Martin 1960; Baker *et al.* 1983; Spillman 1984). An account of the function of reduced wettability, as

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a basis of a "self-cleaning" mechanism ("Lotus-effect") is in preparation. Water droplets that roll off the leaf surfaces remove quantitatively all contaminating particles (e.g. dust algae, bacteria, fungal spores).

There are extensive studies in botanical literature on the wettability of leaf surfaces. The introduction of the SEM also intensified the investigation of plant surfaces. The mostly group-specific features of leaf surfaces can be related to their wettability. Unlike smooth surfaces, those with a rough microsculpture are comparatively difficult to wet. This effect was also quantified by measuring the angle of contact between drops of water and the surface. Furthermore, unwettable leaf surfaces have a "self-cleaning effect", due to the fact that drop run-off washes away dirt particles and fungus spores (Barthlott & Ehler 1977; Barthlott 1990). Thus, a relationship between high unwettability and low contaminability was derived from these results. It was supposed that the "Lotus-effect" is present in all terrestrial organisms exposed to sun, dust and rain. Their surfaces usually show microsculptures in specific dimensions. According to these results, the influence of microsculptures on the wettability and contamination of insect surfaces, especially wings, was investigated.

In this context, biophysical aspects permit the identification of distinct selection factors for the development of specific structures, particulary in flying insects. Hence, there are definite differences between certain groups as regards the mechanics and aerodynamics of flight (Nachtigall 1974; Weis-Fogh 1976). Distal contamination and wetting of the wings increase the moments of inertia, with the result that inertial power-consumption is more in long wings than in short wings.

According to the working hypothesis, long-winged or relatively large-winged insects should have microsculptures which reduce the wettability of the wings and thus cause a "self-cleaning effect", especially due to the fact that long-winged taxa are usually unable to clean their wings with their extremities, as they are too short for this purpose.

Material and Methods

Material

In order to obtain a general overview of the microsculptures of insect cuticles, the following 97 species were examined:

Auchenorrhyncha: *Philaenus spumarius* (L.), *Tettigia orni* (L.).—Blattariae: *Blaberus cranifer* (Fabricius), *Ectobius sylvestris* (Poda), *Periplaneta americana* (L.).—Coleoptera: *Agabus bipustulatus* (L.), *Asaphidion flavipes* (L.), *Atheta crassicornis* Fabricius, *Cetonia aurata* (L.), *Cidnorhinus quadrimaculatus* (L.), *Ctenicera pectinicornis* Fabricius, *Elaphrus cupreus* (L.), *Hydroporus palustris* (L.), *Lagria hirta* (L.), *Pachnoda marginata* Drury, *Ptomaphagus sericatus* (Chaudoir), *Quedius nitipennis* Stephens, *Stenus juno* (Paykull), *Tachinus signatus* (Gravenhorst), *Trechus obtusus* Erichson, *Urodon rufipes* (Olivier), *Zophobas morio* Fabricius.—Diptera: *Episyrphus balteatus* (L.), *Eristalis tenax* (L.), *Mesembrina meridiana* (Meigen), *Myathropa florea* (L.), *Tabanus bovinus* Loew, *Tipula oleracea* (L.), *Volucella bombylans* Geoffroy.—Ephemeroptera: *Ephemera vulgata* (L.), *Ephemerella ignita* (Poda), *Ephoron virgo* (Olivier).—Heteroptera: *Carpocoris fuscispinus* (Boheman), *Coreus marginatus* (L.), *Gerris lacustris* F., *Kleidocerys resedae* (Panzer), *Nepa rubra* L., *Piezodorus lituratus* (L.), *Stenodema calcaratum* Fallou.—Megaloptera: *Sialis lutaria* (L.).—Hymenoptera: *Apis mellifera* (L.), *Bombus pascuorum* (Scopoli), *Ophion luteus* (Fabricius), *Paravespula germanica* (Fabricius), *Polistes gallicus* (L.), *Tenthredo arcuata* (L.).—Lepidoptera: *Aglais urticae* (L.), *Antheraea pernyi* Guerin-Méneville, *Apamaea monoglypha* (Hufnagel), *Anthocharis cardamines* (L.), *Arashnia levana* (L.), *Artogeia napi* (L.), *Autographa gamma* (L.), *Boarmia ribeata* Clerck, *Callimorpha dominula* (L.), *Cidaria rivata* Hübner, *Colias hyale* (L.), *Eudia pavonia* (L.), *Hepialus hecta* (L.), *Hyles galii* (L.), *Lymantria dispar* (L.), *Lysandra bellargus* Rottemburg, *Mamestra pisi* (L.), *Melanargia galathea* (L.), *Melitaea cinxia* (L.), *Micropterix calthella* (L.), *Notodonta dromedarius* (L.), *Operophthera brumata* (L.), *Parnassius apollo* (L.), *Pieris brassicae* (L.), *Phragmatobia fuliginosa* (L.), *Pyronia tithonus* (L.), *Scotia exclamationis* (L.), *Spilosoma lubricipeda* (L.), *Sterrha aversata* (L.), *Thymelicus sylvestris* (Hübner), *Xanthorrhoe fluctuata* (L.).—Mecoptera: *Panorpa vulgaris* Imhoff.—Odonata: *Ischnura elegans* (v.d. Linden), *Lestes sponsa* Hansem., *Libellula depressa* (L.), *Sympetrum sanguineum* (Müller).—Planipennia: *Chrysoperla carnea* (Stephens), *Euroleon nostras* (Fourcroy), *Palpares libelluloides* (Scopoli).—Plecoptera: *Perla burmeisteriana* Clas.—Psocoptera: *Caecilius flavidus* (Stephens).—Saltatoria: *Chorthippus brunneus* (Thunberg), *Gryllus campestris* (L.), *Locusta migratoria* (L.), *Myrmeleotettix maculatus* (Thunberg), *Oedipoda caerulescens* (L.), *Phaneroptera falcata* Poda, *Tetrix subulata* (L.).—Sternorrhyncha: *Aphis fabae* Scopoli—Trichoptera: *Hydropsyche pellucidula* Curtis, *Phryganea grandis* (L.).

As the body mass represents an important statistical parameter, live specimens were required. Thirty-eight species were thus selected from the main groups (Table 1), obtained from cultures of various institutes, or bred from larvae, and the remainder obtained from nature. These species were captured at the beginning of the flight period in order to obtain material with a minimum of contamination.

Methods

Measurement of the relative wing surface. The quotient of the total wing surface to the body mass of the fresh insect was determined as a measure of the relative wing surface, the so-called wing surface-body mass index (SM index). With the allometric relationship between surface and mass taken into account, this dimensionless index is expressed as wing area/(body mass)$^{0.67}$. Twelve to 25 specimens of each species were measured. If available, only males or virgin females were used. In contrast to virgin females, females bearing eggs lead to high variation in the mass values.

Measurement of the wettability of the wing surfaces. The wettability of the wing surfaces was determined by measuring the contact angle of drops of distilled water applied to the flat fixed wings. Principal variations of the values caused by the effect of hysteresis were avoided by a constant drop volume of 7 μl for all contact angle measurements (Adam 1963). The surface is wetted completely if the surface tension of the water is equal to that of the wing surface. In this case, the contact angle would be 0°. The other extreme which no known solid surfaces reach is represented by a contact angle of 180°, where a drop touches the surface at only one single point (Linskens 1950; Noble-Nesbitt 1970; Holloway 1971; Weser 1980; Boyce & Berlyn 1988).

Contact angles on insect wings were measured with a goniometer (ERMA Optical Lim., Mod. G3). The wings were fixed on slides with double-sided tape. The contact angles of immobile drops were measured. These measurements were primarily taken on the upper side of the forewing and also on the hindwing. In case of large wings, the contact angle was measured separately in the middle of the basal and apical third of the wing, while for a few taxa, this angle was measured on the underside of the wing. Twenty measurements, on the wings of five individuals, were measured constantly, per species per wing area, and the mean values were calculated (Table 1).

Artificial contamination of the wings. In order to investigate the manner in which particles were removed from the wings, they were contaminated artificially with silicate dust (Quarzwerke Frechen GmbH) and sorted according to particle size. The wings to be contaminated were fixed on SEM slides. The wings of one specimen were used to prepare two slides for each species. One group of preparations was contaminated with silicate dust (Silbond 100 EST) having a medium particle size of 1.26 μm^2, while the other group was contaminated with Silbond 600 MST with a medium particle size of 4.98 μm^2. In order to contaminate the wings, they were enclosed in a tent with a volume of 0.5 m^3. One gram of dust was circulated using pressurized air for 10 min, after which time, the contaminated wings were removed. Slides prepared with plastic film were also contaminated in the same process. These slides were later used as a control for homogeneous contamination, and their particle count was used as a reference value for the subsequent fogging investigations.

Fogging of the contaminated wings. In the tent mentioned above, the contaminated wings were fogged with water ejected from fine-spray

Table 1. *Values of wing surface–body mass (SM index), contact angle and remaining particles after fogging. Mean values and standard deviations (in brackets)*

	1	2	3
Ephemeroptera			
Ephemerella ignita	22.0 (2.32) m	136 (10.6)	—
		—	—
Ephoron virgo	20.9 (1.33) f	135 (6.31)	57.2 (13.4)
		—	—
Odonata			
Ischnura elegans	22.5 (2.85) f/m	127 (11.5)	16.2 (11.2)
		126 (8.85)	—
Blattariae			
Blaberus cranifer	16.9 (1.02) m	83.0 (9.22)	103 (32.1)
		81.6 (8.90)	123 (21.3)
Ectobius sylvestris	22.5 (1.27) m	72.4 (6.22)	68.9 (24.2)
		85.6 (11.4)	129 (61.3)
Periplaneta americana	11.2 (1.54) m	83.5 (9.00)**	58.2 (11.3)
		69.9 (8.72)	73.8 (14.6)
Hymenoptera			
Tenthredo arcuata	4.99 (0.53) f	89.1 (8.80)	62.8 (12.7)
		—	—
Apis mellifera	2.42 (0.06) f	92.8 (6.16)	41.8 (13.6)
		—	—
Bombus pascuorum	3.12 (0.17) f	85.3 (12.61)	41.7 (8.88)
		—	—
Paravespula germanica	3.58 (0.20) m	95.8 (5.58)	42.6 (14.2)
		—	—
Trichoptera			
Hydropsyche pellucidula	17.3 (0.78) m	136 (4.22)	—
		134 (5.64)	—
Lepidoptera			
Boarmia ribeata	51.7 (3.92) m	132 (5.54)	1.38 (1.12)
		130 (6.08)	—
Cidaria rivata	47.9 (2.34) m	137 (3.87)	—
		—	—
Autographa gamma	19.0 (0.78) f/m	134 (6.54)	2.41 (1.98)
		130 (6.12)	—
Antheraea pernyi	37.4 (2.21) m	133 (8.46)	4.69 (3.21)
		123 (10.2)	—
Thymelicus sylvestris	20.8 (1.54) f/m	132 (6.73)	1.79 (0.63)
		135 (5.32)	—
Pieris brassicae	57.0 (3.13) f/m	133 (4.71)	2.20 (1.22)
		131 (6.19)	—
Aglais urticae	38.2 (1.98) m	141 (6.34)**	0.69 (0.54)
		128 (5.32)	—
Melanargia galathea	33.1 (2.23) m	131 (6.13)	0.55 (0.54)
		132 (5.48)	—
Mecoptera			
Panorpa vulgaris	12.2 (0.16) f	112 (16.6)	23.6 (14.2)
		120 (10.6)	—
Saltatoria			
Phaneroptera falcata	22.1 (0.88) m	113 (6.04)	63.8 (15.4)
		107 (9.81)	41.3 (18.4)
Gryllus campestris	9.91 (0.35) f/m	72.5 (18.1)*	68.4 (22.1)
		88.3 (12.5)	79.3 (17.2)
Chorthippus brunneus	10.4 (0.61) m	101 (14.0)	47.8 (9.98)*
		104 (11.3)	14.9 (3.22)
Locusta migratoria	14.6 (0.89) m	78.9 (10.3)**	34.0 (8.55)
		95.2 (7.25)	40.5 (11.3)
Myrmeleotettix maculatus	7.01 (0.23) m	64.7 (18.7)**	49.1 (11.0)*
		93.8 (9.21)	16.2 (7.17)
Auchenorrhyncha			
Tettigia orni	13.8 (1.04) m	86.5 (15.5)	49.8 (12.1)
		92.4 (16.0)	—
Heteroptera			
Coreus marginatus	5.41 (0.19) m	72.0 (16.7)	45.0 (13.1)*
		73.4 (19.3)	89.6 (11.6)
Piezodorus lituratus	4.34 (0.20) f/m	82.6 (9.81)	13.0 (2.89)
		107 (4.95)	18.0 (4.58)
Megaloptera			
Sialis lutaria	—	130 (6.04)	—
		—	—

Continued overleaf

Table 1. (Continued)

	1	2	3
Planipennia			
Chrysoperla carnea	43.9 (2.23) f/m	155 (6.80) 143 (5.83)	0.41 (0.40) —
Coleoptera			
Pachnoda marginata	3.79 (0.09) m	31.6 (6.50)** 82.2 (7.06)	81.9 (12.5)* 56.7 (8.19)
Lagria hirta	15.5 (0.79) m	81.7 (5.81)** 113 (13.3)	— 53.1 (21.3)
Zophobas morio	6.85 (0.37) m	43.0 (12.1)** 86.3 (13.2)	38.9 (7.87) 43.5 (14.2)
Diptera			
Tipula oleracea	9.28 (0.75) m	130 (10.5) —	22.7 (20.1) —
Tabanus bovinus	4.13 (0.22) f	83.3 (20.1) —	64.3 (15.1) —
Episyrphus balteatus	6.74 (0.34) f/m	128 (6.13) —	44.7 (26.9) —
Eristalis tenax	4.53 (0.31) m	90.3 (4.21) —	90.3 (19.5) —
Mesembrina meridiana	4.12 (0.37) f	85.1 (10.8) —	63.4 (13.8) —

1. Wing surface–body mass = SM index ($cm^2/g^{0.67}$) (12–25 individuals per species measured; f: female; m: male; f/m: both sexes).
2. Contact angle (°) (20 measurements per species; above: forewing upper side, below: hindwing upper side).
3. Remaining particles after fogging compared with contaminated but not fogged plastic control (large particles; %); (10 measurements per species; above: forewing upper side; below: hindwing upper side).
Significant differences between fore- and hindwing; confidence intervals <0.05 (*), <0.01 (**).

nozzles. The slides with the contaminated wings were fixed to the bottom of the tent, inclined at an angle of 45° and protected from residual drops of water from the tent ceiling. Hence, the fog could only settle on the wings indirectly from the side. The wings were exposed to the fog for 6 min, after which time, rolling drops or a thin streaming coat of water had developed. After air-drying, the surfaces were sputtered with gold to fix the remaining particles. Fogging is more advantageous than raining in this case, because mechanical distortion by the kinetic energy of falling droplets is excluded.

SEM and image analysis. The wings were subsequently examined in the SEM. The numbers of particles were counted by digital image analysis (TCL Image). Ten wing sections at a magnification of 250 × were counted. These results were compared with those obtained from the contaminated, but not fogged, plastic controls. In this way, the number of particles removed by water could be measured.

Statistics. Most of the species-specific values did not show a normal distribution, which can be explained by the limited sample size for the SM index and the number of remaining particles. In the case of the contact angle, however, this lack of a normal distribution is due to the nature of the angle, i.e. the values approach a maximum. Consequently, only the Kolmogoroff–Smirnoff test was applied. Correlations were always considered linear (r). Confidence intervals with $P < 0.05$, $P < 0.01$ and $P < 0.001$ were indicated by the symbols *, ** and ***.

Results

Variability of the SM index

The SM index varies from 2.42 to 57.0. The arithmetic mean of all values is 17.6. The values within the individual groups show only a slight variation. Hymenoptera, Diptera and most species belonging to groups with elytra have a low SM index (2.42–16.9). This does not apply to more filigree-structured and actively flying species, such as *Phaneroptera falcata*, *Ectobius sylvestris* and *Lagria hirta*. Ephemeroptera, Odonata, Planipennia and most Lepidoptera have high index values (19.0–57.0).

Contact angle as a measure of wettability

The contact angles on the upper side of the forewings vary from 31.6° (*Pachnoda marginata*, elytron) to 155.5° (*Chrysoperla carnea*). The distribution of the investigated species shows two maxima. The first maximum at 80° includes species with smooth or lightly hairy wing surfaces. The second maximum at 130° includes taxa with special wing sculptures. The values for the basal section on the upper side of the fore- and hindwing are generally smaller than those for the end of the wing. Significant differences between the basal and apical values on the forewings could only be found in four species (*Periplaneta americana*, *Phaneroptera falcata*, *Locusta migratoria*, *Tipula oleracea*). A significant difference in the values for the hindwing was also determined in *Phaneroptera falcata*, which was attributed to the distinct difference between the microsculptures at the base and end of the upper side of the hindwing. No significant differences were determined in a comparison of the values for the upper side of the fore- and hindwing in specimens with uniformly sculptured wings; the forewings show somewhat larger contact angles. In the case of *Aglais urticae*, the significantly larger contact angle on the upper side of the forewings as compared with the similarly sculptured upper side of the hindwings is interpreted as a random occurrence. In contrast, this difference is related to the varying sculpture types in species with elytra. A number of significant differences were found in seven of the 14 representatives of Paurometabola, Heteroptera and Coleoptera investigated (Table 1). The elytra are generally much more wettable than the membranous hindwings. Only *Periplaneta americana* shows any significant larger contact angles on the elytra.

The values for the underside of the wings largely correspond to those for the upper side.

Cleansing the wings by fogging

Particle removal during fogging is very high in Lepidoptera and Planipennia, fluctuating between 95.31% and 99.59% in comparison with the non-fogged controls. This means that only 0.41–4.69% of the particles initially applied remained on the wings after fogging took effect and the water drops began to roll off. The other extreme was demonstrated by cockroaches, which even showed some values over 100%, i.e. there were more particles on the wings after fogging, as compared to the mean values of the controls. A comparison of the particle removal from the fore-and hindwing of species with elytra shows that some species have significantly higher values for the hindwings, while other species show slightly more intensive removal on the elytra (Table 1). No significant differences were determined in a comparison of large and small particles.

Correlations—SM index, contact angle and particle removal

Linear regression analysis of the SM index and the contact angle shows a significant relationship (Fig. 1).

Several groups can clearly be identified in the diagram. Beetles have strongly varying contact angles. The elytra of the species investigated show rough sculptures or shaggy, tousled, unkempt, matted hair which proved to be wettable. The elytra of Paurometabola, Heteroptera, and the more weakly sclerotized transparent "flying wings" of Diptera and Hymenoptera are also more effectively wettable, and are located between index values of 2.42 to about 20 on the regression line. The wing surfaces of these species have no special microsculpture or are thin and largely only covered by short hairs. "Sturdy" butterflies (Noctuidae, Sphingidae), dragonflies and mayflies have larger than average contact angles. Together with those of "filigree" butterflies (Geometridae) and lace wings, their contact angles lie within a more narrow range of 131.4–155.5° and span an index range of about 20–57.0. The wing surfaces of these species are particularly characterized by unique microsculptures.

Particle removal and the SM index or contact angle values are negatively correlated (Fig. 2).

Sculpture types and measurement values within the major taxa

Ephemeroptera. Mayflies are relatively large-winged insects with very unwettable wing surfaces. The wings have a fine, irregular, terry cloth-like microsculpture (Fig. 3). In *Ephemera vulgata*, these sculptures are more elongated and dense on the apical section of the wing than on the base section. Artificial contamination was only investigated in *Ephoron virgo*. This species showed below-average poor particle removal with a large contact angle, which is possibly due to the dense hair on the wing peculiar to this species. *Ephoron virgo* is an atypical species because the subimago no longer sheds its skin. The wings appear milky white due to the air pockets between the cuticle of the subimago and that of the imago. The cuticle of the subimago of *Ephoron virgo* is hairy, relatively wrinkled and has no microsculpture (Fig. 4).

Odonata. The shape and size of the wing-surface microsculpture of the dragonflies correspond to those of the mayflies (Fig. 5). The contact angles are similarly large, the particle removal in *Ischnura elegans* (Figs 6 and 7) being markedly stronger than that of *Ephoron virgo*. In both taxa, there are relatively lightly erodable wing surfaces. The tertiary sculpture can easily be removed by being wiped with a thin brush. However, this sculpture changes only insignificantly in hot chloroform, but does break away in "sheets" from the underlying wax-layer (cf. Neville 1975).

Plecoptera. The surface of the wings of the investigated stonefly shows a slightly wavy background with no microsculpture and dense, long, false hairs. The image, as a whole, can best be compared with the wings of *Ephoron virgo*. Individual measurements of the contact angle on the wings resulted in values between 118° and 125°.

Blattariae. The elytra of cockroaches have a polygonal scale structure, where a polygon corresponds to one underlying epidermal cell (Hinton 1969).

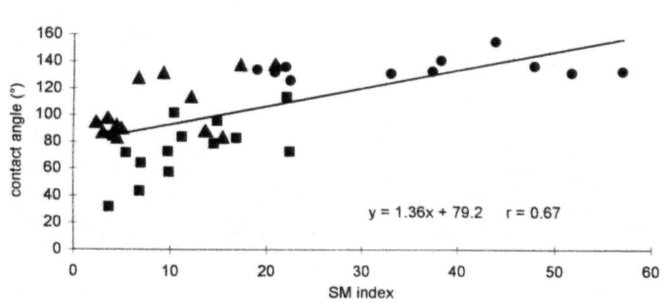


Fig. 1. Correlation between SM index and contact angle (38 species). ■ with elytra, ▲ without elytra and microsculpture, ● without elytra and with microsculpture.

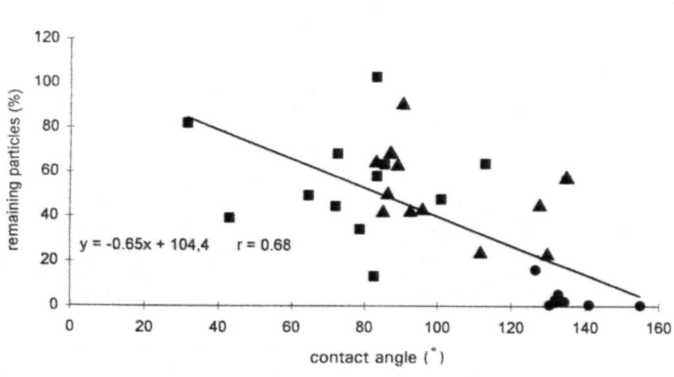
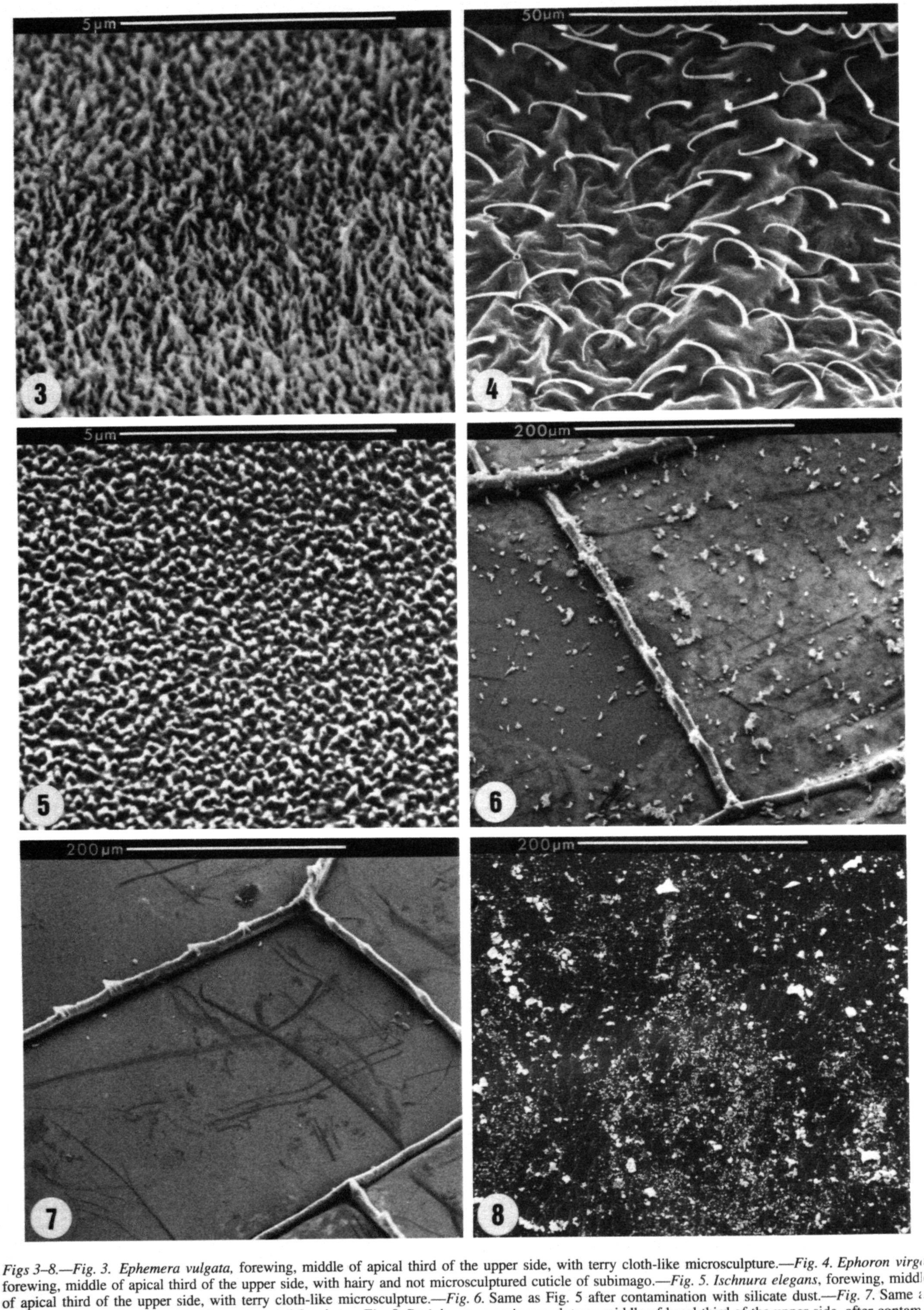


Fig. 2. Correlation between contact angle and remaining particles (32 species). ■ with elytra, ▲ without elytra and microsculpture, ● without elytra and with microsculpture.



Figs 3–8.—Fig. 3. Ephemera vulgata, forewing, middle of apical third of the upper side, with terry cloth-like microsculpture.—*Fig. 4. Ephoron virgo*, forewing, middle of apical third of the upper side, with hairy and not microsculptured cuticle of subimago.—*Fig. 5. Ischnura elegans*, forewing, middle of apical third of the upper side, with terry cloth-like microsculpture.—*Fig. 6.* Same as Fig. 5 after contamination with silicate dust.—*Fig. 7.* Same as Fig. 5 after contamination with silicate dust and fogging.—*Fig. 8. Periplaneta americana*, elytron, middle of basal third of the upper side, after contamination with silicate dust and fogging.

At a higher magnification, uniform and shallow indentations of the epicuticle become visible. Apart from a few sensory hairs, the elytra are bald. The scale structure is only weakly visible on the hindwings, and gradually changes over to short and thin false hairs in the anal region of the wing.

These surfaces have contact angles below 90°. In *Blaberus cranifer* and *Periplaneta americana*, the contact angles of the elytra are larger than those of the hindwings, while *Ectobius sylvestris* has markedly more wettable elytra. The particle removal is generally low in all species (Fig. 8), and usually lower on the hindwings than on the elytra, with occasionally no removal occurring at all.

Saltatoria. The locusts and crickets typically have a wing surface similar to that of cockroaches with a polygonal structure on the elytra and fine, short hairs and a smooth or slightly wavy surface on the hindwings. Uniform protrusions are found on the wings of the very xerophilic *Oedipoda caerulescens*, whose elytra are covered by irregular, erect and plate-like scales (Fig. 9). The elytra of *Locusta migratoria* show a similar sculpture, with the protrusions being flatter and covered by a finely structured layer.

The relatively large-winged *Phaneroptera falcata* has a toothed sculpture on the elytra which is located on the apical (also green) part of the hindwing (Fig. 10). Similar to the microsculptured elytra of *Locusta migratoria*, a high particle removal was determined here, which, however, does not coincide with a larger than average contact angle in *Locusta migratoria*. Instead, this species shows a significantly smaller contact angle on the elytra as compared with the hindwing. The same effect was also determined in *Gryllus campestris*. Both species were obtained from insect breeding facilities, where more severe contamination of the elytra is to be expected due to the often restricted breeding conditions.

Psocodea. All book lice are small insects with body lengths between 0.5 and 7.0 mm. A single species may include winged and also short-winged and wingless forms. However, most species have fully-developed wings with no microsculpture, but rather only short and thin false hairs.

Hemiptera (Auchenorrhyncha, Sternorrhyncha, Heteroptera). Bugs and most of the cicadas have forewings which have developed into tough elytra. The investigated water bugs, *Gerris lacustris* and *Nepa rubra*, also have these types of elytra, in addition to very dense hair. Contact angles of up to 151° were measured on the elytra of *Gerris lacustris* (Fig. 11).

In the case of land bugs and Cercopidae (here: *Philaenus spumarius*), the hair is primarily thin and located on the basal part of the elytra (the corium), often being reduced to short bristles set in indentations or protruding in front of them. Except for a polygonal structure, only *Coreus marginatus* showed a fine, slightly wavy microsculpture. The contact angles on the bug wings were under 90°. Values up to 112° were only measured on the wavier hindwings of *Piezodorus lituratus*. Particle removal was relatively high in his species, and considerably lower in *Coreus marginatus*. The elytra of the latter species were also often severely contaminated in individuals taken from the field.

The transparent wings of the singing cicadas have a completely different sculpture. An extremely fine and irregular microsculpture only becomes visible at a magnification of 3000 (Figs 12, 13). The surface material appears to contain water-soluble components, as the particles often appear to be encrusted on the surface after fogging; the particle removal is also below average. The wing surfaces of *Aphis fabae* were selected for investigation from the Sternorrhyncha. These surfaces show dense, uniformly distributed scales—a sculpture which is at best comparable with the elytron scales of *Oedipoda caerulescens* or *Locusta migratoria*.

Megaloptera. Alderflies have wings with two types of hair. The shorter hairs are false hairs, uniformly covering the entire surface of the wings in a relatively dense manner. The upper sides of the wings additionally have hairs which are four times longer and primarly arranged in rows. The contact angle of 130.5° is relatively large.

Planipennia. All species of lace wings investigated have a microsculpture similar to that of the mayflies and dragonflies (Fig. 14). The shape of the wing surfaces and also the entire wing structure, with its pronounced longitudinal and transverse network of veins and relatively large size, are comparable in these groups. A difference exists only in the long bristles located along the veins of Planipennia, where Palaeoptera have very short hairs, if any at all.

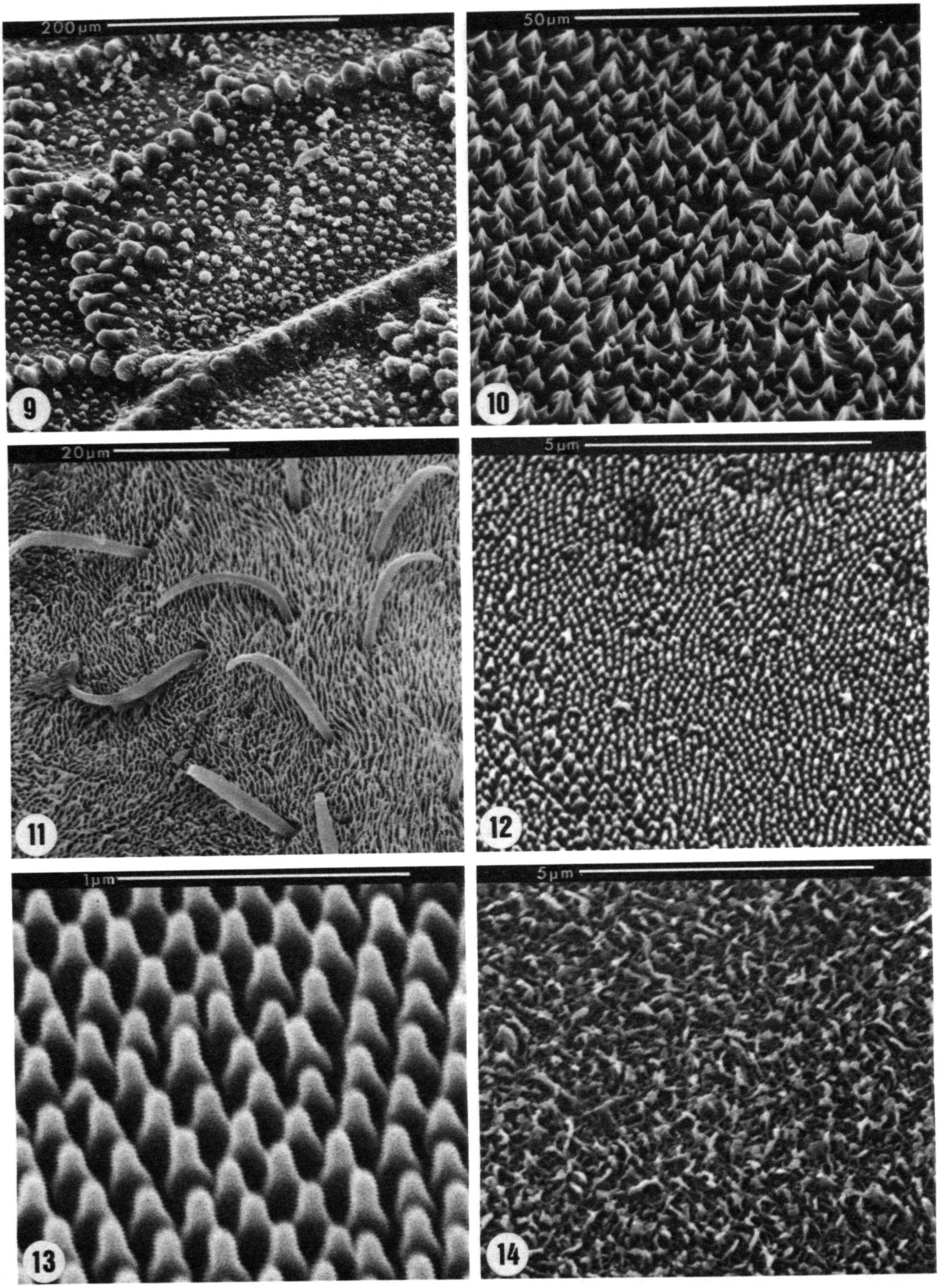
The structural similarity of the groups is also reflected in the low wettability and high particle removal. For *Chrysoperla carnea*, these parameters reach maximum values of 155.5° and 0.26%, respectively, for all species investigated.

Coleoptera. The elytra of beetles have highly diverse microsculptures. A polygonal pattern and parallel ridges represent the main types. The latter type particularly dominate the iridescent structural colours of many beetles (Hinton 1969). Some taxa have hairy wings which reach a maximum length in some Lagriidae (*Lagria hirta*). Some groups of Scarabaeidae and Curculionidae in particular have scaly elytral surfaces.

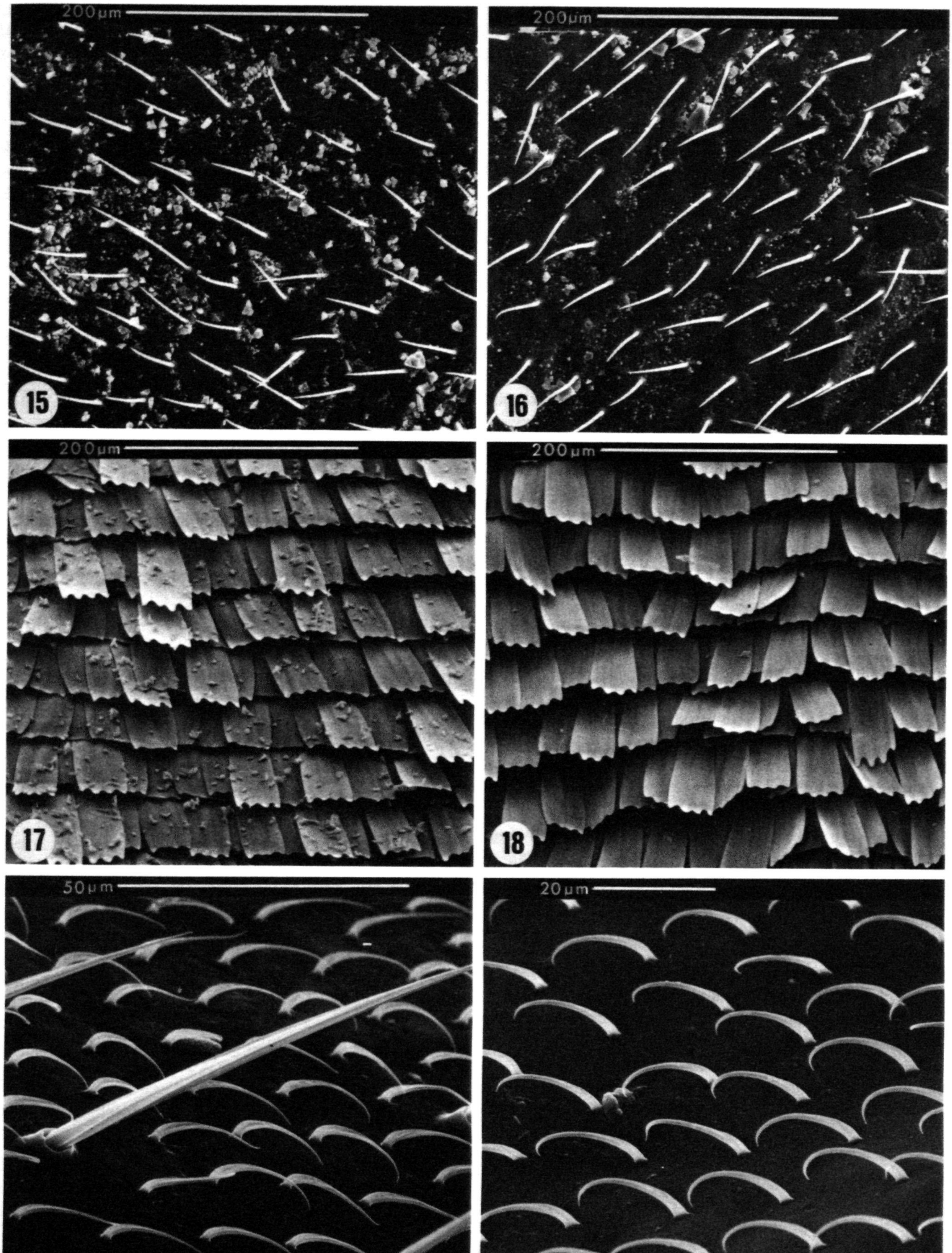
In contrast, the surface of the hindwings of all species is covered very uniformly by thin, short hairs and has no microsculpture. These hairs are absent in the rose-chafers (*Pachnoda marginata, Cetonia aurata*).

At 82.2–86.3°, the contact angles on the hindwings are significantly larger than those on the elytra of 31.6–43.0°. The partially large and roughly sculptured elytra of *Zophobas morio* and *Pachnoda marginata* proved to be the most wettable of all surfaces investigated. The particle removal after fogging is also very low (81.9% remaining particles) for *Pachnoda marginata*, in particular.

Hymenoptera. The sawflies and wasps have very uniformly sculptured wing surfaces. The smooth, at most only slightly microsculptured surface usually has straight, false hairs twisted around their longitudinal axis. These hairs can be dense and long, as in *Paravespula germanica*, or short and thick, as in *Apis mellifera*. In most species, the hair is longer and more dense on the tip of the wing than at the base. The contact angles are generally small, and fluctuate between 85° and 95°, with the particle removal roughly corresponding to the expected value in the contact angle/remaining-particles diagram. An average of about 50% of the particles are removed by fogging (Figs 15, 16).



Figs 9–14.—Fig. 9. Oedipoda caerulescens, elytron, middle of basal third of the upper side, with erected plate-like scales.—*Fig. 10. Phaneroptera falcata*, hindwing, middle of apical third of the upper side, with toothed sculpture.—*Fig. 11. Gerris lacustris*, elytron, middle of the upper side, with dense short hairs.—*Fig. 12. Tettigia orni*, forewing, middle of apical third of the upper side, with extremely fine regular microsculpture.—*Fig. 13.* Same as Fig. 12, higher magnification.—*Fig. 14. Chrysoperla carnea*, forewing, middle of apical third of the upper side, with terry cloth-like microsculpture.



Figs 15–20.—Fig. 15. Paravespula germanica, forewing, middle of the upper side, after contamination with silicate dust.—*Fig. 16.* Same as Fig. 15 after contamination with silicate dust and fogging.—*Fig. 17. Lysandra bellargus*, forewing, middle of the upper side, after contamination with silicate dust.—*Fig. 18.* Same as Fig. 17 after contamination with silicate dust and fogging.—*Fig. 19. Panorpa vulgaris*, forewing, middle of the upper side, with real and false hairs.—*Fig. 20. Episyrphus balteatus*, wing, middle of the upper side, only with false hairs.

Trichoptera. In addition to a basic hair coverage consisting of false hairs, the caddisflies also have uniformly distributed and considerably larger hairs which are seven to eight times longer and slightly flattened. The dense hair clearly leads to the large contact angles on the wings, such as 136.5° in *Hydropsyche pellucidula,* for example.

Lepidoptera. A characteristic feature of the butterflies and moths are the scales consisting of individual epidermal cells. The upper side of these scales has a fine structure of raised ridges which are connected to the bottom of the scales via extensions. The bottom side is flat and turned towards the wing surface. The contact angles are all large. Values between 131.4° and 141.4° were measured for the upper side of the forewings. Many butterflies have larger contact angles at the tip of the wings than at the base. The same effect is also seen in a comparison of the fore- and hindwings. The values on the wing base are probably lower due to the denser hair which disrupts the uniformity of the scale surfaces.

During fogging, butterfly wings are more or less completely cleansed by the water drops which form and roll off (Figs 17, 18). Only 0.55–4.69% of the particles remain on the wings following fogging and after the "dew drops" roll off. Only very small particles which lodge between the ridges, or those on the scale edges were hardly removed by drops.

Mecoptera. In addition to a basic hair coverage consisting of curved hairs fully corresponding to those of the Diptera, the scorpionfly *Panorpa vulgaris* also has longer, straight hairs which are, however, restricted to the central area of the wing cells (Fig. 19). The wettability is higher than for *Hydropsyche pellucidula* and *Sialis lutaria*, which have the same type of hair coverage. In contrast, the particle removal is above average for these species.

Diptera. With uniform and fine hair covering the wings (with the exception of *Eristalis tenax*) and a structure of slightly raised protrusions, the flies have wing surfaces which are comparable with those of Hymenoptera. The hairs are bent at the tip or even along the entire length, and often so extremely that the tip touches the cuticle (Fig. 19). In the case of *Eristalis tenax*, the wings only have hairs in the region of the wing veins and are otherwise completely bald. The more sturdy species (*Eristalis tenax, Mesembrina meridiana, Tabanus bovinus*) have contact angles ranging from 83° to 90° and SM indices between 4.13 and 4.53. The more "delicate" *Episyrphus balteatus* and *Tipula oleracea* (SM indices 6.74 and 9.26) have markedly higher contact angle values (just under 130°). The hair coverage is more dense and the particle removal higher in these species than in more sturdy forms.

Discussion

In the present study, taxa-specific sculptures and/or hair coverage were identified on the wing surfaces of most of the major insect groups. The selection factors which led to this variety are considered in the following sections.

It must be considered that only an infinitely small fraction of the insects were studied. Other sculptures can be expected, or are already known (e.g. wings with long bristles at the edge of Ptiliidae (Coleoptera), Mymaridae (Hymenoptera) or Thysanoptera), particularly among very small insects which have a very different "relationship" to the medium of air due to their low Reynolds values. However, these groups cannot be investigated in quantitative serial studies of this kind, due to the fact that index calculations and, in particular, contact angle measurements present methodological difficulties.

Elytra are wettable and not self-cleaning

Among the insects, the tendency for the forewings to develop into more sclerotic elytra is found repeatedly in Paurometabola, Paraneoptera and Holometabola (Hennig 1969). The primary function of the elytra is to protect the membranous hindwings and the entire abdomen. These elytra have a negative effect on aerodynamics (Nachtigall 1982). Species with elytra usually flee from predators by hiding in the substrate. Some groups (Dermaptera; Staphylinidae, Coleoptera) are especially adapted by means of high mobility in the longitudinal direction and drastically shortening the elytra, under which the membranous hindwings are folded.

The elytron surfaces have very heterogeneous sculptures: smooth with a scaled pattern (cockroaches and many crickets and grasshoppers), hairy (some bugs and beetles), roughly structured as the result of protrusions on the exocuticle (e.g. *Phaneroptera falcata, Cetonia aurata* and *Pachnoda marginata*) or, in a few cases, with an epicuticle microsculpture (*Oedipoda caerulescens*). This diversity stands in contrast to the thinly haired, smooth, non-microsculptured hindwings common to all groups having elytra (with the exception of Pentatomidae, Heteroptera).

The present study results show comparable effects for all species investigated in these groups. Insects with elytra primarily have low SM indices. They have relatively large bodies and small wings, and are largely poor fliers. The elytra are wettable and contact angles greater than 90° are only found in a few species (e.g. *Phaneroptera falcata*). Fogging after artificial contamination results in lower than average particle removal values. Hardly any drops form on the wings which would be able to take up particles when rolling off. The entire surface is homogeneously wetted. The water flows off the inclined samples in sheets. The wing surfaces of species with elytra are thus easily contaminable and wettable.

Both effects are probably of only insignificant importance for these species. The animals live on the ground or in the vegetation. Additional weight on the wings due to contamination is of no consequence. They are able to clean their wings with their extremities or simply by crawling through the substrate. Therefore, the diverse microsculptures on insect elytra cannot be explained by the biophysical aspects of flight.

Short wings can be cleansed by extremities

The elytra of the taxa described above are a contrast to the membranous forewings of the remaining insects. The false hairs and non-microsculptured wings can be considered a plesiomorph form of the wings of Neoptera, and probably of all Pterygota also. This type is found among the stoneflies and among the sawflies/wasps and flies. These species generally have small SM indices and relatively wettable wings with contact angles between 85° and 95°. The more "delicate" *Episyrphus balteatus* and *Tipula oleracea*, with their considerably finer and denser hair coverage, have substantially larger contact angles (just under 130°) and thus stand out among the other, "more sturdy" Diptera. However, particle removal is low among the sawflies/wasps and flies and lower than average in comparison with all other species investigated.

Both taxa differ from the other insect groups with membranous wings in an important aspect to the argument presented here: the wings are so short and of such small surface area that the extremities can reach all points on the wings and thus clean them. This made the evolution of "self-cleaning" surfaces unnecessary, so that groups such as sawflies/wasps and flies have retained the plesiomorph form of the wings of Neoptera.

The ability to clean the wings using the extremities is only conditionally possible among Mecoptera, Megaloptera and Trichoptera. The species investigated in these taxa take on a middle rank as regards wettability (contact angles between 112° and 136.5°, particle removal and the SM indices 12.2–17.3). The convergently evolved "double" hair coverage on the wings of these taxa, with real and false hairs can be regarded as improved protection against wetting. Contamination effects were only investigated extensively on *Panorpa vulgaris*, which shows relatively good particle removal with 23.6% remaining particles.

Large wings are self-cleaning due to the microsculpture

The last of this category are insects with large wings which cannot be cleaned by the extremities as these are too short. Additional weight due to contamination has a negative effect on the flight capabilities of the taxa Palaeoptera, Planipennia and Lepidoptera. The following selection factors can be proposed for these groups: individuals whose wings remain uncontaminated as long as possible have a higher fitness due to the fact that the potential flight time, and thus the reproduction time, is extended.

Theoretical considerations confirm that unwettable surfaces must be roughened. Certain parameters, such as the size of the protrusions and the distance between them, are important in this context (Adam 1963). The wing surfaces of the taxa mentioned above fully correspond to these physical parameters. Palaeoptera and Planipennia convergently evolved a fine, terry cloth-like microsculpture on the epicuticle. The individual structures are only 0.3–0.5 μm apart. The roughness and the obviously strong hydrophobic nature of the surfaces result in highly unwettable wings. The effect is so strong, e.g. in *Chrysoperla carnea*, that it is extremely difficult to place a drop of water on the wing at all. The roughness leads to more than just high unwettability; it also means that contamination particles only have a small surface on the tips of the individual structures on which to lodge themselves. The adhesion forces of the particles to the surface are thus reduced. These particles can be removed by drops of water, in the form of dew, and probably also by wind.

This "self-cleaning effect" is even more extreme among the butterflies and moths. The ridge structure of the wing scales corresponds ideally to the mathematical and physical requirements of unwettable surfaces. According to theoretical findings on the unwettability of surfaces (Cassie & Baxter 1944), the quotient $(r + d)/r$ (r: radius of the raised scale ridges on the wing; d: half the distance between ridges) is a decisive parameter. The scale ridges were measured on ten species in special investigations and also on 11 other species based on SEM photos. The quotients are largely consistent within the species, fluctuating between 4.53 and 8.99, and thus all lying within the range of optimum unwettability.

These values are remarkably similar to those for other unwettable natural surfaces existing in nature. For example, a value of 5 was determined for the density and distances of radioli of duck breast feathers.

Phylogenetic aspects

In this paragraph, only important results of the current study concerning phylogeny of some insects groups are described. For a general discussion on insect phylogeny, see Hennig (1969) and Kristensen (1981, 1991).

Various authors (e.g. Börner 1904; Lemche 1940; Schwanwitsch 1958; Hennig 1969; Boudreaux 1979; Kristensen 1981, 1991; Kukalova-Peck 1985) have considered all possible sister-group relationships for the monophyletic groups of Ephemeroptera, Odonata and Neoptera. Hennig (1969) and Kukalova-Peck (1985) prefer a monophylum Palaeoptera (Ephemeroptera + Odonata), which is the adelphotaxon to the Neoptera, and justifies this based on characteristics of the wing structure, wing articulation and formation of a basal wing brace, in particular. This estimation can be confirmed as regards the identical microsculpture of the imaginal wing cuticle of Ephemeroptera and Odonata. The special shape of the epicuticle could be considered to be an autapomorphy of the stem species of the Palaeoptera, where a smooth, non-microsculptured and possibly hairy wing surface would represent the plesiomorph characteristic.

In this context, the comparable sculpture of Planipennia should be considered to be a convergent development. This hypothesis is also supported by the fact that the fine microsculpture of the Planipennia also covers the veins, which have no microsculpture in Palaeoptera. Furthermore, the Palaeoptera lack the long bristles on the veins which are typical in the Planipennia.

The sister-group relationship between the Trichoptera and Lepidoptera and their combination as Amphiesmenoptera is generally accepted and excellently substantiated (Hennig 1969; Kristensen 1981). The ripple pattern of the butterfly and moth scales also occurs on the long hairs (with an oval cross-section) of Trichoptera, the adelphotaxon of Lepidoptera. The stem species of both taxa probably already had hair with ripples, which the Trichoptera maintain in a plesiomorph form, and which represents a preadaptation of the ridges on the butterfly scales.

The Antliophora (Mecoptera + Diptera + the secondary wingless Siphonaptera) are also a well defined monophylum (e.g. Kristensen 1981). The Mecoptera and Diptera can be confirmed as a part of this monophyletic group due to their coverage of false hairs. Both taxa have extremely curved false hairs on the wings, which are hardly "twisted" at all along the longitudinal axis, in contrast to the straight and twisted hair of the Hymenoptera.

The Mecoptera, Megaloptera and Trichoptera convergently developed "double hair" coverage. The differences are apparent in the structure and distribution of the real hairs.

The development of such complex characteristics, as "double" hair coverage, microsculptured epicuticles and rippled scales (only externally) cannot be a random occurrence but is rather the result of an evolutionary process. The idea of the evolution of these structures as regards protection against wetting and contamination is relatively easy to support based on the biophysical factors.

Comparison of plant leaves and insect wings surface structures

Similar to the sculptures of leaf surfaces (Barthlott 1990), those of insect wing cuticles can be divided into certain categories. Discernible cells or their derivatives are called the "primary sculpture". In contrast to insects, the borders of epidermal cells in plants are often visible. However, insects often have hairs and scales which develop from individual epidermal cells, and thus correspond to the single-celled trichoms of plants.

The relief-like formation of the procuticle, i.e. irregularities in thickness and hair-like growths, is called the "secondary sculpture", as demonstrated, for example, by the sculptures of the elytra of *Pachnoda* and *Phaneroptera*. However, the generally most frequent secondary sculpture in insects is the false hairs, as found on the wings, of Hymenoptera and Diptera species, for example.

The structures and coatings of the epicuticle form the tertiary sculpture. Plants show extraordinarily high diversity as regards this structure. In contrast, only three types of tertiary sculptures could be found on insect wings: smooth and non-sculptured coats in most insects; fine, terry cloth-like microsculptures in mayflies, dragonflies and lace wings; and finely scaled wing surfaces in some locusts and plant-lice.

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References

Adam, N. K. 1963. Principles of water-repellency. In J. L. Moilliet (ed.): *Waterproofing and Water-Repellency*, pp. 1–23. Elsevier, Amsterdam.

Baker, E. A., Hunt, G. M. & Stevens, P. J. G. 1983. Studies of plant cuticle and spray droplet interactions: A fresh approach.—*Pesticide Science* 14: 645–658.

Barthlott, W. 1990. Scanning electron microscopy of the epidermal surface plants. In D. Claugher (ed.): *Scanning Electron Microscopy in Taxonomy and Functional Morphology*, pp. 69–94. Clarendon Press, Oxford.

Barthlott, W. & Ehler, N. 1977. Rasterelektronenmikroskopie der Epidermisoberflächen von Spermatophyten.—*Tropische und Subtropische Pflanzenwelt* 19: 367–467. Steiner, Wiesbaden.

Barthlott, W., Riede, K. & Wolter, M. 1994. Mimicry and ultrastructural analogy between the semi-aquatic grasshopper *Paulinia acuminata* (Arthropoda; Pauliniidae) and its foodplant, the water-fern *Salvinia auriculata* (Filicatae; Salviniaceae).—*Amazoniana* 13: 47–58.

Barthlott, W. & Wollenweber, E. 1981. Zur Feinstruktur, Chemie und taxonomischen Signifikanz epikutikulärer Wachse und ähnlicher Sekrete.—*Tropische und Subtropische Pflanzenwelt* 32: 7–67. Steiner, Wiesbaden.

Börner, C. 1904. Zur Systematik der Hexapoden.—*Zoologica Anzeiger* 27: 511–533.

Boudreaux, H. B. 1979. *Arthropod phylogeny, with special reference to insects*. Wiley, New York.

Boyce, R. L. & Berlyn, G. P. 1988. Measuring the contact angle of water droplets on foliar surfaces.—*Canadian Journal of Botany* 66: 2599–2602.

Cassie, A. B. D. & Baxter, S. 1944. Wettability of porous surfaces.—*Transactions of the Faraday Society* 40: 546–551.

Croghan, P. C. & Noble-Nesbitt, J. 1989. A note of the diffusion of water across oil and wax layers on insect cuticles.—*Journal of Experimental Biology* 143: 537–541.

Gilby, A. R. 1984. Cuticle and insecticides. In J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards (eds): *Biology of the integument*, pp. 694–702. Springer, Berlin.

Hadley, N. F. & Hendricks, G. M. 1984. Cuticular microstructures and their relationship to structural color and transpiration in the terrestrial Isopod *Porcellionides pruinosus*.—*Canadian Journal of Zoology* 63: 649–656.

Hennig, W. 1969. *Die Stammesgeschichte der Insekten*. W. Kramer, Frankfurt.

Hinton, H. E. 1969. Some little known surface structures. In A. C. Neville (ed.): *Insect ultrastructure*. Symposia of the Royal Entomological Society 5, pp. 41–58. Blackwell, Oxford.

Hinton, H. E. 1976. Recent work on physical colours of insect cuticle. In H. R. Hepburn (ed.): *The insect integument*. Elsevier, Amsterdam.

Holloway, P. J. 1970. Surface factors affecting the wetting of leaves.—*Pesticide Science* 1: 156–163.

Holloway, P. J. 1971. The chemical and physical characteristics of leaf surfaces. In T. F. Preece & C. H. Dickinson (eds): *Ecology of leaf surface micro-organisms*, pp. 39–53. Academic Press, London.

Kristensen, N. P. 1981. The phylogeny of insect orders.—*Annual Review of Entomology* 26: 135–157.

Kristensen, N. P. 1991. Phylogeny of extant Hexapods. In Criso, I. (ed.): *The insects of Australia*, 2nd edn, pp. 125–140. Melbourne University Press, Melbourne.

Kukalova-Peck, J. 1985. Ephemeroid wing venation based upon new gigantic carboniferous mayflies and basis morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemerida).—*Canadian Journal of Zoology* 63: 933–955.

Lemche, H. 1940. The origin of winged insects.—*Videnskabelige Meddelelser Dansk naturhistorisk Forening i Kjobenhavn* 104: 255–297.

Linskens, H. F. 1950. Quantitative Bestimmung der Benetzbarkeit von Blattoberflächen.—*Planta* 38: 591–600.

Martin, J. T. 1960. The plant cuticle: its structure and relation to spraying problems.—*Annual Report of the East Malling Research Station* 47: 40–45.

Massoud, Z. 1969. Etude sur l'ornamentation epicuticulaire du tegument des Collemboles au microscopeelectronique a'balayage.—*Compte rendu de l'Academie des Sciences, Paris* 268: 1407–1409.

Nachtigall, W. 1974. *Insects in flight*. Allen & Unwin, London.

Nachtigall, W. 1976. Wing movements and the generation of aerodynamic forces by some medium-sized insects. In R. C. Rainey: *Insect Flight*. Blackwell, Oxford.

Nachtigall, W. 1982. *Biona Report 1 & 2 Insektenflug I & II*.—Akademie der Wissenschaften Literatur Mainz. Fischer, Stuttgart.

Neville, A. C. 1975. *Biology of the Arthropod Cuticle*. Springer, Berlin.

Noble-Nesbitt, J. 1963*a*. Transpiration in *Podura aquatica* L. (Collembola, Isotomidae) and wetting properties of its cuticle.—*Journal of Experimental Biology* 40: 681–700.

Noble-Nesbitt, J. 1963*b*. The fully formed intermoult cuticle and associated structures of *Podura aquatica* (Collembola).—*Quarterly Journal of Microscopical Science* 104: 253–270.

Noble-Nesbitt, J. 1970. Structural aspects of penetration through insect cuticles.—*Pesticide Science* 1: 204–208.

Pal, R. 1950. The wetting of insect cuticle.—*Bulletin of Entomological Research* 41: 121–129.

Roonwal, M. L. 1985. Wing microsculpturing in Termites (Isoptera) under the scanning electron microscope.—*Zoologischer Anzeiger, Jena* 215: 219–230.

Schawaller, W. 1987. Discolomidae aus Nepal, Himalaya; Coleoptera.—*Stuttgarter Beiträge zur Naturkdunde, Serie A (Biologie)* 410: 1–9.

Schwanwitsch, B. N. 1958. Alary system as a basis of the system of pterygote insects.—*Proceedings of the 10th International Congress of Entomology* (1956) 1: 605–610.

Seifert, G. 1966. Die Cuticula von *Polyxenus lagurus* (Diplopoda).—*Zeitschrift für Morphologie Ökologie der Tiere* 59: 42–53.

Smith, W. K. & McClean, T. M. 1989. Adaptive relationship between leaf water repellency, stomatal distribution, and gas exchange.—*American Journal of Botany* 76: 465–469.

Spillman, J. J. 1984. Spray impaction, retention and adhesion: an introduction to basic characteristics.—*Pesticide Science* 15: 97–106.

Süffert, F. 1925. Morphologie und Optik der Schmetterlingsschuppen, insbesondere die Schillerfarben der Schmetterlinge.—*Zeitschrift für Morphologie und Ökologie der Tiere* 1: 171–308.

Thorpe, W. H. & Crisp, D. J. 1947. The biology of *Aphelocheirus* and the mechanism of plastron retention.—*Journal of Experimental Biology* 24: 227–273.

Wegensteiner, R. 1982. Licht- und elektronenmikroskopische Untersuchungen bei den Cuticulaaufbau von *Polyzonium germanicum* (Diplopoda).—*Mikroskopie* (Wien) 39: 198–206.

Weis-Fogh, T. 1976. Energetics and aerodynamics of flapping flight: a synthesis. In R. C. Rainey (ed.): *Insect Flight*, pp. 48–72. Blackwell, Oxford.

Weser, C. 1980. Die Messung der Grenz- und Oberflächenspannung von Flüssigkeiten—eine Gesamtdarstellung für den Praktiker.—*GIT Fachzeitschrift für das Laboratorium* 24: 642–648, 734–742.