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WING-SCALE MORPHOLOGY AND NOMENCLATURE

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In our more detailed studies of scale ultrastructure we have been troubled periodically by a lack of nomenclatural reference for specific structures and areas. Such basic scale research as Kellogg (1894) and Mayer (1896) were accomplished with light microscopes and without the need of a specialized terminology. Even after the development of electron microscopy we are struck by the paucity of labels on the numerous published scale drawings and photographs. Those structures usually identified included such universal and apparent things as "upper surface, lower surface, longitudinal rib, or cross-support", but the ultrastructure of these features demands greater attention to terminology.

Some pre-electron microscope vocabulary is given in Freiling (1909) and Kuznetsov (1967), and post-EM, ultrastructural terms have been used, identified or modified in Anderson and Richards (1942), and in Hirata *et al* (1957, 1959, 1966). More recently, Greenstein (1972a, 1972b) and Ghiradella (1974) have used a modest terminology particularly important in scale development. It is our intention that the review and discussion here might help develop and standardize a vocabulary for work on scale ultrastructure.

CUTICULAR OUTGROWTHS OF BUTTERFLY WINGS

Most entomologists are well aware of the name "scales" as applying to the tiny, overlapping, "dusty"-coating on butterfly and moth wings. Perhaps some do not realize that these highly modified integumental structures also cover the entire body, including legs and antennae, and that they have a similar origin to many other appendages and processes of the cuticular cover of insects. They also occur in other insect groups, for example some beetles and Thysanura, despite disparate phyletic positions.

There are many morphological types of scales, and we are beginning to realize that their physiological functions may be just as variable. For example, the "battledore" (or tennis racket) shaped scales found only on the male wings of certain Lycaenidae are presumed to be scent or odor producing. Their basic similarity to scales taken from male sex-brands or patches also argue for utilization in some sexual way and reinforce the thought that odors are involved. While certain odors can be detected from the living insect, it takes some extremely careful biochemical techniques to isolate chemicals from specific scale types. While the lack of chemical and functional knowledge of specific scales is unfortunate, it does not prevent a morphological survey of scale types, and based on comparative anatomical properties, permit some inferences on comparative functions. Nonetheless, it should be stressed that names for scale types based on presumed function is dangerous, and until more is known about their physiological properties, it would be advisable to stress morphological similarities and differences.

Our description of scales may reflect efforts to give precise exactness and conformance to a character state (or definition) where none exists. Nevertheless, attention to such details heightens our understanding of variability in these structures and certainly augments communications on observed differences.

The descriptive (comparative) value of scales is found in characters such as: 1) form and general outline; 2) socket; 3) pedicel; 4) base and margin; 5) apex; 6) position and arrangement; and 7) surface and internal structure. Each of these will be briefly discussed and graphically illustrated. Under each category, an abbreviated list termed *character states* is given in outline or telephonic style. This is basically a series of nouns, adverbs and/or adjectives associated with the particular scale character under discussion and is meant to indicate vocabulary involved rather than a treatise on the kinds of morphological variability.

Following the character-states are comments concerning the structures which generally could not be treated in the definitions. An alphabetical lexicon follows.

In the listing and discussion of the character states, very little attention is given to quantitative characters such as length, height, arcs or angles, number of structures, ratios, or other comparative statistics. These features, which may in fact be diagnostic of certain scale types, would add little to the vocabulary and stability of communication on scale structures. Many secondary sources contain good to excellent summaries of scale types with references. These include entomology texts (Berlese, 1909; Weber, 1933, 1954; Imms, 1957; and R. Chapman, 1969), morphological treatises (Richards, 1951 and Smith, 1968), general works on Lepidoptera (Bourgogne, 1951 and Forster, 1954) and popular accounts of color and iridescence (Simon, 1971). However, these sources do not add to scale vocabulary and are not herein utilized. Similarly we have omitted from the literature cited many excellent scale papers (examples would include Barth, Gentil, Von Linden, A. Mueller, Pictet and W. Schmidt) where there was no significant addition to scale vocabulary. The great variety of androconial structures leads us also to suspect that a more thorough vocabulary will be needed in that area, particularly extending such excellent studies as begun by Freiling (1909) to studies involving scanning electron microscopy (SEM) or transmission electron microscopy (TEM).

NOMENCLATURE OF SCALE PARTS

FORM AND GENERAL OUTLINE

Character states:

General: teneral or mature; solid or hollow; flat, flexed or twisted; sculptured or smooth; porous, scabrous or crenulate surface, categories by general shape.

1) Piliform (see Fig. **21, 22**)
2) Lamellar (Fig. **20**)
3) Other (variable form).
   a) Symmetrical (Fig. **14**)
      1. Spiral or twisted form
      2. Non-spiral
         saccate, capsular, with irregular appendages or surface structures.
   b) Asymmetrical (Fig. **41**)
      1. Single axis *in situ*
      2. Multiple axis *in situ* heart, folded or fan shape.

There is some evidence (see Kuznetsov, 1967: 152) that physical factors may alter scale shape. In fact, the effect of various agents on variation in color, shape and pattern of scales has been the subject of numerous investigations of which the following are examples: *cauterization,* Urquhart, 1972; *DNA,* Nawa, 1968; *electricity,* Wagner, 1865, Wier, 1876; *parabiosis,* Yagi, 1954; *starvation,* Koehler, 1940; *seasons,* numerous authors, T. Chapman, 1914, Warren, 1961; *sex,* numerous authors, Aurivillius, 1880, Scudder, 1877; *transplants,* Kuehn and Piepho, 1940; *U-V light,* Koehler, 1941; *x-ray,* Picken, 1949.

The main categories of scales may be distinguished by cross section; round to ellipitical, *piliform,* or hair-like scales (Fig. **21, 22**); flattened, leaf-like, *lamellar* scales (Fig. **5, 8, 9**), which exhibit a great variety of shapes; and *irregular* scales (Fig. **12, 14**), which may be bag shaped and pouchy (Fig. **14**) or with portions of the scale enlarged to form capsules or other specialized bodies. Hair scales were considered by Kellogg (1894: 55) to be the generalized scale condition, with lamellar scales the more specialized. Hirata and Ohsako (1966) were the latest to furnish data showing that "hair" scales preceded flat scales, and suggested also that marginal wing scales (Fig. **16**) which are extremely elongate and sculptured on both sides, may be transitional between the two extremes. They also furnish the descriptive morphology and vocabulary for hair scales.

While there is great variability in the form of most scale types, the essential character of cover scales for example, usually can be detected even though their apical margins, and length may change rather markedly on the same individual. Rather different phylogenetic lines, on the other hand, may develop at least superficially similar scale types. Note for example, the similar flask-shaped scales in the males of *Lampides boeticus* (Fig. **5**) and *Parnassius apollo* (Fig. **6**). The latter type androconium is rather similar to other scales on the wing of *Parnassius* (Fig. **10**), even though less than half the size.

Various scale shapes have been described using some of the vocabulary borrowed from the botanical sciences for leaf shape. Thus ovate shapes (Fig. **14**), obovate (Fig. **9**), oblong (Fig. **8**) and lanceolate types (Fig. **17**), among others, have been noted.

In certain primitive moth families (Mnesarchaeidae), Kristensen (1970) found that the upper and lower surfaces of the scale were fused, forming a solid scale: minute lumens were found in other scales beneath the longitudinal ridges. Even though most moth scales cannot be distinguished from butterfly types on the basis of ultrastructure, at least at this point, their great numbers argue for a multitude of scale types, of which the "solid" scale, without a lumen, is an example. Figure **50** shows a moth scale with a rather solid appearing longitudinal ridge, apparently lacking scutes or any fluting.

SOCKET

Character states:

Erect or repressed; truncate or with apex; double-sack or vase-shaped; goblet or eliptical collar; regular or irregular placement; rows or non-tiered; single or multiple rows; parallel or non-parallel.

Sockets are generally arranged in single (Fig. **30**) or multiple (Fig. **20**) sub-parallel rows running transversely across the wing. They are roughly arranged in concentric circles around an unspecified (imaginary) point, which in the forewing is generally positioned somewhere in the thorax; the imaginary center of the concentric socket-lines for the hindwing, however, is usually not as easily placed, and often is to the right of the body. Sockets have an open outer cup (collar) at the base of which, a chitinous retaining ring (Fig. **32**, arrow) constricts the diameter of the passage through which the pedicel fits. The retaining ring helps anchor the scale. Below the retaining ring is the lower chamber with rather heavy walls (theca) and at its proximal base a more elastic, thinner wall articulates with the pedicel base.

According to Kellogg (1894: 50) scales are held in position by the elasticity of the (retaining-wall in the) cup which closely clasps the pedicel. After death, this elasticity is lost by desiccation of the wing membrane, and the pedicels are more easily brushed from the wing than when the insect was alive.

Sockets may be erect, (Fig. **35**) standing almost at right angles to the surface of the wing membrane, or they may be semi-erect (Fig. **41**) or repressed against the membrane. The latter is the "normal" or average condition which occurs even when the scales held by the sockets are in an upright position (Fig. **43**). Hair sockets (Fig. **29**) are also angled or repressed, even when irregularly scattered between the regular rows of other types of scales.

The socket collar may have a prominent lip or projection (Fig. **28**) on the medial margin; usually, however, the collar is truncate (Fig. **34, 35**) apical with level margins. In many species with pulvinus pedicels, the outer collar may be enlarged and basket-shaped (Fig. **31**) to accommodate the swollen element, and may have a more eliptical collar-margin (Fig. **32**). Stossberg (1938) found a high positive correlation between the length of the fully developed scale and both the width of the collar opening and the inner diameter of the socket. She also found (*loc.cit.*) in *Ephestia* that the sockets of color-pattern forming scales (cover scales) were wider in mean average width than non-color pattern forming scales (middle and basal scales).

Significant studies on the development and structure of sockets, their pattern and direction of angle include Piepho (1955a, 1955b), Piepho and Marcus (1957) and Henke (1945), but no new vocabulary is given.

PEDICEL

Character states:

Short (socket-length) or elongate; pulvinus, parallel sides or attenuate; sulcate or smooth; straight or arched; solid or hollow; attached to obverse, basal margin or reverse surface of lamella.

The stalk may be long and narrow (Fig. **20**) or so short that it lies completely within the scale socket (Fig. **34**). Not infrequently it is pulvinus, (Fig. **9, 13, 31**), and the position of the enlargement is quite diagnostic. Hollow scales generally have hollow pedicels (Fig. **33**) and those primitive moth groups with solid scales are assumed also to have solid pedicels. Longitudinal grooves (sulcate base) along the pedicel surface are common, but the surface may be smooth.

Just as the orientation of the socket is related to the positional elevation of wing scales, the articulation of the pedicel with the blade has evolved with scale position and function. Semi-erect androconia, lying between cover and basal scales may be angled like a pancake-turner, (see Fig. **26**) with the pedicel-blade junction lying rather dorsad than medial on the basal margin. Many androconia, however, have the "normal" junction, where the pedicel and blade are in the same axis (Fig. **20**). Ventral blade attachments occur in many satyrid androconia

(Fig. **27**), which might preclude the supine position for such scale types. In the Niphandini of the Lycaenidae, the curious "hieroglyphic" androconia (Fig. **36**) have minute pedicels which are also attached to the reverse surface of the blade (Fig. **25**).

The pedicel tapers toward its apex in the androconia of some lycaenid genera (*Catochrysops* and *Rysops*) and its attachment to the blade is weak; extracted scales may thus appear to lack stalks.

SCALE BASE AND MARGINS

Character states:

With or without basal margin; base truncate, obtuse or auriculate; basal groove (sinus) present or absent; lateral margins parallel, crenate or attenuate; margins upturned (concave) or flat.

A basal margin is most obvious in scales where it is truncate (Fig. **13**), at right angles to its attachment to the pedicel. Margins may develop a small ear-lobe like (auricle) basal extension on either side of the pedicel (Fig. **34**), in which case their is a marginal sinus (Fig. **35**, arrow), or basal groove, between the auricle and the junction of the margin with the pedicel. In some cases where the stalk is joined to the blade of the scale on the reverse membrane (rather than marginally), a basal scale margin may be complete (Fig. **25**, arrow) and project basad of the pedicel-blade juncture. Not infrequently such scale bases are concave, and do not lie flat.

With piliform and other elongate and narrow scales, the base may lack definite margins, or be so gradually attenuate that both lateral and basalar margins do not exist. (Fig. **7**).

APEX

Character states:

Simple (unadorned) margin: obtuse, acute, caudate, aristate, scalloped, truncate, dentate (bi-, tri,-etc.).

Complex margin: coma, fimbria or crown; multicapitate; with several finger-like, to ciliate, filiform, flabelliform or tendril-like structures; parts in single axis or multiple (cluster); appendicular apex acute or clavate, porous or smooth.

The margin of the distal end of the scale varies considerably. In the typical basal scales there is a tendency for the margin to be gently rounded (obtuse) (Fig. **19, 20**). Cover scales, on the other hand, may be rather variable including straight (Fig. **43**), caudate (Fig. **17**), acute, dentate (Fig. **16, 18**), or scalloped (Fig. **40**). The number of teeth (bidentate (Fig. **11**), tridentate (Fig. **16**), etc.) may vary slightly from region to region on the wing, and is apparently also influenced by environmental factors (particularly temperature) at critical times during pupal development. The depth of the incised area between the tubercles appears also subject to both individual and specific variation.

Depending on the number and depth of the incisions, the apical margin may have evolved from a relatively simple structure with few appendages, to a crested, fimbriate or crowned tip (Fig. **12, 23, 24**). Many androconial scales, perhaps in response to their odor dispensing functions, have rather complex structures at their apices. The penicillate apex of the androconia of *Appias drusilla* (Fig. **13**) appears rather intermediate between a less complicated multi-dentate terminal margin, to a highly complex form such as the satyrid *Cyllopsis nayarit* R. Cher. (Fig. **24**) with its coma of clavate cilia.

POSITION AND ARRANGEMENT

Character states:

Supine, semi-erect (cupped), navicular or erect; flexed or twisted; cover-, middle-, or basal vertical positions; origin on margin, vein or membrane; mixture of scale types or homogenous patch; degree of overlap or external exposure; density.

Wing scales normally overlap one another like shingles on a roof (Fig. **37, 38**). Scale sockets and basal margins are thus covered, and only the mesal and apical parts of the upper surface of the scale are exposed. A single type of scale may cover or appear to cover most wing areas (Fig. **19, 40**) with slightly modified shapes in the region of wing veins and margins. Where several types of scales occur together (Fig. **38, 39**), they are usually arranged in definite layers; the uppermost scales with the greatest surface exposure are called cover scales. Depending on position, there may be middle or basal scales, and all three types have been characterized by sculptural features (see below). Basal scales are often brown or black in color, containing greater amounts of melanin than the cover scales for which they often form a light-absorbing or reflecting layer.

The importance of scale arrangement, at least as far as the cover-scales are concerned, is attested by the regularity of color pattern such that taxonomists describe consistent variables associated with geographical or temporal populations. Color pattern has been the subject of much research (see for example Schwanwitsch, 1949; Janin, 1968). Middle scales, particularly androconial types, seem to be more given to both individual and specific variability in density and wing position and arrangement. Eliot (1973) particularly notes such androconial variation in males of Lycaenidae, and Warren (1936, 1961, 1963, 1965, etc.) has recorded much on androconial variability in Pieridae and Satyridae.

Marginal scales (Fig. **16**) are usually rather elongate compared with other scales on the wing, and in addition, show sculpturing such as longitudinal ridges on both sids. In the Thysanura who respire, at least in part, directly through their integument, the longitudinal ridges on both surfaces of their scale keeps the latter apart and no doubt increases ambient air circulation. In marginal scales, it would seem their position would make them more vulnerable to contact and damage from objects (twigs, grass) touched by the wings in flight, and the increased suuport of bracing and struts on both surfaces would therefore be a distinct advantage.

Scales may lie flat or supine (Fig. **40**), semi-"erect" (Fig. **41**) or fully erect (Fig. **43**) with apical magins at a 90° angle to the wing membrane. In the latter case, the sockets usually retain their repressed condition, and either the pedicel, or the scale base, or both are flexed so that the body of the scale is upright. In the upright scales of *Jamadia gnetus* (Fabr.) (Fig. **43**), the blade of the scale is also folded into corrugated pleats.

Many iridescent type cover-scales, such as the copper colored *Lycaena hyllus* (Cram.) [=*thoe* (Guer.)] (Fig. **42**), show torsion such that their distal margins are tilted partially exposing the dark middle and basal scales beneath. The simple flection shown in *Urania* scales (Fig. **39**) exposes less area of the basal scales.

Clumps of androconial scales may form "scent spots" or patches on various parts of the wing. These may have associated scent glands, or dispersion scales, but they are usually visual distinctive because of their scale sculpturing, and subsequent difference in optical properties, or their arrangement and pattern, which accomplishes the same thing. The "polished" appearance of the scales in the area of wing overlap (basad on the caudal margins of the forewing and on the costal margin of the hindwing) is a visual indication of their morphological similarity, even at the ultrastructure level.

SURFACE AND INTERNAL STRUCTURES

Character states: (given with each character below).

1) *General:* external; sculptured or smooth; irregular or regular; all surfaces similar or sculpturing localized on one surface or margin; internal; solid or hollow.
2) *Longitudinal ridges. Character states:* present or absent, solid or with cavities; on all surfaces; parallel or non-parallel; flexuous (sinuous), spiral or straight; shelves parallel or alternate; scutes prominent or obscure; scute apex acute, truncate, upturned or recurved; refractive or non-refractive; inter-shelf groove deep (with fluting apparent) or shallow; inter-shelf sinus present or absent; fluting vertical or oblique; ratio of flute ridge number to number of transverse flutes; microribs (crenulations) apparent on larger flutes.

The longitudinal ribs are usually the most obvious of the surface sculpturing. They are absent only in relatively few scales, and these obviously specialized for particular functions such as the saccate (Fig. **51**) or hieroglyphic (Fig. **36**) androconia. Reverse surfaces (Fig. **9**) are usually devoid of ridges except near their marginal areas. Other sculpturing, particularly linear ribbon-like extrusions such as on the obverse of hieroglyphic (Fig. **36**) scales, are presumed to have a different origin from the ridges. The relation of such cytological structures as microfibril bundles to the ridges in the developing (or teneral) scale is given by Greenstein (1972b) and by Ghiradella (1974).

Longitudinal ridges may be arranged in a spiral (Fig. **14**), or run obliquely (Fig. **55**) across the longitudinal axis of the scale. The latter occurs in all heart-shaped, presumed odor-producing scales (Fig. **41**) in a marginal patch in the basal area of the forewing undersurface. These scales are found in both males and females of all species examined, and are therefore thought to produce some species specific, odorous recognition signal. Figure **55** also shows a light shadow of the longitudinal ridges on the obverse membrane in these scales, which run in the main axis; the two surfaces thus have ridges running in different directions.

Parallel ridges are the most common, but in scales which have constrictions or outlines of extreme shape (see flask scales, Fig. **5, 6, 10**), the ridges must fuse, or end blindly (Fig. **59**). Parallel ridges also run together basally (Fig. **28**) or show this tendency (Fig. **10, 13, 15**) even though they may not fuse. Naviculoid or other scales with concave-rounded bases or apices may also have non-parallel ridges (Fig. **27**) in those areas. Picken (1949: 16) notes that *Eilema lurideola* (Zincken) has scales whose lower surface is covered with a fan-like system of diverging ridges, while the ridges are parallel on the obverse surface. When ridge systems are on both surfaces, they usually unite along distal (or even basal) margins to form loops, which have been described by several authors (Suffert, 1924).

The scutes along the crest of the ridges are most marked on reverse surfaces (Fig. **55**) or on hair-scales (Fig. **21, 11**) where such features indicate the direction of "curl" of the hair-scale, with the obverse surface inner-most. Scutes are also obvious on high longitudinal ridges (Fig. **56**) particularly in lateral view (Fig. **60**) or where they appear to be more heavily sclerotized (Fig. **58, 60**). As indicated above, some primitive moth families have what appears to be solid ridges (Fig. **50**) which lack scutes, or noticeable lateral fluting. The remaining cross-elements and external sculpturing appears typical, however.

Differences in the highly diffractive, elongate, longitudinal ridges between *Morpho* and pierid types may be noted in Figures **3** and **4**. It should be noted in the *Morpho* scale that the width of the ridge shelves and central column are essentially equal wherever they are vertically placed on the longitudinal ridge. It is assumed that light will be refracted to the same degree in such a structure. This uniformity in depth of the refractive material is maintained in the pierid scale through the development of ridge sinuses (**rs,** Fig. 3). Optical properties of such systems have been discussed by several authors (see Ghiradella, 1974).

The very high iridescent-type ridges may undulate back and forth near their crests along their longitudinal axis (Fig. **44, 45**). This may cause some artifacts and confusion with certain light microscope (low power) observation, but apparently does not change the optical properties of the scales.

3) *Flutes. Character states:* present or absent; prominent or obscure; vertical or oblique rows; forming many or (few to) no transverse flutes.

The strengthening flutes (Fig. **57**, arrow) on lateral margins of the ridges may be noted on almost every figure at 5,000 diameters (see Fig. **52, 59,** etc.). Hirata *et al* (1957, 1959, 1966) have used the name *barb lines* for the flutes, alluding to the distinctly pinnate (feather-like) appearance imparted to certain scales (Fig. **49**) by these prominent structures. Their position and number (compare Fig. **52, 53**) may eventually be found to be diagnostic of scale types, but parameters of variability have not been established for flutes in this study.

The ridges of certain flutes continue across the obverse membrane (Fig. **49**) or the crossribs (Fig. **57**, arrow) as a transverse flute. This structure is usually visible on the crest of cross-struts, even when they are net-like (Fig. **53**).

4) *Cross Ribs. Character states:* present or absent; parallel to numerous non-parallel elements, or non-parallel; ladder-like or sinuous (appearing net-like); with narrow horizontal width or broad rungs (cross-piece or septum); transverse flutes on crest or not; attachment with trabeculae marked (as viewed externally) or obscure.

Cross ribs may be noticeable at relatively low magnification (Fig. **18**), particularly where they form very regular ladder-like rungs (Fig. **62**) even when they hold pigment granules (Fig. **46**) which may disrupt the regularity of the ribbing. The slender, rung-like pieces may occasionally branch, or run at an angle between the longitudinal ribs; the number of these oblique elements in otherwise rather regular and parallel, right-angle ribs, is distinctive of some scale types. Kobayashi and Yano (1957) used the term septal lines for the cross-meshes and linear network separating windows into a series of fenestrations.

Cross ribs are absent in some moth families (Micropterigidae and Eriocranidae, acc. Kristensen, 1970) and in specialized scales (Fig. **15, 20**) or surfaces (Fig. **9**), among the more numerous and normally ribbed types.

Care must be taken to distinguish the exact nature of cross ribs. It can be noted on Figures **1, 3,** and **4** for example, that the cross rib element forms the main lateral strengthening struts on the obverse surface. They are often noticeably supported by trabeculae, even in their central span (Fig. **60**) as well as positions beneath the ridges. However, where the obverse membrane is retained in the mature scale, and forms a broad supportive septum, there is less need for the cross rib struts. They may still be present, but obscured beneath the membrane. Further, the latter may be thrown into a series of strengthening pleats (Fig. **48**) or reinforced by transverse fluting (Fig. **49**). The fluting is usually distinguishable by its origin high on the lateral margins of the longitudinal ridges, but could easily be mistaken for the cross rib, where the latter is obscured by the membrane.

5) *Windows. Character states:* present or absent; regularly or irregularly spaced; prominent and large or small and pore-like; window membrane visible (at least in some spaces) or absent.

Internal structures are apparent from above in many scales because of large open windows (see Figs. **60, 63**). Where they are smaller (Fig. **55, 57**), their lateral parameters are more obvious, and they take on the appearance of portholes or large pores. Large windows are identified as lacunae by some authors; smaller openings have been termed areolae, particularly where they are numerous. All windows communicate directly with the lumen, or internal cavity between the obverse and reverse layers. When the cross-ribbing is net-like or has numerous sinuous elements, the inter-ridge area appears alveolate, (Fig. **53**) honey-combed with numerous areolae. The fenestration may be regular and rather central in location (Fig. **49**) or less-regular, pore-like, and scattered over the surface (Fig. **48**). It is even more apparent in capsular scent scales which lack longitudinal ridges (Fig. **51**).

6) *Trabeculae. Character states:* present, infrequent or absent; irregular pattern, but uniform density or degree of clustering (beneath longitudinal ridges, etc.); simple (unbranched) or branched and extremely diverse vertical column.

Trabeculae anchor the longitudinal ridges and cross ribs of the obverse surface to the underside lamella (Fig. **47**, arrow). They are, of course, absent in scales lacking a lumen, and are replaced in cells whose lumen is filled with latticed-lamellae (see Fig. **2**) by cuticular bars. The latter are micro-trabeculae, small rods or pillars which serve to hold the transverse lamellae at uniform distance apart. The bases of these may be noted on the lamellar plate fragment in figure **62**.

The random placement and irregular columnar nature of the trabeculae suggest tiny stalactites and stalagmites which have grown together to form a pillar. Perhaps a more realistic analogy might be imagined by pulling apart two rigid, flat surfaces between which has been place some viscous, tacky material. The adhering properties of the material would cause it to stretch between the surfaces, at a great number of points forming connecting and highly irregular columns, perhaps with no two alike. If the surfaces were separated a sufficient distance, the columns would snap, and the material would be pulled back toward the surface forming small hillocks. These trabecular hillocks are often visible along the internal surface of the reverse membrance in broken scales, or those with extremely high lumen spaces.

7) *Internal lamellae. Character states:* present or absent; extensive throughout scale, or of more limited extent; porous surface or smooth (to scabrous) plates; cuticular bars numerous between plates or less-obvious (inter-lamellar sinuses as wide as plate or not); extending vertically into lumenar trough beneath longitudinal ridges or confined primarily to reverse membrane portion of lumen.

The internal lamellae often lie in the scale lumen in its lower areas, adjacent to the reverse membrane (Fig. **62**). The iridescent scales of *Urania* (shown in figure **62**) has a considerable space between the uppermost plate and the obverse cross ribs and ridge-bases. Depending on the number of plates and their types, the lamellae may fill the lumen (see *Papilio* scales in Huxley, 1975) except for plate interstices. In most Lycaenidae examined, the plates rarely fill 2/3 of the distance between upper and lower surfaces, and are usually positioned in the lower half of the lumen, adjacent the reverse membrane.

Plate lamellae, as in *Urania* and *Papilio,* are distinguished from porous lamellae, found in lycaenids (Fig. **52, 54, 59, 61**) by the extremely punctate uppermost plates in the latter. Eliot (1973) termed this as a pepper-pot appearance. The porous surface apparently forms walls ("grains" or "cubes") between the holes of quite uniform thickness and quality such that incident light from any direction will have the correct orientation to produce a diffraction phenomena (Morris, 1975).

Thus there are at least two types of internal lamellar plates producing structural colors (both of which have types completely filling the lumen, or incompletely filling the lumen): plate lamellae and porous lamellae.

8) *Pigment bodies. Character states:* present or absent; spheroid or elliptical; attached broadly or at restricted points on pigment body; site of attachment to scale (cross ribs, longitudinal ridge base, lower lamellae, etc.).

In scales where they occur, the pigment bodies are very visible from above, clustered to the cross ribs (Fig. **46**, arrow). Even in the iridescent scales of those pierids such as *Colias, Eurema* and *Phoebis,* in which the longitudinal ridges are very high, the pigment bodies may be noted. It can be extracted from the scales with appropriate solvents, without apparent change in other scale parts. The darker pigments, such as the melanins, are apparently carried in the trabeculae and reverse lamellae. Occasionally it may also be in more obverse parts of scales, in the cross-ribs and base of the longitudinal ridges.

LEXICON OF SCALES AND SCALE STRUCTURES

Italicized words are archaic, or usage is not recommended; an asterisk (*) precedes words of foreign extraction referred to English equivalents (if any).

air film.	Air space between the longitudinal ridges particularly in *Morpho* type iridescent scales where the ridges are very high; see inter-ridge channel.
androconia.	See under *scale types.*
apex of scute.	Distal tip of the scaly process on the crest of longitudinal ridges; very marked on hair-scales, and ridges on reverse surfaces. (Fig. **55**, arrow; Fig. **56**, arrow).
areola (-ae).	A small space or window on the obverse surface; the openings between the meshes (septal lines) in a net-like inter-ridge arrangement; see also window.
articular membrane.	The thin somewhat pliable membrane uniting the base of a scale (petiole) with the sclerotized walls of the socket; usually visible only on sectioning.
articular socket.	The cup-like basal depression forming the joint or place where the scale attaches to the body wall; *cf.* socket, theca.
**Balg*(-e), or *Schuppenbalgen.*	Scale socket or follicle; see articular socket and socket.
barb line.	Hirata and Kubota (1957) term for *flutes* (*cf.*) or corrugations forming pinnulate striations on sides of the longitudinal ridges.
basal membrane.	Archaic and non-descript term; Onslow's (1921) name for the upper and lower scale membranes (and contents) taken together as distinct from the elevated longitudinal ridges.
battledore scales.	See under *scale types.*
beams.	Supportive struts connecting the outer layer of the hair-wall (in hair-scales) with the inner wall; probably homologous to trabeculae; sometimes erroneously used as "cross-beams" referring to cross ribs (*cf.*)
blade.	The expanded, usually flattened, leaf-like portion of scales as distinct from their stalk or pedicel; see lamina.

**cannelures*.	Sellier's (1971) term for *flutes* (*cf.*)
canaliculi.	Tiny (0.1u or less) openings in the inner wall of a hair-like scale which communicates to the hair chamber; usually more numerous and larger toward the distal part of the hair-scale; less distinct in wing hair-scales.
chitin pillars.	See trabecula.
**Chitinbrucken.*	See trabecula.
cilia.	See marginal scales under scale types.
color granules.	See pigment bodies.
costules.	See longitudinal ridges.
cross ribs.	Prominent struts or braces arranged transversely between the longitudinal ridges; may be supported by trabeculae below, and traversed by transverse flutes above, and may anchor pigment bodies along their ventral surfaces (Fig. **1**); when wider than one-half their length (between ridges) the word "rib" is not appropriate and the neutral term cross-piece or (*cf.*) septum used; when arranged in a geometric, or honey-comb pattern (dividing the windows into several components) the term septal line (Kobayashi and Yano, 1957) rather than ribs may be used.
cuticular bars (=**Stutzpfeilerchen*).	Small support rods or pillars which appear to maintain the distance between the transverse lamellae in the lumen of *Urania*-type iridescent scales (Fig. **2**).
Doppel-sackchen* (=Schuppenbalg*).	Double-pouch scale socket; see articular socket and socket.
envelope.	Huxley's (1975: 21) term for the obverse surface lamellae in iridescent scales of *Papilio;* it differs from the internal lamellae beneath it, not only by its outer position, but by the microribs on its superior surface.
fimbria (-ae).	The processes or fringe-like border on the apex of many androconia because of which these may be descriptively called plume scales or brush-tip scales (*cf.*).
flute (fluting).	Corrugations, grooves and micro-ridges, which form vertical or oblique pinnulate striations on the lateral margins of the longitudinal ridges (Fig. **60**, arrow); probably strengthening ridges or wrinkles, when continuous between adjacent ridges (along crests of cross bars or septa) they may be more appropriately termed transverse flutes (*cf.*) (Fig. **57**, arrow); around windows (areolae or lacunae) in the obverse surface they are termed marginal flutes; the *barb lines* of Hirata and Kubota (1957), the comb-like *teeth* of the *unit-keel* of Kobayashi and Yano (1957) and the

	cannelures of Sellier (1971) are synonyms. See also transverse and marginal flutes.
hair-chamber.	Central cavity or lumen of a cylindrical hair-like scale.
hairs.	See under *scale types*.
**Haltering*.	See retaining ring in scale socket.
horizontal mullion.	See mullion.
inter-ridge channel.	The air space between two longitudinal ridges usually occupying a V-or U-shaped valley or depression depending on the proximity and heighth of the adjacent ridges (Fig. **4**); equals *air film* of Onslow (1921).
inter-shelf groove.	A shallow longitudinal furrow or channel between the shelves along the lateral margins of the longitudinal ridges (Fig. **3**); may be crossed vertically or obliquely by flutes giving a cancellate appearance (cross-barred or latticed) with the longitudinal furrows and shelves decussate by transverse lines (Fig. **56**).
intra-shelf sinus.	See ridge sinus.
inter-lamellar sinus.	The interstices in the porous element between and around the lamellar-layers and microribs (Fig. **2**); Huxley (1975) believed these form internal air films and are continuous with one another and the external atmosphere; see also inter-trabecular sinus.
interstice (*-ces*).	A space between one thing and another; term used for windows (Miller, 1974), the major perforations in the upper scale surface between longitudinal ridges.
inter-trabecular sinus.	A space or cavity surrounding the trabeculae and between the upper and lower lamellae (Fig. **3**); also called the lumen, particularly where the trabeculae are obscure, infrequent or wanting; in *Urania* type scales with many lamellae lying in the same plane as the surface layers, these spaces should termed inter-lamellar sinuses; see also inter-lamellar sinus.
keel.	Term used (Kobayashi and Yano, 1957) for longitudinal ridges.
lacuna (*-ae*).	A space or gap where something has been omitted; often used (Davis, 1975) synonymously for areola, or a window, gap or pore in the obverse membrane.
lamella (-lae).	A thin plate, scale or layer (see lamina); often restricted (or distinguished in context) to either the upper or lower scale surface; also used for the variable number of (porous element) refractive

layers in the lumen of iridescent scales of the *Urania*-type (see latticed-lamellae).

lamina(-nae). A thin sheet or surface composed of a flat layer or layers; used by some authors (lamella) to refer to the expanded, usually flattened leaf-like part of the scale as distinguished from the petiole, or scale stalk; other authors use the same term to refer to the upper and or the lower surfaces of a single scale (or refer to these surfaces as being laminated, *i.e.* composed of several layers); usually distinctive in context.

**Langsriefen.* See longitudinal ridges.

latticed-lamellae. Another name for porous element (*cf.*); the multistratified, intersticed striae between the upper and lower scale surfaces in the *Lycaena* type iridescent scales (Fig. **2**); the lamellae are separated by cuticular bars (*cf.*) and the inter-lamellar sinuses are connected with one another through pores; its latticed appearance is particularly marked in dorsal view where numerous punctations (pores) break up the surface into a granular mosaic (Fig. **52, 61**); (*cf.*) plate-lamellae.

longitudinal ridge. Prominent elevated structures usually running from basal to apical areas, rarely obliquely on the lamellar surface (Fig. **49, 50**); composed of one or more scutes, and often with flutes and other features on their lateral margins; usually of higher elevation and closer spacing in U-V and highly reflectant (iridescent) (Fig. **34**) scales; lower and further apart (fewer per scale) in non-reflecting scales (Fig. **35**).

lumen. The main cavity or space between the obverse and reverse surfaces; also called the inter-trabecular sinus (Fig. **1**) (*cf.*) in *Morpho*-type scales.

marginal flute. The micro-ridge or bordering flute on the edge of a window or areola in the obverse membrane; characteristic of primitive moth families (Neopseustidae, Davis, 1975) and generally not present in more specialized lepidopteron groups.

micro-filaments. Fibrous material arranged in longitudinal bundles beneath the developing cross ribs and just above the under-surface lamella during pupal development in the early stages of ridge formation; according to Ghiradella (1974: 397) the microfilaments are contractile elements of a cell and may contribute to scale structure by causing flection and tension (and consequent wrinkling and buckling) in the developing scale.

microribs. Extremely minute (50-60nm) thickenings on the obverse scale surface forming a close pattern of parallel or sinusoidal ridges or wrinkles and depressions resembling fingerprints; usually not visible except with electron microscopes.

microtubules. Extremely fine ducts in the cell (prescale) body and which form a fine webbing concentrated in the three major axes (fontal, sagittal, and transverse) and which form a cytoskeletal structural support for the cell body; it is presumed they are involved in the development and orientation of the final internal supportive framework of the scale.

mullion (-ns). A slender vertical bar or pier between lights of windows, screens, etc., "to furnish with or divide by mullions"; see flutes.

obverse surface. The top or principal scale surface which usually lies away from the wing surface; the opposite of reverse.

oval bodies. See pigment bodies.

pedicel. A slender stalk or base of the scale which functions in articulation and support (Fig. **20**, arrow); a narrow basal part to which a larger part is attached; equals petiole or **stiel.*

pepper-pot structure. Eliot's (1973) term for the porous element (*cf.*) in the lumen of certain scale types (Fig. **52**).

petiole(-lus). Another term for the slender stem or base which supports the blade of the scale, as distinguished from the blade; see pedicel.

**pfeiler* (=pillar). See trabeculae.

pigment bodies. Cluster of pigment (or pigments) in roundish, elliptical or rod shape structure in the inter-trabecular sinuses of the Pieridae (Fig. **46**, arrow); appear to be attached by one point to trabeculae, cross ribs, and inner hair wall (of hair scales) and hang downwards by gravity (Fig. **1, 3**).

pillar. See trabecula.

plate-lamellae. The multistratified, intersticed striae between the upper and lower scale surfaces in the *Urania* type iridescent scales; the lamellae are separated by cuticular bars (*cf.*) and the inter-lamellar sinuses may be connected by inconspicuous pores; the lamellae lack the conspicuous and rather regular pores which characterize the porous element (=latticed lamellae) (Fig. **62**, arrow).

plume scales. See under *scale types.*

porous element. An interlacing, sclerotized material lying in the lumen which appears latticed or porous from above (Fig. **52, 61**), but laminated in lateral view; the punctations are surrounded by a matrix which forms a framework of solid or sclerotized material of smooth texture, and often with similar width between holes; in some species the matrix appears to have been laid down by serpentine and latticed fibers in several dimensions rather than horizontal or vertical sheets; equals the "pepper-pot" structure of Eliot (1973); in cross-section schematics the synonym latticed-lamellae (*cf.*) might seem more appropriate; found in iridescent scales of the *Lycaena* type; not to be confused with plate-lamellae, (*df.*).

process. — Term referring to a prolongation of a surface or margin; the distal scale margin (apex) bearing "teeth" of varying number and shape; not used in recent literature.

**Querbalkchen.* — Cross beams or rungs; see cross ribs.

retaining ring. — A collar-like chitinous ridge on the inner margin of the scale socket serving to bind or hold the shaft or pedicel of the scale (Fig. **32**, arrow); when viewed with transmitted light, it divides the socket into a basal (proximal) part (which appears slightly bulging because of its thinner walls) and a collar-like distal part.

reverse surface. — The layer opposite the top or obverse surface; on a prone, flat scale, the adwing surface next to the wing membrane (Fig. **1, 2, rm**); the surface is often devoid of structures (except at its margins, or is slightly scabriculous (Fig. **9**); Kobayashi and Yano (1957) refer to the layer as the reverse membrane.

ribs — A bar, rod, or the like, used for support or strenthening structures; see *cross ribs, microribs, flutes.*

ridges. — Another name for the longitudinal ridges; confused by some who mistakenly use it for longitudinal shelves, or flutes, or other prominent upswellings of a surface forming noticeable striations.

ridge sinus. — A small space or lacuna inside a longitudinal ridge (Fig. **3, rs**); they are between the ridge shelves in those scales with opposite (as opposed to alternate) ridges and usually are of a number one less than the number of shelves (the scute on the summit of the longitudinal ridge usually lacks a sinus); might also be designated as intra-shelf sinuses.

scale(-es) or squama (-ae). — A usually flat, highly modified unicellular outgrowth of the body wall; of a wide variety of shapes, sizes and functions, but usually distinguishable by external and/or internal ultrastructure. *Scale types* have been identified as follows:

Scale Types: — **Androconia.** Specialized scent scales found in males; may be localized and concentrated (see scent spots or patches), or scattered among other scale types; may be phylliform (Fig. **15, 20**), or capsular with comate (Fig. **12, 13**), or cirrose apex; Aurivillius (1880) distinguish several kinds on the basis of general shape and outline; recent authors continue this practice and name androconia by shape (viz, battledore, racket, dagger or flask) or other prominent feature (hieroglyphic, hair-pencil, brush-like organelle, etc).

Androconial macules (spots, patches). Clusters of androconial scales on the wing or within pouches, veins, or coiled-scales forming prominent spots; the secondary sexual characters of males of certain species.

Basales. See basal scales.

Basal scale (Tiefenschuppen, basales). Scales distinguished by their vertical position adjacent to the wing membrane and usually covered entirely or partially by other scale types (Fig. **38**, arrow); usually darker scales (contain more melanin) and with attenuated (rather than auricular) bases; when scale sockets are arranged in alternate or sub-parralled rows, the basal scale sockets are usually proximad to other scale sockets.

Battledore scales. A scent (androconial) scale shaped somewhat like a tennis racket (Fig. **20, 15**) where the petiole forms the handle; found commonly in males of Plebejinae and other Lycaenidae; named after a bat or racket used in striking a shuttlecock in an old game.

Brush-tip scales. Any one of a number of scale types (usually androconia) whose apical margins end in a tuft or cluster of structures (fimbria or coma) whose function is probably associated with dissemination of odors (pheromones) (Fig. **23, 24**); Miller (1974) used the term brush-like organelles for this apical cluster in satyrid scales.

Cover scales (=*Deckschuppen, tegentes*). Scales distinguished by their superior position overlying other (particularly basal) scales (Fig. **37**, arrow); usually highly sculptured on obverse surface and the source of much of the structural color in the wing.

**Deckschuppen.* Top or cover scales on wing; one of 3 main categories of wing scales (as used by Kuehn & Henke, 1929-36, Koehler, 1943 and Schmidt, 1965) characterized by being 4 1/2 to 5 times as long as wide, and having small windows between the longtitudinal ridges. See cover scales.

Fringe scales. See marginal scales.

**Gitterplattentyp.* A type of scale earlier called *Leitertypus,* characterized by having longitudinal ridges in rather low profile, and with rather apparent cross ribs and windows in the obverse surface between the ridges.

Hair-like scales (pili). Elongate, thread-like scales, cylindrical (usually elliptical, rarely circular) in transverse section (Fig. **21, 22**); composed of the same elements as a phylliform wing scale, except coiled around itself forming an inner hollow core.

Iridescent scales. Highly reflectant structures which diffract light physically such that they appear to "change color" (usually metallic) when viewed from slightly different angles; of two basic types (Suffert, 1924):
a) *Urania-type* iridescent scales (Fig. **39**); the structures (plate-lamellae) producing the optical properties are in the lumen of the scale (between its upper and lower surfaces).
b) *Morpho-type* iridescent scales; the structures producing the optical properties are the longitudinal ridges on the obverse scale surface (Fig. **4, 34**).

Ladder-type scale (=*Leitertypus*) Distinguished by having numerous, closely-spaced, parallel cross-ribs between the longitudinal ridges, with relatively open windows between (Suffert, 1924) (Fig. **46**).

**Leitertypus* (=ladder-type). One of 3 categories of scale types proposed by Suffert (1924) and based on characters of the cross ribs and punctations between the longitudinal ridges; inter-rib area cribrate; see perforated-type scales.

Marginal scales. Scales occurring along the margins of the wings which are characterized by being very long, usually attenuate, and having longitudinal ridges and other features of the obverse surface also on the reverse side (Fig. **16**).

Middle scales (=*Mittelschuppen*). Scale distinguished by their vertical position intermediate between *cover scales* and *basal scales* and showing some characters of both (Fig. **11**, arrow).

**Mittelschuppen.* Intermediate or middle scales; one of 3 main categories of wing scales (see Kuehn and Henke, 1929-36; Koehler, 1943) characterized by having lateral margins parallel; being 3-4 times as long as wide and other features; see middle scales.

Net-type scale (=Netztypus). Distinguished on the basis of having an irregular net-like pattern of interconnecting chitinous bridges arranged in the area bordered by the cross ribs and longitudinal ridges (Suffert, 1924) (Fig. **53**).

**Netztypus* (=net-type). One of 3 categories of scale types proposed by Suffert (1924) and based on characters of the cross ribs between the longitudinal ridges; see net-type scales.

Pepper-pot scales. Term used by Eliot (1973) for the *Urania*-type iridescent scales found in the Theclinae/Lycaeninae/Polyommatinae branches of the Lycaenidae (Fig. **52**); however, these differ from the true *Urania* type in that the latter has a non-porous plate-lamellae, while the lycaenids have porous (pepper-pot) lamellae.

Perforated-type scales (=*Lochreihentypus*). Distinguished on the basis of having numerous pores or punctations on the obverse surface of the scale between the cross ribs and longitudinal ridges (Suffert, 1924) (Fig. **61**).

Plume scales. A type of scent scale (androconia) whose distal margins are provided with a "tuft" of densely packed short hair-like structures (Fig. **12**).

Sensilla squamiformia. Innervated sense scales as noted by Freihling (1909) and other workers (see Snodgrass, 1935); usually of elongate fusiform (=spindle) shape.

Tegentes. See *cover scales.*

**Tiefenschuppen.* One of 3 main categories of wing scales (see Kuehn & Henke, 1929-36; Koehler, 1943) characterized by having many ladder-like cross rungs and large windows between the longitudinal ridges; lateral margins are usually not parallel; see *basal scales.*

**Wellenplattentyp.* A type of scale earlier called *Lochreihentypus,* with extremely high longitudinal ridges and strengthening flutes, which give a corrugated appearance to the scale; *Morpho* type scales (*cf.* iridescent scales)

scaly process. Hirata and Kubota (1957) term for scute (*cf.*)

scent brush. A cluster or "tuft" of specialized scales (usually elongate piliform or filiform shaped) which function to aid in emitting or diffusing odors from glands usually at their bases; see under scales, brush-tipped.

scent glands. See scent organs.

scent organs.	Structure which form or diffuse odors which may serve as pheromones or as repellents; usually associated with one sex as a secondary sexual character.
scent scales.	See androconia under *scale types.*
scent tufts.	See scent brush.
*Schuppenbalg (=*Doppelsackchen*).	Double-pouch scale socket; see articular socket and socket.
scute.	Linear, narrow sclerotized process on the crest of the longitudinal ridge (Fig. **55, 58**), they are inclined at a slight angle to the main axis of the scale so that they project distally from under the apex of more proximal scutes (Fig. **56**, arrow); the distal part of the lamellar shelves in a longitudinal ridge; the scaly process of Hirata and Kubota (1957) and the *squamule* of Sellier (1971).
sensory scale.	See sensilla squamiformia under scale types.
septum (-ta).	A thin wall or partition usually dividing two cavities; the "meshes" dividing the areolae (giving a honey-combed appearance) may be termed septal lines, in contrast to the broad septal areas when the areolar openings are sparse; sometimes narrowly restricted (Kobayashi and Yano, 1957) to the upper elements in the obverse surface between the longitudinal ridges, which overlie the obverse (window) membrane.
seta(-ae).	Slender hair-like unicellular appendages of the cuticle; which are hollow and have membranes (joints) at their base which permits some flexibility; scales are presumed to have arisen from setae.
shelf(-lves).	More or less conspicuous ledges forming parallel lines along the lateral margins of the longitudinal ridges, and which terminate in a scute on the vannal ridge (Fig. **4**); usually prominent in iridescent scales and best observed in cross section preparation, where the projection of the shelf from the surface may be exaggerated by shrinking during preparation, particularly resulting in deepening of the (*cf.*.) *inter-shelf groove.*
sinus (-ses).	An opening, hole or cavity usually specified in context; rather inappropriately used for the slight marginal indention at the base of auriculate scales, between the lobe and the petiole.
socket.	The exocuticular swelling in the wing membrane with which the scale articulates (*cf.* articular socket, theca and retaining ring) (Fig. **28, 30, 34**), may be upturned or appressed against the wing surface such that its scale lies flat against the membrane.

socket apex (=lip). — A prominent lip or projection (in the same axis as the scale) on the medial margin of the collar of the scale socket (Fig. **28**), without such an apex the socket has a truncate outer margin (they appear even).

squama (*-ae*). — A scale; the usually flattened single cell outgrowth of the body wall; see *scales* and *scale types*.

**squamule*. — Sellier's (1971) term for scutes (*cf.*)

stalk. — Another name for pedicel.

**Stege*. — A cross bar; see cross ribs.

**Stiel*. — A stalk or pedicel; see pedicel.

striae. — Non-descript term; usually referring to a series of parallel lines; could be any of the following (as may sometimes be determined by other descriptions in the text of an author), (*cf.*) barb lines or flutes, cross ribs, longitudinal ridges.

**Stutzpfeilerchen*. — See cuticular bars.

supports. — Used by Japanese authors for trabeculae.

theca. — The sclerolized wall forming the socket on the wing membrane with which the scale articulates; (*cf.*) articular socket.

trabecula (-lae). — (See synonyms below). A small chitinous pillar or rod forming a supporting framework between the upper and lower surface of a scale (Fig. **1, 4;** Fig. **47,** arrow).
- *beams* (in hair-like scales).
- *Brucken* (of Spuler 1895) or *Chitinbrucken* of several authors).
- *pillars* (of authors)
- *supports* (of Japanese authors).

**Trabekeln* (*=Pfeiler*). — See trabecula.

transverse flute. — An extension of the vertical or oblique *flutes* to the top of the cross ribs so that they form a continuous (albeit sometimes sinuous) bar between the longitudinal ridges (Fig. **57**, arrow); cross ribs may have as many as three such strengthening flutes along their crest; when the cross-ribs are buried or obscured by window membranes, etc., the transverse flutes may appear as the main external cross member between longitudinal ridges (Fig. **49, 57**).

unit-keel. — Term used (Kobayashi and Yano, 1957) for scutes.

**Unterseiten-lamelle*. — See reverse surface.

vane. Anderson and Richards (1942) name for both the vertical and horizontal elements in a hypothetical model of a longitudinal ridge; Hirata & Kubota (1957) attempted to preserve the term, but it was abandon by Hirata & Uehara (1959) and further modified by Hirata & Ohsaka (1966); the scute of the crest of the longitudinal ridge may be said to be on the (*cf.*) *vanal ridge.*

vanal ridge. A non-structural term designating the crest of a longitudinal ridge; in iridescent scales the crest is covered with a linear series of scutes which overlie one another like shingles on a roof; not to be confused with longitudinal (*cf.*) *shelves,* which are structures forming parallel lines along the lateral margins of the longitudinal ridges and terminate in a scute on the vanal ridge.

vertical mullion. See mullion.

window. A space or opening in the upper lamellae between both the longitudinal ridges and the cross ribs (Fig. **21**, arrow); the window communicates with the inter-ridge channel dorsally, and the inter-trabecular sinus ventrally; it may be "closed" by a thin transparent membrane only distinguishable by appropriate TEM shadow casting techniques; windows also occur on hair scales where they may be conspicuous in a parallel series of transverse flutes (*cf.*); windows may be reduced in size to a point where the terms "pores" or "slits" might seem more appropriate; also called lacuna (*cf.*) or areoles (*cf.*) particularly when the septal lines between form a sinuous net-like mesh.

window membrane. The transparent membrane which "covers" some windows or lacunae in the obverse surface; sometimes narrowly referred to (Kobayashi and Yano, 1957) as the obverse membrane proper.

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APPENDIX:
DESCRIPTIVE TERMINOLOGY USED IN SCALE LITERATURE
(NOT EXHAUSTIVE)

abwing surface.	Side away from the wing; in flattened scales, the "upper" surface.
adwing surface.	Side next to the wing; in flattened scales, the "lower" surface.
acicular.	Needle-shaped, roundish in cross section, with a long, slender point.
acute.	Sharp pointed; terminating in or forming less than a right angle.
alveolate.	Honey-combed or resembling such by geometrical uniformity.
annular.	Ring-shaped or ring-like.
apex.	The point furthest removed from the base end; the "tip" end.
aristate.	Having or bearing a bristle or hair.
articulate.	To connect by a joint; jointed or segmented.
attenuate.	Gradually enlarging apically; drawn out.
cancellate	Cross-barred or latticed in appearance.
capsular.	Bladder, flask or swollen-shape.
cribrate.	Pierced with closely set, small holes or pores.

Schematic cross-sections of parts of mature scales: Fig. 1. Yellow-colored scale where color stems from internal pigments (modified from Hirata & Uehara, 1959); Fig. 2. Iridescent scale of the plebeid type in which the structural colors are produced by an internal porous element of latticed-lamellae which extend upwards beneath the longitudinal ridges (modified from Schmidt and Paulus, 1970). *Urania* type scales produce structural colors by internal plate-lamellae, which are non-porous, and do not extend upward into the arch of the lumen beneath longitudinal ridges; Fig. 3-4. Iridescent scales in which structural colors are produced mainly in the longitudinal ridges; Fig. 3. Pierid type with ridge-sinuses and pigment-bodies (modified from Ghiradella, 1974); Fig. 4. *Morpho* type with solid ridges (modified from Lippert and Gentil, 1959). Abbreviations: *cb,* cuticular bar; *cr,* cross rib; *ilp,* inter-lamellar pore; *ils,* inter-lamellar sinus; *irc,* inter-ridge channel; *isg,* inter-shelf groove; *its,* inter-trabecular sinus; *lr,* longitudinal ridge; *mr,* microrib; *pe,* porous element; *pg,* pigment body; *rm,* reverse membrane; *rs,* ridge or inter-shelf sinus; *sc,* scute; *sh,* shelf; *tr,* trabecula.

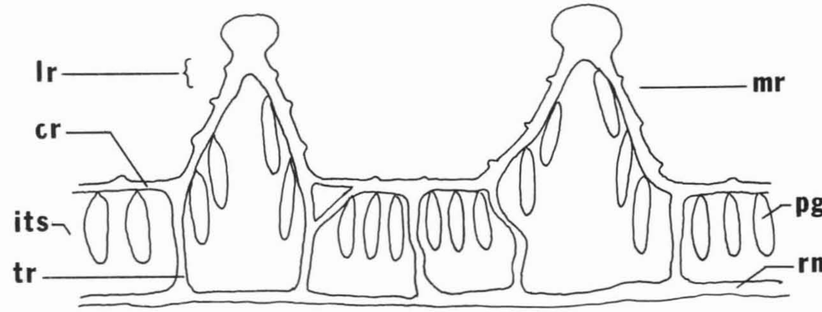


FIG. 1

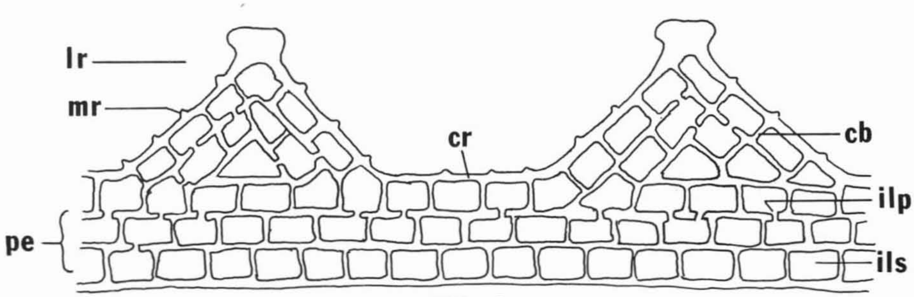


FIG. 2

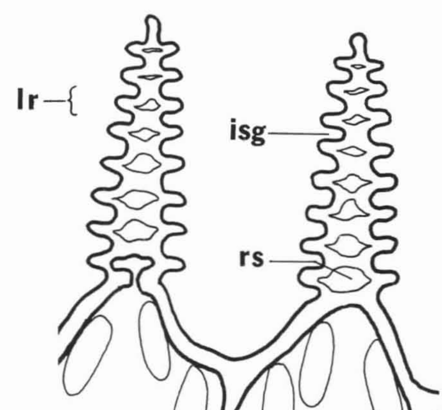


FIG. 3

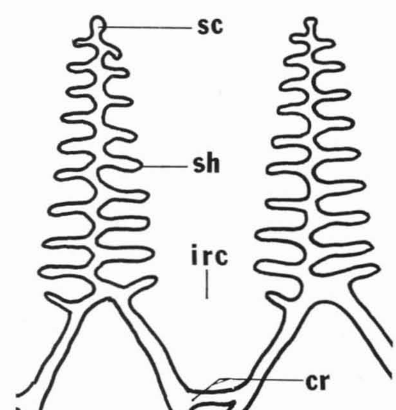
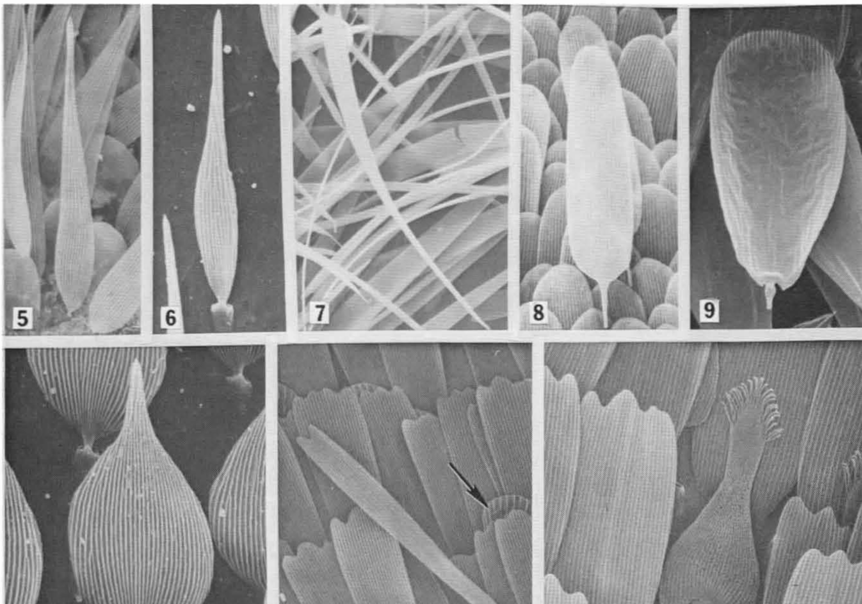
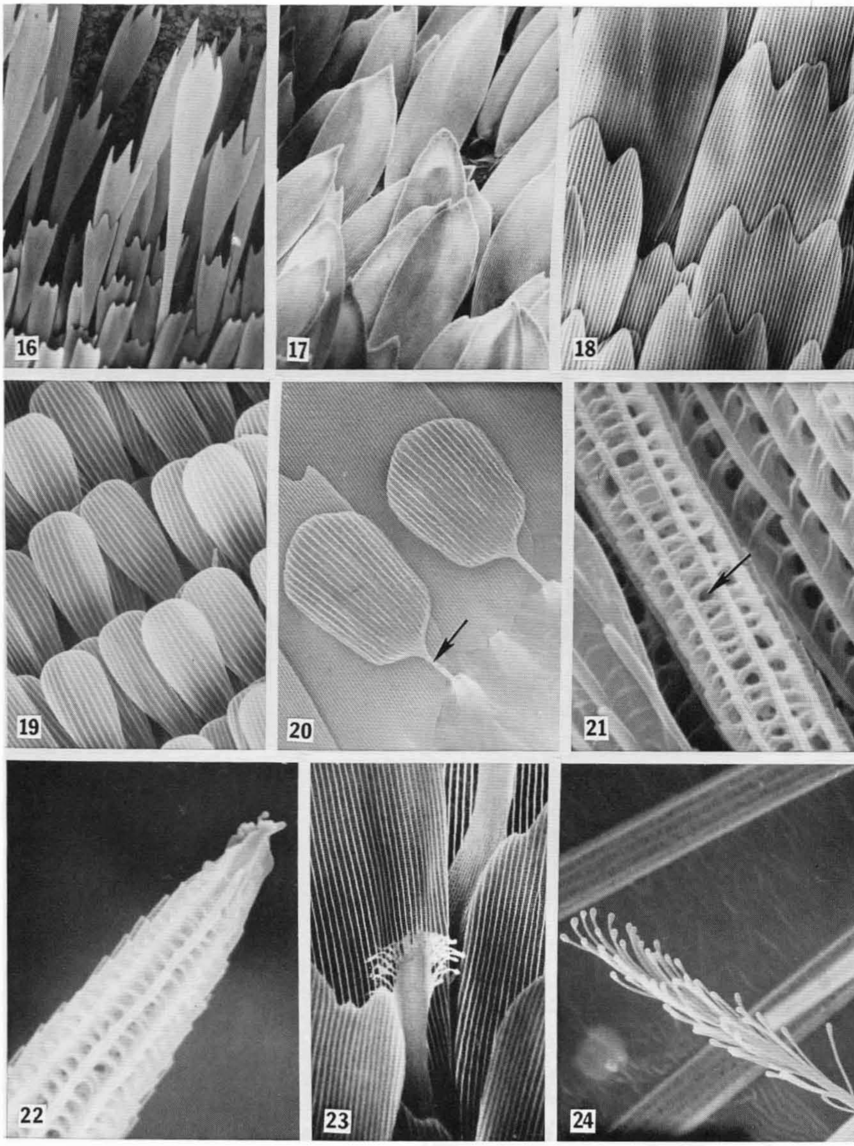


FIG. 4

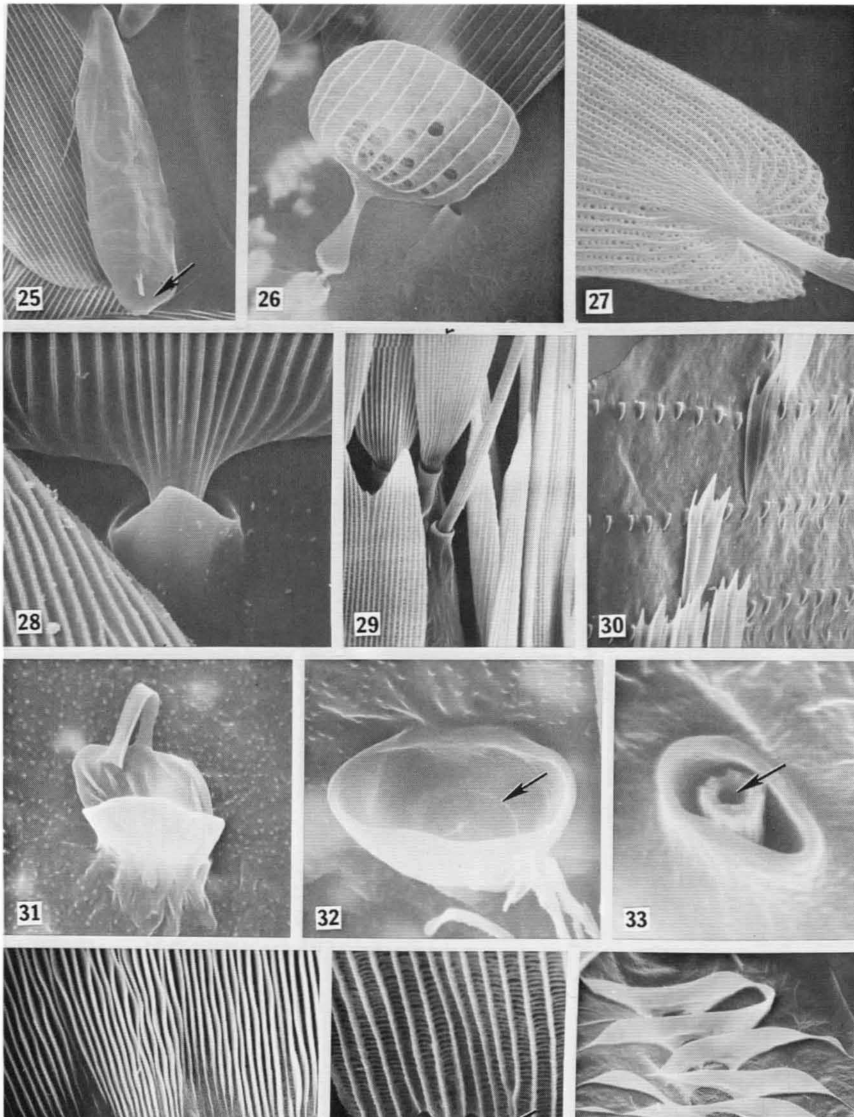
cirrhose (cirrose).	Ending with filiform tips, coiling as a tendril.
coma.	A tuft of hairs; a leafy crown or head.
clavate.	Distal end enlarged or clubbed.
dentate.	Bearing tooth-like prominences or saw-like teeth.
distal.	Away from; more distant from point of orign.
fenestrate.	Perforated by obtuse window-like openings.
filiform.	Thread-like; long, slender and of equal diameter.
flection(=flexion).	A bending of the blade of the scale in the transverse axis; usually a gentle arching of the blade which elevates its middle portions and proportionately lowers the apical margin; in some species the flexion is strongest along the apex, where it approaches a complete curl *cf.* torsion.
fusiform.	Spindle-shaped; broadest at the middle and narrowing toward both ends.
lacunate.	Having a pit, a gap or an empty space, or irregular cavities.
lamellate.	Extended and flat, as a blade of a leaf.
laminate.	Formed of thin flat layers or leaves.
lanceolate.	With acute apex and base, tapered at two ends as the head of a lance.
navicular.	Boat shaped; concave, with elevated margins.
obovate.	Pear-shaped; broadest above middle.
obtuse.	Rounded or blunt (not sharp) or pointed; forming greater than a right angle.
ovate.	Egg shaped; broadest below the middle.
pandurate.	Fiddle shaped; modification of an ovate type.
penicillate.	Tipped with a tuft of fine "hairs".
pertuse.	Perforated with a hole or slit.
petiolate.	Bearing a stalk or pedicel; placed upon a pedicel.
phylliform.	Leaf-shaped.
piliform.	Hair-like; very slender and long.
pinnate.	Feather-like or with markings resembling a feather.
proximal.	Closer, nearer to a point of attachment or origin.
punctate.	Having pits, depressions or a series of impressed points.
saccate.	Pouchy or bag-shaped.
scabrous.	Rough, irregular surface.
scabriculous.	Regularly and finely wrinkled.
spatulate.	Flat and broad at the top, attenuate at the base.
striate.	Marked by repeated, parallel, ridges and furrows or lines.
sulcate.	Furrowed with longitudinal grooves.
teneral.	The condition of the pharate and newly emerged adult when it is not entirely expanded hardened, or fully colored; not fully mature.
torsion (of scale).	A twisting or turning of the blade of the scale along its longitudinal (or horizontal) axis, *cf.* flection.



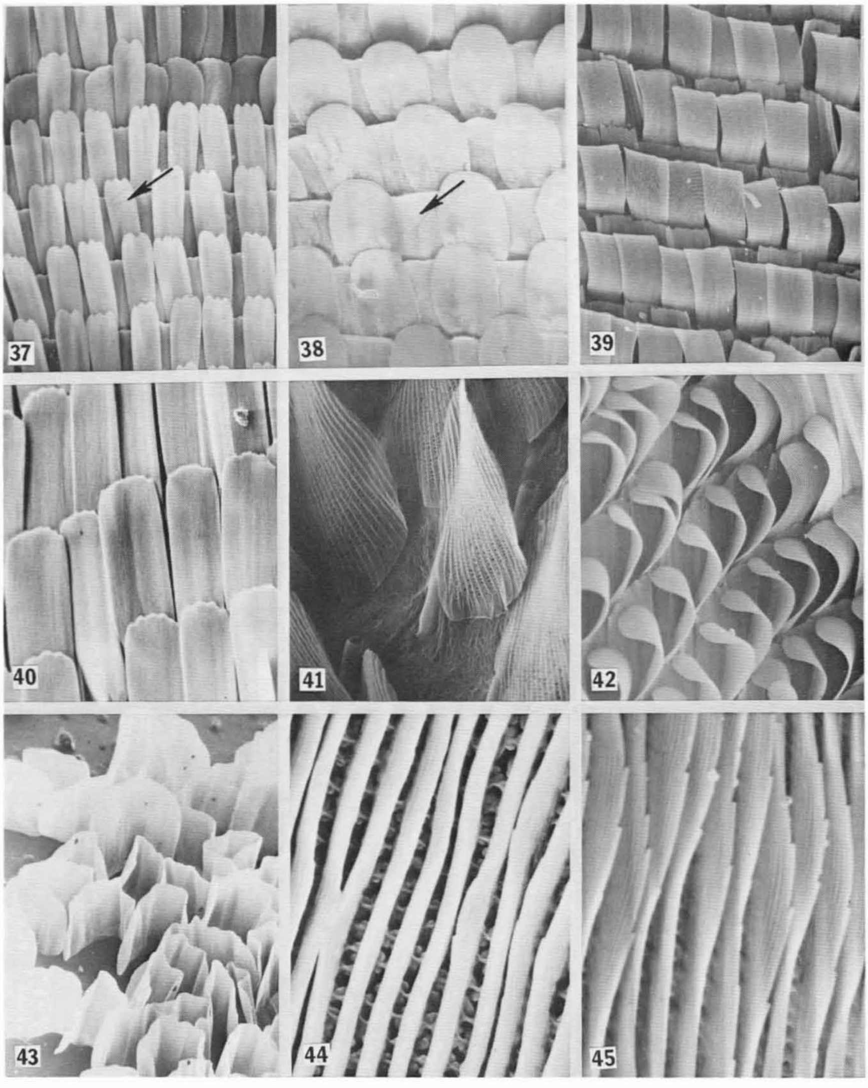
Figures 5-15, Examples of scales from male butterflies; see text. 5, *Lampides boeticus* (L), 150 × .6, *Parnassius apollo* (L), 170 × .7, *Callophrys rubi* (L), 2,000 × .8, *Satyrium calanus falacer* (Godt.), 300 × .9, *Phoebis philea* (L), reverse surface, 325 × .10, *P. apollo* (L), 200 × .11, *Jamides celano* Cram., 200 × .12, *Pieris rapae* (L), 300 × .13, *Appias drusilla* Cram., 600 × .14, *Haeteca piera diaphana* d'Alm., 750 × .15, *J. celano* Cram., 850 ×.



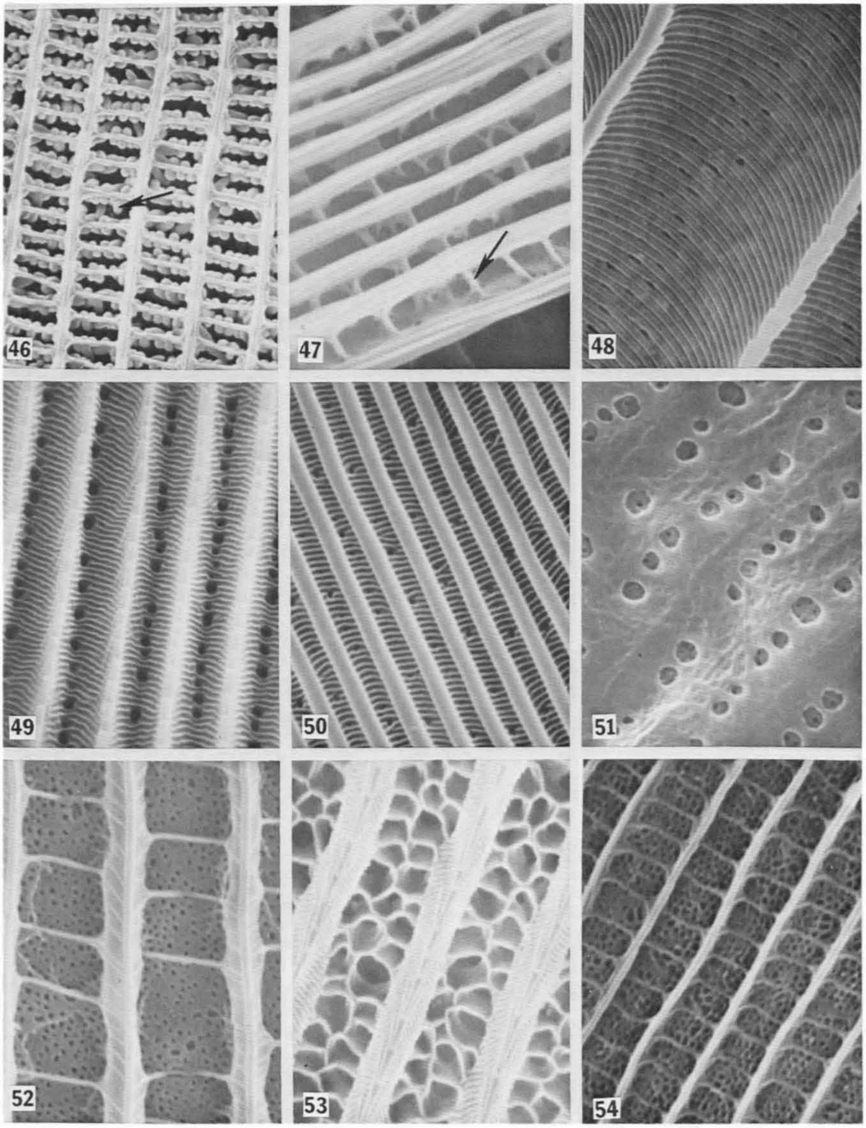
Figures 16-24. Scales and scale apices; see text. 16, *Eumaeus minyas* Hbn., 75 × .17, *Delias harpalyce* Donovan, 150 × .18, *P. philea* (L), 250 × .19, *P. philea* (L), 200 × .20, *Lycaena editha* Mead, 400 × .21, *Leptotes cassius* (Cram.), 5,000 × .22, *Heliophorus brahma* (Moore), 5,000 × .23, *Pereute leucodrosime* Kollar, 500 × .24, *Cyllopsis nayarit* R. Chermock, 1,000 ×.



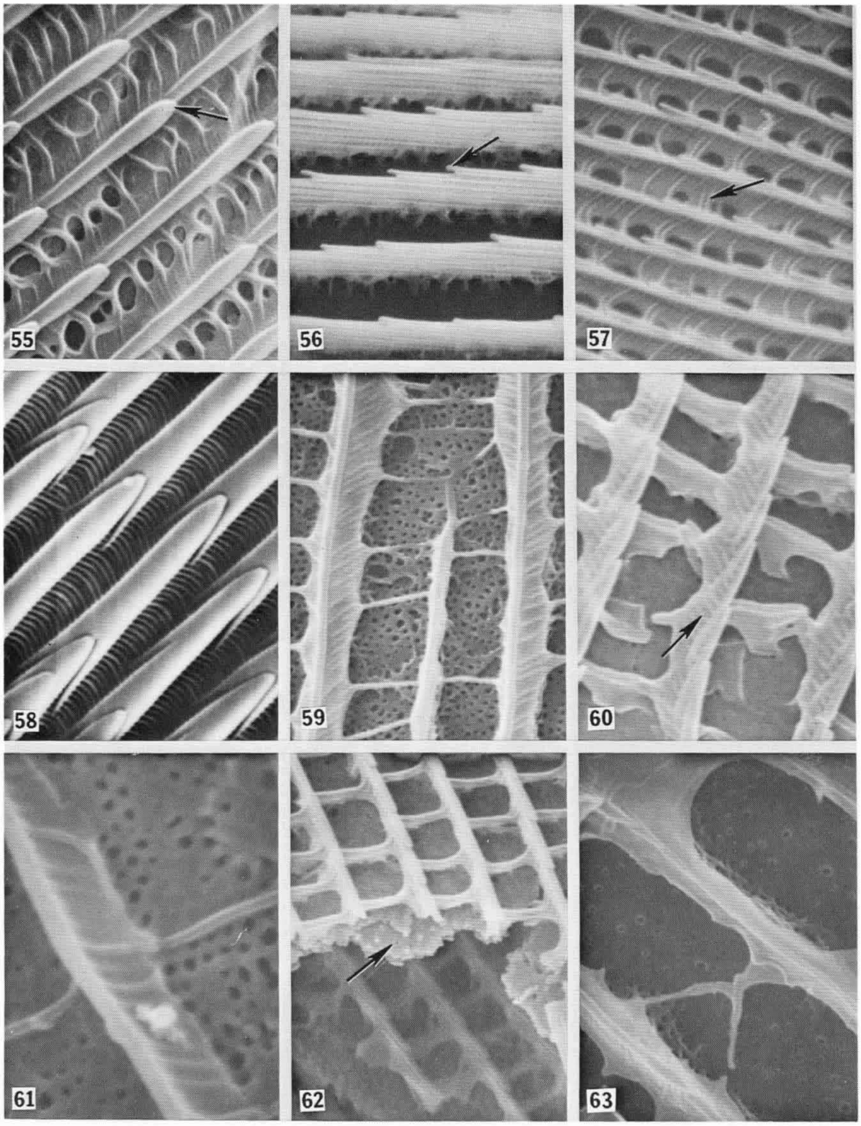
Figures 25-36. Scales and scale sockets; see text. 25, *Niphanda fusca* Brem. & Gr., reverse surface 425 × .26, *L. cassius* Cram., 800 × .27, *C. nayarit* R. Cher., reverse surface, 2,000 × .28, *P. apollo* (L.), 1,000 × .29, *Perisama humboldtii* Guer.-Mene., 500 × .30, *Morpho polyphemus* Westw. & Hew., 100 × .31, *P. rapae* (L), 1,250 × .32, same, 2,500 × .33, *Glaucopsyche lygdamus* Dbldy., broken pedicel in socket, 5,000 × .34, *Morpho aega* Hbn., 1,500 × .35, *P. leucodrosime* Koll., 1,500 × .36, *N. fusca* Brem & Gray, 1,500 × .



Figures 37-45. Scales and longitudinal ridges, see text. 37, *P. philea* (L) 100 × .38, *Gonepteryx cleopatra* (L), 150 × .39, *Urania leilus* (L), 75 × .40, *M. aega* Hbn., 150 × .41, *L. cassius* Cram., 750 × .42, *Lycaena hyllus* Cram. (=*thoe* Guer.), 200 × .43, *Jamadia gnetus* (Fabr.), 150 × .44, *Phoebis thalestris* (Illiger), 5,000 × .45, *P. philea* (L), 5,000 × .



Figures 46-54. Obverse surfaces of scales; see text. All 5,000 × .46, *Phoebis avellaneda* Herr.-Schaef. 47, *M. aega* Hbn. 48, *P. avellaneda* Herr.-Schaef. 49, *Papilio ariarathes* Esper. 50, *Cephalospargeta elongata* Moesch. 51, *J. celano* Cram. 52, *L. boeticus* (L). 53, *Papilio machaon* (L). 54, *L. boeticus* (L).



Figures 55-63. External and internal structures of mature scales; see text. All 5,000 × except as noted. 55, *S. calanus falacer* (Godt.), reverse surface. 56, *Morpho menelaus* Bdv. 57, *M. polyphemus* Westw. & Hew. 58, *P. philea* (L), 59, *L. boeticus*(L) 60, *U. leilus*(L), 7,500 x .61, *N. fusca* Br. & G., 15,000 x .62, *U. leilus*(L) 63, *J. celano* Cram.