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THE PTILINAL ARMATURE OF FLIES (DIPTERA, SCHIZOPHORA)[1]

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Abstract

The ptilinum of schizophoran flies usually is described as a simple protrusible bladder, the function of which is that of bursting the puparium immediately prior to the escape of the adult. A few observers had, however, recorded that it may be provided with scalelike projections. An examination of the ptilina of approximately 150 species of flies, representing 40 families, indicates that these scales are a characteristic of all schizophoran families. Many of these are described and their structure is compared. Nearly all of the extreme variations can be correlated with similar structures on the proboscis of a conopid. In the majority of families, they are very small and usually conform rather closely with four major types which merge into each other. Exceptions to this general rule occur in certain genera in widely separated families which include Ephydridae, Tetanoceridae, Anthomyidae, and Tachinidae. The action of the ptilinum in recently emerged Calliphoridae indicates that its armature of scales may render it an effective digging organ and that these flies employ it energetically for this purpose. With it, *Cyanomyia cadaverina* Desv. can remove the smoked surface from a block of plaster of Paris. Extreme scale development occurs on the ptilina of those genera of Tachinidae in which the adults escape from subterranean earthen cells of phalaenid hosts. Their heavy sclerotization may be completed in the pupa several weeks before the adult normally emerges. They are relatively about ten times as long as are those of many related genera. Among field-captured specimens many show that a high percentage of the scales on the upper and lower surfaces of the ptilinum have their apices missing, indicating extensive abrasion as the fly scraped its way through the consolidated earthen cell of the host. From their armature, it appears that the buccal bladders at the anterior base of the rostrum may, in certain families, assist in effecting an escape.

Introduction

The first published record regarding the ptilinum of schizophorous Diptera appears to have been that of Réaumur (11) in 1738. He correctly ascribed to it the universal function of assisting the adult to escape from the puparium by its intermittent expansion and contraction.

Though several subsequent writers have discussed the structure of the ptilinum of individual species of flies, few have suggested that it is capable of performing anything other than that of rupturing the puparium by simple pressure. It is, in fact, most frequently referred to simply as a "protrusible bladder" or words to that effect.

In 1911, Knab (7) drew attention to the fact that, as early as in 1863, Becher recorded that the ptilina of *Musca*, *Calliphora*, *Lucilia*, and *Sarcophaga* spp. are beset with "lozenge-shaped scales". Despite this, subsequent investigators do not appear to have attached much importance to a possible

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use for these structures. Knab, however, also quoted Reising to the effect that newly emerged Tachinidae use their ptilina to "push obstacles out of the way" after their escape from the puparia, though he did not elaborate upon how this is accomplished.

In 1916 Graham-Smith (2) stated that recently emerged *Calliphora erythrocephala* distend their ptilina in order to "obtain a purchase against neighboring particles", thus suggesting an appreciation of a possible use for the scales. Jobling (6), who carefully figured the ptilinal scales of *Glossina palpalis*, states, simply, that the pulsation of the ptilinum helps the fly to pass through earth and decaying humus.

Laing (9), in a valuable contribution on the development and the function of the calliphorid ptilinum, paid particular attention to its musculature. She described and illustrated the scales, which she termed "spinules", but did not discuss their possible function. Neither the word "scale" nor "spinule" describes the varying forms in which these structures occur in different Schizophora. In the interests of brevity, the earlier designation, "scale", is here adopted to cover all types.

How universal these are on ptilina and the extent to which their structure may vary are matters which do not appear to have been given much attention. Imms (5), in his *Textbook of Entomology*, states that the "ptilinum is roughened owing to the presence of minute scales or spines of various forms". Hendel (3), in the *Handbuch der Zoologie*, describes them as *often* beset with "chitinige Dörnchen". Other recent textbooks to which we have referred still give a reader the impression that the ptilinum is a simple smooth-walled bladder. In the most recent treatise on the ptilinum which we have seen, Atkins (1) mentions their occurrence in *Drosophila melanogaster* Mg. but does not suggest that they might be put to any use. They are, admittedly, much smaller and more indefinite in this family than is usual and, in comparison with others, can probably be correctly described as "degenerate".

Our attention was drawn to them in a series of the tachinid *Bonnetia compta* Fall. which, some years previously, had been reared from the subterranean cells of a phalaenid, *Agrotis orthogonia* Morr. One specimen had failed to retract its ptilinum before it was killed and "pinned". The powerful black spurlike scales on this could not fail to attact the attention of an unaided eye (Fig. 7).

This led to an examination of the ptilina of representatives of all schizophoran families available in the University of Alberta collection. Practically every one of nearly one hundred and fifty species, representing about 40 families, possessed scales. These, normally, are so closely crowded together over the entire ptilinal surface that they overlap. Exceptions occurred in certain of the ephydrids and tetanocerids in a few species of which they were completely suppressed. In the only coelopid available to us the small, almost circular, scales are rather widely scattered.

We feel, therefore, justified in concluding that the ptilinum of all Schizophora normally is densely clothed with an armature of scales.

The Origin of Ptilinal Scales

Künckel d'Herculais (8) demonstrated, in 1875, that the ptilinum is identical in structure with the rest of the body integument. Laing, in studying its larval and pupal development in *Calliphora*, confirmed this but showed that, subsequent to emergence, the underlying epidermis, and much of the chitin itself, disappears.

An examination of the epicranium reveals that scales frequently extend, from the ptilinum, over much of its surface. Of considerable interest is the fact that in certain families, of which Conopidae is a good example, they extend, chiefly in the connective membrane, right to the apex of the proboscis. Along its course, they change in structure in such a manner that they conform with nearly all of the variations which we have found on the ptilina of the different schizophoran families that we have examined (Fig. 1).

Furthermore, similar scales are of widespread occurrence on the integument, particularly in association with connective membrane, throughout the Arthropoda. Their structure embraces a wide variation of which, it appears, the villi on the wings of many insects are an example. Laing and others have established that the ptilinal scales are merely excrescences of the cuticle.

In addition to the cuticular scales, the ptilina of representatives of every family examined possess some 14 or more simple setae scattered over their surface. Each can be seen to arise through a circular pore in the cuticle from the underlying epidermis of recently emerged flies. In certain tachinid species, there appeared to be at least 50 setae. Whether or not these have a sensory function was not established. Usually they do not project upwards for much more than the average length of individual scales. Rarely, as in a helomyzid, *Suilla nemorum* (Fig. 31), though they are of normal size over the greater part of the ptilinum, they gradually lengthen towards its dorsal margin, near which they are produced into a row of elongate pigmented bristles.

Material and Methods

Practically all of the material examined consisted of pinned specimens from the University collection. Recently emerged calliphorids and tachinids, examined before the ptilinum had been permanently withdrawn, revealed no external structures which differed from dried material.

For the preparation of microscope slides, heads were removed and were boiled for a minute or two in 10% potassium hydroxide. Following this treatment it is sometimes possible to extrude the ptilinum by forcing water or air into the head through a fine glass tube inserted in the occipital foramen. This method, however, is not suited to microscopic examination and, owing to the extreme thinness of the "mature" ptilinum, it is not often successful. It is, however, readily accomplished in recently emerged and untreated adults. In such cases, permanent mounts can be made by employing the technique used in inflating larvae (Fig. 6).

Dissection of potassium hydroxide treated heads is a practical alternative in preparing microscope slide mounts. This was most satisfactorily accomplished

in a drop of water on the slide on which the permanent mount was to be made. The eyes were first removed with a scalpel fashioned from a razor blade chip. The proboscis was then cut off, as was the posterior half of the head. After living adults had been observed attempting to escape through glass it was realized that the proboscis should have been retained. Its "buccal bladders" frequently are armed with powerful scales which, in the species which possess them, probably play some part in effecting an escape. What now remains is the front of the head, less the eyes, from the vertex to the oral margin. If it is turned over, the relative volume of the retracted ptilinum can be observed, whether it hangs down medially (Fig. 11) or is simply "bunched up" behind the suture.

On account of its hemispherical shape, the ptilinum cannot be flattened out and it must be cut or torn in order that much of its surface may be examined.

What is left of the epicranium is, therefore, turned face up once more, the frons is bisected by a vertical cut to the frontal suture, and, unless the lower ends of the latter extend to the genal angles, they are continued by vertical cuts to the severed margin of the epicranium. At this time, it is advisable to flood the specimen with 96% alcohol since this reduces, but rarely entirely overcomes, the tendency for the ptilinum to double back on itself when traction is released. The severed halves of the *frons* are now pulled apart resulting in the dorsal half of the ptilinum tearing along its median line to its apex. Two further floodings with 96% alcohol suffice to remove sufficient water for the preparation to be mounted by the addition of a drop of diaphane just before the last of the alcohol has evaporated (Fig. 2).

This technique is satisfactory for preparing the majority of ptilina for examination though it can be approximated only in the case of very small species. Unfortunately, the ptilina of a few species are so extremely fragile that they tear into small pieces under the most careful manipulation. In these cases, fragments only can be examined.

Variations in the Size and the Structure of Ptilina

In the majority of families, particularly among the Acalyptrata, the ptilina are moderately uniform in size and, when distended, they occupy about the same depth from front to back as does the head itself. Those of Conopidae, despite the fact that the frontal suture is unusually short and extends downward to less than one-third the distance from the bases of the antennae to the genal angles, are voluminous and represent the most "rugged" type of ptilinum which we encountered. Their texture is reminiscent of chamois leather. We could not expel them through the suture with occipitally applied pressure and they were too wrinkled in all of our preparations for us to be able to measure their dimensions with any accuracy. Their size was unexpected since, on other characteristics, these flies are usually considered to have closer affinities with the aschizan Syrphidae than has any other schizophoran family.

Dissections of several species of Syrphidae failed to reveal any structures which could, by any similarities, be homologized with a ptilinum, a frontal suture or a frontal lunule. Künckel D'Herculais (8) asserted that, while escaping from their puparia, Syrphidae strongly inflate their frontal region, and cause a small bladder to appear. He stated, however, that all traces of this disappear before the adult is ready to fly. It is certain that, in the syrphid species which we examined, there were no suggestions of ptilinal scales in the sparse connective membrane of this area. It is most unlikely that these would disappear completely after the emergence of the adult had they ever been present. The nearest approach to them were very small short comblike scales on the membrances of the antennal fossae. Becker, according to Knab, denied a ptilinal function in Syrphidae while Laing failed to demonstrate ptilinal muscles in this area.

In other families, with the exception of certain Tetanoceridae, a few Ephydridae and Hippoboscidae, the frontal suture extends nearly, but rarely quite, to the genal angles. In most of the Tetanoceridae the suture is horizontal and lies almost entirely above the antennae. It bends downwards, slightly at the most, at its ends. In some genera, however, it is perfectly normal and the ptilinum is fully developed whereas, in the majority, it is reduced to a mere ribbon which, though armed with an unusual type of flattened scale (Fig. 28), must, surely, be nonfunctional. Attempts to inflate this with occipital pressure merely caused it to bulge outward slightly. In the genus *Sepedon*, the narrow ptilinal area is as heavily sclerotized as is the rest of the epicranium; it is a flat exposed sclerite which is completely devoid of scales (Fig. 10).

In the majority of Ephydridae, despite the greatly swollen face, the ptilinum is normal in development and in armature. In a small group, of which *Ochthera* and *Parydra* are examples, the suture resembles that of the Tetanoceridae, though the ptilinum is voluminous and is armed with a very unusual type of scale (Fig. 25).

Hippoboscidae possess narrow ribbonlike ptilina, which, in this respect, resemble those of some Tetanoceridae. Their scales are, however, of a very different type (Fig. 50).

The greatest relative ptilinal size was encountered in a helomyzid, *Anorostoma currani* Garr. (Fig. 11), though that of *Gasterophilus intestinalis* de G. is almost as large. In many species examined, the retracted ptilinum lies in a crumpled arc-shaped mass immediately behind the suture. In *A. currani*, however, it assumes somewhat the shape of a mushroom of which the stout "stem" is free and projects downwards between the antennae almost to the oral margin. Intermediate stages between these extremes are not uncommon.

Since all of the ptilina here discussed were boiled in 10% potassium hydroxide before examination, they consisted only of such of the cuticle as had been retained at the time of capture. Laing (9) indicates that the underlying epithelium is never robust and that it, with its ptilinal muscles, degenerates soon after the emergence of the adult. In *Calliphora erythrocephala* she finds that the cuticle itself undergoes a marked dissolution. Three

days after emergence it has been reduced in thickness from 25 μ to 5 μ, while, by the 15th day, only the finest layer which connects the bases of the scales remains.

We do not know the individual ages of many of the pinned specimens which we examined but were impressed by the unusual thickness of the cuticle in the ptilina of all Conopidae in comparison with its extreme fragility at the other end of the series, as represented by Tachinidae. Here, it may be almost invisible and is so thin that it is almost impossible to flatten it on a slide without dismembering it. This reduction is even more pronounced in the anthomyid genus *Fannia*, in all species of which it appears to be reduced to the extremely fine layer of cuticulin from which the scales arise.

In individual species of many of the families which were examined, scales, resembling those on the ptilinum, extend from it to additional areas of the epicranium. These occur most frequently on the frons where they may extend to the vertex on either side of the ocellar triangle. They differ from those on the ptilinum chiefly by their tendency to fuse together into compound rods.

Observations made on recently emerged *Cyanomyia cadaverina* and *Phormia regina* during their attempts to penetrate glass with their ptilina proved that, in these flies, the frons functions with the ptilinum at this time. It retains its flexibility and ability to expand until a normal escape has been effected, after which it is contracted longitudinally and becomes sclerotized as part of the inflexible epicranium. Such, however, is not the case in an agromyzid, *Agromyza angulata* Lw. (Fig. 9). In this and other related species, the transparent ptilinum is armed with unusually powerful black scales. These extend, without change in disposition or structure, on to the permanently flexible and transparent frons and reach the vertex on either side of the heavily sclerotized ocellar triangle. It is evident that, in these flies, the two areas constitute a single functional unit of very unusual dimensions.

Scales may also extend from the ptilinum to the frontal lunule and thence down the face as a narrow band between the antennae. This, frequently, widens below the fossae of the latter to cover much of the area between them and the oral margin. In several genera in which the frontal suture does not attain the genal angles, additional scales flare out from its ends and cover much of the genae themselves.

Particularly among many of the smaller species of Acalyptrata, an independent development of scales so heavily arms the rostral membranes that they have every appearance of serving some function. They are particularly well developed on the so-called "buccal bladders" (Fig. 9, *d*). Though these are almost unarmed in Calliphoridae (Fig. 4) they are occasionally pressed by these flies against, and forced in a downward direction over, a glass obstruction which the fly is attempting to penetrate.

Variations in the Structure of Ptilinal Scales

By far the most prevalent types of scales encountered in the species of the 40 families which were examined look, in side view, much like rose thorns (Fig. 1). From above, however, these scales appear as flattened blades of which the outline varies sufficiently for them to be likened to three major types. These can be roughly described as resembling a wheat, barley, or oat grain, respectively.

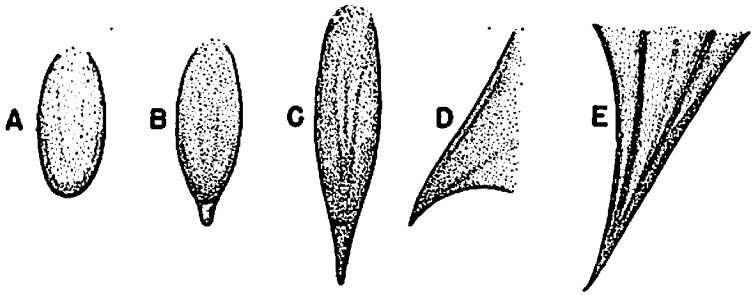


FIG. 1. Normal ptilinal scales (diagrammatic). A, B, and C upper views to types 1, 2, and 3, respectively. D. Side-view of an average 1-3 type. E. Type 4, which varies much in length and degree of attenuation; this type is frequently confined to the median areas of the ptilinum.

Type 1

Approximately twice as long as wide, with a rounded apex.

Type 2

Resembling 1, but the apex is pointed to a varying degree from an obtuse angle through a stout tapered spine to an elongate bristle.

Type 3

Three to five times as long as wide, apex acute and occasionally produced into a spine of varying length or diameter.

In all of these types, the base tends to contract, but it may be parallel-sided or, less frequently, flaring.

Without exception, the apices of all of these types of scales are directed upwards and backwards, i.e. towards the vertex, on the upper half of the ptilinum, and downwards and backwards on its lower half. The change in direction occurs along a transverse belt, of which the width includes about half-a-dozen scales. This "equatorial" area passes through or just below the ptilinal apex (Fig. 6). At the apex itself, the scales are usually reduced in size, are vertical, and somewhat mammiform in appearance. Laterally in this belt they tend to be directed outwards. As will be realized later, during a discussion of their function, this disposition is well suited to their purpose.

Type 4

Any of the above types may merge through intermediate forms into conical structures the sides of which are reinforced by about six deeply pigmented

"rods". Usually this type, which is not often encountered in the "earlier" acalyptrate families, is interspersed with the more normal armature only on certain areas of the ptilinum, which are more frequently median than otherwise. In only a dryomyzid species were the majority of scales of this type. Typically, they are only slightly diverted from a vertical position on whatever part of the ptilinum they occur. It appears, however, that the greatly enlarged scales which are developed (Figs. 48 and 49) on the "working" surfaces of certain tachinid ptilina have been derived from this type of scale. These are numerous and are semirecumbent.

In color, scales vary from unpigmented through light yellow to dark brown, or through gray to opaque black. No reason for the second variation in pigmentation was deduced, though in certain species, there was slight evidence that the grayish pigmentation increased with the age of the individuals. Tachinid scales, if greatly enlarged, are always of the very dark-brown color which is associated with powerful sclerotization on other parts of the body, such as at the tips of the mandibles. Around the periphery and near the apex of these ptilina the scales are not enlarged and may be entirely unpigmented. This suggests that in these flies, these relatively immense "working" scales possess an unusual ability to withstand abrasion and that, whenever this color predominates, it is associated with this characteristic.

For purposes of comparison with a number of other types of scale, it is assumed that type 1 or, possibly, type 2, represents the basic pattern from which, through a variety of modifications, other types, which less frequently occur on the ptilina of different flies, have been derived. In so doing, it is realized that there may be little justification in assuming one type to be more "primitive" for ptilina than any other. Its occurrence is, however, by far the most widespread and it is very rarely entirely replaced. Furthermore, approximations to this type can be found in the connective membrane, or other structures, of very diverse representatives of Arthropoda. Those on the cheliceral shields of the tick *Amblyomma americana* Koch. are almost identical with it though they are more recumbent. Similar scales occur in the connective membrane associated with the maxillae of cockroaches and between the tarsal joints of certain grasshoppers. In the beetle *Harpalus caliginosus* Fabr. many maxillary scales resemble type 2, while some approach type 4.

An examination of the entire ptilinum of all species of flies reveals some variation in the outline and relative size of the scales on different areas of its surface. In many, for example, they are smaller and more blunt with a tendency to fuse longitudinally in the downward extensions of the frontal suture; in others they are more strongly developed medially than they are laterally, while in all the reversal of direction at the apex is, normally, accompanied by a shortening in length of the individual scales and a tendency for a higher percentage of type 4 scales to occur here than elsewhere. Unless such variations are marked, the scales are described as "uniform". Where illustrations have been made, individuals which are of the average size and shape have been selected unless otherwise stated.

Action of the Ptilinum

The action of the ptilina was observed in two species of Calliphoridae; *Cyanomyia* (*Cyanomyopsis*) *cadaverina* R.D., and *Phormia regina* Mg. Puparia were placed in cells consisting of short lengths of glass tubing, of which the inner walls were lined with fine emery paper in order to provide a purchase for the ungues and the dorsocentral bristles. The puparia were held in place, at about half their length from the tops of the cells, with plugs of cotton. The cells were closed above either with clear cover glasses or with plaster of Paris caps of which the lower sides were either smoked or painted black. All covers were held in place with adhesive tape.

Laing (9) describes and illustrates the internal points of attachment of important ptilino-oesophageal muscles along the anterior portion (equatorial region) of the ptilinum. Over this the scales are small and, near its center, are vertical. As already stated, all scales are directed towards the vertex above this region and towards the oral margin below it. When an escaping calliphorid attempts to penetrate glass, the ptilinum, normally, is partly inflated and pressed firmly against the glass with this area withdrawn. This brings the centers of the upper and lower surfaces of the ptilinum together along its infolded margins. A more powerful inflation follows, during which the muscles gradually relax. This relaxation causes the entire upper and lower surfaces of the ptilinum to scarify the obstruction as the tips of the opposing scales are forced apart. Thus, the "working" surfaces of the ptilinum are confined chiefly to the upper and lower median areas. Fig. 3 illustrates the ptilinum of a calliphorid which was inflated before the muscles had disintegrated. It shows a partial withdrawal of the "equatorial region" as a result of a slight contraction of these muscles. In life, at the inception of its withdrawal, five points of muscular attachment are plainly seen along its length as small temporary depressions. In this species, this region is slightly below the morphological apex of the ptilinum whereas in the majority of flies it appears to pass through it.

As can be seen in the photograph (Fig. 4), the partial inflation of the ptilinum is accompanied by a great distension of the buccal bladders. In Calliphoridae these are armed only with relatively weak villuslike scales. They were, however, occasionally brought against the glass with the result that the final inflation of the ptilinum forced them downwards over its surface. This action appeared to be more accidental than purposeful. The shape of the cell, however,—a cylinder with a flat smooth top—is unnatural. Observations made upon species in which the bladders are as heavily armed as is the ptilinum itself may reveal, under more normal conditions, a definite employment of these structures in assisting the escape of the fly.

In an unobstructed emergence, the ptilinum undergoes a series of pulsations for a period of up to about ten minutes before it is permanently withdrawn. It would appear that these pulsations may be essential for the removal of small particles of foreign matter which become lodged between the scales

(Fig. 7). When, however, emergence is obstructed, ptilinal activity may persist intermittently for several hours and it ceases entirely only when the weakened fly approaches the point of death from exhaustion.

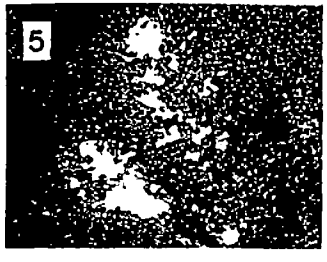
The activities of a *C. cadaverina* which was watched continuously for the greater part of a day exemplify, in general, those of a number of specimens which have been under observation. This burst its puparium at some time between 9.00 a.m. and 9.30 a.m. As soon as it made contact with the glass it explored its surface with its fully distended ptilinum. The apex was then withdrawn and the "scarifying" activity was initiated. This was repeated over and over again. In the early stages of expansion minor, apparently exploratory, pulsations suggested an attempt to engage the scales in something that would give a purchase. After about two hours of fruitless endeavor, the glass surface was seen rather suddenly to be bathed in a copious liquid. Michl, as quoted by Knab (7), states that occasionally *Muscina stabulans* will rupture its ptilinum in its efforts to penetrate paper. Nothing so drastic was observed in *C. cadaverina* or in *P. regina*. Later observations, made upon *regina*, showed that this fluid is liberated through the pseudotracheae. In one fly, three large drops were seen in rapid succession to cover the labellae. Extreme activity caused this liquid to flow over the entire head, including the ptilinum, and thence to the obstruction. Only about 50% of the flies under observation employed this liquid and usually only after an hour or so of fruitless endeavor, though one did so only four minutes after it reached the glass. No attempt was seen to place the liquid directly on the obstruction. Its liberation in no way reduced subsequent ptilinal activity though its employment was not observed to occur more than once during lengthy attempts to escape.

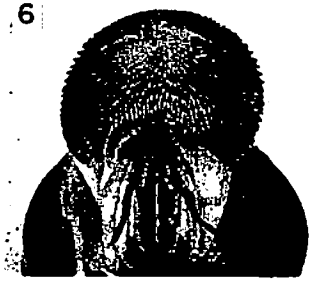
After approximately three hours of constant activity, the fly appeared to suffer from temporary exhaustion. During a half-hour rest, the only continuous movement was a slight and regular pulsation, at exactly one-second

FIG. 2. Muscid (*Musca domestica* L.) ptilinum exposed by technique described. Some tearing has occurred in flattening, a defect that is less liable to occur with more "rugged" types. FIG. 3. Calliphorid (*Phormia regina* Mg.) head, with ptilinum partially inflated to show a slight retraction of the apex as a result of muscular contraction. Prior to an attempt to penetrate on obstacle the apex is completely withdrawn, thus bringing together the centers of the upper and lower ptilinal surfaces. The photograph is of an artificially inflated, and dried, ptilinum, which is somewhat less completely dilated than it may be in life. FIG. 4. Calliphorid (*Phormia regina* Mg.) head with buccal bladders distended. Preparation as above. FIG. 5. Smoked surface of plaster of Paris ×16 after an emerging *Calliphora cadaverina* R.D. has attempted to penetrate it with the aid of its ptilinum. The structure of the plaster probably has been weakened during smoking since similar scarifying did not occur when *Phormia regina* Mg. attempted to penetrate plaster painted with India ink. FIG. 6. Tachinid (*Gonia* sp.) ptilinum artificially inflated and dried. This specimen, dissected from a mature pupa, shows that the scales are fully sclerotized before the adult escapes from the puparium. A narrow "equatorial band" of reduced and vertical scales passes through the ptilinal apex. FIG. 7. Portion of the ptilinum of a tachinid (*Bonnetia compta* Fall.), killed as soon as it emerged from its host's pupation cell, showing particles of sand lodged among the enlarged scales.

All photographs taken by the courtesy of Prof. Brian Hocking.

PLATE I





intervals, of the apex of the frontal lunule below the almost completely withdrawn ptilinum. This was accompanied by a gradual lateral contraction of the frons followed by a rather sudden relaxation at 15 sec. intervals. Activity was now resumed with increased intensity. At times, a portion of the ptilinum would enter a small crevice between the tube and the cover glass. This resulted in what can be described only as "frantic" struggling, followed, invariably, by a careful re-exploration of the rest of the surface with the fully distended ptilinum, of which the apex was now expanded, prior to the resumption of a major effort to escape. These efforts usually lasted for about 30 to 45 min., each followed by somewhat longer periods of almost complete inactivity. During the afternoon, activity became steadily less violent, while the ptilinum assumed an increasingly opaque yellowish coloration. This stage was accompanied by lateral contractions of the hitherto relaxed frons which, temporarily, reduced it to about its normal diameter. By 5 p.m., i.e. about eight hours after emergence, the epicranium showed definite signs of sclerotization and the "leathery" ptilinum appeared to be incapable of further distension. This contrasted with the ptilina of adults which made a normal escape. In all of these, the ptilinum was readily distended, up to at least three days after emergence, by the simple expedient of squeezing the abdomen.

One inexplicable variation in this procedure occurred in a male *P. regina*. In every fly it was seen that the blood, when first forced into the ptilinum, is clear. After about a half-hour of strenuous activity there is an increasing abundance of what appear to be small aggregates of cells suspended in it. These we assume to be haemocytes, possibly with the function of fat body. With the pulsation of the ptilinum they can be seen, passing from the median ventral region of the head through the buccal bladders, to and from the ptilinal cavity. In this specimen, however, they were accompanied by bubbles of "gas". These could be seen, through the still transparent thorax, to be welling upwards along its dorsal wall. During periods of reduced activity those still in the thorax moved with a pulsating motion which, apparently, was induced by the heartbeat. The "gas" was so abundant that it almost completely replaced the blood in the ptilinum and filled the anterior end of the thorax to such an extent that cell aggregates could be observed, high but not dry, held to its wall by a film of blood. Since only an anterior view of the fly was possible the origin of this gas could not be ascertained. Within half an hour of our having first observed these bubbles, the thorax became too opaque for further observation and the ptilinum was permanently withdrawn. In this connection it may be recalled that Réaumur is reported to have stated that the ptilinum is inflated with gas. Possibly he was not so universally incorrect as subsequent observers have assumed. All of this activity, including pigmentation, had occurred in less than two hours from the time that the fly emerged from its puparium. Other flies, which fail to escape, remain unpigmented for at least 24 hr. Four hours after emergence this fly was liberated. It was fully pigmented and normally active though it failed to expand its wings.

The Penetrating Capability of Ptilinal Scales

At the time of writing there has, unfortunately, been no opportunity to ascertain the "digging" power of ptilina in which the scales are abnormally large. Fig. 49 shows the relatively enormous scales on the ptilinum of a tachinid of which the adult normally escapes from the earthen pupation cell of a phalaenid moth. This, surely, must be capable of penetrating far more resistant obstacles than is possible to the majority of flies. In August, 1952, Mr. Jacobson, of the Dominion Entomological Laboratory at Lethbridge, very kindly provided us with a number of pupae of *Agrotis orthogonia* Morr. which contained the puparia of a species of *Gonia*. This tachinid is univoltine and we have failed to break its pupal diapause in the laboratory.

Experiments in which calliphorids were obstructed by plaster of Paris while escaping from their puparia indicated that *C. cadaverina* was capable of making some impression on this material with its ptilinum. Fig. 5 is a photograph of the abrasion which, apparently, was produced by a *cadaverina* in its attempts to penetrate plaster the surface of which had been smoked by holding it over burning xylol. It is probable that the consistency of the plaster had been somewhat broken down by heat during the smoking since, though several of the smoked surfaces showed definite signs of abrasion, nothing comparable could be observed when the plaster was painted with India ink.

From the table of the relative sizes of ptilinal scales in different flies, page 291, it will be seen that those of *cadaverina* are rather below the average but, from the systematic manner in which it "scarifies" an obstruction with them, we are of the opinion that the marked variation in their size in different flies may be an important factor in determining the locations in which individual species can pupate with prospects of successful adult emergence.

Variations in the Structure of Scales on a Conopid Proboscis

Although, with minor variations, the scales on the majority of ptilina are very similar in structure, one or two remarkable exceptions were encountered. These appeared to bear little relationship with the more usual types. It was, therefore, of particular interest to find that, on the proboscis of the conopid, *Zenilla furcillata* Will. (Fig. 8), there is a progressive modification from the "normal" type of ptilinal scale to several of the others which, occasionally, predominate on the ptilina in certain families.

Immediately ventrad of the upturned oral margin a frontal view reveals two large membranous areas, one on either side of the sclerotized clypeus. These, when dilated, constitute the buccal bladders. In Conopidae, the entire rostral membrane is clothed with scales. Over much of the basoanterior region, i.e. on either side of the clypeus, these are of the normal type 2 of many ptilina and are directed downward. Laterally, along the margin of the oral orifice, they turn outward and develop short black tubercles along what is now their ventral side. Meanwhile, the "body" of the scale becomes progressively more narrow and its dorsal side more indefinite until it resembles a comblike structure with from 3 to 12 downwardly directed teeth. This type

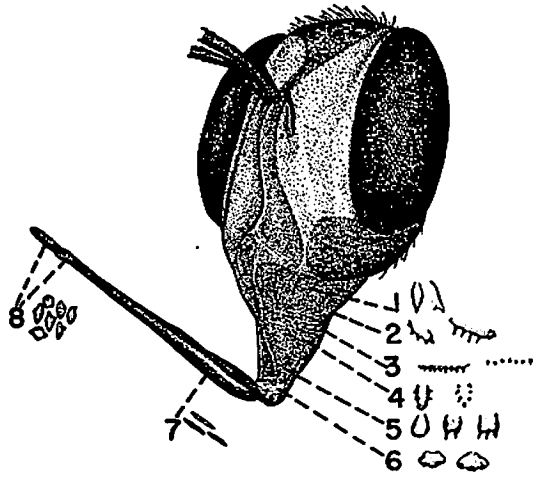


FIG. 8. Conopid (*P. furcillata* Will.) head showing transition of normal ptilinal-like types of scales on proboscis membranes to unusual types found on ptilina of certain families. 1. Normal type 2 scales. 2 and 3. Transition comblike scales degenerating to "villi" posteriorly as on certain ephydrid ptilina. 4. Degeneration of scales to villi in a manner not observed on any ptilinum. 5. Scales with widened or split apices resembling those on chamaemyid ptilina. 6. Reduction of split apices to tubercles as seen on ptilinal apices of certain Agromyzidae. 7. Narrowed tuberculate scales resembling those near genae of chamaemyid ptilina. 8. Flattened scales resembling somewhat the ptilinar scales of certain Tetanoceridae.

of scale covers most of the posterior side of the rostrum but, near its lower end, the "body" frequently disappears completely leaving only a row of minute black spots the majority of which bear a central, very short to rather elongate, unpigmented spine. Similar comblike scales or their residua of black spots constitute the only type of armature present on the ptilina of certain Ephydridae (Fig. 25).

More anteriorly, many scales develop black spurs along both sides and the disappearance of the "body" in these cases leaves a residuum of small clusters of black spiniform spots. Similar structures have not been observed on the ptilina of any flies.

Immediately adjacent to the clypeus the scales tend to sink to the general membrane level and to become more polygonal owing to the widening of the apex. Near the lower end of the rostrum the apex frequently splits into two or more fairly elongate spurs. A similar modification is found among the ptilinal scales in Chamaemyidae (Fig. 26). At the junction with the haustellum they are very irregularly polygonal and are usually armed with from two to four short upwardly directed tubercles. Similar scales occur near the apex of the ptilinum in certain agromyzid species (Fig. 21).

The labrum is unarmed but the rest of the haustellum bears very narrow elongate scales each with a single series of small black spiniform tubercles

throughout its length. Similar structures were observed only on the ptilinum of a chamaemyid, where they were confined to the genal ends of the suture. Near the apex of the haustellum, as well as on the upper surface of the labellae, these scales widen out once more into apparently flattened polygonal structures which, however, in side view are seen to bulge outward in the center. Somewhat similar scales occur on the ptilina of many Tetanoceridae (Fig. 28).

In one species of Conopidae, *Myopa vicaria* Walk., the labellar scales are circular with a central short spur or spine similar in structure to those on coelopid ptilina (Fig. 30).

Comparisons Between the Ptilinal Scales of Schizophoran Families

Conopidae

General

In all species examined the frontal suture is very short and narrow (Fig. 8). It extends downwards only to about one-third the distance from the base of antennae to the genal angles. Despite this, the ptilinum is voluminous and is more "rugged" in texture than is that of representatives of any other family which we have examined. The scales are very closely crowded and they overlap over the greater part of the ptilinum.

Conops fronto Will. Scales type 1. Normal; unpigmented.

Physocephala furcillata Will. Fig. 12. Scales very deeply pigmented with brown. They are so crowded near the center of the ptilinum that this area appears to be completely black under the binoculars and it contrasts strongly with the cream color of the bordering epicranium. Laterally, they are type 1, but medially, particularly on the lower half, the base develops bluntly pointed processes which give their outline somewhat the appearance of holly leaves when viewed from above. The lateral view, however, retains its normal rose-thorn outline. The unpigmented short ptilinal setae are unusually conspicuous since each arises from a transparent pore which, at first glance, resembles a pinprick in the otherwise blackened ptilinum.

Physocephala texana Will. Closely resembles *P. furcillata* though the scales are light yellow in color.

Myopa vicaria Walk. Fig. 13. Scales type 3, with apex produced into a moderately long, highly refractive spine; unpigmented. Under a low microscopic magnification the entire ptilinum appears to be "hairy" owing to the high refraction of both sides of these spines.

Zodion fulvifrons Say. Scales type 2, with a short blunt apex; unpigmented.

Otitidae (Ortalidae)

General

The frontal suture reaches the genal angles, but the ptilinum within its lower ends is partly sclerotized and the scales fuse together into heavily sclerotized rods.

Seioptera vibrans L. Fig. 14. Scales chiefly type 1, varying to 2; unpigmented. They extend to the face between the antennae and tend to fuse to elongate ridges at its center though they separate into a patch of individual scales just above the oral margin.

Chrysomyza demandata Fall. Very similar to *S. vibrans* though the scales are confined to the ptilinum.

Eurycephalomyia myopaeformis V.R. (*Tetanops aldrichi* Hend.). Fig. 15. Scales type 2, apices of those on lower half of the ptilinum produced. Though this species pupates below ground, the scales are small and very light yellow in color.

Trupaneidae (Trypetidae)

General

In three genera examined, the ptilinum is voluminous and it hangs as a median fold internally to about opposite the end of the second antennal joint. The suture is evanescent before the genal angles and its contained ptilinum is lightly sclerotized from about level with the apices of the antennae. Scales are chiefly type 3, with a slightly produced apex. They are closely crowded and overlap.

Epochra canadensis Lw. The very light yellow scales are uniform over the entire ptilinal surface.

Rhagoletis pomonella Walsh. As above with somewhat wider scales.

Eurosta solidaginis Ft. (Fig. 16) and *E. comma* Wd. Scales as above except that they are distinctly yellow and, surrounding the ptilinal apex, where as is usual they are mammiform and reduced in size, there is a wide band of flat scales which are widely flared basally. Their apices are frequently divided into two or three rather shorter spines. The scales on this area impart to it a most unusual "imbricated" appearance. In so far as we are aware, all flies of this genus escape, as adults, from stem-galls.

Pallopteridae

Palloptera jucunda Lw. Scales type 2, apex stoutly tapering; unpigmented to very light yellow. They continue medially on the face to below the antennal fossae where they fuse to form rods. The membranes of the fossae, also, are rather copiously armed with type 2 scales above but, below the antennae, they merge through a mammiform to a horizontal type somewhat resembling those on the conopid proboscis (3, Fig. 8).

Lonchaeidae

Lonchea polita Say. Fig. 17. The majority of the smoky-black scales are type 1 or 2. Medially, on the lower half of the ptilinum, they are transformed to type 4. The suture extends to the genal angles where the contained ptilinum remains membranous though, here, the scales are united to form long rods on which, from near the apex of each component scale, arises a long black bristle. A narrow band of scales extends on the face from the lunule to the oral margin. Only between the antennae do they fuse to form rodlike structures. The membranes of the antennal fossae possess a few transverse scales. The buccal bladders are densely clothed with a mammiform type with an elongate dark-brown central bristle.

Tanypezidae

Tanypeza luteipennis K. & S. Fig. 18. The majority of the light yellow scales are type 2 with an acuminate apex. On the lower half of the ptilinum their bases flare. Scales extend to the vertex as simple rods whereas, on the face, they extend to the oral margin as individual, though connected, scales.

Calobatidae

Cnodacophora nasoni Cr. Normal type 1 to 2 light-yellow scales over the ptilinum but fuse in the downward extensions of the suture, which terminate shortly below the antennal fossae.

Micropezidae

Micropeza lineata V.D. Despite the unusual shape of the head, the ptilinum is normal and extends to the genal angles. The unpigmented scales are chiefly type 1 but, near the equatorial region, many are widened and resemble somewhat the bracts of a pine cone.

Piophilidae

Piophila affinis Mah. Scales type 1, rather longer than in related families; almost unpigmented.

SEPSIDAE

General

The ptilinum is voluminous and somewhat pendulous when withdrawn.

Nemopoda cylindrica Fab. Scales type 1 to 2. The latter tend to be produced into a refractive apex resembling that of *Myopa vicaria*, Fig. 2; very lightly yellow pigmented. On the face, a narrow band of hardly modified scales extends to the oral margin.

Themira putris L. Fig. 19. The dark-brown to gray scales are not very uniform, chiefly type 1 but elongate towards the upper end of the ptilinum with a tendency to fuse to compound rods. Above the antennae they are bractlike. Compound rods similar to those on the ptilinum extend on the face to the oral margin.

LAUXANIIDAE (SAPROMYZIDAE)

Camptoprosopella borealis Shew. Scales type 2, apex hardly produced; almost unpigmented. Ptilinum of normal size though the suture extends only about halfway to the genal angles.

Miniella lupulina Fab. Scales vary from type 3 with an acuminate apex to a type 4 which closely resembles that of a dryomyzid, Fig. 32. All are "delicate" and are rather poorly defined; faintly pigmented with brown. The suture does not extend to below the lower margins of the antennal fossae and the ptilinum is unusually narrow. Its brown setae are stout and prominent.

DROSOPHILIDAE

General

The ptilinum is relatively small and the scales are very poorly developed in comparison with related families. With the possible exception of *D. funebris*, it would appear that the weakly sclerotized irregular areas which represent the scales over the greater part of the ptilinum cannot perform any useful function.

Drosophila funebris Fab. The light-yellow scales are moderately well developed. The majority are of type 1, tending to become club-shaped near the genal angles. This species pupates below ground.

Drosophila melanogaster Mg. Fig. 20. Over the greater part of the ptilinum the outline of the scales is poorly defined, though each appears to terminate in a fine spine. Laterally and near its upper margin they are more regularly conical with an acuminate apex while in the downward extensions of the suture they are irregularly club-shaped with a tendency to fuse near the genal angles.

Drosophila buscki Coq. The scales over the entire surface of the small ptilinum are even more fragile and irregular than they are in *melanogaster*. They resemble weakly developed examples of the type found on the ptilina of certain Tetanoceridae, Fig. 28.

ASTEIIDAE

Asteia multipunctata Sab. Scales type 2, widened basally and with a long tapering apex; delicate and unpigmented. Unlike *Drosophila*, they are well-developed and are similar over the entire surface of the ptilinum. Almost identical scales heavily invest the antennae but are not present elsewhere on the epicranium.

OPOMYZIDAE

Anthomyza tenuis Lw. Scales type 2, similar to *Asteia* but rather wider and less clearly defined. Those on the antennae are spiniform.

AGROMYZIDAE

General

A number of the species examined possess a large ptilinum with heavily sclerotized scales. Since these are better developed on the median area than they are laterally it would appear that they may perform a definite function.

Though the majority of species are believed to be leaf-miners the fact that several pupate below ground may have some bearing on the fact that these small flies possess scales which are far better developed than are those of their close relatives.

A feature which appears to be unique to this family is the complete suppression of sclerotization on the frons in a number of species. This is associated with the development of powerful separate scales on this area. Among the species examined, this tendency was not particularly apparent in *Agromyza perpusilla* Mg. but was increasingly so in *A. artemesiae* Kalt., *A. pusilla* Mg., *A. neptis* Lw., and *A. dubitata* Mall. It reached its climax in *A. angulata* Lw. (1, Fig. 9) and *Disygomyza lateralis* (2, Fig. 9). In these two species, the frons is completely membranous and lacks a distinct demarkation between it and the ptilinum which therefore extends as a perfectly transparent membrane to the vertex on either side of the ocellar triangle which, in addition

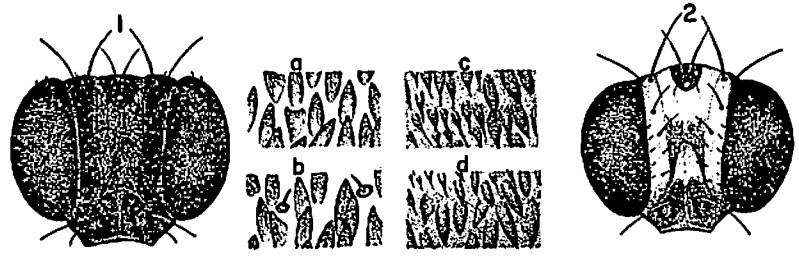


FIG. 9. Agromyzidae. 1. *A. angulata* Lw. "Ptilinum" extends as a heavily scaled transparent membrane to the vertex. *a*. Scales on the permanently flexible frons. *b*. Scales and setae on the ptilinum. *c*. Scales on the partly transparent but rigid lunule. *d*. Scales on the partly pigmented buccal bladders. All scales are drawn at a magnification of ×500. 2. *D. lateralis* Mg. (*A. coquilletti* Mall.) Black ptilinal scales extend about half way on the transparent and flexible frons to the ocellar triangle. Reduced and unpigmented scales extend almost to the vertex. Though the parafrontia are unpigmented, they are rigidly sclerotized.

to the parafrontia, acquires its normal sclerotization. In *A. angulata* the ptilinal scales extend, without interruption or change in structure, to the vertex whereas in *D. lateralis* they are much reduced in size and lose their pigmentation at a short distance below the ocellar triangle. In both species the dorsal and lateral boundaries of this membranous area are sharply defined and it is evident that it is, functionally, part of the ptilinum.

Agromyza dubitata Mall. (Fig. 21) and *A. neptis* Lw. Both appear to be very similar with heavily sclerotized blackish-gray scales chiefly of type 2, with tendencies towards type 4. A rather lightly pigmented band covers the "equatorial" region of the ptilinum. Where this passes through its apex the scales are much widened basally and have their apices separated into from two to about four short blunt teeth. They thus closely resemble the scales on the conopid proboscis (6, Fig. 8).

Surrounding this area a number of scales are asymmetrical. The frons is partially sclerotized and its scales are fused into compound rods.

Agromyza angulata Lw. Fig. 22. Scales type 3, with tendencies towards type 4, unusually large medially where they are dark gray to almost black. Those on the completely transparent frons are black and of type 3 (1*a*, Fig. 9). There is a slight reduction in their size

near the vertex. The sclerotized ocellar triangle and the parafrontia carry a normal complement of delicate "villi". The large sclerotized frontal lunule (1*c*, Fig. 9) and the antennal joints are heavily armed with black, type 2, scales, while the centrally pigmented buccal bladders, also, are armed with brown type 2 scales, which are almost as well-developed centrally as are those of the ptilinum. Around the edges of the bladders they are reduced to a weak villiform type (1*d*, Fig. 9). Webster and Parks (14) state that this species attacks timothy grass leaves and pupates in the mine that it has produced.

Disygomyza lateralis Fab. Scales type 1 over most of the ptilinum but type 2 in the lateral sutural grooves. Several of the latter have their apices divided. The frons is as completely membranous as it is in *A. angulata*, but the black scales lose their pigment before, and become evanescent at about, the apex of the ocellar triangle with the result that a transparent membrane extends on either side of it to the vertex. In untreated examples of this species the head, with the exception of the triangle and the antennae, is white when viewed from in front. Just above the frontal suture, however, it is marked with very fine grayish irregular longitudinal lines which are, in fact, the dark "ptilinal" scales of this area (2, Fig. 9). Webster and Parks (14) record this species under the name *Agromyza coquilletti* Mall. as mining in the basal leaves of volunteer wheat and oats.

Pseudonoapomyza atra Mg. Scales of normal size, chiefly type 1; uniform and gray in color. Frons only partly sclerotized as in *A. dubitata*.

Phytagromyza orbitalis Mel. Scales of normal size, chiefly type 1; brownish-gray. Consistencies of the frons and scales resemble these characters in *A. dubitata*.

Phyllomyzidae

General

The ptilina and their armatures vary so much in the few species supposedly belonging to this family which are available to us that some doubt arises as to whether they are correctly associated.

Pholcomyia indecora Lw. The scales are rather large, chiefly of type 2 with an acuminate apex; rather dark gray-brown; heavily sclerotized. The ptilinum is voluminous and is pendulous medially when withdrawn. It reaches to about the apices of the antennae. The partly sclerotized frons resembles that of *Agromyza dubitata*.

Anthomyza sp. Scales small, poorly defined, many somewhat truncate-cone to club-shaped with an elongate terminal bristle; very lightly sclerotized and unpigmented. Frons partly sclerotized; surface longitudinally wrinkled.

Desmometopa latipes Meig. Scales very similar to *Anthomyza*, as is the frons though it is more heavily sclerotized.

Desmomyza confusa Curr. Scales well-defined, type 2, uniform; majority light brown-yellow with scattered individuals more deeply stained. All are heavily sclerotized. The frons is very heavily sclerotized throughout and is sharply differentiated from the ptilinum.

Chloropidae

General

Nothing unusual was observed in any of the species examined. The scales are small, poorly developed, uniform type 2 with apex produced; practically unpigmented.

Thaumatomyia glabra Mg. Scales not contracted basally. Though this fly pupates below ground the scales appear to be very weak.

Meromyza americana Fit. Almost identical with *T. glabra*.

Oscinella frit L. Fig. 23. Scales somewhat more contracted basally than in preceding species and relatively larger. Similar scales cover the buccal bladders but, posteriorly, on the rostrum, they become comblike.

Ephydridae

General

Despite the greatly swollen face of many species, the ptilinum and its armature usually is normal. It extends within the frontal suture to the genal angles.

In one group, however, comprising *Ochthera*, *Parydra*, and some others, neither the ptilinum itself nor its armature in any way resembles that of other families which we have examined. Taxonomically, they do not appear to be closely associated with the other genera which are included in this family.

Ephydra millbrae Jones. Scales normal type 3 with a tendency to flare basally and with the apex somewhat produced; dark gray. The equatorial region shows as an unusually light transverse band.

Paracoenia turbida Curr. Fig. 24. Scales type 3 terminating in a long, stout, spine. Heavily sclerotized, dark brown. Immediately above the antennae they are much dilated and many are nearly circular behind the apical spine.

Ochthera mantis DeG. Fig. 25. The frontal suture is transverse and is not produced downward laterally. In this respect it resembles members of the family Tetanoceridae. In dried specimens it appears to continue downward, rather close to the inner eye margins, before bending inwards to the genal angles. This furrow, however, is completely sclerotized and inflexible. The ptilinum terminates abruptly at its upper end in a series of rodlike sclerotized folds.

The somewhat voluminous and intensely wrinkled ptilinum is armed on its dorsal third with transversely elongate comblike gray scales, armed on their upper margin with about twenty powerful dark-brown teeth. They somewhat resemble the comb scales on the posterior base of the conopid proboscis (3, Fig. 8). Over this area, the wrinkling of the ptilinum is, for the greater part, transverse. At the equatorial region, wrinkling is more irregular and the scales, as such, disappear though the teeth occasionally persist as a few scattered black tubercles on the ridges of the ptilinal folds. This parallels the disappearance of the similar scales on the conopid proboscis. The ventral half of the ptilinum is most irregularly and intensely wrinkled in a manner reminiscent of the convolutions of a mammalian brain surface. Very rarely do the summits of the folds bear one or two black tubercles. The entire ptilinum is lightly stained with brown.

Parydra nitida Cr. The disposition and structure of the ptilinum closely resemble that of *O. mantis* but it is completely devoid of scales. The summits of the wrinkles are very finely crenulate.

Borboridae

Borborus equinus Fall. Scales light yellow, chiefly a wide type 2, except in the downward extensions of the suture where, in contrast, they become unusually elongate with a tendency to fuse together to form yellow sclerotized rods.

Clusiidae

Clusiodes melanostoma Lw. Scales type 2, base not contracted, apex produced to a long bristle; unpigmented and delicate. Resemble Chloropidae.

Chamaemyidae

Chamaemyia polystigma Mg. Fig. 26. The moderate sized, light brown scales vary in shape on different areas of the ptilinum. Nowhere have they a regular "grain"-shaped outline. Over the greater part of the ptilinum the apex is bifurcate or trifurcate; laterally on the dorsal surface they are reduced in size and are mammiform with a long apical bristle. Ventrally, the lateral scales are enlarged and fuse together to form elongate structures of which the component scales retain their spinelike apices. At the genal ends of the suture they are reduced to spiniform rods resembling those on the haustellum of a conopid (7, Fig. 8). On the median area above the antennae the apical bristle is reduced or absent and the apices of many scales are widened and obliquely truncate.

Tetanoceridae (Sciomyzidae)

General

Earlier observers have drawn attention to the fact that representatives of this family, generally speaking, possess only a transverse frontal suture above the antennae which lacks lateral extensions towards the genal angles. There is, however, a wide variation in this character among the representatives of different genera. In *Melina* the suture almost reaches the genal angles and it contains a normally voluminous ptilinum. In *Tetanocera* it terminates just below the lower margins of the antennal bases and the ptilinum is moderately voluminous. It appears to be capable of normal evagination. The scales,

for the greater part, are modified into irregular plates with a stout, frequently elongate, central spur. In *Limnia* and *Hadroneura*, however, the suture terminates above the antennal bases and is only slightly arcuate above them.

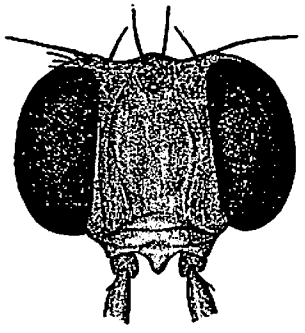


FIG. 10. Tetanoceridae = Sciomyzidae. (*S. fuscipennis* Lw.) All species of the genus *Sepedon* which have been examined are devoid of a ptilinum. It is replaced by a rigid transverse sclerite above the biarcuate frontal lunule.

Here, the ptilinum is ribbonlike and is only slightly invaginated. Water pressure, applied through the foramen, hardly bulges it outwards. The scales vary in development. The most extreme modification is exemplified in flies of the genus *Sepedon* (Fig. 10). These possess *no* ptilinum. The permanently exposed "ptilinal" area is smooth, rigid, and flat. It holds the narrow transverse suture open as a sclerotized area connecting the frons with the transverse frontal lunule.

Melina (*Pherbellia*) *schoenheri* Fall. Fig. 27. Scales normal, chiefly type 1 to 3, merging to type 4; almost unpigmented. Though the downward extensions of the suture reach the genal angles, the ptilinum is flexible for only about one-third of these extensions below the bases of the antennae. This is, however, not uncommon in other families. Type 3 scales, which tend to fuse near the genal angles, clothe the sclerotized portions.

Melina nana Fall. is similar but the scales are brown.

Tetanocera valida Lw. Fig. 28. Though the suture extends only to the center of the antennal fossae the ptilinum is moderately voluminous and is armed over most of its surface with irregular unpigmented scales of which the bases, when viewed from above, resemble rather closely placed pieces of a jigsaw puzzle. In side view the majority appear to be subconical while the apices of those near the median margins of the ptilinum are produced into stout semirecumbent spurs.

Limnia saratogensis Fit. Fig. 29. The subarcuate transverse suture terminates laterally above the level of the antennal bases. Its ribbonlike ptilinum is armed with mammiform scales which are produced to moderately long central spines. Dorsally these unpigmented scales are wide basally and they overlap; ventrally their bases tend to be quadrate. Over the narrow equatorial region they are of the jigsaw puzzle type as in *T. valida*, though they become comblike laterally.

Hedroneura rufa Panz. The ptilinum is even narrower than is that of *Limnia* and it appears to be armed throughout with jigsaw puzzle type of scales which are very weak and perfectly flat over the greater part of its area.

Sepedon armipes Lw. and *S. pacifica* Cr. In common with three other available species (Fig. 10) of this genus, the permanently exposed ptilinal area is as heavily sclerotized as are the neighboring areas of the epicranium. It is smooth and shining. By transmitted light, subtransverse darkened areas are visible, but there is no suggestion of scales.

CHRYOMYIDAE

Trixoscellis fumipennis Mall. Scales, type 1; unpigmented. The suture nearly reaches the genal angles. Nothing abnormal.

PSILIDAE

Pseudopsila perpolita Joh. Scales chiefly narrow type 3 with the apex of many produced into a fine spine; unpigmented. The ptilinum extends to the genal angles. Nothing abnormal, though the ptilinum is rather larger than in related families.

COELOPIDAE

Coelopa frigida Fab. Fig. 30. All of the scales are nearly circular and mammiform; they are only slightly deflected from a vertical position above and below the ptilinar apex. They are moderate closely crowded except in the area across the "equatorial" region where they are separated by more than their own diameters.

HELOMYZIDAE

General

Although in *Suilla* and *Neoleria* the ptilinum is rather more voluminous than usual, it assumes a transverse position within the head when retracted. In *Anorostoma* and *Helomyza*, it is relatively enormous and it extends, as a median fold, almost to the oral margin (Fig. 11 *a*). A distended *Anorostoma*

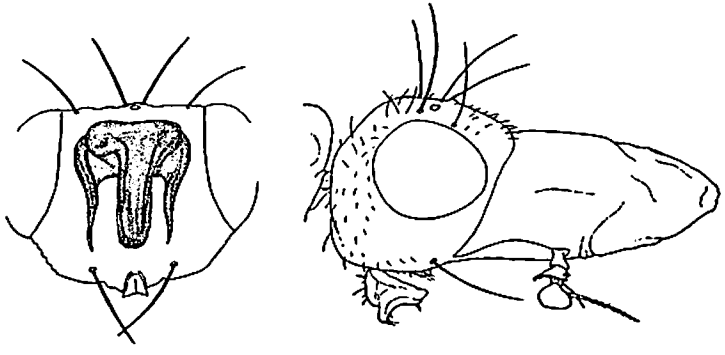


FIG. 11. Helomyzidae. (*A. currani* Garr.) An example of the largest ptilinum seen on any fly. Other species in this family equal it in size but this is rarely approached in those of other families. As seen from behind after removal of the back of the head and almost fully extended from a potassium hydroxide treated head.

ptilinum is conical and, even when slightly collapsed, is nearly one and a half times the length of the head (Fig. 11 *b*). The finely wrinked frons rarely bears traces of scales. They usually are well-developed on the face, particularly between the antennal sockets.

Suilla nemorum Mg. Fig. 31. Scales, type 2 tending to fuse near the upper end of the ptilinum; almost unpigmented. Similar fused scales occur on the lunule and extend between the antennae to below their bases. The most remarkable feature of the ptilinum is its setae. Over the greater part of its surface they are colorless and of a normal size but they gradually increase in length and pigmentation towards its upper margin near which they are transformed into a row of about six excessively long bristles which are about five times the length of the average scale.

Neoleria fuscolinea Garr. Resembles *S. nemorum* but with less tendency for scale fusion while the dorsal setae are less than half as long.

Anorostoma marginata Lw., *A. currani* Garr. and *Helomyza serrata* L. Apart from the unusual size of the ptilinum there is nothing abnormal. Scales, type 1 tending to become somewhat truncate apically and to fuse together near the upper ptilinal margin; almost unpigmented.

DRYOMYZIDAE

Neuroctena anilis Fall. Fig. 32. Nearly all of the scales are type 4, with a bristlelike apex sharply differentiated; rather uniform structurally over the greater part of the ptilinum though, around its periphery, they tend to revert to type 2 with a long apical bristle. The frontal suture extends to only a short distance below the antennal fossae but the ptilinum is of normal volume.

CORDYLURIDAE AND SCOPEUMATIDAE (SCATOPHAGIDAE)

General

In both families the frontal suture extends at least to the vibrissae and is filled to its extremities with flexible unsclerotized ptilinum. The scales are uniform, chiefly type 3 with a tendency to approach type 4 medially on the ptilinum. The frons is armed, at the most with very weak scales, they may, however, be well-developed on the frontal lunule.

Cordilura confusa Lw. Scales medially brownish-black, laterally yellow becoming pigmentless at the extremities of the suture. The frontal lunule is heavily armed with a mammiform type of scale.

Achaetella varipes Walk. Scales longer and more tapered than in *Cordilura*. The suture is longer and the lunule is completely bare.

Scopeuma stercorarium L. Resembles *Cordilura* with more crowded scales which are lightly pigmented on the upper third of the ptilinum in marked contrast with the dark gray-black scales which cover the rest of it. In addition to lunular scales, the antennal fossae of some specimens possess remarkably strongly developed scales on the antennal fossae membranes. These resemble types 5 and 6 of the conopid proboscis.

Scopeuma furcatum Say. resembles *stercorarium* but all scales are uniform yellow in color.

ANTHOMYIDAE

General

Species representing two or more genera of each of the major subfamilies, which have very varied larval habits, were examined. Three types of scales were observed, the most unusual being confined to the genus *Fannia* (Fig. 33). Ptilina in some subfamilies are uniformly more fragile than they are in others. Typically, the frontal suture reaches or exceeds the vibrissae but in the majority of species the ptilinum is sclerotized from about half the distance between them and the antennal fossae. Scales invariably extend to the vertex as composite rods. True scales were not seen on the face, but the buccal bladders, usually are weakly armed.

(Phaoninae). *Bigotomyia houghi* Stn. The fragile ptilinum is voluminous and pendant medically when withdrawn. The scales are type 2 to 3 with tendencies to approach type 4. They are evidently heavily sclerotized and are of an almost opaque brown color. In two specimens examined the apices of several scales were missing which suggests that the fly escaped from a subterranean puparium. We have, unfortunately, no information regarding the biology of this species.

Phaonia basiseta Mall. Resembles *houghi* though the scales are smaller and less heavily sclerotized. No sign of abrasion of the apices was observed.

(Mydaeinae). *Helina barpana* V.d.W. and *Mydaea discimana* Mall. Scales rather longer than in Phaoninae with more of type 4. These predominate on the lower half of the *discimana* ptilinum; brown-black in color but apparently not very heavily sclerotized.

(Hydrotaeinae). *Ophyra leucostoma* Wd. Scales shorter than in Phaoninae and rarely overlapping, predominantly type 4 medially; not heavily sclerotized; light brown. The scales on the frons and lunule are unusually powerful; reduced in size, they also extend on the face to the oral margin. The buccal bladders are densely clothed with strong mammiform, centrally spined, scales.

(Fanniinae). *Fannia scalaris* Fab., *serena* Mg., *postica* Stn., *canicularis* L., *spathiophora* Mall., and *howarti* Verr. Fig. 33. The scales of all are practically identical and are quite unlike those of any other anthomyid genus examined. Over the greater part of the ptilina they are of a compound "comb" type with from about three to eight elongate spiniform teeth. On the upper median area of the ptilinum they break down to singly spiniform scales. The color varied in different species from light yellow to gray.

Demarcation between the ptilinum and the lunule is indefinite, but the former folds downward for a short distance below the latter and, here, it is sparingly wrinkled longitudinally and is completely devoid of scales. The ptilinum is extremely fragile and it breaks into fragments too readily to permit its being flattened. It is, however, sclerotized in the suture from about opposite the antennal bases, below which point the scales form continuous spiniform rods.

Azelia gibbera Mg. Though this genus is included in the Fanniinae, the scales are normal type 1 to 2, lightly pigmented brown but not heavily sclerotized. The ptilinum is more voluminous and stronger than in *Fannia*. In two specimens examined there were faint lateral ptilinal stains resembling those of *Hylemyia antiqua*, Fig. 36.

(Lispinae). *Lispe salina* Ald. Scales all appear to be type 2 and tend to fuse together. They are very heavily sclerotized and crowded.

Lispe nasoni Stein. Fig. 34. The heavily sclerotized median scales are all of a type 4 which approaches the shape of the enlarged median scales of certain Tachinidae. All, however, remain small and no sign of abrasion to their apices was observed in the specimens that were examined.

Incidentally, it was observed that these flies possess extremely large prestomal teeth, a characteristic shared by all genera of Coenosiinae and, to a less extent, Limnophorinae. Hobby (4) has recorded that a number of European Cordyluridae and Anthomyidae are predaceous on various flies, and Perron and Lafrance (10) recently observed adults of *Coenosia tigrina* F., one of the species recorded by Hobby, feeding on adults of the onion maggot in Quebec. From the development of the teeth on the proboscides of every species that we have examined in these three subfamilies, it would appear that all are capable of predatory activities.

(Limnophorinae). *Lispocephala alma pallipalpis* Zett. Fig. 35. Over the greater part of the ptilinum the scales are of type 2 to 3, with or without a somewhat produced apex. All are rather heavily sclerotized. Above the antennae, however, there is a rather large and plainly differentiated patch of smaller, more slender and transparent type 2 scales, each armed with a long apical spine. The prestomal teeth are smaller than in *Lispa* spp.

Limnophora tetracheata Mall. and *Lasiops melanderi* Hall. Similar to *pallipes* but types 2 and 4 scales appear to be similar in structure through the ptilinum, which is bare in the fold above the lunule as in *Fannia* spp. Ptilinum very fragile.

(Coenosiinae). *Coenosia cilicauda* Mall. and *anthracina* Mall. Scales deep gray-black, type 3, apex slightly produced, a few approach type 4. The rather long-triangular frontal lunule is sharply demarked from the ptilinum which is wrinkled and bare along its margin.

(Anthomyinae). In this subfamily, only, are the scales light yellow to unpigmented and all are of types 1 to 2 with a few merging to type 4. The ptilinum is noticeably more robust than it is in other subfamilies.

Hylemyia antiqua Mg. Fig. 36. The transparent scales are typical type 1 to 2, with a few merging into type 4. To a varying degree a lateral area, which underlies about 50 scales on each side of the ptilinum, is stained from a light to a deep opaque brown. Around its edges, detached dark areas underlie individual scales but, in the center of each area, the entire membrane is uniformly stained.

Hylemyia cerealis Coq. Resembles *antiqua* but with only a light median staining above the lunule.

Pegomyia connexa Stn. Resembles *antiqua* but scales are yellow and show a greater tendency to be transformed into type 4.

MUSCIDAE

General

All species examined possessed normal type 1 to 2 scales with little tendency to be transformed into type 4. The frontal suture terminates opposite to or well above the vibrissae, but the ptilinum is usually sclerotized on the lower half of the face. The frons is armed to the vertex with rodlike structures obviously derived from fused scales. The face is unarmed, while the buccal bladders usually carry rather well-developed mammiform scales.

Musca domestica L. Fig. 37. Scales dark gray, not suggesting heavy sclerotization; types 1 and 2, with tendencies towards 4. They are densely crowded on the whole of the ptilinum except at the apex. The ptilinum is only moderately robust. Rods of "fused" scales extend on the frons to the vertex.

Muscina stabulans Fall., *Stomoxys calcitrans* L., and *Lyperosia irritans* L. are all similar to *domestica* though the scales are slightly longer and are definitely more heavily sclerotized. They are largest in *irritans* and tend to fall into diagonal rows with a higher frequency of type 4, while the bare wrinkled area immediately under the lunule, which was first observed in *Fannia* spp., is pronounced in *stabulans*.

Orthellia caesarion Mg. The type 3 scales are more slender in proportion to their length than are those of the preceding genera and, though of a gray color, they appear to be less heavily sclerotized.

GASTEROPHILIDAE

Gasterophilus intestinalis deG. Fig. 38. Scales small, type 1; evanescent basally, unpigmented. They are extremely numerous over the entire ptilinum, overlapping slightly laterally and for about one-third of their length. The ptilinum is very large and it hangs downward when at rest much as does that of the helomyzid illustrated in Fig. 11. The frontal suture terminates indefinitely at about the lower level of the eye-margins but the genae, with the intervening membranous "buccal" area, are almost completely clothed with unmodified "ptilinal" scales. It is estimated that there must be approximately 150,000 of them on the entire area.

CALLIPHORIDAE

General

In all species examined, with the exception of *Pollenia rudis* in which it reaches almost to the vibrissae, the frontal suture terminates at about halfway between the antennal fossae and the vibrissae. Scales, however, continue beyond its ends and flare outwards over much of the genae where they tend to fuse together. They extend, also, on the frons to the vertex, again with a tendency to fuse. The face is scaleless, though the buccal bladders may be moderately heavily armed with small mammiform scales. The majority of ptilinal scales are of type 2 with tendencies to vary to other normal types. There is a varying degree of scale fusion on the ptilinum itself. The latter is moderately robust, of a medium size, and is always stained brown near the extremities of the suture.

Phormia regina Mg. Fig. 39. At the time of emergence, the scales are unpigmented, but they turn to yellowish-brown after a few hours. At this time, the ptilinum is moderately strong and could be readily inflated. Among captured specimens classified as this species there was some variation. In the most extreme case, as illustrated, the blackish scales over much of the ptilinum were fused into compound rods and the ptilinum was unusually thin. Possibly the latter characteristic is correlated with the age of the individuals though similar variations have not been observed in other species.

Protophormia terra-novae R.D. Scales gray, majority type 2, merging to 1 medially. Laterally there is a slight tendency to scale fusion.

Cynomyia (*Cynomyopsis*) *cadaverina* Desv. (Fig. 40) and *Calliphora vomitoria* L. Scales type 2 to 3, with a distinct tendency to approach type 4 laterally; bases tending to flare basally; rather more refractive than are those of other species; light gray to brown. Normal.

Pollenia rudis Fab. Scales uniform type 2 to 3; dark gray; ptilinum sclerotized from about halfway between the antennal fossae and the vibrissae. Though these are parasites of earthworms the scales are not larger than are those of cadavorous species.

SARCOPHAGIDAE

General

The ptilina and armament closely resemble those of Calliphoridae. The chief difference is that, in all species examined, the suture extends to a point about opposite to the vibrissae and its contained ptilinum is membranous and unpigmented to its extremities. Despite differences in larval habits, the ptilina and their scales are very uniform. Among the latter, type 2 predominate

with a varying tendency to type 4 medially. There is a marked tendency for them to be laid down in diagonal, slightly overlapping, rows. Separate or fused scales extend on the frons to the vertex, but not on the face. The buccal bladders bear numerous, but weak, "villi".

Sarcophaga Pherminieri Desv. Fig. 41. A dung inhabiting species. The medium-brown scales are relatively smaller and more numerous than are those of species which parasitize grasshoppers.

Sarcophaga nearctica Park. Supposedly sarcophagous; scales as in *Pherminieri* but darker in color.

Sarcophaga (*Kellymyia*) kellyi Ald. and *S.* (*Protodexia*) *hunteri* Hgh. Grasshopper parasites. The ptilina are relatively more voluminous than they are in the larger species while the scales may be, in actuality, slightly longer with less tendency to be transformed to type 4.

Wohlfahrtia opaca Coq. A myiasis producing species. The light brown scales are normal type 1 to 2; possibly more approach type 4 than in *Sarcophaga*. The ptilinum is stained in the somewhat abbreviated lateral sutures.

Agria affinis Fall. Rhopaloceran parasite. The dark brown scales are less crowded than they are in other genera.

METOPIIDAE

Metopia leucocephala Rossi. Fig. 42. Bee parasite. Scales chiefly type 1, relatively larger and distinctly wider than in Sarcophagidae. The medium-brown scales are rather densely crowded on the voluminous ptilinum which, also, is stained a light brown.

CUTEREBRIDAE

Cuterebra tenebrosa Coq. Fig. 43. Despite the unusually large size of this fly, the ptilinal scales are relatively small; chiefly of type 2 merging to type 1 laterally and to type 4 medially. The upper surface of the majority of scales is stained to a dark brown but the central support is seen, in side view, to be unpigmented. They are uniform in size throughout the ptilinum but, medially, a few tend to assume in shape the modified type 4 which predominates in certain tachinids. The ptilinum is unusually large, its volume being due more to lateral development than to its length. The rather contracted frontal suture extends to the level of the antennal apices and it is completely filled with flexible ptilinum.

HYPODERMATIDAE

Hypoderma lineatum DeVil. Fig. 44. The scales are gray and the majority are type 2 but they vary considerably in shape and size on different areas of the ptilinum. They are largest medially where their bases are unusually flaring. A scattering of individuals are abnormally enlarged in the area bordering the ptilinal apex on which, as is usual, they are reduced in size. Many taper rather asymmetrically from base to apex. Laterally, they are less crowded than they are elsewhere, are smaller, and less deeply pigmented. The ptilinum does not extend medially to below the apices of the short antennae and it is less voluminous and rugged in texture than is that of *Gasterophilus*. Scales do not extend to the genae or to the membranous frons.

OESTRIDAE

Oestrus ovis L. The light-yellow, type 2 scales are slightly larger and more uniform in size than are those of *Hypoderma*. The suture does not extend to below the lower eye-margin. Despite this, the ptilinum is voluminous and rugged.

TACHINIDAE (LARVAEVORIDAE)

General

The ptilinal armature of the various species in this large family is of unusual interest because the habits of the host usually impose upon the escaping fly the environment from which it must liberate itself as it leaves its puparium. Of those which parasitize holometabolous hosts the majority do not escape from them until the latter have formed their own pupal protection. Among

lepidopterous hosts this protection may be completely lacking, as in Rhopalocera; more frequently it consists of a silken cocoon while, in the most extreme cases, it is a hard-walled earthen cell constructed about one to three inches below the soil surface by Phalaenidae.

The adults of many Tachinidae oviposit on leaves and depend either upon their liberated larvae successfully attaching themselves to, and entering a satisfactory host, or upon a suitable host swallowing their minute eggs with its food. Their first biological problem thereafter is that the larvae may be adapted to live in the large variety of hosts into which they may thus gain a somewhat fortuitous entrance. The writer (12) has discussed this problem in connection with certain species which could, or could not, be reared in different species of Phalaenidae. Later, it is essential that, should the larvae succeed in maturing in a specific host, their adults shall be equipped to penetrate its pupal protective covering.

From the following observations, it appears to be self-evident that the type of ptilinal armature possessed by different species of tachinids constitutes an important factor in determining this ability. It can hardly be maintained that the relatively enormous scales possessed by species which are known to escape from subterranean phalaenid cells were evolved as a "ready-made" adaptation with this end in view, but it would appear that only those species which are so equipped stand much chance of becoming successful parasites of hosts which form earthen cells prior to the escape of their larvae.

An examination of a number of Tachinidae indicates that the majority of species possess ptilinal scales which, though rather longer than are those in related families such as Calliphoridae, do not reveal other modifications. They are not very heavily sclerotized and are chiefly of type 3 with only a normal complement of short moderately vertical type 4 scales.

Information regarding the known hosts of many tachinids is available from a variety of sources. The most complete list is the catalogue prepared under the direction of W. R. Thompson (13), while, for local species, Essig's book *Insects of Western North America* is a useful source of additional data. It is, however, most unlikely that, even in the case of the best-known species, we possess information regarding the entire range of hosts which they parasitize successfully. Their relationships have, in almost every case, been recorded only in so far as they concern hosts which are of particular economic interest.

Species which are believed to be limited to essentially superterranean hosts, such as Orthoptera, Hemiptera, butterflies, and leaf-eating moth-caterpillars possess unmodified ptilinal scales. Even in the case of *Doryphorophaga doryphorae* Ry., which may escape from the subterranean pupal cavity of the potato beetle, the scales are normal in structure and size. Certain species which are known to parasitize subterranean phalaenid larvae, also, have normal scales. We do not know in what stage of host development the larvae of these species kill their hosts but suspect that they do so before the latter form their pupation cells.

The ptilina of all species in genera in which it is known that the adult tachinid normally escapes from a subterranean phalaenid cell, however, are armed with extremely powerful scales on the median dorsal surface (Figs. 6 and 7). They are only slightly smaller on the corresponding ventral surface. These scales are invariably very heavily sclerotized here though, laterally, they are usually much smaller and are frequently unpigmented. With the exception of species in the genus *Echinomyia* (*Fabriciella* or *Cnephaliodes*) in which they are of type 3, these are greatly lengthened and semidecumbent type 4 scales.

Field-captured representatives of many of these species reveal that the apices of a varying percentage of these enlarged scales are lacking and have every appearance of having been "eroded" away rather than having been broken off. This, it is assumed, is due to their having been vigorously employed in scraping through the earthen wall of a pupation cell.

Frontal scales, generally, are weak and appear to be nonfunctional; those on the face when present are villiform.

The few examples discussed below are arranged in accordance with the manner in which the habits of their known hosts may result in increasing difficulty for the adult tachinids to penetrate their pupal protection. It is unfortunate that generic concepts in this large family are still in a state of flux. In the following list, species are recorded under generic names which, until recently, have been most frequently employed. These are followed by alternative names (in brackets) under which they may also be recorded in the literature.

Gymnosoma (*Rhodogyne*) *fuliginosa* Desv. Fig. 45. A bug parasite. The scales are uniform, elongate type 3, with very few slightly modified to type 4; relatively small. They are light brown in color and, apparently, are only lightly sclerotized.

Acemyia (*Euacemyia*) *tibialis* Coq. A grasshopper parasite. The scales resemble those of *Gymnosoma* but are more gray than brown.

Zenilla futilis O.S. Fig. 46. A butterfly parasite. The scales resemble those of *Gymnosoma* but with a much greater tendency to be modified to type 4. They are distinctly more heavily sclerotized, moderately crowded, and overlap for about one-third of their length.

Zenilla affinis Fall. (*Aplomya estigmensis* Sell.). An arctiid parasite. The scales resemble those of *futilis* but are a little longer and more crowded, overlapping for about half their length.

Winthemia quadripustulata Fab. and *Frontina* (*Achaetoneura*) *frenchi* Will. Rather general parasites of Lasiocampidae, Arctiidae, Sphingidae, &c. Similar to *Zenilla* spp.

Hystricia (*Bombyliomyia*) *abrupta* Wied. An arctiid parasite. The scales on the ptilinum of this excessively bristly fly resemble those of *Zenilla* and they are, relatively, no larger.

Doryphorophaga doryphorae Ry. A beetle parasite, including *Leptinotarsa*. The scales are not very heavily sclerotized but are wider than are those of any preceding species and they completely conceal the ptilinal membrane over much of its surface.

Belvosia bifasciata Fab. A saturniid parasite. This is the largest tachinid taken locally. The narrow scales are heavily sclerotized and are essentially of type 3 with tendencies, over the whole to the ptilinum to approach type 4. They are relatively larger than in any of the foregoing species.

Tachinomyia variata Curran. A liparid parasite which has, also, been recorded as having parasitized the phalaenid *Agrotis orthogonia*. The ptilinum is voluminous and pendulous when withdrawn. The scales are not modified or enlarged and they resemble those of *Zenilla*. In one specimen examined a few scales had the apices missing but they appeared to be broken rather than eroded.

Aphria ocypterata Twns. A parasite of *Euxoa*. The scales of this rather small fly resemble *Zenilla*. Information is lacking as to when *T. variata* and this species kill and leave their hosts. We suspect that they do so before the latter have formed pupation cells.

Echinomyia spp., later synonymized with *Fabriciella* and *Cnephaliodes*, and still later separated into several genera. These appear to represent an intermediate stage between those

genera in which the scales are unmodified and those which possess the relatively enormous type 4 scales to be discussed later. All, in so far as is known, are phalaenid parasites. In all species of this genus which we have examined, the scales are distinctly enlarged medially but to a less extent than are those of the following genera. They are, however, typically of type 3, with slight tendencies towards type 4 near the lower edge of the ptilinum. *Echinomyia (Rhacogaster) algens* Wd. Fig. 47, a parasite of cutworms and *E. (R.) latifrons* Toth., reared from *Agrotis orthogonia* Morr., exemplify this genus. Several specimens examined showed abrasion of the scale apices.

Epalpus (Argenteopalpus) signiferus Wlk. Fig. 48 is a locally abundant early-spring flyer which is recorded as parasitizing a phalaenid, *Lithophane* sp. This is an example of a tachinid which possesses flattened type 4 scales on the upper and lower median surfaces of its ptilinum. They are, however, smaller in this species than in any other with this character which we have examined.

Peleteria (Peletieria) spp. Host records of species in this genus indicate that they are essentially phalaenid parasites. It has recently been divided into a number of separate genera. *Peleteria (Sphyromyia) campestris* Curr., a parasite of *A. orthogonia*, exemplifies the generic ptilinum and it resembles that of *Gonia* S.L., discussed below.

Bonnetia (Linnaemyia) compta Fall. An abundant parasite of *A. orthogonia* Morr. and other Phalaenidae. It normally kills its host after the later has formed its pupation cell and has entered the prepupal stage. Its scales resemble those of *Gonia* spp. They are among the largest we have observed. Among captured specimens, a number of these large scales have the apices missing.

Gonia spp. This large group of undoubtedly closely related flies has recently been separated into several genera. They are essentially phalaenid parasites which allow their hosts to pupate before killing them. All of the species with which we are familiar are univoltine and hibernate in their hosts' pupal cells. It is many years since the writer had an opportunity to study the habits of these flies in the field but, in so far as he can remember, adult moths always escaped from their cells by a reasonably circular hole whereas tachinids did so through a jagged opening.

This genus, however, contains one species *Gonia (Knabia) frontosa* Say. which, we believe, is normally a parasite of tree-foliage eating caterpillars and it pupates in the aerial cocoons of its hosts. In common with related species, its ptilinum is armed with greatly enlarged type 4 scales. Since these are as large as are those of many which parasitize Phalaenidae it would appear that, should its larva be capable of developing in cutworms, the adult should have no difficulty in penetrating their pupation cells.

Gonia (Knabia) frontosa Say. Parasite of *Malacosoma disstria* Hub. Enlarged, heavily sclerotized, decumbent type 4 scales are confined to the upper and lower median surfaces of the ptilinum. Around its periphery, as well as at its apex, they gradually reduce in size and pigmentation. Apically, they are very short vertical type 4, about one twentieth the length of the enlarged dorsal scales; around the periphery the very light-yellow scales are of type 3 about one tenth the length of the dorsal ones. As is the case with all tachinids with enlarged scales, those on the dorsal half of the ptilinum are about 10% longer than are those on the lower half. There was no abrasion of the scale apices on any specimen that was examined.

Gonia (Reamuria) aldrichi Toth. A parasite of *Agrotis orthogonia* Resembles *G. frontosa*, scales about one and one-half times as long. It is believed that the inflated ptilinum shown in Fig. 6 represents this species.

Gonia (Reamuria) longiforceps Toth. Fig. 49. A parasite of *A. orthogonia*. No species examined possessed larger scales. These are somewhat variable in size and the largest one observed is illustrated. Its apex is missing. In this species the scales at the ptilinal apex are less inclined to tend towards type 4 than they are in *frontosa*. A ptilinal seta is included in the drawing to show its comparative length. On account of lack of pigmentation in all lateral scales, including those in the lateral sutural grooves, a gross examination of the ptilinum gives the impression of its being transparent with a wide median black band which does not quite reach its upper and lower margins.

HIPPOBOSCIDAE

General

In two species examined the frontal suture is wide and transverse, as it is in many Tetanoceridae. It bends down slightly at its extremities. The ptilinum is ribbonlike but tends to be sclerotized. It folds inwards by a single fold along its equatorial area and does not appear to be capable of protrusion.

Melophagus ovinus L. Fig. 50. Medially the ventral scales are asymmetrical and somewhat bractlike. Laterally they become increasingly narrowed and, finally, fuse to form longitudinal flattened "rods". All dorsal scales are fused to form horizontal, irregularly wrinkled and flattened rods. The entire ptilinum is sclerotized.

Ornithomyia fringillina Curt. Resembles *M. ovinus* but the scales are less definitely outlined and appear to fuse together to form "zig-zag" transverse bands which cover the greater part of the more flexible ptilinum. Rarely, only, can the outline of a sharply tapering asymmetrical scale be distinguished.

The Relative Size of Ptilinal Scales in Different Species of Flies

Extreme specific variations in the size of flies obviously affects the actual length of their ptilinal scales. This can be inferred from the accompanying illustrations, all of which have been drawn with a camera lucida at a magnification of 500. More significant, regarding possible function, is their size in relation with that of their possessors. In gauging this, the best method appears to be to record their length in proportion to the width of the flies' heads. All measurements are given in millimeters. In order to save space, data are grouped where variations in proportion appear to have little significance. The species included in each group can, however, be deduced from the foregoing individual discussions of them.

No significant sexual difference was observed either in head-width or scale-length. Scales, however, vary in size on different parts of the same ptilinum. Attempts were made to measure the average length of those near the median center of the upper half of the ptilina. It was not always possible to pin point this area in our dissections while extensive overlapping of scales here frequently rendered exact measurements impossible. Furthermore, in many species, the bases of the scales are evanescent. Measurements, as given, must therefore be considered as approximate. Errors much in excess of 10% are improbable, but this possibility exists.

For scales which terminate in an elongate apical bristle, the lengths, as given, refer to that of the body only. Because of their unusual structure, scale lengths in the ephydrid, *O. mantis*, several Tetanoceridae, and all species in the anthomyid genus, *Fannia*, are hardly comparable with those of more typical flies.

Despite these inherent shortcomings, the list indicates for each species the extent to which any unusual variation in size might, in some manner, be correlated with its ability to escape, as a recently emerged adult, from its immediate surroundings.

Family	Species	Scale length	Head width	Ratio, scale: head
CONOPIDAE	4 species	0.014–0.021	2.08–2.90	0.005–0.009
	Z. fulvifrons	0.021	1.70	0.012
OTITIDAE	3 species	0.014–0.015	1.50–2.14	0.007–0.010
TRUPANEIDAE	3 species	0.017–0.019	1.42–1.95	0.010–0.013
PALLOPTERIDAE	*P. jucunda*	0.014	1.00	0.014
LONCHAEIDAE	*L. polita*	0.019	1.66	0.011
TANYPEZIDAE	*T. luteipennis*	0.018	1.39	0.013
CALOBATIDAE	*C. nasoni*	0.013	0.92	0.014
MICROPEZIDAE	*M. lineata*	0.013	0.81	0.016
PIOPHILIDAE	*P. affinis*	0.010	1.03	0.010
SEPSIDAE	2 species	0.014–0.017	0.94–1.03	0.015–0.017

Family	Species	Scale length	Head width	Ratio, scale: head
LAUXANIIDAE	2 species	0.012–0.016	1.09–1.25	0.010–0.015
DROSOPHILIDAE	3 species	0.005–0.010	0.67–1.00	0.007–0.010
ASTEIIDAE	*A. multipunctata*	0.008	0.69	0.012
OPOMYZIDAE	*A. tenuis*	0.008	0.61	0.013
AGROMYZIDAE	5 species	0.008–0.013	0.47–0.86	0.012–0.019
	A. angulata	0.019	0.72	0.026
PHYLLOMYZIDAE	4 species	0.004–0.006	0.64–1.03	0.006–0.008
CHLOROPIDAE	3 species	0.006–0.007	0.61–1.00	0.006–0.010
EPHYDRIDAE	2 species	0.014	1.39–1.53	0.009–0.010
	O. mantis	0.004	1.69	0.002
	P. nilida	None	1.50	—
BORBORIDAE	*B. equinus*	0.008	1.03	0.008
CLUSIIDAE	*C. melanostoma*	0.010	0.89	0.011
CHAMAEMYIDAE	*C. polystigma*	0.014	0.78	0.005
TETANOCERIDAE	2 species	0.010–0.011	0.92–1.16	0.009–0.011
	3 species	Not comparable with others	1.39–1.66	Not comparable with others
	Sepedon spp. (5)	None	1.26–1.72	—
CHIROMYIDAE	*T. fumipennis*	0.008	0.72	0.011
PSILIDAE	*P. perpolita*	0.009	0.83	0.011
COELOPIDAE	*C. frigida*	0.004	0.97	0.004
HELOMYZIDAE	5 species	0.009–0.014	1.03–1.42	0.007–0.012
DRYOMYZIDAE	*N. anilis*	0.012	1.44	0.008
CORDYLURIDAE	*C. confusa*	0.015	1.66	0.009
	A. varipes	0.021	1.25	0.017
SCOPEUMATIDAE	2 species	0.017–0.018	1.61–2.19	0.008–0.011
ANTHOMYIDAE	Phaoninae (2)	0.017–0.022	1.84–2.17	0.009–0.010
	Mydaeinae (2)	0.022–0.023	2.09–2.25	0.010–0.011
	Hydrotaeinae (1)	0.018	2.22	0.008
	Faniinae *A. gibbera*	0.009	0.72	0.013
	6 species of *Fannia*	0.002–0.004	1.09–1.84	0.002–0.003
	Lispinae (2)	0.017	1.88–1.94	0.009
	Limnophorinae (3)	0.013–0.017	1.42–1.64	0.009
	Coenosiinae (2)	0.014	0.83–1.16	0.012–0.017
	Anthomyinae (4)	0.012–0.014	1.31–1.75	0.008–0.011
MUSCIDAE	4 species	0.014–0.017	2.28–2.67	0.006–0.007
	L. irritans	0.014	1.16	0.012
GASTEROPHILIDAE	*G. intestinalis*	0.019	3.94	0.005
CALLIPHORIDAE	6 species	0.014–0.016	2.75–3.84	0.004–0.005
	P. rudis	0.018	2.91	0.006
SARCOPHAGIDAE	4 species	0.016–0.022	2.30–3.70	0.005–0.007
	S. kellyi and *hunteri*	0.017–0.019	2.03–2.47	0.008
METOPIIDAE	*M. leucocephala*	0.020	1.50	0.013
CUTEREBRIDAE	*C. tenebrosa*	0.029	9.50	0.003
HYPODERMATIDAE	*H. lineata*	0.021	4.10	0.005
OESTRIDAE	*O. ovis*	0.025	3.75	0.007
TACHINIDAE	12 species. Hosts superterranean	0.071–0.096	1.84–6.00	0.006–0.016
	T. variata	0.031	3.00	0.010
	A. ocypterata	0.029	3.00	0.010
	E. algens	0.076	4.00	0.019
	E. signiferus	0.116	3.50	0.033
	G. frontosa	0.130	3.20	0.041
	3 species of *Gonia* Phalaenid pupae	0.130–0.215	3.20–4.00	0.041–0.054
	P. campestris	0.177	3.80	0.047
	B. compta	0.190	3.50	0.054
DEXIIDAE	*P. tibialis*	0.021	2.35	0.009
HIPPOBOSCIDAE	*M. ovinus*	0.014	1.25	0.011
	O. fringilaria	0.010	1.25	0.009

In the foregoing list it will be seen that, on the ptilina of flies, representing the majority of families, the ratio of head width to scale length varies between 1 : 0.005 and 1 : 0.015, which is approximately ×200 to ×66. Only in species in which the scale structure is abnormal is this ratio appreciably exceeded. On the other hand, apart from in certain Tachinidae, it appears to be significantly reduced only in certain Agromyzidae, e.g. *A. angulata* (1 : 0.026 or ×40) and, possibly, though to a lesser degree, in Anthomyidae, subfamily Coenosiinae.

Among those species of Tachinidae which penetrate phalaenid pupation cells, however, it may be reduced to as little as 1 : 0.054, or approximately ×20. This is approached in at least four genera which are not particularly closely related to each other.

Discussion and Summary

From an examination of about 150 species of Schizophora, it is evident that the ptilina of this entire group normally are armed with thousands of minute, to occasionally very large, cuticular projections to which the name "scale" has been applied. Only in 2 of the 40 families examined were any species found in which they are lacking.

In size, the vast majority vary in length from about 1/200 to 1/66 of the width of the head, i.e. 0.005 : 1 to 0.015 : 1.

The apices of these scales are directed upwards and backwards on the dorsal half of the ptilinum and downwards and backwards on its ventral half. On a narrow transverse band, which is about six scale-lengths in width and which passes through the ptilinal apex, they are vertical and are usually reduced in length. Underlying this band retractile muscles are attached to the inner wall of the ptilinum.

Scales vary in structure in different families but, in general, all appear to be derived from a "primitive" type which, in side view, resembles a rose-thorn. From above, the dorsal surface is seen as a widened blade. Variations in its outline can be likened to a wheat, barley, or oat grain respectively. The most frequently encountered variant from this general type is conical and is strengthened from its base to its apex with about six heavily sclerotized rods. These give it the appearance of a partially collapsed "bell" tent. Scales which are intermediate in structure between these two types are not uncommon on all ptilina on which the latter are represented.

On the ptilina of a few widely separated families these normal types are entirely replaced with others which, when first observed, appear to have no relationship with them. Cuticular scales are of wide occurrence on the connective membranes of Arthropoda and they assume a great variety of forms. Elsewhere than on ptilina they usually are small and rather widely scattered. Particularly among the Acalyptrata, however, the buccal bladders at the base of the proboscis may be as heavily armed with scales resembling those of the ptilina as are the latter, themselves. On the proboscis of the

conopid, *P. furcillata* Will., these crowded scales undergo a gradual transformation, between its base and its apex, which includes nearly all of the infrequently encountered variations which are peculiar to the ptilina of different families. This indicates that all are variations of the same structure and may throw some light upon their possible functional adaptations.

In the majority of ptilina both the structure and the disposition of scales indicate that they may be capable of being employed, after the fly has escaped from its puparium, in assisting it to penetrate obstructions, such as moderately consolidated soil. The actions of several species of Calliphoridae in attempting to penetrate glass at this time support this view, despite the fact that, in these flies, the scales are only about 0.005 of the head-width and they belong in the group in which they are of the minimum normal size.

As soon as the ptilinum encounters glass, while the fly is leaving its puparium, it explores the surface of the obstruction. Following this, the apex is withdrawn by muscular contraction to produce a temporary transverse fold which brings together along its edges the centers of the upper and lower surfaces of the ptilinum. Both surfaces (together with the frons) are pressed firmly against the glass. Greatly increased internal blood pressure follows and is accompanied by a gradual release of the ptilinal apex. This causes the tips of the opposed scales on the two surfaces to be forced apart and to scarify the obstruction. This scarifying action may be repeated dozens of times during the next few hours. It is obviously "purposeful". After about an hour of fruitless endeavor, about 50% of the flies under observation released a copious fluid from their pseudotracheae. This flooded the obstruction and probably would soften certain types. Its liberation was invariably followed by extreme exertion. Its use appears, however, to entail some risk, unless, as a result of its employment, a rapid escape is effected. On evaporation, it firmly cements small particles together.

In many species of flies scales extend from the ptilinum to other parts of the epicranium. This applies, chiefly, to the frons in Calyptratae or to the face in Acalyptratae. Less frequently, they flare out from the lower ends of the frontal suture and cover the genae. Epicranial scales tend to be rather smaller than are those on the ptilinum and they are frequently fused together longitudinally. Prior to its sclerotization, those on the frons are definitely employed by Calliphoridae in conjunction with the ptilinum in efforts to escape. In Agromyzidae the frons may be exceptionally heavily armed with separate scales. It retains its flexibility throughout the life of the fly and is, undoubtedly, functionally a part of the ptilinum.

Powerful armature on the buccal bladders is more common among Acalyptratae than it is in Calyptratae. The latter rarely possess more than a scattering of "villi", or similar weak structures, on this area. This applies to Calliphoridae. Despite this, these flies inflate them to the utmost whenever they make a major effort to penetrate an obstruction with their ptilina. Though they may occasionally be brought against the glass and forced over its surface they do not appear to be put to any specific use. It would appear

that Acalyptratae in which these structures are heavily armed with scales may have a definite use for them. No flies, so equipped, have, however, been observed attempting to penetrate an obstruction.

In a few, unrelated, species the ptilinal scales are abnormally large in size and this character is usually accompanied by their being unusually heavily sclerotized. This combination is most pronounced in those species of Tachinidae which normally allow their phalaenid hosts to construct subterranean pupation cells before their larvae kill them. These flies must, therefore, ultimately penetrate these cells by their own efforts. That they do so with the aid of their ptilinal scales is indicated by the relatively enormous development of these structures on all species which are known to have this habit. In several of these the length is over 0.05 of the head width. This is, at least, 10 times their relative size in Calliphoridae. Not only does their size and structure suggest that they are particularly well-adapted to powerful digging but the fact that many field-captured adults have the tips of many of them abraded suggests that they have, undoubtedly, been employed for this purpose.

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* *Papers marked with an asterisk have not been seen by the writer.*

EXPLANATION OF FIGS. 12–50

All illustrations of individual scales have been made, with the aid of a camera lucida, at a magnification of 500. The text explains whether each illustration refers to the prevailing type of scale for the species concerned or whether it is of some unusual modification which is confined to part of the ptilinum. Scales drawn with their apices directed upwards are from the upper half of the ptilinum and those with it downward are from its lower half.

Unless otherwise stated, average-sized scales were selected for drawing. Where more than one scale is illustrated from the same ptilinum the first description refers to the one on the left.

CONOPIDAE: FIG. 12. *P. furcillata* Will. Lower and upper outlines of a ventral scale as seen from above. FIG. 13. *M. vicaria* Walk. Upper and side view of scale.

OTITIDAE: FIG. 14. *S. vibrans* L. Upper and side view of scale. FIG. 15. *E. myopaeformia* V.R. Upper and side view of scale.

TRUPANEIDAE: FIG. 16. *E. solidaginis* Fit. Imbricated scales near ptilinal apex, and a normal type 3 on its upper surface.

LONCHAEIDAE: FIG. 17. *L. polita* Say. Type 4 scale from median ventral ptilinal surface and "rods" of fused scales from near the genal angles.

TANYPEZIDAE: FIG. 18. *T. luteipennis* K. & S. Normal scale and one with flared base from lower half of ptilinum.

SEPSIDAE: FIG. 19. *T. putris* L. Bractlike scale from above frontal lunule and fused scales near upper edge of ptilinum.

DROSOPHILIDAE: FIG. 20. *D. melanogaster* Mg. Indefinite scales near center of ptilinum. Laterally, and near genal angles they are better defined, as shown.

AGROMYZIDAE: FIG. 21. *A dubitata* Mall. Scale with divided apex from apex of ptilinum and an asymmetrical one from near this area. FIG. 22. *A. angulata* Lw. Upper and side view of one of the larger scales.

CHLOROPIDAE: FIG. 23. *O. frit* L. Upper and side view of scale. This was the smallest species of fly dissected.

EPHYDRIDAE: FIG. 24. *P. turbida* Curr. Upper and side view of typical scale and upper view of one from just above the frontal lunule. FIG. 25. *O. mantis* DeG. Portion of ptilinum from near its center showing comb-scales on dorsal one-third and intensive wrinkling of ventral two-thirds.

CHAMAEMYIDAE: FIG. 26. *C. polystigma* Mg. Variations in ptilinal scales, all of which are of unusual shapes.

TETANOCERIDAE: FIG. 27. *M. schoenheri* Fall. Normal scales on a normally developed ptilinum. FIG. 28. *T. valida* Lw. "Jigsaw puzzle" type of scales which cover the greater part of a ribbonlike ptilinum and a side view of those near its upper margin. FIG. 29. *L. saratogensis* Fit. Imbricate scales near upper center of ribbonlike ptilinum, and one on lower half.

COELOPIDAE: FIG. 30. *C. frigida* Fab. Circular scales which arm the entire ptilinum.

HELOMYZIDAE: FIG. 31. *S. nemorum* Mg. Partly fused scales and one of the greatly enlarged ptilinal setae near the dorsal margin of the ptilinum.

DRYOMYZIDAE: FIG. 32. *N. anilis* Fall. Upper and side view of the unusual type 4 scale which arms the entire ptilinum.

ANTHOMYIDAE: FIG. 33. *F. scalaris* Fab. This type of scale predominates on the ptilina of all species examined in the genus *Fannia* and was never observed elsewhere. FIG. 34. *L. nasoni* Stein. Upper and side view of scales which approach, in structure, the greatly enlarged scales of certain genera of Tachinidae. FIG. 35. *L. a. pallipalpis* Zett. Side view of typical scale; side and upper view of scales from a small differentiated patch just above the frontal lunule. FIG. 36. *H. antiqua* Mg. Portion of the edge of one of the lateral areas on the ptilinum which is stained black.

MUSCIDAE: FIG. 37. *M. domestica* L. Upper and side view of scales; fused scales which arm the frons.

GASTEROPHILIDAE: FIG. 38. *G. intestinalis* DeG. Upper and side view of small scales which arm the ptilinum and the buccal area.

CALLIPHORIDAE: FIG. 39. *P. regina* Mg. Upper and side view of fused ptilinal scales. This fusion and heavy pigmentation is atypical for the majority of specimens examined. FIG. 40. *C. cadaverina* Desv. Scales which are either somewhat flaring or parallel sided basally; a lateral type 4 scale.

SARCOPHAGIDAE: FIG. 41. *S. l'herminieri* Desv. Upper and side view of scale from median area of ptilinum.

METOPIIDAE: FIG. 42. *M. leucocephala* Rossi. Upper and side view of scale.

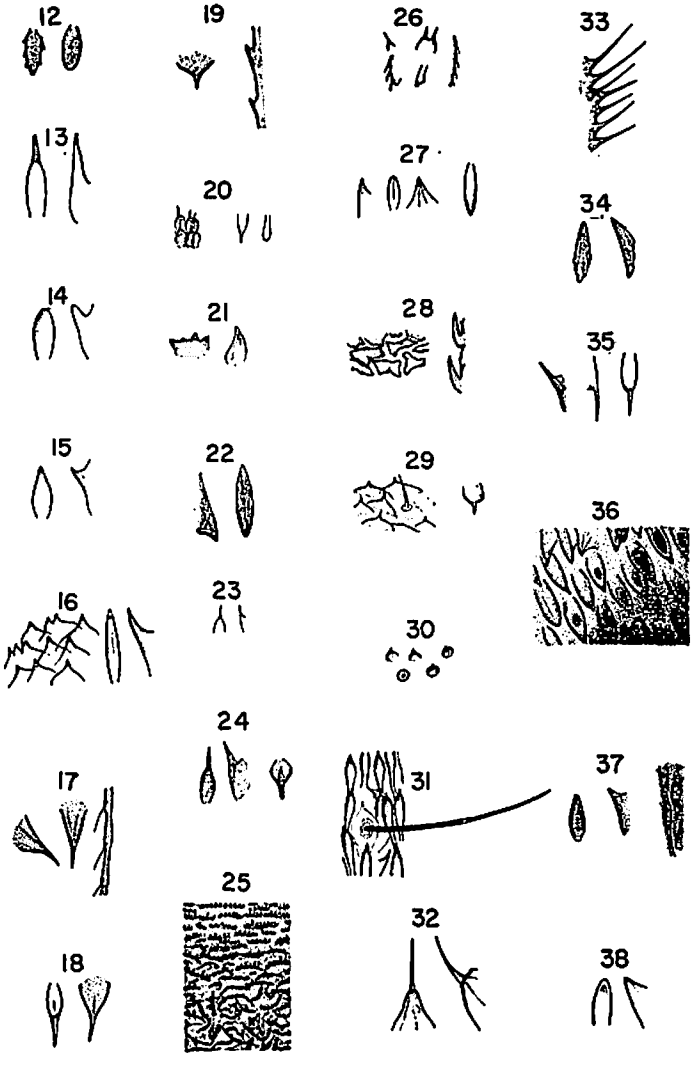
CUTEREBRIDAE: FIG. 43. *C. tenebrosa* Coq. Upper and side view of scale.

HYPODERMATIDAE: FIG. 44. *H. lineatum* DeV. Normal lateral scale; a slightly asymmetrical median scale; an individually enlarged median scale.

TACHINIDAE: FIG. 45. *G. fuliginosa* Desv. A bug parasite. Typical type 3 scales which clothe the entire ptilinum. FIG. 46. *Z. futilis* O.S. A rhopaloceran parasite. Typical type 4 scales which cover most of the ptilinum. FIG. 47. *E. algens* Wd. A phalaenid parasite. Enlarged type 3 scales which cover the upper and lower median ptilinal areas. FIG. 48. *E. signiferus* Wlk. A phalaenid parasite. Enlarged type 4 scales which cover the upper and lower median ptilinal areas. FIG. 49. *G. longiforceps* Toth. A phalaenid parasite. *a*. The largest individual type 4 scale observed in any fly though those of *B. compta* are very similar in size and structure. The apex of this scale appeared to have been abraded away while the fly penetrated the pupation cell of its host. *b*. An unpigmented lateral type 3 scale. *c*. and *d*. Two apical scales. In this species they are not modified to type 4. *e*. An unpigmented type 4 scale from near the upper ptilinal margin. *f*. A ptilinal seta drawn to the same magnification as are the scales.

HIPPOBOSCIDAE: FIG. 50. *M. ovinus* L. Portion of the ribbonlike ptilinum from near one lateral extremity and near its center.

(Note: Figs. 12-50 follow.)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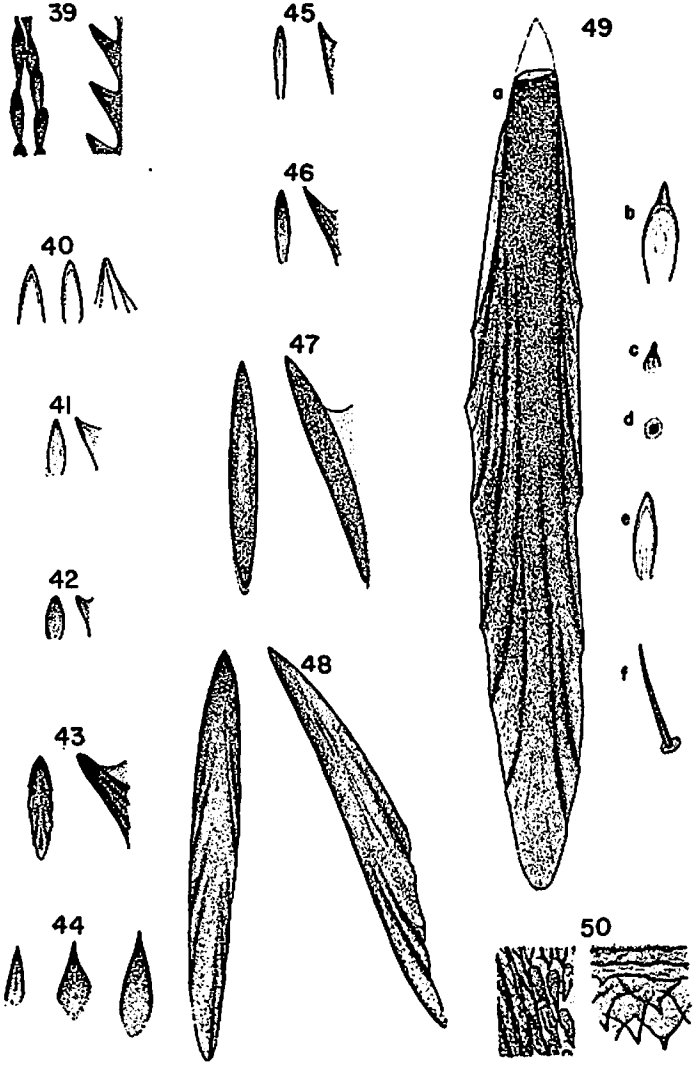
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