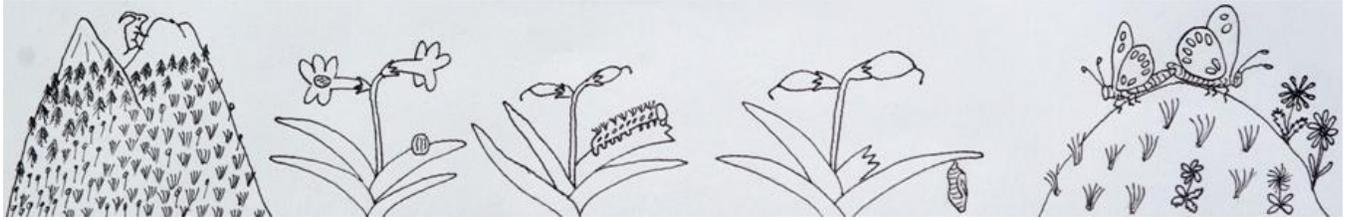


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## CHAETOTAXY OF FIRST-STAGE BUTTERFLY LARVAE, WITH IMPROVED HOMOLOGIES AND NOMENCLATURE FOR LEPIDOPTERA SETAE AND SENSILLA

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{Note: The following paper was finished in ~1990, when I hoped to include setal maps of >100 species of Colorado butterflies collected thereafter, but I did not find the time or patience to finish those. So the paper is published here without those >species, and without the hundred+ available setal maps published elsewhere in the literature by other persons.}

### INTRODUCTION

One of the mysteries of the universe as we know it, is that the objects we see continue to display shape and structure at both the infinitely microscopic and the infinitely astronomic frontiers of our search, without apparent limits, no matter how powerful the microscope or cyclotron or telescope; the "elementary particles" and galaxies both continue to multiply. Caterpillars are no exception to this rule: their bodies are covered with a forest of strange structures, whose shapes are as varied as the plants in a landscape, and the closer we look the more structures we see. But the caterpillar's small size has retarded our investigations: the structure of first stage larvae is one of the last frontiers of butterfly study.

Study of the small forest of caterpillars is challenging. Merely seeing some tiny structures is a challenge in microscopy. Following their changes in position and form from one taxon to the next, and from one larval stage to the next, is a challenge. Naming the structures is another challenge, especially as the names of the structures are inextricably linked with theories on their homology.

Butterflies have thousands of setae on mature larvae, which usually cannot be individually homologized with setae of other Lepidoptera. But most first-stage butterfly larvae have few setae, the same setae present in most Lepidoptera, so the first stage represents a unique opportunity to compare butterflies to other Lepidoptera to determine their evolution. The presence of extra setae in some first-stage butterflies provides excellent characters for use in determining evolution within butterflies, and provides unique opportunities not available in most Lepidoptera for determining homologies of the basic Lepidoptera setae.

This paper has two goals. The first goal, of interest to all Lepidopterists, is to improve the names given to the setae and olfactory pores and sensillae: new homologies of the setae are presented

including those on the last abdomen segment (good homologies on this segment are presented for the first time); a name is assigned for every seta and sensilla of the entire body including mouthparts, building upon Hinton (1946); different names are assigned to non-homologous setae that formerly were confused by having the same name; figures and an alphabetical glossary of structures are presented for users. The second goal is to present new data on butterflies, including setal maps for every subfamily known (only Pseudopontiinae and Calinaginae now lack setal maps), an improved key that includes additional subfamilies and genera, and diagnostic characters for each family, subfamily, and tribe. Scott (1986a) presented setal maps for selected first stage butterfly larvae and presented a key to all known North American subfamilies. Scott (1985, 1986b) and Scott and Wright (1990) used characters of first stage larvae as well as many other characters to deduce the phylogeny of butterflies.

## LABORATORY TECHNIQUES

When describing structures, it is standard to figure and describe only the structures of the LEFT half of the body (Figs. 1-2 of Scott 1986a); for example, a statement that the prothoracic shield has three olfactory pores means that the left side has three and the right side has an additional three). In addition, setal maps should illustrate EVERY segment from T1 to A10, because there are nearly always at least minor differences from segment to segment, and readers may wonder about possible differences if some segments are omitted. Every setal map of the head should adopt the OBLIQUE LEFT side view (of Figs. 1-2 of Scott 1986a, for instance) in which the lower flange of the head is bent outward to show the SO and PG setae and pores. Because setal maps are quite detailed, and the names of the structures may have to be changed for various reasons, tedious redrawing and inking setal maps involves a definite probability of creating errors, so the author recommends that the drawings be made and labeled in pencil, not inked, and photocopies of the drawings be used for publication, minimizing errors and minimizing enormous waste of time.

The larger tactile setae can be seen with a binocular microscope having only 15-45X. But the smaller tactile setae (V1 beneath the thorax for instance), all the proprioceptor setae, and nearly all the olfactory pores (except Fa is often visible under low power), require much higher power to find. Most of the smaller structures can be found on whole larvae using high quality 100-1000X binocular microscopes. But to find the small structures with ~400X using lesser quality microscopes, and to find the smallest structures on the least accessible areas with high quality microscopes, one must prepare the head and carcass on a glycerine slide. In a dish of alcohol, remove the head by grasping the neck as close to the head as possible with fine forceps, and prying off the head with a #00 pin. The body must now be cut down the right side: insert one point of fine dissecting forceps into the interior of the body through the neck opening, squeeze the forceps holding the larval integument so that the two halves of the forceps run parallel along the right side of the body, and run the point of a #00 insect pin down the groove formed by the two halves of the forceps tips, to neatly scissor the larval integument on the right side; repeat this maneuver until the integument is cut all along the right side. Now soak head and integument in KOH: place 5-10% KOH in the bottom of a small vial with a screw-cap (loosely screwed on so that air pressure cannot cause the vial to explode), cover eyes with goggles for safety, heat the vial over an alcohol lamp until it begins to boil, then swirl the vial or swirl the fluid with an eyedropper until it cools. Rinse head and carcass in a dish of alcohol, place them on a slide with a drop of glycerine, arrange them for viewing (flatten the carcass), and place a cover glass slowly (to avoid bubbles) on top. After microscope viewing, store the head and integument in a genitalia vial with glycerine (these parts are so small that they will become lost in a large 3 cm vial), and place this vial in a larger vial with label. Lacking a high-quality microscope, breaking the head into pieces is sometimes necessary to

get the head rim and mouthparts in a flat position for better viewing; and several larvae are always desirable because a given individual may have the exoskeleton folded to hide a particular structure. Scanning electron microscopy is great for realistic photos; but light microscopes are superior for detecting olfactory pores (because light shining from below makes the pore appear as a bright spot), and are just as good or better for detecting proprioceptor setae (a good-quality binocular microscope with 50X, 100X, and 400-100X is ideal).

Interpretation of published setal maps. Because first stage larvae are so small, and many authors lack the highest quality microscopes, some errors or omissions occur on most published setal maps. Most maps show only the tactile setae, miss the smallest tactile setae such as the ventral V1 setae, and show none of the proprioceptor setae. In interpreting setal maps, the rule is that if a tiny tactile seta is not shown, it is probably present but was missed; and if a proprioceptor seta is not shown, it is almost certainly present but was missed. No matter what the magnification and quality of the microscope used, there will always be structures at the limit of resolution that tantalize the viewer but are difficult to interpret. Therefore, the smallest structures shown on any drawing are most subject to error, and one must interpret the drawing according to the quality of the microscopes used to prepare it. Luckily, the proprioceptor setae of butterflies show little variation, so that studies of the larger tactile setae are still very valuable. Some of the present setal maps--those lacking proprioceptor setae--do not show many of the smaller setae and olfactory pores.

## **HOMOLOGY (and see Figs. 2-5)**

Two problems must be surmounted in naming setae. The names should be linked to the evolution of the animals by being homologous from one species and family to the next (true evolutionary homology) and should be homologous from one body segment to the next (serial homology). And the names themselves must be clear (the names of separate structures must not be confused) and usable (the names must be as simple as possible for ease of labeling drawings and typing manuscripts).

The fact that most setae of primitive Lepidoptera larvae are homologous to those of advanced Lepidoptera is well known; the setae of Lepidoptera are more uniform than those of any other large insect order (Hinton 1946). Even the related orders Mecoptera and Trichoptera have similar larval setae (Stehr 1987), and future work will no doubt homologize at least some of their setae with those of Lepidoptera.

Serial homology ("homotypy" of Hinton 1946) is the determination of which setae on a given segment are homologous with which setae on another segment. Serial homology can be difficult to study: basically, when a single genetic mutation deletes one of the normal setae (or greatly alters its shape or position), we assume that a seta absent on one segment (or greatly altered the same way in shape or position) is homologous with the absent (or altered) seta on another segment. There are various methods for determining serial homology. In Drosophila flies, gene mutants have been found that alter the presence or absence or alter the structure of a seta, so that by examining which segments are affected by the mutation homologies can be established. These genetic mutants are not known in Lepidoptera, and because few workers study Lepidoptera setae, and few individual larvae are studied, few mutations will be found. The next best evidence comes from using differences of setal patterns between closely related species, and assuming that because they are closely related, their differences in each structure are probably due to a single mutation: a mutation during evolution may have deleted or changed a seta in one species, so the location of the absent or changed seta from segment to segment indicates serial homology. Other evidence involves the shape of a seta: the length and shape of homologous setae are likely to be similar from one segment to the next. A species that has gained a few secondary setae through the division of a primary seta

(or lost a primary seta) can be compared to a related species having only primary setae to help determine serial homology. Finally, the positions of homologous setae are likely to be similar from one segment to the next.

Hinton (1946), following half a dozen pioneering workers (W. Mueller, H. Dyar, W. Forbes, S. Fracker, C. Heinrich, A. Gerasimov, etc.), polished the modern system of naming Lepidoptera setae, and his system is now used nearly universally (Mutuura 1956 renamed ALL the setae, which was too drastic a step because almost all subsequent authors ignored his names). Hinton's head setae mostly use names developed by C. Heinrich from 1916-1921, while his body setae were named by Hinton himself. The Hinton system of naming setae involves a capitalized one- or two-letter abbreviation of the seta name, followed by a number, for instance F1. Olfactory pores are named with the capitalized letter(s) of the associated seta followed by an uncapitalized letter, for instance Fa.

The Hinton system is used in this paper with the few modifications explained below. The changes involve improvements in the homology of setae, slight alterations of the names of some head setae to avoid confusing them with those of the body (see Clarity of Terminology and the Glossary below), some new names for structures ignored by Hinton (setae and sensilla of the mouthparts and legs), and a system for naming lenticles and scoli. For the first time, names are presented for ALL the setae and visible olfactory pores and related visible sensilla of the entire larva; each name is unique so that no two structures on the larva can be confused. The alphabetical glossary below lists the name of each structure and related terminology.

MacKay (1963) discussed some problems in naming setae, and compared the naming systems of Hinton (1946) and Mutuura (1956) (however, MacKay was wrong in claiming that the prothorax shield terminology of Hinton differed from 1946 to 1956--it does not). MacKay suggested--correctly I think--that Hinton's postnatal ("subprimary") L3 seta on the abdomen actually is a SV seta.

It would of course be useful to examine larvae of all the families of Lepidoptera on a comparative basis to study the homology of setae. However, most Lepidoptera families have only primary setae, and therefore do not display enough variation to be suitable for drawing conclusions regarding homology. Butterflies are ideally suited for study of homology, both because first-stage larvae have primary setae in some taxa and some secondary setae in others, and because older larvae develop secondary setae in all taxa. Only such moth groups as Zygaenidae are likely to be as useful as are butterflies for the study of setal homology.

MSD2. A major error of homology made by Hinton (1946) is his designation of MSD2 on the abdomen as SD2 (the SD2 column on his Table 6 should be renamed MSD2 and transferred to Table 3); MSD2 occurs on the abdomen as well as on T2-3 in nearly all Lepidoptera. David M. Wright first informed me of this error. It is difficult to decide which of the two MSD's on T2-3 is homologous to the single MSD on A1-8, but MSD2 of T2-3 is usually more similar in position to the single MSD on A1-8, so the abdominal proprioceptor is here named MSD2. There is no good evidence that any Lepidopteran tactile seta on the body has become a proprioceptor, although some tactile setae on the heads of leaf mining moths and some dorsal head setae of Lycaenidae (in which the head is retracted into the prothorax) are reduced and evidently serve a proprioceptor function. Hinton (1946) stated that MSD2 has lengthened into a tactile seta on at least older larvae of Hepialidae, some Tineidae, and some Pyralidae; however, Hepialus (Hinton's Figs. 18, 21) has both MSD2 and SD2 on T2-3, and SD2 and SD1 have the same lengths on thorax and abdomen, so it is my opinion that MSD2 has been lost on the abdomen of Hepialus, where SD2 has been gained from the thorax, and MSD2 has NOT enlarged to become SD2 on the abdomen as Hinton thought.

SD Setae of Thorax. The arrangement of SD setae and lenticles in Piruna (Hesperiinae) indicates the correctness of Hinton's designation of SD1 as anteroventral to SD2 on T1-3. In Piruna (Fig. 20)

a long SD1 seta is anteroventral to a SDr ring gland=lenticle on T1-3 (Hesperiid setae are known to become lenticles, Franzl et al. 1984), and on A1-8 SD1 is posterodorsal to the SDr lenticle, and SD1 occurs alone on A9-10. The more-anterior SD seta on T1-3 is usually longer so is SD1, the posterior seta is SD2.

SV Setae of Thorax. On T1, the posterior SV1 is usually longer than the anterior SV2, which seems to prove that these names are correct, as previous authors thought.

D Setae. Comparison of D and SD on thorax and abdomen of Danainae gives the appearance that D2 on abdomen is actually SD2, but in Ithomiinae T2-3 has five D and SD setae, which seems to indicate that on both Ithomiinae and Danainae the extra seta is D1.2 on both thorax and abdomen.

Dorsal Setae of A10 Including L Setae. Hinton (1946) did not discuss the setae of A10 at all. They are often useful to distinguish between butterfly species and higher taxa. The dorsal setae of A10 have usually not been named or homologized with those of the body, but various authors (including Hardwick 1958, and B. Rankin [in Common 1974]) name the four primary setae on the suranal plate, and these names were used by Scott (1986a).

The homology of D1 on A10 is rather certain. Evidence includes: D1 is long on both A9-10 in Aegiale (Megathyminae, Fig. 24) and some Trapezitinae (Figs. 13-19), longest on both A9-10 of Erebia (Satyrinae, Fig. 39), short on both A9-10 in Euschemoninae (Fig. 6) and Coeliadinae (Fig. 7), in Speyeria (Nymphalinae, Fig. 51) A9 and A10 have an extra D1 seta, and Boloria improba (Nymphalinae, Fig. 50) has three D1 setae and two SD1 setae on A9 and has an extra A10 seta that is nearest D1.

Likewise there is no reason to question the homology of SD1 on A10. Parnassius (Parnassiinae, Fig. 26) has secondary SD1 setae on every body segment, and the three SD setae on A10 (SD1, SD1.2, SD1.3) are positioned consistent with accepted homology. In Curetis (Curetinae, Fig. 55) and Lycaena (Lycaeninae, Fig. 56) the very short and spatulate setae of T1-A9 are all SD setae, and Curetis and L. cupreus (David M. Wright, pers. comm.) have one anteroventral SD seta on A10 very short and spatulate, proving that it is SD.

However, current evidence suggests that D2 and L1 on A10 should be switched on the drawings of the above three persons, so that L1 is posteroventral (ventromedial) to D2 and usually smaller than D2, as suggested by the first person to name A10 setae (Ripley 1923; Dugdale 1961 and McGuffin 1977, both cited by Stehr 1987, also use Ripley's system), for the following reasons. One case involves the number of secondary D setae on A9 versus A10: Mechanitis (Danainae, Ithomiini, Figs. 2, 36) has two D1 setae on T2-A8 (D1 and D1.2), and has two setae in the position of my D2 on A10, which seems to prove the new serial homology that these A10 setae are D setae and not L setae (even though the extra seta D1.2 is nearest D2 instead of D1 on A10; the name of this extra seta would be D2.2 if we looked only at A10, but it seems best to call it D1.2 because it is closer to D1 on T2-A8). Most of the evidence for the new homology of D2 and L1 involves the relative lengths of the setae on A10 versus more anterior abdomen segments. L1 is generally the shortest dorsal seta on A10 of butterflies, and D2 is often the next shortest seta. These lengths may help warn against predators; evidently the A10 setae are adjusted in position and length so that they extend to the rear a more similar amount than if they were all of equal length. Thus the most posterior seta (L1) is shortest, and the next most posterior (D2) is next shortest. So deviations from these normal lengths may help determine homology. The Pyrrhopyge (Pyrrhopyginae, Fig. 8) A9 has D1 short, L1 twice as long, SD1 extremely long, and D2 even longer, and on A10 D1 is very short, my L1 is twice as long, and SD1 and my D2 four times as long as D1, which seems to prove the new serial homology. In Coeliadinae in which L1 is longer than D1-2 and SD1 on A9, L1 is as long as D2 on A10 (both are very long, and SD1 is almost as long). In Epargyreus (Pyrginae, Fig. 12) in which L1 is longer than D1-2 and SD1 on A9, L1 and D2 and SD1 are very long on A10. Euschemon (Euschemoninae, Fig. 6) has SD1 greatly lengthened and L1 lengthened less (doubled)

on A9, and D2 and SD1 are greatly lengthened on A10 where L1 is lengthened somewhat and is the same size on A9-10. In Nathalis (Coliadinae, Fig. 30) L1 is shorter than the other dorsal setae on T1-A9 and is also much shorter on A10. In Nymphalis (Nymphalinae, Fig. 46) and Polygonia (Nymphalinae, Fig. 45) L1 is shortest on A9 and on A10. In Actinote (Nymphalinae, Fig. 48) the lengths decrease gradually from D1 to D2 to SD1 to L1 on A9 and on A10. Many Trapezitinae have D1 and SD1 very long on A9, and these also have D1, D2, and SD1 greatly lengthened on A10 (L1 lengthened only slightly), which may also help prove the new homology of L1.

The SV setae of A10 have moved to the rear of the segment (see below), which helps support the rear position of L on A10; apparently all the lateralmost setae of A1-9 (L and SV) moved posteriorly on A10.

But the toughest test for the new homology of D2 and L1 on A10 is Lycaena (setal maps prepared by David M. Wright), which has up to seven setae on the suranal part of A10: a dorsal seta presumably D1 behind a plate of lenticles and an olfactory pore, two posterior setae that are often tufted and are apparently L setae, a seta anteroventrad of D1 that is apparently D2, and two anterior setae that are apparently SD setae, and the seventh very short spatulate SD seta above the latter two SD setae. The problem in Lycaena is that the three anterior long setae (SD, SD, D2) are in line so that it is tempting to label them L setae because T1-A8 have three or four L setae in line, and especially because most Lycaena have three L setae on A1-8 and two "L" setae on A10, whereas L. cupreus has four L on A1-8 and three "L" on A10. This homology, if true, would be a variant of the old homology in which the L setae include several setae below SD1 and posteroventral to SD1. However, other Lycaenidae do not support this variant homology well. Curetis (Curetinae, Fig. 55) is similar to Lycaena in having the "L" setae on A10 in one row, but the A1-8 L setae are in two rows, and the D setae also form a row on A10, which weakens the variant homology. And in Feniseca (Miletinae, Fig. 54) the lowermost SD setae on A1-9 are one long above one short, and the two anteriormost setae on A10 are also long above short indicating that both are probably SD, which breaks up the variant homology theory which places "L" setae in a line on A10. In Strymon (Lycaeninae, Fig. 57) there are four anterior then two posterior setae on A10, without a conspicuous line, and comparing these to the number and position of setae on A1-7 indicates that the anterior four could be D1 and D2 above two SD's, and the two posterior could be L's. And when comparing Callophrys (Lycaeninae, Fig. 58) to Strymon (Lycaeninae), Callophrys has only three L's on A1-8 (Strymon has four) and the lowermost of the two posterior setae of the six setae on A10 is very short; presumably the loss of the fourth L seta on A1-8 genetically caused a drastic reduction in size of one L on A10 because of genetic homology. So, I am rejecting this Lycaena variant homology. The two posterior L setae (my homology) are often tufted on Lycaena, which would help determine homology if previous segments had tufted setae, but they do not; the only other locations of tufted setae on Lycaena are P1 and P2 on the A10 proleg.

L Setae Prior to A10. The homology of the L setae between thorax and abdomen seems to be elucidated by the secondary setae of Polygonia (Figs. 3, 45), in which the normally-single anteroventral L seta on A1-8 and the normally-single L1 seta on T3 consist of one large and one small seta on a single plate which resembles the usual T1 plate containing L1 and L2. All of these plates seem definitely homologous, which indicates that the following names should apply to the L setae of the Polygonia body: T1 has a posteroventral L1 and a shorter anterodorsal L2 on one plate, T2 has one long L1, T3 has a long posteroventral L1 and a shorter L2 on one plate, A1-8 have a long posteroventral L1 and a shorter anterodorsal L2 on one plate anteroventral to spiracle and have a long L3 posteroventral to spiracle, A9 has one long L1; the secondary seta on T3 and A1-8 should be called L2 because of its correspondence with L2 of T1. Thus the usual two L setae on A1-8 of most butterflies and Macrolepidoptera should be called L1 (not L2) anteriorly and L3 (not L1) posteriorly.

This conclusion seems to be confirmed by the following arguments. L1 is always anterior to the spiracle on T1 so should logically be anterior to the spiracle also on A1-8; and L1 generally occupies an anterior position on T2-3 so should logically occupy the anterior position on A1-8. That the usual one anterior L1 seta on T2-3 is homologous with the anterior L1 seta on A1-8 is proven by Asterocampa (Apaturinae, Figs. 4, 42) which has two L setae on T2-3 (the anterior is L1, the secondary posterodorsal is L3) in the same positions as those of A1-8. I accept the view of MacKay (1963) and Mutuura (1956) that the postnatal (subprimary) "L3" abdominal seta of Hinton (1946), which he used to determine homology, is really SV1, so I reject Hinton's homologies of L setae on the abdomen (Hinton's L1-3 on the thorax evidently ARE L setae). (Most readers will be confused about which setae are primary or postnatal [=subprimary], so here is a list of all the postnatal setae that occur on most Lepidoptera: L3 on T1 in the superfamilies prior to Pyraloidea-Macrolepidoptera, L2 and L3 on T2-3, SV1 [Hinton's L3] on A1-9, P3 [Hinton's SV3] on A3-6.) Hinton (1946) shows L1 posterior to L2 on the abdomen of Hepialidae and Noctuidae, but MacKay (1963) (following Mutuura 1956) indicates that they should be switched in position, to homologize them with the L setae of the thorax, in accordance with my homology. Larvae of the Lepidoptera suborder Ditrysia prior to Macrolepidoptera (except for several of the earliest Ditrysiian families, Tineidae-Lyonetiidae-Acrolophidae-Yponomeutidae) have the abdominal L setae close together, but in Macrolepidoptera these setae are far apart. Hinton (1946) noted this dichotomy of families; almost no taxa have the setae intermediate in position. My homology explains why these two L setae are either close together, or far apart: in families with abdominal L1-2 close together, the anterior seta is in general smaller, so it is apparently L2, the longer posterior seta is L1; in Tineidae etc. and in Macrolepidoptera where both are far apart, they are of equal size, and are apparently L1 (anterior) and L3 (posterior). (An independent origin of the far-apart L setae in the two groups Tineidae-etc. and Macrolepidoptera is possible, but unlikely according to Mutuura.) Furthermore, many segments have three L setae in various Lepidoptera so it is reasonable to apply the name L3 to one of the L setae of abdomen segments A1-8: in the Ditrysia prior to Pyraloidea-Macrolepidoptera there are three setae L1-3 on the prothorax (two primary, one postnatal--postnatal seta L3 was lost on T1 by the ancestor of Pyraloidea-Macrolepidoptera); T2-3 have three setae after the first stage larva in most Lepidoptera; there are several L setae on A9 (all L setae except L1 were lost on A9 by the ancestor of Pyraloidea-Macrolepidoptera); and Mecoptera have three L setae on most body segments (G. Byers, in Stehr 1987). Hinton (1946, top p. 33) states that A9 has L2 short and dorsal to L1, which is in accordance with the positions of these two setae using my homology. Hinton's (1946) drawing of T2 of Noctuidae (Fig. 22) shows L1 anteroventral to L3, the same positions as I am labeling these setae on the abdomen. The only problem with this homology of L1-3 is that during the evolution of the two groups that have L1 and L3 far apart, the loss of L2 and the reappearance of L3 on the abdomen would have to have taken place simultaneously; this may seem unlikely, but evidently it happened.

On Mechanitis (Danainae, Ithomiini, Fig. 36) the posterior L seta on A1-8 is twice as long as the anterior, an unusual condition; the single L seta on A9 is halfway between the two in length but its anterior position on the segment suggests that it should be called L1 and not L3.

SV and P setae, Including Ventral Setae of A10. MacKay (1963) and Mutuura (1956) correctly showed that Hinton's postnatal ("subprimary") seta "L3", positioned just above the prolegs, is really an SV seta, and should be named SV, so the proleg setae of the same segment can be named P without conflict of homology. To accept Hinton's and others' name L3 for this seta requires two simultaneous assumptions: the assumption that SV1 (present on T2-3) disappeared on A3-6 and, simultaneously, the assumption that L3 (present on T2-3) moved down to replace it on A3-6; both assumptions are unlikely by themselves, and are ludicrous in combination. This paper assumes neither and labels "L3" SV1 on A3-6, based on its position. Lithosiinae (Arctiidae) seem to prove

this homology: SV consists of two setae on a plate on segments T1-3 AND on A1-7 (Stehr [1987] fig. 26.370).

The SV setae of Hinton often occur in two longitudinal rows (just above the prolegs, and on the prolegs) in various Lepidoptera including butterflies, so designating both rows by one name SV is a nuisance. Therefore, many authors have given two names to them, including the name P (or sometimes PL) for proleg setae; in this paper the upper row is named SV, and the lower row (on the abdominal proleg region) is named P (Scott 1986a). Because SV setae are usually lacking above the prolegs on A3-6 of first-stage larvae, it could be assumed that the SV setae on these segments moved to the prolegs. But this view seems wrong for several reasons: SV1 is a postnatal seta, so it and the proleg setae are BOTH present on A3-6 on older larvae, proving that they are not homologous and deserve separate names (SV1 and P); some first-stage larvae have secondary setae that include the true SV setae that appear in the usual spot ABOVE the A3-6 prolegs indicating that the proleg setae are not SV setae; and T2-3 and A1-2 and A7-9 generally have only one SV seta yet the prolegs have several.

The ventral setae of A10 were named by Scott (1986a), who used SV for the two setae ventrolateral to the intestine, and used P for the proleg setae which were named P1-6 in a reversed-S shape starting clockwise with the dorsalmost seta. Scott (1986a) named the P setae of the preceding body segments (P2 and P4 on A3-6, and P6 on A2) based on their positional equivalents on A10. It would be possible to name the two setae on the A3-6 proleg P1 and P2, and then try to apply these names to A10, but A10 has six P setae versus usually only two on A3-6 and only one on A2, so Scott's names P2, P4, and P6 maintain the same spatial relation to each other on A1-9 as they do on A10 (instead of jumping back and forth on A10 which would be required if the A3-6 setae were P1 and P2) and indicate apparent homologies better.

The Megathyminae (Figs. 5, 23-24) seem to prove the homology of the P and SV names used here. Megathyminae have two secondary P setae (P1 and P3) on the side of the A3-6 prolegs, making a total of four P setae there, which are arranged in the same positions as are the four primary P1-4 setae on the side of the A10 proleg; this proves that the proleg setae on A3-6 and A10 are homologous (obviously disproving that any A10 proleg seta is "L" as labeled by Stehr [1987] and authors he cites), and seems strong proof that the usual two setae on A3-6 are P2 and P4 and the two secondary setae are P1 and P3, and proves that the postnatal proleg seta between P2 and P4 in most Lepidoptera is P3 (Hinton's postnatal "SV3" seta is my P3). Agathymus (Megathyminae, Figs. 5, 23) has four setae below the L setae on A1-2 (and has a SV1 seta above the proleg on A3-6), which thus on A1-2 seem to be SV1, P1, P6, and V1.

The identity of the usual two setae below the anus on the rear of A10 has been questioned. But Megathyminae have SV1 on A7-8 split into two setae, one behind the other, and SV1 on A10 (the upper of the usual two setae) is identically split into two setae, one behind the other, which seems to prove conclusively their serial homology (and proves that the usual lower seta is not SV1 and the usual upper seta is not "PP1" or "PP" or "CD1", names used or tabulated by Stehr [1987]).

Mechanitis (Danainae, Ithomiini, Fig. 36) have two SV1 setae (one secondary) on A10, one above the other, and two SV1 setae (or one SV1 and one P6?) on A2, one above the other, which perhaps also supports the serial homology of the A10 SV setae.

Stehr's (1987) homologies for A10 are based on Gerasimov (1952, but he died in 1942 so this work is 49 years old or more), in which D1-2 and SD1 homologies are in turn based on Gerasimov (1935 fig.4); these homologies are rejected totally here, because they are contrary to the homologies established above, and are rejected for other reasons, as follows. On A10 it seems ridiculous to separate the two setae that I call SV (just below anus) and give them two different names ("PP1" and "SV1"), because these two are always close in position and nearly identical in shape and size. Labeling three of the proleg setae L seems grossly wrong (one of several reasons being the great

distance between L setae and prolegs on prior segments). Splitting up the proleg setae and giving them two different names (L1-3 and SV2-4) also seems totally wrong. And using the same name for setae in two different places--SV for one seta below anus and SV for three proleg setae--seems ludicrous. None of the authors cited by Stehr (1987) offered any evidence for serial homology of A10 setae other than setae D1-2. Ripley (1923) was the first person to name A10 setae and seems to have been the most correct (except his proleg names are wrong); his D1-2, L1, SD1 are all in the correct positions, and his two SV setae are also my two SV (though reversed in position).

Scoli Homology. Some similarities occur between the positions of primary setae on first stage larvae and the positions of scoli (branching spines) on older larvae. For instance the two setae on the proleg of first stage Nymphalinae larvae at first glance appear homologous to the two tiny scoli above the proleg on some older larvae. But further analysis indicates that scoli are NOT homologous with primary setae, as first shown by Muller 1886. Study of the setal patterns of all larval stages of Nymphalinae (*Polygonia prognegrozephyrus*, Scott 1988, and Fig. 45) indicates that the Nymphalinae scoli are new developments and are not homologous with primary setae; most of the primary setae (such as D1-2, SD1, L1 on A10, L1-2 on T2-3, etc.) are still recognizable on the second stage body near newly-developed scoli, and an unpigmented spot on A10 in the first-stage larva, independent of the primary setae, is the forerunner of the BSD1 scolus of older larvae. (The proliferation of secondary setae in butterflies sometimes makes the recognition of primary setae difficult on second stage to mature larvae.) Thus the scoli must have separate names. They cannot be named S- (such as SD1 or SV1 for scoli near D1 and V1) because of confusion with other named setae (such as setae SD1, SV1, etc.), so they should be named B- for branching spine then the name of the nearest primary seta (for instance BD1 for the scolus nearest seta D1)

Conclusion Regarding Homology. If there is any general conclusion to be gathered about the improvements in homology given in this paper, it is that the position occupied on the body by a seta does not change during evolution as much as some previous authors thought. Most notably, an L3 seta did not migrate ventrally to the position of a SV seta, the L1 seta did not migrate from front to rear of a segment, other L and SV setae did not migrate onto the prolegs, and the setae of A10 are in the same positions as on prior segments except for some vertical compression of positions and moderate posterior travel of the most lateral setae (L and SV).

### **CLARITY OF TERMINOLOGY (see Figs. 1-2 of Scott 1986a)**

Not only must names of structures correctly reflect their homology, they must also be easy to use and be clearly understood, and each name must be clearly different from the name given to a different structure.

Body Segments. The names for body segments must be standardized to T1-3 for thorax and A1-10 for abdomen. Some people use numbers I-III for thorax segments and 1-10 for abdomen segments, but this system is unwise because there is confusion about the meaning of I-III and 1-10 because some morphologists number the abdomen segments I-X, and the British persist in numbering the segments of the larva 1-13 starting with the prothorax. For clarity more specific names are needed, and T1-3 and A1-10 (the system used by Peterson [1965]) are easier to remember than mere numbers or roman numerals.

Head Setae and Head Olfactory Pores. Hinton (1946) totally revised the setae of the body, but he unfortunately retained most of the names for the head setae given by earlier workers such as Heinrich and Gerasimov. This was unfortunate because many of the head names are the same as those of the body, causing much confusion (when making descriptions or lists of characters, one often forgets to specify whether head or body is meant, and then later one often becomes confused and must look up the drawings to find which was meant). Some minor changes in names of setae and olfactory pores of the head are required to make the names of the head and body structures

different in order to avoid this confusion (it is better to modify names for head setae because the head setae must be drawn and labeled only once, versus many times for the setae of the thirteen body segments). Hinton's names also misapplied the word gena.

Hinton's "gena" is actually the gena + postgena. During the evolution of the larval head of the ancestor of the orders Mecoptera-Trichoptera-Lepidoptera, three developments are notable: 1) the larval antenna moved ventrally along the adfrontal (antennal) sulcus (as a result, in the developing pupa the adult antenna develops from a row of cells beneath this sulcus, Eassa 1963, and then pops to the surface to make the adult antenna base dorsal in position as in most insects) and ended up at the base of the mandible; 2) the occipital sulcus disappeared (it formerly separated gena from postgena, and ran from the posterior articulation of the mandible dorsally behind the eyes and then ran dorsally around the top of the head); 3) the hypostoma extended ventrally so that the two hypostoma now nearly meet behind the labium at the mid-ventral line (the hypostoma has been misidentified as "postgena" by some authors; morphologically, the hypostoma is a sclerite anteroventral to posterior tentorial pit, and is the posterior portion of the subgena, Chapman 1969). The true gena is the lower part of the head posterior to the adfrontal sulcus and anterior to the occipital sulcus (anterior to the posterior articulation of the mandible, because the occipital sulcus in insects which possess it runs from the posterior mandible articulation dorsally around the posterodorsal rim of the head, in front of the postoccipital sulcus). The true postgena is the lower part of the head posterior to the occipital sulcus (posterior to the posterior articulation of the mandible). And the posterior tentorial pit is on the rear edge of the postgena in all insects, which proves that PG1 and PGa are on the postgena in Lepidoptera. Comparing the Lepidoptera larval head to the head of insects that have an occipital sulcus, the postgena is even wider in Lepidoptera than in these other insects, because the postgena and hypostoma have extended posteromedially such that the two hypostoma almost meet on the posterior mid-ventral line. Applying this anatomy to the larval head, the eyes and setae O1 and S02 occur on the gena, whereas the setae SO1, SO3, O2-3, and PG1 occur on the postgena. On the top of the head, because of the loss of the occipital sulcus the vertex anterior to the sulcus and the occiput posterior to the sulcus can no longer be readily distinguished, but the anterior-facing dorsal part should be named vertex, the posterior-facing dorsal part of the head named occiput. The previously named "genal" structures "G1" and "Ga" actually occur on the postgena, NOT on the gena; thus these names are anatomically imprecise so should be corrected. Stehr (1987)--using the prefix M- for microscopic or proprioceptor--changed "G1" and "Ga" to "MG1" and "MGa" to mean microscopic genal. These names are modified here to PG1 and PGa, for Postgenal, because these structures are on the postgena, not the gena.

The "V1-3" proprioceptor setae on the head must be renamed because "V1" is confused with the usually-tiny V1 seta on the body. Stehr (1987) changed "V1-3" and "Va" to "MD1-3" and "MDa", but "MD1-3" is confused with body proprioceptor seta MD1, and the name "MD" implies that these head and body setae are homologous. This homology seems exceedingly doubtful; not only are these head setae posterior, the body seta anterior on each segment, there is no proof that ANY head seta or pore is homologous with any body seta or pore. The practical reason to name head and body setae differently to avoid confusion overshadows any infinitesimal possibility that a head seta is homologous with a body seta, so Stehr's names are rejected. Stehr's addition of M- to the front of these setae is admirable to indicate that they are proprioceptors. But adding M- to V1-3 forms "MV1-3", which can be confused with MV1-3 on the body. Altering them to "MVT1-3" for microscopic vertex setae would work but is too long to label drawings. "MT1-3" and "MTa" is possible as a compromise for Microscopic verTex setae, but is too different from the old "V1-3" name, so VT1-3 is used here. VT setae usually start (VT1 etc.) on the vertex, but they usually (VT3) end on the occiput and rarely even end on the postocciput (the narrow rim of the head around

the neck, posterior to the postoccipital sulcus/suture); thus the name VT for vertex setae is often wrong, but is not changed because these setae vary considerably in position, and because a name such as "MO" would be interpreted as "microscopic ommatidial" by many people.

Microscopic proprioceptor setae on the body (except TF1) have names beginning with M (MXD, MD, MSD, MV, MC). Ideally, this convention should be applied on the head as well, but unfortunately doing so causes too many name changes and destroys too many usefully-mnemonic names. On the body, the trochanter-femur proprioceptor seta TF1 has a mnemonic name rather than one beginning with M- (and MTF1 is too long). On the head, the vertex setae VT1-3, postgena seta PG1, antenna setae AN3-10, labium seta LB2, maxillary palp setae MP1-3-etc., and laciniogalea setae LG1-3-etc. are proprioceptors in part, but have mnemonic names rather than names starting with M-. And on the head, mandible setae MA1-2 and maxillary setae MX1-4 on the head have mnemonic names that begin with M-, even though they are not as small as proprioceptors (though their function is similar). The ease of remembering these names outweighs the desire to have every proprioceptor name preceded by M-, and naming them all starting with M- would produce too many structures with similarly-spelled names.

The "A1-3" head setae must be renamed because the name is confused with abdomen segments A1-3; they occur on the gena so are renamed AG1-3 (for anterior genal seta); for consistency, the pore "Aa" must be renamed AGa. The "L1" head seta must be renamed LH1 (for lateral head) because the name is confused with the L1 body seta; for consistency "La" must be renamed LHa. The "P1-2" parietal setae on the head must be renamed PA1-2 because "P1-2" is confused with the P1-2 proleg setae (it is better to rename the head "P" setae because there are fewer of them than the many proleg P setae; some people use "PL" for proleg setae, but P is preferable for brevity, particularly on drawings of A10 which is crowded with six P setae); likewise, "Pa" and "Pb" olfactory pores on the head must be renamed PAa and PAb because the names are confused with anal proleg pores Pa and Pb. The C1-2 head setae actually occur on the anteclypeus (the ventral part of the frontoclypeus) rather than on the clypeus, and the names C1-2 are similar to the names of the CX1-8 coxal setae; but this is a minor problem so no changes are required, and the name "AC" for anteclypeus could be confused with the name AG on small drawings. The name SV was Hinton's (1946) abbreviation of "subventral", but because these setae are really sublateral they should be called "SL", however the name SV is so entrenched that changing it would be wrong, and the simple solution to this problem is to call these setae supraventral, which has the same abbreviation SV; so the name SV is retained, but they are called supraventral, not subventral.

Stehr changed Hinton's O1-3 and Oa-b to "S1-3" and "Sa-b", on the grounds that "ocelli" are really stemmata (true ocelli are limited to two on the head of adult moths). But larval "ocelli" are actually ommatidia (larval Mecoptera have a compound eye of ommatidia from which the Lepidoptera larval eyes evolved by reduction in number of ommatidia), similar to adult ommatidia in structure, and the name stemmata is excess terminology, so names O1-3 and Oa-b must be retained and simply called ommatidial or ocular structures. Stehr changed SO1-3 and SOa to "SS1-3" and "SSa"; these changes are rejected by the same logic, so SO1-3 and SOa are retained here and called subommatidial or subocular structures.

Lenticles. Lenticles (ring glands) should be named with the capitalized letter(s) of the nearest primary seta followed by an uncapitalized -r (for ring gland) and then followed by uncapitalized letters designating which lenticle is meant if there are more than one. For instance, Xra, Xrb for lenticles on the prothoracic shield of some Lycaenidae. The letter -l cannot be used, for instance "SDl" instead of SDr, because "SDl" is too easily confused with SD1 (the letter l is too easily confused with the number 1).

Secondary Setae. Finally, a system of naming secondary setae is needed. When hundreds of secondary setae cover the head or body, names for each seta are not practical or desirable. But if a

species has mostly primary setae and just a few secondary setae, these few secondary setae may be usefully named. Three principles seem desirable to guide these names: 1) when a primary seta splits into two setae, if the primary seta is still recognizable it must keep its old primary name; 2) the extra seta must be given a name that is different but still shows its origin from that particular primary seta; 3) the new name given to the extra seta must have numbers rather than letters at its end because letters are reserved for olfactory pores and lenticles and other non-setal structures. Only one system seems to fulfill these three requirements: for example, if seta D2 has split into two setae, if one of them closely resembles D2 of other species whereas the second seta differs, the former should remain D2, while the extra second seta should be called D2.2 (a third seta would be called D2.3); if both setae are identical (so that neither can be called D2), one should be called D2.1, the second D2.2 (a third D2.3). The second seta should never be called D2.1 because the name D2.1 should be reserved for the first seta on species on which it is no longer recognizable as the primary seta. If a particular large taxon has a certain seta in most included taxa, perhaps for convenience it could be given a larger-numbered name such as D3 that is not a primary seta in most Lepidoptera, but this decision should be left up to individual researchers.

Sometimes a seta/structure occurs on some individuals but not on others, or on one side of the body but not the other. To indicate this on a drawing, the seta/structure should be drawn as a dashed line.

## **GLOSSARY OF NAMES OF SETAE, OLFATORY PORES, RING GLANDS (LENTICLES), SCOLI, AND OTHER CUTICULAR STRUCTURES**

An alphabetical glossary is useful for reference, and an alphabetical list is required to make certain that the names of the various structures are different enough from the names of other structures to prevent confusion. Structures within quotes " " are recently-used names that should not be used or have been renamed as noted (long-obsolete names of N. McIndoo, S. Fracker, A. Gerasimov, etc. are not listed).

1-6--Eye names (counterclockwise from top).

"1-10"--Should not be used for names of abdomen segments (A1-10 should be used); T1-3 should be used for names of thorax segments (I-III should not be used).

"A1-3"--Obsolete name for AG1-3.

A1-10--Abdomen segments (1-10 should not be used; some morphologists number them I-X though this should not be done); T1-3 should be used for thorax segments (I-III and 1-3 should not be used for thorax).

"Aa-b"--Obsolete name for AGa-b.

AF1-2--Adfrontal tactile setae on gena beside frontoclypeus on head.

AFa--Adfrontal olfactory pore near AF2 on head.

AG1-3--Anterior genal tactile setae on gena of head (were "A1-3", renamed to avoid confusion with abdomen segments 1-3).

AGa-b--Anterior genal olfactory pores anterior to eyes; AGa is near AG2 on head (was "Aa", renamed for consistency with AG1-3); AGb is just anterior to eye #4 (was "Ab" of Peterson 1965 and Allyson 1976, renamed for consistency with AG1-3; was "Ob" of Gerasimov 1935, which is rejected because all other O setae and pores are posterior to eyes).

AN1-2--Antennal tactile setae, on end of pedicel.

AN3-10-- Antennal sensilla (as many as seven): AN3-6 on end of pedicel (AN5 small and often overlooked), AN7-10 (AN9 small and often overlooked) on end of flagellum.

ANa-e--Antennal olfactory pores: a ventrally and b (c rarely) dorsally on scape, d (and very rarely e) on pedicel.

BD1-2, BSD1, BL1, BSV1--Branching spines (scoli) on the body, named from the nearest primary seta (BD1 is nearest D1, etc.); they are not named S- (such as SD1) because of confusion with primary seta SD1, etc. (See also H- for horn and T- for tubercle/tail.)

C1-2--Anteclypeal (ventral part of frontoclypeus) ("clypeal") tactile setae on head (some previous authors used "CL1-2", but C1-2 is simpler).

Ca--Anteclypeus ("clypeal") olfactory pore (rare) between C1 and C2 on head.  
 "CL1-2"--Obsolete name for C1-2.  
 "CLa"--Obsolete name for Ca.

CM1-2--Comb, CM1 above anus (the usual position), CM2 below anus.

CX1-5--Coxal tactile setae from front to rear.

D1-2--Dorsal tactile setae on body.

Dr--Dorsal ring gland, near D setae on body.

EP1-3--Epipharyngeal tactile setae, wide from base to tip, appressed to inner wall (epipharynx) of labrum, numbered from medial to lateral.

EPa-b--Epipharyngeal olfactory pores on inner wall (epipharynx) of labrum, numbered from top to bottom.

F1--Frontoclypeal tactile seta on lower frontoclypeus of head.

Fa--Frontoclypeal olfactory pore medial to F1 on head.

FE1-2--Femoral tactile setae, from front to rear (the trochanter and femur are fused together but a membranous medial rift evidently is the joint between them).

"G1"--Obsolete name for PG1.  
 "Ga"--Obsolete name for PGa.

H- (prefixed to name of nearest primary seta)--Horn, any hardened protuberance mostly lacking setae (if setae are present it is a scolus) such as an antler. (See also T- for tubercle/tail, and B- for branching spine or scolus.)

HG--Honey gland (in Lycaenidae).

I-III--Should not be used for names of thorax segments (T1-3 should be used); A1-10 should be used for names of abdomen segments (1-10 should not be used).

"L1"--Obsolete name for LH1 on head.

L1-3--Lateral tactile setae on side of body.

"La"--Obsolete name for LHa on head.

LB1--Labial tactile seta on postmentum.

LB2--Labial proprioceptor seta on prementum.

LB3-4--Labial sensilla on labial palp (LB4 a sensillum styloconicum).

LBa-d--Labial olfactory pores (LBa-c on rhaphe [= "palpiger", which should not be used because of confusion with "palpifer"] [LBc is rare], LBd on oval-shaped sclerite [fusuliger] surrounding spinneret [fusulus]).

LG1-8--Laciniogaleal setae/sensilla (named "STI, STII, STIII, LSS, MSS, LSB, CSB, MSB" respectively by Grimes and Neunzig 1986b): LG1 is a tactile seta (sensillum trichodeum) usually dorsal to the terminal lobe, LG2-3 are wider tactile sensilla (sensilla trichodea)(both usually dorsal to the terminal lobe on a slight ridge homologous to the lacinia), LG4-5 are sensilla styloconica chemoreceptors/ mechanoreceptors (each two-segmented as are all s. styloconica), LG6-8 are small sensilla basiconica chemoreceptors/mechanoreceptors; LG4-8 are on a terminal lobe homologous to the galea.

LGa--Laciniogaleal olfactory pore or sensillum campaniformium (oddly, this was missed by Grimes and Neunzig [1986b], though I found it on every Papilionoidea and Hesperioidea examined

except Morpho, and it was found in Everes [Lawrence and Downey 1966], Leptotes [Downey and Allyn 1979], and by Forbes [1910 Fig. 26] and McIndoo [1919]).

LH1--Lateral head seta (was "L1", renamed LH1 because of confusion with L setae of body).

LHa--Lateral head olfactory pore near LH1 on side of head (was "La", renamed LHa for consistency with LH1 of head).

Lr--Lateral ring glands, near L setae.

LR1-6--Labral tactile setae on front on head, clockwise from top. LR1 and LR2 are longest, LR4 is generally fairly long, LR3 and especially LR5-6 are often quite small.

LRA-c--Labral olfactory pores on front, from top to bottom.

MA1-2--Mandibular tactile setae, MA1 basal (longer) and MA2 distal.

MAa-b--Mandibular olfactory pores on rear base and anteromedial base of mandible (McIndoo 1919 uses "MDa-b" for the mandible pores but this causes confusion with MD1 proprioceptor seta of body).

MC1-3--Microscopic coxal proprioceptor setae, from front to rear.

MD1--Microscopic dorsal proprioceptor seta far in front of D2 on T2-3 and A1-9.

"MD1-3"--Obsolete name on head (of Stehr 1987) for VT1-3.

"MDa"--Obsolete name on head (of Stehr 1987) for VTa.

"MG1"--Obsolete name (of Stehr 1987) for PG1.

"MGa"--Obsolete name (of Stehr 1987) for PGa.

MP1-8--Maxillary palp (on tip) sensilla basiconica (the same as the medial "M1-2", apical "A1-3", and lateral "L1-3" sensilla names respectively of Grimes and Neunzig 1986a; all function in olfaction/taste/touch).

MPa-f--Maxillary palp (on sides) oval and elongate sensilla (on the dorsal side of last palp segment, MPa is the elongated "SD" sensillum digitiformium mechanoreceptor of Grimes and Neunzig 1986a, MPb is their "SC1", MPc is "SC2", MPd is "SC4", MPe is "SC3" [apparently absent in most or all butterflies]; on the ventral side of the second-from-last palp segment, MPf is "SC5" of Grimes and Neunzig 1986a; MPb-f are campaniform sensilla that detect bending of the palp wall).

MS--Microspines, very minute cuticular projections even smaller than proprioceptor setae, common near anus (name of Peterson 1965; wrongly called "spinules" by Stehr [1987], a name Peterson used for scolus setae).

MSD1-2--Microscopic subdorsal proprioceptor setae, above level of spiracles on T2-3 (for MSD1) and on T2-3 and A1-8 (for MSD2).

MV1-3--Microscopic ventral proprioceptor body setae at level of legs and prolegs.

MX1-4--Maxilla tactile setae (MX1-2 on basistipes, MX3 on first dististipes segment, MX4 on second dististipes segment ("palpifer", which should NOT be used because of great confusion with "palpiger" of labium).

MXa-d--Maxilla sensilla (MXa on basistipes, MXb on first dististipes segment, MXc-d on second dististipes segment).

MXD1--Microscopic extra dorsal proprioceptor seta, just behind prothoracic shield.

N--Navel, middorsally between T2 and T3, only on first-stage larvae.

O1-3--Ommatidial or ocular (not "ocellar") setae within and behind eyes of head (note: butterflies lack ocelli, which are the two single-lens-multiple-nerve eyes on top of the head of adult moths; the eyes of butterfly larvae are properly named ommatidia because each eye's structure is very similar to that of a single adult ommatidium).

Oa--Ommatidial or ocular (not "ocellar") olfactory pore on head behind sixth eye (the "Ob" of Gerasimov 1935 = the "Ab" of Peterson 1965 and Allyson 1976 have been renamed AGb).

OS--Osmeterium, found only on top of Papilionidae prothorax.

"P1-2"--Obsolete names for PA1-2.

P1-6--Proleg tactile setae: generally only two, P4 in front of P2, on A3-6, but six on A10 where they are numbered clockwise (P5 is generally medial to P4, while P6 is generally on anteromedial base of proleg anterodorsal to Pb).

"Pa-b"--Obsolete names for PAa-b.

Pa-c--Proleg olfactory pores on A10 (a laterally, b anteromedially, rarely c anterolaterally).

PA1-2--Parietal tactile setae on vertex of head (were "P1-2", renamed PA1-2 to avoid confusion with P on prolegs).

PAa-b--Parietal olfactory pores on head (PAa is above AG2 on head [and perhaps is properly named AGc], PAb is near PA2 on top of head) (were "Pa" and "Pb", renamed PAa-b to avoid confusion with Pa and Pb on A10 proleg).

PG1--Postgenal proprioceptor seta on head (was "G1", renamed PG1 because it is on the postgena, not the gena).

PGa--Postgenal olfactory pore near PG1 on posteroventral corner of head (was "Ga", renamed PGa because it is on the postgena, not the gena).

"PP1"--Obsolete seta (of Stehr 1987) for SV1 on A10.

"S1-3"--Obsolete names (of Stehr 1987) for O1-3.

"Sa-b"--Obsolete name (of Stehr 1987) for Oa and AGb respectively.

"SS1-3"--Obsolete names (of Stehr 1987) for SO1-3.

"SSa"--Obsolete name (of Stehr 1987) for SOa.

SD1-2--Subdorsal tactile setae on body for

SDr--Subdorsal ring gland, near SD setae.

SO1-3--Subommatidial or subocular (not "subocellar") tactile setae on head.

SOa-f--Subommatidial or subocular (not "subocellar") olfactory pores below eyes, the sequence of name forming a water dipper.

sp--spiracle.

SPa-b--Suranal plate olfactory pores, from top to side; these occur only in Lycaenidae.

SPr--Suranal plate ring glands.

SV1-2--Supraventral (sublateral, not "subventral") tactile setae on body.

SVr--Supraventral (sublateral, not "subventral") ring gland, near SV setae.

T- (prefixed to name of nearest primary seta)--Tubercle or tail; a "tubercle" is any thick fleshy protuberance with few setae (if several setae are present it is a scolus), a tail is fleshy, or sclerotized if on suranal plate; for example the usual tail is named TD2 because it incorporates seta D2 (tails TL1 and TSD1 are unknown thus far). (See also H- for horn and B- for branching spine or scolus.)

T1-3--Thorax segments (I-III and 1-3 should not be used); A1-10 should be used for names of abdomen segments (1-10 should not be used for abdomen).

TA1-4--Tarsal tactile setae (TA1-2 lateral and TA3-4 medial; TA3-4 are small, but are 50-100% longer than MC1-3 so are not named as proprioceptors).

TAA--Tarsal olfactory pore, on lateral tip near claw (McIndoo 1919 used "Ta" for this pore but there are so many other TB, TF, etc. names that TAA is better to avoid confusion).

TB1-6--Tibial tactile setae.

TBa--Tibial olfactory pore, on posterior side.

TE--Tentacle organ (in Lycaenidae).

TF1--Trochanter-femur proprioceptor seta, on membranous rift between trochanter and femur.

TFa-c--Trochanter-femur olfactory pores, from front to rear on membranous rift of trochanter-femur (McIndoo 1919 used b for anterior, a for middle, and c for posterior pore, which is harder to remember than a simple abc sequence so is not accepted).

TP--Tonofibrillary platelet (a minute cuticular plate marking the site of a muscle attachment, Stehr and Neunzig 1981).

"V1-3"--Obsolete names for VT1-3.

V1--Ventral tactile seta on body.

"Va"--Obsolete name for VTa.

VNG--Ventral neck gland (usually present only on older larvae, but found on first stage larvae of Trapezitinae such as *Trapezites eliena* and Hesperinae such as *Calpodes*).

VT1-3--Vertex proprioceptor setae on top of head (were "V1-3", renamed VT1-3 to avoid confusion with V1 of body).

VTa--Vertex olfactory pore near VT2 on head (was "Va", renamed VTa for consistency with VT1-3).

WG--Wax gland (in Hesperidae).

Xa-c--Extra olfactory pores from top to bottom on prothoracic shield (McIndoo 1919 used the names "T1a-c" which are not as descriptive; Hinton 1946 used "XDb, XDa, XDc" from top to bottom, which is harder to remember than the simpler Xa, Xb, Xc sequence from top to bottom).

XD1-2--Extra dorsal tactile setae on prothorax.

"XDb,a,c"--Obsolete names for Xa-c.

Xra-Xrc--Extra prothoracic shield ring glands.

XSD1-4--Extra subdorsal tactile setae on prothorax of Lycaenidae.

## DESCRIPTION OF EXOSKELETAL STRUCTURES

Setae. There are two basic types of setae in Lepidoptera based on their usual size. **Tactile setae** are longer and usually require only 15-100X to see, although a few of these may become very small in some groups and require greater magnification, or are sometimes lost. **Proprioceptor setae** are minute, requiring 400X microscopy to see well. Proprioceptor setae function to detect the position of the segment in relation to an adjacent segment that can move against or telescope over the proprioceptor. **Microspines** (name of Peterson [1965], misnamed "spinules" by Stehr [1987]; Peterson used the name spinules for scoli spines) are very minute seta-like structures, each consisting of a conelike base and a hairlike tip, that are common near the anus to repel fecal pellets.

There are three types of setae based on their occurrence among the superfamilies of the suborder Ditrysia and on their occurrence in the various larval stages. **Primary setae** are setae that occur in all Lepidoptera superfamilies (in fact, the setae of the larvae of the order Mecoptera are very similar to Lepidoptera setae, so it is likely that the Lepidoptera setal names can be applied to Mecoptera as well). All proprioceptor setae are primary setae, because the same proprioceptor setae occur on nearly all Lepidoptera and the same proprioceptor setae occur on mature larvae as on first stage larvae. Tactile setae may be either primary or secondary. **Postnatal setae** ("**subprimary**" setae) are those few basically primary setae that do not occur on first stage larvae but do occur on later larval stages (the following is a list of all the postnatal setae that occur in most Lepidoptera: seta L3 on T1 in most Lepidoptera except Pyraloidea and Macrolepidoptera [which includes butterflies]; setae L2 and L3 on T2-3; SV1 [Hinton's L3] on A1-9; and P3 [Hinton's SV3] on the A3-6 prolegs); Hinton (1946) named them "subprimary" setae, but this name is not as appropriate as postnatal (which means "after birth", referring to presence only after the first stage). **Secondary setae** are extra setae, in addition to the primary setae, that developed later in evolution, generally by individual species or genera or tribes or superfamilies. Most moth larvae have only primary setae on first stage and mature larvae (mature larvae add the few postnatal setae), but in butterflies and some moths (Zygaenidae for instance) first stage larvae usually have only primary setae while

mature larvae always have thousands of secondary setae. Postnatal setae are therefore important in most moths, which are studied as mature larvae, because mature larvae of most moths have only primary setae and the few postnatal setae; in butterflies however, because older larvae (and most second stage larvae) have numerous secondary setae, the postnatal setae can be seen only on second stage larvae of some groups.

Secondary setae occur on first stage larvae of some butterfly groups. Usually they have been named by merely incrementing the number, thus if L1 and L2 are primary setae a third secondary seta would be L3. However, to indicate the derivation of the secondary setae, a better naming system is to add a decimal point and a number after the primary seta name; thus if L1 has become two setae the names of the three setae should be named L1.1, L1.2, and L2 if the former two are similar; or if a new seta occurs near L1 but the true L1 is still obviously recognizable as L1 the three setae should be named L1, L1.2, and L2; this system would solve the problem under the old naming system that the name of the seta L3 is misleading because it implies that L3 is near L2 when L3 is actually close to L1 and far from L2. Of course, when the number of secondary setae becomes large, any naming system becomes unwieldy, and names are no longer applied to individual setae, unless these are so distinctive as to be still recognizable as primary setae.

Proprioceptor Setae. Proprioceptor setae are tactile setae so small that their function is to detect when adjacent flexible exoskeleton overlaps the seta, such as when one segment overlaps another or the leg base moves. The antenna, maxilla, and labium have tiny setae or seta-like sensilla many of which have a similar role in detecting the physical presence of food or the position of the mouthparts. Microspines are even smaller, and in butterflies are common around the anus where they apparently serve to repel pellets and probably have no attached nerves.

Olfactory Pores. Pore is a good name for these structures because with a light microscope, these pores appear as a round or oval light spot in the cuticle (McIndoo 1919), due to a ventral cavity in the exoskeleton at that spot and due to a small hole in the center that permits nerve dendrites to contact the exterior (the cavity may be spherical and filled with a bulb of nerves, David M. Wright pers. comm.). Pores are often misnamed "punctures" because of their microscopic appearance. Some of these pores may be sensilla campaniformia, which also appear as a pale spot using the light microscope, though true *s. campaniformia* should exhibit an arched dome (Chapman 1969 p. 615) and cross sections of larval pores do not show the dome (McIndoo, 1919, 1929, Grimes and Neunzig 1986a; however the known *s. campaniformia* on the wing base do not show the dome either, McIndoo 1929), and *s. campaniformia* are known to be in areas of the body subject to bending stress (such as wing bases) which does not fit most pore locations on larvae. So the term "olfactory pore" will be used as a general term for those sensilla lacking an external projection and incorporating an internal hollowing of the exoskeleton, even though some of these could be *s. campaniformia*.

Butterflies have all the usual olfactory pores found in Lepidoptera. About 58 pores are typical in butterflies (on the left side of course). McIndoo (1919, 1929) noticed 51 olfactory pores on Noctuidae larvae, but he probably missed three SO pores, four labrum pores, and two antenna pores, so that about 60 olfactory pores are present; evidently most Lepidoptera have a similar number. Olfactory pores on hardened body sclerites have the same structure as those of the head. Olfactory pores similar in structure can occur in membranous cuticle on the body (for instance Pb on A10) by occupying the center of a chitinous ring that strengthens the membrane.

Ring Glands. Ring glands (the proper technical name is lenticle, and synonyms that should not be used are perforated cupolas = porrenkupeln = annuli = rings = ring-pores) are present in Hesperidae and Lycaenidae first stage (and older) larvae. Tactile seta in first stage larvae of Hesperidae can change into ring glands during the molt to the second stage larva, and a ring gland can become bare cuticle and then become a ring gland again in successive molts (lenticles never

molt into setae) (Franzl et al. 1984). Ring glands should be named from the capitalized-letter name of the nearest seta, with uncapitalized "r" appended and then an uncapitalized letter appended if there is more than one ring gland there; for instance SVra, SVrb, SVrc for three ring glands near SV setae, plus the Dr, SDr, Lr, SPr, Xr, ring glands etc. (r is not capitalized because olfactory pores are similar to ring glands in appearance with poor microscopy and are also not capitalized; r is used rather than l because the uncapitalized letter l for lenticle is too easy to confuse with the number 1 [on most typewriters l=1] and the capitalized letter L is too easy to confuse with the L setae).

Other Structures. First stage larvae may have a sclerotized prothoracic shield, suranal plate, and proleg shields, or these areas may be membranous like the rest of the integument. The larva may have horns, scoli, fleshy bumps, fleshy tails, sclerotized tails, and rarely an osmeterium, ventral neck gland, or honey glands. A sclerotized anal comb CM1 above the anus may be present but is usually absent; this structure has undoubtedly evolved independently several times (*Hasora khoda*, Coeliadinae, Fig. 7, has a comb consisting of dozens of very long anal spikes, not fused with each other, suggesting that the anal comb evolves from the microspines ubiquitous in butterflies; and *Curetis*, Curetinae, Fig. 55, has an anal comb CM2 below the anus in contrast to the usual position above the anus). The comb above anus can be named CM1, that below anus CM2. The setae may be single with a platelike sclerotized base (a pinaculum), single with a domelike sclerotized base (a chalaza), clustered on a sclerotized flat base (a verricule), clustered on a domelike sclerotized base (a verruca), or clustered on a fleshy or sclerotized cone (a scolus). Spiracles are always present of course, and are always larger in size on T1 and A8 because these spiracles must supply air to the head and rear respectively. Crochets are always present on the prolegs, though they vary in number and position, and they may occur in several different sizes (the lateral crochets often smaller than the medial). The anterior eight prolegs have the crochets usually in a circle, though they are a mesoserries (limited to medial half of the proleg) in some Papilionidae, Lycaenidae, Satyrinae (*Cyllopsis*, Fig. 37), and Trapezitinae (*Anisynta*, Fig. 18); the A10 prolegs always have the crochets only on the anterior and medial sides of proleg. A middorsal navel N is always present between T2 and T3 of first-stage but not older larvae; this is a minute pit stretching from side to side, a remnant of the invagination of the midgut during embryology (Kume and Dan 1968; David M. Wright will present a paper on it). The ventral A7-8 powder glands of mature Hesperidae larvae is apparently absent on all first stage larvae. The ventral neck gland is present on older larvae of many butterflies, but is absent on all first stage larvae except some Trapezitinae (*Trapezites eliena*, Fig. 14, etc., Hesperidae).

Cranium. Butterflies have all the usual structures found in Lepidoptera, including tactile setae C1, C2 (Stehr [1987] switched C1-2 from the normal positions [of Hinton {1946} figs. 12-13, etc.], though other authors' drawings in Stehr [1987] label C1 and C2 in Hinton's positions) with no apparent reason, so the switch is rejected, F1, AF1, AF2, AG1, AG2, AG3, PA1, PA2, LH1, O1, O2, O3, SO1, SO2, SO3, proprioceptor setae PG1, VT1, VT2, and VT3, and olfactory pores Fa (medial to F1), AFa (generally between AF1 and AF2), AGa (in front of or above first eye) AGb (just anterior to fourth eye), PAa, PAb, VTa (VTa varies in position in various butterflies from between VT2 and VT3 [the typical Lepidoptera condition] to between VT1 and VT2), LHa, Oa, PGa (PGb is also present in *Morpho*, Fig. 40), SOa, SOb, SOc, SOd, SOe, SOf (David M. Wright and I have found six SOa-f pores in various butterflies: SOc, SOe, and SOf are often on the edge of the cranial rim, and the ventralmost SO pores are often hard to see. A pore Ca between C1 and C2 on the anteclypeus (=lower division of frontoclypeus) is apparently unique to some Lycaenidae.

Labrum and Epipharynx. The labrum has six anterior tactile setae in roughly the same positions in all butterflies (naming the setae clockwise, LR1 mediodorsally, LR2 about on the middle of left half of labrum, and LR3-6 from side to bottom on the rim). Forbes (1910) illustrated the six labrum setae of various butterflies and showed that Papilioninae and Danainae etc. gain secondary labrum

setae as the larva matures (the mature butterfly labrum generally has many setae). The labrum has no proprioceptor setae, although LR5-6 and sometimes LR3-4 may be small. The inner wall of the labrum (epipharynx) has three large, very wide, flattened (wider at base than at tip!) sensillae appressed to the inner wall (named EP1-3 from medial to lateral). The typical butterfly labrum evidently has three pores LRA-c on the front (LRA above LR1-2, the most visible labrum seta, LRB-c below LR2 near the lateral end of a pale streak formed from thinner exoskeleton inside the labrum)(one pore LRD was found just dorsal to LRA in Trapezites [Figs. 13-14] but this may be a freak individual variant); the epipharynx has two pores EPA-b near pore LRA. Most or all butterflies probably have all five pores (LRA-c and EPA-b), because the five were seen in Apodemia mormo (David M. Wright, pers. comm.), Feniseca (Fig. 54), Curetis (Fig. 55), Hypaurotis, Strymon (Fig. 57) (all David M. Wright), Euchloe (Fig. 32), Morpho, Trapezites, and Pyrrhopyge (Fig. 8). LRA was seen in every butterfly examined; LRB-c were not seen in about a third of the species, but better microscopy would probably reveal them (in a few species a pore in the position of LRB-c appeared to be on the epipharynx but is assumed to be LRB or LRC on the front); EPA-b was seen in nearly all butterflies and probably occurs in all.

Antenna. The antenna was studied in detail by Dethier (1941), who noted no change of sensilla or seta number between first-stage and mature larvae. Each scape (first segment) has one olfactory pore ANa on the ventral side, and one or two pores ANb-c on the dorsal side (ANa was seen in many butterflies; ANb was seen in Apodemia mormo [David M. Wright, pers. comm.], Baronia, Morpho, Trapezites, Hesperia; ANb and ANc were seen in Libytheana, Calpodus, Euschemon, Chaetocneme, Netrocoryne and could possibly occur in all butterflies; ANa-c may occur in most or all butterflies). The pedicel (second segment) has one or two pores ANd-e on its ventral side (ANe was rarely seen so may just be an individual variation, but both ANd and ANe were seen in Aegiale [Dampf 1923] and on at least one side of Piruna head; ANd probably occurs in all butterflies). ANd is a sensillum campaniformium (not an olfactory pore)(Peterson 1965), so perhaps ANa-e are also. The pedicel also has one seta AN1 near its end, and on the terminal membrane is one very long seta AN2 and four olfactory sensilla basiconica AN3-6 (the long round-tipped AN3, the long pointed AN4, a very small AN5, and a small AN6); AN5 is difficult to see, and seldom drawn by Dethier (1941), who noted AN3-4 and AN6 as typical of butterflies, but most butterflies may have AN5 because it was seen in all the families (Feniseca [David M Wright], Baronia, Euchloe, Cyllopsis, and Trapezites). The flagellum (third segment) tip has four sensilla AN7-10: a long round-tipped AN7, a shorter pointed AN8, a tiny pointed AN9 (AN7-9 are olfactory sensilla basiconica), and a two-segmented sensillum styloconicum AN10; AN9 is difficult to see, but was shown in nearly all butterflies drawn by Dethier (1941), was seen by me in both superfamilies (Baronia, Morpho, Chaetocneme, Netrocoryne) and was shown on the "typical Lepidoptera antenna" by Peterson (1965, Fig. L1R), so is present in most or all butterflies, though is evidently absent in Trapezitinae-Heteropterinae-Hesperinae-Megathyminae.

Mandible. Each mandible has two setae MA1-2 on the lateral side (only one in Morpho, more than two in some Riodininae); many older butterfly larvae have more than two setae. There are no proprioceptor setae. Each mandible evidently has two pores, MAa on posterior base and MAb on proximal medial base, the former difficult and the latter very difficult to see.

Labium. The postmentum has a long LB1 seta in all butterflies. The prementum has one tiny LB2 proprioceptor seta (present in all butterflies, except absent in Feniseca [David M. Wright pers. comm.], very minute or absent in Euschemon and Chaetocneme). The rhaps (= "palpiger", which name should NOT be used because of enormous confusion with "palpifer" on the maxilla; numerous published papers manage to confuse these two words) has two ventral pores near its attachment to the prementum (LBA-c from rear to front; LBC is rare). Each fusuliger (the oval ring surrounding the true spinneret) has one lateral pore (LBD). The spinneret (fusulus, the distal long projection that

applies silk) has no sensillae or pores. Each labial palp has two setae LB3-4 on the tip, the longest LB4 a sensillum styloconicum (which always has two segments).

Maxilla. The basistipes has two long MX1-2 setae (older larvae such as Baronia, Everes, etc. have more than two here), and one pore just posterior to them. The first segment of the dististipes has one ventral MX3 seta (just beyond the sclerite), and one pore MXb (this is evidently very difficult to see, but on the lateral edge of the segment Lawrence and Downey 1966 found it in Everes, and I may have seen it in Libytheana and Chaetocneme; McIndoo's [1919] draws MXb in Noctuidae on the medial edge of the dorsal side of the sclerite, which could be its usual position in butterflies, or perhaps the different position is merely an artifact of how he positioned this segment for drawing). The second segment of the dististipes has one small medial MX4 seta (just beyond the sclerite), and two pores, MXc on ventrolateral side and MXd on ventromedial side (McIndoo found only one on this segment on three butterflies, and I saw MXc on most butterflies; MXd occurs only in Lycaenidae, where David M. Wright found both MXc-d on Apodemia, Feniseca, Curetis, Strymon, and Lycaena)(the "MXd" of McIndoo [1919] is my LGa).

The maxillary palp tip (Grimes and Neunzig 1986a, who studied mature larvae), found eight sensilla basiconica, which I name MP1-8 (the same as their medial "M1-2", apical "A1-3", and lateral "L1-3" sensilla names respectively; all function in olfaction/taste/touch). First-stage butterfly larvae may typically have only 7 MP sensilla (about 3 small and about 4 even smaller), because I have seen 7 in many species, but have seen 8 in only one (Calpodes, Hesperinae). On the dorsal side of the last maxillary palp segment, Grimes and Neunzig (1986a) found one sensilla digitiformium (touch detector) which I name MPa (their "SD"), several sensilla campaniformia (touch detectors) which I name MPb-e (their "SC1-4")(MPe is apparently absent in most or all butterflies). On the ventral side of the next-to-last palp segment, Grimes and Neunzig 1986a found one sensillum campaniformium which I name MPf (their "SC5").

The homology of the second segment of dististipes is controversial; it is called 2nd dististipes by Hinton (1958), but is labeled first segment of maxillary palp by many authors (or the "palpifer", which should NOT be used because of endless confusion with the "palpiger" on the labium). In primitive Lepidoptera it appears to be the basal segment of maxillary palp (in outward appearance, Zeugloptera have the palp 3 segmented, stipes undivided; Dacnonypha and Heterobathmiina have palp 3 segmented and dististipes 1 segmented; Aglossata palp 2 segmented and dististipes 1 segmented). But in defense of the 2-segmented dististipes, seta MX4 appears to be limited to advanced Lepidoptera and is similar to MX3 on the first dististipes segment, and in Lyonetiidae (Bedellia, Stehr 1987 Fig. 26.43j) the dististipes appears apparently two-segmented. If this segment is the first of three maxillary palp segments rather than the second dististipes segment, the seta and two pores on it may require name changes (MX4 will become MP9, MXc-d will become MPg-h), so to minimize the possible disruption to other maxilla names I have named the maxillary palp structures from terminal to basal segments.

The laciniogalea has a ventral olfactory pore LGa (present on all the butterflies I have examined except Morpho). Each laciniogalea (Grimes and Neunzig 1986b) has 8 setae/long sensilla: the terminal lobe (containing LG4-8) represents the galea, and LG1-3 usually occur dorsal to the terminal lobe on a slight ridge representing the lacinia; my names LG1-8 were named "STI, STII, STIII, LSS, MSS, LSB, CSB, MSB" respectively by Grimes and Neunzig 1986b; LG1 is a tactile seta (sensillum trichodea), LG2-3 are wider tactile sensilla (sensilla trichodea), LG4-5 are sensilla styloconica chemoreceptors/mechanoreceptors (these are two-segmented), LG6-8 are small sensilla basiconica chemoreceptors/mechanoreceptors. All eight LG1-8 (as well as the olfactory pore LGa missed by Grimes and Neunzig 1986b) are apparently present in most or all butterflies (I have seen all 8 and LGa in Libytheana, Morpho, Euschemon, Pyrrhopyge, Netrocoryne, Epargyreus).

**Body.** Butterflies have all the usual tactile setae, D1, D2, SD1, SD2, L1, L2, SV1, SV2, P1-6, and V1. (These are all primary setae, contrary to Stehr [1987, Table 26.5] who listed P2, P5, and P6 as postnatal setae on A10.) The prothorax has additional XD1 and XD2 tactile setae (and Lycaenidae have four or more additional XSD1, XSD2, XSD3, XSD4 setae).

The usual Lepidoptera proprioceptor setae occur, including MXD1 on T1 behind the prothoracic shield (anterodorsal to MD1 on T2), MD1 (generally anterior to D2) on T1-2 and A1-9, MSD1 on T2-3, MSD2 on T2-3 and A1-8 (the MSD's just anterodorsal to each abdominal spiracle), MV1 on T2-3, MV2 on T1-3, MV3 on T1-3 (MV1-3 form an oblique triangle on T1-3 centered at the level of the top of the leg) and A1-9. There is some question as to which of the three MV setae found on T2-3 occur on T1 and on the abdomen, because the position of "MV3" (MV2?) jumps up and down somewhat between abdominal segments (it is often more dorsal on A1-2), but I can contribute little to the problem's resolution; MV3 may be the best name pending more research (perhaps some moth larva will be found to have more than one MV seta on an abdomen segment?). MV3 is generally immediately anterior to the proleg on A3-6.

Microspines, each with a conelike base and a hairlike tip, always occur around the anus to repel fecal pellets (the exoskeleton of the rest of the body generally is covered with exceedingly tiny cones or similar structures, which lack spearlike tips). Microspines are as small as proprioceptor setae but evidently function differently.

Butterflies have all the usual olfactory pores on the body found in Lepidoptera (figured in moths by McIndoo 1919, 1929), including two or three on the prothoracic shield (Xa-c from top to bottom; McIndoo named them T1a-c but Xa-c is simpler and takes advantage of the name of the nearby XD tactile setae), none to two on the suranal plate (named SPa-b from top to side, and found only in Lycaenidae), one named Pa on the A10 proleg plate ("APa" of McIndoo 1919), rarely one anterior to this proleg plate (Pc in Curetis, Fig. 55, Strymon, Fig. 57, etc.), and one large pore named Pb on the anteromedial base of the A10 proleg ("APb" of McIndoo 1919). One pore Pa occurs on the side of each A3-6 proleg of Apodemia mormo (David M. Wright, pers. comm.).

**Leg.** The coxa has five tactile setae CX1-5 and three proprioceptor setae MC1-3 (MC1-2 anterior, MC3 posterior). The coxa is sclerotized more anteriorly than posteriorly in some Lycaenidae and Euschemon, divided into two sclerites in Libytheana, MC1 is on an unsclerotized area in Morpho, and MC3 is often just posterior to the coxal sclerite. The trochanter has no structures, but it is fused to the femur except on a long lateral rift. This trochanter-femur rift has a proprioceptor seta TF1 and three pores (TFa just behind TF1, TFb, and the posterior TFc)(the names of TFa and TFb have been exchanged from McIndoo's [1919] locations to maintain a proper front-to-back sequence). The femur has two distal medial setae FE1-2. The tibia has one lateroposterior pore TBa (a second and third pore occurred on one tibia of one individual of Limenitis archippus, McIndoo 1919, a freak occurrence), and six distal setae TB1-6 (named anterolateral to anterior to medial to posterior to posterolateral). The tarsus has two setae (TA1 and the posterior TA2) lateral to the claw (both have peculiar wide flaplike tips in Euschemoninae-Coeliadinae, Fig. 6), two shorter setae (TA3 and the posterior TA4) medial to the claw, and one lateral pore TAa near the base of the claw. The end of the tarsus itself is peculiarly widened in Actinote.

## KEY TO FIRST STAGE LARVAE

Gaps are left between the numbers of the key so that new taxa can be conveniently entered and the additions numbered.

- 100(600) Prolegs with fleshy lobe at the tip, with a gap in the crochets next to the lobe, usually only four to five crochets present (but up to a dozen in some species), usually not in a complete circle; hypostomal bridge has a gap as wide as the mandibles; ring glands present on body, usually both subdorsally and sublaterally; secondary setae present on body, often including SV setae above the prolegs; three or four XSD setae present on prothorax; long setae (including D, XD, XSD) on prothorax often overhang head; head seta F1 usually missing, if present usually tiny; head setae C1 and C2 far apart; abdomen segments 9 and 10 often appear fused; **Lycaenidae**, go to 200, 300, 400, and 500
- 200(300,400,500) About a dozen crochets on first eight prolegs, arranged in a circle, the circle interrupted in front and back and near the lobe; often more than two setae on mandible; head setae usually the same length on top of head as on front of head (but short on top in the Mexican Anatole); F1 a pore or pit (not a seta); VT2 present; body sometimes has hardened subdorsal and sublateral setae-bearing plates on every segment (tropical Anatole and Menander lack the plates); prothorax covers less than half of the normal-size head.....**Riodininae**
- 300(200,400,500) About a dozen crochets on first eight prolegs, arranged in a circle, the circle interrupted in front and back and near the lobe; only two mandible setae; head setae much shorter on top of head than on lower front of head; F1 a pore or pit (not a seta); VT2 absent on head; hardened body plates only on T1 and A10; prothorax covers less than half of the normal-size head.....**Curetinae**
- 400(200,300,500) Only four crochets present on first eight prolegs, arranged in an inner semicircle; only two mandible setae; AF2 long near top of head; F1 present; VT2 present (as well as VT1, VT3, VTa); hardened body plates only on prothorax and rear; prothorax covers less than half of the normal-size head.....**Miletinae**
- 500(200,300,400) Usually only four crochets present on first eight prolegs, arranged in an inner semicircle; only two mandible setae; head setae much shorter on top of head than on lower front of head; F1 rarely present as a seta, usually absent; VT2 present or absent; hardened body plates only on prothorax and rear; prothorax extends forward to cover half of the often-small head.....**Lycaeninae**
- 600(100) Prolegs lack a fleshy lobe, the crochets continuous at least on inner margin and usually in a complete circle;; hypostomal bridge has only a hairline gap; ring glands present only in skippers; setae vary; go to 700 and 2500
- 700(2500) Hardened ring glands present on body, always sublaterally (and often subdorsally in Hesperinae-Megathyminae); head and body have only primary setae (including two L setae on prothorax); setae generally short and clubbed or forked at tip, but SD1 long on T1 and D2 and SD1 long on A10, setae sometimes longer and hairlike on the middle of the body of Pyrrhopyginae and Megathyminae; head usually much wider than thorax; **Hesperiidae**, go to 800 and 1500
- 800(1500) Only one SD seta (SD1) on mesothorax, one on metathorax (SD2 is replaced there by one or more ring glands, often in pairs); go to 900 and 1200
- 900(1200) Supralateral ring glands paired (like a figure-8) or clustered on T2 and T3; ring glands on A8-9 below spiracles; go to 1000 and 1100
- 1000(1100) Setae on middle of body all short and broadened at tip.....**Hesperiinae**
- 1100(1000) Setae on middle of body long and hairlike.....**Megathyminae**
- 1200(900) No paired ring glands, the ring gland single on T2-3; ring glands absent or above spiracles on A8-9; go to 1300 and 1400

- 1300(1400) Supralateral ring gland on T1-3 and A1-8; a sublateral ring gland on A1-2; one V seta on A10 as usual; terminal two tarsus setae hairlike; crochets few (~17-23); VTa present on head.....**Heteropterinae**
- 1400(1300) No ring glands on A3-10; a supralateral ring gland on T2-3 and a sublateral ring gland on A1-2; two V setae on A10; terminal two tarsus setae flaplike; crochets very numerous (~60 on A3-6, ~91 on A`10); VTa absent on head.....**Euschemoninae**
- 1500(800) Two SD setae on mesothorax, two on metathorax; paired ring glands rare (on T1 of Epargyreus clarus, on A1-2 and/or A7-8 of some Trapezitinae) (but there may be clusters of ring glands); go to 1600 and 1700
- 1600(1700) Ring gland present sublaterally on T1-3 and A1-2, absent on A3-9; P1 on A10 replaced by a ring gland P1r; terminal two tarsus setae have flaplike tips; anal comb newly evolved from spikelets.....**Coeliadinae**
- 1700(1600) Ring glands absent on T2 and T3; ring glands if present on A8 and A9 above or below spiracles; terminal two tarsus setae hairlike; anal comb large as far as known; go to 1800 and 1900
- 1800(1900) Only one sublateral ring gland on A1-2, below P6 (occasionally a second near spiracle); no sublateral ring glands on A7-8 as far as known; setae clubbed or forked at tip; head neither flattened nor bumpy.....**Pyrginae**
- 1900(1800) A cluster of 2-6 sublateral ring glands on A1-2; sublateral ring glands present on A7-8 except in some Trapezitinae; go to 2000 and 2100
- 2000(2100) Setae short (less than or equal to the front-to-back length of the segment, except long on top of A9-10 and L1 long on T1), the D2 setae not longer; head neither flattened nor bumpy.....**Trapezitinae**
- 2100(2000) Setae long, the D2 setae much longer than the others all along body (about three times the length of the segment on A7-9); head flattened (ringed with a conspicuous ridge on top and sides), slightly bumpy, with a network of dark "veins".....**Pyrrhopyginae**
- 2500(700) Ring glands absent; secondary setae present in some species; setae various in shape; head usually about as wide as thorax; go to 2600 and 7100
- 2600(7100) Secondary setae (at least one) present on body or head; Nymphalidae and Papilionidae, go to 2700, 4500, 5000
- 2700(4500,5000) Body has some scoli (sometimes only BD2 scoli, or a fleshy bump at base of D2 on T2-A9); SV setae present above first eight prolegs, and other secondary body setae may occur; clusters of setae do not arise from plates; go to 2800 and 3500
- 2800(3500) Head has only primary setae; setae unforked; go to 2900 and 3200
- 2900(3200) Abdominal scoli associated with D2 seta; **Parnassiinae, Zerynthiini**; go to 3000 and 3100
- 3000(3100) Many D2 setae from BD2 scoli on T2-A9, secondary L setae on A2-A8;..... **Sericinus**
- 3100(3000) Only one D2 seta from D2 fleshy bump ("scolus") on T2-A9, no secondary L setae;..... **Bhutanitis**
- 3200(2900) Abdominal scoli associated with D1 seta and SD1 seta; Papilioninae, Graphiini; go to 3300 and 3400
- 3300(3400) No body setae forked.....Meandrusa payeni
- 3400(3300) Some body setae forked.....Graphium sarpedon
- 3500(2800) Head has at least one secondary seta; setae may be hairlike or forked; Papilioninae, go to 3600 and 3700
- 3600(3700) No body scoli present.....Chilasa epycides (**Troidini**)

- 3700(3600) Body scoli present; go to 3800 and 4100
- 3800(4100) Setae, but not scoli, present slightly above abdominal spiracles 2-8 (scoli may occur above this row on top of abdomen); **Battus**, **Tribe Troidini**, go to 3900 and 4000
- 3900(4000) Scoli present on top of abdomen.....Battus polydamas (Fig. 27) (**Troidini**)
- 4000(3900) Setae, but no scoli, on top of abdomen.....Battus philenor (**Troidini**)
- 4100(3800) A row of scoli slightly above abdominal spiracles 2-8; go to 4200 and 4300
- 4200(4300) Some setae on scoli forked at tip.....Parides (**Troidini**) and Eurytides (**Leptocircini**)
- 4300(4200) No forked setae.....Papilio (**Papilionini**)
- 4500(2700,5000) No body scoli, although body usually has fleshy subdorsal tubercles on T2 and sometimes on A2 and/or A8 (in tropics probably also on metathorax); secondary setae limited to a D3 seta (and Ithomiini may have a SV3 on A10) (head has only primary setae); SV setae absent above first eight prolegs; XD1 absent; XD2 present; setae hairlike; a few clusters of setae may or may not arise from plates; Danainae, go to 4600 and 4900 (the key characters distinguishing Danaini and Ithomiini may not hold up when more genera are studied)
- 4600(4900) A secondary D3 seta present only on abdomen; prothoracic shield sclerotized; **Danaini**, go to 4700 and 4800
- 4700(4800) Small fleshy subdorsal tubercles on T2, A2, and A8.....Danaus gilippus (Fig. 35)
- 4800(4700) Small fleshy subdorsal tubercles only on T2 and A8.....Danaus plexippus (Fig. 34)
- 4900(4600) A secondary D3 seta present on thorax as well as abdomen; prothoracic shield not sclerotized.....**Ithomiini**
- 5000(2700,4500) No body scoli (Baronia, Fig. 25, has a low hairy bump on A10); XD1 present; XD2 present; go to 5100, 5900
- 5100(5900) Prolegs have secondary setae; secondary SV setae present above first 8 prolegs (except perhaps in Morphinae, which have hundreds of secondary head setae); go to 5200 and 5300
- 5200(5300) Only primary setae (all hairlike) present on head (except one secondary seta near LH1 in Archon); all setae hairlike; SV setae present above first eight prolegs, other secondary setae sometimes present including SD, L, D1; clusters of setae occasionally arise from plates.....most **Parnassiinae**
- 5300(5200) Numerous secondary setae present on head; head setae hairlike or forked (forked at least in Morpho, Fig. 40), but setae hairlike on body; secondary setae numerous everywhere on body and head; no plates except prothoracic shield and usually suranal plate; go to 5400, 5700, and 5800
- 5400(5700,5800) Two tails which are part of sclerotized suranal plate; dorsal setae very long on head and body; head smooth, with or without a middorsal forked horn; **Morphinae**, go to 5500 and 5600
- 5500(5600) With a middorsal forked horn on head.....Morpho
- 5600(5500) Without a middorsal forked horn on head .....Caligo
- 5700(5400,5800) Two long tails, apparently fleshy; dorsal setae moderately long on head and body; head bumpy, with horns (a long lateral, a long subdorsal, and a short near-middorsal horn).....Charaxes marieps (**Charaxinae**)
- 5800(5400,5700) No tails; all setae very short on head and body; head bumpy, without horns.....**Baroniinae**
- 5900(5100) Prolegs lack secondary setae; no SV setae present above first 8 prolegs; go to 6000 and 6600

- 6000(6600) Secondary setae limited to two or three secondary L setae (L2.1-L2.4 present) on thorax and abdomen in all species, secondary D1 setae in most species, and secondary SD setae (three or more on thorax segments, two or more on abdomen segments) in some species (head has only primary setae); setae usually slightly clubbed at tip; clusters of setae usually arise from plates; **Boloria** and **Speyeria (Heliconiini)**, go to 6100, 6200, and 6500
- 6100(6200,6500) No secondary D1 setae (only D1 present); no secondary setae other than L.....**Boloria titania**
- 6200(6100,6500) One secondary D1 seta (D1.1 and D1.2) present; go to 6300 and 6400
- 6300(6400) Two secondary SD setae on most segments (SD1.1-SD1.3 present).....**Boloria eunomia**
- 6400(6300) No secondary SD setae (only the usual two SD present on T2-3, one on A1-9).....**Speyeria nokomis** (Fig. 51)
- 6500(6100,6200) Two to three secondary D1 setae (D1.1-D1.3 present), three to four secondary SD setae (SD1.1-SD1.5 present).....**Boloria improba** (Fig. 50)
- 6600(6000) Secondary setae limited to L setae; setae hairlike; clusters of setae may or may not arise from plates; go to 6700 and 7000
- 6700(7000) Two short tails on rear; secondary setae limited to L setae on T2-3 and L on A10; **Apaturinae**, go to 6800 and 6900
- 6800(6900) Head has several (up to ten) tiny 'horn' bumps along dorsal and lateral rim.....**Asterocampa celtis** (Fig. 42) and some **Doxocopa**
- 6900(6800) Head lacks tiny 'horn' bumps along dorsal and lateral rim.....**Asterocampa clyton** and some **Doxocopa**
- 7000(6700) No tails on rear; secondary setae limited to L setae on T3 and A1-8; no bumps on head.....**Polygonia** (Fig. 45)(**Nymphalinae**)
- 7100(2600) Only primary setae present on head and body; no D3 seta present on each abdomen segment; XD1 present; Nymphalidae, Libytheinae, Pieridae, go to 7200, 7300, and 7400
- 7200(7300,7400) Body has about ten fleshy cones on top (on T2 to A8); setae clubbed.....**Limenitis** (Fig. 43)(and perhaps a few other **Nymphalinae**)
- 7300(7200,7400) Body with a small fleshy subdorsal bump on A2 and two tails; setae probably clubbed.....**Prepona omphale (Charaxinae)**
- 7400(7200,7300) No fleshy tubercles or cones on body; setae hairlike or clubbed; go to 7500 and 8000
- 7500(8000) Third eye 50 percent larger than the others, first eye usually vestigial; head much taller than thorax; two P3 setae; **Satyrinae**, go to 7600 and 7700
- 7600(7700) Head has two conelike bumps or "horns" on top; body setae clubbed (short or long); usually two short to long tails on rear (except for **Megisto** and others).....**Lethe**, **Cyllopsis** (Fig. 37), **Megisto**, **Neonympha**, and others
- 7700(7600) Head has neither bumps nor horns; body and often head setae clubbed (short or long) or bladelike (like a scythe in **Cercyonis**, Fig. 38); go to 7800 and 7900
- 7800(7900) Two fleshy tails; setae very long and clubbed.....**Paratisiphone**, **Tisiphone**
- 7900(7800) Only a trace of two fleshy tails (none in **Erebia**); setae short and clubbed.....**Cercyonis** (Fig. 38), **Oeneis**, **Erebia** (Fig. 39), and others
- 8000(7500) Third eye the same size as the other five; head generally about as tall as thorax; go to 8100 and 8200
- 8100(8200) Head has several (up to ten) small 'horns' along dorsal and lateral rim; body setae all hairlike; two short tails on rear.....**Asterocampa celtis** (Fig. 42) and some **Doxocopa (Apaturinae)**

- 8200(8100) Head has neither bumps nor horns (some Anaea have two very small rounded bumps on top of head); body setae hairlike or clubbed; no tails on rear; go to 8300, 8400, and 8900
- 8300(8400,8900) XD2 absent on prothorax; two L setae on prothorax; one SD seta each on mesothorax and metathorax; VTa absent on head; setae around rim of labrum minute, and all body setae very short, most of them slightly widened at tip; prothorax as large as mesothorax, with slight shoulders..... **Libytheinae**
- 8400(8300,8900) XD2 missing on prothorax; 1-2 L setae on prothorax; usually two (one in Dismorphiinae) SD setae on mesothorax, always one on metathorax; VTa present on head; body setae vary; prothorax a bit smaller than mesothorax; **Pieridae**, go to 8500 and 8600
- 8500(8600) Two L setae on prothorax; one SD seta on mesothorax; body setae T-shaped (long hairlike setae only on T1, A10, and head); AF2 absent on head..... **Dismorphiinae**
- 8600(8500) One L seta on prothorax; two SD setae on mesothorax; body setae slightly forked (clubbed) or hairlike; AF2 present on head; go to 8700 and 8800
- 8700(8800) Body setae clubbed and often glandular (the forked tips of D1 and D2 dispense honeydew attractive to ants), varying from very short (except on the rear in Colias) to long (as long as a body segment in Pierinae and Eurema)..... **all Pierinae and most Coliadinae**
- 8800(8700) Body setae hairlike (perhaps very slightly enlarged at the tapered tip, perhaps not glandular) and almost as long as a body segment..... **some Coliadinae** (Nathalis, Fig. 30, perhaps others)
- 8900(8300,8400) XD2 present on prothorax; two L setae on prothorax; two SD setae each on mesothorax and metathorax; VTa present on head; body setae hairlike, varying from short to very long; prothorax a bit smaller than mesothorax; **Nymphalidae**, go to 9000 and 9100
- 9000(9100) Body and head setae very short and clubbed, not visible to the naked eye; head and body mottled with pale dots (the head of Anaea andria, Fig. 41, is smooth, but A. pithyusa and A. itys may have two low bumps on top of head; some tropical species have two to six head horns and two tails)..... **Charaxinae**
- 9100(9000) Body setae long, visible to the naked eye; go to 9200 and 9500
- 9200(9500) XD1 and XD2 present; go to 9300 and 9400
- 9300(9400) MXD1 present on T1; tarsus narrowed at base of claw and not bilobed (both conditions typical of nearly all butterflies)..... **Nymphalini and Melitaeini (Nymphalinae); Calinaginae** (not seen) probably fits here
- 9400(9300) MXD1 absent on T1; tarsus wide at base of claw and bilobed mediolaterally..... **Acraeini**
- 9500(9200) XD1 absent, XD2 present..... **all Heliconiini including Euptoieta (Nymphalinae)** (Speyeria-Boloria have XD1 but are presented in numbers 6100-6500 above in this key)

## CHARACTERISTICS OF HIGHER TAXA

**HESPERIIDAE.** Ring glands present on body, always including one sublaterally on A1-2 (except in some Megathyminae); only primary setae present; SD1 long on T1, D2 and SD1 long on A10; VT1a23 sequence on head (in all five subfamilies); anal comb present (except in Megathyminae, and the Coeliadinae anal comb newly evolved from spikelets).

**Euschemoninae.** Seta SD2 has become a single ring gland SDr on T2-3, only one sublateral ring gland on A1-2, ring glands absent on T1 and A3-10; only one SD seta SD1 on T2-3; only primary setae present; short setae slightly clubbed at tip; setae short (less than or equal

to the front-to-back length of the segment, except on A9-10), the D2 setae not longer, D1 short on A10, L1 long on T2-3; terminal two legtip setae flaplike; two V setae on A10 (V1.1 and V1.2); crochets numerous (about 60-62 on A3-6, about 91 on A10); head neither flattened nor bumpy; mandible with teeth; VTa (=Va) absent on head. This taxon is closer to Coeliadinae than to Pyrginae. Examples: Euschemon rafflesia (Fig. 6).

**Coeliadinae.** Only one sublateral ring gland on A1-2 and T1-3, P1 on A10 is a ring gland P1r, ring glands absent on A3-9, paired ring glands absent; only primary setae present; two SD setae on T2-3; setae trumpetlike at tip; setae short (less than or equal to the front-to-back length of the segment, except on rear), the D2 setae not longer, D1 short on A10; L1 long on T2-3, moderately long on T1 and A9; terminal two legtip setae flaplike; anal comb newly evolved from spikelets; head neither flattened nor bumpy; mandible with teeth. Examples: Hasora khoda (Fig. 7).

**Pyrrhopyginae.** No paired ring glands (but there are clusters of sublateral ring glands on A1-2), a sublateral ring gland on T1 and A7-8, ring glands absent on T2-3, A3-6, A9-10; only primary setae present; two SD setae on T2-3; setae hairlike, the D2 setae much longer than the others all along body (about three times the length of the segment on A7-9), L1 moderately long on T1-3, but D1 short on A10; head flattened (ringed with a conspicuous ridge on top and sides), slightly bumpy, with a network of dark "veins"; mandible with teeth. Examples: Pyrrhopyge araxes (Fig. 8).

**Pyrginae.** Only one sublateral ring gland on A1-2, ring gland sometimes present subdorsally and sublaterally on T1, a ring gland sometimes present on A1-8 below spiracles (L2r) and on A9 above spiracles (D1r), P1 usually a ring gland P1r on A10, but ring glands absent on T2-3, paired ring glands occasionally present (on T1 of Epargyreus clarus) but no clusters of ring glands; only primary setae present; two SD on T2-3; setae clubbed or forked at tip; setae short but moderately long in Pyrgus (less than or equal to the front-to-back length of the segment except on rear), D1 short (long in Pyrgus) on A10, the D2 setae not longer, L1 short (moderately long in Pyrgus) on T1-3; head neither flattened nor bumpy; mandible with teeth. Examples: Chaetocneme beata (Fig. 9), Netrocoryne repanda (Fig. 10), Pyrgus centaureae (Fig. 11), Epargyreus clarus (Fig. 12). Published examples: Epargyreus clarus (gross appearance, Scudder 1889), Thorybes pylades gross appearance (Scudder 1889), Achalarus lyciades gross appearance (Scudder 1889), Erynnis lucilius gross appearance (Scudder 1889).

**Trapezitinae.** Clusters of 2-6 sublateral ring glands on A1 and A2, 1-2 sublateral ring glands sometimes present on A7-8, these ring glands sometimes paired, ring glands absent on other segments except P1 sometimes a ring gland on A10; only primary setae present; two SD setae on T2-3; setae clubbed at tip or hairlike; setae on top of A9-10 long (D1 long on A10), all other setae short (less than or equal to the front-to-back length of the segment, the D2 setae not longer) including L1 short on T1-3; A3-6 crochets usually in a circle but sometimes in a mesoseries; ventral neck gland sometimes present; head neither flattened nor bumpy; mandible of first stage larva has fairly small teeth; AN9 evidently absent. Examples: Trapezites iacchoides (Fig. 13), T. eliena (Fig. 14), Toxidia doubledayi (Fig. 15), T. peron (Fig. 16), Hesperilla ornata (Fig. 17), Anisynta cynone (Fig. 18), Mesodina halyzia (Fig. 19). Published examples: Trapezites maheta and T. praxedes (Sands et al. 1984).

**Heteropterinae.** A ring gland SD2r on T1-3 and A1-8 above spiracle (and another below spiracle on A1-2), seta SD2 has become a single ring gland SD2r on T2-3 and A1-8; only primary setae present; only one SD seta SD1 on T2-3; setae on middle of body all short but not broadened at tip, D1 long on A10, L1 short on T1-3; mandible of first stage larva has very shallow teeth; AN9 evidently absent. Because this taxon (Piruna pirus) is more

different from Hesperinae-Megathyminae than the latter two subfamilies are to each other, Heteropterinae must be removed from Hesperinae to its own subfamily. Examples: Piruna pirus (Fig. 20).

**Hesperinae.** Ring glands on A7-9 below spiracles, SD2 has become a pair (like a figure 8) or cluster of ring glands on T2-3; only primary setae present; only one SD seta SD1 on T2-3; setae on middle of body all short and broadened at tip, D1 long (sometimes short) on A10, L1 short on T1-3; mandible of first stage larva lacks teeth; AN9 evidently absent. Examples: Calpodes ethlius (Fig. 21), Hesperia leonardus montana (Fig. 22). Published examples: Ancyloxypha numitor gross appearance (Scudder 1889), Hesperia sassacus gross appearance (Scudder 1889), Hesperia setae (10 species; seta D1 on A10 is very short and spatulate in H. juba, short and spatulate in H. comma tildeni, H. comma ochracea, H. comma colorado, and H. lindseyi, longer and spatulate in H. nevada, long and pointed in H. ottoe, H. columbia, H. viridis, H. uncas, H. pahaska pahaska, H. pahaska martini, H. leonardus pawnee, and H. leonardus montana; D2 on T1 is present or absent) (Scott 1975), Hesperia leonardus setae and gross appearance (Scudder 1889, Scott 1986a), Polites origenes gross appearance (Scudder 1889), Wallengrenia egeremet gross appearance (Scudder 1889), Calpodes ethlius ring glands (Franzl et al. 1984).

**Megathyminae.** Ring glands present on A7-9 below spiracles, SD2 has become a paired (like a figure-8) ring gland on T2-3; only primary setae present, except two SV1 setae on A7-8 and A10, and four P setae on A3-6 proleg, a P6 and at least sometimes a P1 seta on A1-2; only one SD seta SD1 on T2-3; setae on middle of body long and hairlike, and D1 setae gradually lengthening from T1 to A10 (long on A10), L1 short on T1-3; mandible of first stage larva lacks teeth; anal comb absent; AN9 evidently absent. Examples: Agathymus alliae (Fig. 23), Aegiale hesperiaris (Fig. 24). Published examples: A. hesperiaris (Fig. 24, Dampf 1923), Megathymus yuccae gross appearance (Riley 1876).

**PAPILIONIDAE.** Many secondary setae on side of body and on prolegs. VT12a3 sequence on head.

**Baroniinae.** Many forked secondary setae on head, many secondary body setae. Examples: Baronia brevicornis (Fig. 25). Published examples: B. brevicornis (Vazquez and Perez 1961, Ruiz 1969).

**Parnassiinae.** SV setae present above prolegs, secondary P setae present, one to several secondary setae on A10 suranal plate, only primary setae on head (except one secondary seta near LH1 on Archon).

**Zerynthiini.** Characters of the subfamily, with one to several secondary dorsal seta on A10, only primary setae on head, scoli present in Sericinus and Bhutanitis. Published examples: Luehdorfia japonica, Parnalius cerisy, Sericinus montela (all Igarashi 1984), Bhutanitis lidderdalei (Igarashi 1989).

**Parnassiini.** Characters of the subfamily, with several secondary dorsal setae on A10, secondary SD and L setae in Parnassius and Archon, secondary D1 setae in some Parnassius, only primary setae on head (except one secondary seta on Archon). Examples: Parnassius phoebus (Fig. 26). Published examples: P. phoebus (Scott 1986a), P. glacialis, Archon apollinus, Hypermnestra helios (all Igarashi 1984).

**Papilioninae.** Scoli present on body; secondary setae common on body (secondary L setae always present) and sometimes on head.

**Troidini.** Setae hairlike, except forked in Parides photinus; scoli present on body; D1 a seta in Battus philenor but a scolus in B. polydamas and all other genera, D2 remained a seta (this seta is away from the D1 scolus in Parides, near it in Battus, and is on its posteroventral base

in the other genera); secondary setae common on body, very few to many secondary setae on head (typically near LH1, but only one in Battus polydamas and Parides photinus); extra sensilla basiconica on pedicel tip (Dethier 1941). Examples: Battus polydamas (Fig. 27). Published examples: Parides photinus (Ross 1964b), Battus philenor gross appearance (Scott 1986a, Scudder 1889), Cressida cressida, Euryades corethus, Pachliopta aristolochiae, Pharmacophagus antenor, Troides aecus, Ornithoptera priamus, Atrophaneura alcinous, Chilasa epycides, C. clytia (all Igarashi 1984; note that some Papilioninae genera such as Chilasa and Meandrusa are assigned to different tribes than those of Igarashi and others, as explained by Scott and Wright 1990).

**Papilionini.** Setae not forked; D1 remained a seta; scoli present on body; D2 became a scolus, a unique trait in Papilionidae (except independently in some Zerynthiini); secondary setae common on body, some to usually many secondary setae on head. Examples: Papilio polyxenes (Fig. 28). Published examples: Papilio polyxenes olfactory pores (McIndoo 1919) and gross appearance (Scudder 1889), Papilio zelicaon f. nitra (Scott 1986a), Papilio cresphontes gross appearance (Scudder 1889), Papilio thoas (Ross 1964b), Papilio troilus gross appearance (Scudder 1889), Agehana maraho, Papilio demoleus, Euchenor euchenor, Menelaides protenor (all Igarashi 1984).

**Teinopalpini.** Setae not forked; no scoli present; D1 and D2 remained setae; secondary setae somewhat common on body and on head. Published examples: Teinpalpus imperialis (Igarashi, 1987).

**Leptocircini.** Some body setae forked (except Meandrusa payeni); scoli present on body (except on Meandrusa payeni and Graphium sarpedon); D1 became a scolus; D2 remained a seta; secondary setae common on body, only primary setae present on head (except Iphiclides podalirius). Published examples: Eurytides marcellus gross appearance (Scudder 1889, Scott 1986a), Meandrusa payeni, Iphiclides podalirius, Graphium sarpedon (Igarashi 1984).

**PIERIDAE.** Only primary setae present; XD2 seta absent on T1, only one SD seta on T3; D1 and D2 are forked and dispense honeydew attractive to ants.

**Pseudopontiinae.** Unknown.

**Dismorphiinae.** Only primary setae present; XD2 absent on T1, only one SD seta on T2-T3; all body setae T-shaped except long and hairlike on front of T1 and on A10 (and on lower part of head); sequence VT12a3 on head. Examples: Leptidea amurensis (Fig. 29). Published examples: Dismorphia virgo (Young 1972), D. amphiona (Aiello 1980).

**Coliadinae.** Only primary setae present; XD2 absent on T1, only one SD seta on T3 (two on T2), only one L seta on T1; sequence VT12a (Colias) or VT1a23 (Nathalis) on head. Examples: Nathalis iole (Fig. 30), Colias alexandra (Fig. 31). Published examples: Colias philodice gross appearance (Scudder 1889, Scott 1986a).

**Pierinae.** Only primary setae present; XD2 absent on T1, MXD1 absent on T1, only one SD seta on T3 (two on T2), only one L seta on T1; sequence VT12a (Pieris) or VT123a (Euchloe) on head. Examples: Euchloe ausonia (Fig. 32). Published examples: Pieris brassicae (Hinton 1946, Scott 1986a), Pieris rapae olfactory pores (McIndoo 1919) and gross appearance (Scudder 1889), Anthocharis midea gross appearance (Scudder 1889, Scott 1986a).

**NYMPHALIDAE.** Only primary setae present in most groups.

**Libytheinae.** Only primary setae present; VTa absent, XD2 absent, only one SD seta on T2-3; all setae small. Examples: Libytheana carinenta bachmanii (Fig. 33). Published examples: L. carinenta bachmanii (Scott 1986a).

**Danainae** (includes Ithomiini). XD1 absent on T1; secondary D1.2 seta on abdomen and sometimes thorax; fleshy subdorsal bumps sometimes present; only primary setae on head; sequence VT12a3 on head; extra sensillae occur on antennal pedicel tip (Dethier, 1941), at least in Danaus.

**Danaini.** XD1 absent on T1; secondary D1.2 seta on A1-9; fleshy subdorsal bumps sometimes present (on the segments which gain long filaments in older larvae); only primary setae on head. Examples: Danaus plexippus (Fig. 34), D. gilippus (Fig. 35). Published examples: Danaus gilippus (Kitching 1984), Danaus plexippus gross appearance (Scudder 1889, Scott 1986a).

**Tellervini.** Unknown.

**Ithomiini.** XD1 absent on T1; secondary D3 seta on T2-3 and A1-8, several secondary D and SV on A10; (fleshy subdorsal bumps probably present in a few genera?); only primary setae on head. Examples: Mechanitis polymnia dorissides (Fig. 37).

**Calinaginae.** Setae unknown, but the brief mention of first stage larva and the gross appearance of the figured third stage Calinaga buddha (Ashizawa and Muroya 1967) suggests that only primary setae are present and that the head is smooth without horns and that A10 lacks tails.

**Satyrinae.** Third eye larger than the others; eye #1 of first stage larva (and older larvae?) vestigial in most species (except Cyllopsis); only primary setae present in most genera except a secondary P seta (P3.2) present on A10, and Acrophtalmia artemis and Ragadia luzonia are drawn with secondary head setae (Fukuda 1983); two tails present (sometimes only a trace of tails); PA1 nearly as dorsal as PA2 on head of first stage larva; sequence VT1a23 on head; mandible of first stage larva lacks teeth; extra sensillae on pedicel tip in a few genera (Dethier 1941). Examples: Cyllopsis pertepida dorothea (Fig. 37), Cercyonis oetus (Fig. 38), Erebia epipsodea (Fig. 39). Published examples: Lethe eurydice gross appearance (Scudder 1889), Lethe portlandia gross appearance (Scudder 1889), Lethe europa (Fukuda 1985), Acrophtalmia artemis and Ragadia luzonia (Fukuda 1983), Ypthima asterope (Hesselbarth 1983), Ypthima praenubilia (Matsumura 1988), Ypthima pandocus, Mycalesis sp., Orsotriaena medus, Elymnias melias, Zethera pimplea, Ptychandra lorquinii (all Fukuda 1985), Paratisiphone and Tisiphone (Holloway 1974), C. pertepida dorothea (Scott 1986a), Neonympha areolata gross appearance (Scudder 1889, Scott 1986a), Megisto cymela gross appearance (Scudder 1889), Cercyonis pegala gross appearance (Scudder 1889, Scott 1986a; the setal map of Emmel and Mattoon 1972 has several errors), Oeneis jutta gross appearance (Scudder 1889), Oeneis melissa gross appearance (Scudder 1889, Scott 1986a), Erebia meta, aethiops, spp. (Roos and Arnscheid 1989, and see references cited therein), Satyrus (Garcia Barros 1987).

**Morphinae** (includes Brassolini). Hundreds of setae on head (forked in Morpho) and a few secondary setae on body; two sclerotized tails on rear and often horns on head; sequence VT1a23 on head; mandible of first stage larva lacks teeth (Morpho mandible has only one seta); Morpho has PGa and unique PGb. Examples: Morpho granadensis (Fig. 40). Published example: Caligo beltrao (Casagrande 1979).

**Charaxinae.** Only primary setae present; setae very short; sometimes two tails on rear and sometimes several horns (very long in some species) on head; sequence VT1a23 on head. Examples: Anaea andria (Fig. 41). Published examples: Anaea pithyusa (Muysshondt 1975),

Anaea itys (Muysshondt 1973b), Prepona omphale (Muysshondt 1973a), Charaxes marieps (Williams and Boomker 1980).

**Apaturinae.** Only primary setae present, except one secondary L on T2-3 and three or four secondary L setae on A10; two often-sclerotized tails on rear; small horns sometimes present on rim of head; sequence VT1a23 on head. Examples: Asterocampa celtis (Fig. 42).  
Published examples: A. celtis (Scott 1986a).

**Nymphalinae.** Only primary setae present (except in Polygonia, Speyeria, and Boloria); small subdorsal bumps present on body in a few species (Limnitis); sequence VT1a23 on head (even in Acraeini).

**Limnitudini.** Only primary setae present; small subdorsal bumps present in many or all species; Limnitudini and Nymphalini have all five P1-5 setae on the A10 proleg plate. Examples: Limnitis weidemeyerii (Fig. 43). Published examples: Limnitis archippus olfactory pores (McIndoo 1919) and gross appearance (Scudder 1889, Scott 1986a).

**Biblidini.** Unknown.

**Marpesiini.** Unknown.

**Nymphalini.** (includes Eurytelini, which can be distinguished by the ventral pseudovalve on A8 of adult males, but its phylogenetic distinctness from Nymphalini is unproven). Only primary setae present (except in Polygonia, Speyeria, Argynnis, and Boloria). Nymphalini and Limnitudini have all five P1-5 setae on the A10 proleg plate. Examples: Precis coenia (Fig. 44), Polygonia progne nigrozephyrus (Fig. 45), Nymphalis milberti (Fig. 46).  
Published examples: Vanessa atalanta gross appearance (Scudder 1889), Polygonia faunus gross appearance (Scudder 1889), Nymphalis antiopa gross appearance (Scudder 1889, Scott 1986a), Anartia fatima and jatrophae ((Silberglied, Aiello, and Lamas 1979).

**Melitaeini.** Only primary setae present. Examples: Phyciodes orseis herlani (Fig. 47).

Published examples: Chlosyne harrisii gross appearance (Scudder 1889), Phyciodes tharos gross appearance (Scudder 1889), P. orseis herlani (Scott 1973).

**Acraeini** Only primary setae present (a tiny secondary SV seta on T1); MXD1 absent on T1. Examples: Actinote carycina (Fig. 48).

**Heliconiini** (includes Argynnini). Only primary setae on head; body has only primary setae in most species (except Heliconius ricini lacks L2 on T1, Heliconius wallacei and alipha have L3 on A1-8, Dione juno and Heliconius doris have SV2 on T2-3 [Fleming 1960], and Speyeria and Boloria have secondary L setae and often other secondary setae); XD1 absent (except in Speyeria and Boloria); extra sensillae on pedicel tip only in Euptoieta (Dethier 1941). Examples: Euptoieta claudia (Fig. 49), Boloria improba acrocneuma (Fig. 50), Speyeria nokomis nokomis (Fig. 51). Published examples: Dryadula, Philaethria, Dione, Dryas, Heliconius (all Fleming 1960), Heliconius isabella (Ross 1964b), H. erato (Ross 1964b), Dryas iulia (Ross 1964b), Speyeria nokomis (Scott 1982b), Speyeria aphrodite gross appearance (Scudder 1889), Speyeria idalia gross appearance (Scudder 1889), Boloria improba (Scott 1982a, 1986a), Boloria selene gross appearance (Scudder 1889).

**LYCAENIDAE.** VT12a3 sequence on head (but VT2 or VT3 lost in some groups); gap in hypostomal bridge very wide; ring glands present on body; many secondary setae on body including SV setae above prolegs and on top of A10; unique XSD1-4 setae present on T1; V1 absent on T1 (the drawing of Scott 1986a shows V1 in error); MXd present (on ventromedial side of 2nd dististipes segment); posterior third of each coxa membranous (David M. Wright pers. comm.); a medial gap interrupts row of crochets (except first stage Feniseca). Many of the following subfamily traits are from Scott and Wright (1990).

**Riodininae** (includes Styx). Ca absent on head (it is absent in all butterflies except the remaining Lycaenidae); F1 lost at least sometimes (it became a sunken pit or pore in Apodemia); fusulus not fused to fusuliger (fused in other Lycaenidae subfamilies); prementum seta near midventral line; about ten or more crochets, including many small ones on lateral edge of proleg. Examples: Apodemia nais (Fig. 53). Published examples: A. nais (Scott 1986a), Anatole rossi (Ross 1964a), Menander felsina (Callaghan 1977). Styx infernalis belongs to Riodininae (Robbins 1988).

**Poritiinae**. Unknown to me.

**Miletinae**. Ca present on head; Ab absent on head; AF1 absent on head; prementum seta absent; four crochets, all medial but without a medial gap. Examples: Feniseca tarquinius (Fig. 54).

**Curetinae**. Ca present on head; F1 lost (it became a sunken pit or pore); VT2 lost on head; about ten or more crochets, including many small ones on lateral edge of proleg; some SD setae short and spatulate, including a short spatulate SD3 seta near MD1; a supraspiracular row of ring glands present; cuticle sculpturing microtuberculate. Examples: Curetis acuta (Fig. 55).

**Lycaeninae**. Ca present on head; VT3 lost on head; head retracts into prothorax strongly; only 4-16 crochets, on medial side of proleg or almost a complete circle; some (or all) SD setae short and spatulate, including a short spatulate SD3 seta near MD1; several A10 setae tufted on the rear (apparently L setae); a supraspiracular row of ring glands present; cuticle sculpturing microtuberculate. Clark and Dickson (1956) figure structures on an abdominal segment of many S. Africa species, including Liptenini, Miletini, Aphnaeini, Lycaenini, Theclini, and Polyommadini. Examples: Lycaena heteronea (Fig. 56), Strymon melinus (Fig. 57), Callophrys affinis homoperplexa (Fig. 58). Published examples: Lycaena epixanthe (Wright 1983), Lycaena phlaeas gross appearance (Scudder 1889), Eumaeus minyas (Ross 1964b), Satyrium liparops gross appearance (Scudder 1889), Callophrys gryneus gross appearance (Scudder 1889), Callophrys affinis homoperplexa (Scott 1986a), Strymon melinus (Scott 1986a), Plebejus idas gross appearance (Scudder 1889, Scott 1986a), Leptotes cassius (Downey and Allyn 1979), Everes comyntas setae (Lawrence and Downey 1966) and gross appearance (Scudder 1889), Hemiargus ceraunus (Downey and Allyn 1984).

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## FIGURE LEGENDS

- Figs. 1 (see figs. 1-2 of Scott 1866a). Typical major larval structures and their names.
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- Fig. 2. Mechanitis polymnia dorissides (Danainae, Ithomiini).
- Fig. 3. Polygonia progne nigrozephyrus (Nymphalinae, Nymphalini).
- Fig. 4. Asterocampa celtis antonia (Apaturinae).
- Fig. 5. Agathymus alliae (Megathyminae).
- Fig. 6. Euschemon rafflesia (Euschemoninae).
- Fig. 7. Hasora khoda (Coeliadinae).
- Fig. 8. Pyrrhopyge araxes (Pyrrhopyginae).
- Fig. 9. Chaetocneme beata (Pyrginae).

- Fig. 10. Netrocoryne repanda (Pyrginae).  
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 Fig. 49. Euptoieta claudia (Nymphalinae, Heliconiini, "Argynnini").  
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 Fig. 51. Speyeria nokomis nokomis (Nymphalinae, Heliconiini, "Argynnini").  
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 Fig. 54. Feniseca tarquinius (Lycaenidae, Miletinae), redrawn from David M. Wright (pers. comm.).  
 Fig. 55. Curetis acuta (Lycaenidae, Curetinae).  
 Fig. 56. Lycaena heteronea (Lycaenidae, Lycaenini).

Fig. 57. Strymon melinus (Lycaenidae, Eumaeini).

Fig. 58. Callophrys affinis homoperplexa (Lycaenidae, Eumaeini).

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FIG. 2. MECHANITIS

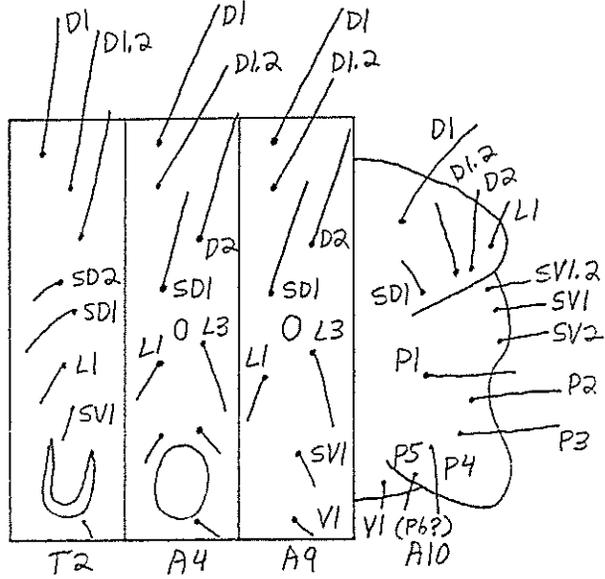


FIG. 3. POLYGONIA

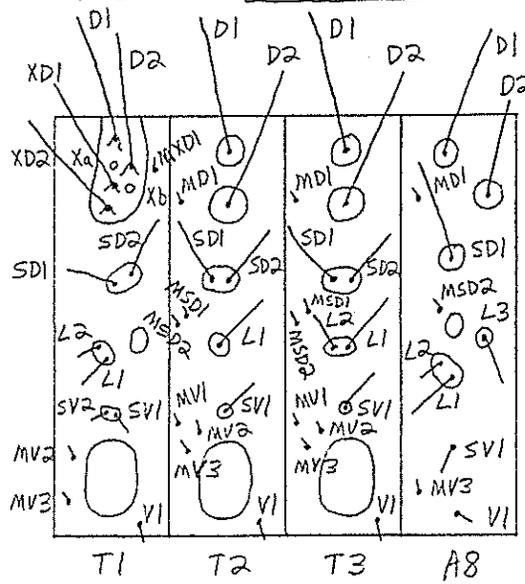


FIG. 4. ASTEROCAMPA

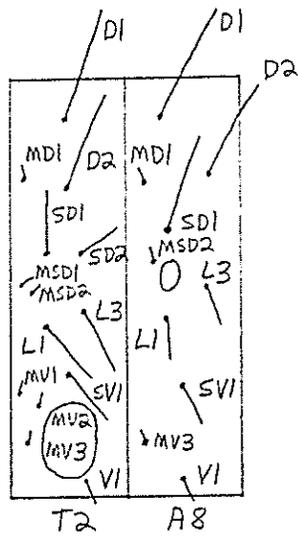


FIG. 5. AGATHYMUS

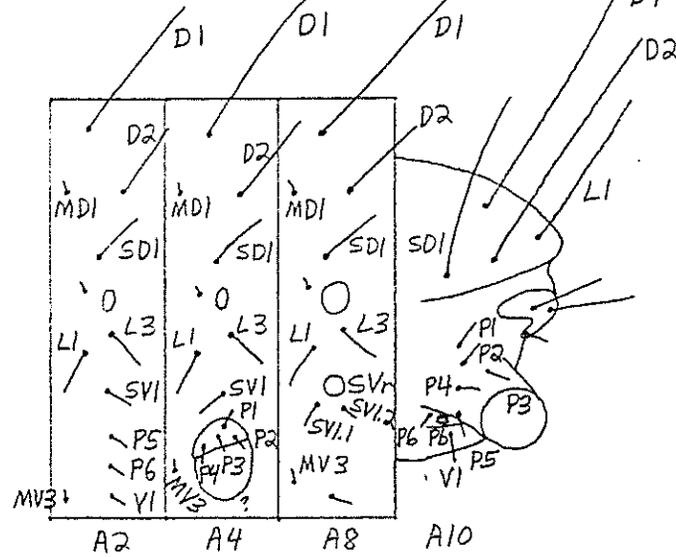
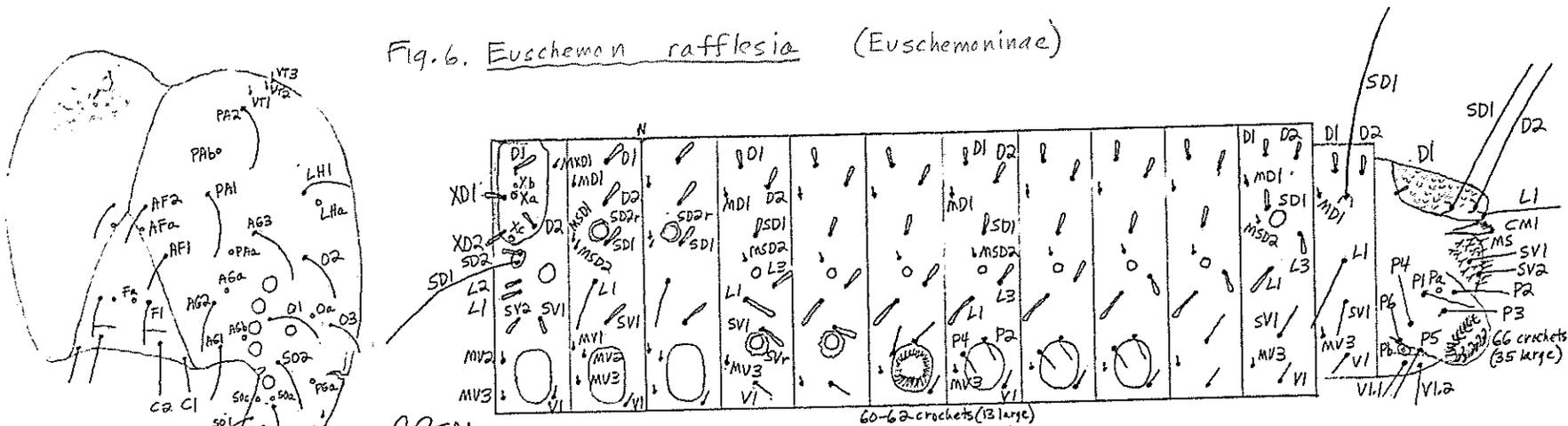
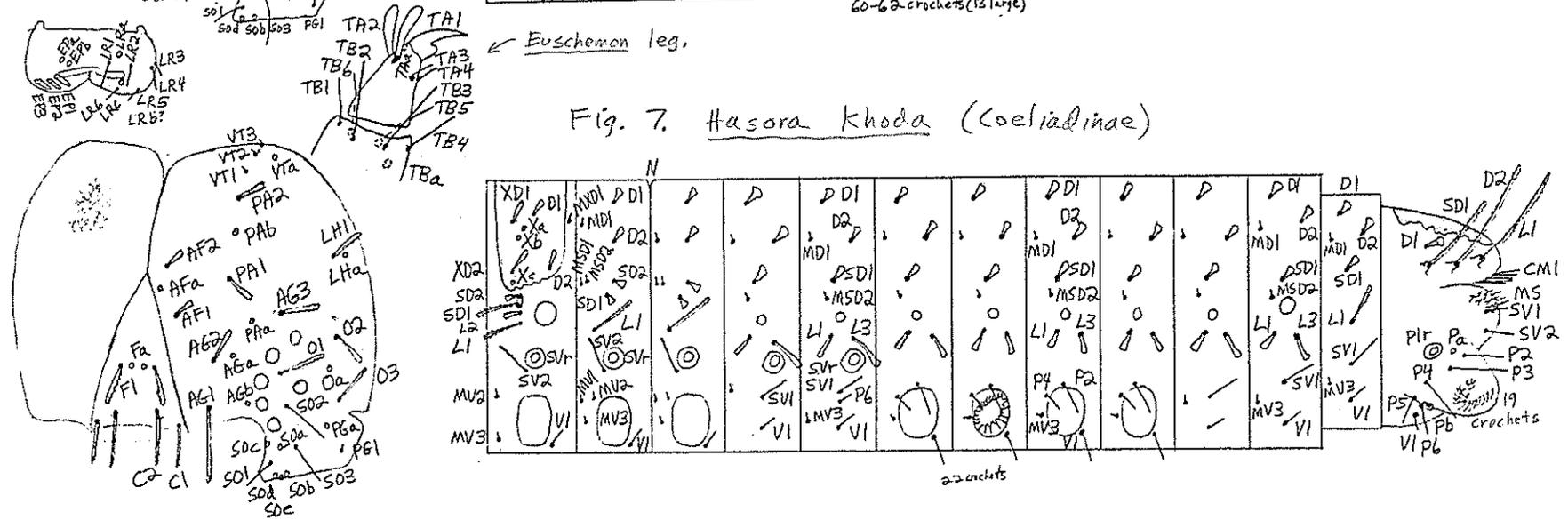


Fig. 6. Euschemon rafflesia (Euschemoninae)



← Euschemon leg.

Fig. 7. Hasora khoda (Coeliadinae)









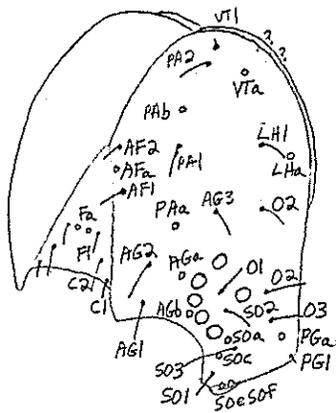


Fig. 14. *Trapezites eliena* (Trapezitiinae)

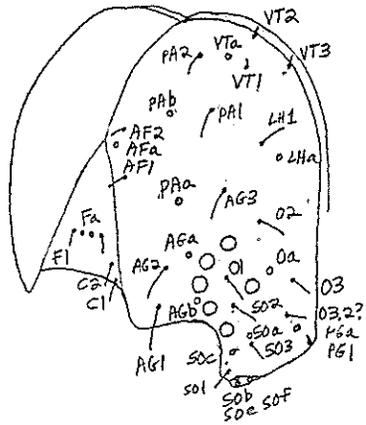
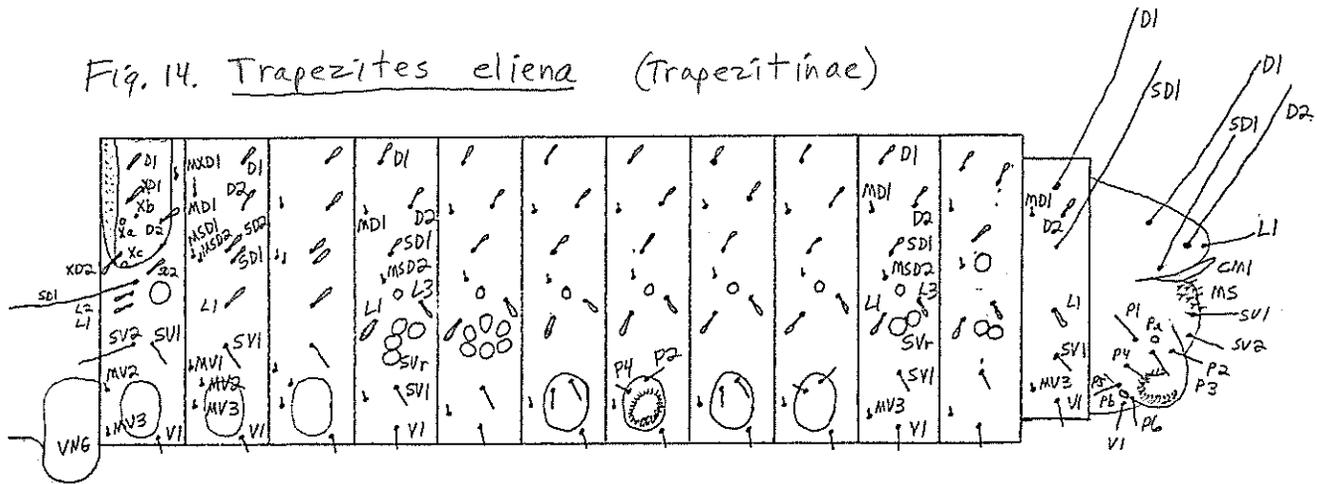


Fig. 15. *Toxidia doubleayi* (Trapezitiinae)

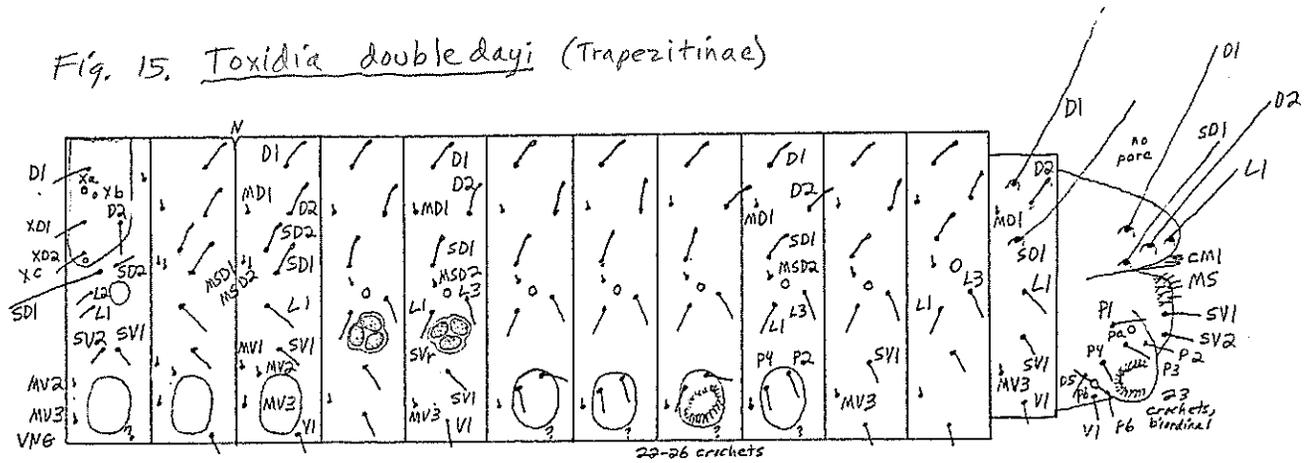


Fig. 16. *Toxidia peron* (Trapezitinae)

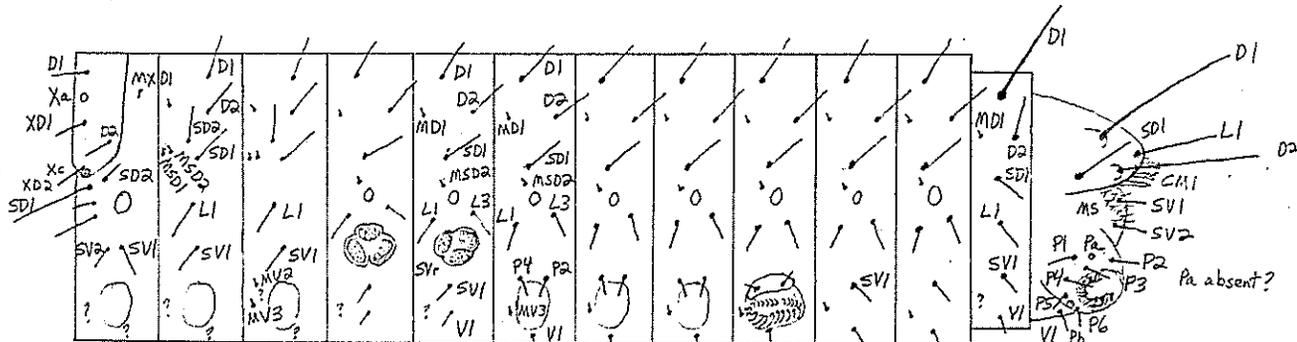
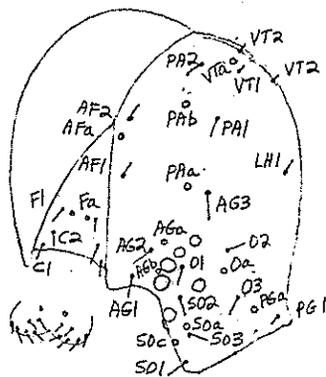


Fig. 17. *Hesperilla ornata* (Trapezitinae)

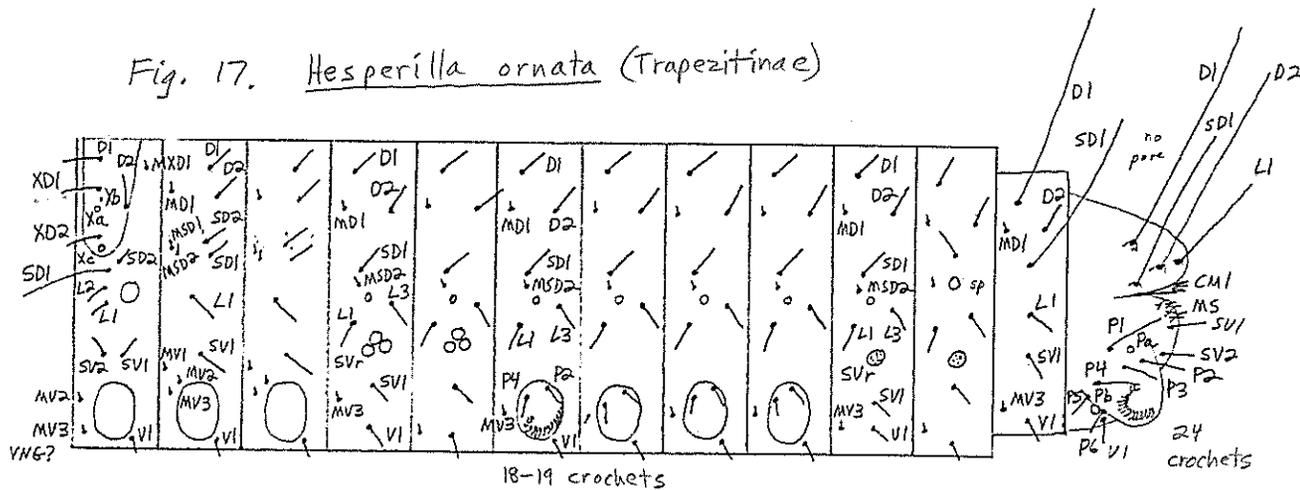
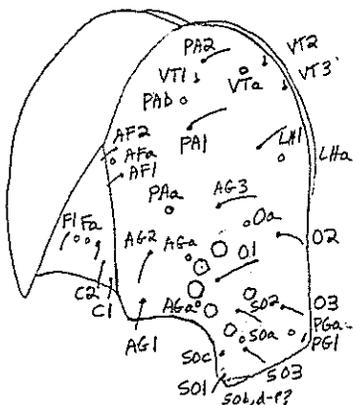


Fig. 18. Anisynta cynone (Trapezitinae)

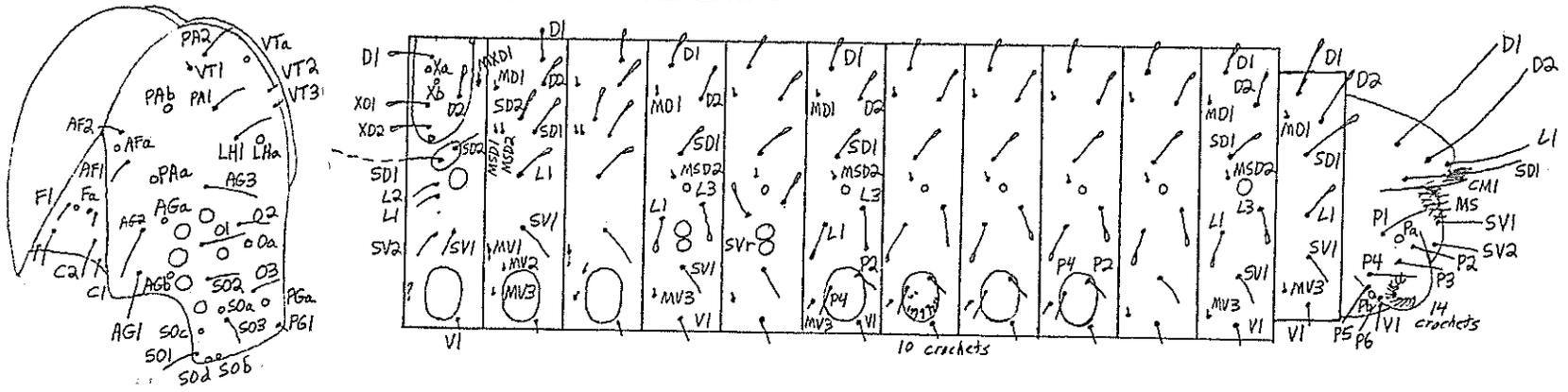


Fig. 19. Mesodina halgzia (Trapezitinae)

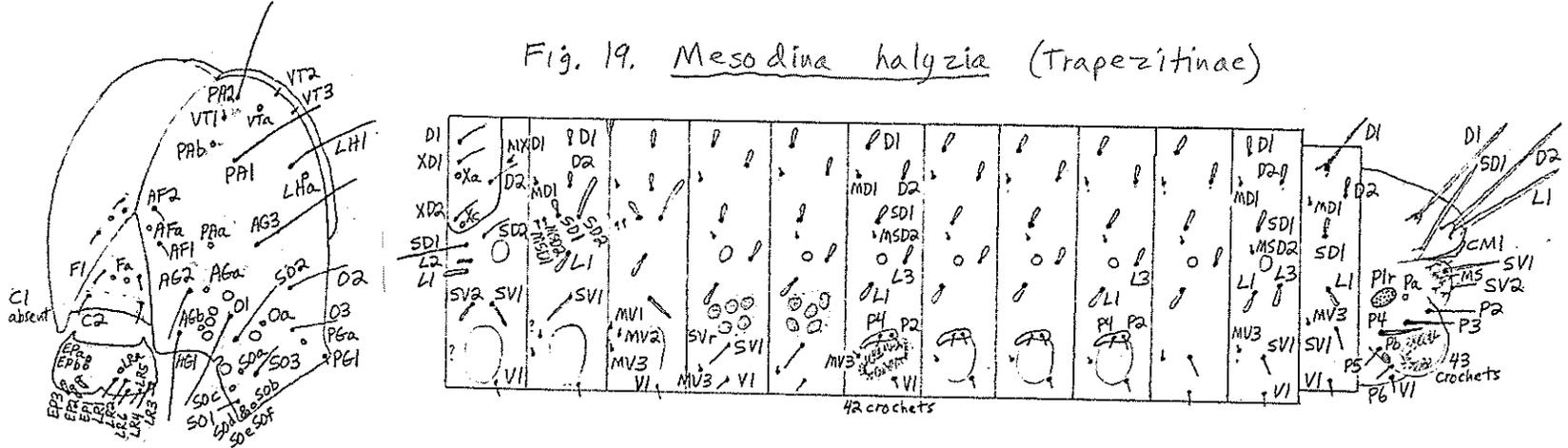






Fig. 24. *Aegiale hesperiaris* (Megathyminae), redrawn from Dampf (1923-1924)

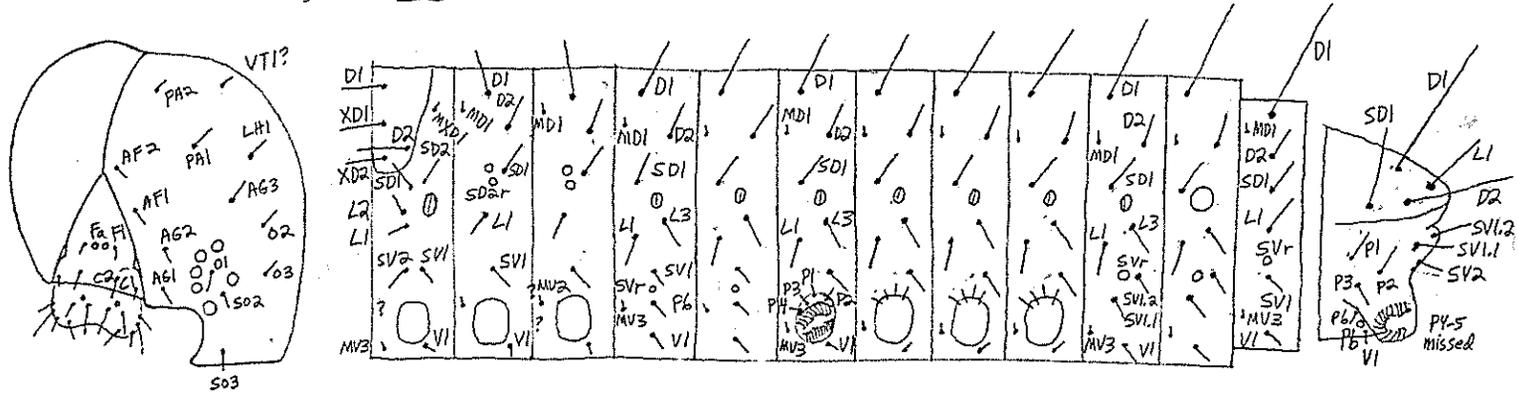


Fig. 25. *Baronia brevicornis* (Baroniinae), redrawn from Ruiz (1969)

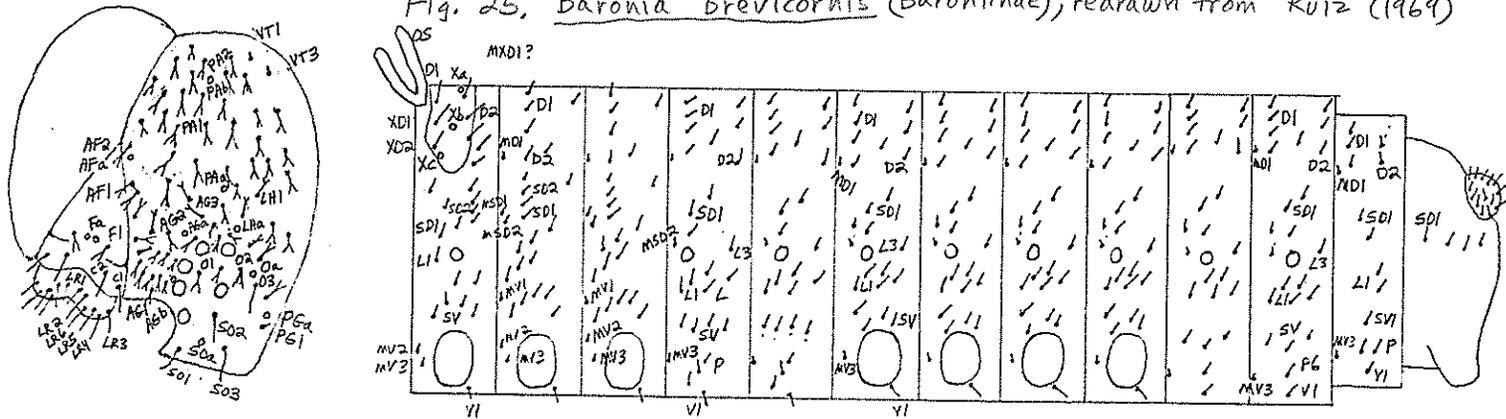


Fig. 26. *Parnassius phoebus* (Parnassiinae)

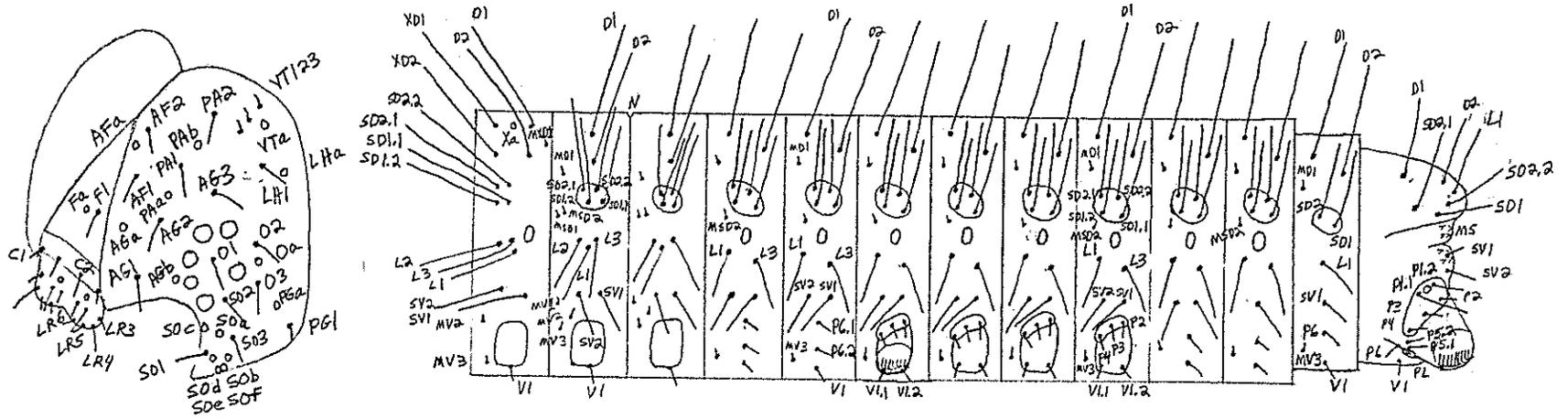


Fig. 27. *Battus philenor* (Papilioninae, Troidini)

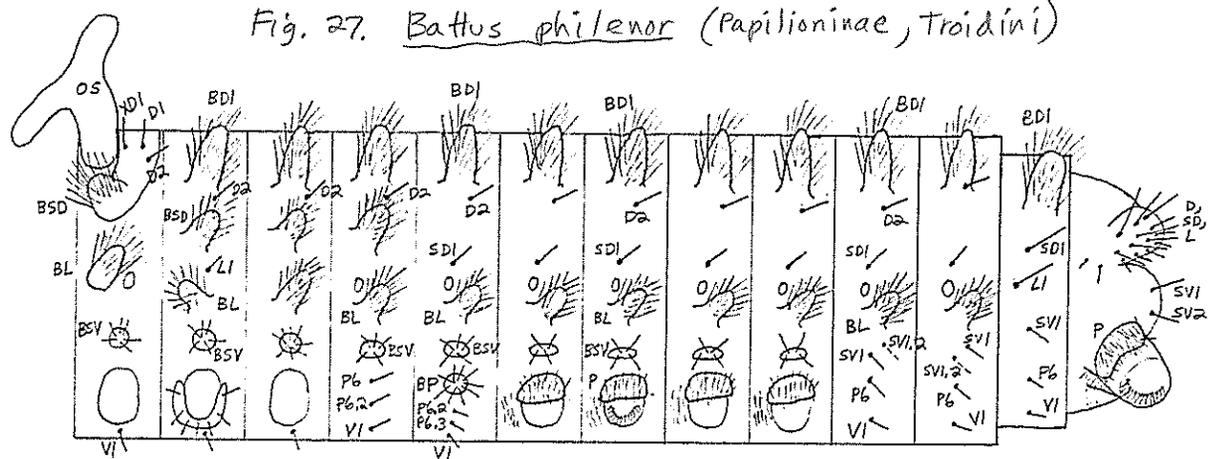
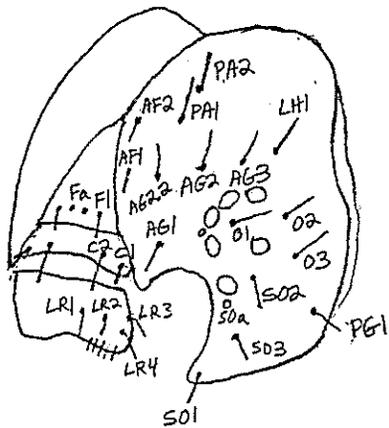




Fig. 30. Nathalis iole (Coliadinae)

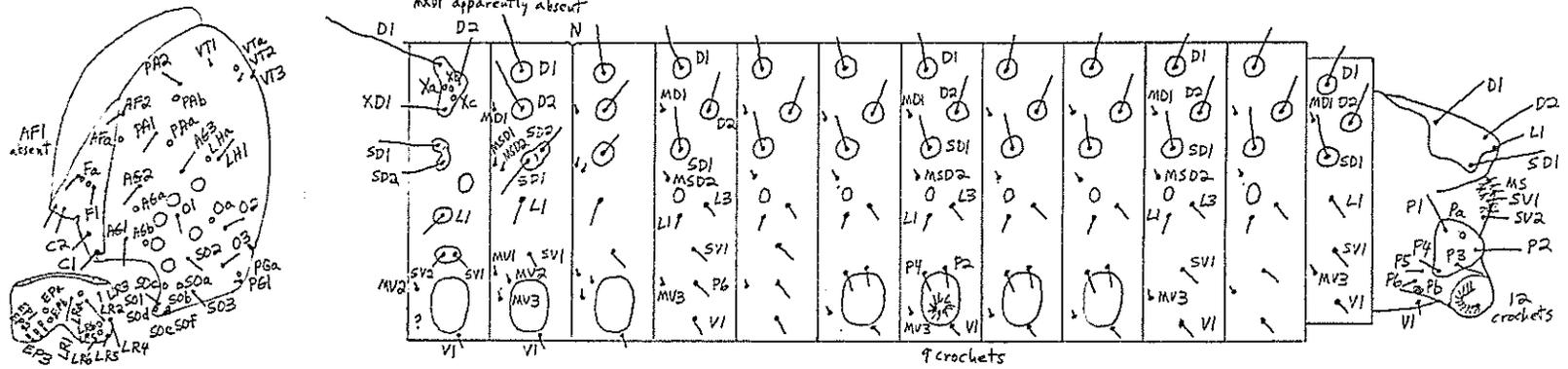


Fig. 31. Colias alexandra (Coliadinae)

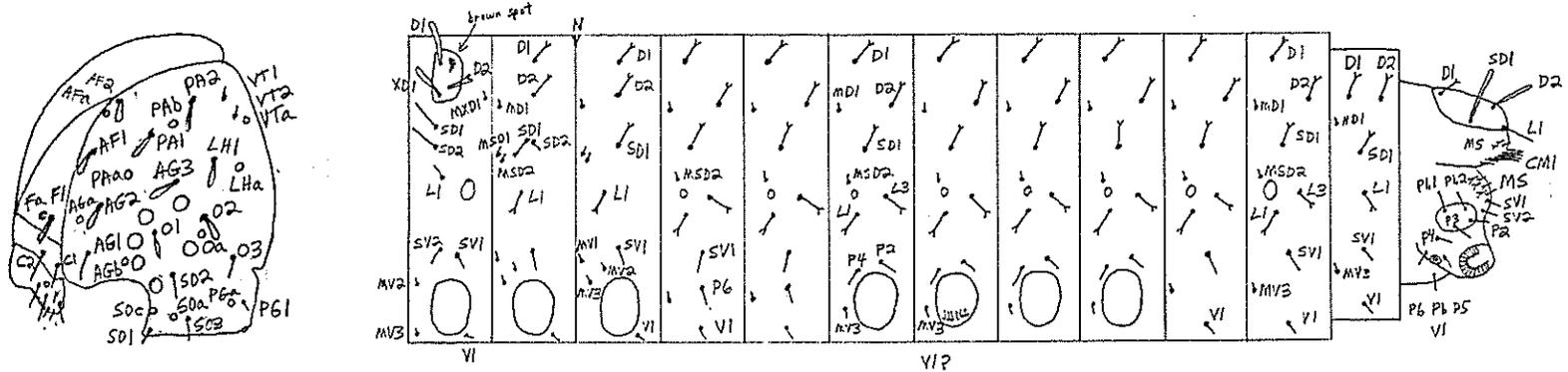




Fig. 34. Danaus plexippus (Danainae)

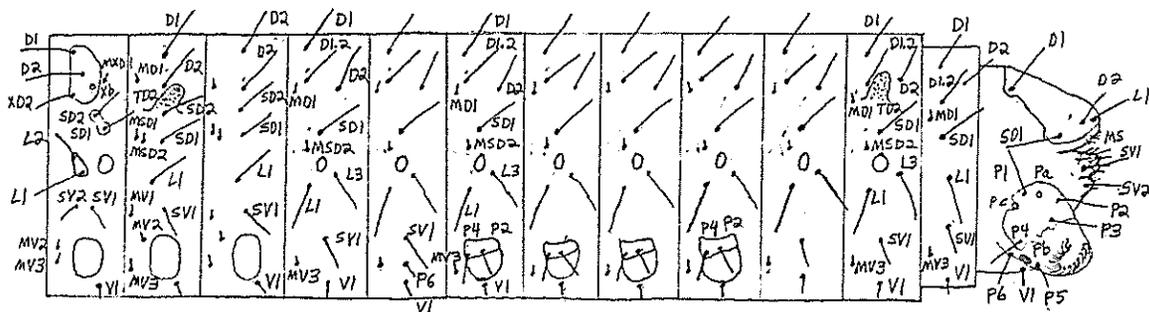
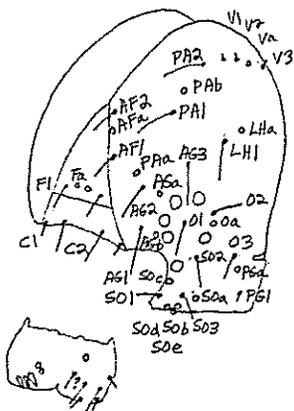


Fig. 35. Danaus gilippus (Danainae), redrawn from Kitching (1984)

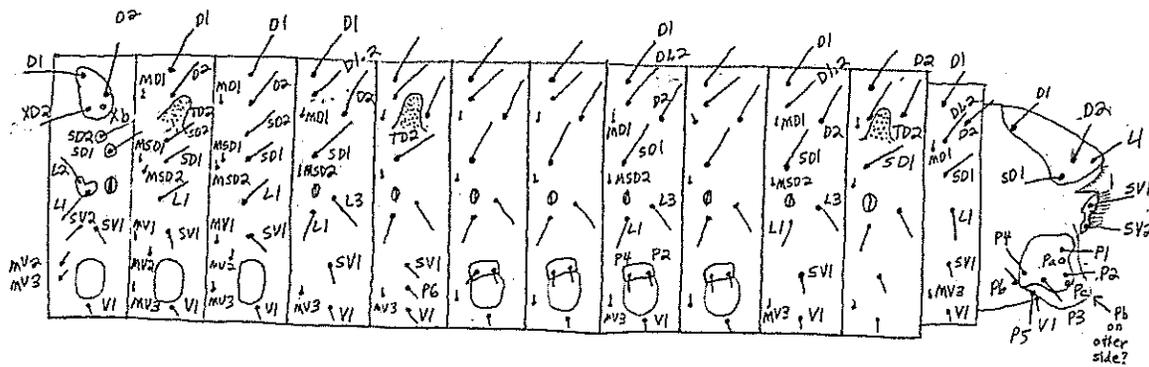
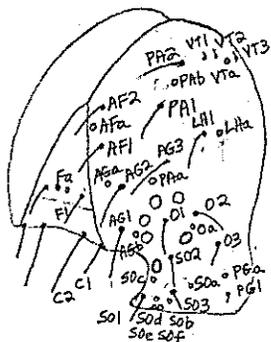


Fig. 36. *Mechanitis polymnia dorissides* (Danainae, "Ithomiinae")

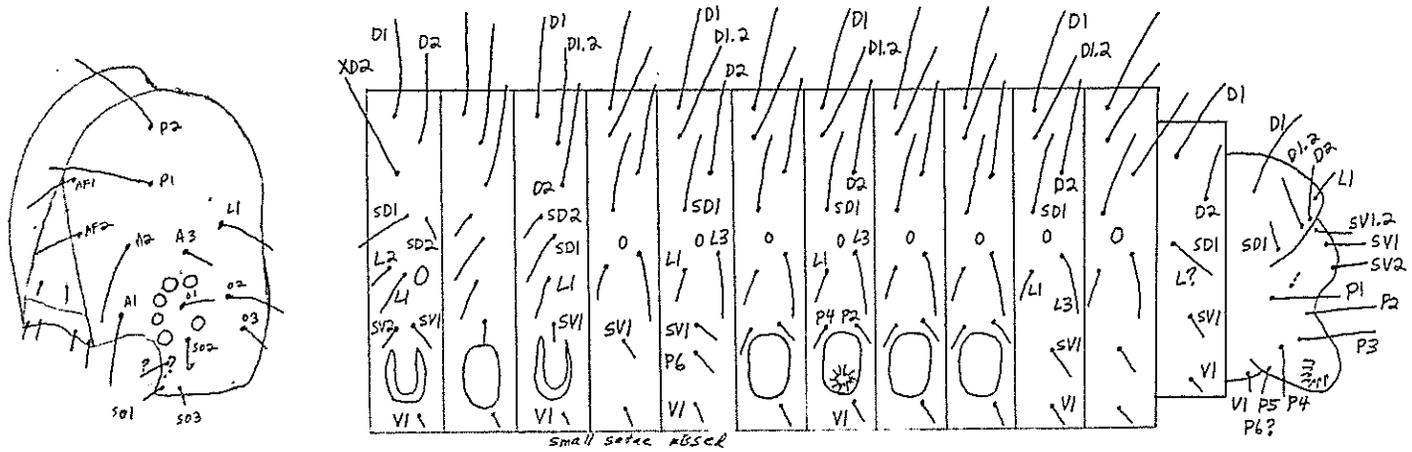


Fig. 37. *Cyllopsis pertepida dorothea* (Satyrinae)

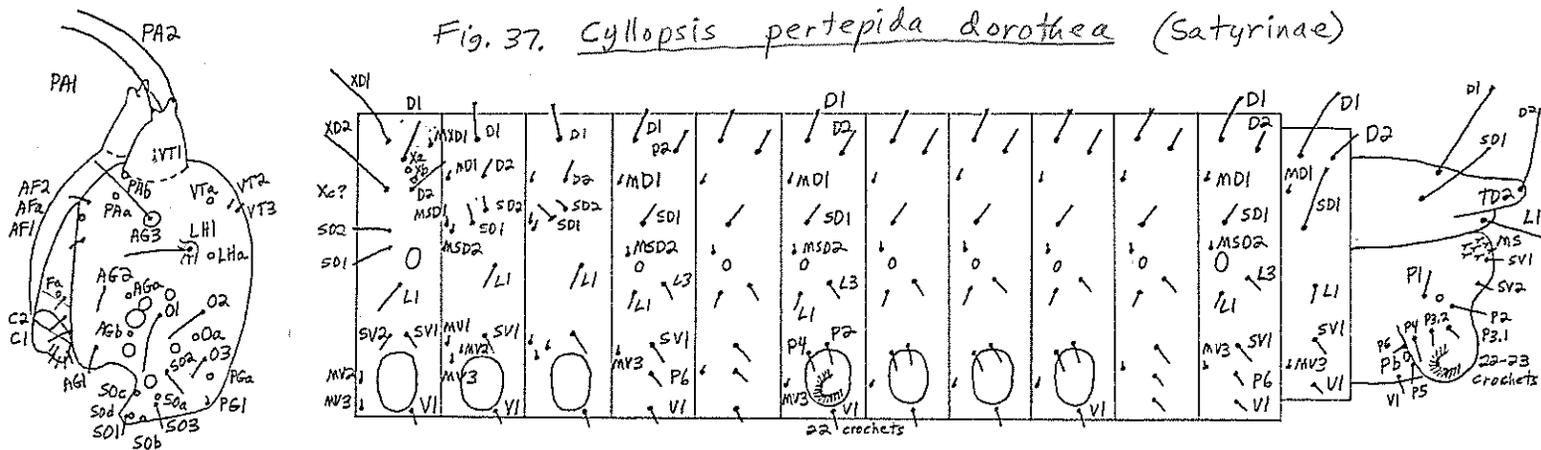






Fig. 42. *Asterocampa celtis* (Apaturinae)

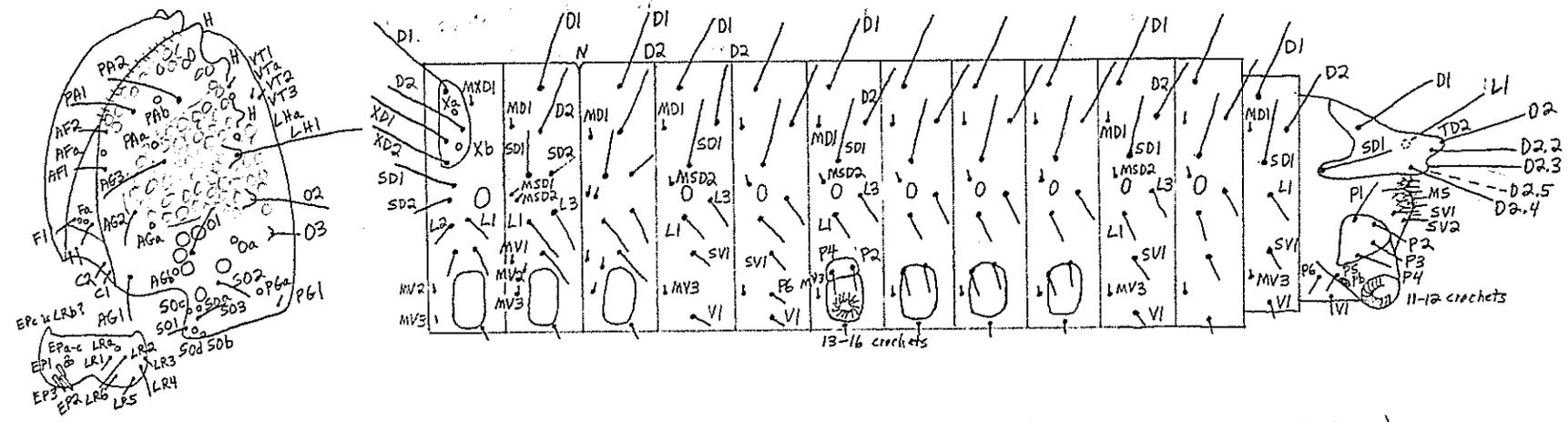


Fig. 43. *Limnitis weidemeyeri* (Nymphalinae, Limenitidini)

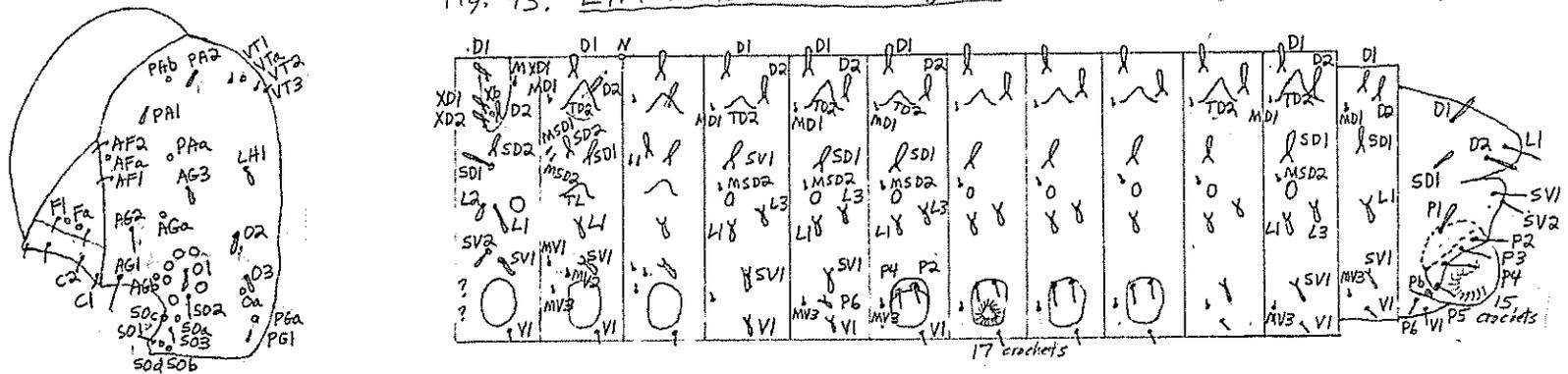




Fig. 46. Nymphalis milberti (Nymphalinae, Nymphalini)

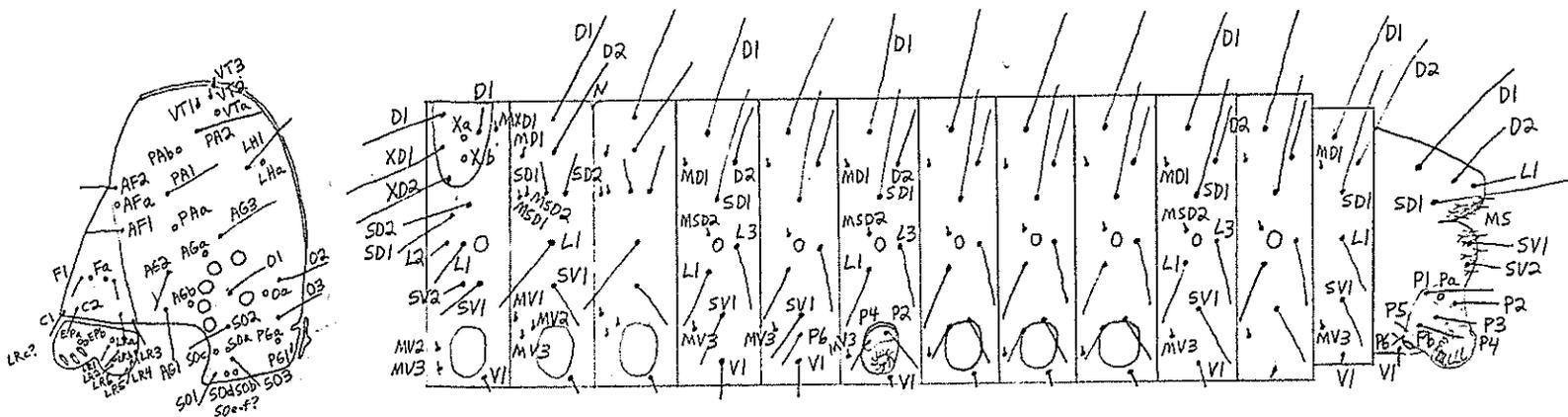


Fig. 47. Phyciodes orseis (Nymphalinae, Melitaeini)

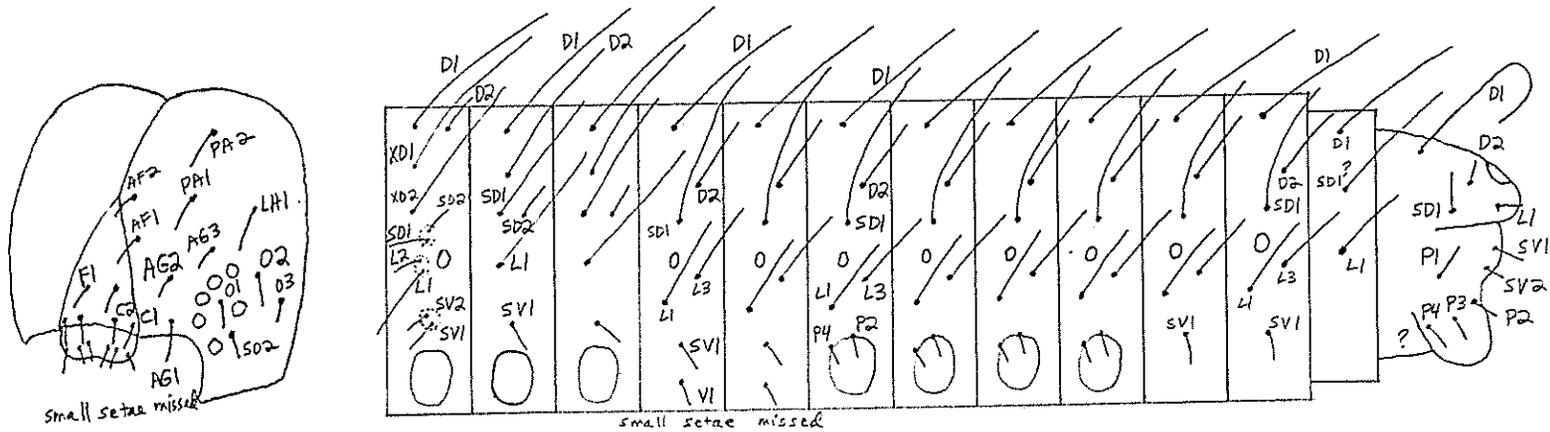




Fig. 50, *Boloria improba acrocnema* (Nymphalinae, Heliconiini, "Argynnini")

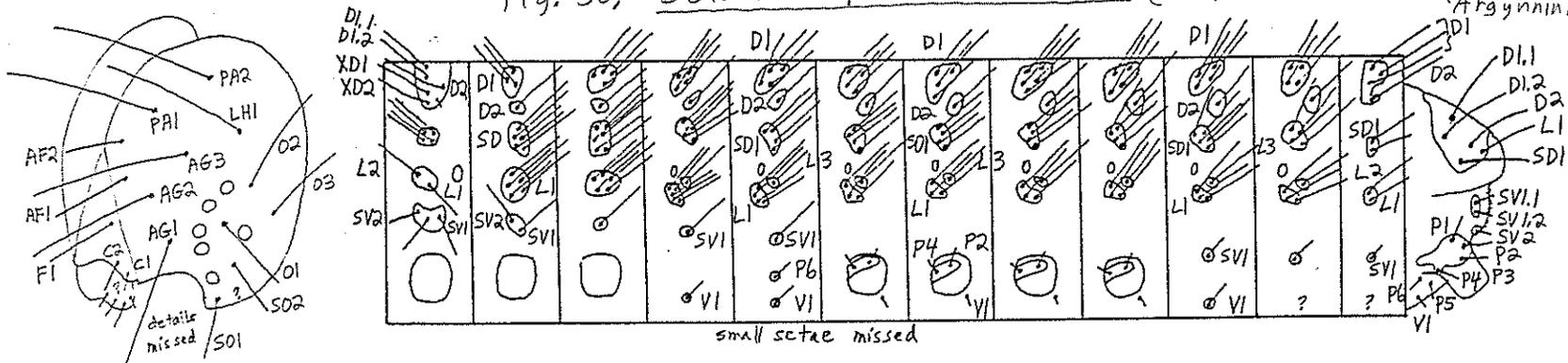


Fig. 51, *Speyeria nokomis nokomis* (Nymphalinae, Heliconiini, "Argynnini")

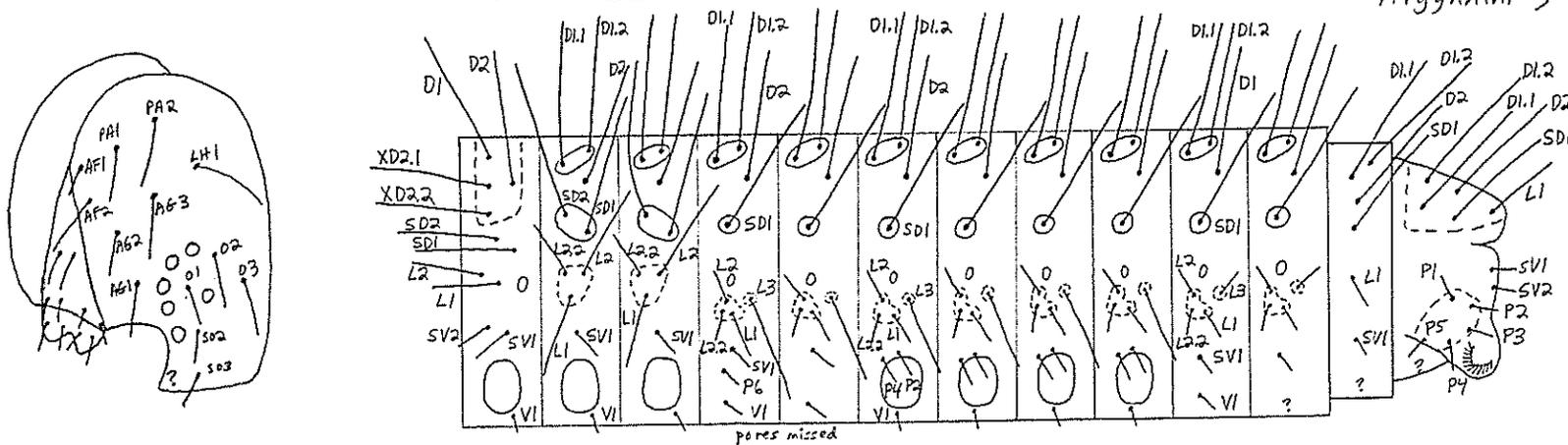




Fig. 54. Feniseca tarquinius (Lycaenidae, Miletinae), redrawn  
From David M. Wright  
(pers. comm.)

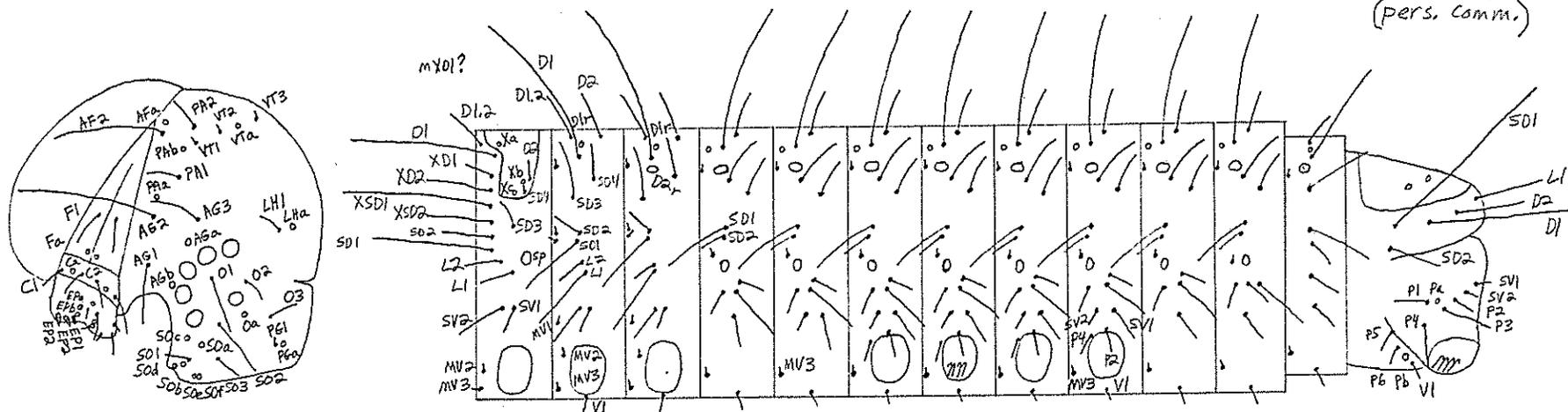


Fig. 55. Curetis acuta (Lycaenidae, Curetinae)

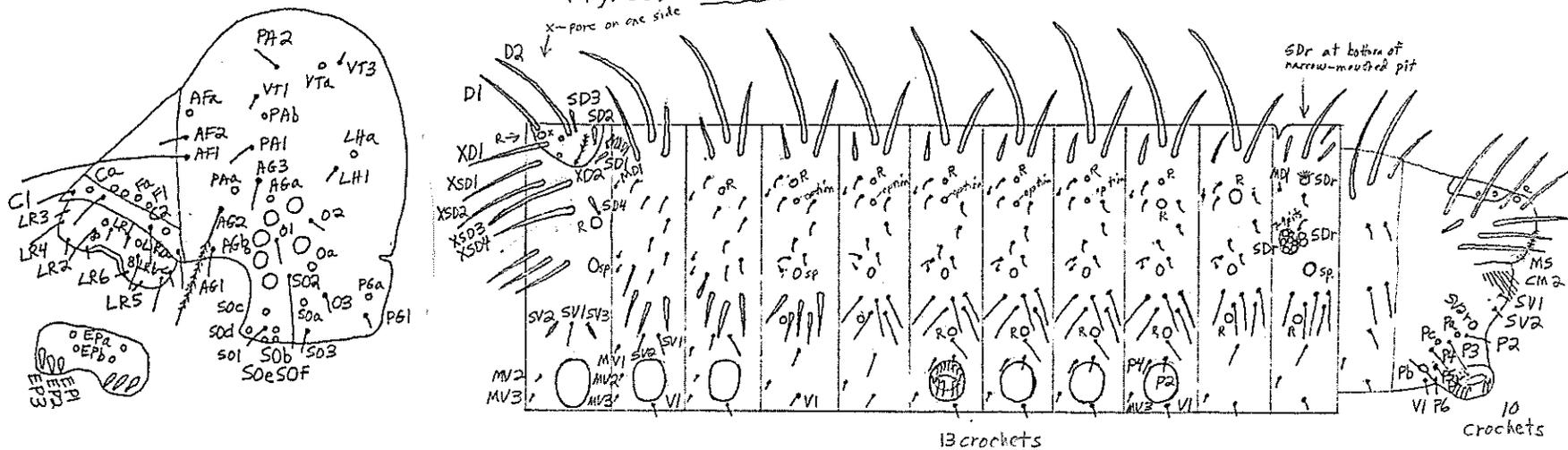




Fig. 58. Callophrys affinis homoperplexa (Lycaeninae, Eumaeini)

