Zoomorphology (1999) 119:143–162

ORIGINAL ARTICLE

Ivar Hasenfuss

The adhesive devices in larvae of Lepidoptera (Insecta, Pterygota)

Accepted: 29 July 1999

Abstract Adhesion to smooth surfaces by means of thin fluid lipid film was studied on living larvae of 71 species of Lepidoptera by a simple "light reflection method". The method made it possible to localize exactly the sites of adhesion and to estimate roughly the film thickness, within a certain range. Furthermore, it revealed the general presence of mobile lipid on the entire insect surface. The observations on living larvae were complemented by comparative structural studies of the adhesive parts with light and scanning electron microscopes on preserved specimens of 161 species. Specialized adhesive devices were found in great diversity on larval legs and prolegs, especially in larvae living in the open air on their food plants. Two main surface types of adhesive cuticle were found: (1) cuticle with a flexible smooth surface and (2) cuticle with very numerous small projections (microtrichia) with spatulate and recurved apices. Both the functional implications of the adhesive cuticular structure and the role of the adhesive fluid as well as the evolution of the adhesive devices are discussed. The adhesive effect is due to "capillary" or meniscus forces.

Abbreviations *L1*, *L2*, *L3*: instars of larvae · *Lm*: mature larva(e)

A. Introduction

Adhesion to smooth substrate surfaces utilizing thin fluid film is a widely observed phenomenon in insects. The presence of fluid is obvious from the fact that tiny droplets remain at the substrate after detachment. Since the days of Rombouts (1884) and Dahl (1885) it is well known that this fluid is an oily lipid immiscible with water. The sole existing reference on its chemical nature is Bauchhenß (1979). She sampled the droplets of flies walking in a vessel and, using thin-layer chromatography, found the substance to be composed mainly of hydrocarbons. As already stated by Hasenfuss (1977), the adhesive fluid is secreted through the cuticle and is part of a general superficial mobile lipid coating in insects. The presence of this fluid and the accurate location of adhesion are demonstrable by a simple "light reflection method" described here. Furthermore, the method allows rough estimates of the thickness of the fluid coating. Edwards and Tarkanian (1970) had already argued that adhesion by fluid film is due to "meniscus forces".

Observation by stereomicroscope revealed the ability of many caterpillars to cling to polished glass surfaces utilizing adhesion in this way. During the last two decades, representatives of most lepidopteran families were studied for adhesive effects by use of the "light reflection method". As far as possible, all larval instars were taken into account. Body parts which normally make contact with a substrate are often more or less specialized for adhesion. The structure of such cuticular parts was studied by ordinary and polarized light as well as by scanning electron microscopy (SEM). Some of the adhesive devices were mentioned in earlier descriptive work, but their function remained more or less obscure (Hinton 1955; Beck 1960; Stehr 1987a). It was the aim of the present study to obtain an overview of the adhesive structures in the larvae of Lepidoptera and to discuss the corresponding morphological, functional and evolutionary aspects.

B. Materials and methods

I. Animals

Most of the larvae were reared from eggs which were deposited by females captured with light traps in the vicinity of Erlangen in northern Bavaria. Some material was provided by colleagues or purchased. A list of the investigated species is given in the Appendix.

I. Hasenfuss
Zoologisches Institut der Friedrich-Alexander Universität
Erlangen-Nürnberg, Germany

Present address:
Karlsbader Strasse 9, D-91083 Baiersdorf, Germany
Tel.: +49-9133-1426, Fax: +49-9133-603998

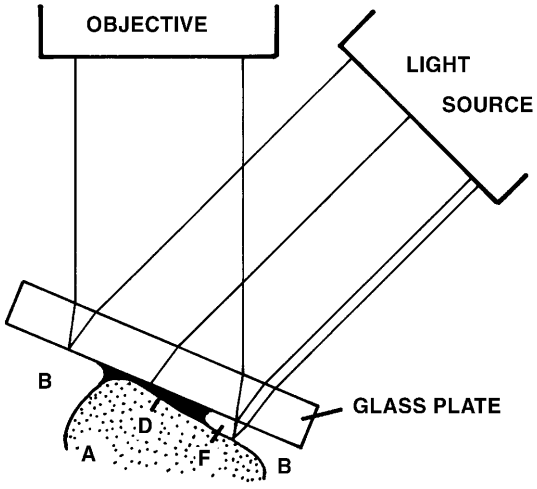

Fig. 1 Principle of "light reflection method". An extended light source and a glass plate with the adhering object are so arranged under the objective of a microscope that the image of the light source is seen reflected from the underside of the glass plate. Superficial fluid film of adhering objects (*A*) appears as dark spots (*D*) within a bright field (*B*). *F* Zone of interference fringes

II. Light microscopy

Living larvae were studied with a stereomicroscope with gradually adjustable magnification between 8× and 164×. The light source was a Schott fibre glass illuminator equipped with a 150 W low voltage halogen bulb. For observation by the "light reflection method", the light source and the animal clinging to the underside of a suitable glass plate were arranged as shown in Fig. 1. Dark spots appear within the bright reflection of the light source where adhesive fluid fills the gap between the animal and the glass plate (Fig. 2A,B). By tilting the glass plate slightly, the reflection is turned away and the cuticular surface becomes visible. Very accurate locations of the adhesive parts are thus possible.

Rough estimates of fluid film thickness within a certain range were possible by observing the presence, absence or number of interference fringes around the points or zones of contact. Interference was caused by coherent light reflected from the underside of the glass plate and from the surface of the object below. Wedge-shaped air-filled gaps exhibited interference fringes in the range 0.2–2.2 µm distance between both surfaces. The restriction to this range is due to the fact that maximally seven fringes were observable with the used light source. Neighbouring fringes indicate a distance difference of roughly half the light wavelength. If no dark fringes were seen around the dark spots of adhesion, the thickness of the fluid film was at least 2 µm. By slightly pressing a glass plate on any cuticular part, it was possible to test the animals for the presence of a general superficial fluid film. It is certainly present if none or not all seven fringes are observable around the tiny dark spots of contact; if all fringes are seen, the fluid film must be thinner than 0.2 µm or be absent.

The presence of a general superficial lipid fluid was tested additionally by applying small particles of the lipid-soluble dye sudan red III to the surface of living animals. For the application, the animals were forced to walk for some hours in a glass vessel internally coated with the dye. The coating was prepared by dissolving some dye in acetone, wetting the inner side of the vessel with the solution and evaporating the solvent. In the presence of fluid lipid, the dye particles on the animal lose their dusty appearance and are converted into pasty masses by soaking up the fluid in the course of one to several days. Very thin fluid films thus become apparent which are otherwise not detectable. Larger lipid amounts in the depressions appear clearly stained (Hasenfuss 1977).

The cuticular structure was studied by light microscopy on mounts of adhesive appendages or on hand-made sections of specimens preserved in alcohol. All sections were mounted in water or glycerol. The main orientation of the cuticular micellar fibrils, indicated by their optical form birefringence, was observed by using polarized light and a first-order red compensator plate.

III. Scanning electron microscopy

For SEM of adhesive devices, the preserved specimens were cleaned, as far as possible, by treating them with a strong stream of running water. Freshly killed animals were shaken with detergent solution before this treatment. The parts of interest were cut off, freeze dried or transferred to acetone and dried in air. For demonstration of the arrangement of non-proteinaceous fibrillary micelles, thick sections were made with a razor blade, incubated overnight in a protease K solution (TRIS buffer, pH 7.5, 37°C), washed with water and acetone, transferred to water and freeze dried. By this treatment the protein matrix of unsclerotized cuticle was cleanly removed without affecting the other micelles and without disturbing their arrangement. Judging from the known general structure and chemical composition of insect cuticle (Neville 1975) these are certainly chitin micelles.

C. Results

I. General

Observation of larvae of Lepidoptera by the reflection method not only accurately revealed the location of adhesion but also revealed the general presence of a liquid or semi-liquid lipid film of at least 2 µm thickness on all cuticular surfaces. No interference fringes were observed around the dark points of contact between any part of the cuticle and the cover glass. Lipid-soluble dye particles applied to the cuticular surface turned to pasty masses by soaking up the lipid in the course of the following 24 h. Dye particles on mechanoreceptive sensillae (setae) were observed to be the first to turn to pasty masses; the depressions on their surface (for example, rillae) contain comparatively more lipid stained by the dye.

The surface of normal cuticle is sculptured in diverse manner and exhibits frequently sharply pointed or stout small projections (microtrichia) which reduce considerably the observable area of contact. In adhesive devices the area of contact is greatly enlarged, either by a large number of points of contact or by a smooth flexible surface.

Locomotion in lepidopteran larvae takes place by "wave-like creeping". Beginning with the caudal end, the segments are released from their support, brought forward by a contraction and set down immediately behind the foregoing segment which starts with the same process. The segmental adhesive parts become detached when lifted up, whereas the adhesive parts of the other segments remain effective. The larvae are thus always clinging safely to the support.

II. Cuticular structure

Detailed ultrastructural studies with transmission electron microscopy on the cuticle under consideration have

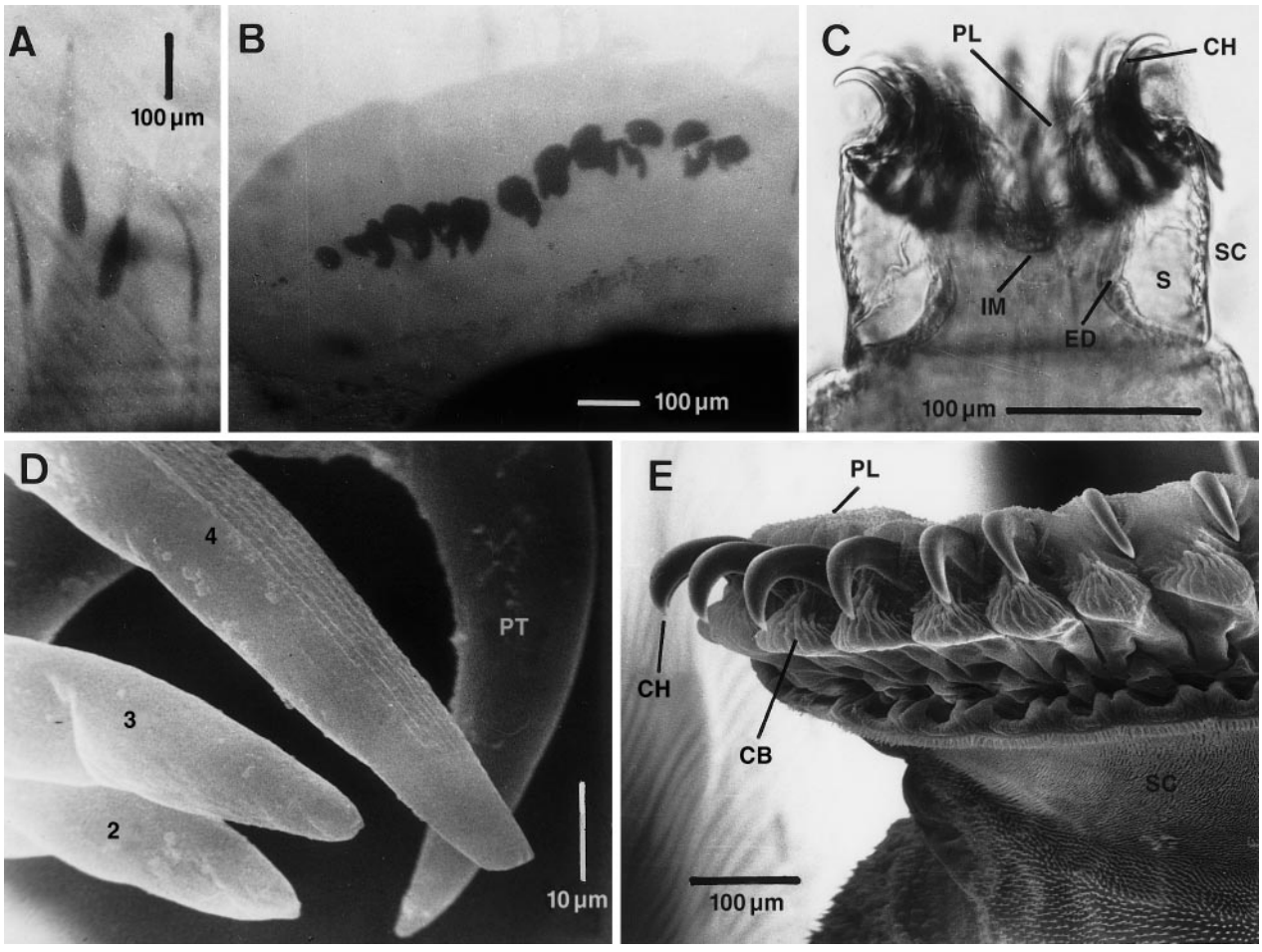

Fig. 2A, B Effect of "light reflection method", dark spots indicate locations of adhesion in *Mamestra brassicae* (Noctuidae), Lm. **A** Adhesion of mesal tarsal and tibial setae. **B** Mesal side of clasping prolegs, adhesion of coronal blisters between the invisible coronal crochets. **C** *Plodia interpunctella* (Pyralidae), Lm, ventral proleg with full circle corona, lateral view, Feulgen's stain, space (*S*) within the cuticle contains a watery liquid, on left side thin sheets of cuticle are seen traversing the space. **D** *Eudia pavonia* (Saturniidae), L1, SEM, distal parts of adhesive tarsal setae *2–4*, ventral side with smooth surface. **E** *Orthosia cruda* (Noctuidae), Lm, SEM, clasping-type abdominal proleg, mesal view. *CB* Adhesive coronal blisters, *CH* coronal crochets, *ED* epidermis, *IM* insertion of retractor muscles, *PL* planta, *PT* pretarsus, *SC* subcorona. *Scales* in µm

not as yet been done. To obtain information of the main arrangement of cuticular fibrils, hand-made sections were observed by polarized light in as many species as possible. In some instances, the arrangement of the chitin micelles were observed directly on protease-treated sections using SEM. Three types of main orientation of fibrils were discernible:

1. Cuticle in which at least the main bulk of fibrillary micelles are arranged parallel to the cuticular surface. This is likewise a feature of the "normal" cuticle generally found in insects (for details and references see Neville 1975). Cuticular parts with this appearance in polarized light are, therefore, referred to as "normal" in the text. This appearance is characteristic of thin flexible cuticle as well as of sclerotized parts. It is likewise found in many adhesive cuticular parts with smooth surfaces.
2. Cuticle which contains "undulated layers" and which seems to be a slight modification of the former type. SEMs of protease-treated sections show sinuous chitin micelles (Fig. 3D,E). That this "wavy" structure is not an artifact is evident by its appearance in polarized light; cross-sections of native cuticle of this type appear to be "banded" indicating the locally different orientation of the main part of fibrils (Figs. 3F, 13B–D). Observed in any orientation with polarized light, the cuticle appears as if it were composed of a mosaic of sharply bounded patches with differently arranged fibrils. The internal surface is uneven and bumpy (Fig. 13D), often with excessive projections (*SCL* in Fig. 8G). This type is called here "undulated cuticle" and is found in thick flexible cuticle of larger larvae (Figs. 3D,E, 13B–D). In such larvae, the main part of the truncal flexible cuticle is of this type.
3. In structures here called "pad cuticle", the main part of fibrillary micelles appears to be arranged obliquely to the surface, the angle being nearly 45°. The apex of the angle is always directed to the apex of the corresponding seta or proleg. This orientation is seen both with polarized light as well as with SEM (Figs. 3A,

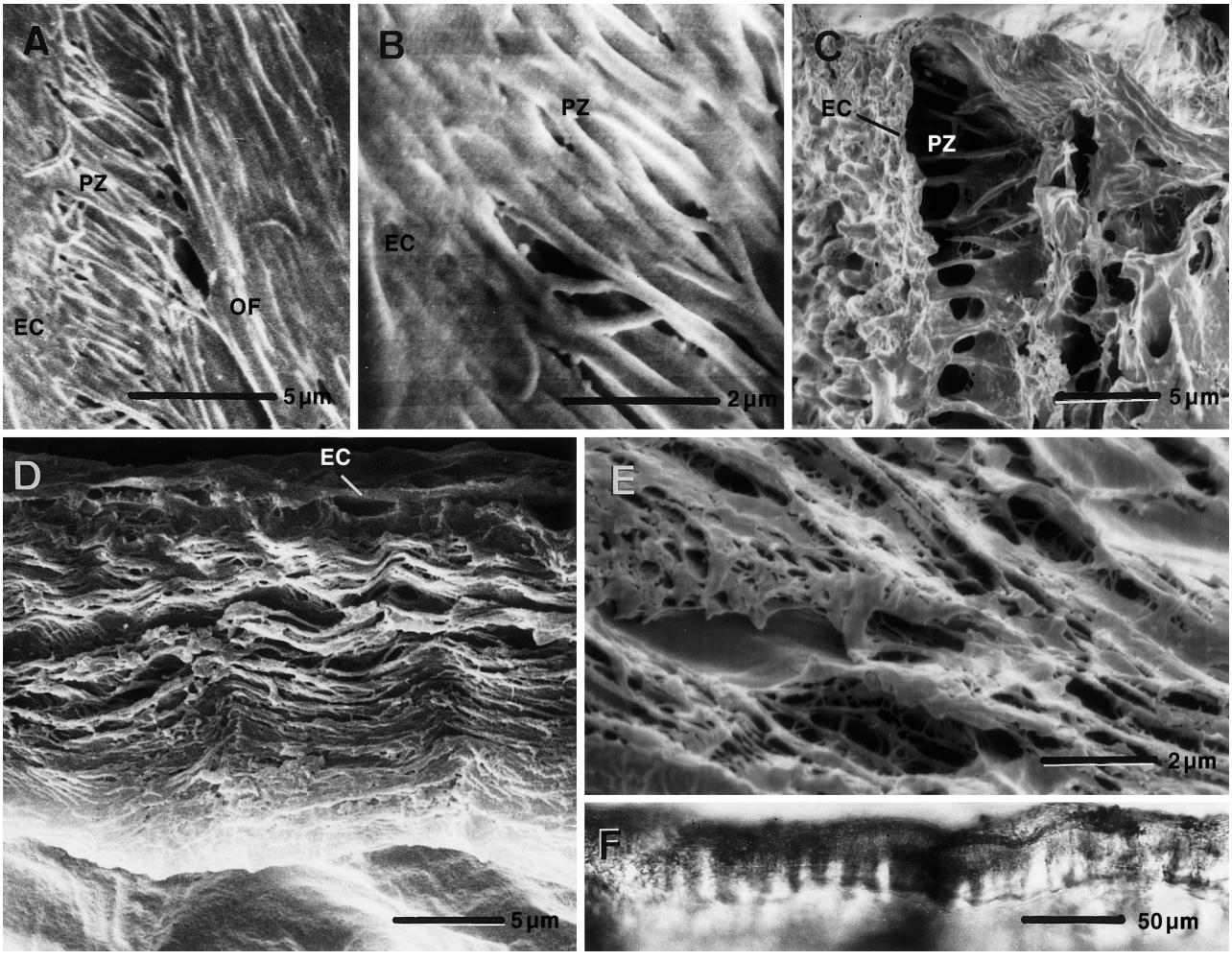

Fig. 3A–E Micellar structure of cuticle, longitudinal sections of Lm prolegs, mesal side, protease-treated. **A, B** *Spilosoma luteum* (Arctiidae), SEM, peripheral zone of pad cuticle of coronal blisters, zone of connection of the oblique fibrils to the thin peripheral layer. **C** *Hyles euphorbiae* (Sphingidae), SEM, peripheral zone of distal subcorona. **D, E** *H. euphorbiae*, SEM, proximal subcorona, cuticle with undulated layers. **F** *Epirrhoe alternata* (Geometridae), subcorona, longitudinal section, cuticle with undulated layers observed with polarized light and compensator plate, dark and bright zones indicate differently oriented fibrils. *EC* Peripheral layer, externally lined by epicuticle, *OF* oblique fibrils, *PZ* zone between the peripheral layer and the oblique fibrils. *Scales* in µm

12E,F, 13). In very small larvae it is frequently difficult to recognize even with an oil immersion objective. The micelles of the oblique fibrils appear as comparatively thick parallel rods without chitinous interconnections in between. They are connected with the thin peripheral subepicuticular chitin layer by brushing out in finer fibrils (Fig. 3A,B). The peculiar micellar arrangement shown in Fig. 3C is located peripherally to the zone of oblique fibrils in members of Bombycoidea. The pad cuticle is comparatively thick, usually much thicker than the adjacent cuticle (Fig. 13).

III. Adhesion in Zeugloptera

All instars of the soil-inhabiting larva of *Micropterix aruncella* are able to walk even on the underside of glass surfaces and to climb plants by “wave-like creeping”. Very effective adhesive devices are the non-retractile prolegs on abdominal segments 1–8 and the smooth eversible perianal membrane (Figs. 4, 10F). The prolegs are ventral projections with laterally bent distal flexible parts. Their medioventral sides make contact with the substrate and show thin normal cuticle. The flexibility of the distal part is facilitated by a series of external circular constrictions. The perianal membrane consists of thin cuticle of normal type, and the cuticular fibrils are arranged parallel to the surface. The small thoracic legs do not participate in adhesion.

IV. Adhesion in Neolepidoptera

‘Primitive’ larvae of Neolepidoptera (Fig. 5) have short thoracic legs and retractile prolegs on abdominal segments 3–6 (“ventral prolegs” according to Hinton 1955) and on segment 10 (“anal prolegs”). Generally, the larvae produce silken threads with the labial spinning apparatus terminating in the spinneret. The threads are used

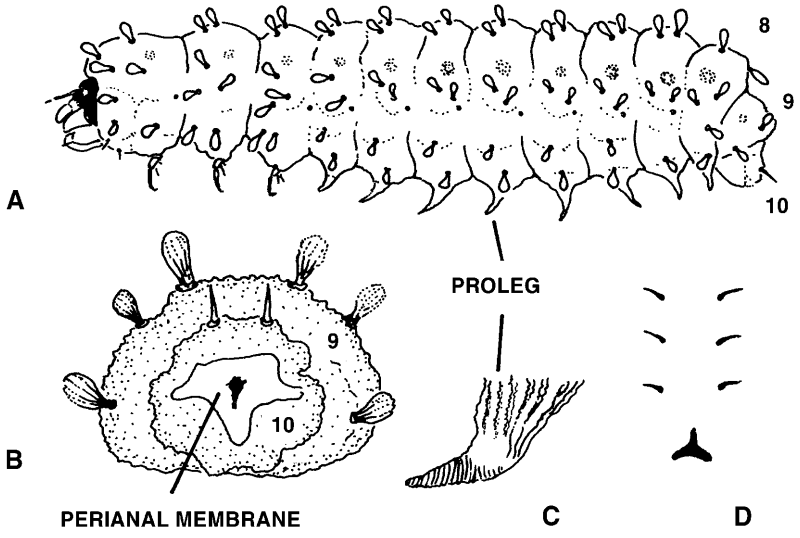

Fig. 4A–D *Micropterix aruncella* (Zeugloptera). **A** Mature larva, left side, total length 3.3 mm. **B** Abdominal segments *9* and *10*, caudal view. **C** Proleg, caudal view. **D** Dark spots of adhesion observed by the reflection method

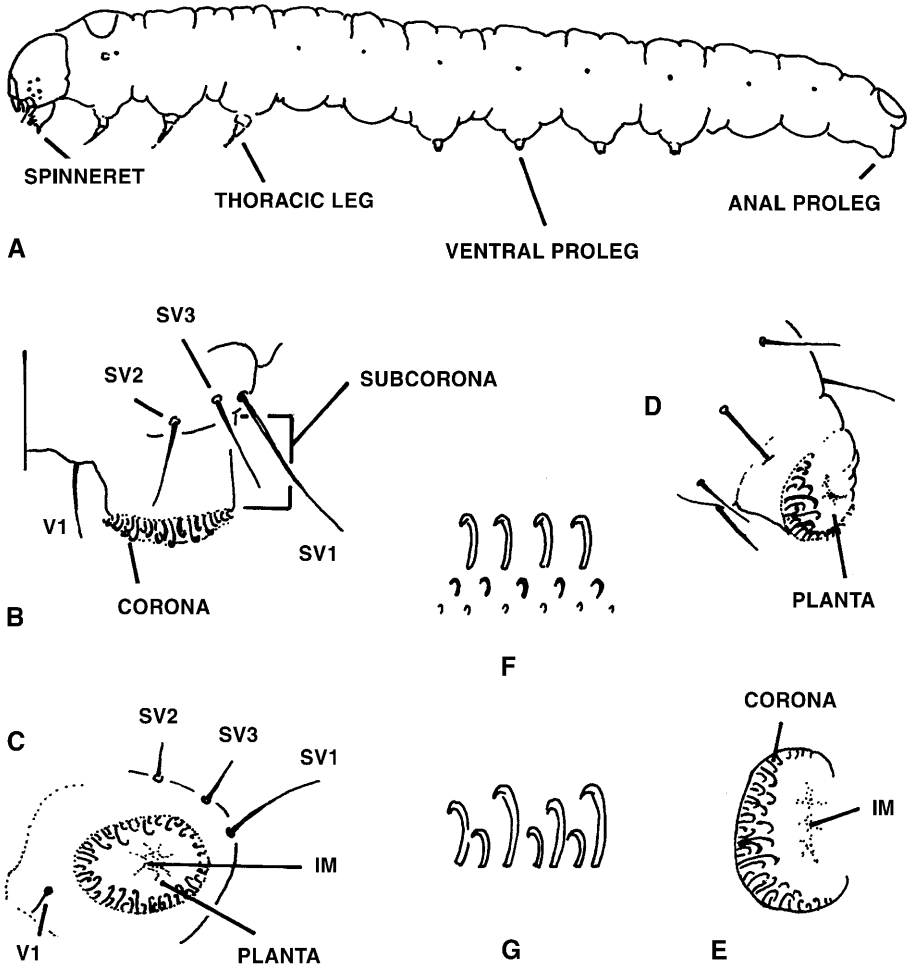

Fig. 5A–G Neolepidoptera, 'primitive'-type larva. **A** Left side, setae omitted. **B,C** Ventral proleg, anterior view (**B**) and ventral view (**C**). **D,E** Anal proleg, lateral view (**D**) and ventral view (**E**). **F** Primitive multiserial corona. **G** Advanced multiordinal corona. *IM* Insertion of plantal retractor muscles, *SV1–3* subventral setae, *V1* ventral seta

for different purposes: for making tubes and other retreats and for securing a hold during walking and resting by threads laid down on the substrate. Accordingly, the thoracic legs and prolegs are organized in such a way that they easily link up with the threads. Each pretarsal claw of the thoracic legs has a ventral notch into which the threads fit well (Fig. 7F). The retractable prolegs bear sclerotized crochets at the periphery of the flexible sole (Fig. 5B–G). Following Hinton (1955), this sole is called the planta. For the crochets the term "corona" is

proposed here. The flexible zone proximal to the corona is the subcorona. (In Stehr 1987a, the whole retractable part, including the subcorona, is considered to be the "planta".) The subcorona is more or less invaginated when the proleg is retracted by muscles which are inserted at the middle of the planta (Figs. 2C, 5C–E). By contraction of these muscles the corona is disengaged; the opposite occurs when turgor pressure evaginates the planta.

The cuticular apparatus of the corona is very thick and contains, in between the external part and the proximal cuticular layer, a large space filled with a watery liquid (*S* in Figs. 2C, 7D,E, 8G). The liquid filling is confirmed by dissection under the stereomicroscope. Frequently the space is traversed by thin sheets of cuticle (Fig. 2C). This indicates that the epidermis secretes intermittently cuticular substance and liquid when, during ecdysis, a new cuticle is produced.

The corona of ventral prolegs of the primitive type (Gerasimov 1952; Hinton 1955) is a complete circle or ellipse around the planta (Figs. 2C, 5C), and the whole plantal area makes contact with the substrate. Coronae supposed to be in the primitive state are composed of two or more series of crochets, and they are multiserial (Fig. 5F). The crochets of the same series are of almost equal size (uniordinal crochets), and those of the more peripheral series are usually smaller. In first instar larvae, only the most distal series of crochets is realized; the other series of smaller crochets appear in later instars. In coronae thought to be advanced, there is only one series of multiordinal crochets (Fig. 5G). This type differs from the former by proximal elongation of the crochets to the same level. In first instar larvae, the corona is uniordinal; the smaller crochets appear in later instars.

Prolegs in oblique orientation towards the substrate have interrupted coronae; crochets are absent on that side which never makes contact with the substrate or web. This is generally the case in anal prolegs (Fig. 5A,D,E) as well as in slender, elongated, laterally diverging ventral prolegs. In such ventral prolegs, the lateral crochets are reduced or absent (Fig. 7B,C), and the basal part of the subcorona is usually not invaginated when the proleg is retracted.

In Zygaenidae and Macrolepidoptera, the prolegs of all or only the later instars are of the clasping type, adapted for clasping twigs and stalks of the food plants. In these prolegs, only the mesal part of the corona is well developed and the crochets are arranged in "mesoseries" on the mesal edge (Figs. 2E, 8E, 10B–D,G,H, 11, 12). The clasping movements are executed by muscles of a fleshy protrusion of the body wall on which the prolegs are located. The protrusion bears the subventral group of setae and a ventral seta (Fig. 5B,C). These setae are likewise present on the proleg-free segments 1, 2, 7–9. In contrast to prolegs and except for adhesive devices, the thoracic legs are very uniform (Fig. 9A).

Flexible parts of legs, prolegs and setae of Neolepidoptera exhibit great diversity in adhesive devices, examples of which are shown in Figs. 6, 7, 8, 9, 10, 11, 12 and 13. Many larvae are able to walk on the underside of polished glass plates without the aid of silken threads. Larvae with clasping prolegs are frequently able to take hold on glass rods of comparatively large diameter.

1. Concealed living larvae

For food uptake, the larvae leave their retreats and walk, normally, some distance on more or less smooth surfaces. To hold on the support with claws and crochets, many larvae lay down loops of silken threads. Additionally, holding on in this way is sometimes assisted by adhesion. If adhesion is effective enough, the spinning of threads is often omitted. Larvae which are freshly hatched from the eggs have to rely on adhesion.

Many small young larvae take sufficient hold by adhesion with the thin apical flexible cuticle of their prolegs and with tarsal setae. Tarsal setae, engaged in this way, are broadened and dorsoventrally flattened. Later instars usually lose the ability for adhesion. For example, in *Agriphila tristella* (Crambidae), adhesion takes place in L1 and L2 on tarsal seta 4 and the apices of prolegs (Fig. 6A–C). The zone of proleg adhesion includes the planta, the somewhat swollen corona and part of the subcorona. The crochets are partly invaginated, only their apices and basal parts are exposed. Adhesion disappears in L3. In many other Crambidae and some Pyralidae, tarsal seta 4 has a similar broadened shape in L1 and sometimes in L2; in later instars it is more or less of normal shape (Hasenfuss 1963). The very effective tarsal seta 4 in L1 of *Galleria mellonella* (Pyralidae) has an apically flat surface and is not, as formerly thought, apically excavated. Effective adhesion is confined to apically slightly extended prolegs in L1–Lm of *Anthophila fabriciana* (Choreutidae) and to plantae in L1 of *Thyris fenestrella* (Thyrididae). Lm of *Epermenia illigerella* (Epermeniidae) exhibits only broadened tarsal setae (Fig. 6D).

In some Gelechiidae, adhesive devices are developed even in Lm. Lm of members of *Teleiodes, Anarsia, Brachmia* and *Anacampsis* have distally diverging ventral prolegs (Fig. 6F). Medially these bear a plantal bulge extending more or less into the coronal zone; in this zone the crochets are small or missing (*PB* in Fig. 6E,F). A similar lobe is present in the anal proleg corona. All tarsal setae of Lm are normal or the tarsal seta 4 is broadened (Fig. 6G).

Within Elachistidae (sensu Minet 1990) some species of *Agonopterix* show plantal adhesion in L1 and/or later instars and sometimes the tarsal setae 1 and 4 are broadened as in Fig. 6D. No adhesive devices were found in the members of the Oecophoridae, Chimabachidae, Carcinidae and Coleophoridae. In Tortricidae, effective adhesive devices are normally missing and the tarsal setae are of normal shape. However, setae 4 and 1 are sometimes broadened as in Fig. 6D.

In all concealed living larvae mentioned, no signs of pad cuticle was found. No effective adhesion and/or no adhesive devices have as yet been observed in members

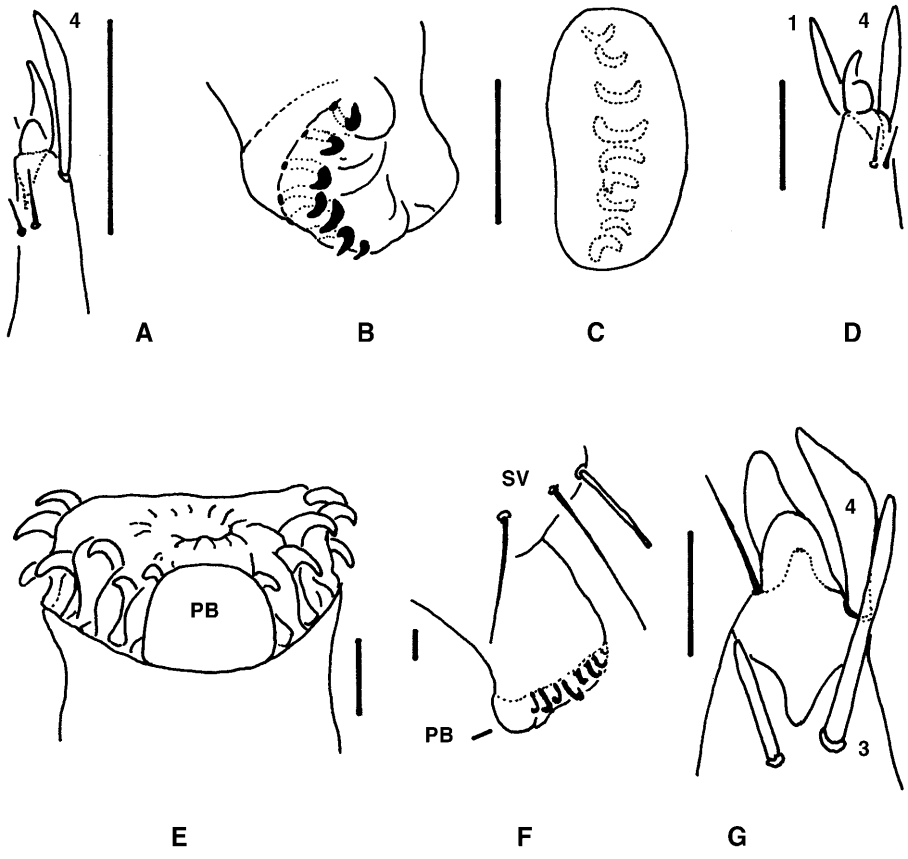

Fig. 6A–G Adhesive devices of concealed living larvae. **A–C** *Agriphila tristella* (Crambidae), L1, median view of left tarsus (**A**), lateral view of anal proleg (**B**) and adhesive area of anal proleg (**C**). **D** *Epermenia illigerella* (Epermeniidae), Lm, median view of left tarsus. **E–G** *Anacampsis populella* (Gelechiidae), Lm, median side of ventral proleg (**E**), anterior view of ventral proleg (**F**) and median view of left tarsus (**G**). *PB* Plantal bulge, *SV* subventral setae, *1*, *3*, *4* tarsal setae. *Scales* 0.05 mm

of the Hepialidae, Incurvariidae, Psychidae, Gracillariidae, Yponomeutidae, Plutellidae, Sesiidae and Cossidae (see Appendix for species). The following taxa contain mainly free-living larvae which are resting on their food plants in the open air.

2. Pterophoridae and Schreckensteiniidae

No adhesive devices were observed in Lm of the exophagous *Agdistis tamaricis* (Agdistinae) and the endophagous species (Platyptilinae, part of Pterophorinae). However, in L1 of *Agdistis*, tarsal seta 4 is typically broadened (Fig. 7A). The exophagous species of Pterophorinae, which are living in the open, exhibit effective adhesion in all larval instars. The prolegs are of the slender, distally diverging type; their apices are flexible, whereas the slender part is stabilized by more sclerotized cuticle (Fig. 7B,C). In L1, the apex is like a vesicle, it bears only a few crochets and its medioapical flexible adhesive cuticle is thin normal cuticle (Fig. 7B). In Lm, the subcoronal zone which makes contact with the support exhibits smooth adhesive pad cuticle (Figs. 7D, 10A). The proximal parts of crochets are invaginated and held in position by a thick internal cuticular sheet (*SCL* in Fig. 7D) which is separated from the external cuticular layer in the region of the pad cuticle. [In *Agdistis*, the liquid-filled space extends from the subcoronal zone to the insertion of the planta retractor muscles (*SCL* in Fig. 7E).] The tarsal setae 3 and 4 and, to a lesser degree, 1 bear pad cuticle and participate in adhesion (Fig. 7F). In young larvae, tarsal setae 3 and 4 or 1 and 4 are broadened; seta 2 is always small. In Lm of *Schreckensteinia festaliella*, the size and shape of tarsal setae are similar to Fig. 7A; the prolegs are small, slender and do not diverge laterally. Their apices are slightly vesicle-like and bear five crochets in a circle.

3. Zygaenidae and Limacodidae

The larvae of Zygaenidae live in the open on their food plants. *Zygaena lonicerae* (Zygaeninae) and *Rhagades pruni* (Procridinae) have nearly identical, very effective adhesive devices in all instars (Fig. 8). In L1, the ventral prolegs on segments 3–6 bear four crochets caudally. The anterior parts of the prolegs lack crochets and bear, in the coronal zone, areas of adhesion with normal cuticle (*AA* in Fig. 8C,D). Additionally, setae SV1 and 2 are apically extended to knob-like structures, they seem to have pad cuticle and are engaged in adhesion. In later instars, the corresponding subventral setae are normal. In L2 through Lm, the prolegs are of the clasping type; the corona is a mesoseries and contains two series of crochets (Fig. 8E–G). The distal series consists of normal functional crochets. The proximal crochets are totally invaginated, and the flexible cuticle in between forms protruding blisters which seem to consist mainly of a com-

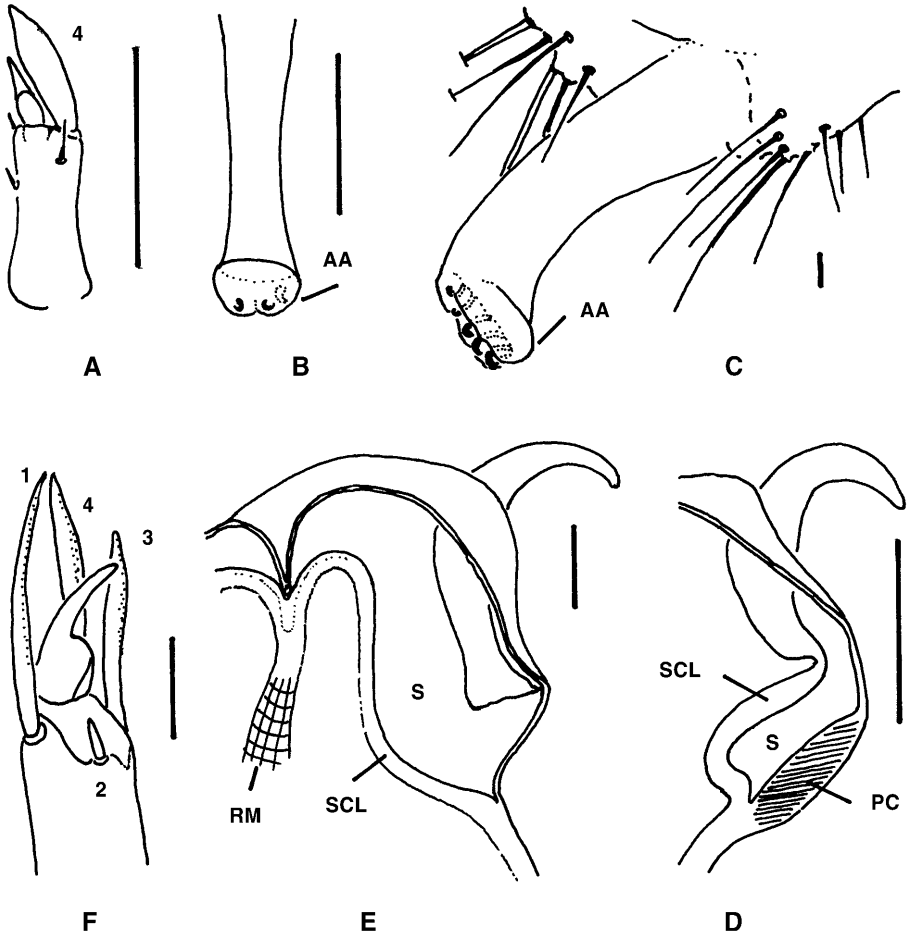

Fig. 7A–F Adhesive devices in Pterophoridae. **A, E** *Agdistis tamaricis*. **B–D, F** *Pterophorus pentadactyla*. **A** L1, left tarsus, median view. **B** L1, median view on ventral proleg. **C** Lm, caudal view on left ventral proleg. **D, E** Lm, longitudinal section of ventral proleg, coronal zone. **F** Lm, left tarsus, anterior view, adhesive cuticle is punctured. *AA* Adhesive area, *PC* pad cuticle, *RM* retractor muscle, *SCL* cuticular layer proximal to the liquid-filled space (*S*), *1*–4 tarsal setae. Scales 0.05 mm

paratively thin layer of pad cuticle. The surfaces of mesal subcoronae bear numerous tiny spines; they are much smaller than the spines of the other body parts. The tarsal setae 3 and 4 are adhesive devices in all instars (Fig. 8A,B). In the later instars, they are fan-shaped and bear, on the ventral side, typical pad cuticle distally. Tarsal seta 2 and some ventral tibial setae have thin layers of pad cuticle ventrally.

In *Apoda limacodes* (Limacodidae), the thoracic legs are reduced to small appendages. The prolegs are completely absent and the ventral surface of the abdomen is flattened to a very effective adhesive sole exhibiting close analogies to the sole of snails. In contrast to snails, the adhesive fluid is, of course, of lipid nature. Locomotion is by the usual wave-like creeping.

4. Macrolepidoptera

This group comprises the majority of the larger Lepidoptera (see Kristensen 1999). The larvae of most Macrolepidoptera live on their food plants in the open, climbing on them with the aid of clasping type prolegs (Figs. 2E, 10B–D,H, 11, 12). The corona of these prolegs is usually restricted to the mesal edge of the planta (“mesoseries”) even in the anal prolegs. In early instars the prolegs are often of the ‘primitive’ type. Adhesive devices are absent only in species which make, in all instars, extensive webs on which they sit and walk. Among these species are some Lasiocampidae (for example, species of *Lasiocampa* and *Malacosoma*), the Rhopalocera (with the exception of Lycaenidae and some Pieridae) and species of the Thaumetopoeinae (Notodontidae).

Thoracic legs. In Macrolepidoptera, the tarsal setae 2–4 are, in most taxa, adhesive devices, at least in young larvae (Figs. 2D, 9A–C). They are more or less broadened and depressed, and those parts of the setae which make contact with the support usually have pad cuticle structure. In older instars, especially in very large Lm, the pad cuticle is more or less replaced by normal cuticle and the shape of the setae is less broadened or normal (Fig. 9D). Frequently, however, the adhesiveness of the setae is maintained in Lm, as in species of *Drepana* and *Watsonalla* (Fig. 9C), most Geometridae and Noctuoidea (Figs. 9A, 13A). In some Geometridae only the tarsal setae 2 and 3 are broadened (Fig. 9E).

Older instars with clasping legs and prolegs show, in some taxa, vesicle-like bulges on the mesal side of some of the leg articulations (*MB* in Fig. 9A,D). If the larvae embrace a glass rod, the bulges are pressed against the support and show dark spots when observed using the light reflection method. They are called “Tastbläschen”

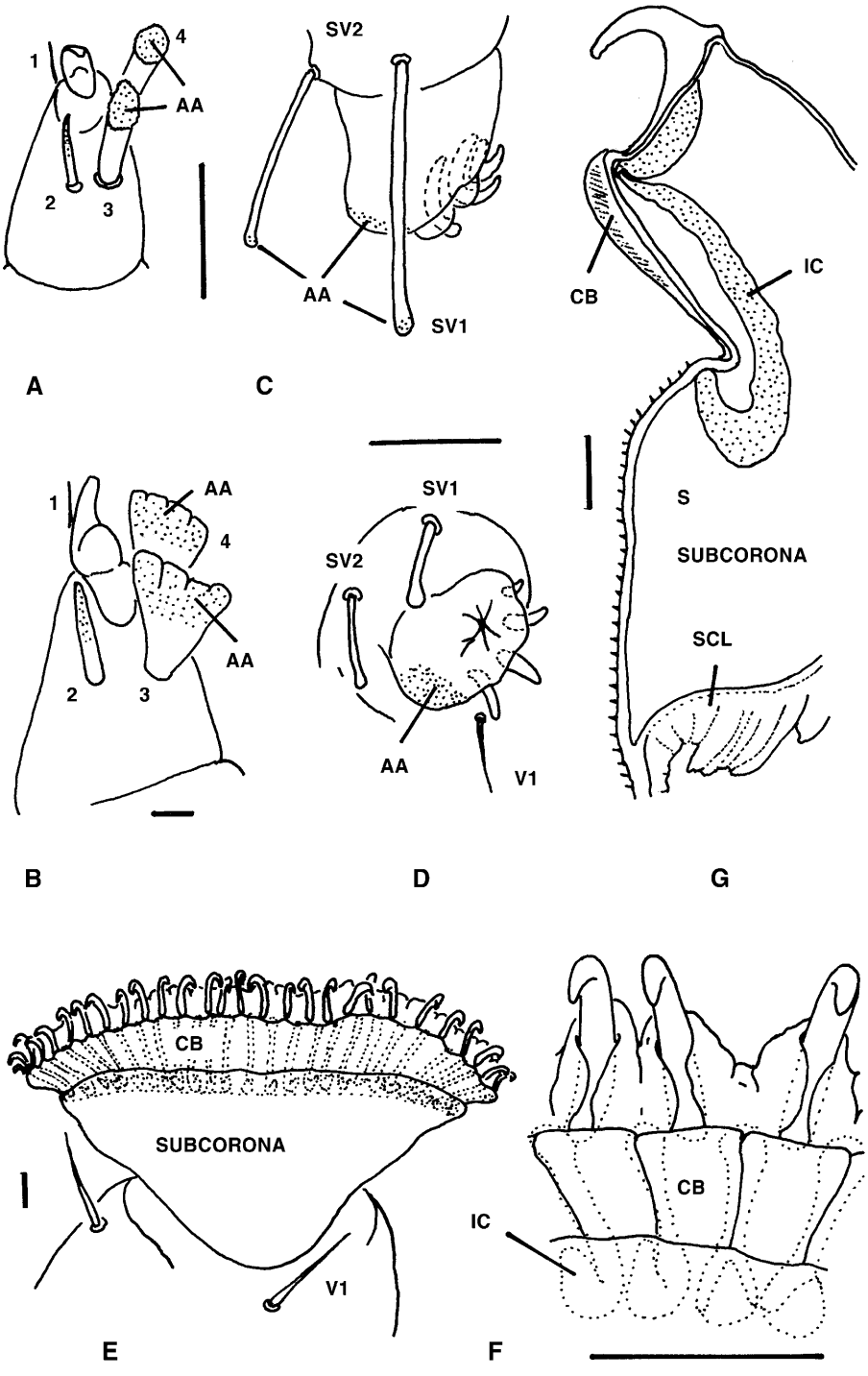

Fig. 8A–G Adhesive devices of *Zygaena lonicerae* (Zygaenidae). **A, B** Left tarsus, ventral view in L1 (**A**) and Lm (**B**). **C,D** Left ventral proleg in L1, lateral view (**C**) and ventral view (**D**). **E** Ventral proleg, Lm, median view. **F** Part of proleg corona in L2. **G** Ventral proleg, Lm, longitudinal section, median side. *AA* Adhesive area, *CB* coronal blisters, *IC* invaginated crochets, *SCL* cuticular layer proximal to the liquid-filled space (*S*), *SV1*, *2* subventral setae, *V1* ventral seta, *1–4* tarsal setae. *Scales* 0.05 mm

by Beck (1960) and are effective adhesive devices. The bulges always exhibit normal cuticle structure with fibrils parallel to the surface. Bulges on the tarsus and tibia are present in *Citheronia splendens* (Saturniidae) and other Bombycoidea (Sphingidae, *Bombyx mori*, *Endromis versicolora*, *Lemonia dumi* and *Brahmaea* species; Fig. 9D). In most Saturniidae, only the tarsal bulges are developed. In many Geometridae (Larentiinae and Boarmiinae) and many Noctuidae, such bulges are present on the tibia, femur and, to some extent, on the coxa (Fig. 9A). In other Geometridae (Archiearinae, Geometrinae and Sterrhinae) they are absent. In Notodontidae, they are present on the tarsus and tibia. Adhesive bulges were not found on the thoracic legs in representatives of the Lasiocampidae, Drepanidae, Uraniidae, Rhopalocera, Arctiidae and Lymantriidae.

Prolegs, plantae. Proleg adhesive devices are plantal, coronal, or subcoronal. Plantal devices are most widely distributed. In prolegs of the unspecialized type in young

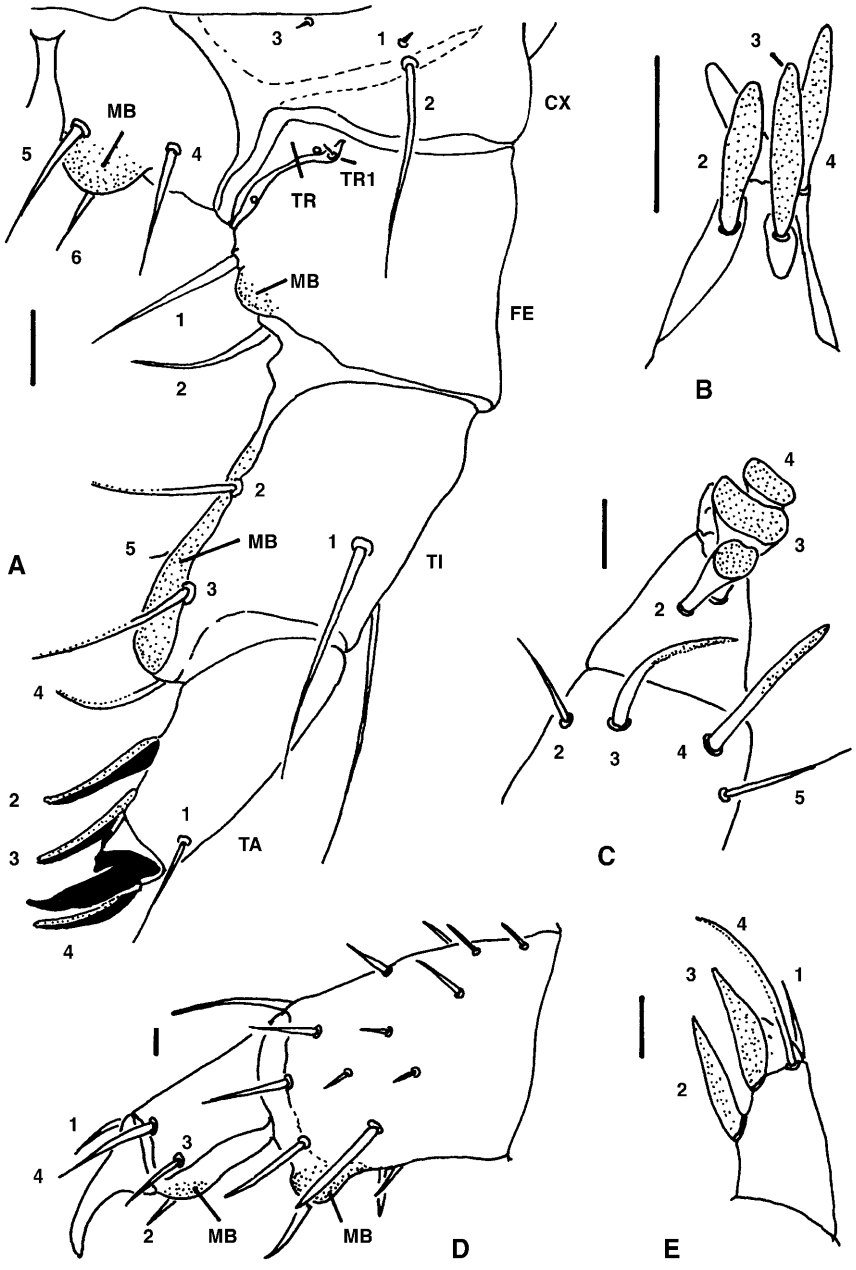

Fig. 9A–E Macrolepidoptera, thoracic legs, adhesive surfaces punctured. **A** *Callistege mi* (Noctuidae), Lm, left thoracic leg, anterior view. **B** *Eudia pavonia* (Saturniidae), L1, left tarsus, median view. **C** *Drepana falcataria* (Drepanidae), Lm, left tarsus and tibia, median view. **D** *Hyles euphorbiae* (Sphingidae), Lm, left tarsus and tibia, posterior view. **E** *Epirrhoe alternata* (Geometridae), Lm, left tarsus, posterior view. *CX* Coxa, *FE* femur, *MB* bulge with flexible cuticle, *TA* tarsus, *TI* tibia, *TR* trochanter. Numbering of setae according to Hasenfuss (1980). *Scales* 0.1 mm

larvae, the thin, normally structured plantal flexible cuticle usually shows effective adhesion (Fig. 12A,B). In the clasping-type prolegs of later instars, the mesal side comes into contact with the substrate and an adhesive plantal bulge extends more or less into the corona. The crochets below the bulge are more or less diminished or completely absent (*PB* in Figs. 10B, 11A–C). The prominent bulges exhibit pad cuticle (Fig. 13B) even if they are present in L1 (exceptions are noted in the following text).

All instars of the Lycaenidae have very elaborate plantal bulges (Fig. 11C). Young larvae of some Pieridae show slight adhesion of the normal apical plantal flexible cuticle. In Geometridae, plantal bulges are generally present on the clasping-type prolegs of segments 6 and 10 (Fig. 10B). (The prolegs of segments 3–5 are normally reduced or, if some of them are present, they are diminished and of a simplified unspecialized type.) In part of the Boarmiinae and Sterrhinae, the bulge is completely reduced in the older larvae, especially in Lm; in such cases the corona shows a normal row of crochets or there is a remnant of smaller crochets indicating the presence of the bulge in the young larvae (Fig. 11D). The bulge is absent in Lm of *Archiearis notha*.

Plantal bulges are present on ventral prolegs in young larvae (L1–L3/L4) of Drepaninae and *Palimpsestis or* (Thyatirinae). The crochets proximal to the bulges are only slightly diminished. In L1 and L2 of *Thyatira batis* no plantal bulges are present; however, there is effective plantal adhesion of ventral and anal prolegs by means of the apical normal cuticle. No adhesion is observable in

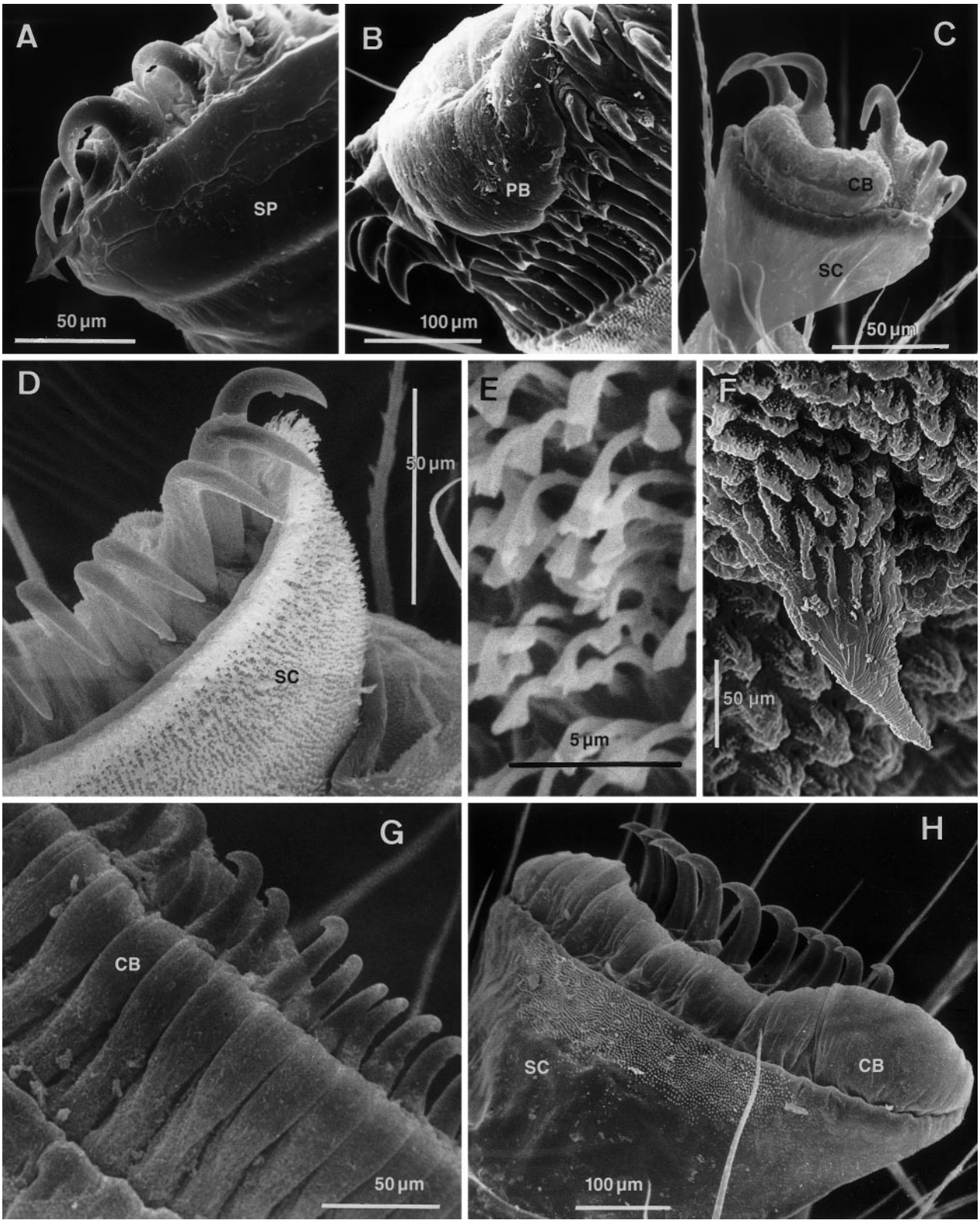

Fig. 10 Adhesive devices of ventral prolegs, SEM, mesal view in **A–E, G, H** and anterior view in **F**. **A** *Pterophorus pentadactyla* (Pterophoridae), Lm, subcoronal pad (*SP*). **B** *Epirrhoe alternata* (Geometridae), Lm, plantal bulge (*PB*). **C** *Lymantria dispar* (Lymantriidae), L1, fused central coronal blisters, central crochets invaginated and apically reduced. **D, E** *Orgyia antiqua* (Lymantriidae), L2, subcorona, spatulate recurved microtrichia. **F** *Micropterix aruncella* (Zeugloptera), proleg. **G** *Zygaena lonicerae* (Zygaenidae), Lm, coronal blisters of a second series of invaginated coronal crochets. **H** *Phragmatobia fuliginosa* (Arctiidae), L4, fused coronal blisters, marginal hooks apically reduced. *CB* Coronal blisters, *SC* subcorona. *Scales* in µm

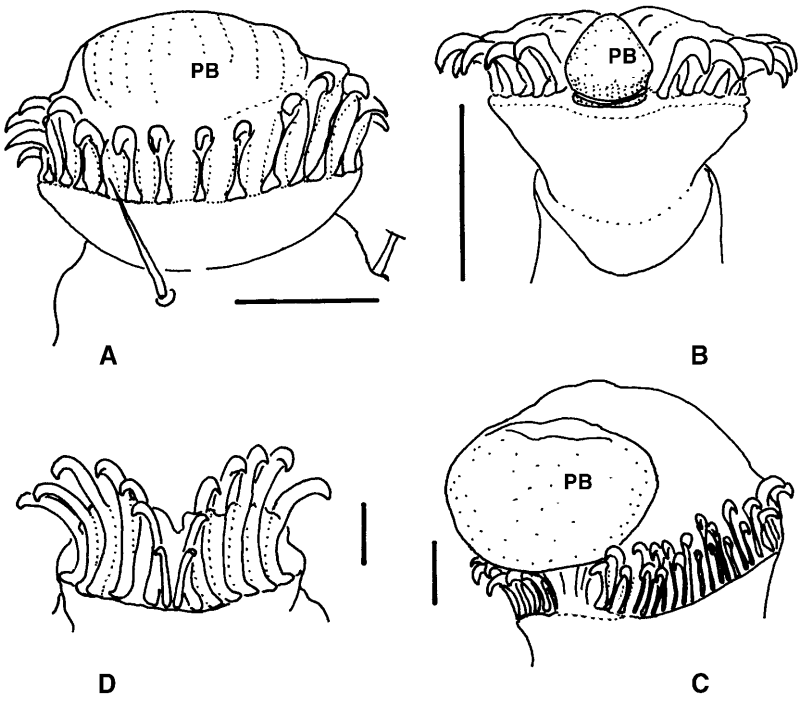

Fig. 11A–D Macrolepidoptera, plantal bulges (*PB*), median view. **A** *Eudia pavonia* (Saturniidae), L1. **B** *Macrothylacia rubi* (Lasiocampidae), L1. **C** *Hamearis lucina* (Lycaenidae), Lm. **D** *Idaea seriata* (Geometridae), atrophied plantal bulge in Lm. *Scales* 0.1 mm

older larvae of this species. Plantal bulges are likewise present in young larvae of many Bombycoidea. They are present either in L1, L1+L2 (representatives of *Brahmaea*, *Lemonia* and most Lasiocampidae) or in L1–L3 (*Bombyx mori* and most Saturniidae); in later instars, the bulges disappear without any residue. Sphingidae lack plantal bulges.

In Noctuoidea, plantal bulges without pad cuticle and with centrally diminished crochets were sometimes found in L1. Except for several Notodontidae they disappear with the first moult and their function is normally taken over by coronal blisters described in the next section. However, in part of the Notodontidae, the plantal adhesion in L1 is followed by a plantal bulge with pad cuticle in L2 and L3. This is found in *Cerura vinula*, *C. erminea*, *Furcula bicuspis*, *Harpyia milhauseri*, *Pheosia gnoma*, *Ptilodon capucina* and *Clostera pigra*. The bulge extends more or less into the central part of the corona, the crochets below being more or less diminished. In L4 and L5(=Lm), the bulges are reduced, and adhesion takes place with coronal blisters; only in *C. vinula*, *C. erminea* and *F. bicuspis* are the blisters too small for adhesion.

Prolegs, coronae. In young larvae, especially in L1, the crochets are very frequently invaginated except for their apices (Fig. 12A,B). Thus, not only the plantae but also the protruding flexible cuticle between the crochets are engaged in adhesion. In older larvae with clasping-type prolegs, they frequently maintain adhesion as elaborate "coronal blisters" (Figs. 2B,E, 12) constituting an alternative to plantal bulges. Apart from the exceptions mentioned below, the adhesive coronal parts are always thin normal cuticle in which the fibrils are arranged parallel to the surface. Coronal blisters were only found in Sphingidae and Noctuoidea.

In Sphingidae, coronal blisters are confined to L1–L3/L4; the cuticle was found to be of normal type in all species, except for *Laothoe populi* (its blisters contain typical pad cuticle). Despite the presence of coronal blisters, the crochets are arranged in multiordinal mesoseries. Contrary to the other Macrolepidoptera studied, the Noctuoidea have generally uniordinal coronal crochets even in later instars (Figs. 2E, 10D,H, 12C). This feature is combined with the general presence of coronal blisters in the late instars. A few Noctuidae (for example, Plusiinae) are exceptional in having slightly biordinal crochets which, however, does not conflict with the blisters. With few exceptions, the typical coronal blisters appear in Noctuoidea after the first larval moult and are normally maintained in the later instars (Fig. 12A–C). Part of the Notodontidae are exceptional in developing temporary plantal bulges (with pad cuticle and diminished central crochets) which are present only in L2 and L3 (see section above). The later instars usually show adhesion by coronal blisters.

In many species of Noctuoidea, the larvae are able to move their prolegs laterally so far that the blisters come into contact even with flat surfaces; all instars or only young larvae are thus able to cling to the plain surface of leaves solely by adhesion. This is especially found in taxa in which the coronal blisters are peripherally fused into a coherent adhesive strip (Figs. 10C,H, 12D,F). Contrary to ordinary blisters, the cuticle consists of pad cuticle (Fig. 12E,F). This type of blister is present in L2–Lm of all Arctiidae and several quadrifine Noctuidae (*Herminia tarsicrinalis*, *Scoliopteryx libatrix* and *Nycteola revayana*). It is likewise found in Lymantriidae in

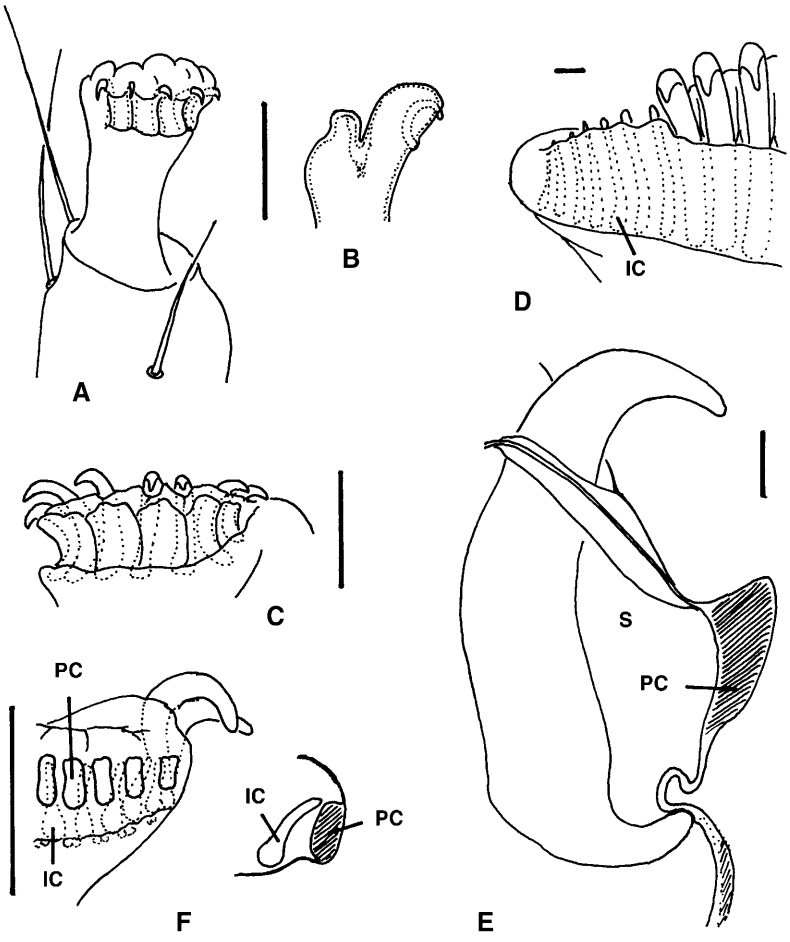

Fig. 12A–F Macrolepidoptera, coronal blisters. **A–C** *Autographa gamma* (Noctuidae), ventral proleg. **A** L1, anteromesal view. **B** L1, optical longitudinal section. **C** L2, posteromesal view. **D** *Spilosoma luteum* (Arctiidae), Lm, margin of corona, mesal view, heteroideous crochets, fused blisters. **E** *Spilosoma luteum*, Lm, longitudinal section, coronal zone. **F** *Orgyia antiqua* (Lymantriidae), L1, mesal view and optical longitudinal section. *PC* Pad cuticle, *IC* crochets with atrophied hooks, *S* space with liquid. Invaginated parts of crochets are punctuated. *Scales* 0.05 mm

which it is confined to L1 (Figs. 10C, 12F). Frequently, the adhesive strips are enlarged by extending the corona at both ends; the extensions are equipped with almost completely invaginated hookless crochets (Figs. 10H, 12D). Such coronae are called heteroideous and are found in many Arctiidae and in *Scoliopteryx libatrix*. In some Arctiidae, for example in species of *Syntomis* and *Setina*, the coronae are homoideous, i.e. all crochets have well-developed hooks. The adhesive coronal strips of Arctiidae, *H. tarsicrinalis* and *S. libatrix* are alike in having a sharp distal margin (Figs. 10H, 12E). In *Nycteola revayana*, the sharp margin is on the proximal side of the strip; all crochets have hooks.

In first instar Lymantriidae, the adhesive organ superficially resembles a plantal bulge because it is developed only in the central part of the corona (Fig. 10C). However, the typical pad cuticle is subdivided into a series of patches which are located between the invaginated hookless crochets (Fig. 12F). The organ disappears with the first moult and it is replaced by crochets of normal shape and size in instars L2–Lm (Fig. 10D). In these instars, adhesion of the prolegs is executed only by the subcoronae, as described in the next section. All larval instars of Lymantriidae are able to cling to the underside of glass plates by adhesion. In non-lymantriid Noctuoidea, the pad cuticle of fused blisters is never divided into patches; it forms, in every proleg, a continuous strip.

Prolegs, subcoronae. The median subcoronal zone, proximal to the corona, always comes into contact with the substrate when the larva is clinging to stalks, twigs or leaf margins. The surface of this part generally bears very numerous small microtrichia (Figs. 2E, 10B,D,E,H). Observation using the light reflection method reveals that only their apices make contact with the substrate. In L1, the microtrichia are normally small, rounded or sharply pointed elevations. Later, or at least in Lm, the more distal microtrichia are usually apically spatulate and frequently somewhat recurved (similar to Fig. 10D,E), the more proximal ones are rounded or end in a sharp point. The microtrichia are very small, the apical edge of the spatulate ones is only 1–2 µm long (Fig. 10E).

Except for Rhopalocera, such microtrichia were found in representatives of all the main groups of Macrolepidoptera (Bombycoidea, Uraniidae, Geometridae, Drepanidae and Noctuoidea). In members of the Hesperiidae and Pieridae, the mesal part of the subcorona is smooth and lacks microtrichia in all instars. In the early instars of other Rhopalocera, the subcorona is similarly nearly always smooth. However, in later in-

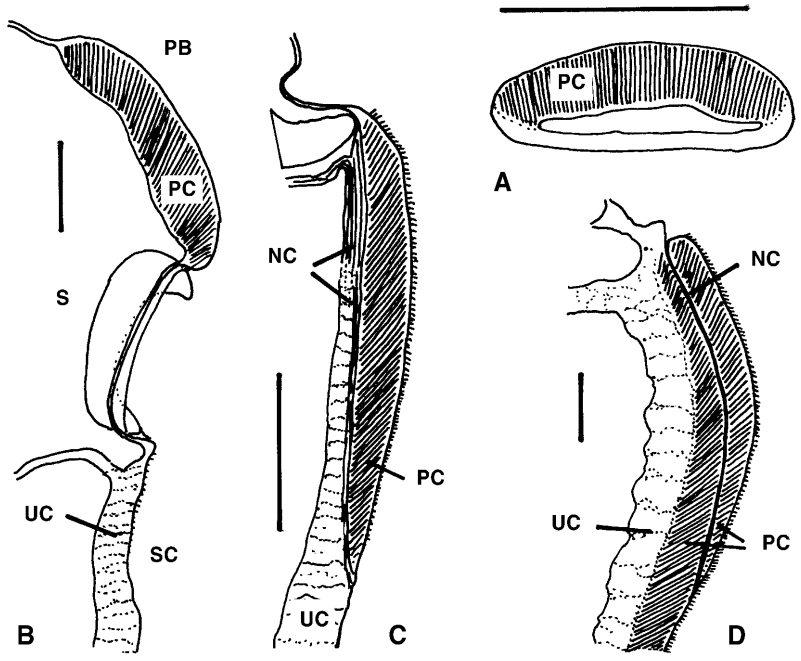

Fig. 13A–D Macrolepidoptera. **A** *Colocasia coryli* (Noctuidae), Lm, cross-section of an adhesive tarsal seta. **B–D** Longitudinal sections of prolegs, mesal side. **B** *Epirrhoe alternata* (Geometridae), Lm. **C** *Agriopis marginaria* (Geometridae), Lm, subcorona. **D** *Eudia pavonia* (Saturniidae), Lm, subcorona. *NC* Normal cuticle, *PB* plantal bulge, *PC* pad cuticle, *S* space with liquid, *SC* subcorona, *UC* undulated cuticle. *Scales* 0.05 mm

stars there are microtrichia on the mesal zone exhibiting some diversity in shape and size. Few scattered microtrichia were found in species of Lycaenidae. In members of the Papilionidae, they are densely arranged and more or less dactyliform. In representatives of the Nymphalidae, the projections of the distal median subcoronal zone are general spatulate recurved microtrichia. However, they differ from these in shape and size. Normally, the spatulate microtrichia have no or little adhesive effect. However, in L2–Lm of Lymantriidae, the spatulate microtrichia are more recurved and have enlarged apices (Fig. 10D,E). They are effective adhesive devices.

In young larvae, the subcoronal cuticle is of normal type. In older larvae of Macrolepidoptera, the cuticle is composed of some normal cuticle, much undulated-type cuticle and, very frequently, a subepicuticular layer of typical pad cuticle in the more distal median part (Fig. 13C,D). In all Bombycoidea studied, the subcoronal pad cuticle is unique in being "doubled", i.e. there are two layers of pad cuticle separated by a thin sheet of normal cuticle (Fig. 13D).

D. Discussion

I. Principle of adhesion and properties of the fluid

Adhesion of two solid surfaces by means of a thin fluid film is due to "capillary" or meniscus forces which are explained in Fig. 14. The force of adhesion depends on the reciprocal of the radius of curvature (r) and, hence, on the reciprocal of the distance between both surfaces. The contact angles of the adhesive fluid to the solid should be as small as possible, and this means that the fluid surface tension should not be much larger than the solid surface tension. The main objects to which the animals are to cling are plant leaves and stalks which are covered by a "wax layer" (Cutler et al. 1982), i.e. lipids with low surface tensions. The surface of insects is likewise of lipid nature, as indicated by the large contact angles of water droplets on the cuticle (Holdgate 1955). Hence, liquid lipids with comparatively low surface tension will properly work as adhesive fluids.

Information on adhesive fluids in insects is very scanty. Bauchhenß (1979) sampled traces of the fluid from flies of a *Calliphora* species walking in a vessel. Thin-layer chromatography of the comparatively viscous substance revealed that it consists of hydrocarbons and traces of more polar lipids. Furthermore, contact angles were measured on the surface of a variety of solids, including glass, plant leaves, polyethylene, etc.; the observed angles were between 16 and 28°. The measured angle of 50° on polytetrafluoroethylene (surface tension 0.0188 N/m) allows estimation of the surface tension of the fluid with equations presented by Driedger et al. (1965). The data give an estimate of 0.027 N/m, in good accordance with the chemical nature of the fluid. Surface tension depends generally on the molecular parts exposed on the surface. Apolar lipids such as saturated aliphatic hydrocarbons (-CH_3 and -CH_2 groups) cause especially low tension (0.020–0.031 N/m according to Shafrin and Zisman 1960). The surface tension grows with increasing polarity of the atomic groups, for example, 0.035–0.042 N/m for -CH_2-CHOH groups (Ray et al. 1958).

Measurements of contact angles of water on the smooth cuticular surfaces of insects and on plant leaves similarly allows estimates of surface tensions of the solids with the equations presented by Driedger et al.

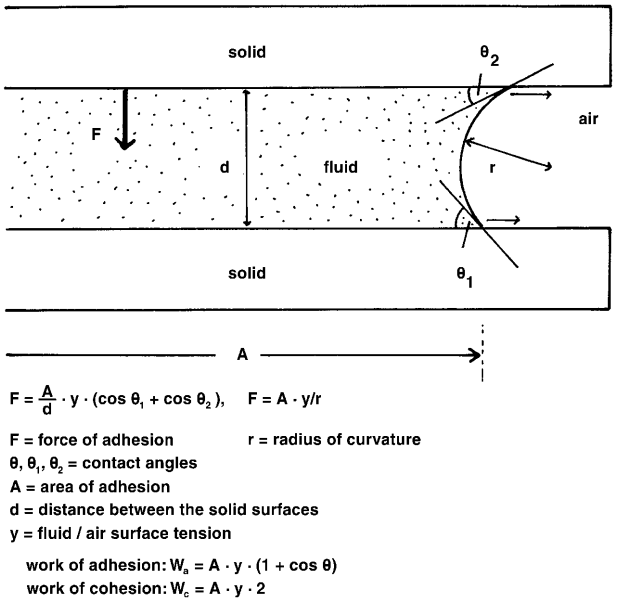

Fig. 14 Principle of adhesion. Surface tension causes negative pressure within the fluid. The equations for *F* are verified by modelling experiments

(1965). According to Holdgate (1955), the mean advancing angle of terrestrial insects is 105° and that of the retreating angle 87°. The corresponding surface tension estimates are 0.020 and 0.033 N/m, respectively. From these data, the contact angle of the adhesive fluid is estimated to be 46 and 0°, respectively. It is to be expected that the real angle will be somewhere in between. Water contact angles on smooth leaves are usually smaller and hence the surface tension of the lipid is somewhat larger than in insects (Linskens 1950; Bauchhenß 1979).

Since work of adhesion and work of cohesion are nearly the same (Fig. 14), the fluid will rupture anywhere during detachment. The result is tiny droplets left adhering to the substrate. The lost fluid will certainly be replaced by fluid from neighbouring parts thus maintaining the surface ready for the next action. The droplets left behind are involatile and have the same appearance as paraffin oil for which I measured a surface tension of 0.026 N/m. Exposed to air, the droplets remain liquid for months and solidify thereafter by autoxidation (Atkinson and Gilby 1970). Solidification was prevented by keeping the droplets in an oxygen-free atmosphere (Hasenfuss, unpublished observation).

II. General fluid lipid covering

Everywhere on the surface of caterpillars, the light reflection method and the application of sudan dye revealed the presence of a thin mobile lipid coating which is at least 2 µm thick. These findings are supported by similar observations in other insects (Hasenfuss 1977). The lipid coating is likewise present in adult Lepidoptera on the cuticle below the scales; however, it is absent or extremely thin on the scales. These exhibit, when observed by the light reflection method, the full set of interference fringes around each zone of contact (Hasenfuss 1977).

There is a large bulk of published work on the chemistry and physiology of cuticular lipids (see Lockey 1988; Noble-Nesbitt 1991; Renobales et al. 1991 for review). These are complicated mixtures of aliphatic apolar and polar lipids exhibiting great diversity in composition. Lipids easily pass the cuticle and the cuticular lipids are secreted through it. Their main function is to minimize water loss from the body surface and they support the epicuticle as a barrier by making it waterproof. However, there is a discrepancy in the appearance of cuticular lipids when extracted with solvents and when observed in situ using the light reflection method. In situ observation shows liquid or semi-liquid surface lipids even in insects of which the extracted cuticular lipids are known to be solid wax-like substances (Hasenfuss, unpublished observations).

The impression is that the superficial mobile lipid film acts, additionally, as a smear which protects the very thin epicuticle from becoming scratched when touching objects. If the epicuticle is locally damaged (for example, by rubbing with alumina), severe water loss by evaporation is the result (Wigglesworth 1945). Under natural conditions, damage is minimized by small projections (microtrichia, trichomes, etc.) which make the area of contact as small as possible. Mechanoreceptive sensillae are, in particular, mechanically stressed by contact and especially rich in superficial fluid.

III. Evolution of adhesive devices, functional aspects

The general fluid lipid coating causes some adhesive effect of any body part which comes into contact with the substrate. Normally, this effect is minimized by appropriate sculpturing of the cuticular surface, i.e. by minimizing the area of contact. Adhesive devices evolved by improving the effect. This was achieved by reducing the distance between the adhering solid surfaces and by enlarging the area. Since the surface of natural objects is more or less bumpy, there are generally two ways to meet these conditions:

1. Improvement by evolving comparatively large areas of smooth, flexible cuticle which cling closely to uneven surfaces. The negative pressure within the adhesive fluid pulls the cuticular surface towards the support and makes the film as thin as possible, thus increasing the force of adhesion.
2. Optimizing the adhesive effect of small cuticular projections by increasing their number, by making them elastic in a certain range perpendicular to the substrate and by making the apices curved and spatulate. The projections are then likely to compensate for irregularities of the substrate surface. In both cuticular types, the cuticle should be stiff enough to prevent the animal becoming detached by its own weight.

In Lepidoptera, the second type of adhesive cuticle is rare. It is found especially in larval subcoronae of Lymantriidae (Fig. 10D,E). In other insects, however, this type of organ is frequent, for example tibia in Heteroptera (Gillett and Wigglesworth 1932; Edwards 1962; Edwards and Tarkanian 1970), tarsal setae in Coleoptera (Stork 1980) and tarsal pulvilli in Diptera (Hasenfuss 1977; Bauchhenß 1979; Röder 1986). Very similar adhesive structures are also found in spiders (Hill 1977) as well as in gekkonid and anolid lizards (Ruibal and Ernst 1965; Hiller 1968). Adhesion by means of numerous curved spatulate elastic projections has the advantage that slipping is prevented in the direction of the apical edge (Gillett and Wigglesworth 1932). This seems to be the main role of the short recurved subcoronal spatulate projections found on the median side of prolegs in Macrolepidoptera; the projections improve the hold when the prolegs are clasping plant stalks. Starting from this condition, it was possible to improve adhesion by enlarging the apical areas of the microtrichia (in Lymantriidae). The other adhesive parts in lepidopteran larvae consist of flexible cuticle with a smooth surface. They sometimes show a special micellar arrangement of cuticular fibrils which is discussed in the following section.

IV. Cuticular structure

In sclerotized and normal flexible cuticle, the fibrils are arranged in parallel layers below the epicuticle (for review see Neville 1975). This texture is suited to the mechanical stress mainly acting within the plane of the cuticle. However, the adhesive force is directed almost perpendicularly to the cuticular surface. Notwithstanding this fact, normal cuticle texture is maintained in many adhesive devices with a smooth cuticular surface. In other devices pad cuticle evolved, i.e. a comparatively thick layer of parallel rod-like fibrils making an acute angle to the surface (Figs. 3A,B, 7D, 12E,F, 13). This texture is especially able to withstand combined vertical and horizontal pulling forces. The acute angle between the parallel fibrils and the surface, in Lepidoptera, always points to the apex of the leg or proleg. The fibrils are thus arranged almost within the direction of the pulling force when the leg or proleg adheres to the substrate. The absence of chitinous micellar interconnections between the rods possibly improves the flexibility of the cuticular surface. A very similar cuticular structure is found in tarsal arolia of adult Lepidoptera as well as of many other insects, for example orthopteroid insects (Slifer 1950; Roth and Willis 1952; Kendall 1970).

The developmental realization of the patterns of pad cuticle is surprisingly coincident with the patterns of adhesive contact. This is especially apparent in adhesive setae of caterpillars. The shaft of the seta is normally sclerotized and shows a sculptured surface, for example rillae, in which assemblages of liquid lipids are observable by the application of sudan dye. The adhesive effect is improved by enlarging the area of substrate contact and by developing pad cuticle within this area. Indeed, pad cuticle is found exclusively in that zone and only on that side of the seta which actually comes into contact with the substrate (Figs. 2D, 8B,C, 13A).

Furthermore, pad cuticle is especially frequent on the mesal side of clasping-type prolegs. It was observed in plantal bulges (Fig. 13B), coronal blisters (Fig. 12E,F) and the mesal zone of subcorona (Figs. 7D, 13C,D). Plantal bulges and coronal blisters are typical adhesive devices with smooth surfaces. However, the pad cuticle in the subcorona of Macrolepidoptera seems to be primarily engaged in other functions. For clasping twigs and stalks, it is important that the prolegs do not slide off the support. This is achieved by very numerous small spatulate and recurved microtrichia, as discussed in the previous section. The resulting shearing forces within the cuticle are met by the oblique fibrils of the pad cuticle. There is an additional pulling force from the crochets which are hooked into the support. This force is transmitted to the proximal parts by a thin layer of normal cuticle (*NC* in Fig. 13C) underlain by undulated cuticle. Sometimes the whole mesal subcoronal cuticle is of the undulated type (Fig. 13B). All studied Bombycoidea (including Sphingidae) form an exception; there is a second layer of pad cuticle below the thin internal sheet of normal cuticle (Fig. 13D). This peculiarity seems to be an autapomorphy of Bombycoidea.

Undulated layers are generally found in the flexible cuticle of large larvae (Fig. 13B–D). The “wavy” texture of fibrils seems to be a means of maintaining sufficient flexibility even in thicker cuticle.

V. Peculiarities of some lepidopteran groups

Since every body part which comes into contact with the substrate has the chance to become an adhesive device, convergent evolution was easily possible. Only unusual adhesive devices can be regarded as synapomorphies for cladistical argumentation.

1. Zygaenoidea

Together with some other families, the Zygaenidae and the limacodid group (with Megalopygidae, Aididae, Dalceridae and Limacodidae) are members of the Zygaenoidea (see Epstein 1996; Epstein et al. 1999). The abdominal adhesive devices of both groups are very unusual and seem to have a common base. The larvae of all instars live exposed to the open air and either cling to their food plants with clasping-type prolegs (Zygaenidae and Megalopygidae) or the prolegs are diminished or reduced and adhesion is taken over by the ventral body surface [Aididae, Dalceridae and Limacodidae (see Epstein 1996)].

It seems that, except for the first instar, the common ancestor of Zygaenidae and the limacodod group had clasping-type prolegs with two mesoseries of crochets on

abdominal segments 3–6 and 10. Furthermore there was a tendency to establish a functionally single row of uniordinal crochets and to increase the adhesive area. This is indicated by the two series of crochets in L2–Lm in Zygaenidae in which the distal series contains normally hooked crochets; the crochets of the proximal series are invaginated and the coronal blisters form an adhesive strip (Fig. 8E–G).

The first instar prolegs in Megalopygidae are similar to those in Zygaenidae (Fig. 8C,D) and have pads anterolateral to the single row of crochets (Epstein 1996). In contrast to Zygaenidae, these pads are maintained in post-first instars as adhesive devices. In these instars the corona is completed by the development of the anterior part of the mesoseries which is not continuous with the posterior part already present in L1. Normally, there is a gap between both parts. However, in a *Norape* species, both parts overlap for a short distance, the anterior part being more proximal than the other (see Fig. 26.176d in Stehr 1987b). This indicates that the mesoseries of the limacodid group are composed of parts of the two original series of crochets which tend to be functionally arranged in a single row. The composed nature of the corona explains its subdivision.

It seems that adhesion, in the ancestor of the limacodid group, was improved by developing additional prolegs on segments 2 and 7. These additional prolegs are an autapomorphy of this group and they are, in Megalopygidae, usually without crochets, exhibiting only the adhesive pads. The slug caterpillars of the limacodid group evolved by integrating neighbouring body parts into the adhesive surface. The corresponding transformations are discussed by Epstein (1996).

2. Macrolepidoptera

The Macrolepidoptera are now regarded as a clade (Minet 1991; Kristensen 1999) and prolegs of the climbing type are, except for Mimallonidae, clear ground plan characters. In contrast to the prolegs in Zygaenoidea, their coronae are uniserial and multiordinal. Uniserial coronae have the advantage that the hooking action of the crochets is more simultaneous and more easily controlled than the multiserial ones.

The independent evolution of clasping prolegs in Zygaenoidea and Macrolepidoptera is indicated by the different types of ancestral coronae and, additionally, by the different sculpturing of the median surface of the subcoronae. As pointed out in the previous section, the sculpturing improves the hold of the prolegs when clinging to food plant stalks. In Zygaenidae, the projections are small simple spines, and, in Macroplepidoptera, they are small, very numerous and have spatulate and often recurved apices. This type of projection is generally found in Macroleidoptera, except for Rhopalocera.

The prolegs of Rhopalocera are somewhat unusual and show more or less the characteristics of unspecialized-type prolegs. The coronae are sometimes complete or nearly complete circles of crochets even in mature larvae (for example in many Hesperiidae). Microtrichia on median subcoronae are missing or of a different type and of considerable diversity. The adhesive tarsal setae 2–4 (Fig. 9) are of normal shape. The larvae make extensive webs of silken threads on the substrate on which they are resting and walking. All this suggests that the ancestor of Rhopalocera had lost the adhesive devices formerly present and regained the unspecialized features of prolegs by continuously living on the webs. Only in young larvae of some Pieridae and in all instars of Lycaenidae was plantal adhesion observed. Lycaenidae exhibit a very specialized bulge which is a clear autapomorphy of the family (Fig. 11C), whereas in Pieridae there is some ineffective adhesion of the unspecialized planta.

3. Noctuoidea

The Noctuoidea have coronal adhesive blisters combined with uniordinal coronae. Both are ground plan characters of Noctuoidea maintained in nearly all members. Only in part of the Noctuidae are the crochets slightly biordinal (Beck 1960), but the differences in length are so small that they do not interfere with the the blisters. The other Macrolepidoptera exhibit multiordinal coronae, and there is no doubt that the uniordinal state is due to the evolution of adhesive coronal blisters in the ancestor of the Noctuoidea. Accordingly, the plantal bulges in some Notodontidae should be secondary. Except for members of the Noctuoidea discussed below, the blisters are structures of thin normal flexible cuticle.

Comparable coronal blisters were found elsewhere only in Sphingidae (Bombycoidea). However, in these, the blisters are small and seem to be of less importance, especially in large larvae. Contrary to Noctuoidea, the multiordinal state of coronae is maintained. Doubtless, the blisters of Sphingidae evolved independently of those in Noctuoidea.

In part of the Noctuoidea, the coronal blisters are fused into a protruding adhesive strip; it is built up of pad cuticle and its distal margin is sharply edged (Figs. 10C,H, 12D–F). This structure is present in Arctiidae, Lymantriidae and some quadrifine Noctuidae (*Herminia tarsicrinalis* and *Scoliopteryx libatrix*). Except for the Lymantriidae, which are discussed below, the adhesive strips are missing in the first instar and appear with the first moult. It is likely that these structures are synapomorphies. This is supported by the presence of an internal tympanum-like membrane in the adult tympanal organ found in the above-mentioned taxa and some other members of quadrifine Noctuidae (Hasenfuss 2000). From this hypothesis it follows that the quadrifine Noctuidae are not monophyletic in terms of Arctiidae and Lymantriidae, a result which is in accordance with conclusions from molecular data (Weller et al. 1994).

It should be mentioned that a similar strip of fused coronal blisters with pad cuticle is present in the larva of *Nycteola revayana* (Noctuidae, Sarrothripinae), the adult

of which lacks the internal tympanum-like membrane. However, the sharp edge of the fused blisters is on the proximal (instead of the distal) margin of the strip, and this is probably a sign of its independent origin.

In all Lymantriidae studied, the adhesive devices are extremely modified, probably as a result of passive dispersion of first instar larvae by wind. Wind dispersion is, actually, at least well known from *Lymantria dispar* (see Speight and Wainhouse 1989). The adhesive pads of L1 are well exposed in the central part of the coronae and seem to be especially effective when landing on a leaf. The exposure of the pads is facilitated by reduction of the apical hooks of the crochets within the pads (Fig. 10C, 12F). The large crochets at both sides of the central pads will support a hold on rough surfaces. A series of isolated patches of pad cuticle indicate clearly that the pads are fused coronal blisters. It seems that the development of hookless crochets, in Lymantriidae, was closely connected with the development of blisters. In later instars, normally hooked crochets are needed in the central part of the coronae; the blisters are, therefore, reduced and the subcoronae have taken on the task of adhesion by microtrichia (see Discussion, section III). The developmental programme of invaginated hookless crochets is likewise realized at both ends of the coronae in *Scoliopteryx libatrix* and nearly all Arctiidae ("heteroideous coronae"; Figs. 10H, 12D).

Summing up, it is apparent that the functional interrelations between organisms and their environment are, in regard to locomotion and attachment, comparatively simple and easy to observe directly in extant organisms. The comparative study of these interrelations makes it possible to understand one or other feature of the considered parts of the organisms as adaptations resulting from selection. Frequently such adaptations are convergent; however, sometimes they are unique solutions to a problem. In these cases it is possible to assign the corresponding traits to a single specific evolutionary event. The apparent interrelationships to the environment then throw some light on the mode of life of the corresponding ancestor and help to understand the further evolution of its descendants.

Acknowledgements I am obliged to Dr. W. Heimler for help with the SEM and to Dr. H. Beck, D. Lees, Prof. Dr. L. Kobes and I. Schulz for providing me with living or alcohol-preserved specimens of some lepidopteran larvae.

Appendix

List of investigated species

Species studied in the vital state are marked with an *asterisk*. Absence or type of adhesion is noted in brackets behind the instar notation L1, L2, etc.: – no adhesion or, if not marked with an asterisk, no adhesive devices morphologically recognizable, *T* adhesion with tarsal setae, *TL* adhesion with bulges on thoracic legs, *P* adhesion with prolegs

- Micropterigidae: **Micropterix aruncella* (Scopoli, 1763) L1, Lm (P)
- Hepialidae: **Triodia sylvina* (Linné, 1761) L1, Lm (–). Incurvariidae: *Incurvaria masculella* ([Denis and Schiffermüller], 1775) Lm (–)
- Tineidae: **Morophaga choragella* ([Denis and Schiffermüller], 1775) L1 (P), Lm (–); *Monopis rusticella* (Hübner, 1796) Lm (–); *Triaxomera parasitella* (Hübner, 1796) Lm (–); **Tineola bisselliella* (Hummel, 1823) Lm (–)
- Psychidae: **Psyche casta* (Pallas, 1767) L1, Lm (–); **Lepidopsyche unicolor* (Hufnagel, 1766) L1, L2, Lm (–). Gracillariidae: *Caloptilia syringella* (Fabricius, 1794) Lm (–).
- Yponomeutidae: *Yponomeuta plumbella* ([Denis and Schiffermüller], 1775) Lm (–); *Y. vigintipunctata* (Retzius, 1783) Lm (–)
- Plutellidae: **Plutella xylostella* (Linné, 1758) Lm (–)
- Gelechiidae: **Anacampsis populella* (Clerck, 1759) L3–Lm (T, P); *Anarsia spartiella* (Schrank, 1802) Lm (P); **Brachmia lutatella* (Herrich-Schäffer, 1854) Lm (T,P); *Gelechia muscosella* (Zeller, 1839) Lm (–); *Teleiodes proximella* (Hübner, 1796) Lm (P); *T. notatella* (Hübner, 1813) Lm (P). Elachistidae (sensu Minet 1990): **Agonopterix assimilella* (Treitschke, 1832) L1,L2 (T, P); **A. heracliana* (Linné, 1758) L3–Lm (P); *A. vendettella* Chrétien, 1908 Lm (T); *Anchinia cristalis* (Scopoli, 1763) Lm (T); **Ethmia bipunctella* (Fabricius, 1775) L1, Lm (–)
- Carcinidae: **Carcina quercana* (Fabricius, 1775) Lm (–). Chimabachidae: *Diurnea fagella* ([Denis and Schiffermüller], 1775) Lm (–)
- Oecophoridae: **Harpella forficella* (Scopoli, 1763) Lm (–). Coleophoridae: several undetermined species, Lm (–)
- Zygaenidae: **Zygaena lonicerae* (Scheven, 1777) L1–L3, Lm (T, P); *Rhagades pruni* ([Denis and Schiffermüller], 1775) L1–Lm (T, P)
- Limacodidae: **Apoda limacodes* (Hufnagel, 1766) L1–Lm (P, entire ventral surface)
- Sesiidae: **Pennisetia hylaeiformis* (Laspeyres, 1801) Lm (–); *Chamaesphecia tenthrediniformis* ([Denis and Schiffermüller], 1775) L1 (–)
- Cossidae: **Cossus cossus* (Linné, 1758) L1–Lm (–); *Phragmataecia castaneae* (Hübner, 1790) Lm (–)
- Tortricidae: several undetermined species L1,Lm (– or T)
- Choreutidae: **Anthophila fabriciana* (Linné, 1767) L1–Lm (P)
- Epermeniidae: *Epermenia illigerella* (Hübner, 1813) Lm (T). Schreckensteiniidae: *Schreckensteinia festaliella* (Hübner, 1819) Lm (T, P?)
- Pterophoridae: *Agdistis tamaricis* Zeller, 1847 L1 (T), Lm (–); *Marasmarcha lunaedactyla* (Haworth, 1811) Lm (–); **Pterophorus pentadactyla* (Linné, 1758) L1–Lm (T, P); *Oidaematophorus lithodactyla* (Treitschke, 1833) Lm (T, P); *Emmelina monodactyla* (Linné, 1758) L1–Lm (T, P); *Leioptilus scorodactyla* (Hübner, 1813) Lm (–)
- Thyrididae: **Thyris fenestrella* (Scopoli, 1763) L1 (P), Lm (–)
- Pyralidae: **Galleria mellonella* (Linné, 1758) L1 (T, P), Lm (–); *Plodia interpunctella* (Hübner, 1813) Lm(–)
- Crambidae: **Agriphila tristella* ([Denis and Schiffermüller], 1775) L1, L2 (T, P), Lm (–); **Dolicharthria punctalis* ([Denis and Schiffermüller], 1775) L1 (P), Lm (–); *Nomophila noctuella* ([Denis and Schiffer-müller], 1775) Lm (–); **Pleuroptya ruralis* (Scopoli, 1763) L2 (T,P), Lm (–)

- Macrolepidoptera
  – Bombycoidea. Lasiocampidae: *Poecilocampa populi* (Linné, 1758) L1 (T, P), L2–Lm (T); **Malacosoma castrensis* (Linné, 1758) L1, Lm (–); **Lasiocampa trifolii* ([Denis and Schiffermüller], 1775) L1–Lm (–); *Macrothylacia rubi* (Linné, 1758) L1 (T, P), L2 (T), Lm (–); *Cosmotriche lunigera* (Esper, 1784) L1, L2 (T, P), Lm (–); *Euthrix potatoria* (Linné, 1758) L1 (P), L2–Lm (–); *Gastropacha quercifolia* (Linné, 1758) L1 (T, P), L2 (T), L3–Lm (–); **Odonestis pruni* (Linné, 1758) L1 (T, P), L2 (T). Endromidae: *Endromis versicolora* (Linné, 1758) L1 (T, TL), Lm (TL). Saturniidae: *Citheronia splendens* (Druce, 1886) L1 (T, P), L2 (T, TL, P), Lm (TL); *Argema mittrei* (Guérin-Méneville, 1847) L1 (T, P), L2–L3 (T, TL, P);

Eudia pavonia (Linné, 1758) L1 (T, P), L2–L3 (T, TL, P), L4–Lm (TL); *Callosamia promethea* (Drury, 1773) L1 (T, P), L2–L3 (T, TL, P), L4 (T, TL); *Eupackardia calleta* (Westwood, 1853) L1 (T, P), L2 (T, TL, P), Lm (TL); **Aglia tau* (Linné, 1758) L1 (T, P), L2 (T, TL, P), Lm (TL). Bombycidae: **Bombyx mori* (Linné, 1758) L1–L3 (P), L4–Lm (TL). Lemoniidae: **Lemonia dumi* (Linné, 1761) L1 (P), L2, Lm (TL). Brahmaeidae: **Brahmaea certhia* (Fabricius, 1793) L1 (P), L2, Lm (TL); *B. wallichi* (Gray, 1831) L1 (P), L2 (TL). Sphingidae: **Hyloicus pinastri* (Linné, 1758) L1–L3 (T, P), L4–Lm (TL); *Laothoe populi* (Linné, 1758) L1–L2 (T, P), Lm (TL); **Hyles euphorbiae* (Linné, 1758) L1–L3 (T, P), L4–Lm (TL); **Deilephila elpenor* (Linné, 1758) L1–L2 (T, P), L4–Lm (TL)

– Geometroidea. Geometridae: *Archiearis notha* (Hübner, 1803) Lm (T); **Chlorissa viridata* (Linné, 1758) L1 (T, P); **Hemistola chrysoprasaria* (Esper, 1794) L1–Lm (T, P); *Idaea seriata* (Schrank, 1802) Lm (T); *Cyclophora punctaria* (Linné, 1758) L2–Lm (T, P); *Rhodostrophia calabra* (Petagna, 1787) L1 (T, P); *Horisme* sp. Lm (T, TL, P); **Epirrhoe alternata* (Müller, 1764) L1–L2 (T, P), L3–Lm (T, TL, P); **Selenia lunaria* (Hübner, 1788) L1–L2 (T, P), Lm (T, TL, P); *Biston betularia* (Linné, 1758) Lm (T, TL); *Agriopis marginaria* (Fabricius, 1777) Lm (T, TL). Uraniidae: *Chrysiridia rhipheus* (Drury, 1773) L1 (T, P), submature larva (–)

– Drepanoidea. Drepanidae: **Drepana falcataria* (Linné, 1758) L1–L3 (T, P), L4–Lm (T); *Watsonalla binaria* (Hufnagel, 1767) L1 (T, P); *W. cultraria* (Fabricius, 1775) L1 (T, L), Lm (T); * *Cilix glaucata* (Scopoli, 1763) L1–L4 (T, P); **Thyatira batis* (Linné, 1758) L1–L2 (T, P), Lm (–); **Tethea or* ([Denis and Schiffermüller], 1775) L1–L2 (T, P), Lm (–)

– Rhopalocera. Hesperiidae: *Carterocephalus palaemon* (Pallas, 1771) L1 (–); *Thymelicus lineolus* (Ochsenheimer, 1808) Lm (–). Papilionidae: *Papilio machaon* (Linné, 1758) L1–Lm (–); *Iphiclides podalirius* (Scopoli, 1963) L1–Lm (–). Pieridae: **Pieris rapae* (Linné, 1758) L1–L3 (P), L4–Lm (–); **Pieris napi* (Linné, 1758) L1 (P); **Gonepteryx rhamni* (Linné, 1758) L1–L2 (P), Lm (–). Nymphalidae: *Apatura iris* (Linné, 1758) L1, Lm (–); *Inachis io* (Linné, 1758) L1–Lm (–); **Mellicta athalia* (Rottemburg, 1775) L1–Lm (–); *Melanargia galathea* (Linné, 1758) L1–Lm (–). Lycaenidae: **Hamearis lucina* (Linné, 1758), *Cupido minumus* (Fuessly, 1775) L1–Lm (P); **Celastrina argiolus* (Linné, 1758) Lm (P); **Polyommatus icarus* (Rottemburg, 1775) L1–Lm (P)

– Noctuoidea. Notodontidae: **Phalera bucephala* (Linné, 1758) L1 (T, P), L2 (T), Lm (TL); **Cerura vinula* (Linné, 1758) L1–L3 (T, P), L4–Lm (T, TL); *C. erminea* (Esper, 1784) L1–L2 (T, P), Lm (T, TL); *Furcula bicuspis* (Borkhausen, 1790) L1–L3 (T, P), Lm (T, TL); **Harpyia milhauseri* (Fabricius, 1775) L1–L2 (T, P), Lm (T, TL, P); **Peridea anceps* (Goeze, 1781) L1–L3 (T, P), L5 (T, TL, P); **Drymonia ruficornis* (Hufnagel, 1766) L1–L2 (T, P), Lm (T, TL, P); **Eligmodonta ziczac* (Linné, 1758) L1–L3 (T, P), Lm (TL, P); *Pheosia gnoma* (Fabricius, 1777) L1–L3 (T, P), Lm (T, TL, P); **Ptilodon capucina* (Linné, 1758) L1–L2 (T, P), Lm (T, TL, P); **Clostera pigra* (Hufnagel, 1766) L1–L3 (T, P), Lm (T, TL, P); **Rhegmatophila alpina* (Bellier, 1881) L1–L3 (T, P), Lm (–); *Traumatocampa pityocampa* ([Denis and Schiffermüller], 1775) L1–Lm (–). Noctuidae: *Euxoa* sp. L1–L3 (T, P), L4–Lm (–); *Noctua comes* (Hübner, 1813) Lm (T, TL, P); *Discestra trifolii* (Hufnagel, 1766) L1–L2 (T, P), L3–Lm (T, TL, P); **Mamestra brassicae* (Linné, 1758) L1 (T, P), Lm (T, TL, P); *M. persicariae* (Linné, 1761) Lm (T, TL, P); *Orthosia cruda* ([Denis and Schiffermüller], 1775) Lm (T, TL, P); *Cucullia artemisiae* (Hufnagel, 1766) Lm (T, P); *C. verbasci* (Linné, 1758) Lm (T, P); *Allophyes oxyacanthae* (Linné, 1758) Lm (T, P); *Euplexia lucipara* (Linné, 1758) Lm (T, P); **Autographa gamma* (Linné, 1758) L1–L3 (T, P), L4–Lm (T, TL, P); **Acronicta alni* (Linné, 1767) L1–Lm (T, P); **A. rumicis* (Linné, 1758) Lm (–); **Colocasia coryli* (Linné, 1758) Lm (T, P); *Pseudoips prasinanus* (Fabricius, 1781) L1–Lm (T, P), *Nycteola revayana* (Scopoli, 1772) Lm (T, P); **Callistege mi* (Clerck, 1759) Lm (T, TL, P); *Euclidia glyphica* (Linné, 1758) Lm (T, TL, P); *Apopestes spectrum* (Esper, 1787) Lm (T, TL, P); *Rivula sericealis* (Scopoli, 1763) Lm (T, P); *Hypena proboscidalis* (Linné, 1758) Lm (T, P); *Parascotia fuliginaria* (Linné, 1761) Lm (–); *Herminia tarsicrinalis* (Knoch, 1782) Lm (T, P); *Scoliopteryx libatrix* (Linné, 1758) Lm (T, TL, P). Arctiidae: *Eilema complana* (Linné, 1758) L1–Lm (T, P); *Tyria jacobaeae* (Linné, 1758) L1–Lm (T, P); **Diacrisia sannio* (Linné, 1758) L1–Lm (T, P); *Spilosoma luteum* (Hufnagel, 1766) L1–Lm (T, P); **S. lubricipeda* (Linné, 1758) L1–Lm (T, P); *Parasemia plantaginis* (Linné, 1758) L1–Lm (T, P); **Arctia villica* (Linné, 1758) L1–L2 (T, P); *Phragmatobia fuliginosa* (Linné, 1758) L1–Lm (T, P); *Euplagia quadripunctaria* (Poda, 1761) L1–Lm (T, P); *Setina roscida* ([Denis and Schiffermüller], 1775) L1–Lm (T, P); *Syntomis phegea* (Linné, 1758) L1–Lm (T, P). Lymantriidae; **Calliteara pudibunda* (Linné, 1758) L3–Lm (T, P); **Orgyia antiqua* (Linné, 1758) L1–Lm (T, P); **Lymantria dispar* (Linné, 1758) L1–Lm (T, P); *L. monacha* (Linné, 1758), **Sphrageidus similis* (Fuessly, 1775) L1–L2 (T, P)

References

Atkinson PW, Gilby AR (1970) Autoxidation of insect lipids: inhibition on the cuticle of the American cockroach. Science 168: 992

Bauchhenß E (1979) Die Pulvillen von *Calliphora erythrocephala* Meig. als Adhäsionsorgan. Dissertation, Fakultät für Biologie, Ludwig-Maximilians-Universität München

Beck H (1960) Die Larvalsystematik der Eulen (Noctuidae). Akademie, Berlin

Cutler DF, Alvin KL, Price CE (1982) The plant cuticle. Academic Press, London

Dahl F (1885) Die Fußdrüsen der Insekten. Arch Mikrosk Anat 25:236–262

Driedger O, Neumann AW, Sell P-J (1965) Über die grenzflächenenergetische Zustandsfunktion, II. Kolloid Z Z Polym 204:101–105

Edwards JS (1962) Observations on the development and predatory habit of two reduviid Heteroptera, *Rhinocoris carmelita* Stal and *Platymeris rhadamanthus* Gerst. Proc R Entomol Soc Lond A 37:89–98

Edwards JS, Tarkanian M (1970) The adhesive pads of Heteroptera: a re-examination. Proc R Entomol Soc Lond A 45:1–5

Epstein ME (1996) Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea). Smithson Contrib Zool 582:1–102

Epstein ME, Geertsema H, Naumann CM, Tarmann GM (1999) The Zygaenoidea. In: Kristensen NP (ed) Lepidoptera, moths and butterflies, vol 1. Handbook of zoology 35. de Gruyter, Berlin, pp 159–180

Gerasimov AM (1952) Lepidoptera, part 1, caterpillars (in Russian). Zool Inst Acad Nauk USSR New Ser no. 56. Fauna USSR. Insects – Lepidoptera 2:1–338

Gillett JD, Wigglesworth VB (1932) A climbing organ of an insect, *Rhodnius prolixus* (Hemiptera; Reduviidae). Proc R Soc Lond B 111:364–376

Hasenfuss I (1963) Basale Prolongation in der Larvalentwicklung der Wachsmotte *Galleria mellonella* L. (Pyralidae, Lepidoptera). Verh Dtsch Zool Ges 1963:587–602

Hasenfuss I (1977) Die Herkunft der Adhäsionsflüssigkeit bei Insekten. Zoomorphologie 87:51–64

Hasenfuss I (1980) Die Präimaginalstadien von *Thyris fenestrella* Scopoli (Thyrididae, Lepidoptera). Bonn Zool Beitr 31:168–190

Hasenfuss I (2000) Evolutionary pathways of truncal tympanal organs in Lepidoptera (Insecta: Holometabola). Zool Anz 239 (in press)

Hill DE (1977) The pretarsus of salticid spiders. Zool J Linn Soc 60:319–338
Hiller U (1968) Untersuchungen zum Feinbau und zur Funktion der Haftborsten von Reptilien. Z Morphol Tiere 62:307–362
Hinton HE (1955) On the structure, function, and distribution of the prolegs of the Panorpoidea, with a criticism of the Berlese-Imms theory. Trans R Entomol Soc Lond 106:455–541
Holdgate MW (1955) The wetting of insects cuticle by water. J Exp Biol 32:591–617
Kendall UD (1970) The anatomy of the tarsi of *Schistocerca gregaria* Forskal. Z Zellforsch 109:112–137
Kristensen NP (1999) Lepidoptera, moths and butterflies, vol 1. Handbook of zoology 35. de Gruyter, Berlin
Linskens HF (1950) Quantitative Bestimmung der Benetzbarkeit von Blattoberflächen. Planta 38:591–600
Lockey KH (1988) Lipids of the insect cuticle: origin, composition and function. Comp Biochem Physiol 89B:595–645
Minet J (1990) Remaniement partiel de la classification des Gelechioidea, essentiellement en fonction de charactères pré-imaginaux (Lepidoptera Ditrysia). Alexanor Rev Lepid Fr 16: 239–255
Minet J (1991) Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). Entomol Scand 22:69–95
Neville AC (1975) Biology of the arthropod cuticle. Springer, Berlin Heidelberg New York
Noble-Nesbitt J (1991) Cuticular permeability and its control. In: Binnington K, Retnakaran A (eds) The physiology of insect epidermis. CSIRO Publ, East Melbourne, pp 252–283
Ray RJR, Anderson JR, Scholz JJ (1958) Wetting on polymer surfaces. I. Contact angles of liquids on starch, amylose, amylopectin, cellulose and polyvinyl alcohol. J Phys Chem 62: 1220–1227
Renobales Mde, Nelson DR, Blomquist GJ (1991) Cuticular lipids. In: Binnington K, Retnakaran A (eds) The physiology of insect epidermis. CSIRO Publ, East Melbourne, pp 240–251
Röder G (1986) Zur Morphologie des Praetarsus der Diptera und Mecoptera. Zool Jahrb Anat 114:465–502
Rombouts JE (1884) Über die Fortbewegung der Fliegen an glatten Flächen. Zool Anz 7:619–623
Roth LM, Willis ER (1952) Tarsal structure and climbing ability of cockroaches. J Exp Zool 119:483–517
Ruibal R, Ernst V (1965) The structure of the digital setae in lizards. J Morphol 117:271–294
Shafrin EG, Zisman WA (1960) Constitutive relations in the wetting of low energy surfaces and the theory of the retraction method of preparing monolayers. J Phys Chem 64:519–524
Slifer EH (1950) Vulnerable areas on the surface of the tarsus and pretarsus of the grasshopper (Acrididae, Orthoptera); with special reference to the arolium. Ann Entomol Soc Am 43: 173–188
Speight MR, Wainhouse D (1989) Ecology and management of forest insects. Clarendon Press, Oxford
Stehr FW (1987a) Immature insects, vol 2. Order Lepidoptera. Kendall/Hunt Dubuque, Iowa, pp 288–596
Stehr FW (1987b) Megalopygidae. In: Stehr FW (ed) Immature insects, vol 2. Kendall/Hunt Dubuque, Iowa, pp 454–456
Stork NE (1980) A scanning electron microscope study of tarsal adhesive setae in the Coleoptera. Zool J Linn Soc 68:173–306
Weller SJ, Pashley DP, Martin JA, Constable JL (1994) Phylogeny of noctuoid moths and the utility of combining independent nuclear and mitochondrial genes. Syst Biol 43:194–211
Wigglesworth VB (1945) Transpiration through the cuticle of insects. J Exp Biol 21:97–114