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# Ultrastructure of a Scent Scale Organ with Pressure Discharge in Male *Caligo eurilochus brasiliensis* (Fldr.) (Lepidoptera: Brassolidae)*

Lutz Thilo Wasserthal and Wiltrud Wasserthal
Lehrstuhl für Spezielle Zoologie, Ruhr-Universität Bochum, Bochum, Federal Republic of Germany

**Summary.** The abdominal scent apparatus of male *Caligo eurilochus* was examined at different ages by light, scanning and transmission electron microscopy. The glandular epithelium is covered with specialized scales and forms a pad on each side of the 4th to 6th abdominal segments. The pads are surrounded by smooth, elastic cuticle and can protrude toward the opposite hind wing hair pencil. The scales have a poreless cuticle with a fibrillar texture. They are impregnated by an oily, slowly volatile substance. The scales are elongated toward the base, forming hoods over the long cone-shaped sockets. The scale pedicel is anchored tension-free by rootlets in the central socket base. The slightly asymmetric cuticular sockets are very elastic, due to their high water content. They are stabilized by internal epicuticular rods. The release of the secretions from the cell and a possibly active microvillar transport is discussed. Different secretions are found in the space between the microvillar surface of the gland cell and the socket floor. They are probably discharged from the supraglandular space into the scale lumen by means of pressure and bending of the sockets. A flowback might be prevented by capillary effect of a "ball" of vesicles, which lies exactly above the outlet of the scale pedicel.

**Key words:** Scent scales – Lepidoptera – Secretion discharge – Gland cells – Insect cuticle.

**Zusammenfassung.** Der abdominale Duftapparat männlicher *Caligo eurilochus* wurde licht-, raster- und transmissions-elektronenmikroskopisch bei Tieren verschiedenen Alters untersucht. Das Drüsenepithel ist mit spezialisierten Schuppen bedeckt und bildet seitliche Polster auf den Abdominalseg-

*Send offprint requests to:* Dr. Lutz Thilo Wasserthal, Lehrstuhl für Spezielle Zoologie der Ruhr-Universität, Postfach 102148, D-4630 Bochum-Querenburg, Federal Republic of Germany

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menten 4 bis 6. Diese Polster sind von nackter, elastischer Kutikula umgeben und können gegen eine glatte Reibefläche des anliegenden Hinterflügelbereiches gepreßt werden, auf der sich ein Borstenpinsel befindet. Die porenlose Schuppenkutikula weist eine ungeordnete Fibrillentextur auf und ist mit einer ölartigen, langsam flüchtigen Substanz durchtränkt. Die Schuppenbasis ist zu einer Haube umgebildet, die einem konisch verlängerten Schuppenbalg dicht aufsitzt. Der Schuppenstiel ist durch wurzelartige Ausläufer spannungsfrei im basalen Balg verankert. Infolge eines hohen Wassergehalts sind die Schuppenbälge sehr elastisch. Sie sind durch innere asymmetrisch angeordnete Epikutikula-Pfeiler stabilisiert. Die Sekretabgabe aus der Zelle und ein möglicherweise aktiver Mikrovilli-Transport werden diskutiert. In einem Raum zwischen der Mikrovilli-Oberfläche und der Schuppenbalgbasis sind verschiedene Sekrete angereichert. Diese werden wahrscheinlich durch Einengen des supraglandulären Raumes bei Druck auf den biegsamen Schuppenbalg in die Schuppe entleert. Ein Rückfluß der Sekrete wird möglicherweise durch Kapillarwirkung eines Vesikelbällchens verhindert, das genau über der Austrittstelle des Schuppenstieles liegt.

## Introduction

A large variety of lepidopterous scales is specialized as scent dispensers. Many different structural types have been described (Freiling, 1909; Müller, 1877; Seibt et al., 1972; Sellier, 1971, 1972; Vane-Wright, 1972; Vogel, 1910), but the mode of transport of the secretion from the scent gland to the cell surface has not yet been revealed even in recent investigations (Birch, 1970; Pliske and Salpeter, 1971; Grant et al., 1971–1973; Clearwater, 1975). In this paper a new type of scent scale organ is described with unique specializations for the extrusion of the secretory products.

## Materials and Methods

Chrysalids of *Caligo eurilochus brasiliensis* (Fldr.) 1862 were received from a breeder in Brasil. The butterflies emerged in an air-conditioned room and were kept at 23° C and above 90% relative humidity. Fed with squashed ripe bananas, they lived for about 2 months.

Abdominal scent scale areas were taken from 4 animals 6.5 h, 8 h, 2 days and 18 days after eclosion. Fixation: Injection of 4% glutaraldehyde, buffered in 0.08 M cacodylate (pH 7.2) with 4% sucrose; preparation at room temperature, subsequently stored in the fixative at 4° C for 16.5 h (Fix. I) or 12 h (Fix. II); washing and postfixation with 1% $OsO_4$ in cacodylate buffer. During dehydration the specimens were block-stained in 1% uranyl acetate in 70% ethanol; embedding in Epon. Ultrathin sections were cut with glass knives on a Reichert Om U2 microtome and examined on a Zeiss EM 9S electron microscope. The semi-thin sections were stained with methylene blue polychrome Unna (Serva).

The less dense appearance of the interior socket material in Fix. I is possibly due to the 4.5 h longer time of fixation in glutaraldehyde and/or to the different succession of mixing the components of the fixative solution: in Fix. II sucrose was added to cold buffer 1.5 h before mixing with glutaraldehyde; in Fix. I glutaraldehyde was added first and a slight precipitation occurred during fixation.

In order to examine whether the scent organs of butterflies are exposed during wing opening, two males were photographed with a self-timer from the rear and from the dorsal side. The butterflies were glued at the mesonotum perpendicularly to a stable rod, which allowed unrestricted wing movements. A fine wire contact was oriented in such a way that a slight touch by the wings in any desired stroke-position released a motor camera with a stroboscopic flash emitter.

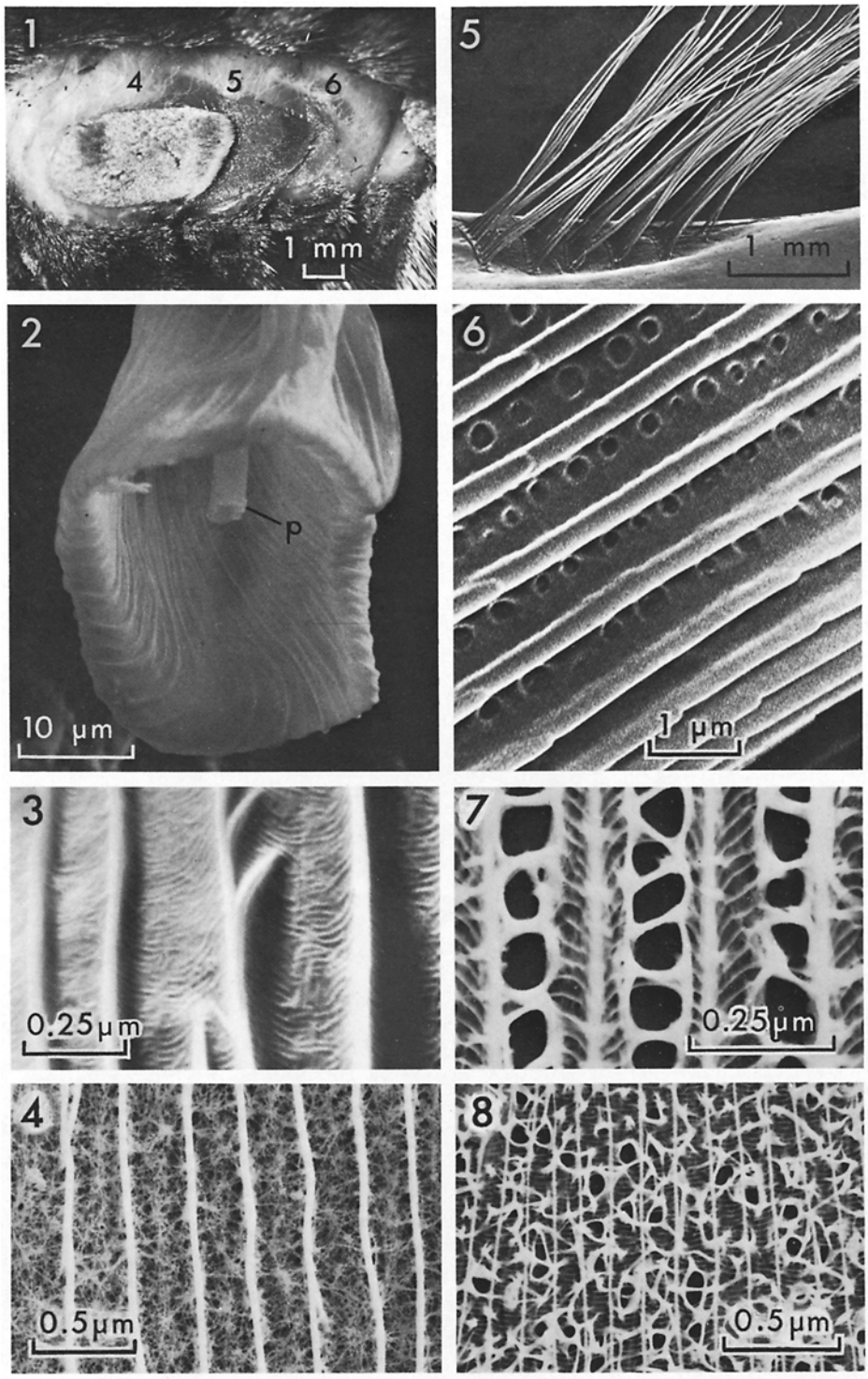
## Results

The males of *Caligo eurilochus* have a large oval field of brown soft scales on each side along the abdominal segments 4, 5 and 6. It is surrounded by smooth, elastic cuticle (Fig. 1). The entire area can be protruded by abdominal pressure. The scale surfaces appear wet and oily (Fig. 30). However, if exposed to air, they will dry within 30–60 min. The scent can be perceived by human olfaction and is reminiscent of smoked ham. In the resting position dessication is prevented by the anal part of the hindwings which fits tightly to the body. This wing area bears a pencil of hairs near the anal vein (1A+2A, Fig. 5). This area is also surrounded by smooth cuticle. Stroboscopic pictures in tethered flight show that the scent pads remain covered by the pencil area of the hindwing borders, independent of the wing position. It is therefore likely that the scent pads and pencils are only exposed by a special behavior. Unfortunately, the butterflies did not exhibit courtship or territorial behavior in captivity. Although we have repeatedly observed that females sat closely besides the more passive males, no mating display occurred.

The lateral abdominal scent organs consist of hundreds of scent producing units, each consisting of a gland cell, a conical socket and a scale. The most conspicuous characteristics of the gland cells are a broad microvillous apex, concave toward the socket, and a highly increased basal cell surface (Figs. 9, 13). The socket is an extremely elastic, long cone with an internal tube. The scent scale consists of a long pedicel, a hoodlike basis and a slightly undulating lamina, bent backwards, thus partly covering posterior scales (Figs. 9, 28, 31).

In general, the gland cells are quite similar to other insect epidermal secretory cells (Noirot and Quennedey, 1974). The cells are separated from the hemocoel by a loose extracellular basement membrane. The basal cell surface shows multiple invaginations of extracellular spaces, forming a broad border (Fig. 13). The large nucleus seems to be polyploid and has a lobed surface (Fig. 9), which is less prominent in older specimens. The cytoplasm has an abundance of free ribosomes, but a poorly developed endoplasmic reticulum and Golgi apparatus. The numerous mitochondria and microtubuli are longitudinally orientated.

Two different types of granules can be discerned in the gland cell. The first type has a globular crystalline structure, surrounded by a membrane. It is found throughout the cytoplasm of the gland cell and the neighboring small hypodermal cells (Fig. 14). This type of granule occurs in all ages, but more frequently in the cells of older specimens (2 and 18 days). In the young butterflies, 6.5 and 8 h after eclosion, such large granules are found with less organized contents and with more electron dense material between the globules. The second type of granules is evenly electron dense. It is restricted to the gland cells and occurs mainly in young specimens. The granules are more concen-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trated below the microvilli of the apical cell border, lie within cell vacuoles but are not directly surrounded by a membrane (Fig. 21).

The microvilli are arranged in clusters in young specimens, their tips oriented towards the basal socket tube. The structure of the microvilli with peripherally ill-defined axial filaments differs in complexity from the normal types (Fawcett, 1967) by the existence of a central channel. This was, however, repeatedly observed in insect secretory cells (Quennedey, 1969, 1971; Waku and Sumimoto, 1969). In the 18 day-old specimen the brush border is more regular than in the younger ones and does not show clustering (Fig. 12).

The supraglandular space between the microvillar surface and the cuticular basis of the socket is filled with a substance of fibrillar or grainy appearance with a higher density in the older specimens (Fig. 15). This substance seems to be concentrated and attached to the darkened microvillar tips (Figs. 18, 19). In the young specimens this material is also found along some darkened contours of the bases of microvillar clusters (Figs. 18, 19). In the small hypodermal cells a comparatively loose substance was found supracellularly and between the short microvilli, which also have dark tips.

The granules of the dense type can normally be seen extracellularly in the niches between the microvilli (Figs. 20, 31) but also within the clusters surrounded directly by microvilli (Fig. 17). In Figure 20 the extrusion of one granule is visible. Membranous remnants lying at the microvilli bases are found mainly in the older specimens (Fig. 15).

The supraglandular space between the microvillous surface and socket base always contains only very few single, dense granules. In the 2 and 18 day-old specimens there is, however, a mass of dense material like that of the dense granules, which originates with a few processes between single microvillar clusters and extends from the center of the supraglandular space into the lumen of the scent scale pedicel (Figs. 9, 15, 31).

Near the entrance of the pedicel in addition to the secretory mass some different material is found. It gives the impression of clustered winding tubes with an outer membrane and seems to be degenerated (Fig. 16). The homogeneous material of the secretory mass dissolves into granules again in the upper pedicel lumen. A "ball" of vesicles always occurs upon the outlet of the lumen

**Fig. 1.** Scent pads on the abdominal segments 4 to 6 (*4, 5, 6*) surrounded by smooth cuticle; on segment 4 scale impregnation volatilized

**Fig. 2.** View into a scent scale hood, pedicel (*p*) broken. Scanning electron micrograph (SEM)

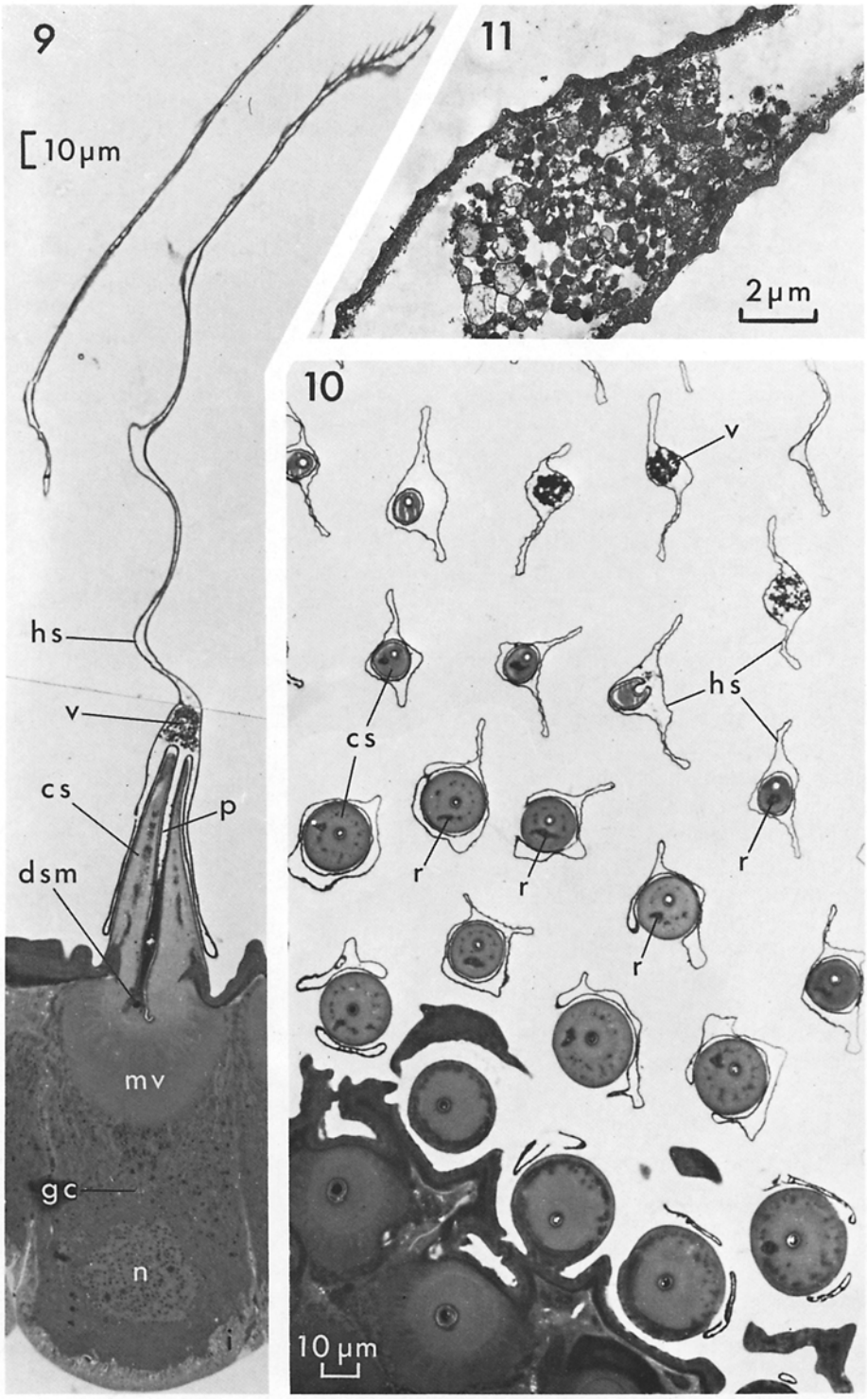
**Fig. 3.** Scent scale lamina, medium part, upper side. SEM

**Fig. 4.** Unperforated scent scale lamina, medium part Transmission electron micrograph (TEM)

**Fig. 5.** Hair pencil on smooth hindwing area. SEM

**Fig. 6.** Hair of the wing pencil; pores in the upper part. SEM

**Figs. 7 and 8.** Normal body scales, showing two typical perforation patterns. TEM. (Figs. 4, 7 and 8, prints from internegatives)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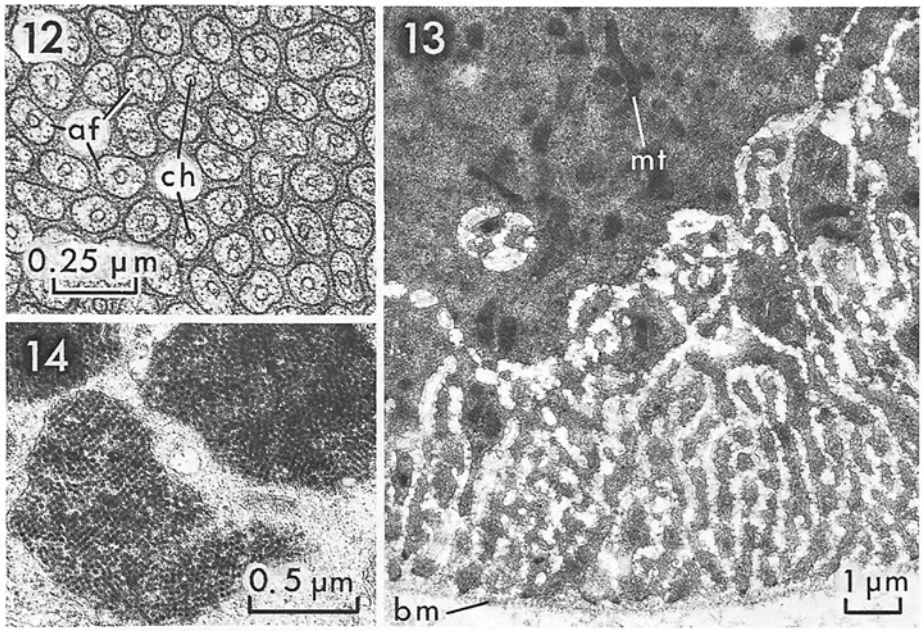



**Fig. 12.** Microvillous cell border; *af* axial filament; *ch* central channel

**Fig. 13.** Invaginations at the basis of the glandular cell; *bm* basement membrane; *mt* mitochondrium

**Fig. 14.** Globular granules in the cytoplasm of a gland cell. (Figs. 12–14. 18 days old)

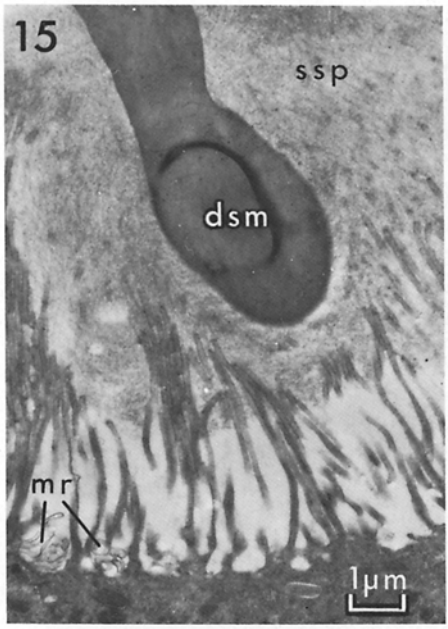
of the scale pedicel (Figs. 9–11, 31). Single vesicles are never found in other parts of the scales. These vesicles have a larger diameter than the secretions in the pedicel and seem to be different. They contain an amorphous or granular substance of a variable amount. In the lumen of the scale lamina, however, homogeneous droplets of a still larger size than the "ball" vesicles exist: in the light microscope, scales are found to be densely packed with refracting droplets after dehydration in ethanol. In semi-thin sections droplets of the same size are also present, some of which stain with methylene blue, while most of them remain transparent (Fig. 29).

The scent scale sockets are prolonged and have an obliquely cone-shaped form, bent slightly caudad (Fig. 9), while scale sockets normally are less prominent and have stiff annular holes around the scale insertion. The scent scale

**Fig. 9.** Semithin longitudinal section of a scent organ unit; 18 days old. *cs* Cone socket; *dsm* dense secretory material; *gc* gland cell; *hs* hood scale; *i* invaginations of the basal cell membrane; *mv* microvilli; *n* nucleus; *p* pedicel; *v* "ball" of vesicles

**Fig. 10.** Semithin cross section of sockets with hood scales, showing the preferred orientation of the anterior thick rods (*r*); 18 days old

**Fig. 11.** "Ball" of vesicles in the scent scale lumen; cross section; 18 days old. TEM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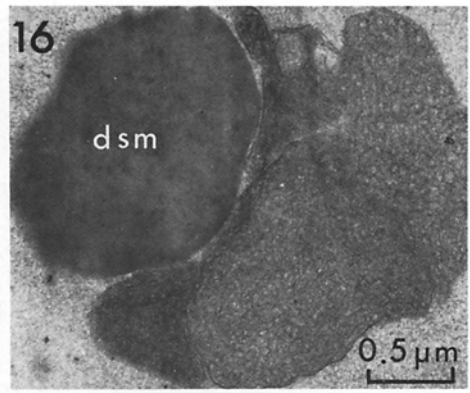
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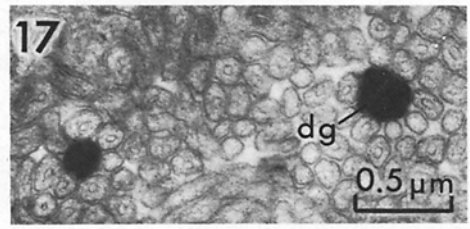
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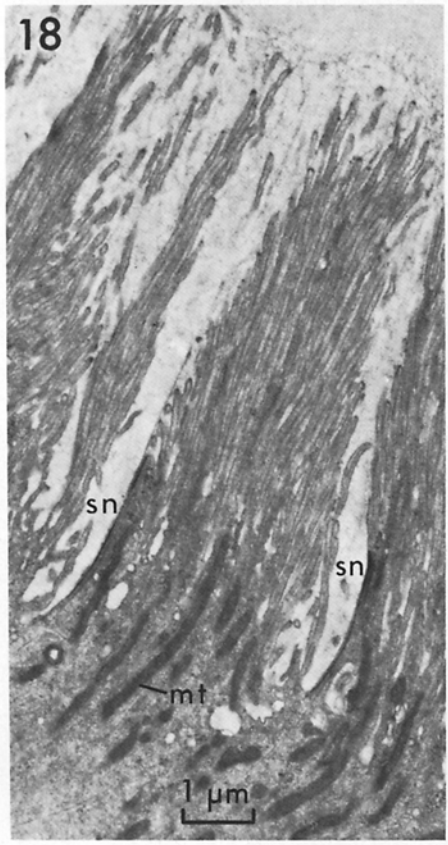
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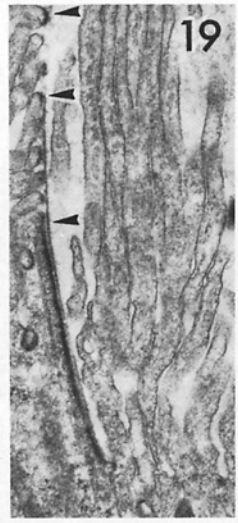
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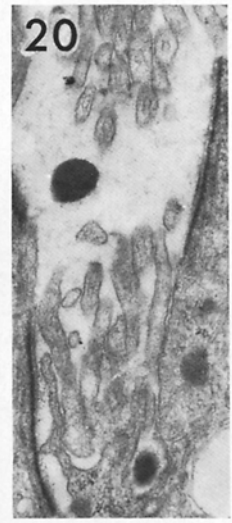
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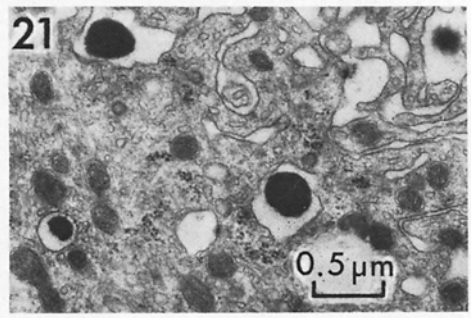
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sockets feel like elastic gum piles when gently touched with a fine needle under the stereo-microscope. In the transmission electron microscope (TEM) their interior reveals a rather homogeneous material of a moderate electron density (Fix. II, Figs. 9, 22; Fix. I, Figs. 24, 26). The thin electron dense cuticle of the outer cone and the central tube are followed inside by some fibrillar, less distinct material (Figs. 24, 27). The upper half of the cone contains some kind of fiber-like cuticular material, loosely arranged below the outer cuticle. The orientation of these fibers is partly concentric, partly curled (Figs. 22, 23). After freeze-fracturing and -drying of the fixed cone sockets, no substance is found with the SEM in their interior except for about 6–12 cuticular rods. These rods arise from the thick basal socket wall, branching towards the apex and anastomosing with one another (Fig. 31). The anterior rod is much thicker than the others (Figs. 10, 24, 31). The material of this network is identical to that of the outer socket wall. Most rods are longitudinally traversed by a canal, the anterior rod by several, all of them filled with an amorphous dark substance ("Wachskanäle", Neville, 1975) (Fig. 24). Tiny branches of the rods lead upward to the outside socket cuticle.

The central socket tube does not run exactly longitudinally through the socket axis: the basal end, with the insertion of the scale, lies eccentric towards the anterior side; the distal end is shifted towards the posterior side. The interior socket floor is identical to the "roof" of the supraglandular space. It is constructed of some very delicate fibrillar cuticle (Fig. 26).

The scent scale inserts in the socket base with laterally extending coiled, rootlike appendages of the proximal pedicel (Fig. 27). There are two sets of "rootlets" which lie close together, one over the other, fitting into the correspondingly formed channels of the socket cuticle (Fig. 31). The socket channels are, however, broader than the rootlets, thus facilitating a non-tension anchorage of the scale, when the sockets are bent. It is impossible to pull off the scent scales without breaking their pedicels (Fig. 2). The scent scale hoods cover almost the whole surface of the cones. Most hoods have a longitudinal cleft and show bizarre outgrowths of their margins without regularity of

**Fig. 15.** Confluence of the electron dense secretory mass (*dsm*) in the supraglandular space (*ssp*), surrounded by loose secretory substance; *mr* membranous remnants; 2 days old

**Fig. 16.** Dense secretory mass (*dsm*) and membranous structured material, possibly degenerated cell remnants, below the inner pedicel entrance; 18 days old; cross section

**Fig. 17.** Dense granules (*dg*) surrounded by microvilli

**Fig. 18.** Clustered microvilli with secretory niches (*sn*); *mt* mitochondrium

**Fig. 19.** Electron dense cell surface and plaques (arrows) on microvilli tips in a secretory niche (same scale as Fig. 21)

**Fig. 20.** Extrusion of dense granules at the base of a secretory niche (same scale as Fig. 21)

**Fig. 21.** Secretory granules in vacuoles of the cytoplasm below the microvillar cell border. (Figs. 17–21: 6.5 h old)

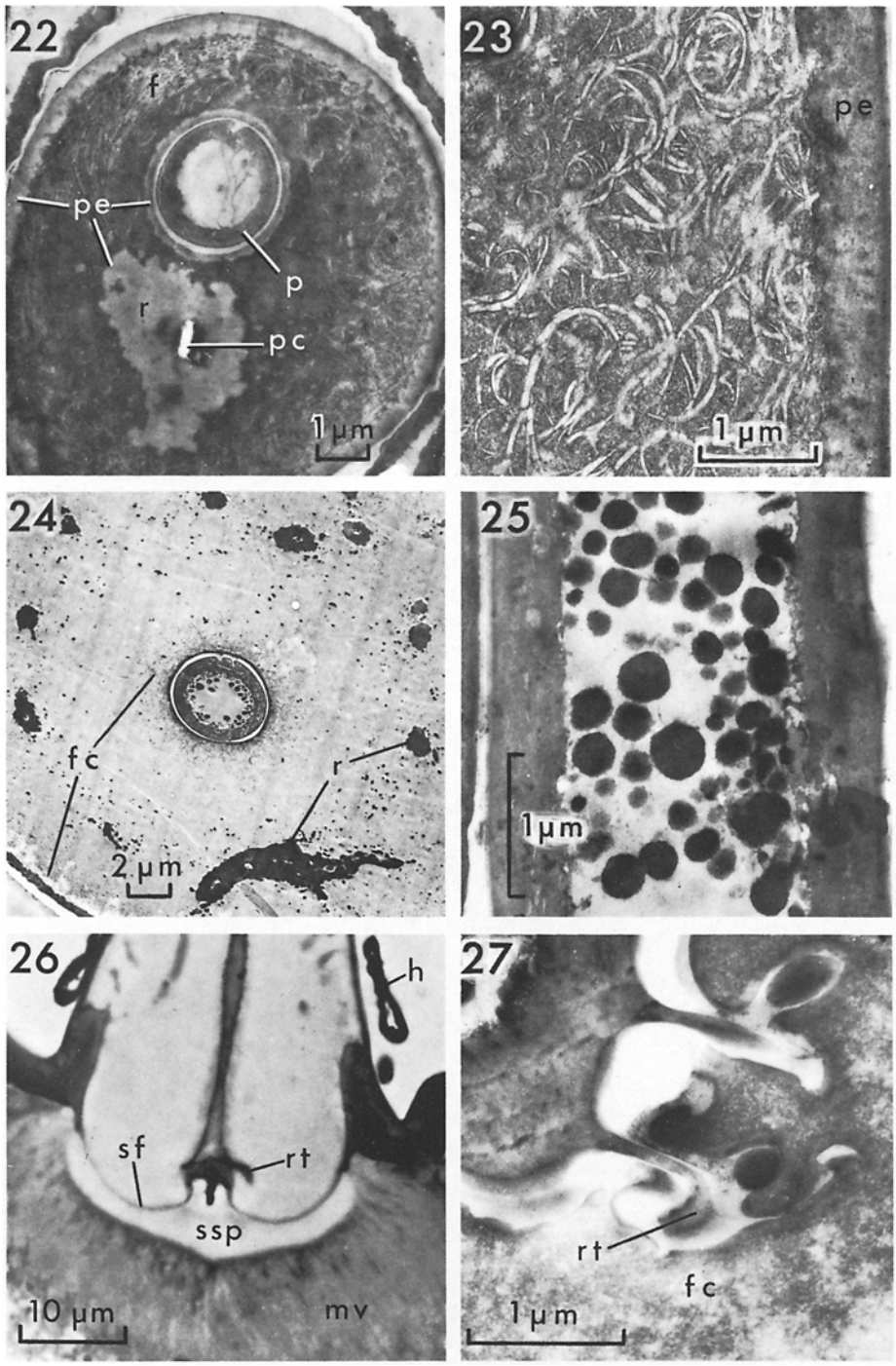


**Fig. 22.** Cone socket; cross section near the tip, showing fibrous material (*f*) under the protein epicuticle (*pe*); *p* pedicel; *r* anterior rod with pore canal (*pc*); 18 days old (Fix. II)

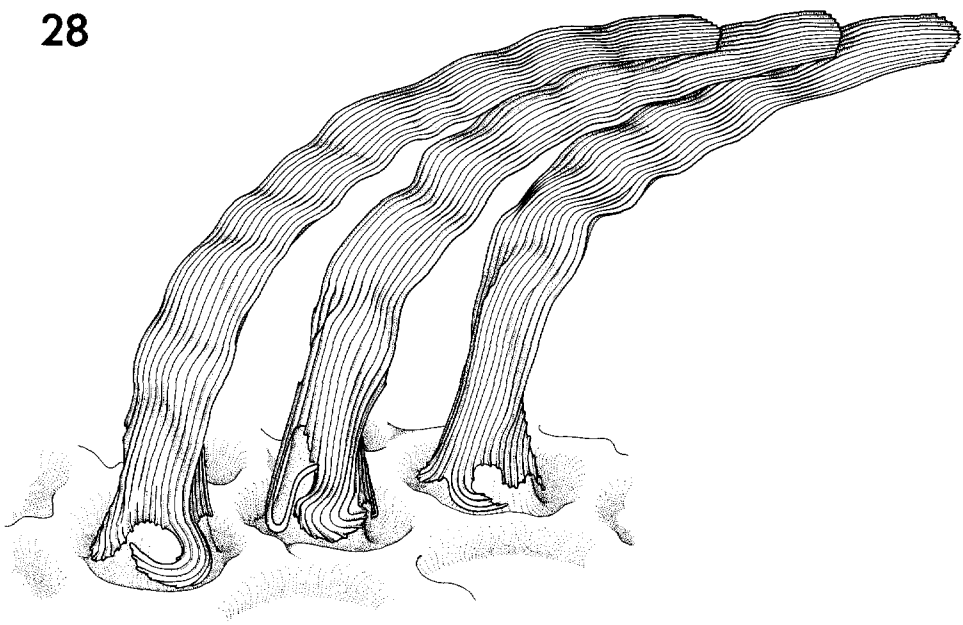


**Fig. 28.** Hood scales of Caligo ♂ scent pads with irregular outgrowths of the hood margins

form and orientation (Fig. 28). The lamina of the scale originates from lateral longitudinal folds of the hood and is bent backwards (Figs. 10, 28).

In ultrathin sections the outer scale wall is a homogeneous solid layer with longitudinal ridges (Fig. 11). In the SEM, also, no perforations of the surface can be found (Fig. 3). Untreated scent scales mounted on grids in the TEM show an irregular fibrillar network between the ridges (Fig. 4). This texture is similar to the intermediate stage of normal scale formation before the development of the holes and cross ridges (Paweletz and Schlote, 1964; Schmidt, 1965). It is thus much less complicated than the normal body scales (Figs. 7, 8).

The scent scale cuticle is impregnated by an oily, slowly volatile secretion. This is documented by the traces which untreated scales leave behind on the

**Fig. 23.** Same as Fig. 22, longitudinal section

**Fig. 24.** Cone socket with asymmetric arrangement of cuticular rods (*r*) in the less dense aqueous ground substance; cross section in the proximal third; *fc* fibrillar cuticle; 6.5 h old (Fix. II)

**Fig. 25.** Scent scale pedicel with dense secretory granules; longitudinal section; 6.5 h old

**Fig. 26.** Basis of the cone socket, showing the delicate rounded socket floor (*sf*) and supraglandular space (*ssp*); *h* process of hood-shaped scale basis; *mv* microvilli; *rt* rootlet, anchorage of the pedicel; semithin section (Fix. I)

**Fig. 27.** Rootlike appendages (*rt*) of the pedicel cuticle, penetrating into the cone socket

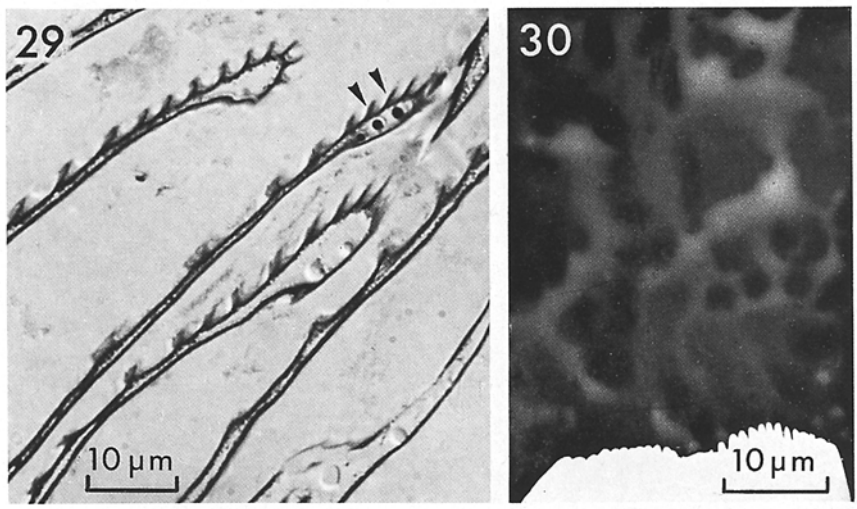


**Fig. 29.** Stained (*arrow*) and unstained droplets in the scent scale lumen (methylene blue; longitudinal semi-thin section, interference contrast)

**Fig. 30.** Tip of the scent scale, leaving behind a trace of oily substance on a coated grid. TEM (print of an internegative)

Formvar coating of the grids when they are moved by thermal effects of the electron beam (Fig. 30). Even in two month-old males this impregnation can be found, which might be due to the fact that no scent consuming behavior had occurred.

The hairs of the wing pencils opposite to the scent organs have pores, which are larger and arranged more densely in the distal half (Fig. 6) than along their bases.

## Discussion

### *Secretions and Secretory Process*

In the scent organs of male Caligo eurilochus (Fldr.) several secretory products of different appearance have been found. Some products are not gland specific but also occur in the neighboring hypodermal cells. Moreover, the age dependent and spatial occurrence of the secretions within the scent organ gives a better understanding of the secretory process. The dense homogeneous secretions are restricted to the gland cells. They are supposed to consist of identical material (perhaps a lipid), despite their different forms and size. In the 6.5 and 8 h specimens the synthesis of this substance seems already to be completed; the dense material was found only within vacuoles of the apical cell region. The granules are discharged already soon after emergence. From the bases of the niches in the brush border, they enter into the supraglandular space

(Figs. 18–20, 31). They seem to leave no membranous remnants behind when expelled from the cell (Figs. 20, 21), but only vacuoles. Such vacuoles were very common 6.5 to 8 h after emergence. In the 2 and 18 day-old specimens only few dense granules were found in the cell and around the microvilli, but the dense mass in the center of the supraglandular space, which was absent in the young specimens, could well be a confluence of these dense granules (Fig. 15). The possibility of such a change is indicated by the dissolving of the dense mass into granules in the upper pedicel lumen.

It can not be decided whether the droplets in the scale lamina and the oily impregnation are different substances or only different stages of the same material. Both materials may be derived from dense granules. Two types of scale droplets can be distinguished by virtue of their different staining characteristics (Fig. 29), and thus might also be different in nature or represent the same substance changing in form by chemical conversion.

The loose material in the supraglandular space of the gland cell and the small hypodermal cells is possibly a mucous substance. It is attached to the tips of the microvilli and thus reminds one of the "antennular glycocalyx" (Fawcett, 1967; Bennett, 1969), which according to Bennett is generally mucous in microvillar cell borders. Such a loose extracellular material may still be produced after emergence, as it becomes denser within the more aged males. The globular granules, which also occur in both cell types, have never been observed extracellularly. They might be the precursor form of the loose extracellular secretions. Their quantity is also increased in the adults.

Although the electron dense microvillous tips and the attached "glycocalyx" are a common occurrence, the interpretation of the interdependence and function of both structures is unclear. Locke (1969) discussed the microvillous "plaques" with regard to transport and assembly of cuticular precursor material or determination of the orientation of the completed microfibers in cuticle formation. In the Caligo gland cells dense microvillar tips could be found in a continuous arrangement with the dense cell membranes of the basal microvillar clusters (Fig. 19) in the secretory niches. The dense membranes arising from the niches may have similar properties as the dense tips and may help in the transport and orientation of secretions from the releasing vacuoles towards the center of the supraglandular space. This may be indicated by the thin layer of a "glycocalyx" spread continuously over the dense cell membrane of the secretory niche and the microvillar tips.

Another interpretation is a direct secretory function of the microvillar membrane. Comparable amorphous dense material attached to the membranes of the "Faltensaum" in the pheromone cells of Bombyx females is supposed to be a lipoid, secreted directly from the "microvilli" surface after passage in their central channels (Waku and Sumimoto, 1969). These central channels are regarded as a part of the smooth endoplasmic reticulum (Quennedey, 1969, 1971).

As the microvilli contain axial filaments and show variable orientation in relation to different ages, active positional changes and movements can be assumed. An active transport function of the microvilli has not been considered in insect gland cells so far (Noirot and Quennedey, 1974; Pliske and Salpeter, 1971; Quennedey, 1969; Steinbrecht, 1964). It is discussed, however, with respect

to insect cuticle deposition by Neville and Luke (1969) and suggested by Locke (1969). The "undisturbed" regular appearance of the brush border in Caligo after 18 days, when secretory activity has ended, may support the idea of a transport activity of the microvilli during secretion.

The different types of secretion found in Caligo scent organs do not allow a decision as to which secretion contains the odor efficient molecules, expected to be only a minimal portion of the visible substances (Steinbrecht, 1964; Waku and Sumimoto, 1969). The dense homogeneous substance, which could be traced from the cell into the scent scale pedicel, probably represents the main portion of the extruded secretions. It is suggested to have a carrier function and to produce the oily scale impregnation.

In this connection the "ball" of vesicles above the outlet of the scale pedicel deserves some attention. It has its definite size and form already in the 6.5 h specimen and persists throughout the entire lifetime. The vesicles might be remnants of the scale forming cell, which normally degenerates at the end of the scale development (Stoßberg, 1938). The trichogen cells of the hair pencil in young adults of Danaus, however, persist and become gland cells (Pliske and Salpeter, 1971). The "ball" vesicles could possibly be some kind of secretion, which is produced in an earlier age than that of the examined specimens; but could also be a degenerative element. Since many "ball" vesicles still show some granular contents in the 18 day-old specimen, it must be a rather stable product. We speculate that it could be some kind of secretory deposit, lying at exactly the site where all further secretions such as the presumed carrier substance must pass by.

### *Cuticular Structures of the Scent Organ and Mechanism of Secretion Discharge*

The wing scale pencil of Caligo males was already mentioned by Müller (1877) and the corresponding abdominal scent pads by Stichel (1909). The microanatomical investigations of the scent organ have revealed an unknown type of construction and allow reconstruction of its mode of operation. The most interesting functional part of this organ is the coneshaped elastic socket. Its elasticity is due to the interior aqueous substance, providing it with the mechanical characteristics of a water cushion. The high content of water in the inner socket "cuticle" is deduced from its property to shrink by air drying. In fact, only the stabilizing rods seem to prevent a complete collapse. In fixed and freeze-dried sockets the outer cuticle remains smooth, but the interior of the cones is empty except for the rods. In the living, turgescent condition the sockets are supposedly elastically deformable by pressure of the wing-pencil-area against the actively protruded scent pads. As the furrows around the socket bases are deeper at their posterior side with a thinner cuticle and the anterior side is better stabilized by the thick asymmetric rod, it is presumed that the sockets can be bent backwards. In this position the soft socket floor would be pressed inwards and reduce the supraglandular space. The consequence would be that the dense secretions, which are deposited at the entrance of the scale pedicel (see above and Fig. 31), are extruded into the scale pedicel. It is not clear

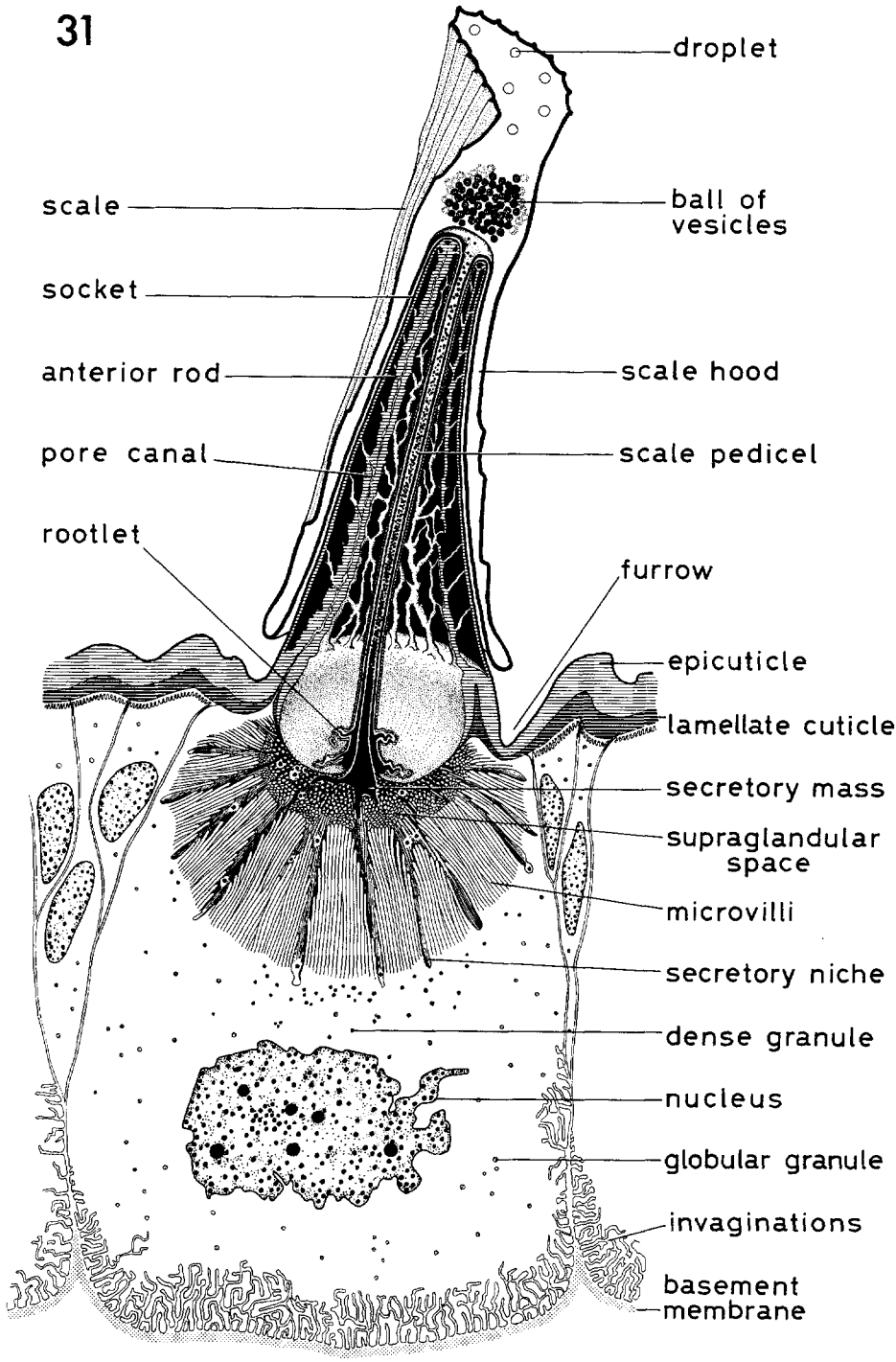


**Fig. 31.** Semi-schematic view of one unit of the scent scale organ, showing the passage of the secretions. The loose secretory substance filling the supraglandular space and the aqueous ground substance of the cone socket are omitted

whether the "ball" of vesicles, which always could be found exactly above the outlet of the pedicel, is a distinct secretion or simply a degenerative by-product (see above). The position and structure of the "ball" would be appropriate for soaking up the secretions, which have left the pedicel outlet under pressure of the socket. A flowback of all secretions into the basal pedicel, when the pressure ceases under the relief of the socket, would thus be prevented. The impregnations stored in the "ball" could then pass into the scale by capillary force.

The firm but tension-free anchorage of the scent scale and the large rest upon the socket by the hood can be understood as adaptations to the mechanical strain during depletion.

The distribution of the secretions within the scale may happen by capillary force of the wick-like scale cuticle. The hairs of the wing pencil could then be impregnated by the secretions when touching the scent pads. The cuticle around the scent pads as well as the wing area with the hair pencil is smooth, and thus the capillary distribution of secretion is restricted to the scent apparatus. The scales of the hair pencil possess pores like other scent scales, which receive substances indirectly for distribution (Birch, 1970; Clearwater, 1975; Grant and Eaton, 1973). The hair pencils are supposed to produce no additional own secretion, because no enlarged cells were found at their bases.

The role of scent in the behavior of Caligo is still unknown (see above). Territorial recognition behavior among males, as is described for Ithomiine butterflies (Pliske, 1975) might be considered in addition to a stimulatory function in courtship display.

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