

THE TAXONOMY AND BIOLOGY OF THE

BRITISH CHRYSOMELIDAE

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by

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# VOLUME 2



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## B. THE TAXONOMY OF CHRYSOMELID LARVAE

### A. Introduction.

Many workers have studied individual British species but there have been few comprehensive studies of the subfamilies. However, Oglobin and Medvedev (1971) compiled a subfamily key, generic and specific keys to many British species. They illustrated but did not describe a Lamprosoma species. Little has been done on the Donaciinae, Orsodacninae, Zeugophorinae, Criocerinae, Cryptocephalinae and Clytrinae whereas the Chrysomelinae, Galerucinae, Haliicinae and Cassidinae have been covered in more detail ( Appendix Table 3 ).

Few workers have attempted to homologise the setae on the head or the tubercles and setae on the body of Chrysomelid larvae, merely giving them their own nomenclature. The first worker to produce a generally applicable notation for the tubercles of the Chrysomelid larvae was Sanderson (1901). Paterson (1931) stated that in the primitive condition every segment of the body bears two rows of setae, each seta on a small round tubercle. There were six groups of tubercles : Dorsals, dorso-laterals, subspiraculars, pleurals, ventro-laterals and ventrals. The dorsals bear four setae, the dorsolaterals four, subspiraculars two, pleurals two, ventrolaterals two and ventrals two. All the setal forms in the British Chrysomelidae were described using this nomenclature. This nomenclature was criticised by Hennig (1938) who worked on German Chrysomelinae and divided them into two groups. The Oligochaeten Larvengruppe contains the genera Plagiodera, Chrysomela, Phyllodecta, Hydrothassa, Prasocuris, Phaedon and Gastroidea which generally have fewer setae and glanduliferous tubercles on the meso and metathorax and the first seven abdominal segments. The Polychaeten Larvengruppe contains the genera Chrysolina, Phytodecta and Leptinotarsa in which there are many setae and the glanduliferous tubercles are absent.

In a later nomenclature one tubercle was homologised to another irrespective of the number of setae on them. The tubercle arrangement rather than setal arrangement was used in the taxonomy of the Chrysomelinae larvae (Kimoto, 1962).

## B. Materials and Methods.

### i. Culturing.

Larvae used in this study were obtained from several sources. The most suitable method was to collect wild adults, identify them and culture the eggs, larvae and pupae from them in the laboratory. Success was usually achieved by placing several adults in airtight plastic containers with the fresh foodplant which was replaced every 2 or 3 days. The humidity was maintained by placing moist filter paper at the base of each container. Any eggs laid were removed immediately and placed on filter paper or cotton gauze over moistened vermiculite in an airtight plastic container. Adults, eggs and larvae were kept in an incubator at a constant temperature of 19°C. The eggs were inspected daily and any hatched larvae were cultured as the adults.

### ii. Fixation and Preservation.

All larval instars and pupae were fixed in Petersons KAAD which consists of 1 part kerosene, 1 part glacial acetic acid, 1 part Dioxan and 8 parts 95% ethyl alcohol. KAAD was found to be an excellent fixative both of external features (setae, coloration) and also internal structures. After 2-3 hours the larvae and pupae were transferred to 70% alcohol for preservation. Fixation and preservation in alcohol only, resulted in discoloration, shrivelling up and hardening of the specimens.

### iii. Slide preparation for chaetotaxy.

The preserved larva was held with fine forceps and the head carefully removed using a sharp scalpel. The larva was held on its back so that its dorsal surface was adjacent to a piece of soft plastic on the microscope stage. The tip of the scalpel blade was inserted into the prothorax via the aperture left by the removal of the head.

A downward cut was then carefully made along the mid-dorsal line of the thorax. The scalpel blade was then further inserted into the abdomen and more cuts made along the mid dorsal line until eventually the 10th abdominal segment was reached. Thus even in the convex Chrysolina sp. this process ensured that the larval skins could be opened out and mounted flat. The body and severed head were then placed in 10% KOH and heated at 60-80°C on a hot plate for 30-60 minutes until muscles etc were removed. For later instars or larger species 60 minutes was usually necessary. The skin and the head were then washed in distilled water and each mounted separately in Berlese's Mountant on a microscope slide. Chaetotaxy drawings were made using a Wilde binocular microscope with drawing tube attachment.

C. Typical Chrysomelid larval structure.

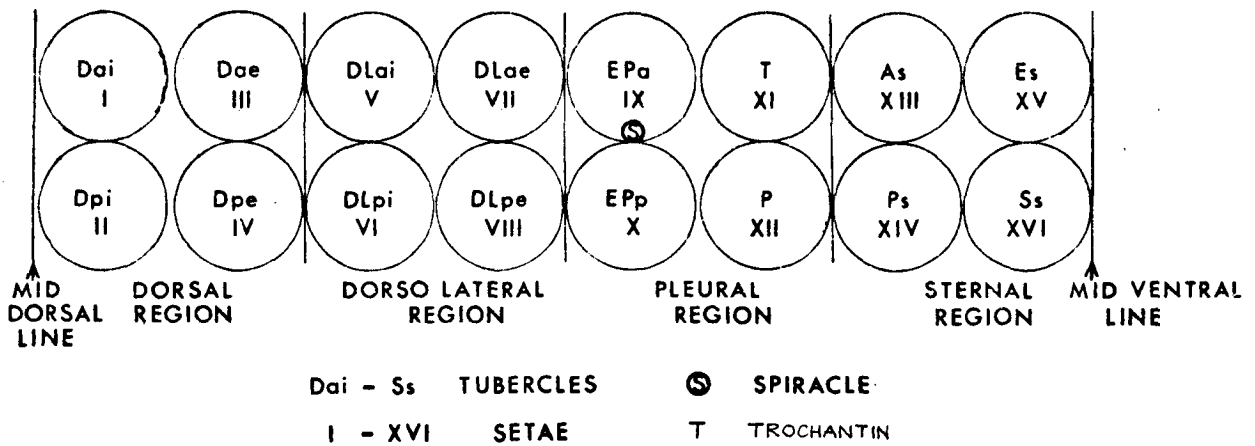
I. Head. Plate L1. Fig. 2a,b,c.

The head is bilaterally symmetrical, orthognathous with a well developed epicranial suture separating the vertex and frons. The distal limit of the frons is located where the branches of the epicranial suture end. The frons is bisected by a clearly defined mid-dorsal longitudinal invagination. A transverse clypeal suture separates the post and ante-clypeus. The gena is usually demarcated anteriorly into a small triangular hypostomal area, at the anterior extremity of which the socket for the ventral mandibular articulation is located. On each side of the head capsule six ocelli are arranged into two groups, four on the vertex, postero-dorsal to the antennae, and a ventral group of two, located anteriorly on the gena. 2-5 primary setae are present on each side of the frons whereas the number on the vertex varies from 3-7. The number of setae associated with the ocelli varies from 2-4 and on the gena 2-5. The post clypeus usually bears 3 pairs of short setae and the labrum two pairs of relatively long dorsal setae. The antennae are typically 3-segmented. The first 2 segments are rather short whilst the third is elongate and bears 6 tactile processes at the apex. An accessory conical process sometimes longer than the third segment is located antero-ventrally on the second segment. The broad 5-toothed mandible articulates with the hypostome by a prominent rounded condyle. The inner and outer teeth are usually smaller than the three middle teeth. The mandible bears two long primary setae on its dorsal surface and there may be a tuft of setae (the penicillus) arranged along its inner margin. The maxilla is highly variable. The cardo is a small triangular sclerite which articulates ventrally with the head near the hypostome. The variably chitinised stipes is typically elongate and rectangular with a pair of long primary ventral setae and often with a pair of minute distal setae. Distally on the stipes a shoulder like palpifer is usually demarcated

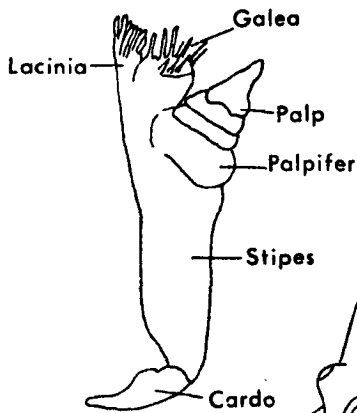
# PLATE L1

## FIG. 1 ARRANGEMENT OF TUBERCLES AND SETAE FOR

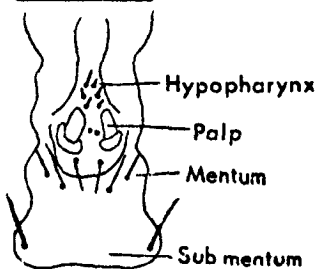
THE MOST GENERALISED CHRYSOMELID LARVA (After Kimoto 1962)



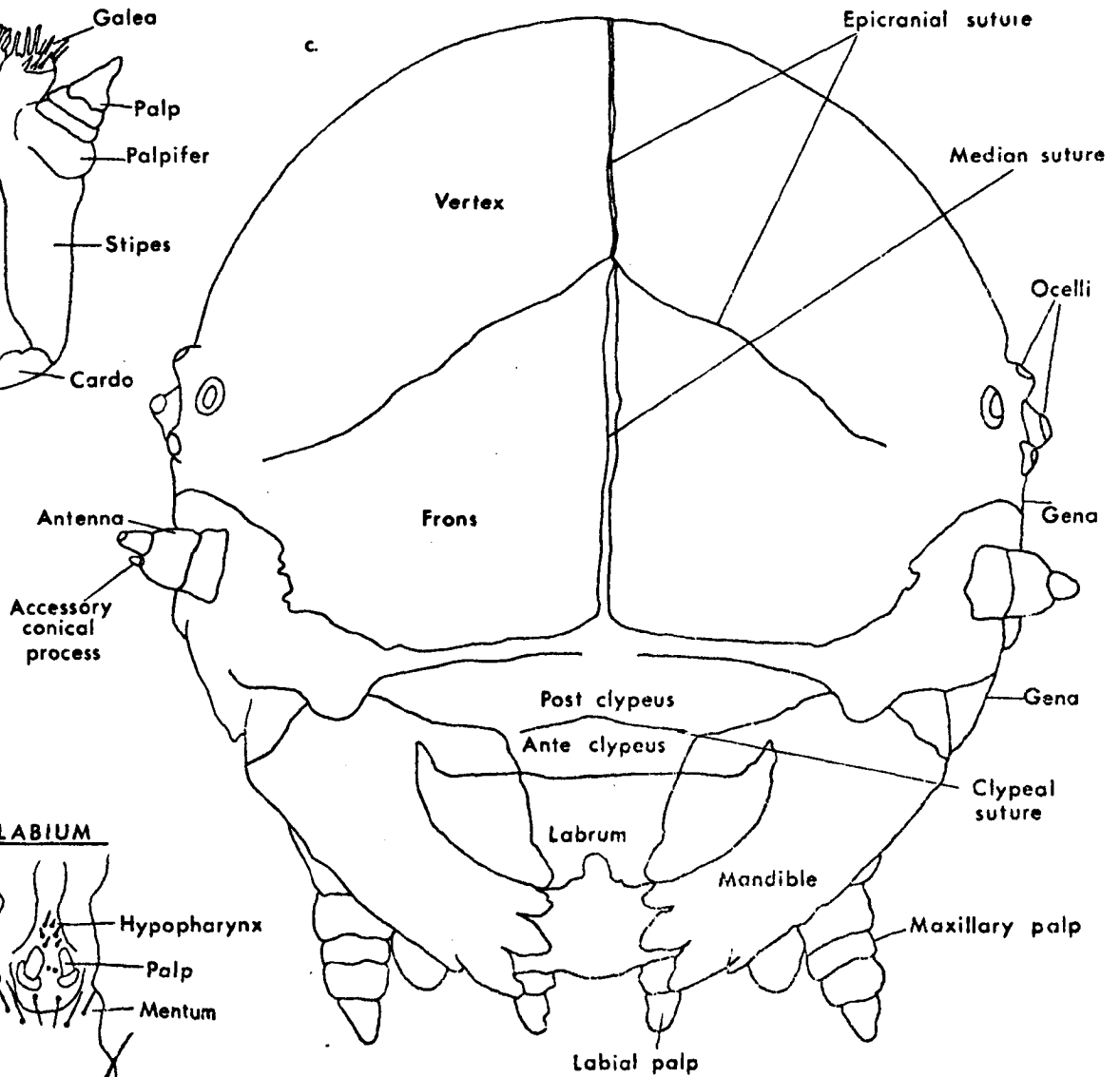
### a. MAXILLA



### b. LABIUM



### FIG. 2 GENERAL MORPHOLOGY OF CHRYSOMELID LARVAL HEAD



### c. HEAD ANTERIOR VIEW

FIG. 3   DONACIINAE

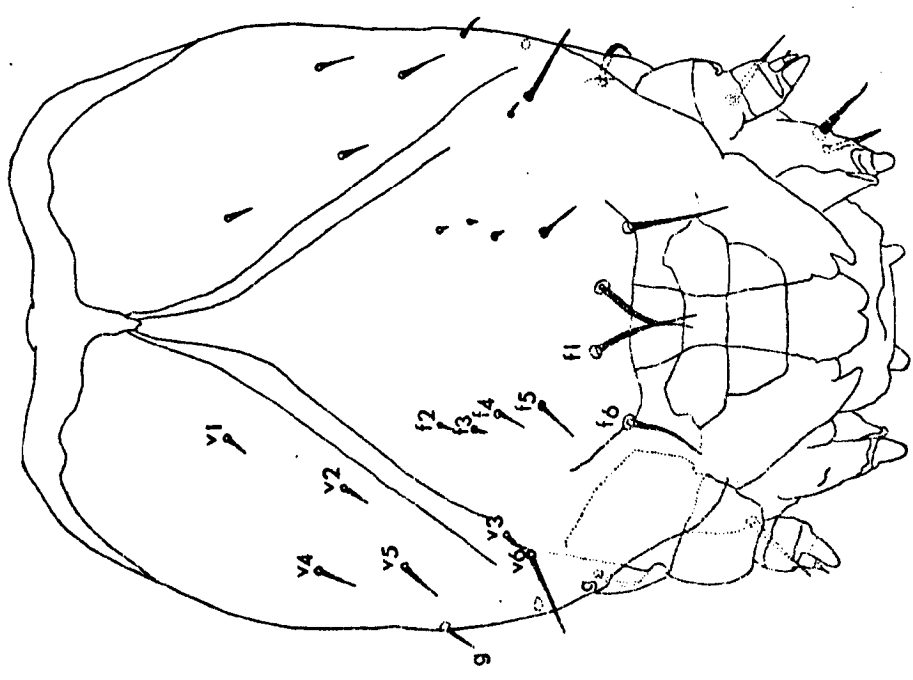


FIG. 4   CRIOCERINAE

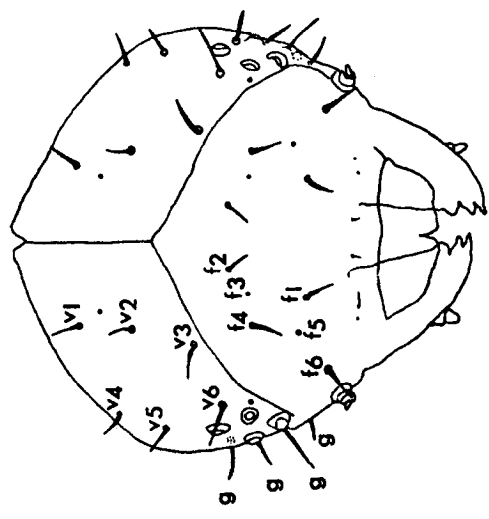
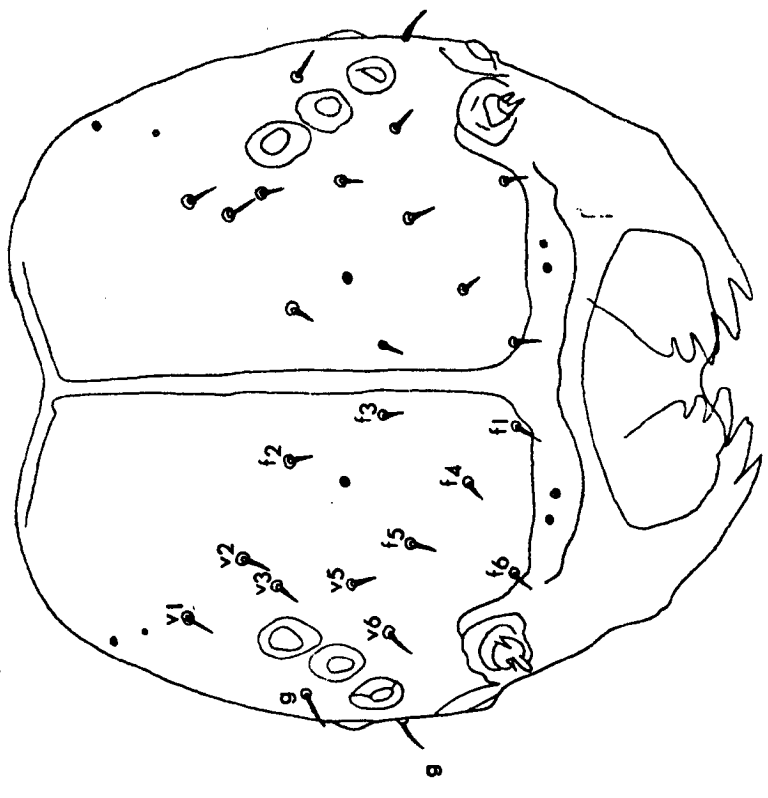
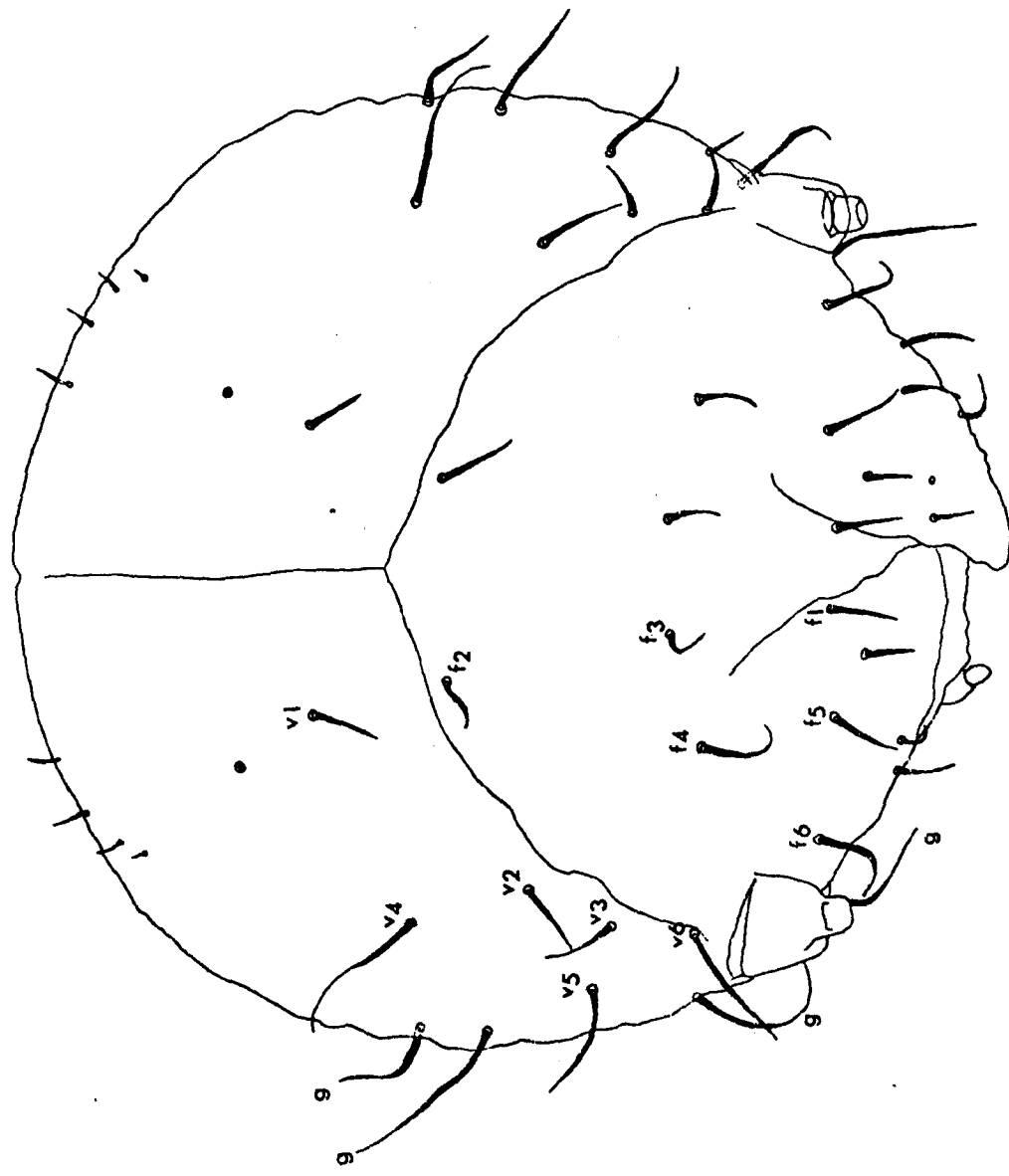


FIG. 5   CASSIDINAE

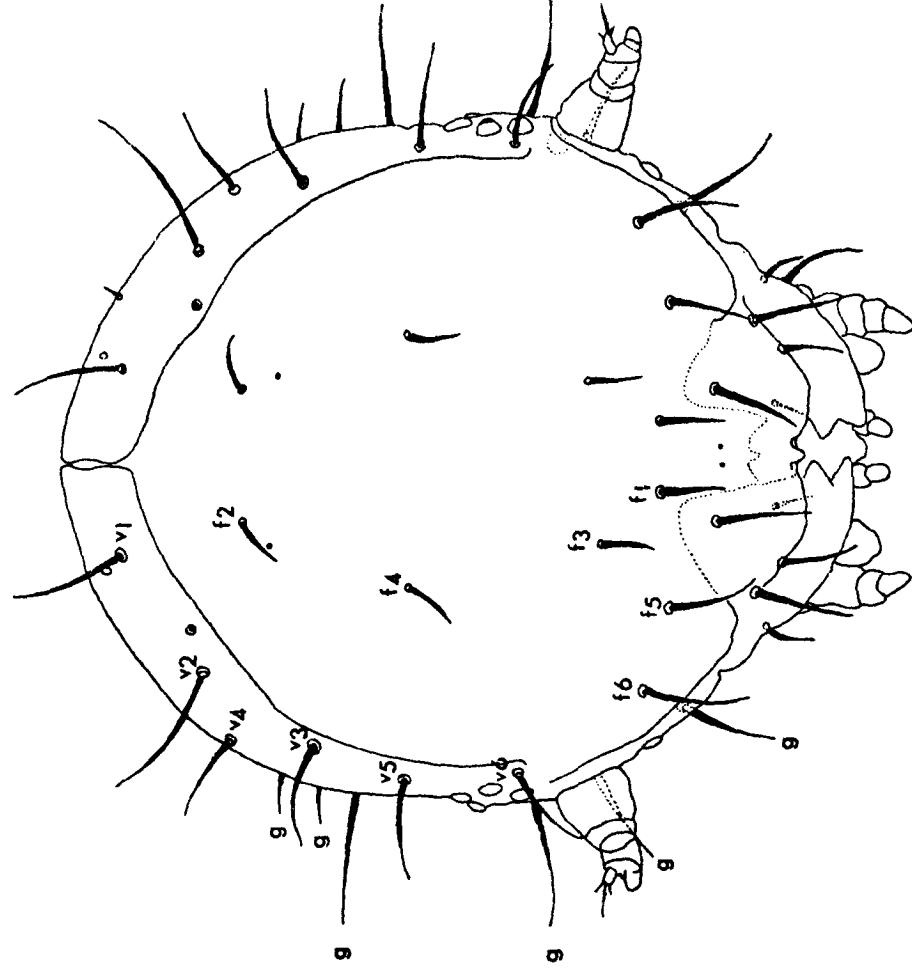




**FIG. 6** CLYTRINAE & LAMPROSOMATINAE



**FIG. 7 CRYPTOCEPHALINAE**



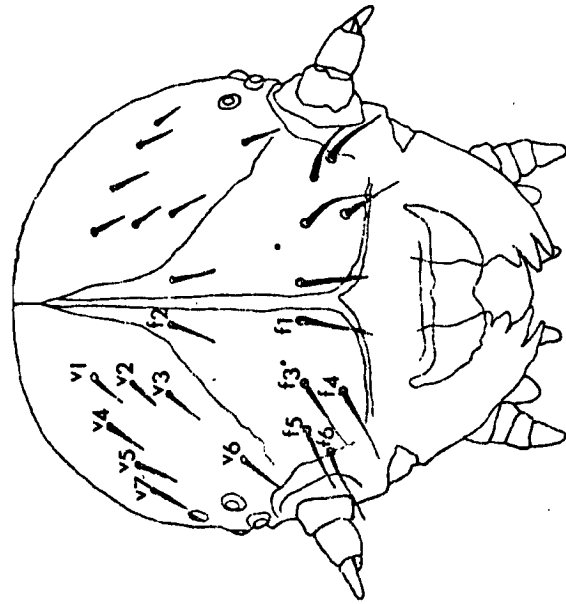


FIG. 8   CHRYSOMELINAE

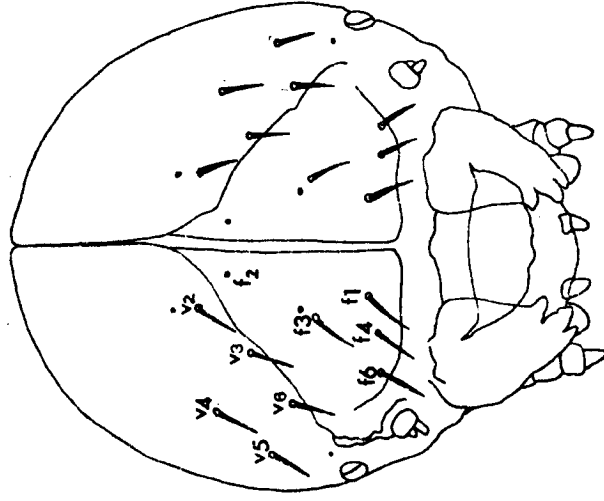


FIG. 9   GALERUCINAE

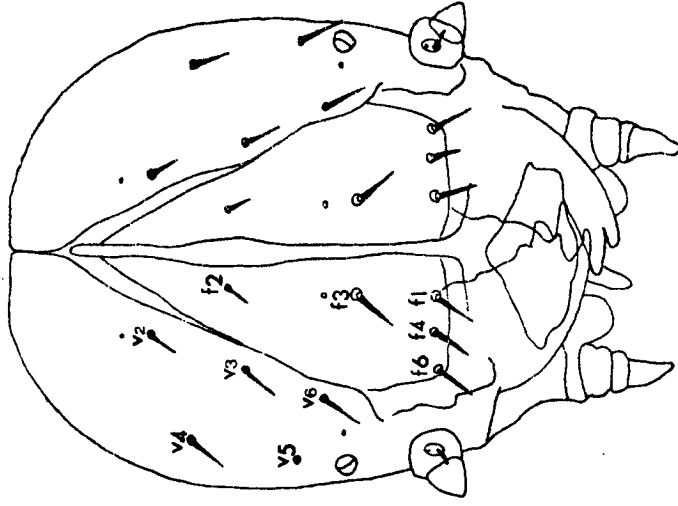


FIG. 10   HALTICINAE

bearing a pair of long ventro-lateral setae. The typically 3-segmented maxillary palpus is situated at the distal extremity of the palpifer. The second palpal segment usually bears 3 short setae while a minute seta is always located on the inner lateral margin of the third segment. A lacinia is sometimes demarcated at the distal extremity of the stipes. It is pouch-like with a distal fringe of broad blade-like setae. The galea, a well defined triangular arm possessing several conspicuous setae is located distally on the palpifer at the inner base of the maxillary palp. Many of the parts of the labium are fused in Chrysomelid larvae. The structure and chaetotaxy of the labium is constant. The gula is a short membranous region between the base of the labium and the prosternum. The submentum and mentum are not clearly demarcated. The mentum is usually more membranous and situated distally, anterior to a strongly chitinised transverse semi-circular sclerite, the post-labial chitinisation. As this latter sclerite is close to the bases of the 2-jointed labial palpi it probably originates by the fusion and reinforcement of the bases of the palpifers. The hypopharynx is a convex membranous region, distal to the labial palpi, and is directly continuous with the labium. It is supported by a pair of lateral chitinisations which are sometimes closely associated anteriorly with the lateral extremities of the semi-circular labial sclerite. The hypopharynx bears 3 pairs of minute setae mid-dorsally. The superlinguae are a pair of dilated lobular structures situated postero-laterally on the hypopharynx. Dorsally they bear minute setae which may occasionally be lightly pigmented. The epipharynx is attached anteriorly to the margin of the labrum and posteriorly a transparent membrane connects it with the hypopharynx. Its ventral wall bears a number of sensory areas and olfactory pores while its anterior margin has several strong setae which usually project beneath the labrum.

## ii. Thorax and Abdomen.

The body is typically eruciform and elongate with the dorsal surface of the abdomen only slightly convex. The prothorax is rarely broader nor very much longer than the metathorax and the body narrows gradually. There are three thoracic and ten abdominal segments with the tenth segment very reduced. The three pairs of thoracic legs are usually short and stout and each consists of five segments ending in a single tarsal claw. Spiracles are always present on the mesothorax and usually on the first eight abdominal segments. Tubercles bearing setae are arranged on the segments. Setae are structures developed as extensions of the exocuticle and each is produced by a single, usually enlarged epidermal cell or trichogen. The tubercles are chitinated or pigmented plates which probably originated by the chitination of the integument at the base of a single setae. Occasionally however, small tubercles lacking setae may occur in first instar larvae. These tubercles may not have arisen by the chitination of the base of a setae or setae may have been lost. In all Chrysomelid larvae, the dorsal tubercles of the prothorax, and usually those of the 8th and 9th abdominal segments have fused to form entire tergal plates, around the margins of which the dorsal setae are arranged.

The body wall may be divided into five parts. These are the dorsal part, dorso-lateral part, epipleural part, pleural part and the sternal part. The tubercles situated in each of these parts are the dorsal tubercle (D), dorso-lateral tubercle (DL), epipleural tubercle (EP), pleural tubercle (P) and sternal tubercle (S). Changes in tubercular arrangement through the different instars occur in only a very few genera. Primary tubercles exist from the first instar whereas secondary tubercles appear at later instars.. However, the majority of the tubercles appear in the same position in all instars of a species and these can be given names based on homology. The tubercular nomenclature (Plate L1, Fig.1) is that of Kimoto (1962). The dorso-anterior tubercle (Da) and the dorso-posterior tubercle (Dp) occur in the dorsal region. These may be

further divided into a dorso-interior tubercle (Di) and dorso-exterior tubercle (De). In the dorso-lateral region, anterior and posterior tubercles (DLa and DLp) are present but these may be divided into interior and exterior tubercles ( DLi and DLe ). On the meso and metathorax only one tubercle (DL) may be present. In the epipleural region of the abdominal segments one tubercle, the epipleural tubercle (Ep) is present. In the same region on the meso and metathorax the two tubercles EPa and EPp are present. In the pleural region of the abdomen there is always a single pleural tubercle (P), whereas on the thoracic segments there appear to be two tubercles (T) and (P). However, (T), the anterior of the two tubercles was considered by Kimoto (1962) as trochantin, a basal chitinised plate to which the coxa attaches. In the sternal region there are typically 3 tubercles, the eusternal tubercle (Es), sternellar tubercle (Ss) and parasternal tubercle (Ps). A tubercle (As) is rarely present anterior to (Ps) in the abdominal segments and is assumed to be fused with this latter tubercle. On the abdominal segments, Ps is sometimes divided into two tubercles Psi and Pse.

D. Subfamily, Generic and Specific larval descriptions.

I. SUBFAMILY CASSIDINAE

a. GENUS Cassida

First and Final instar larvae. Plate LP13, Figs. 42-45, PLB 27 Figs. 63-67.

Body pale green, pale yellow or yellow brown. Body dorso-ventrally flattened and broadened. Each segment with large peripheral spines each with numerous side branches (setiferous scoli). (Plate LB 27, Figs. 64-67). Each side of body carries 16 spines, 4 on the prothorax, 2 on the meso and metathorax and 1 on each of the first 8 abdominal segments. 8th abdominal segment poorly developed. Scoli on 9th abdominal segment (the terminal fork) anteriorly directed and thus dorsal in position. Terminal fork in the majority of species carries the cast exuviae and the excrement. The scoli and terminal fork are sometimes grey brown and are darker than the rest of the integument. The mesothoracic spiracle is located on the dorsal surface of the 4th scoli, whereas the abdominal spiracles are situated dorsally at the bases of the lateral scoli in the first 8 segments. The spiracular peritremes are concolorous with the integument, pale to dark brown.

HEAD: PLB: 27 Fig. 63 Oval in anterior view, usually mottled with very pale grey brown or pale brown patches, paler near the ocelli, epicranial suture absent, but head paler in this region, median suture distinct, dark brown in first instar, paler in later instars, vertex bearing 5 large ( $v_1 - v_6$ ) and several smaller setae, gena bearing 4 setae, frons usually paler than rest of head, bearing 6 large setae ( $f_1 - f_6$ ).

Ocelli, 5, dark brown, 4 arranged in a semicircle posterior to antennae, 1 laterally on the gena; Antennae, 2 segmented, short, 3rd segment inconspicuous, accessory conical process well developed, as long as the 2nd segment, Clypeus, post clypeus bearing 1 or 2 pairs of setae, Labrum, bearing 2 pairs of setae posteriorly, anterior edge bearing 5 pairs setae; Maxillae, (Fig. 63b) cardo frequently indistinctly demarcated from stipes, stipes broad bearing a pair of long lateral

setae, palpifer long and broad, maxillary palps short, 2 segmented, segments equal in length, galea well developed bearing 7 setae, an indistinct setiferous membranous structure probably the lacinia lies dorsal to the galea; Labium, labial palps a single cylindrical segment bearing at the apex 10 sensillae; Mandibles, (Fig. 63b) darker brown than rest of head, broad, 5 dentate, inner 2 teeth the largest, short ventral ridge present.

THORAX AND ABDOMEN: As the integument does not exhibit a definite arrangement of segmental tubercles and setae it is impossible to homologise the situation in Cassida larvae with the generalised type. Sometimes there are indications of pale grey brown dorsal setiferous areas. Dorsally and ventrally, bearing spinules, variable in colour, size and position. Setae situated at extremities of short papilla-like protuberances, and are somewhat irregularly arranged. Pronotum is broad and conceals the head. Pronotum is usually indistinct, and mottled with brown patches. Hatching spines absent in first instar larvae. Legs, (Fig. 63c) well developed, coxa, femur, tibia, tarsungulus present, concolorous with integument or scoli, claws usually golden brown to dark brown.

## ii. SUBFAMILY DONACIINAE

### a. GENUS Donacia D. cinerea Hbst.

#### Final instar larvae. (PLH.29 Figs.71,72, PLB.26, Fig.62)

Body white or cream. Tubercles not chitinised, indistinct, demarcated by folds in the integument and the presence of small setae. Setae, short, numerous and very pale yellow brown. Body curved, usually tapering anteriorly and posteriorly from the middle of the body, sometimes not tapering posteriorly. Dorsum of 7th segment rounded transversely and is in a dorsal or posterior position. 8th abdominal segment with a pair of caudal spines.

HEAD: small, oval, directed forward, partly or completely retracted into the prothorax, very pale yellow brown, epicranial stem very short, epicranial suture distinct, moderately long, median suture indistinct, vertex bearing 3-6 small setae, ( $v_1 - v_6$ ), gena 4 setae, frons pentagonal, antero-lateral border heavily chitinised, bearing 6 setae ( $f_1 - f_6$ ) on each side of the head; Ocelli, 5 in 2 rows, postero-ventral to the antennae, first row nearest the antennae with 3 ocelli, next with 2 ocelli, each ocellus composed of about 5 brown or black spots; Antennae, well-developed, 3 segmented, interior edge of basal segment darker brown than rest of head, 1st segment,  $1\frac{1}{2}$  times longer than the 2nd, 2nd segment bearing a large accessory conical process and the 3rd segment, conical process longer than the 3rd segment, apex of 3rd segment bearing a short and a long seta; Clypeus, post-clypeus, darker brown bearing 3 pairs of large setae; Labrum, mid-region with heavily chitinised band, bearing on ventral surface an anteriorly curved process or hook, labrum bearing 16 setae, dorsal face with 4 pit-like structures or sensory spots, one seta (the angular seta) at latero-anterior angle, 6 discal setae projecting from dorsal face, 2 proximal setae close to caudal margin, 2 distal setae just caudal to mid-anterior edge, 2 median setae, each lateral to the distal setae and median to the lateral seta, 2 lateral setae near the lateral labral edges; Maxillae, maxillary palps



apparently 2 segmented, 2nd segment half the length of the 1st, lacinia, ear-shaped projection from anterior part of the heavily chitinised band of the stipes and is dorso-medial to the palpus, dorsal side in form of a niche opening toward the mouth, on medial side of niche is a heavily chitinised bow-shaped band bearing 2 keel-shaped chitinous folds on its niche side and continues laterad as a thin chitinised basin, caudal part of bow-shaped portion connects with the distal medial chitinised band of the stipes, on dorso-lateral side of niche is a strongly chitinised process, jagged at the posterior end, serving as a muscle attachment, on anterior edge of outer face of chitinous process are 2 rows of hair-like projections, extending over the niche and obliquely cephalad, at anterior end of bow-shaped band is a needle-like structure united to the band by a joint, ventral to needle-like structure is a soft scalpel-like blade which is possibly the galea, projecting into the niche and continuing along the side of the needle-shaped portion is a boat-shaped structure, bifurcate, forming 2 setae, stipes not attached to mentum as in other Chrysomelid larvae; Labium, mentum, unisetate, free laterally and fused posteriorly with the submentum bearing 5 setae on each side of the head, labial palps small, one-segmented, highly chitinised region or chitinised bow, semicircular or V-shaped, anterior to which is a pair of large setae; Mandibles, darker brown, flat, triangular, 2 dentate, cutting surface curved with definite concave region just proximad to inner tooth, this region serrate, denticulate, or smooth, round condyle on basal portion of ventral side of each mandible, 2 setae present, one on lateral surface, one on dorsal surface just distad to the neck of the condyle.

THORAX: Prothorax, Pronotum distinct, small, yellow, same colour as legs, bearing about 10 large and numerous smaller setae, EPa possibly fused with EPp forming a large tubercle bearing 10-11 large setae and numerous small setae, a small tubercle possibly EPa bearing small setae anterior to legs, a small tubercle P with 1 large and a few small setae dorsal to legs, T anterior to legs bearing a few large and numerous small setae, a large

transverse tubercle, possibly As, and Ss fused, bearing numerous small setae, fused across mid-ventral line, and antero-ventral to legs, a tubercle probably Ps and Es fused, bearing numerous small setae lies posterior to As-Ss and is fused across the mid-ventral line; Meso and Metathorax, Dai with 1 large and numerous small setae, Dpi with 1 large and numerous small setae, tending to fuse with Dpe, Dae with 1 large and numerous small setae, tending to fuse with DLai, Dpe and DLpi fused, with 2 large and numerous small setae, tending to fuse with Dpi and DLpe, DLpe distinct with one large and numerous small setae, DLai without large setae but bearing numerous small setae, DLai tending to fuse with Dae, DLae with one large and numerous small setae, EPa large, with 1 large plus numerous small setae and bearing a spiracle in the mesothorax, EPp smaller, tending towards fusion with EPa, bearing 2 large and numerous small setae, other tubercles as in prothorax; Legs, short, stout, 3 segmented, same colour as head capsule or pronotum, coxa short, broad, femur much smaller, tibia terminating in a minute claw-like tarsungulus, claw sickle-shaped, claw base with prominence on inside.

ABDOMEN: Abdominal segments 1-7, Dai large, with 1 large and numerous small setae, Dpi, DLpi, tending towards fusion, tubercle with 3 large and numerous small setae, Dae bearing 1 large and numerous small setae, DLai and DLae small, tending towards fusion, without large setae but with numerous small setae, DLpe tending towards fusion with DLai and DLae, with 1 large and numerous small setae, EPa very small, bearing spiracle but no setae, EPp absent, T and P fused into a large tubercle with 2 large and numerous small setae, Ss and Es possibly fused, but only 1 large and numerous small setae present, tubercle fused across mid-ventral line; 8th Abdominal segment, reduced, arrangement of setae different from those in previous segments, dorsum bearing a pair of dark caudal spines, each consisting of a base and a hook-shaped terminus, base encloses a soft-walled oval space containing the biforous spiracle, which is a slit elongated in an antero-posterior direction, the hook-shaped part

varies in length and curvature in the different species;

9th and 10th Abdominal segments, greatly reduced, indistinct.

b. GENUS Plateumaris

P. discolor (Pz.) (Plate LH 29, Fig. 69, Plate LB 25 Fig. 60 )

Final instar.

Chaetotaxy of head and body similar to D. cinerea. Body setae shorter and more numerous especially ventrally.

c. GENUS Macropilea

M. appendiculata (Pz.) ( Plate LH 29, Fig. 70; Plate LB 25, Fig. 61 )

Chaetotaxy of head and body similar to D. cinerea. However, body setae especially on abdominal segments 6 and 7 dorsal to spiracle are much larger than those in D. cinerea. The caudal spines are nearly two times longer in M. appendiculata than in D. cinerea.

Although the body chaetotaxy was not studied for several species within one genus, MacGillivray (1903), Boving (1910), Hoffmann (1940) and Oglobin and Medvedev (1971) used body chaetotaxy as a specific character within the Donaciinae. Other specific characters used by previous workers for the Donaciinae include mandible shape ( Hoffmann 1940, Oglobin and Medvedev 1971), frons shape (Boving 1910, Hoffmann 1940, Oglobin and Medvedev 1971), shape and chaetotaxy of the labrum (Boving 1910, Hoffmann 1940, Oglobin and Medvedev 1971 ), shape of the lacinia (Boving 1910, Hoffmann 1940 ), shape of the chitinous bow of the labium (Hoffmann 1940 ), shape of the caudal spines (Boving 1910, Hoffmann 1940) and claw shape ( Oglobin and Medvedev 1971 )

### III. SUBFAMILY ORSODACNINAE

#### a. GENUS Orsodacne Plate LH30 , Figs.73-76

Larval material was unavailable but the larva of an Orsodacne species has been described (Boving and Craighead, 1931)

#### Final instar larva.

The body is slightly curved and the head retracted into the prothorax (as in Donacia species). The setae are fewer but larger than in Donacia and tubercles are indistinct as in Donacia. However, abdominal segments 9 and 10 are distinct as in Zeugophora.

HEAD: Elongate, rectangular, prognathous, epicranial stem very long, epicranial suture short, indistinct, median suture absent, vertex without setae, frons without setae, gena bearing 5 setae; Ocelli : 5 on each side of the head in a line posterior to the antennae; Antenna : 3 segmented, well developed, directed anteriorly, segments 1 and 2 subequal in length, 2nd segment bearing at its apex a conical process and the 3rd segment, half the length of segments 1 or 2, conical process same length as 3rd segment; Clypeus, post clypeus without setae; Labrum, semicircular in outline, bearing 3 pairs of setae posteriorly and 5 pairs along the anterior margin; Maxillae, maxillary palps 3 segmented, 1st and 2nd segments subequal in length, 3rd segment slightly shorter, bearing 2 setae at its apex, galea bearing 7 stout spindle-shaped setae and 2 finer, longer setae, lacinia absent; Labium, prementum and mentum separate distinct, prementum bearing 2 pairs of setae and the 2 segmented labial palps inserted well apart at the base of the ligula; Mandibles, one dentate, with inner side excavated, condyle well developed. Thorax:Prothorax, pronotum large, overhanging the head without setae, EPP absent, 3 setae ventrally; Meso and metathorax, bearing one seta dorsally and 3 or 4 setae dorso-laterally (spiracle only present in mesothorax), 2 setae ventrally; Legs, absent. Abdomen: 1st-8th abdominal segments, setae present dorsally only in posterior half of segment, 2 setae dorsally,

3 or 4 minute setae anterior to these, 3 or 4 dorso-laterally, a bisetate, tubercle ventral to spiracle (probably T-P fused), a bisetate tubercle, probably As-Ps fused, 3 or 4 setae near mid-ventral line, there are more setae ventrally in the 7th abdominal segment.

Crowson (1955) described an Orsodaone larva obtained by Dr. F. van Emden. It differs profoundly from that attributed to the genus by Böving and Craighead (1931) but has considerable similarities to the larvae of the Eumolpinae and Galerucinae. In respect of its biforous spiracles it resembles larvae of Criocerinae and Donaciinae, and in the straight simple tarsungulus it resembles Sagra, Clytra and the Eumolpinae; the mandibles have pluridentate apices much as in Galerucinae etc.

iv. SUBFAMILY ZEUGOPHORINAEGENUS Zeugophora ( Z. subspinosa (F.)First instar larva (Plate LB 28, Figs. 68-71)

Colour cream or white. Tubercles absent. Grey chitinated plates present ventrally and dorsally on each segment. Head and body dorso-ventrally flattened. Body tapering gradually from the broad prothorax.

HEAD: triangular, dorso-ventrally flattened, prognathous, uniformly pale brown, epicranial stem absent, epicranial suture long, nearly reaching the antennal bases, indistinct posteriorly, median suture indistinct, vertex bearing 10 or 11 minute setae, gena 3 large setae, frons 6 minute setae on each side of the head; Ocelli absent; however in the final instar of Z. flavicollis there are 2 ocelli dorsally and one ventrolaterally; Antennae 3-segmented, well developed, directed anteriorly, segments 1 and 2 subequal in length, 2nd segment bearing at its apex a conical process and the 3rd segment, half the length of segments 1 or 2, conical process same length as 3rd segment, apex of 3rd segment bearing 4 setae; Clypeus, post-clypeus, bearing 2 pairs of setae; Labrum, semicircular, bearing 2 pairs of large setae posteriorly and 10 pairs along the anterior edge; Maxillae, maxillary palps 3 segmented, 1st segment longest, 3rd and 4th segments subequal in length, galea bearing approximately 6 stout setae, lacinia absent; Labium, labial palps one segmented, inserted close together; prementum, mentum and submentum fused; Mandibles, well-developed 4dentate ( 2 dentate in final instar, and therefore not a good specific character for Zeugophora sp. as proposed by Oglobin and Medvedev (1971)), all teeth subequal in size, molar area as broad as the basal area.

THORAX : Prothorax, pronotum long, narrow, grey, without setae, exterior to the pronotum are a minute hatching spine and seta, outside these along the lateral edge are 2 large and 1 minute seta, ventrally near these latter setae is a minute seta, interior to this is an indistinct tubercle without setae, anterior to this tubercle is a minute seta, a bisetose ventral plate as large as the pronotum, is fused across the mid-ventral line and passes anterior to the indistinct tubercle;

Mesothorax, dorsally with paired, long, narrow chitinated plates, fused across the mid-dorsal line, these plates without setae, interior to the lateral edge are a hatching spine and seta, laterally are a small and large seta, ventrally, near the lateral edge opens a large spiracle, interior to the spiracle is an indistinct tubercle without setae, anterior to which lie 2 minute setae, interior to this tubercle lie 2 long narrow chitinated plates, fused across the mid-ventral line, 2 setae lying on or near the anterior edge of the 2 plates; Metathorax, identical with mesothorax, but dorsally an additional minute seta anterior to hatching spine, ventrally an additional minute seta near the indistinct tubercle; Legs, absent. ABDOMEN: 1st Abdominal segment, dorsally with 5 minute setae, posterior to the anterior chitinated plate, exterior to these, a small seta anterior to a large seta, near the lateral edge are 2 setae and a hatching spine, laterally are a biforous spiracle and a large seta, ventrally and interior to this large seta, are a small and a large seta, interior to these latter setae lie 2 long, narrow chitinated plates, fused, across the mid-ventral line, the anterior one the longer and with 3 small setae posteriorly; 2nd - 7th Abdominal segments, identical with 1st segment but anterior dorsal plate with 2 or 3 minute setae posteriorly, spiracle more dorsal in position, hatching spine on 7th segment reduced; 8th abdominal segment, identical with segments 2-7 but dorsal anterior plate much shorter than posterior, hatching spine absent, ventrally with posterior chitinated plate absent; 9th abdominal segment, without dorsal chitinated plates, dorsally with 7 minute setae, laterally with 1 large and 2 small setae, ventrally with a single unisetate chitinated plate, a large and a small seta at extero-posterior edge of this plate; 10th abdominal segment, dorsally with 2 large and 1 small setae, ventrally with 5 small setae.

The 10 setae present interior to the spiracle on the first abdominal segment are probably homologous with setae 1-X in the primitive generalised form, and the 6 lateral ventral setae homologous with setae XI-XVI.

v. SUBFAMILY CRIOCERINAEGENUS Lema

First Instar Larvae. PLH22&23 <sup>Figs.</sup> 55-60; PLB21. <sup>Figs.</sup> 53-55; PLP.11: <sup>Figs.</sup> 36-38.

Colour creamy white. Tubercles small, colourless or very pale brown, very indistinct. Tubercles bearing colourless to very pale grey brown setae. Tubercles and setae are absent on the ventral surface of the abdomen. Integument between tubercles with very small grey brown chitinised plates which may be conical or seta-like. Plates absent ventrally on the abdomen. The body is convex dorsally as in Chrysolina sp., and covered by excrement.

HEAD: pentagonal in anterior view, epicranial stem long, epicranial suture distinct, very long, reaching the antennal base, median suture absent, vertex, gena and frons pale yellow brown, bearing circular plates or blisters or hexagonal plates, vertex 6 ( $v_1-v_6$ ) gena 4-6, frons 4 (+ 1 reduced) large setae on each side of the head capsule, setae pale grey yellow; Ocelli, 6, group of 4 dorsal to the antennae, 1 posterior to the antennae, 1 ventral to the antennae; Antennae, 3 segmented, short, segments subequal in length, short accessory process present, apex of 3rd segment bearing 6 sensillae; Clypeus, post-clypeus, distinct usually same colour as vertex etc., or slightly darker, bearing 3 pairs of setae, paler anterior to the setae; Labrum, bearing 3 pairs of setae, anterior edge with 2 or 4 pairs of setae; Maxillae, maxillary palps moderately short, 3 segmented, segments subequal in length, galea and lacinia distinct, lacinia bearing 3 or 4 stout setae; Labium, mentum and submentum fused, bearing 2 pairs of setae, labial palps consisting of a single conical segment; Mandibles, 5 dentate, sometimes inner and outer teeth reduced, same colour as rest of head, teeth yellow, small teeth sometimes present near the ventral ridge and interior to the first tooth. THORAX: Prothorax, pronotum very pale brown with perimeter paler, setae I-VIII present, setal group 1 trisetate, EPP bisetose,



T unisetate or seta XI reduced, or absent, P unisetate, As and Ps absent, Ss unisetate, Es unisetate, Meso and Metathorax, setae I-VIII on tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLpe, DLae arranged into a single row in the posterior half of each segment, in mesothorax 2 or 4 of these setae and tubercles may be absent, in metathorax 2 or 3 setae may be absent, tubercles DLae, DLpe fused and bearing setae VII, VIII plus an extra small seta, EPa unisetate, bearing a biforous spiracle in the mesothorax, EPp unisetate, T without seta XI, P unisetate, As and Ps absent, Ss unisetate, Es unisetate; Legs, 5 segmented well developed, (PLL 2.14<sup>Fig</sup>) same colour as pronotum or tubercle DLae, DLpe in first abdominal segment, claws completely yellow or yellow brown, claw with basal pulvillus. ABDOMEN: First abdominal segment, setae I-VI appear to be present but setae III and V are reduced, tubercles DLae, DLpe fused to form a large yellow brown tubercle slightly darker than the pronotum, bearing a single large hatching spine and 2 small setae, EPa bearing a biforous spiracle but seta IX absent, EPp absent, T, P, As, Ps, separate, all unisetate, Ss and Es always absent, As, and Ps sometimes absent; 9th abdominal segment, setae I-VIII probably present, all other setae and tubercles absent; 10th abdominal segment, indistinct, without setae.

#### GENUS Crioceris

Final Instar larva Crioceris asparagi (L.) Fig. PLH24, 62; Fig. PLB22, 56.

Body cream to pale yellow brown. Dorsal tubercles almost colourless to pale yellow brown. Ventral tubercles in abdomen almost colourless. Setae short, pale grey brown. Subcylindrical, weakly convex dorsally, posterior end curved abruptly ventrally, narrowed anteriorly from metathorax, and posteriorly from 6th abdominal segment. Between tubercles even in the ventral region numerous variously shaped grey brown chitinised plates occur. Spiracles, biforous, prominent, peritremes slightly darker brown than integument, same colour as legs. Spiracles larger on the mesothorax than the 1st abdominal segment but larger on

that segment than the following 7 segments. HEAD: Pale brown, epicranial stem long, apicranial suture distinct, long, reaching antennal bases, median suture absent, frons bearing 6 small setae, gena bearing 3 setae, vertex bearing 6 small setae; Ocelli, 6, paler than rest of head, position as in Lema; Antennae, short, 2 segmented, 2nd segment bearing a chitinated plate with a long seta and one papilla probably the rudimentary 3rd segment, 2nd segment also bearing papillae and one large conical accessory process, shorter than the seta on the chitinated plate; Clypeus, post-clypeus broad bearing 2 pairs of minute setae; Labrum, posteriorly bearing 6 setae, anterior edge bearing 6 setae; Maxillae, cardo unisetate, stipes bearing 3 setae, galea bearing 8 setae, lacinia absent, maxillary palps 3 segmented, segments subequal in length; Labium, postmentum bearing 1 pair of setae, pre-mentum bearing 1 pair of setae, also 1 pair of setae arising from inner margin labial palps. labial palps 1 segmented, maxillae, and labium slightly paler than rest of head; Mandibles, dark brown, 5 dentate, 3rd or median tooth the longest, inner tooth greatly reduced. THORAX: Prothorax, pronotum very pale yellow brown with slightly darker hexagonal areas, median part darker but much lighter than the head, bearing 10 setae, probably setae I-VIII present, setal group I trisetate, Epp large, trisetate, T, P unisetate, A, Ps, absent, Es, Ss fused, trisetate; Mesothorax and Metathorax, (Leg, PLL2 Fig.16) setae I-VIII probably present, DLae bisetate. DLpe bearing 2 large and 1 or 2 small setae, EPa bearing 2-4 setae and a spiracle in mesothorax, EPp unisetate, T without seta, P unisetate, As, Ps absent, Es bearing 2-4 setae, Ss unisetate or bisetose. ABDOMEN: 1st-7th Abdominal segments, tubercles Dal, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe unisetate, DLae sometimes bisetose, EPa without seta IX but bearing spiracle, EPp unisetate, T and P fused, large tubercle bearing 4-5 setae, As, and Ps consisting of 2-5 unisetate tubercles, Ss apparently trisetate, Es apparently unisetate, segments 2-7 bearing 3 pairs suctorial discs on the ventral surface; 8th abdominal segment, tubercles Dpi, Dpe, DLpi probably fused together,

tubercle trisetose, tubercles DLae, DLpe probably fused together, tubercle trisetose, EPp absent, T and P fused together, bisetose, As, Ps, Ss, Es indistinct, 9th abdominal segment, tubercles Dal, Dpl, Dae, Dpe, DLai, DLpi, DLae, DLpe, EPa, EPp represented by 2 setae, T and P fused, trisetose, tubercles T, P, As, Ps, Ss, Es absent, a single suctorial disc present on the ventral surface; 10th abdominal segment, indistinct, without setae.

### GENUS Lilioceris

Final instar larva Lilioceris lili (Scop.) (PLH 24 FIG. 61; PLB 23 FIG. 57)

Body cream or pale yellow brown, convex dorsally, highest at abdominal segments 2 and 3. Body gradually broadening from the head to the 6th abdominal segment, then gradually narrowing to the posterior end. Dorsal area of meso and metathorax and abdomen bearing numerous small brown tubercles. Dorso lateral to ventral tubercles in thorax pale brown, slightly paler than pronotum. Ventral tubercles in abdomen only present on segment 1. Only small tubercles present dorsally and dorso-laterally in abdomen. Setae moderately long, pale grey brown, Numerous very pale brown circular chitinised plates occur between the tubercles. Plates most numerous and distinct in thorax and 1st abdominal segment, but absent ventrally in abdomen. Plates unraised. Spiracles large, peritremes light brown. Mesothoracic and 1st abdominal spiracle equal in size, slightly larger than those on the remaining abdominal segments. HEAD: oval in anterior view, dark brown to black, vertex bearing hexagonal or rounded plates, epicranial stem long, epicranial suture distinct, long, reaching antennal bases, vertex bearing 5, gena 5, frons 4 setae on each side of the head capsule, setae moderately long, pale grey brown; Ocelli, 6, arranged as in Lema, paler than rest of head; Antennae, 2 segmented, short, Clypeus, fronto-clypeal suture indistinct, post clypeus usually bearing 2 pairs of large setae; Labrum bearing 3 pairs of setae posteriorly, 6 pairs along the anterior

edge; Maxillae, cardo without setae, stipes bearing 3 pairs of large setae and a small seta, galea bearing 6 setae, lacinia absent, maxillary palps short, 3 segmented, the apical segment indistinct, segments subequal in length; Labium, mentum bearing 2 pairs of setae, labial palps a single conical segment; Mandibles, basal area dark brown, apical half golden brown, 5-dentate, 3rd or median tooth the longest, 2nd tooth deeply incised on the inner margin, inner tooth greatly reduced.

THORAX: Prothorax, pronotum brown, bearing 10 setae, setae I-VIII probably present, setal group 1 trisetose, EPp large, bearing 4 setae, T, P, unisetate, As, Ps absent, Ss, Es unisetate, neither tubercle fused across the mid ventral line; Mesothorax, posterior part of segment, dorsal to tubercle DLae-DLpe, bearing 7-9 unisetate tubercles, anterior part bearing 2 unisetate tubercles, tubercles DLae, DLpe, fused, large bearing 8 setae, separate tubercle dorsal to DLae-DLpe sometimes absent, EPa apparently divided into 2 by the spiracle, dorsal part bearing 3 setae, ventral part bisetose, EPp bisetose, T without seta XI, P unisetate, As, Ps absent, Ss bearing 5 setae, Es unisetate, neither fused across the mid-ventral line; Metathorax, posterior part of segment dorsal to tubercle DLae, DLpe bearing 17-21 unisetate tubercles, some rarely bisetose, anterior part bearing 2 unisetate tubercles, tubercles DLae, DLpe fused, large, bearing 7-8 setae, EPa with dorsal part absent, but probably represented by 3 unisetate tubercles antero-dorsal to DLae-DLpe, ventral part of EPa bearing 3-5 setae, rudimentary spiracle present, EPp bisetose, T without seta XI, P unisetate, Ss bearing 7 setae, Es bearing 2 or 3 setae, neither tubercle fused across mid-ventral line; Legs, (PLL2 Fig.15) well developed, darker brown than pronotum, same colour as head, claws unicolorous pale brown, with pulvillus, ABDOMEN: First abdominal segment, 30 unisetate tubercles dorsal to spiracle, EPa bearing spiracle, but seta IX absent, EPp absent, T and P possibly represented by 3 unisetate tubercles, As, Ps, unisetate, Ss and Es represented by 3 unisetate and a bisetose tubercle; 2nd-6th abdominal segments,

27-32 unisetate tubercles dorsal to spiracle, EPa bearing spiracle, but seta IX absent, EPp absent, T, P possibly represented by 3-4 unisetate tubercles, As, Ps possibly represented by 4 unisetate tubercles, Ss, Es unisetate, indistinct, ventral surface bearing suctorial discs; 7th abdominal segment, identical with segments 2-6 but Ss absent, no suctorial discs present; 8th abdominal segment, identical with segments 2-6 but 11 unisetate tubercles dorsal to spiracle, Ss, Es, suctorial discs absent; 9th abdominal segment, bearing 9 unisetate tubercles; 10th abdominal segment, bearing 2 setae.

## vi. SUBFAMILY CLYTRINAE

GENUS Clytra

Clytra quadripunctata (L.) - Final Instar larva. (PLH<sup>25</sup> FIG. 63; PLH<sup>26</sup> FIG. 65; PLB<sup>24</sup> FIG. 59)

Colour creamy white with indistinct tubercles. Head, pronotum and legs yellow brown, head slightly darker. Posterior part of the abdomen curved ventrally.

HEAD: In anterior view spherical, yellow brown, epicranial stem and suture long, both indistinct, median suture absent, vertex and gena with darker brown irregular raised areas (sulcations) surrounding lighter brown depressions, frons bearing minute darker brown chitinated plates, vertex with 6 setae, ( $v_1 - v_6$ ), gena with 4 large, 1 small seta, frons 6 large setae ( $f_1 - f_6$ ) on each side of the head, setae colourless, not feathered; Ocelli, 6, a group of 4 postero-dorsal to the antennae, 2 posterior to the antennae, each ocellus consisting of about 7 black spots; Antennae, large, 2 segmented, first segment broad, bearing 3 setae; Fronto - clypeal suture distinct, clypeolabial suture indistinct; Clypeus, post clypeus indistinct, clypeus bearing 4 pairs of large setae; Labrum, bearing 4 pairs of large setae along the ventral edge; Maxillae maxillary palps 3-segmented, lacinia present; Labium, fused mentum and sub-mentum bearing 5 pairs of large setae, labial palps 2-segmented; Mandibles, with 5 indistinct teeth. THORAX: Prothorax, pronotum large, narrow elongate, yellow brown, bearing numerous large setae, EPp unisetate, very small, T apparently unisetate, P unisetate, As and Ps absent, Ss indistinct but seta XVI present, Es indistinct but seta XV present; Meso and Metathorax, Dai unisetate, a unisetate tubercle dorsal to Dai, Dae unisetate, a unisetate tubercle ventral to Dae, Dpi and Dpe unisetate, DLai and DLpi possibly fused into a bisetose tubercle, DLae and DLpe fused, tubercle bearing 5 or 6 large setae, EPa without seta IX and bearing a spiracle in mesothorax, EPa tending towards fusion with DLae - DLpe, EPa indistinct in metathorax, EPp unisetate. T trisetose well chitinated tubercle, P unisetate, As possibly present,

small, unisetate, Ps absent, Es unisetate, Ss and Es tending towards fusion; Legs, very well developed, all of equal length, yellow brown, (PLL2.Fig.12) claws elongate, yellow. ABDOMEN: Abdominal segments 1-8, all tubercles up to EPa probably present, unisetate, tubercles Dai, Dae, Dpe usually indistinct but setae present, EPa bearing spiracle but seta absent, EPp absent, T and P fused, bisetose, As unisetate, P bisetose, Ss unisetate, Es bearing 4 setae, setae III and IV enlarged in abdominal segments 6 and 7, seta III enlarged in segment 8; 9th segment, bearing 10 setae; 10th segment, bearing 8 setae.

#### GENUS Labidostomis

L. tridentata (L.) Plate LH 28, Fig. 67.

Material was unavailable but the larva has been studied by Medvedev (1962).

HEAD: in anterior view oval, epicranial stem and suture long, very distinct, median suture absent, vertex and gena without sulcations, vertex bearing 5 long setae ( $v_1, v_3, v_4, v_5, v_6$ ), seta  $v_3$  x2 longer than the other setae, frons bearing 6 long setae ( $f_1 - f_6$ ) setae  $f_2$  and  $f_4$  x2 longer than the other setae; Ocelli, 6, Antennae 2 segmented; Fronto-clypeal suture absent; Clypeo-labral suture absent; Clypeus, probably bearing 6 pairs of setae; Labrum bearing 4 pairs of setae along the ventral margin; Mandible apparently 4 dentate. Pronotum: bearing 6 large setae along the anterior margin, 2 setae at the lateral edge, 2 setae centrally and 4 setae along the posterior margin.

#### GENUS Gynandrophthalma

G. cyanea Plate LH 28, Fig. 68.

Material was unavailable but the larva of G. cyanea has been studied by Medvedev (1962)

HEAD: in anterior view oval, epicranial stem and suture long, very distinct, median suture absent, vertex and gena without sulcations, vertex bearing 6 moderately long setae ( $v_1 - v_6$ ) seta  $v_3$  the longest,

frons bearing 6 spindle shaped setae ( $f_1 - f_6$ ); Ocelli, 6; Antennae 2 segmented, 2nd segment bearing apically a large seta; Fronto clypeal suture absent; Clypeo-labral suture very indistinct; Clypeus probably bearing 6 pairs of setae; Labrum bearing 4 pairs of setae along the ventral margin; Mandible 2-dentate; Pronotum: bearing 7 large setae along the anterior margin, 2 setae at the lateral edge, 2 setae centrally and 6 setae along the posterior margin.



## vii. SUBFAMILY CRYPTOCEPHALINAE

GENUS Cryptocephalus

First instar larvae. (PLH25 FIG.64; PLH27 FIG.66; PLB24 FIG.58; PLP12 FIGS.39-41)

White or cream, with the pronotum, legs and head yellow brown.

Dorsal tubercles on thorax and abdomen indistinct. Body between tubercles with numerous small round plates. Setae very pale yellow brown. Posterior part of the abdomen curved ventrally.

HEAD: oval in anterior view, epicranial stem and suture short, median suture absent, vertex, gena and frons golden brown bearing slightly darker brown chitinated plates, vertex sometimes with irregular paler areas, vertex bearing 6 large ( $v_1 - v_6$ ) and 1 small seta, gena with 4 large and 2 small setae, frons with 6 large setae ( $f_1 - f_6$ ) on each half of the head capsule, setae on the vertex ventral to the epicranial suture and on frons are feathered; Ocelli, 6, a group of 4 dorsal to the antennae, one posterior to the antennae, one ventral to the antennae; Antennae, same colour as rest of the head, 3 segmented, well developed, first segment two times longer and broader than the second which is one and a half times longer than the third, ventrally at the apex of the second segment arises a conical accessory process which is longer than the third segment, interior dorsal to the accessory process are 2 setae, third antennal segment small, bearing at its apex 5 small setae and a very large seta over 2 times the length of the segment; Fronto-clypeal suture distinct; Clypeo-labral suture indistinct bearing 1 pair of setae, clypeus bearing 6 pairs of setae with 4 pairs of setae along the ventral edge; Maxillae, maxillary palps 3-segmented; lacinia distinct, consisting of 2 stout setae, galea bearing 8 stout setae, Labium, labial palps 2-segmented, segments of equal length, maxillae and labium paler brown than the rest of the head; Mandibles, 4 dentate, inner tooth reduced, outer tooth the largest, ventral ridge distinct.

THORAX: Prothorax, pronotum pale yellow brown with periphery paler, much darker than other tubercles, bearing 11 large and a number of smaller setae, setae 1-VIII probably present, EPa present in cervical region antero-ventral to T, EPp very small, unisetate, paler brown, T bisetose, same colour as the large fused tubercle DLae - DLpe in meso and metathorax, P unisetate, pale, As and Ps absent, Ss unisetate, Es bisetose; Meso and Metathorax, dorsal tubercles indistinct, difficult to homologise, Dai and Dae unisetate, Dpi and Dpe unisetate, tending towards fusion, DLai probably absent, DLpi very pale yellow bearing a hatching spine, one large and one small seta, DLae and DLpe fused into a large tubercle the same colour as DLpi, bearing 2 large and 2 small setae, EPa indistinct and as pale as dorsal tubercles, anterior to and tending towards fusion with tubercle DLae - DLpe, EPa without seta IX but bearing a large spiracle in the mesothorax, spiracle two times size of abdominal spiracles, atrium variously shaped, EPa absent in metathorax, EPp unisetate, colour as dorsal tubercles, T bisetose, colour as DLae - DLpe in meso and metathorax, P unisetate, pale, As probably present, unisetate, Ps absent, Ss and Es fused, bisetate; Legs, very well developed, colour as pronotum, 5-segmented, coxa, femur, tibia long, tarsungulus with claw elongate, completely yellow. ABDOMEN: Abdominal segments 1 - 8, all tubercles in the abdomen very indistinct, tubercles Dai and Dae very indistinct but setae I and III present, tubercles Dpi and Dpe fused, bisetose, seta II and IV present, seta IV greatly enlarged in segments 6 and 7, seta V probably present but tubercle DLai absent, seta VI present, tubercle DLpi absent, this seta is also enlarged on segments 6 and 7, setae IX and X probably present but greatly reduced, EPa small, bearing spiracle, 8 pairs of spiracles in abdomen of approximately the same size, EPp absent, T and P fused, bearing 1 large and 1 small seta, As and Ps fused, bearing 1 large and 1 small seta, Ss unisetate, Es bisetate, fused across mid-ventral line.

## viii. SUBFAMILY CHRYSOMELINAE

GENUS TimarchaFirst instar larva (PLP 1, Fig. 3, PLH1.Fig1,PLB10.Figs. 4.b,c)

Colour dark metallic blue or green, metallic colour absent ventrally. Ventral surface pale or yellow brown. No tubercle dorsal to the spiracles and only weakly chitinised on the ventral surface. Dorsal integument formed by the fusion of numerous very small hexagonal light brown chitinised plates, with less numerous lighter grey brown round chitinised plates in the ventral region. Hexagonal plates cover the pronotum etc. Setae yellow brown to very pale grey yellow. Tubercles with hatching spines black, spiracles black, both slightly darker than the integument.

HEAD: (Fig.1) Pentagonal in anterior view, vertex coming to a point, epicranial stem extremely short, epicranial suture distinct but short, median suture indistinct, short, black fading to pale brown anteriorly, head light brown covered by small plates, the peripheries of which are paler, vertex and frons with numerous small setae, gena with 8-11 large setae, setae very pale grey yellow, base of vertex and vertex interior to antennae with numerous large setae; Ocelli, 6 on each side of the head, arranged as in Chrysolina spp., Antennae, well developed, as long in Chrysolina spp., 3 segmented, second segment nearly x2 as long as the first or third which are almost equal, conical process at least half the length of the third segment, 2 setae near the base of the conical process, apex of 3rd segment with 1 large and 4 small setae; Clypeus, post-clypeus same colour as rest of the head, bearing 15-23 large setae; Labrum, darker than rest of the head with 2 pairs of large setae, very pale yellow areas around setal bases, ventral edge of labrum bearing 6 large setae; Maxillae, maxillary palps 3 segmented, palpiger and 1st segment short, equal in length, 2nd segment x2 the length of these segments, 3rd segment conical, bearing numerous sensillae at the apex and a group of 6 setae on its dorsal surface; Labium, with palps

2 segmented, labial and maxillary palps same colour as rest of head; Mandibles, distinctly 5-dentate, outer tooth well developed, basal half same colour as the labrum, form as in Chrysolina sp., base of mandible bearing 6-9 large setae. THORAX: Prothorax, Pronotum slightly darker than the rest of the body, without a paler periphery, with numerous scattered very small setae, EPa apparently present in the cervical region as a very pale brown tubercle anterior to tubercle T, large EPp present tending towards fusion with the pronotum, and bearing 10-11 large setae, T with 2 large setae, P with 4 large, 2 small setae, As, and Ps absent, Es large, well defined very pale brown bearing a total of 14 large setae, Ss indistinct, bearing 4 setae, tending towards fusion with Es; Meso and metathorax, tubercles absent dorsal to spiracles, a single large one present in mesothorax only, a single large indistinct tubercle bearing numerous large setae, dorsal to T and P, T distinct, bisetose, P distinct, unisetate, paler brown than dorsal surface, Ss and Es indistinct, tending towards fusion, bearing 26 large setae, large golden brown tubercles dorsal to the spiracles bearing single large hatching spines and 3-4 small setae; Legs, 5 segmented, well developed, (PLLI.Fig1) segments light brown, slightly darker than the rest of the body, dorsal apical half of coxa membranous, pale yellow, claw tip golden brown. claw (PLL3.Fig32) without inner tooth. ABDOMEN: 1st-7th abdominal segments, tubercles absent dorsal to spiracles which decrease in size from 1st-7th, 7th x 0.5 size of the first, first abdominal spiracle smaller than the mesothoracic, a single large indistinct tubercle bearing numerous large setae dorsal to T and P, T and P fused, forming an indistinct tubercle bearing approximately 10 large setae, As, and Ps fused forming a slightly more distinct pale brown tubercle bearing up to 15 large setae, tubercle Ss bearing few large setae in the 1st abdominal segment, up to 18 in later segments, Es fused across mid-ventral line, bearing a total of 16 setae, Ss and Es fused in 7th abdominal segment, a hatching spine present on large golden brown tubercle dorsal to spiracle only in 1st abdominal segment, tubercle Ss

raised to form paired papillae on the ventral surface of abdominal segments 4, 5, 6, 7, papillae largest on segments 5 and 6, these probably aid in progression; 8th abdominal segment, similar to segments 1-7 but paired spiracles absent, tubercles Ss and Es fused, papillae not evident; 9th and 10th abdominal segments, very reduced, completely pale yellow, brown hexagonal chitinised plates absent, replaced by numerous very pale brown round chitinised plates, with numerous large setae, 10th segment bearing paired anal papillae, ventral to anus. Glands are absent between abdominal segments 8 and 9.

### Diagnosis.

Post clypeus bearing 15-23 large setae. EPp in prothorax bearing 10-11 setae. Pronotum without large setae. 3rd segment of maxillary palp bearing a group of 6 setae on its dorsal surface. Abdomen with only 7 pairs of spiracles.

### GENUS Chrysolina

#### First instar larvae

PLH2, FIGS 3&4; PLH3, FIGS 5&6; PLH4, FIGS 7&8; PLH5, FIGS 9&10

PLP1 : 1,2, PLP2 : 4-6, PLP3 : 7-9

PLB1, FIGS 1-4; PLB 2, FIGS. 5-8.

Body white, cream, yellow, orange, grey or various shades of brown.

Numerous small, pale grey or grey brown chitinised plates occur between the tubercles which are usually small, distinct and yellow or brown.

Body convex dorsally.

HEAD: Spherical or oval in anterior view, epicranial stem, and suture moderately long, epicranial suture a distinct fine pale line, median suture very distinct and dark brown or black, vertex, gena, frons and antennae light brown, vertex bearing 4-7 ( $v_1 - v_7$ ) gena 4-7 and frons 5 ( $f_1, f_2, f_3, f_4, f_6$ ) large setae on each side of the head capsule, the setae varying in size between species, setae usually pale grey yellow; Ocelli, 6, present on each side, arranged into a dorsal group of 4 posterior to the antennae and a ventro-lateral group of 2 on the gena; Antennae, 3 segmented, the basal segment very short and annular, the length of 2nd and 3rd segments varying between species, 2nd segment

with a conical process on the distal postero-ventral surface, conical process is half the length of the 3rd segment, apex of 3rd segment with 4 short setae; Clypeus, post-clypeus with 3 pairs of setae, anterior to which there is a paler area, post clypeus slightly darker than rest of head; Labrum, usually the same colour as the post-clypeus and bearing 2 pairs of large setae; Maxillae, without lacinia, cardo a small triangular glabrous sclerite, stipes usually with 2 short distal setae near the base of the galea and a pair of long ventral setae, maxillary palps 3 segmented, the apex of the 3rd segment with conspicuous tactile processes; Labium, short and rectangular, submentum with 1 pair of setae, the mentum with 2 pairs of setae, the transverse semi-circular bar at the proximal extremity of the palpi heavily chitinised, the lateral rods of the hypopharynx also well defined, palpi short, 2 jointed; Mandibles, slightly more heavily chitinised, 5-dentate, apex almost as broad as the base, 5th or outer tooth often reduced.

THORAX: Prothorax, Pronotum consisting of fusion of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe and possibly EPp, usually light brown or grey brown with the perimeter lighter, with 12-17 large setae variable in size and position between species, EPa present, T and P unisetate, As, and Ps absent, Es and Ss separate and both unisetate; Meso and metathorax, Tubercles Dai, Dpi, Dae, Dpe unisetate, DLai absent or possibly fused with DLpi, DLpi bearing a 'hatching spine' or 'egg-burster' and 2-4 small setae, DLpi the same colour as or slightly darker than the pronotum, DLae and DLpe fused and bearing 2-4 large setae, EPa bearing 1-3 setae and the spiracle in the mesothorax, EPp unisetate, T without seta and P unisetate, As, and Ps absent, Es and Ss separate and both unisetate, Ss usually indistinct; Legs, 5-segmented, well developed and the same colour as the pronotum, tip of claw yellow, claw with inner tooth in some species. ABDOMEN: 1st-6th abdominal segments, Tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe unisetate, DLpe sometimes indistinct but seta VIII present, DLpi in first abdominal

segment bearing the hatching spine and 0-3 small setae, EPa bearing the spiracle but no setae, EPP absent, T and P fused and bearing 2-3 large setae, As and Ps fused and bearing 2-3 setae, Ss sometimes indistinct and bearing 3-4 setae, Es sometimes indistinct, unisetate; 7th abdominal segment, as previous abdominal segments but Dai, Dpi, Dae, Dpe and DLai sometimes fusing to form a large dorsal tubercle not fused across the middorsal line; 8th abdominal segment, as previous abdominal segments but Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae and DLpe usually fusing to form a large dorsal tubercle, sometimes several tubercles are absent and hence the tubercle bears 5-8 large setae, Ss and Es fused to form a large tubercle; 9th abdominal segment, Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae and DLpe forming a large dorsal tubercle bearing 6-8 large setae, ventral tubercle bearing 3-4 large setae, formed by the fusion of As, Ps and Ss. A small gland opens dorsally posterior to 8th abdominal spiracle between abdominal segments 8 and 9. They are not eversible.

Diagnosis: Ratio of the number of tubercles between the spiracles on the meso or metathorax/number on 1st abdominal segment is 14/16, 12/14, 12/16.

GENUS LeptinotarsaL. decemlineata (Say.)Final instar larvae (PLH10, FIG 28, PLB10, FIG 24a.)

Colour reddish yellow, body strongly convex dorsally. Setae minute, numerous. Very small, circular, grey, weakly chitinised plates occur between the tubercles, especially near the large spiracle and the lateral tubercles.

HEAD: Oval in anterior view, epicranial stem long, epicranial suture moderately long, median suture not strongly chitinised, vertex pale brown with black markings, bearing 6 minute setae ( $v_1 - v_6$ ), frons with dorsal area concolorous with vertex, remainder including ventral slightly raised area creamy yellow, bearing 5 large setae ( $f_1, f_2, f_3, f_4, f_6$ ), gena pale brown, bearing 6 setae; Ocelli, 6, arranged as in Chrysolina.

Antennae, short, 3 segmented; Clypeus, postclypeus creamy yellow bearing 3 pairs of setae; Labrum pale brown, bearing 5 pairs of minute setae dorsally and 4 large pairs along ventral margin; Maxillae without lacinia, pale brown, maxillary palps 3 segmented, pale brown; Labium, pale brown, labial palps 2 segmented; Mandibles, pale brown 5 dentate, inner and outer teeth reduced, apical half including teeth dark brown.

THORAX: Prothorax, Pronotum consisting of fusion of tubercles  $D_{al}, D_{pi}, D_{ae}, D_{pe}, DL_{al}, DL_{pi}, DL_{ae}$  and possibly  $EP_{p}$ , anterior glabrous part concolorous with rest of body, posterior pale brown bearing numerous minute setae,  $EP_{p}$  absent, T unisetate, P bearing 4 minute setae, As and Ps probably absent, Es and Ss probably fused, bearing 3 small setae, anterior to fused Es - Ss are three small setae; Meso and Metathorax, tubercles  $D_{al}, D_{pi}, D_{ae}, D_{pe}, DL_{al}, DL_{pi}$  probably present, usually unisetate but  $D_{pi}$  yellow brown (lighter than other body tubercles) much larger than other tubercles, bearing 3-4 setae,  $DL_{ae}$  and  $DL_{pe}$  fused, light brown, three times the size of  $D_{pi}$ , prominent, bearing 12-14 minute setae,  $EP_{a}$  light brown, 2/3 size of  $DL_{ae}-DL_{pe}$ , bearing 4-6 minute setae and a spiracle in the mesothorax which is three times



the size of the abdominal spiracles, mesothoracic EPa with indications of a spiracle (non functional), EPp small, yellow brown unisetate or with an additional minute seta, T, yellow brown, bearing 2 small and 3 minute setae, P yellow brown bearing 4-6 minute setae, ventral region bearing 5-7 small unisetate tubercles and fused Es-Ss yellow brown, bearing 4 minute setae (Note also there are usually 5 small unisetate tubercles anterior to EPa); <sup>(PLL1.Fig4)</sup> Legs, 5 segmented, well developed basically same colour as vertex, anterior part of coxa creamy brown, posteriorly slightly darker, femur, tibia and claw medium to dark brown, claw tip pale brown, <sup>(PLL3.Fig33)</sup> claw with inner tooth. Abdomen: 1st-7th abdominal segments, tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe indistinct, minute, bearing one minute seta, only rarely are all setae present, EPa large, light brown, decreasing in size from 1st to 7th abdominal segment, bearing a spiracle with black peritreme and 1-13 minute setae (usually 9), EPp probably absent, T and P fused, tubercle large, light brown bearing 5-10 minute setae (usually 9), As and Ps, minute, unisetate, tending towards fusion, Ss bisetose, small, in first segment fused across the mid ventral line, Es minute, unisetate. In 7th abdominal segment, minute tubercle, probably Dpi is fused across the mid-dorsal line; 8th abdominal segment, a light brown dorsal plate probably consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae and DLpe fused, bearing 16 minute setae, EPa greatly reduced, bearing small spiracle but no setae, T-P fused, small, yellow brown, bearing 2 minute setae, As and Ps probably absent, Es and Ss minute, unisetate; 9th abdominal segment, a dorsal plate up to mid-point of eversible gland bearing 12 minute setae, 5 minute setae; ventrally, with a pair of fleshy prolegs. Between 8th and 9th abdominal segments, posterior to spiracle are single small eversible glands.

#### Hatching spines in first instar larvae.

Hatching spines occur on the meso, metathorax and first abdominal segment (Bertrand, 1924).

Diagnosis.

Tubercle EPa in abdominal segment 2 at least 2/3 the size of fused DLae - DLpe in meso and metathorax.

GENUS Phytodecta

First instar larva (PLH 6, FIG 11; PLH 7, FIGS. 13 & 14; PLB 3, FIG. 9; PLB 4, FIG. 10; PLB 5, FIGS. 11a & 11b; PLB 4, FIGS. 10-12.)

Colour pale green or pale grey. Tubercles large, indistinct, the central area pale brown or grey with the periphery paler. Integument between tubercles with very small, grey, chitinated plates. Body elongate and only slightly convex. HEAD: spherical in anterior view, epicranial stem and suture moderately long as in Chrysolina spp., epicranial suture distinct, yellow brown or darker brown but not as heavily chitinated as in Chrysolina spp., vertex, gena, frons and antennae pale yellow brown, the vertex bearing 5 ( $v_1, v_3, v_4, v_5, v_6$ ), gena 5, and frons 5 ( $f_1, f_2, f_3, f_4, f_6$ ) large setae on each side of the head capsule, the setae varying from nearly colourless to pale grey yellow; Ocelli, 6 arranged as in other larvae of the Chrysomelinae; Antennae, as long as in Chrysolina spp., with 3 segments subequal in length, the conical process more than half the length of the third segment; Clypeus, post-clypeus pale yellow brown, bearing 3 pairs of large setae with a paler area anterior to their bases; Labrum, very slightly darker than the rest of the head capsule, bearing 2 pairs of setae, Maxillae and Labium, pale yellow brown, with the same structure as Chrysolina spp. Mandibles, 5 dentate with the outer tooth reduced, of the same shape as in Chrysolina spp., colour as in the labrum but with the tips of the teeth yellow. THORAX: Prothorax, Pronotum pale brown or grey centrally with the periphery paler, consisting of tubercles Dae, Dpi, Dae, DLai, DLpi, DLae, DLpe and possibly EPp, with 10-15 large setae, T and P unisetate, As and Ps absent, Es and Ss separate and both unisetate; Meso and Metathorax, Tubercles Dai and Dae fused and bisetate, the resulting tubercle also fused across the mid-dorsal line, sometimes Dai and Dae separate and

both unisetate, Dpe sometimes absent but when present it is fused with Dpi and also DLpi, Dpi may be unisetate or bisetate, when absent Dpi and DLpi remain separate, DLai sometimes absent but when present without seta V, DLpi bears the 'hatching spine' or 'egg burster', 2 large and 1 small seta and may be the same colour or slightly darker than the other tubercles, the tubercle formed by the fusion of DLae and DLpe bears 3-5 large setae, EPa bears the spiracle in the mesothorax and may be unisetate or rarely bisetose, EPP unisetate, T without seta XI, P unisetate, As, and Ps absent, Es and Ss both unisetate; <sup>(PLL1.Fig.3)</sup> Legs, 5 segmented, well developed and usually yellow brown or the same colour as tubercle DLpi, <sup>claw yellow</sup> (PLL3.Figs.21,22), claw with inner tooth. ABDOMEN: First abdominal segment, Tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi usually separate and unisetate, sometimes Dai fused with Dae, and Dpi with Dpe, DLpi with a hatching spine, DLae and DLpe apparently absent, EPa bearing the spiracle but seta IX absent, EPP absent, T and P fused and bisetose, As and Ps fused and unisetate or bisetate, Es and Ss both unisetate; 2nd-6th abdominal segment, identical with the first abdominal segment but DLpi without a hatching spine and Ss trisetate, 7th abdominal segment, identical with segments 2-6, but Dai, Dpi, Dae, Dpe, DLai, DLpi may be united to form a dorsal plate fused across the mid-dorsal line or DLai and DLpi may remain separate; 8th abdominal segment, identical with segments 2-6 but Dai, Dpi, Dae, Dpe, DLai, and DLpi unite to form a dorsal plate fused across the mid-dorsal line, Es and Ss fused; 9th abdominal segment, identical with segment 8 but EPa, T and P are absent, As, Ps, Es and Ss are fused to form a ventral plate bearing 4 setae. In some species an eversible gland opens dorsally between abdominal segments 7 and 8. These are dorsal to the spiracles.

#### Diagnosis.

Ratio of the number of tubercles between the spiracles on the meso or metathorax/number on 1st abdominal segment 3/6, 8/6, or 12/12, (when 8/6 without eversible glands on meso and metathorax).

**GENUS Phyllodecta**

**First instar larvae** (PLH 8, FIGS 15, 16 & 17; PLB 8, FIGS : 20 a,b,c; PLP 5 : 13-16)

Colour white or cream. Tubercles well developed and very distinct, the central areas pale brown surrounded by paler perimeters. Numerous very small grey or grey brown chitinised plates occur between the tubercles. **HEAD:** Oval in anterior view, epicranial stem and suture longer than in Chrysolina spp., epicranial suture a distinct fine pale line, nearly reaching the antennal base, median suture dark brown and distinct, vertex, gena, frons and antennae pale brown, vertex bearing 4 ( $v_1, v_3, v_4, v_6$ ), gena 4, frons 4 ( $f_1, f_3, f_4, f_6$ ) large setae on each side of the head, setae pale grey yellow; **Ocelli**, as for Chrysolina spp., **Antennae**, conical, 3 segmented, much shorter than in Chrysolina spp., segments approximately the same length but tapering from the much broader basal segment, the conical process slightly shorter than the 3rd segment; **Post-clypeus and Labrum**, the same colour as the rest of the head and both bear two pairs of setae, post clypeus is paler anterior to the setae; **Maxillae and Labrum**, similar to those of Chrysolina spp., however the maxillary and labial palps are much shorter in Phyllodecta spp. **Mandibles**, apparently 5-dentate, outer tooth reduced and difficult to distinguish, teeth golden brown, the apex of the mandible much narrower than the base, the whole mandible more elongate than in Phaedon, Gastroidea, Chrysomela spp. **THORAX: Prothorax**, Pronotum consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae and DLpe, usually yellow brown with the perimeter paler, setae 1-VIII present, setal group 1 bisetose, seta VI reduced. , Epp unisetate, T and P unisetate, As and Ps absent, Es and Ss fused and bisetose; **Meso and Metathorax**, Tubercles Dai and Dae fused and bisetate, Dpi unisetate, Dpe absent, DLai absent or possibly fused with DLpi, DLpi bearing a 'hatching spine' or 'egg-burster', 1 large and 2 small setae and is of the same colour as the pronotum and other tubercles, DLae fused with DLpe and bearing 2 large, 1 small and 2 minute setae,

the openings of single large eversible glands occur on these tubercles, EPa unisetate and bearing a spiracle in the mesothorax, EPP unisetate, T with seta XI absent, P unisetate, As, and Ps absent, Ss and Es separate and unisetate, tubercle Ss usually indistinct; Legs, 5-segmented, (PLL1.Fig.5) well developed and usually the same colour as the pronotum and other tubercles, (PLL3.Figs.18,19,20) claw tip yellow, claw without inner tooth. **ABDOMEN:** 1st abdominal segment, Dai unisetate, Dpi and Dpe fused and bisetose, Dae, DLai and DLpi absent, DLae and DLpe fused and bisetose but without eversible glands, EPa with spiracle but seta IX absent, EPP absent, T and P fused and bisetose, As, and Ps fused and bisetose, Ss very indistinct and with 1-4 small setae, Es unisetate, 2nd-6th abdominal segments, as 1st abdominal segment but Dai absent; 7th abdominal segment, as 2nd-6th segments but Dpi and Dpe fused into dorsal tubercle which is also fused across the mid-dorsal line; 8th abdominal segment, as 2nd-6th abdominal segments but Dpi, Dpe, DLae, DLpe fused into a dorsal tubercle which is also fused across the mid-dorsal line, Es and Ss fused; 9th abdominal segment, as 8th segment but EPa, T and P absent, As-Ps unisetate; 10th abdominal segment, a single ventral plate bearing 12 minute setae. **Diagnosis:** 1st abdominal segment different from remainder as tubercle Dai is absent.

#### GENUS Phaedon

**First instar larvae** (PLH 8, FIGS. 18-20; PLB 6, FIGS 12-14; PLP 6, FIGS. 17-19)

Body dull white. Numerous small pale brown chitinated plates between the tubercles, tubercles large, distinct, and very pale yellow brown with a paler periphery.

**HEAD:** Spherical in anterior view, epicranial stem shorter than in Phyllodecta sp. but epicranial suture as long, median suture very distinct and dark brown or black, vertex, gena, frons and antennae very pale yellow brown to pale brown, vertex bearing 4 ( $v_1, v_3, v_4, v_6$ ), gena 5 and frons 4 ( $f_1, f_3, f_4, f_6$ ) large setae on each side of the head,

setae pale yellow or pale grey yellow; Ocelli, 6 present on each side of the head, their arrangement similar to that of Chrysolina spp., Antennae, 3-segmented and similar to those of Chrysolina sp., with the conical process about half the length of the 3rd segment; Clypeus, post-clypeus, yellow brown or darker, bearing 3 pairs of setae, anterior to which a lighter area occurs; Labrum, same colour as post-clypeus, bearing 2 pairs of large setae; Maxilla and Labium, similar to those of Chrysolina sp., colour similar to that of the rest of the head; Mandibles, usually slightly more heavily chitinated and darker brown, 5 dentate, teeth yellow or golden brown, outer tooth reduced.

**THORAX:** Prothorax, pronotum, usually very pale yellow brown surrounded by a paler area, consisting of fused tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe, setal group 1 sometimes bisetose, seta VI sometimes absent, EPp, T, P unisetate, As, and Ps absent, Ss and Es fused and bisetose; Meso and metathorax, Dai and Dae usually fused and bisetose, Dpi unisetate, Dpe and DLai absent, DLpi with a hatching spine and 1 large and 2 much smaller setae, DLae and DLpe fused and bisetose with a single large eversible gland opening on the tubercle, EPa unisetate and bearing a spiracle in the mesothorax, EPp unisetate, T with seta XI absent, P unisetate, As, and Ps absent, Ss and Es unisetate; Legs, 5 segmented, well developed, the same colour as the pronotum, claw tip yellow, claw without inner tooth (PLLI.Fig7 PLL3.Fig25-27)

**ABDOMEN:** 1st-6th abdominal segment, Dai and Dae when present both unisetate, Dpi and Dpe fused and bisetose, DLai and DLpi absent, DLae and DLpe fused and unisetate or bisetose, EPa with spiracle but without seta IX, EPp absent, T and P fused and bisetose, As and Ps fused, unisetate in 1st segment, bisetose in the following segments, Es bisetose in 1st segment, trisetose in following segments, Ss unisetate; 7th abdominal segment, similar to first 6 abdominal segments but tubercles Dpi and Dpe united to form a tubercle fused across the mid-dorsal line, tubercles Dae, Dai, DLai, DLpi absent, Ss and Es fused to form a trisetose ventral plate; 8th abdominal segment, identical to 7th abdominal segment but tubercles Dpi, Dpe, DLae and DLpe united to form a dorsal tubercle fused across

the mid-dorsal line; 9th abdominal segment, tubercles Dpi, Dpe, DLae, DLpe and possibly T and P fused into a large dorsal plate fused across the mid-dorsal line, As, Ps, Ss and Es possibly fused into a ventral plate.

#### Diagnosis.

(Tubercles Dai and Dae unisetate present on abdominal segments 1-6)

(Tubercles Dai and Dae both absent from abdominal segments 1-6 and EPp present).

### GENUS Gastroidea

#### First instar larvae (PLH 9, FIGS. 24 & 25; PLB 7, FIGS. 17 & 18; PLP 7, FIGS 22 & 23)

Colour grey, finely speckled with brown spots. Tubercles pale brown, periphery very pale grey brown. Integument between tubercles with numerous small grey brown chitinated plates. Setae pale brown to very pale grey-brown. HEAD: Oval in anterior view, epicranial stem long, epicranial suture distinct, moderately long, median suture distinct and very dark brown to black, vertex, gena, frons, and antennae yellow brown, vertex with 4 ( $v_1, v_3, v_4, v_6$ ), gena 5, frons 4 ( $f_1, f_3, f_4, f_6$ ) large setae on each side of the head, setae light brown; Ocelli, 6, arrangement similar to that of Chrysolina spp. Antennae, 3-segmented, segments subequal in length, shorter than other Chrysomelinae except Phyllodecta, conical process half the length of the 3rd segment; Clypeus, post-clypeus very slightly darker than the vertex etc., paler below the 3 pairs of setae; Labrum, darker brown, bearing 2 pairs of large setae; Maxilla and Labium, as in Chrysolina sp., maxillary palps 3-segmented, labial palps 2-segmented, Mandibles, 5-dentate, outer tooth reduced, colour as post-clypeus and labrum, teeth yellow. THORAX: Prothorax, pronotum consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLae, pale brown or pale grey-brown surrounded by a paler area, seta VI reduced, VIII sometimes absent, setal group I bisetose, EPp, T and P unisetate, As, and Ps absent, Ss and Es fused, bisetose, Meso and Metathorax, Dai, Dpi, Dae unisetate, Dpe, DLai absent, DLpi same colour as other dorsal tubercles, bearing a hatching spine, one large and

2 small setae, DLae and DLpe fused, bisetose, bearing the opening of a single large eversible gland, EPa with 1-3 setae, bearing in the mesothorax a spiracle, EPP, P, Ss and Es unisetate, T without seta XI, As, and Ps absent; <sup>(PLLI.Fig.6)</sup> Legs, as in other Chrysomelinae, claw without inner <sup>(PLL3Fig.30-31)</sup> tooth. ABDOMEN: 1st-6th abdominal segments, tubercles Dai, DLai, DLpi absent, Dpi and Dpe fused, bisetose, Dae very small, unisetate, tubercles DLae and DLpe fused, unisetate, EPa bearing spiracle but seta IX absent, EPP absent, T and P fused, bisetose, As, and Ps fused, bisetose, Ss bisetose in first segment, trisetose in the following, Es unisetate; 7th abdominal segment, identical with segments 1-6 but tubercles Dpi and Dpe forming a tubercle fused across the mid-dorsal line, Ss and Es fused, bisetose; 8th abdominal segment, identical with segment 7, but tubercles Dpi, Dpe, Dae, DLae, DLpe fused into a dorsal plate, fused across the mid-dorsal line; 9th abdominal segment, dorsal plate formed from Dpi. Dpe, Dae, DLae, DLpe and EPP bearing 3 or 4 large setae, EPP may be separate and unisetate, T, P absent, ventral plate formed by fusion of As, Ps, Ss and Es.

#### Diagnosis.

EPP present, Dai absent in all abdominal segments but Dae present but reduced.

### GENUS Hydrothassa

First instar larvae (PLH9, FIGS. 21 & 22; PLB6, FIGS 15 & 16; PLP 14, FIG. 46)

Colour grey. Light brown tubercles small but distinct and with numerous small grey brown chitinised plates in between.

HEAD: Oval in anterior view, epicranial stem short but epicranial suture as long as Phyllodecta and Phaedon spp., nearly reaching the antennal bases, median sutures very distinct, dark brown, vertex 3 ( $v_1, v_3, v_6$ ) or 4 ( $v_1, v_3, v_4, v_6$ ), gena 5, frons 3 ( $f_3, f_4, f_6$ ) or 4 ( $f_1, f_3, f_4, f_6$ ) large setae on each side of head, setae very pale yellow; Ocelli, arrangement of 6 ocelli on each side of head capsule identical with Chrysolina spp.,



Antennae, 3 segmented, relatively longer than in Chrysolina spp., segments subequal in length, 3rd segment narrower than in Chrysolina spp., and slightly constricted in the middle, conical process half the length of 3rd segment; Clypeus, post clypeus bearing 2 pairs of setae, lighter anterior to the setae; Labrum, darker brown than rest of head, bearing 2 pairs of setae; Maxillae and Labium, similar in structure to Chrysolina spp., Mandibles, more heavily chitinated, 5-dentate, outer tooth reduced, teeth yellow. TH ORAX: Prothorax, Pronotum consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe and sometimes possibly EPp, pale brown very slightly darker than the other tubercles, periphery paler, seta VI sometimes reduced, group I bisetose, T and P unisetate, As and Ps absent, Es and Ss fused and bisetose; Meso and Metathorax, tubercles Dai and Dpi both unisetate, Dae, Dpe and DLai absent, DLpi slightly darker than the other tubercles and bearing a hatching spine, a large and 2 smaller setae, tubercles DLae and DLpe fused and bisetose, bearing the opening of a single large eversible gland, EPa unisetate, bearing a spiracle in the mesothorax, EPp unisetate, T with seta XI absent, P unisetate, As, and Ps absent, Es and Ss both unisetate; (PLL1 Fig.8)

Legs, 5 segmented, well developed and the same colour as the pronotum, claw (PLL3 Fig.28) claw tips yellow, claw without inner tooth. ABDOMEN: 1st-6th abdominal segments, Tubercles Dai, Dae, Dpe, DLai, DLpi absent, Dpi unisetate, DLae and DLpe fused, bearing 1 large and 2 smaller setae, EPa with spiracle but seta IX absent, EPp absent, T and P fused and bisetose, As, and Ps fused, unisetate in the 1st segment, bisetose in the following, Ss bisetose in the 1st segment, trisetose in the following, Es unisetate; 7th abdominal segment, identical with segments 1-6 but Dpi fused across the mid-dorsal line, Ss and Es fused, with 4 setae; 8th abdominal segment, identical with 7th segment but Dpi, DLae and DLpe united and the tubercle fused across the mid-dorsal line, tubercle Ss-Es bisetose; 9th abdominal segment, dorsal tubercle consisting of Dpi, DLae, DLpe, and possibly T and P fused together, bearing 4 large setae, a ventral

tubercle consisting of As, Ps, Ss, and Es fused together.

### Diagnosis.

EPp if absent in Prothorax then seta  $f_1$  on frons also absent. Also seta  $v_4$  on vertex absent.

EPp if present in Prothorax then seta  $f_1$  on frons also present.

Seta  $v_4$  on vertex present. Distinct Dai in all segments present, but tubercle Dae absent.

### GENUS Prasocuris

#### First instar larvae (PLH 6, FIG. 12; PLH 9, FIG. 23; PLB 7, FIGS. 19 & 20a)

Colour grey. Tubercles pale grey brown, indistinct. Between them occur numerous small grey brown chitinised <sup>plates</sup> slightly darker than the tubercles. HEAD: Oval in anterior view, epicranial stem and suture short, as in Hydrothassa spp., median suture dark brown, distinct, vertex with 3 ( $v_1, v_3, v_6$ ), gena 5, frons 4 ( $f_1, f_3, f_4, f_6$ ) large setae on each side of the head, setae very pale grey brown; Ocelli, arrangement of 6 ocelli on each side of the head as with Chrysolina spp., Antennae, 3 segmented, relatively long, as in Hydrothassa, 3rd segment narrow, slightly longer than the other 2 segments, narrowing slightly after the middle, apex with 5 setae, 1 larger than the rest, conical process half the length of the 3rd segment; Clypeus, post-clypeus, slightly lighter than the median suture, bearing 2 pairs of small setae, paler area anterior to the setae; Labrum, same colour as the post clypeus, bearing 2 pairs of setae; Maxillae and Labium, same colour as vertex etc., Maxillary palps 3 segmented, segments shorter than in Hydrothassa sp., labial palps 1 segmented; Mandibles, 5 dentate, outer tooth reduced, same colour as post clypeus in basal half, apical half, including the teeth yellow. THORAX: Prothorax, Pronotum pale grey brown, same colour as other tubercles, consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe and EPp fused together, seta VI sometimes reduced, setal group I bisetose, T, P, **unisetae**, As, and Ps absent, Ss and Es fused, bisetose; Meso and Metathorax,

tubercles Dai and Dpi unisetate, Dae and Dpe apparently absent, DLae absent, DLpi slightly darker than the other tubercles, bearing a hatching spine, 1 small and 2 minute setae, DLae and DLpe fused together, unisetate, bearing the opening of a large eversible gland, EPa unisetate, bearing a spiracle in the mesothorax, EPp unisetate, T without seta XI, P unisetate, As, and Ps absent, Es and Ss both unisetate; Legs, 5-segmented (PLL1Fig9) well developed, slightly darker than the tubercles, claw tip yellow, claw (PLL3.Fig.29) claw without inner tooth. ABDOMEN: 1st abdominal segment, tubercles Dai, Dae, Dpe, DLai, DLpi absent, tubercles DLae, DLpe fused, unisetate, EPa bearing spiracle but seta IX absent, EPp absent, T and P fused, bisetose, As, and Ps fused, but unisetate, Es bisetose, Ss unisetate; 2nd-6th abdominal segment, identical with the 1st segment but tubercle As-Ps bisetose, Es trisetate; 7th abdominal segment, as segments 2-6 but tubercle Dpi fused across the mid-dorsal line, Ss and Es fused, bisetate; 8th abdominal segment, tubercles Dpi, DLae, DLpe united, forming a large dorsal tubercle fused across the mid-dorsal line, bearing 2 large setae, Ss and Es fused, unisetate; 9th abdominal segment, large dorsal plate bearing 5 large and 6 small setae, ventral plate formed by fusion of As, Ps, Ss, and Es, and trisetate.

#### Diagnosis.

Seta  $v_4$  on vertex absent. EPp in prothorax absent but seta  $f_1$  on frons present.

#### GENUS Chrysomela

##### First instar larvae (PLH 1, FIG.2; PLH 10, FIG. 27; PLB 9, FIGS 22&23; PLP 7, FIGS.20&21)

Colour white or cream. Tubercles large, very distinct, light brown, perimeters paler. Setae very pale grey brown. Integument between tubercles on the dorsal surface with small, grey brown chitinised plates less numerous than in other Chrysomelinae. These plates are absent laterally and ventrally. On dorsal and ventral surfaces of abdominal segments 7, 8 and 9, these plates are conical and seta like.

**HEAD:** Spherical in anterior view, epicranial stem and suture long, distinct, median suture black, distinct, vertex, gena, frons, antennae pale brown, vertex  $5(v_1, v_2, v_3, v_4, v_5)$  or  $4(v_1, v_3, v_4, v_5)$ , gena 5, frons  $5(f_1, f_3, f_4, f_5, f_6)$  or  $4(f_1, f_3, f_4, f_6)$  large setae on each side of the head, setae pale yellow; Ocelli, 6 on each side of the head, their arrangement similar to that in Chrysolina sp., Antennae, 3 segmented, relatively shorter than Chrysolina sp., 1st segment broader but shorter than 2 and 3, 3rd segment the largest, bearing 6 small setae at its apex, conical process about half the length of the final segment; Clypeus, post-clypeus, darker brown than the vertex etc. but paler anterior to the 3 pairs of setae; Labrum, same colour as post-clypeus, bearing 2 pairs of setae; Maxillae, palps 3 segmented, relatively shorter than Chrysolina sp., same colour as post-clypeus and labrum, final segment X2 length of 2nd segment; Labium, palps 2 segmented relatively shorter than Chrysolina sp., same colour as post-clypeus and labrum; Mandibles, 5 dentate, basal half dark brown, apical half with teeth golden brown. **THORAX, Prothorax**, Pronotum, same colour as other tubercles, bearing 10 large setae, consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe, setal group I bisetose, seta VI sometimes reduced, EPp with 1 large and 2 small setae, T unisetate, P with 2 large and 1 small seta, As and Ps absent, Ss and Es fused and with 3 large and 1 small seta; Meso and Metathorax, tubercle Dai fused with Dae, bisetose, Dpi fused with Dpe, bisetose, DLai absent, DLpi grey brown, darker than the majority of tubercles, except DLae-DLpe of meso and metathorax, bearing a hatching spine, 1 large, 2 or 3 small and 2 minute setae, DLae and DLpe fused, bearing 3 large setae and the opening of a single large eversible gland, Epa with 3-5 setae, bearing a spiracle in mesothorax, EPp bearing 5-6 setae, T with seta XI absent, P with 2-3 setae, As, and Ps absent, Ss and Es fused, bisetose, rarely trisetate. Legs, claw with inner tooth. (PLLI.Fig.10; PLL3.Fig.23)

**ABDOMEN:** 1st abdominal segment, Tubercles Dai, Dpi, Dae, Dpe, fused to form a single tubercle bearing 2 large and 3 smaller setae, DLai, DLpi absent, DLae and DLpe fused, bearing 2 large, 3-4 small setae, As, and

Ps fused, bearing 2 large, and 2 small setae, Ss bisetate or trisetate, Es unisetate. 2nd-5th abdominal segments, identical with 1st segment but the number of small setae on tubercles As-Ps and Ss is greater; 6th abdominal segment, identical with segments 2-5 but tubercle consisting of Dae, Dpi, Dae, Dpe becoming fused across the mid-dorsal line; 7th abdominal segment, identical with 6th segment, but tubercles Ss and Es fused and forming a large ventral tubercle, 8th abdominal segment, similar to 7th segment but tubercles DLae-DLpe fusing with the large dorsal plate, 9th abdominal segment, similar to 8th segment but EPa absent, As, Ps, Ss and Es fusing into a ventral plate.

#### Diagnosis.

Seta  $f_2$  on frons absent but  $f_1$  present. EPp present. T-P separate and trisetate in 9th abdominal segment. Dai or Dae not separate in abdominal segment.

#### GENUS Plagiodera (P. versicolora (Laich.))

#### First instar larvae (PLH 10, FIG. 26; PLB 9, FIG. 21)

Colour dull white. Dorsal and lateral tubercles pale yellow brown. Pronotum, DLpi and DLae-DLpe, very slightly darker. Ventral tubercles pale grey yellow. Setae very pale grey brown. Integument between tubercles with numerous small pale brown chitinised plates.

HEAD: Oval in anterior view, yellow brown, epicranial stem long, epicranial suture short, median suture dark brown distinct, vertex 5 ( $v_1, v_2, v_3, v_4, v_6$ ), gena 5, frons 3 ( $f_3, f_4, f_6$ ), large setae on each side of the head; Ocelli, 6 arranged as in Chrysolina sp. Antennae, conical 3 segmented, short, final segment the shortest; Clypeus, post-clypeus bearing 3 pairs of minute setae; Labrum, bearing 2 pairs of setae; Maxillae, palps 3 segmented; Labium, palps 2 segmented; Mandibles, 5 dentate, outer tooth reduced. THORAX: Prothorax, Pronotum consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe, bearing 9 large setae, setal group 1 bisetose, EPp small, unisetate,

T and P unisetate, As, and Ps absent, Es and Ss fused and bisetose;

Meso and Metathorax, Dai, unisetate, Dpi fused with Dpe, bisetose, seta

IV reduced, Dae, DLai absent, DLpi bearing a hatching spine 1 large,

and 2 minute setae, DLae and DLpe fused, bisetose, bearing the opening

of single large eversible glands, EPa bearing 1 large and 2 small setae

and a spiracle in the mesothorax, EPp bearing 1 large and 1 small setae,

T with seta XI absent, P unisetate, As and Ps absent, Ss and Es separate,

(PLLI.Fig.II; PLL3Fig.24)

unisetate. Legs, claw without inner tooth. ABDOMEN: 1st abdominal

segment, Dai and Dpi possibly fused, bisetose, Dae, Dpe, DLai, DLpi

absent, DLae, DLpe fused, bisetose, EPa bearing spiracle but seta IX

absent, EPp absent, T and P fused, bearing 1 large, 1 small and 2 minute

setae, As, and Ps fused, bisetose.

#### Diagnosis

Setae  $f_1$  and  $f_2$  on frons absent. Setae  $v_1 - v_6$  present on vertex.

## IX. SUBFAMILY LAMPROSOMATINAE

Lamprosoma (Late instar larva of L. chorisae Monros)(PLH24.Figs.96;99, PLB29.Fig.29)

Larva bearing a cornet-shaped case, narrowed and curved posteriorly.

Posterior abdominal segments curved ventrally. Tubercles and setae indistinct.

HEAD: Oval in anterior view, pale brown, epicranial stem long, epicranial suture long, almost reaching the antennal bases, median suture absent, vertex bearing 6 setae ( $v_1-v_6$ ), frons pale brown with a yellow circular area ventral to the junction of the 2 arms of the epicranial suture, frons bearing 6 setae ( $f_1-f_6$ ) on each side of the head, gena bearing 18 setae; Ocelli, 5, arranged as in PLH33 Fig.96; Antennae, very short, 2 segmented, accessory conical process present and 2nd segment bearing 1 long and about 4 <sup>short</sup> apical setae; Fronto-clypeal suture distinct; Clypeo-labral suture indistinct; Clypeus, bearing 6 pairs of setae, Labrum bearing 4 pairs of setae along the ventral margin; Maxilla, cardo bearing 2 setae, stipes bearing 2 large and 7 small setae; maxillary palps, short, 3 segmented, segments subequal in length; lacinia present bearing 2 short, stout setae, galea bearing 12 large setae; Labium, submentum bearing 1 pair of large setae, mentum bearing 3 pairs of large setae, labial palps short 2 segments; Mandibles, 2 dentate, with a distinct ventral ridge. THORAX: Prothorax, Pronotum bearing numerous (42) long setae in the anterior half, EPp probably absent, T unisetate, P bisetate, As, Ps probably absent, Ss large, fused across the mid ventral line, bearing 18 setae, Es indistinct but probably bearing 12 setae; Meso and Metathorax, tubercles Dai, Dae, Dpi, Dpe, DLai, DLpi, DLae and DLpe present probably indistinct, unisetate, setae II and IV well developed, EPa very large, bearing approximately 20 setae and a spiracle in the mesothorax, EPp probably unisetate, T indistinct, P bisetate, As, Ps probably absent, Ss and Es indistinct, represented by approximately 20 setae. Legs, well developed. ABDOMEN: segments 1-8, setae I-VIII probably present but tubercles less distinct than in thorax, setae I-IV well developed on segments 6,7,8; DLae, DLpe represented by

numerous setae, EPa, EPp absent, T and P represented by numerous setae, As, Ps probably present, bearing 5 setae, Ss and Es indistinct, represented by approximately 8 setae; 9th segment with a large dorsal plate bearing numerous setae, ventrally bearing approximately 17 setae; 10th segment bearing approximately 12 setae.

The above description of a late instar larva of L.chorisiae was made from material in the British Museum. It does not completely agree with the description of L.chorisiae given by Monros (1949). Monros described the head bearing only 4 pairs of ocelli but it is probable that he missed a pair of ocelli situated posteriorly on the gena.

The larva of Oomorphus concolor Sturm was described by Kasap and Crowson (1976). The description was made from one late instar larva. The larva possessed 5 ocelli on one side of the head which Kasap and Crowson consider represents the basic number, whereas there were only 3 on the other side. The antennae were exceptionally long and consisted of 3 segments. Segments 1 and 2 were more elongate than the 3rd segment. Segment one possessed 2 campaniform sensillae and segment 2 had a long conical sensory appendix. The 3rd segment possessed a strong articulated seta apically, a long slender outgrowth and 3 setae, 2 dorsally and one ventrally. The morphology and chaetotaxy of the head agrees with my and Monros's description of L.chorisiae. However, L.chorisiae has a short 2 segmented antenna, whilst the antennae are long and 3 segmented in O.concolor. This is further evidence for the removal of Lamprosoma concolor from the genus Lamprosoma and the valid generic name for this species is Oomorphus.



## X. SUBFAMILY GALERUCINAE

GENUS Lochmaea

First instar larvae (PLH 14, FIGS. 39-41; PLH 16, FIGS. 43 a, b, c; PLH 17, FIG. 44 b; PLH 18, FIGS. 46 a, b, c; PLB 14, FIGS. 37-39; PLP 8, FIGS. 26 & 27.)

Colour white, cream, pale yellow. Tubercles very pale grey brown to pale brown. Integument between tubercles with numerous small circular very pale grey chitinated plates. Setae very pale grey yellow, those on the dorsal, dorsolateral and epipleural tubercles with knobbed or truncate apices. HEAD: Oval in anterior view, epicranial stem long, epicranial suture very long, distinct, median suture dark brown or black, vertex, gena, frons, yellow brown or pale yellow brown, vertex  $4(v_2v_3v_4v_6)$  or  $3(v_2v_4v_6)$  large setae, gena 2 large and 1 small setae, frons 3 ( $f_1, f_3, f_6$ ) large setae, present on each side of the head; Ocelli, one, postero-dorsal to antenna; Antennae, short, one-segmented; Clypeus, post-clypeus with 4 pairs of small setae; Labrum with 2 pairs of large setae, normally post-clypeus and labrum the same colour as the vertex etc; Maxillae, palps 3 segmented, segments subequal in length, sometimes 3rd segment clearly the longest; Labium, palps 2 segmented; Mandibles, 5 dentate, basal part more heavily chitinated, teeth orange or orange yellow, outer and inner teeth reduced, 3rd or middle tooth the longest, with or without penicillus. THORAX: Prothorax, Pronotum pale brown or pale grey brown bearing 8-9 setae, consisting of tubercles  $Dai, Dpi, Dae, Dpe$

$DLai, DLae, DLpe$ , seta VI absent, setal group I bisetose, setal group I sometimes trisetose, EPP bearing 2-5 setae, T and P unisetate, As and Ps absent, Ss and Es fused and bisetose; Meso and Metathorax, Dai usually absent, when present fused with Dpe and trisetose, Dpi absent, Dae, Dpe, unisetate, DLai present but seta V absent, DLpi unisetate, DLae and DLpe fused, trisetate, EPa unisetate, bearing a spiracle in mesothorax, EPP unisetate or bisetose, T with seta XI absent, P unisetate, As and Ps absent, Ss and Es both unisetate; Legs, well developed, as for Agelastica, claw with pulcillus. ABDOMEN: 1st abdominal

segment, Dai and Dpi usually absent, when present Dai fused with Dae and bisetose, Dae, Dpe, DLai, DLpi, unisetate, DLae absent, DLpe unisetate or bisetose, EPa with seta IX absent but spiracle present, EPp absent, T and P fused, bisetose, As and Ps fused bisetose, Ss bisetose, Es unisetate; 2nd-7th abdominal segment usually identical with first segment but tubercle DLae sometimes present anterior to EPa; 8th abdominal segment, identical with segments 2-7, but tubercle DLpi fused with Dpe and bisetose; 9th abdominal segment, dorsal plate bearing 5-7 large setae, ventral plate bisetose, 10th abdominal segment, a ventral anal plate bearing 10-11 minute setae.

#### GENUS Sermyla (S. halensis (L.))

First instar larvae (PLH 11, FIG. 30; PLH 15, FIG. 42C; PLH 17, FIG. 45b; PLH 18, FIG. 46i; PLB 11, FIG. 25; PLP 9, FIG. 31)

Colour white or cream. Tubercles pale yellow brown, integument between tubercles without chitinised plates. Setae pale yellow. Segmental pores present on all thoracic segments and abdominal segments 1-9, posterior to P in prothorax, dorsal to DLae, DLpe on other segments. HEAD: Spherical in anterior view, epicranial stem long, epicranial suture long, distinct, median suture distinct, medium to dark brown, vertex, gena, frons, yellow brown bearing long pale grey yellow setae, vertex 4, ( $v_2 v_3 v_4 v_6$ ), gena 5, frons ( $f_1, f_3, f_4, f_6$ ), large setae present on each half of the head; Ocelli, absent; Antennae, short, one-segmented, apex with approximately 10 sensillae, accessory conical process as long as the first segment; Clypeus, post-clypeus, anterior darker part with 3 pairs of small setae; Labrum, bearing 2 pairs of large setae, same colour as vertex etc., Maxillae, palps 3 segmented, 3rd segment the longest; Labium, palps 2 segmented; Mandibles, slightly darker than the rest of the head, 5 dentate, outer tooth very reduced, penicillus well developed. THORAX: Prothorax, Pronotum pale yellow brown slightly darker than other tubercles, consisting of tubercles Dai, Dpi, Dae, Dpe, DLai, DLpi, DLae, DLpe, all setae I-VIII present, setal group I bisetose,

Epa distinct, EPp unisetate, T, P, unisetate, As, Ps absent, Ss and Es fused, bisetose; Meso and Metathorax, Dai and Dae fused, bisetose, Dpi and Dpe fused, bisetose, DLai without seta V, DLpi trisetate, DLae and DLpe fused, trisetate, EPA unisetate, bearing spiracle in mesothorax, EPp unisetate, T without seta XI, P unisetate, As, Ps absent, Ss, Es, unisetate; Legs, as Agelastica, claw with pulvillus.

ABDOMEN: 1st abdominal segment, Dai usually unisetate, rarely bisetose, Dpi absent, Dae unisetate, not fused across mid-dorsal line and median to Dai and Dpe, Dpe, DLai, DLpi, DLae, DLpe unisetate, DLae dorso anterior to EPA, EPA bearing a spiracle but seta IX absent, EPp absent, T and P fused, bisetose, As and Ps fused, bisetose, Ss bisetose, rarely trisetose, Es unisetate; 2nd-7th abdominal segments, identical with 1st but a new tubercle bearing a minute seta present anterior to Ss; 8th segment, as 2-7 but Dpe and DLpi fused, bisetose; 9th segment, dorsal plate bearing 7 large setae, consisting of tubercles Dai, Dae, Dpe, DLai, DLpi, DLae and DLpe fused together, EPA, EPp, T, P, absent, ventral plate trisetate, consisting of tubercles As, Ps, Ss and Es fused together; 10th segment, ventral anal plate bearing 13 minute setae.

#### GENUS Phyllobrotica (P. quadrimaculata (L.))

First Instar larvae ( PLH 11, FIG. 29; PLH 15, FIG. 42d; PLH 17, FIG. 45c; PLH 18, FIG. 46g; PLB 11, FIG. 26; PLP 8, FIG. 25 )

Colour creamy white. Tubercles indistinct, composed of many small, very pale cream grey plates. Integument between tubercles with numerous colourless plates similar to those composing the tubercles. Setae colourless to pale yellow, spindle-like or club-shaped in dorsal and epi pleural regions.

HEAD: Oval in anterior view, epicranial stem moderately long, epicranial suture long, distinct, median suture yellow brown, only slightly darker than the rest of the head, vertex, gena and frons yellow brown, vertex  $4(\sqrt{v_2 v_3 v_4 v_6})$   $v_3$  reduced ), gena 5, frons 3 ( $f_1, f_3, f_6$ ) large setae present on each side of the head; Ocelli, absent; Antennae, short, 2 segmented, 2nd antennal

segment reduced, lying postero-dorsal to accessory conical process, conical process as long as 1st segment, 1st segment bearing at its apex 11 sensillae interior to conical process; Clypeus, post-clypeus with 4 pairs of small setae; Labrum, with 2 pairs of setae, post clypeus and labrum same colour as median suture; Maxillae, palps, short, conical; 3 segmented, 2nd segment the shortest; Labium, palps 2 segmented, 2nd segment clearly the longest; Mandibles, dark yellow, 5 dentate, inner and outer teeth reduced, 3rd middle tooth the largest, penicillus well developed. THORAX: Prothorax, Pronotum very pale cream grey bearing 11 setae, setae I-VIII present, setal group I bisetose, possibly setal groups VII and VIII also bisetose, EPp, T, P unisetate, As, and Ps absent, Ss and Es fused, bisetose;

; Meso and

metathorax, Dai and Dae fused, bisetose, Dpi and Dpe fused, bisetose, DLai without seta V, DLpi trisetate, DLae and DLpe fused, trisetate, EPa unisetate, bearing a spiracle in the mesothorax, EPp unisetate, T with seta XI <sup>(PLL2Fig.17)</sup> absent, P unisetate, As, and Ps <sup>(PLL3Fig.35)</sup> absent, Ss and Es both unisetate; Legs, as Agelastica, claw with pulvillus. ABDOMEN:

1st-7th abdominal segments, Dai unisetate, Dae unisetate, moved into median position between Dai and Dpe and fused across mid-dorsal line, Dpi absent, Dpe, DLai, DLpi, unisetate, DLae unisetate, anterior to EPa, DLpe unisetate, EPa without seta IX but bearing a spiracle, EPp absent, T and P fused, bisetose, As, and Ps fused, bisetose, Ss bisetose, Es unisetate; 8th segment, identical with segments 1-7 but DLpi fused with Dpe which becomes bisetose, Ss tending towards fusion with Dpe which becomes bisetose, Ss tending towards fusion across the mid-ventral line; 9th segment, dorsal plate bearing 7 large setae, consisting of tubercles Dai, Dae, Dpe, DLai, DLpi, DLae, DLpe, tubercles, EPa, EPp, T, P, As Ps absent, tubercles Ss and Es fused into a bisetose ventral plate; 10th segment, a ventral anal plate bearing 8 minute setae.

# GENUS Luperus

First Instar larvae (PLH 13, FIGS. 35 & 36; PLH 15, FIG. 42e; PLH 17, FIG. 45a; PLH 18, FIG. 46h.)  
PLB 11, FIG. 27 & 28.

Colour white, very narrow, elongate. Tubercles colourless to very pale yellow, bearing colourless setae. Integument between tubercles without chitinated plates.

HEAD: Oval in anterior view, epicranial stem long, epicranial suture long, distinct, median suture indistinct, same colour as rest of head, vertex, gena and frons pale yellow, bearing very pale yellow setae,

Vertex  $4(v_2, v_3, v_4, v_6, v_3 \text{ reduced})$ , gena 2 large, 3 small, frons 1 minute ( $f_2$ )  
 $3(f_1, f_3, f_6)$  large setae present on each side of the head; Ocelli:

absent; Antennae, comparatively long, one segmented, accessory conical process large, as long as the first segment; Clypeus, post-clypeus

with 4 pairs of minute setae; Labrum with 2 pairs of setae, post clypeus and labrum same colour as rest of head; Maxillae, palps well developed 3 segmented, segments subequal in length; Labium, palps 2 segmented;

Mandibles, 5 dentate, slightly darker, especially the teeth, inner and outer teeth very reduced, middle tooth the longest, penicillus well

developed. THORAX: Prothorax, Pronotum colourless or very pale yellow, bearing 7 large setae, setae I, II, III, IV, V, VII, VIII probably present, seta VI absent,

EPp unisetate, T, P, unisetate, As, Ps, absent, Ss and Es fused,

bisetose; Meso and Metathorax, setae I and II absent, hence tubercles

Dai, Dpi, absent, Dae and Dpe both unisetate, both fused across the mid-dorsal line, DLai without seta V, DLpi with 1 large, 2 small and 1 minute seta, DLae and DLpe fused, with 1 large and 2 small setae,

EPa unisetate, bearing a spiracle in mesothorax, EPp unisetate, T with seta XI absent, P unisetate, As and Ps absent, Ss and Es both unisetate.

ABDOMEN: 1st-7th abdominal segments, Dai unisetate fused across the mid-dorsal line, Dpi absent, Dae unisetate, fused across mid-dorsal line or separate and median to Dai and Dpe, Dpe unisetate, fused across mid-dorsal line, DLai, DLpi, DLae unisetate, DLpe with one large and one small seta, EPa bearing spiracle but seta IX absent, EPp absent,

T and P fused, bisetose, As, and Ps fused and bisetose, Ss bisetose, Es unisetate; 8th segment, identical with 1-7 segments but Dpe and DLpi fused and bisetose; 9th segment, dorsal plate bearing 4 large, 2 small setae, with total of approximately 125 sensory pores, ventral plate bisetose.

### GENUS Galerucella

First instar larvae (PLH 12, FIGS. 33 & 34; PLH 13, FIGS. 37, 38a, b; PLH 16, FIGS. 4.3d-g; PLH 17, FIGS. 4.4a; PLH 18 FIGS. 4.5 d-f; PLB 12, FIGS. 29-31; PLB 13, FIGS. 34-36; PLP 19, FIGS. 28 & 30.)

Colour cream or yellow. Tubercles pale yellow brown or pale brown with perimeters paler. Integument between tubercles usually bearing numerous small pale grey brown chitinised plates. Setae pale grey yellow or light brown. HEAD: Oval in anterior view, epicranial stem short or long, epicranial suture short to long, distinct, median suture dark brown to black, distinct, vertex, gena, and frons pale yellow to pale brown, vertex  $2(v_2v_6)$ ,  $3(v_2v_4v_6)$ , or  $4(v_2v_3v_4v_6; v_3 \text{ reduced})$ , gena 2-4, frons 3 ( $f_1, f_3, f_6$ ), large setae present on each side of the head; Ocelli, one postero-dorsal to antennae; Antennae, short, one-segmented, apex with approximately 11 sensillae, accessory conical process as long as 1st segment; Clypeus, post-clypeus with 4 pairs of small setae; Labrum, with 2 pairs of large setae anterior part of post-clypeus and labrum same colour as vertex etc.; Maxillae, palps 2 or 3 segmented, usually 3; Labium, palps 2 segmented, maxillae and labra paler than elsewhere; Mandibles, 5 dentate, more yellow than rest of head, inner and outer teeth reduced, penicillus present. THORAX, Prothorax, Pronotum pale yellow brown or pale brown with perimeter paler, setae I, II, III, IV, V, VII, VIII, probably present, seta VI absent, setal group I sometimes bisetose, EPp bisetose or trisetose, T and P unisetate, As, and Ps absent, Ss and Es fused, bisetose, Meso and Metathorax, setae I and II absent, hence tubercles Dal, Dpi, absent, Dae, Dpe unisetate, DLai without seta V, DLpi unisetate, sometimes Dae fused with DLai and Dpe fused with DLpi,

DLae and DLpe fused, trisetate, EPa unisetate, bearing a spiracle in mesothorax, EPp unisetate, T without seta XI, P unisetate, As, and Ps absent, Ss and Es both unisetate; Legs, as Agelastica, (PLL3Fig4.0) claw with pulvillus.

ABDOMEN: 1st-7th abdominal segments, setae I and II absent, hence tubercles Dai, Dpi, absent, Dae, Dpe, DLae, DLpi unisetate, sometimes Dae fused with DLai and Dpe fused with DLpi, DLae usually absent, sometimes present anterior to EPa and unisetate, DLpe unisetate, Epa with seta IX absent, but spiracle present, EPp absent, T and P fused, bisetate, As, and Ps fused, bisetate, Ss bisetose, Es unisetate; 8th segment, identical with segments 1-7 but tubercles Dpe and DLpi fused, bisetose; 9th segment, a dorsal plate bearing 5 setae, possibly consisting of tubercles Dae, Dpe, DLai, DLpi, DLae, DLpe, tubercles EPa, EPp, T, P, absent, a bisetose ventral plate consisting of tubercles As-Ps, Ss and Es.

#### GENUS Agelastica (A. alni (L.))

Final instar larvae (PLH 12, FIG 31, PLH 15, FIG 42a; PLH 17, FIG 45d; PLH 18, FIG 46j; PLB 13, FIG 32; PLP 8, FIG. 24)

Colour uniformly brown. Tubercles yellow brown, nearly the same colour as integument. Tubercles and integument covered by very fine brown spots and numerous larger brown spots which are aggregations of the finer spots. The larger spots have a tendency to be raised. Setae are very pale grey yellow. HEAD: Spherical in anterior view, epicranial stem moderately long, epicranial suture long and distinct, median suture dark brown to black, very distinct, vertex, gena and frons light brown, vertex 5, ( $v_2 v_3 v_4 v_5 v_6$ ), gena 5, 4 large, 1 small, frons 3, ( $f_1, f_3, f_6$ ) setae present on each side of the head, Ocelli, one, postero-dorsal to the antennae; Antennae, short 2 segmented, 2nd antennal segment (homologous with 3rd of Chrysomelinae) less broad and shorter than the accessory conical process, 2nd segment interior and slightly dorsal to the conical process and with 3 sensillae; Clypeus, post-clypeus, with 2 or 3 pairs of small setae; Labrum, with 2 pairs of setae, anterior part of post-clypeus and labrum darker brown than

the rest of the head capsule; Maxillae, palps, short, conical 3 segmented concealed by mandibles, 2nd segment the shortest, other segments subequal; Labium, palps 2 segmented; Mandibles, golden brown, apparently 4-dentate, inner and outer teeth reduced, penicillus absent. THORAX: Prothorax, Pronotum yellow brown, same colour as other tubercles, bearing 9 large and 7 much smaller setae, setae I-VIII are present, setal group V bisetose, EPP, T, P unisetate, As and Ps absent, Ss and Es fused, bisetose; Meso and Metathorax, Dai and Dae fused, bisetose, also with 5 much smaller setae, Dpi and Dpe fused, bisetose, also with 3 small setae, DLai bearing 4-5 minute setae, DLpi bisetose, DLae and DLpe fused, bearing 7 large, 5-6 minute setae, EPa with 1 large and 5-8 minute setae, in mesothorax also bearing spiracle, EPP unisetate, T with seta XI absent, P unisetate, As, and Ps difficult to distinguish as many minute setae and tubercles occur in the sternal region, setae XV and XVI on tubercles Ss and Es can be distinguished; Legs, well(PLL2Fig.13) developed, claw with pulvillus. ABDOMEN: 1st-7th abdominal segments, Dai and Dae fused, bisetose, also with 6 minute setae, Dpi and Dpe fused, bisetose, also bearing 3 minute setae, DLai and DLpi both unisetate, DLae and DLpe fused together but also with EPa bearing the spiracle, the resulting tubercle bearing 2-3 large, 2-6 minute setae, and the single apertures of large glands, a very small unisetate tubercle, possibly EPP lies posterior to this large tubercle, T and P fused, bearing 3-4 large and 6 minute setae, As, and Ps fused, bearing 2 large and 4-9 minute setae, Ss usually bisetose, Es unisetate, tubercles Ss and Es indistinct and surrounded by many minute setae; 8th segment, identical with segments 1-7 but DLpi fused with Dpi-Dpe, becoming trisetate. 9th segment, dorsal plate consisting of tubercles Dai, Dae, Dpi, Dpe, DLai, DLpi and bearing 6 large setae and 4 small setae; ventral plate probably T, P, As, Ps, Ss and Es fused together and bearing 4 large setae.



GENUS Galeruca(G. tanacetii (L.))

Final instar larvae (PLH 12, FIG 33; PLH 15, FIG 42b; PLH 18 FIG 46K; PLB 13, FIG 33)

Colour light brown, paler ventrally. Tubercles paler than the surrounding integument. Tubercles and integument speckled with dark brown-black spinules.

HEAD: Spherical in anterior view, epicranial stem long, black, epicranial suture long, distinct, median suture dark brown to black, distinct, frons, vertex, gena, post clypeus, labrum, light brown, vertex 4 ( $v_2, v_3, v_4, v_6$ ),

gena 5, frons 4 ( $f_1, f_3, f_4, f_6$ ) large setae on each side of the head;

Ocelli, one postero-dorsal to antennae, Antennae, short, one segmented;

Clypeus, post clypeus bearing 4 pairs of setae, paler anterior to setae,

Labrum, bearing 2 pairs of setae posteriorly and 2 pairs on the anterior

margin; Maxillae, paler, palps 3 segmented, 2nd and 3rd segments equal

in length, lacinia distinct; Labium, paler, palps 2 segmented; Mandibles,

5 dentate, penicillus absent, THORAX: Prothorax, Pronotum bearing numerous long setae (approximately 25) along its anterior and ventral edges which

are raised, bearing 3 distinct raised tubercles bearing 5-7 large setae each at its posterior edge, tubercles homologous with Dpi-Dpe, and DLpi,

EPp large bearing 8 setae, T bearing 9 setae, P with 4-6 setae, As, Ps

absent, Ss and Es fused, bearing 6 setae; Meso and Metathorax, Tubercle

Dai absent or possibly fused with Dae, bearing 5-8 setae, Tubercle Dpi

absent or possibly fused with Dpe, bearing 5-6 setae, DLae and DLpe fused,

bearing 10-11 setae, DLai with 2-5 setae, DLpi bearing 7-9 setae,

EPa with 3-6 setae and bearing a spiracle in mesothorax, EPp bearing

6 setae, T with 1 large and 2 smaller setae, P bearing 5 setae, As, and

Ps possibly absent or possibly represented by 2 minute unisetate

tubercles dorsal to Ss, Ss fused across midventral line, bearing 9

setae, Es unisetate; Legs, well-developed darker brown than body, claw(PLL3Fig.36)

tip yellow, pulvilli present, coxa, femur, tibia equal length.

ABDOMEN: 1st-7th abdominal segments, Tubercle Dai possibly fused with

Dae, bearing 5 setae, Dpi possibly fused with Dpe, bearing 5 setae, DLai with 4 setae, DLpi with 6 setae, DLae and DLpe fused, bearing 7 setae, EPa bearing spiracle but without setae, EPP absent, T and P fused, bearing 9 setae, As, and Ps fused, bearing 6 setae, Ss bearing 7 setae, Es possibly divided into 2 tubercles, a larger dorsal one bearing 5 setae, and a small unisetate ventral tubercle; 8th segment, identical with segments 1-7 but Dai-Dae fused across mid-dorsal line, bearing 4 setae, Dpi-Dpe fused across the mid-dorsal line, also 2 tubercles comprising Es tending to be united; 9th segment, a dorsal plate, bearing 10 large setae, consisting of tubercles Dai, Dae, Dpi, Dpe, DLai, DLpi, tubercles EPa, EPP, T, and P possibly absent, As, and Ps fused, bisetate, Ss and Es fused, bearing 2 unisetate papillae.

SUBFAMILY HALTICINAEGENUS HalticaFirst instar larvae (PLH 19, FIG. 47; PLB 15, FIGS 40 & 41; PLB 16, FIGS 42 & 43; PLP 10, FIGS 32 & 33)

Colour white or grey brown, body elongate, tubercles pale brown, as distinct ventrally as dorsally. Integument between tubercles bearing paler sparse round chitinised plates. Setae clear grey yellow.

HEAD: pale brown, oval in anterior view, apicranial stem short, epicranial suture moderately long, median suture distinct, vertex bearing 4 ( $v_2 v_3 v_4 v_6$ ) gena 4, frons 3 ( $f_1 f_3 f_6$ ) large setae on each side of the head, setae grey yellow; Ocelli: absent, Antennae, paler brown, short, first segment short but broad, pill-box shape, bearing an accessory conical process as long as the first segment and the second antennal segment shorter than the accessory process; Post-clypeus: bearing 3 pairs of setae; Labrum: darker brown, bearing 2 pairs of large setae dorsally and 6 pairs of setae along the ventral edge; Mandibles: darker brown, broad, 5-dentate, teeth golden brown, inner tooth reduced, penicillus or mesial tuft well developed; Maxillae: maxillary palps 3 segmented, paler brown, all segments subequal in length, lacinia present, galea well developed, bearing 10 setae; Labium: labial palps 2-segmented, paler brown. THORAX: Prothorax, pronotum light brown, very slightly darker than other tubercles bearing 8 or 9 primary setae, seta VI sometimes absent, setal group I bisetose, EPp, T, P unisetate, As, and Ps absent, Ss and Es fused and bisetose.

Meso and Metathorax: tubercles Dai and Dpi absent, tubercles Dae and Dpe unisetate, tending towards fusion across the mid-dorsal line, tubercle DLai distinct but seta 5 absent, tubercle DLpi same colour as pronotum, bisetose, bearing a single hatching spine, rarely two, DLae and DLpe fused and trisetose, EPa unisetate, bearing a spiracle in mesothorax, EPp unisetate, T without seta 11, P unisetate, As and Ps absent, Ss and Es unisetate; Legs: well developed, slightly darker brown than the tubercles, claw tips yellow, pulvilli present (Fig. 41).

ABDOMEN: 1st-7th abdominal segments, tubercles Dai, Dpi absent, tubercles Dae, Dpe, DLai, DLpi, DLae, DLpe unisetate, Epa bearing spiracle but seta 9 absent, T and P fused, bisetose, As and Ps fused bisetose, Ss unisetate, Es bisetose; 8th abdominal segment, as first 7 segments, but tubercles Dpe and DLpi fused and bisetose; 9th abdominal segment, tubercles Dae, Dpe, DLai, DLae and DLpe fused into a large dorsal plate bearing 5 large and 5 small setae, a ventral plate possibly formed by the fusion of Es and Ss, bearing 2 large and 1 minute seta; 10th abdominal segment, a ventral plate bearing 12 minute setae.

#### GENUS Psylliodes

First instar larvae (PLH 21, FIG 53; PLB 18, FIGS. 4.7 & 4.8.)

Body elongate, narrow, parallel-sided, cream or white. Tubercles very pale grey or pale grey brown, ventral tubercles as dark as dorsal tubercles. Integument between tubercles bearing numerous very small very pale grey brown circular chitinised plates.

HEAD: elongate oval in anterior view, pale brown, same colour as dorsal plate of 9th abdominal segment, epicranial stem moderately long, epicranial suture long, broad, clear, median suture distinct, vertex bearing 4 ( $v_2, v_3, v_4, v_6, v_3$  reduced), gena 4, frons 3 large ( $f_1, f_3, f_6$ )

1 small ( $f_2$ ) setae on each side of the head; Ocelli: absent, Antennae: cream, short, first segment pill-box shaped, bearing a large accessory conical process, second segment inconspicuous, represented by 2 setae;

Post-clypeus, bearing 4 pairs of setae; Labrum, <sup>usually</sup> bearing 2 pairs of large setae dorsally, and 6 pairs of large setae along ventral edge,

Mandibles, 5-dentate, inner and outer teeth reduced; Maxillae,

maxillary palps, cream, long, 3-segmented. THORAX: Prothorax, pronotum, colour as other tubercles or darker, usually bearing 7 large setae,

seta VI absent, setal groups I and II sometimes bisetose, EPP unisetate, T and P unisetate, As and Ps absent, Ss and Es fused, bisetose.

Meso and Metathorax, as Haltica sp. tubercle DLpi bearing a hatching spine in some species; Legs, quite well developed, pale grey brown, slightly darker or the same colour as the tubercles, claws with pulvilli. ABDOMEN: 1st-8th abdominal segments; tubercle Dai present, otherwise identical to Haltica, sometimes tubercle Dpe fused with DLpi in 8th segment only; 9th abdominal segment, a large dorsal plate bearing 5 large setae, 2 small setae and a sensory pore, posterior edge with or without a sickle-shaped protuberance, ventral plate bearing 2 large setae.

Psylliodes affinis PLB18 Fig. 48.

DLpi bearing a hatching spine in the meso and metathorax, DLpi fused with Dpe in 8th abdominal segment only, posterior edge of dorsal plate on 9th abdominal segment not bearing a pair of sickle shaped protuberances.

Psylliodes napi PLB. Fig. 47.

DLpi without hatching spine, DLpi not fused with Dpe in 8th abdominal segment, posterior edge of dorsal plate on 9th abdominal segment bearing a pair of sickle-shaped protuberances.

#### GENUS Hippuriphila (PLH 20, FIG. 50; PLB 19, FIG. 50)

HEAD: as Psylliodes, epicranial stem slightly shorter, epicranial suture, broad, clear, median suture broad, very distinct, vertex bearing 2 large ( $v_2, v_6$ ), 2 small ( $v_3, v_4$ ), gena 2 large, 2 small, frons 3 large ( $f_1, f_3, f_6$ ) setae on each side of the head; Ocelli, absent; Antennae, Psylliodes-like; Post-clypeus, Labrum, Mandibles, Maxillae as Psylliodes; Labium, labial palps 2 segmented, long. Thorax: Pro, meso and metathorax as Haltica sp. Legs, well developed as in Haltica. Abdomen: as Psylliodes sp., but dorsal tubercles not fused across mid-dorsal line.

GENUS Hermaphysa (PLH 19, FIG. 48; PIB 19, FIG. 49)

HEAD: as Psylliodes, epicranial suture less broad and less distinct as is the median suture, vertex bearing 4 large ( $v_2, v_3, v_4, v_6$ ), gena 4 large, frons 3 large ( $f_1, f_3, f_6$ ) and 1 small ( $f_2$ ) setae on each side of the head; Ocelli, absent; Antennae, Psylliodes-like; remainder as Psylliodes. Thorax: pro, meso and metathorax as Haltica sp. Legs well developed as in Haltica. Abdomen as Haltica sp.

GENUS Mantura (PLH 20, FIG. 51; PIB 19, FIG. 51)

HEAD: broader and more dorso-ventrally flattened than in Haltica, Psylliodes, Hippuriphila etc., epicranial stem very short, epicranial suture very broad and clear, median suture very broad, dark, vertex bearing 3 large ( $v_2, v_4, v_6$ ) and 1 small ( $v_3$ ), gena 4 large, frons 3 large ( $f_1, f_3, f_6$ ) setae on each side of the head, Ocelli, one large ocellus posterior to the antennae; Antennae, Psylliodes-like, Post-clypeus, Labrum and Mandibles as Psylliodes, Maxillae, maxillary palps 3 segmented, galea bearing a 2 segmented appendage, Labium, labial palps short, one segmented. THORAX: Prothorax, as Haltica. Meso and Metathorax, as Haltica but tubercle DLai absent, tubercle DLpi without hatching spine, tubercles Ss and Es fused together and across mid ventral line. Legs, well developed as in Haltica. Abdomen: as Haltica, but dorsal tubercles not fused across mid-dorsal line. 8th segment, tubercle Dpe absent, DLpi unisetate fused across mid-dorsal line. 9th segment, a dorsal plate bearing 4 large and 1 small seta, a ventral bisetose plate.

GENUS Apteropoda { PLH 20, FIG. 52; PIB 20, FIG. 52 }  
FLP. 14, FIG. 47

HEAD: as Mantura, vertex bearing 2 large ( $v_2, v_6$ ) and 2 small ( $v_3, v_4$ ) gena 2 large, frons 3 large ( $f_1, f_3, f_6$ ) setae on each side of the head; Ocelli, one large ocellus posterior to the antennae;

Antennae, Psylliodes-like; Post-clypeus, Labrum, Mandibles, Maxillae, as Psylliodes; THORAX: Prothorax, pronotum bearing 10 large setae, setae I-VIII present, setal groups I and II bisetose, EPp, unisetate, large, anterior to the lateral edge of the pronotum, otherwise as Haltica; Meso and Metathorax, tubercles Dai and Dpi probably present, Dai unisetate, large in the mesothorax, reduced in the metathorax, tubercles Dae, Dpe, DLai, DLpi very reduced, unisetate, DLpi without hatching spine, DLae, DLpe fused, large, trisetate, EPa bearing spiracle in mesothorax but seta 9 absent, EPa absent in metathorax, EPp unisetate, very reduced, T without seta 11, P unisetate, As and Ps absent, Ss and Es very reduced, unisetate; Legs, well developed as in Haltica. Abdomen: 1st-8th segments, as Psylliodes, but tubercles very reduced in size, dorsal tubercles not fused across mid-dorsal line, As-Ps bearing a single seta, seta XVI absent ; 9th segment, dorsal plate absent but 5 unisetate tubercles present, probably Dpe, DLai, DLpi, DLae, DLpe, 2 ventral tubercles.

GENUS Longitarsus (PLH 19, FIG 4.9; PLB 17, FIG 4.6b)

HEAD: as Psylliodes, but narrower, epicranial stem short, vertex bearing 3 large ( $v_2, v_4, v_6$ ) , gena 4 large, frons 3 large ( $f_1, f_3, f_6$ ) 1 small ( $f_2$ ) setae on each side of the head; Ocelli, absent; Antennae, Post-clypeus, Labrum, Mandibles, Maxillae, Labium, as Psylliodes. THORAX: as Psylliodes, DLpi in meso and metathorax bearing hatching spine. Abdomen: 1st-8th segments, as Psylliodes, 9th segment, a dorsal plate bearing 6 large setae and 2 sensory pores, a ventral bisetose plate. Legs, well developed, as in Haltica.

GENUS Chalcoides PLB 17 Fig. 46a

Similar to Longitarsus . Hatching spines present.

GENUS Derocrepis PLB I7, Fig. 45

Tubercle arrangement and chaetotaxy similar to Luperus longicornis as the three dorsal abdominal tubercles are fused across the mid-dorsal line and each bear a total of 2 large setae each.

GENUS Phyllotreta PLB I7, Fig. 44

Similar to Longitarsus but Es and Ss fused in meso and metathorax and apparently tubercle Dai not fused across mid-dorsal line in abdominal segments I-8.

GENUS Chaetocnema

Similar to Longitarsus.

GENUS Crepidodera

Similar to Hermaeophaga.

Hatching spines in first instar larvae.

Table I4 shows the occurrence of hatching spines in Halticinae species.



E. Larval Instar Number in the Chrysomelidae (PLH 31 and 32 Figs. 77-95 )

Zeugophorinae - 4 instars occur in Z. subspinos

Criocerinae - 4 instars occur in Lema puncticollis

Cryptocephalinae - 4 instars occur in Cryptocephalus parvulus, labiatus  
and pusillus

Chrysomelinae - 4 instars occur in Chrysolina and Phytodecta

3 instars occur in Phyllodecta, Gastroidea, Hydrothassa,  
Prasocuris, Phaedon, Chrysomela

Galerucinae - 3 instars occur in Sermyla, Phyllobrotica, Galerucella,  
Lochmaea

Halticinae - 3 instars occur in Haltica, Apteropeda, Mantura, Hippuriphila

Cassidinae - 5 instars occur in Cassida

Growth is according to Dyars Rule (Dyar, 1890) which can be expressed  
as the equation:  $y = k.p^n$  where:-

y = the length of any measured part (in this case head capsule width)

n = number of ecdyses

k.p are constant, p being the progression factor (Dyar's Factor)

The law is upheld as straight lines were obtained on plotting the  
logarithm of head capsule width (microns) against the number of ecdyses.

$\bar{X}$  Head capsule width (mm.) and growth ratios for each species shown in PLH 31  
and PLH 32, Figs. 77-95 are listed in TABLE 4.

LIST OF ABBREVIATIONS USED IN THE FOLLOWING LARVAL FIGS.

A	ANTENNA
I A	FIRST ABDOMINAL SEGMENT
8 A	EIGHTH II II
C	COXA
cd	CARDO
F	FEMUR
Ff	FAECAL FORK
gl	GALEA
H	HEAD
Hs	HATCHING SPINE
L	LABRUM
Lb	LABIUM
lc	LACINIA
M	MAXILLA
Mst	MESOTHORAX
Mtt	METATHORAX
m	MENTUM
Oc	OCELLUS
P	ACCESSORY CONICAL PROCESS
Pc	POSTCLYPEUS
Pen.	PENICILLUS
Pr-t	PROTHORAX
Pu	PULVILLUS
p	PALP
Sp	SPIRACLE
sm	SUBMENTUM
st	STIPES
S	SCOLUS
T	TIBIA
Tr	TROCHANTER
Ta	TARSUNGULUS

TIMARCHA

CHRYSOMELA

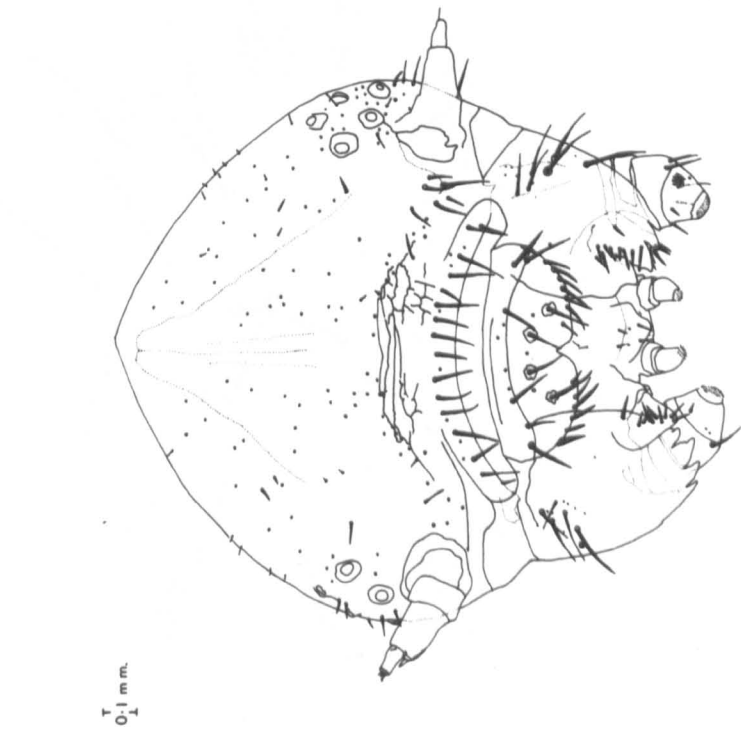


Fig. 1 T. tenebricosa (F.)

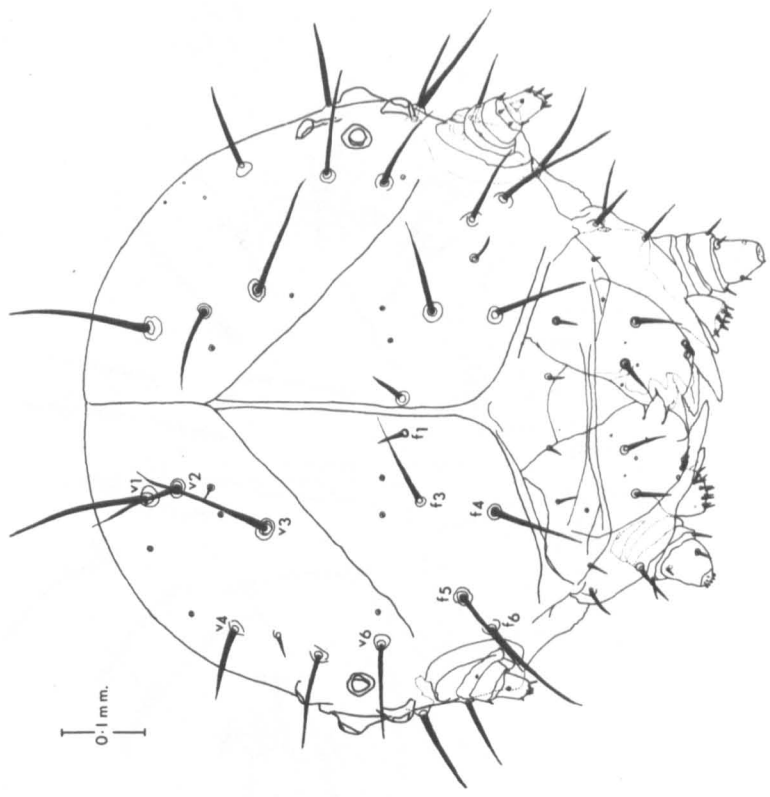


Fig. 2 C. populi L.

PLATE LH2    CHRYSOMELINAE    LARVAL HEADS

CHRYSOLINA    FIRST INSTAR

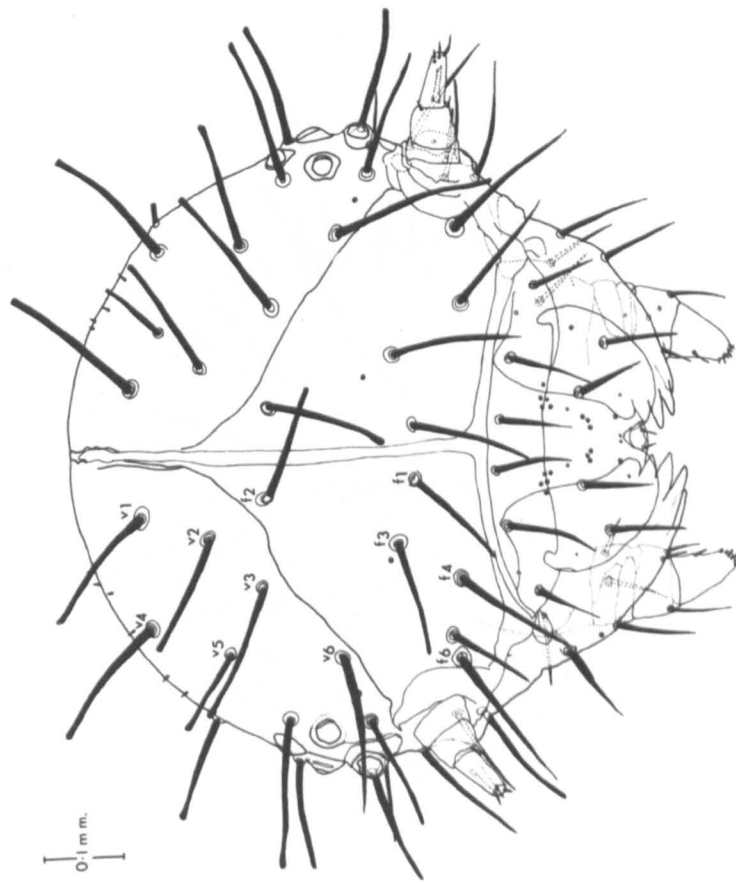


Fig. 3    *C. staphylea* (L.)

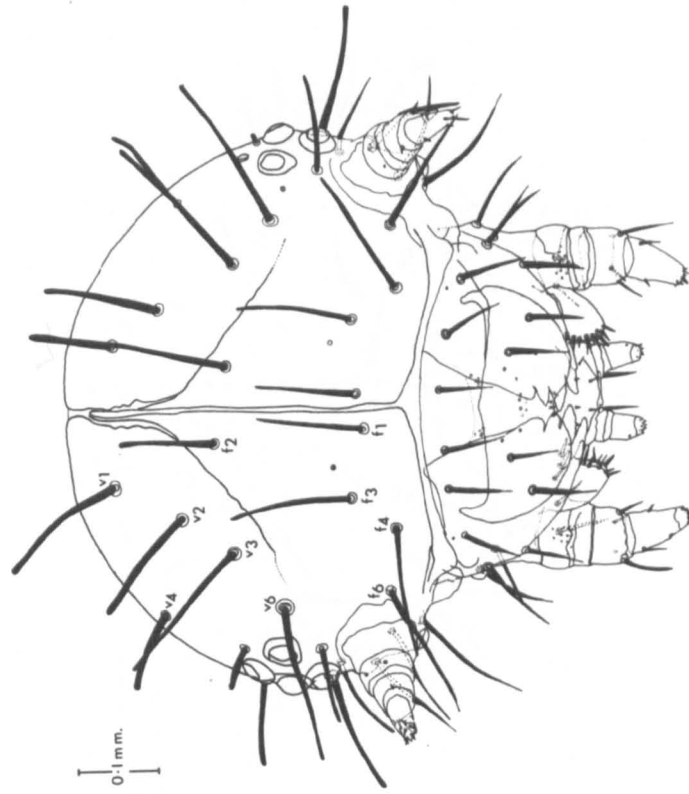


Fig. 4    *C. polita* (L.)

## PLATE LH3

CHRYSOMELINAE

## LARVAL HEADS

CHRY SOLINA

FIRST INSTAR

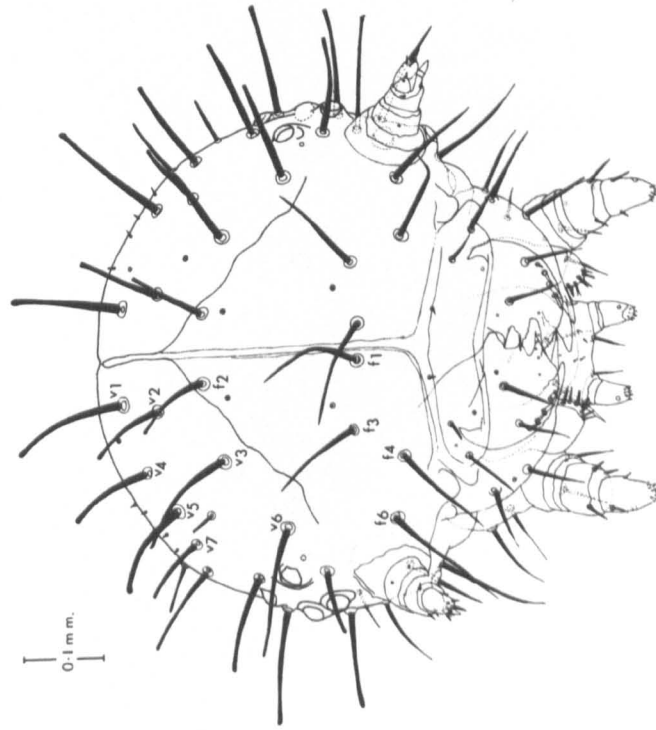
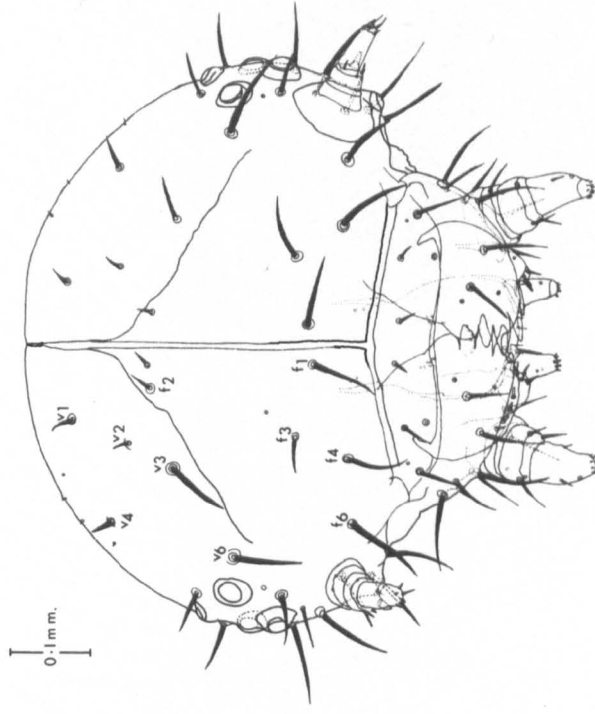


Fig. 5 C. fastuosa (Scop.)



**Fig. 6** C. menthastri (Suf.)

PLATE LH4    CHRYSOMELINAE    LARVAL HEAD CHAETOTAXY    FIRST INSTAR

CHRYSOLINA

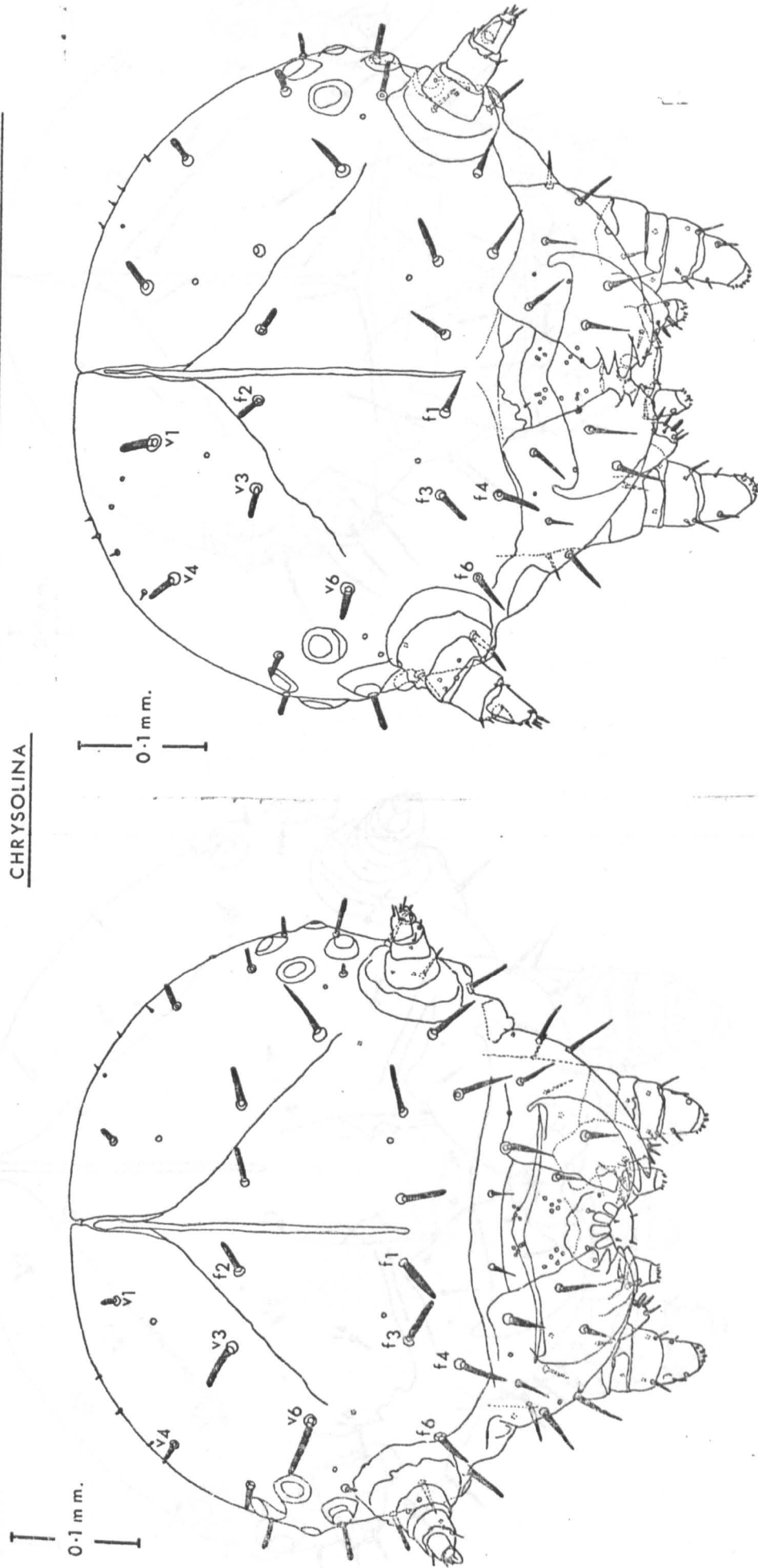


FIG. 7. *C. hyperici* (Forst.)

FIG. 8. *C. brunsvicensis* (Gr.)

CHRYSolINA

0.1 mm.

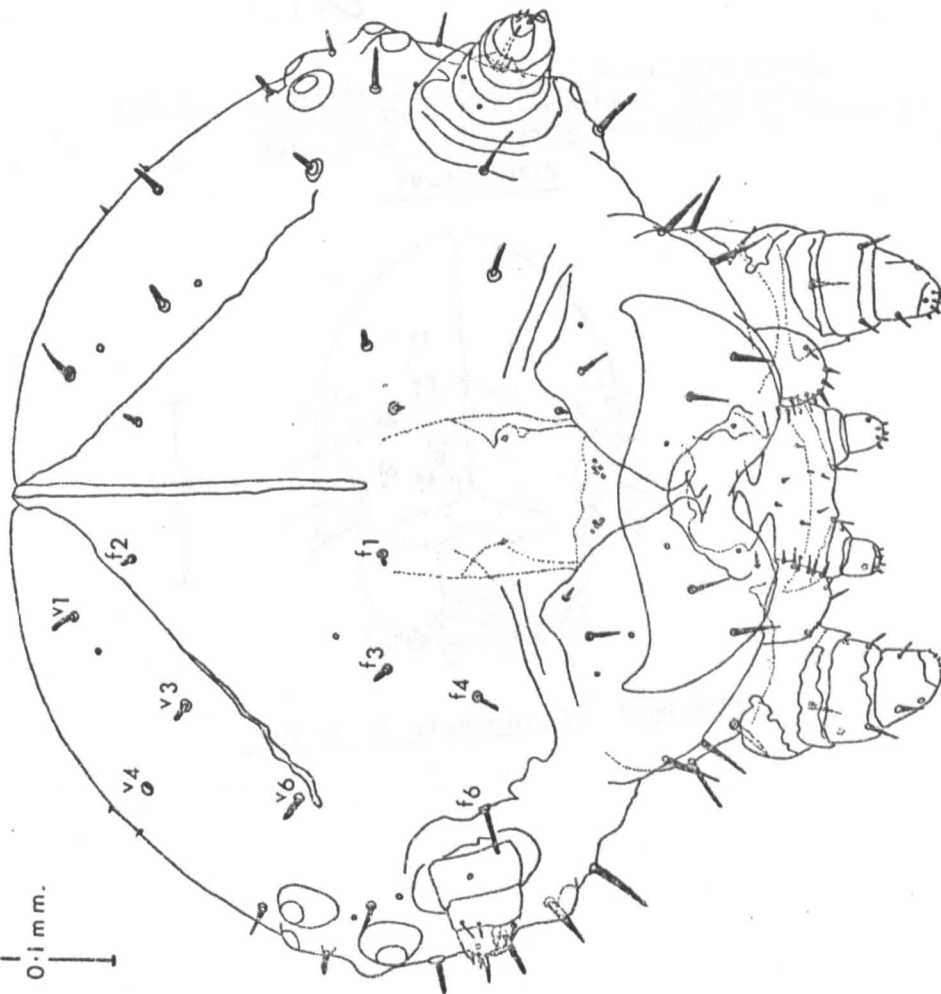


FIG. 9 *C. varians* (Schal.)

0.1 mm.



FIG. 10 *C. graminis* (L.)

PLATE LH6   LARVAL HEAD CHAETOTAXY

PHYTODECTA

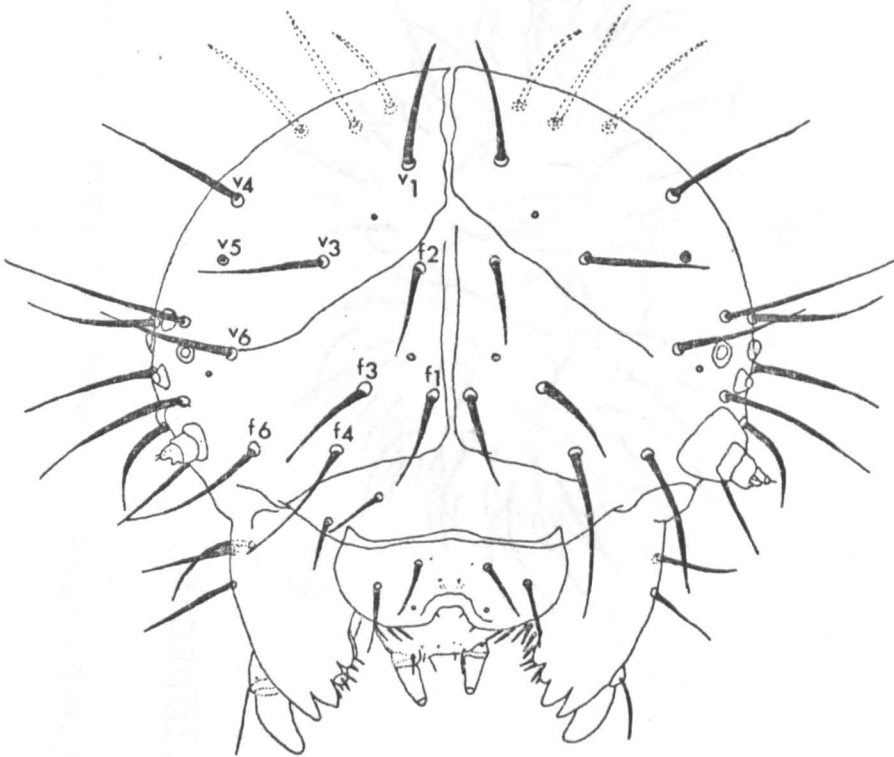


FIG. 11   *P. pallida* (L.) & *P. olivacea* (Forst.) First instar  
*P. rufipes* (De G.) & *P. viminalis* (L.) Final instar  
Extra setae in *P. olivacea* (Forst.) shown by broken line

PRASOCURIS

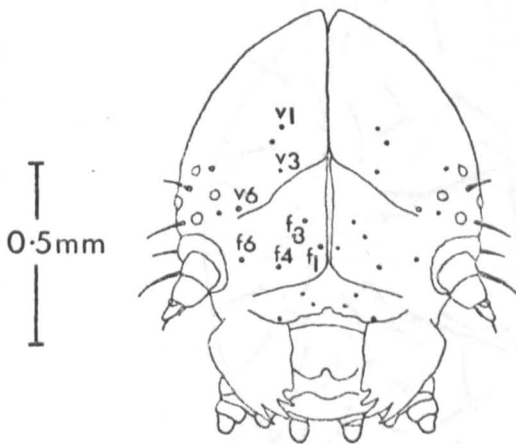


FIG. 12   *P. phellandrii* (L.) Final instar



PHYTODECTA

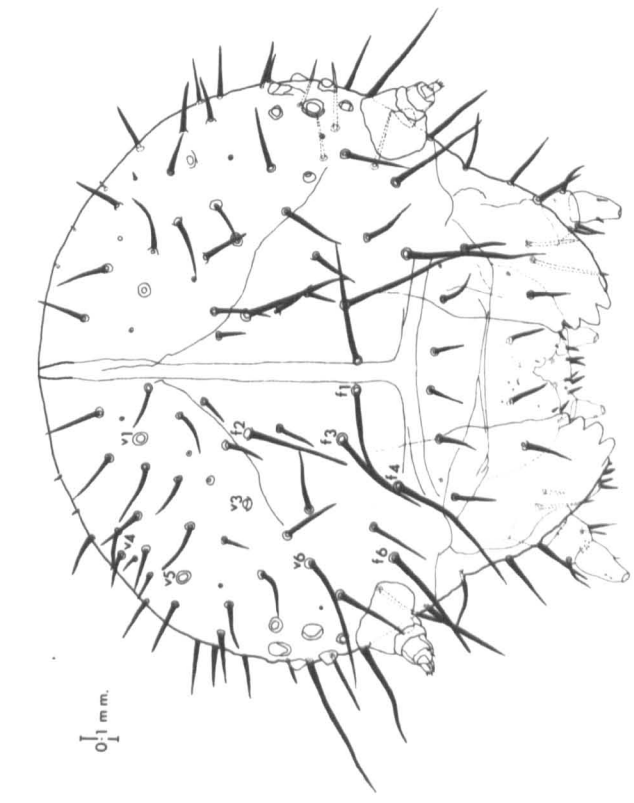


Fig. 13 *P. pallida* (L.)



Fig. 14 *P. olivacea* (Forst.)

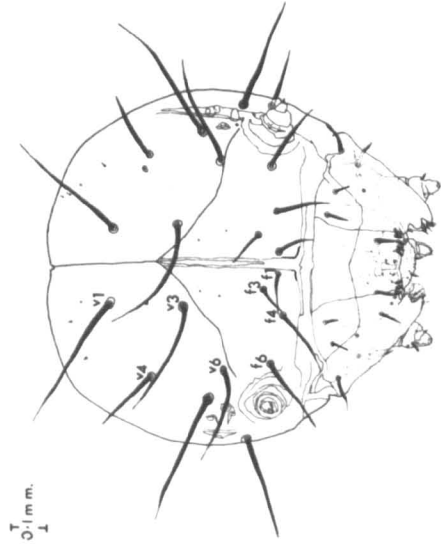


Fig. 15 *P. vitellinae* (L.)

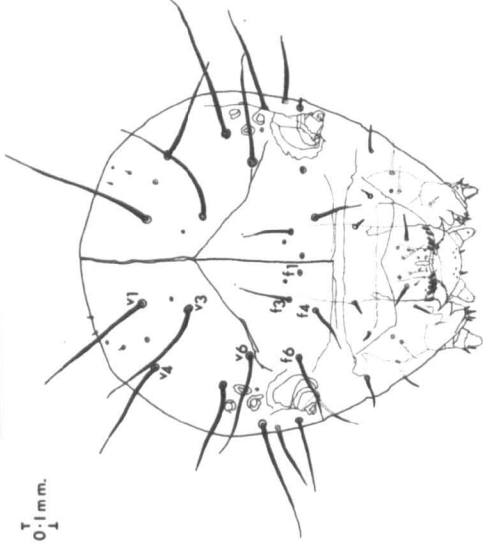


Fig. 16 *P. vulgatissima* (L.)



Fig. 17 *P. laticollis* Suf.

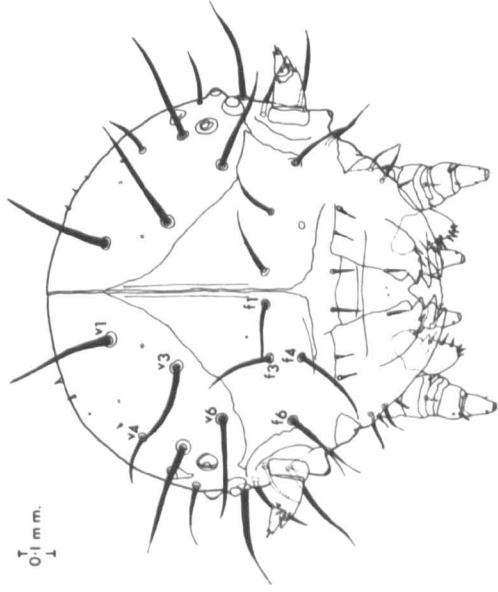


Fig. 18 *P. armoraciae* (L.)

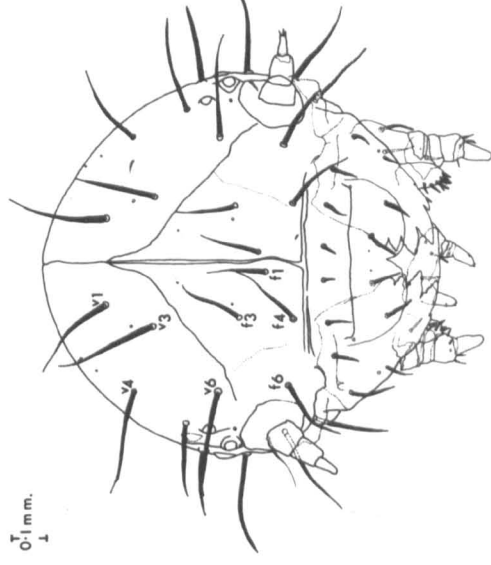


Fig. 19 *P. tumidulus* (Germ.)

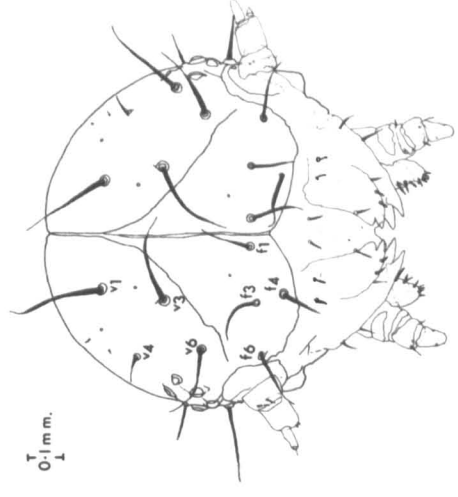


Fig. 20 *P. cochleariae* (F.)

PLATE LH9  
HYDROTHASSA

CHRYSMELINAE

LARVAL HEAD CHAETOTAXY  
FINAL INSTARS

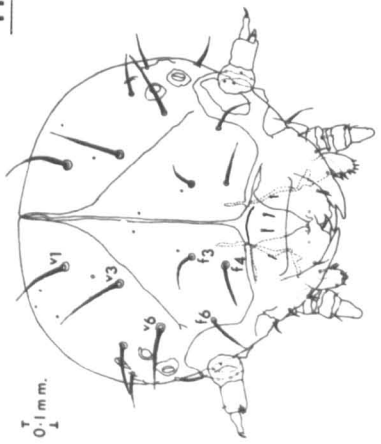


Fig. 21 *H. marginella* (L.)

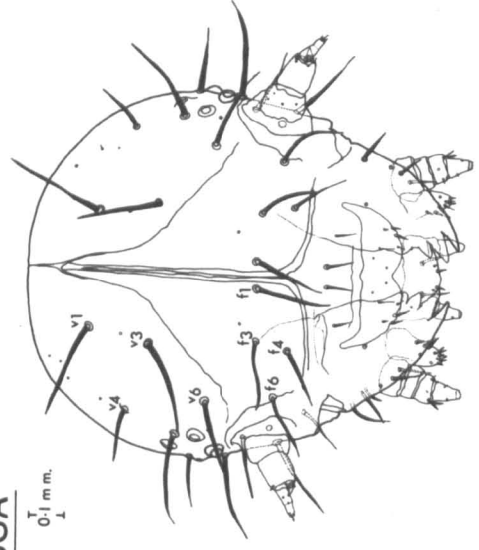


Fig. 22

*H. aucta* (L.)

GASTROIDEA

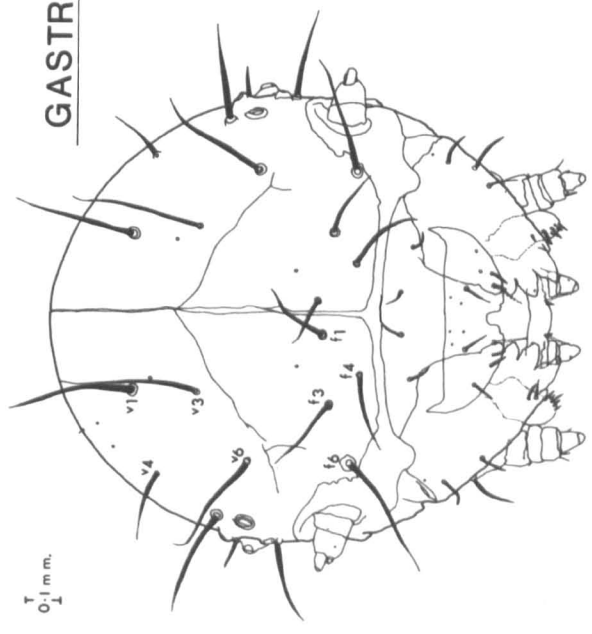


Fig. 24 *G. viridula* (De G.)

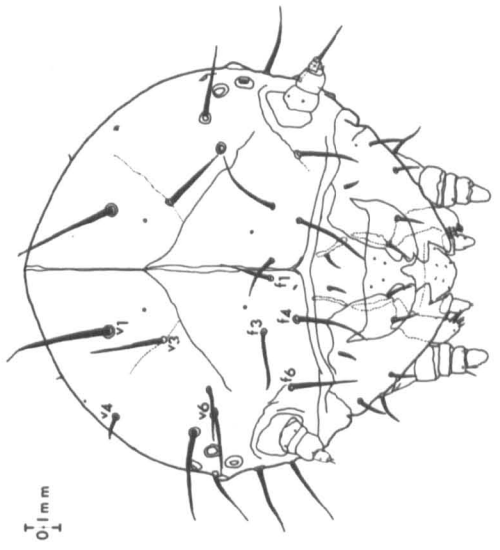


Fig. 25 *G. polygoni* (L.)

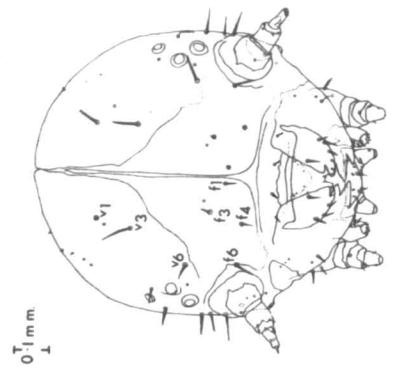
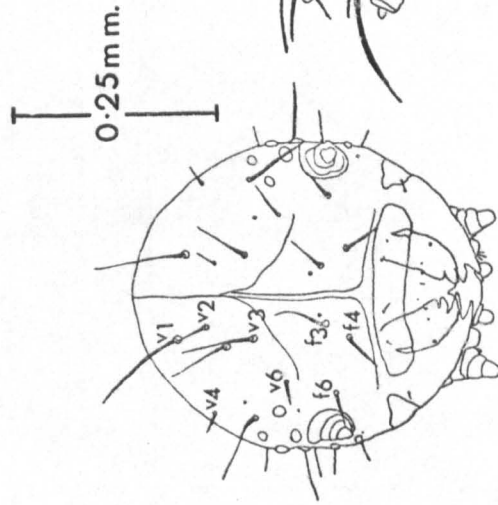


Fig. 23 *Prasocuris junci* (Brahm.)

PLATE LH10
CHRYSMELINAE
LARVAL HEAD
CHAETOTAXY

PLAGIODERA



CHRYSMELA

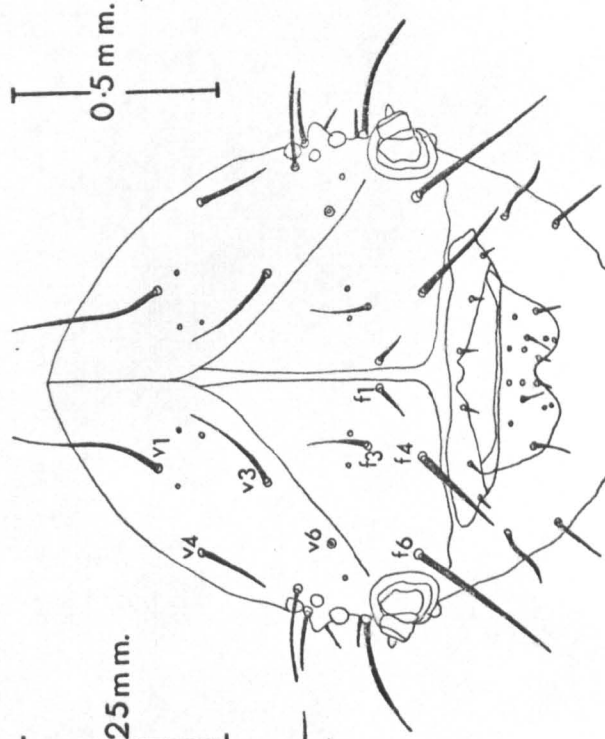


FIG. 26 P. versicolora (Laich.)  
First instar

FIG. 27 C. aenea L.  
Final instar

LEPTINOTARSA

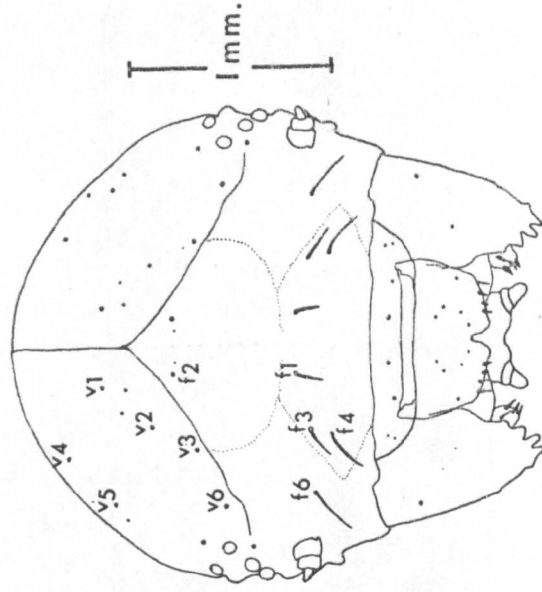


FIG. 28 L. decemlineata (Say.)  
Final instar

PHYLLOBROTICA

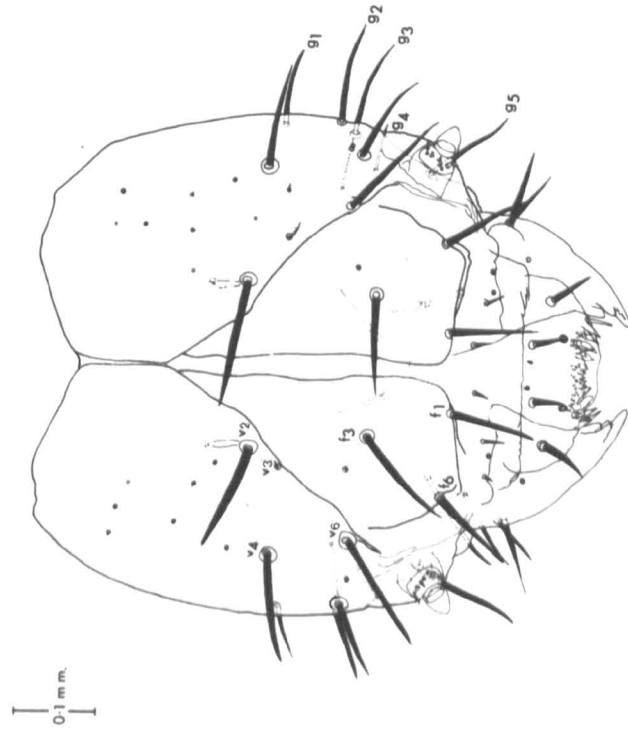


Fig. 29 *P. quadrimaculata* (L.)

Second instar

SERMYLA

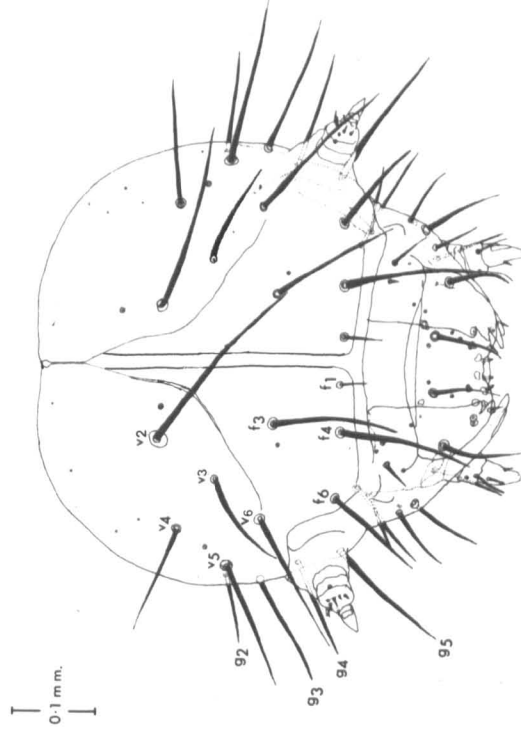


Fig. 30 *S. halensis* (L.)

First instar

PLATE LH12 GALERUCINAE

HEAD CHAETOTAXY

FINAL INSTAR LARVAE

AGELASTICA

GALERUCELLA

GALERUCELLA

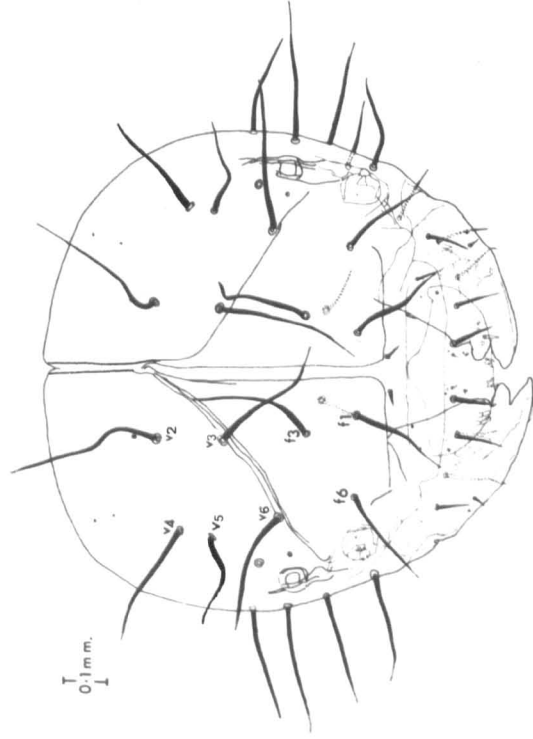


Fig. 31 A. alni (L.)

GALERUCA

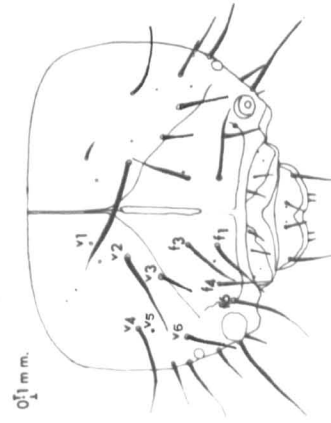


Fig.32 G. tanacetii (L.)

Mouthparts

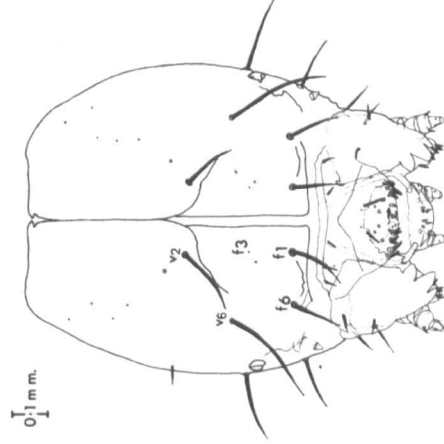
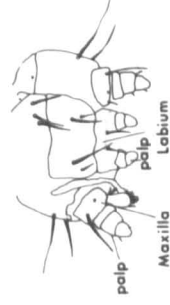


Fig.33 G. lineola (F.)

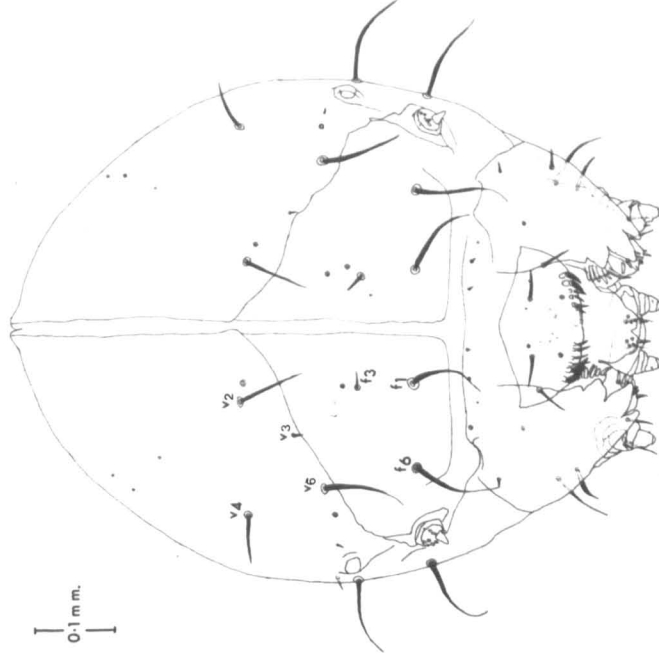


Fig.34 G. sagittariae Brit. Cat.

Second instar

LUPERUS

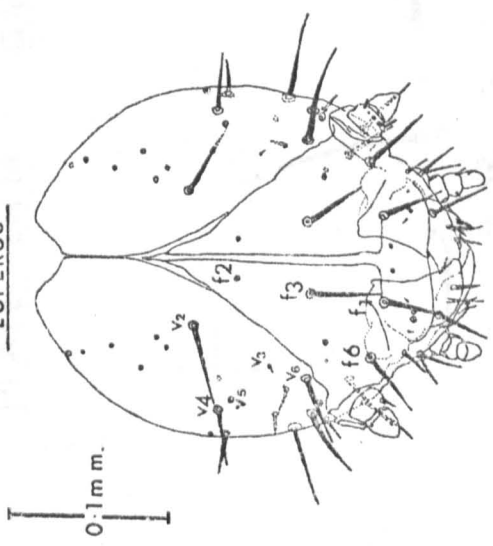


FIG. 35 *L. flavipes* L.

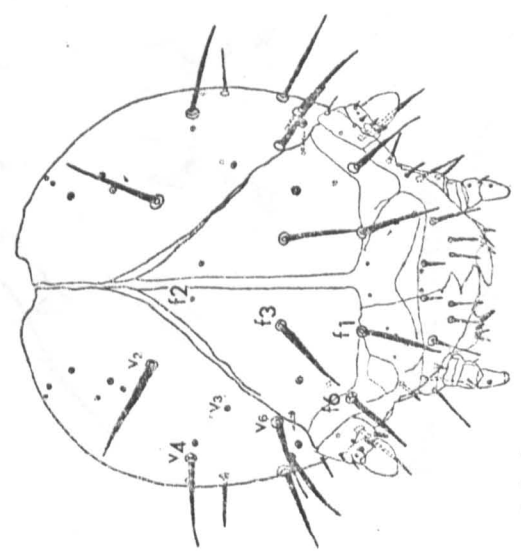


FIG. 36 *L. longicornis* F.

GALERUCELLA

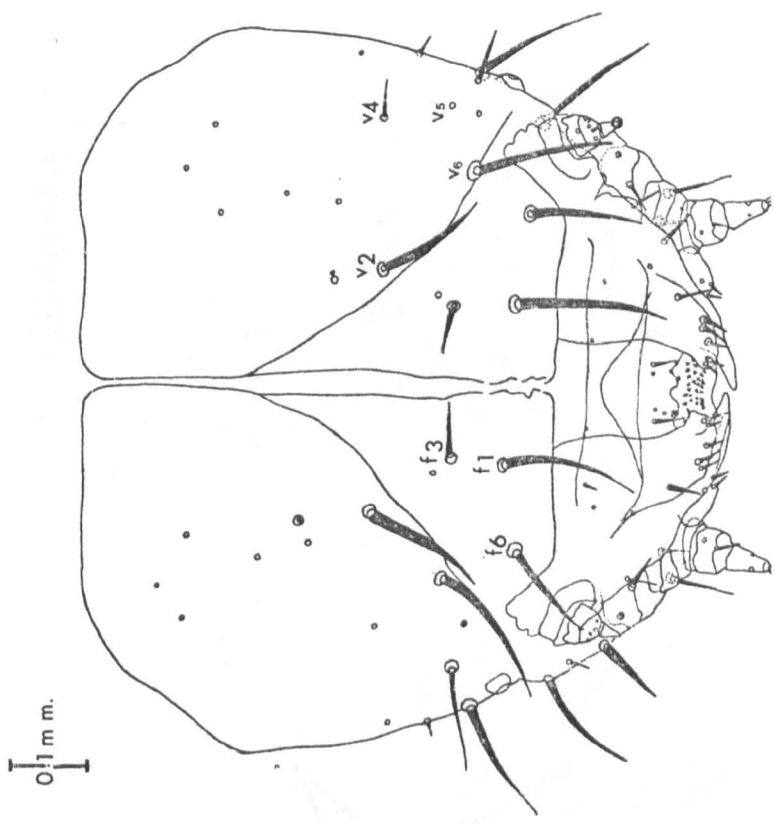
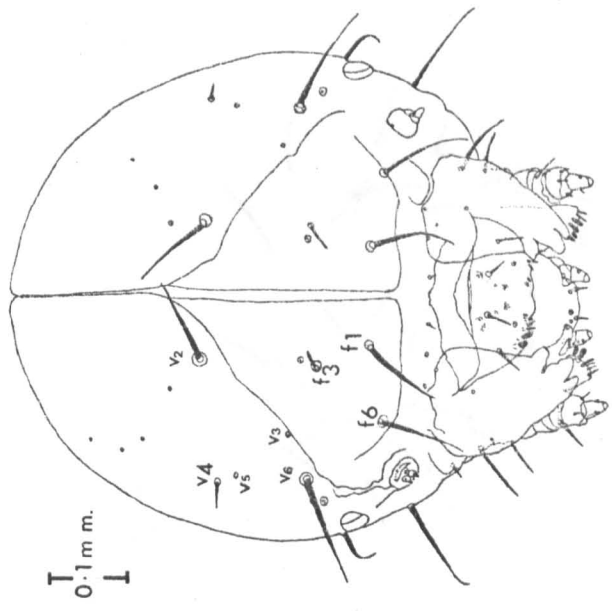
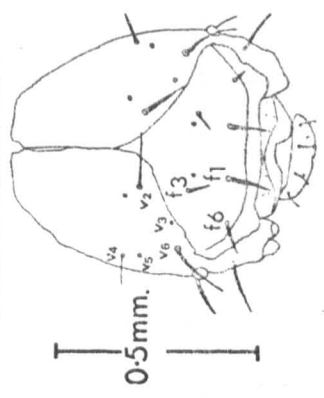


FIG. 37 *G. viburni* (Pk.)

FIG. 38 a *G. tenella* (L.)



b. *G. californiensis* (L.)



LOCHMAEA

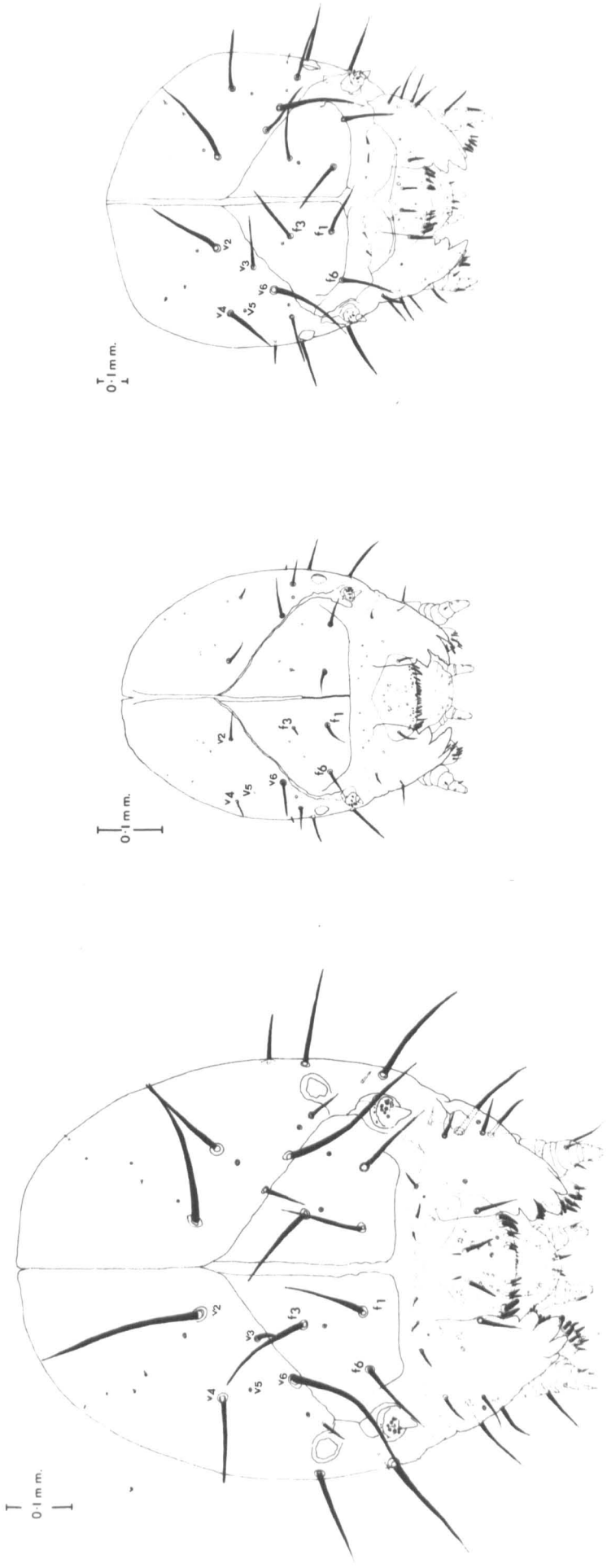


Fig. 39 *L. capreae* (L.)  
Second instar

Fig.40 *L. crataegi* (Forst.)  
First instar

Fig.41 *L. suturalis* (Th.)  
Final instar



PLATE LH15

GALERUCINAE

LARVAL MANDIBLES

FIGS. 42 a-f

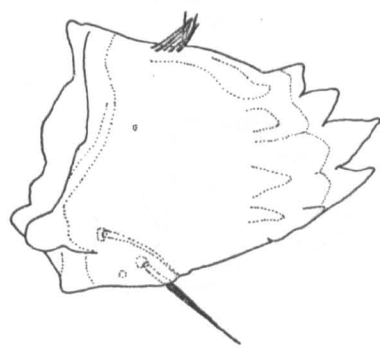
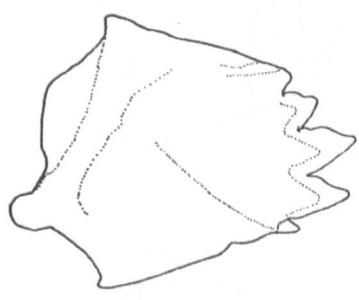
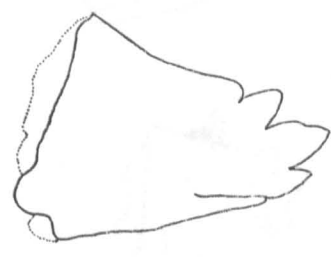
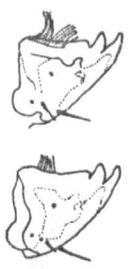
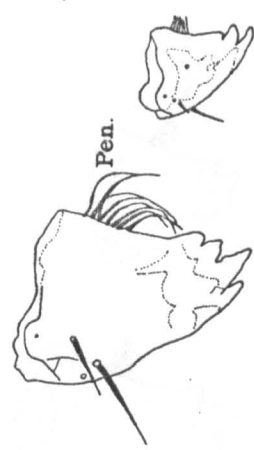
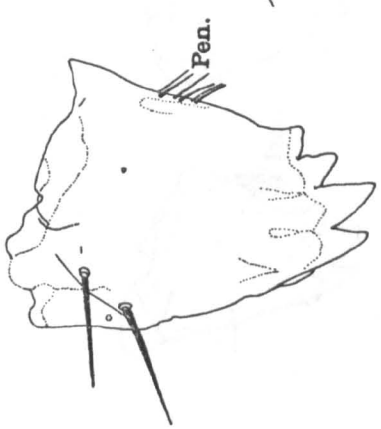
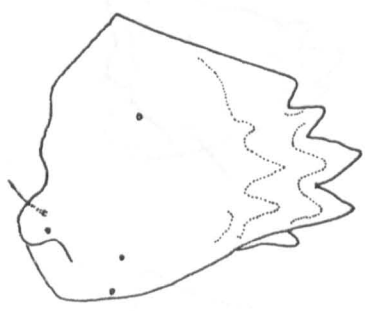
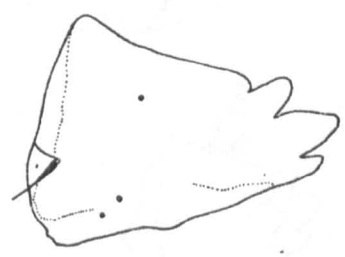
AGELASTICA

GALERUCA

SERMYLA

PHYLLOBROTICA

LUPERUS



0.1 m m.

0.1 m m.

a. *A. alni* (L.)

b. *G. tanacetii* (L.)

c. *S. halensis* (L.)

d. *P. quadrimaculata* (L.) e. *L. f. flavipes longicornis* F. L.

LOCHMAEA      GALERUCINAE      LARVAL MANDIBLES      FIGS 43 a-g  
GALERUCELLA

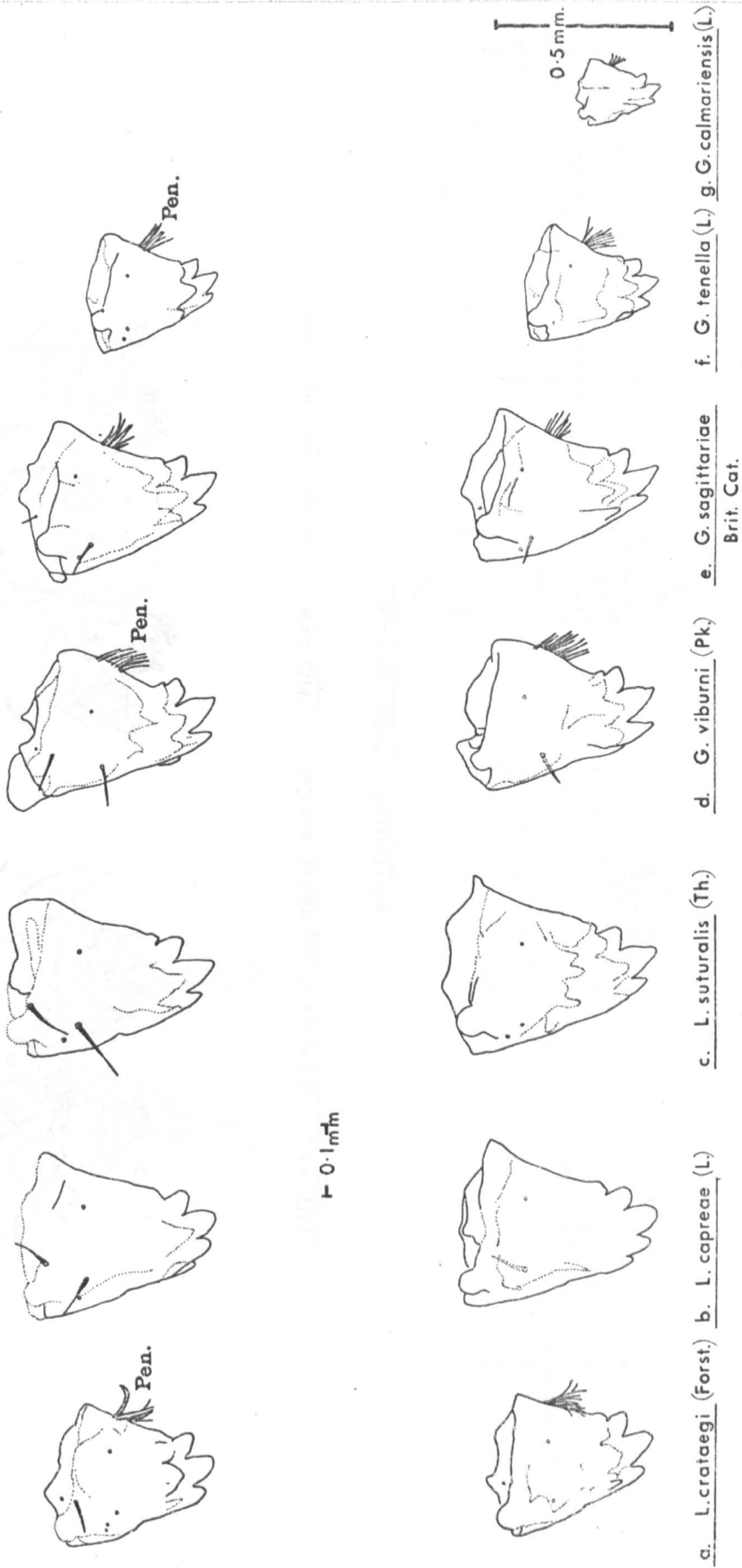


PLATE LH 17 GALERUCINAE LARVAL MOUTHPARTS

MAXILLA & LABIUM

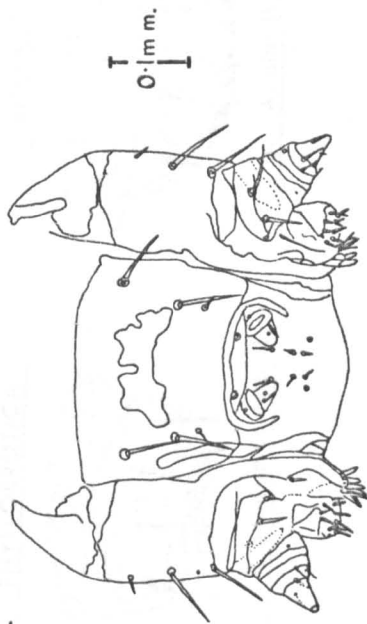
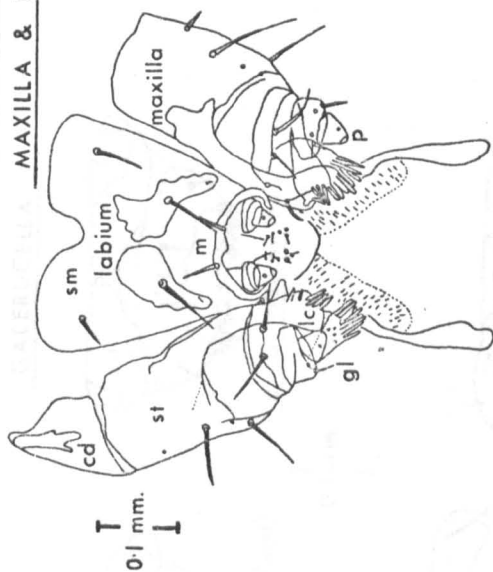
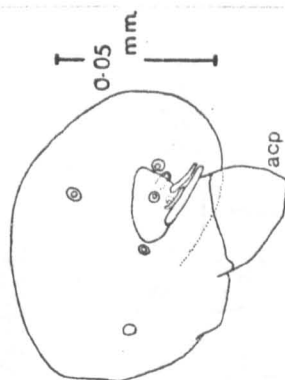
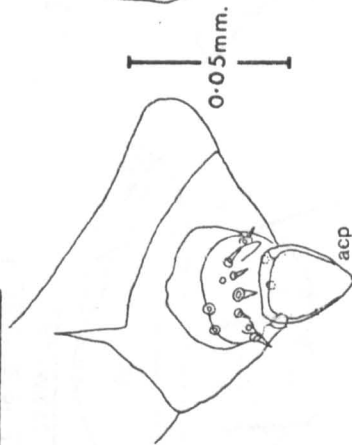
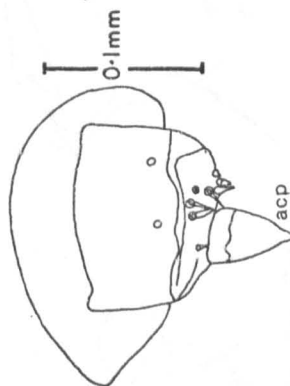
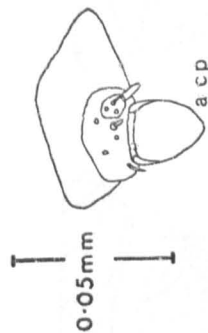


FIG. 44a *Galerucella sagittariae* Brit. Cat. FIG. 44b *Lochmaea crataegi* Forst.

ANTENNAE FIGS. 45 a-d



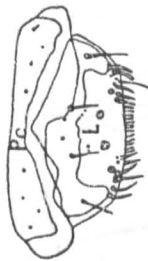
a. *Luperus longicornis* F. b. *Sernyla halensis* (L.) c. *Phyllobrotica quadrimaculata* (L.) d. *Agelastica alni* (L.)

LOCHMAEA

GALERUCELLA

PHYLLOBROTICA

AGELASTICA

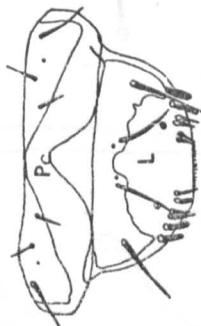


a. L. crataegi (Forst.)



d. G. viburni (Pk.)

T  
0.1mm.  
I



b. L. capreae (L.)



e. G. lineola (F.)

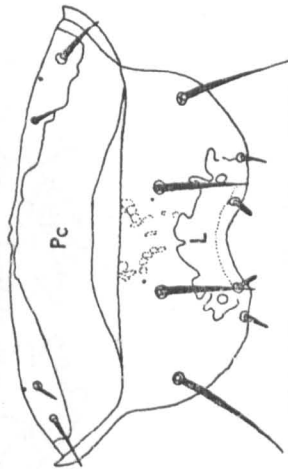
LUPERUS



h. L. longicornis F.

T  
0.05mm.  
I

SERMYLA



i. S. halensis (L.)



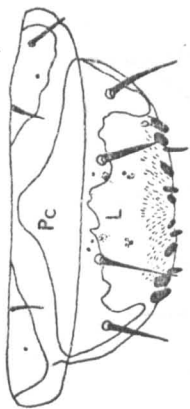
c. L. suturalis (Th.)



f. G. sagittariae Brit Cat.



g. P. quadrimaculata (L.)



j. A. alni (L.)

GALERUCA



k. G. tanacetii (L.)

T  
0.1mm  
I

HALTICA

HERMAEOPHAGA

LONGITARSUS

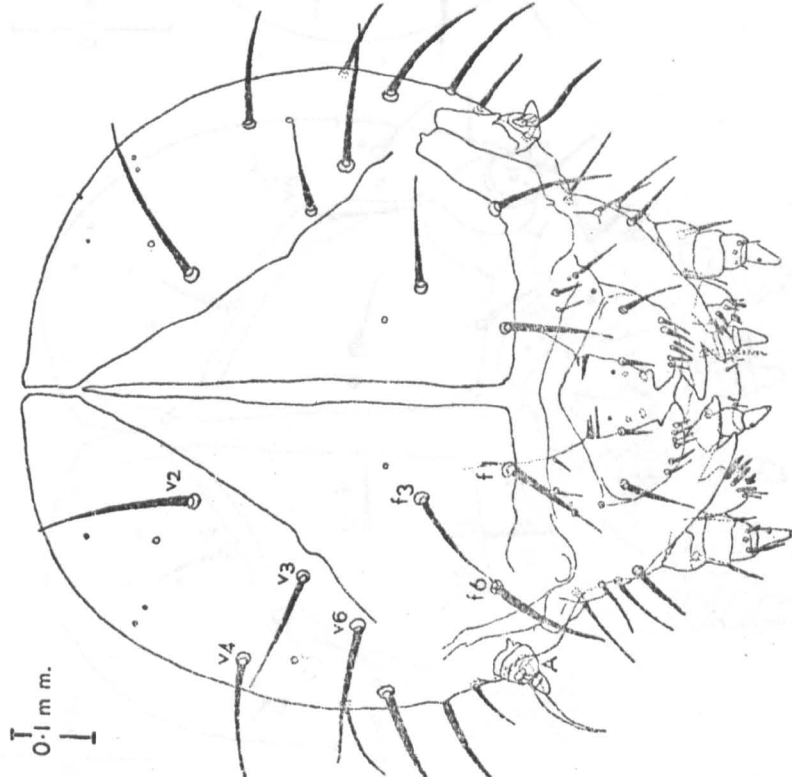


FIG. 47 *H. britteni* Shp. Final instar

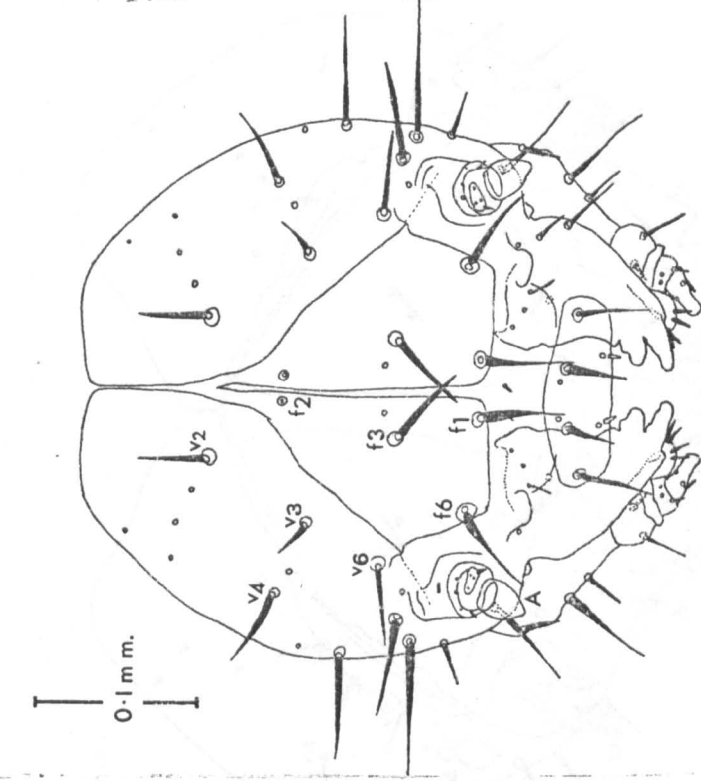


FIG. 48 *H. mercurialis* (F) First instar

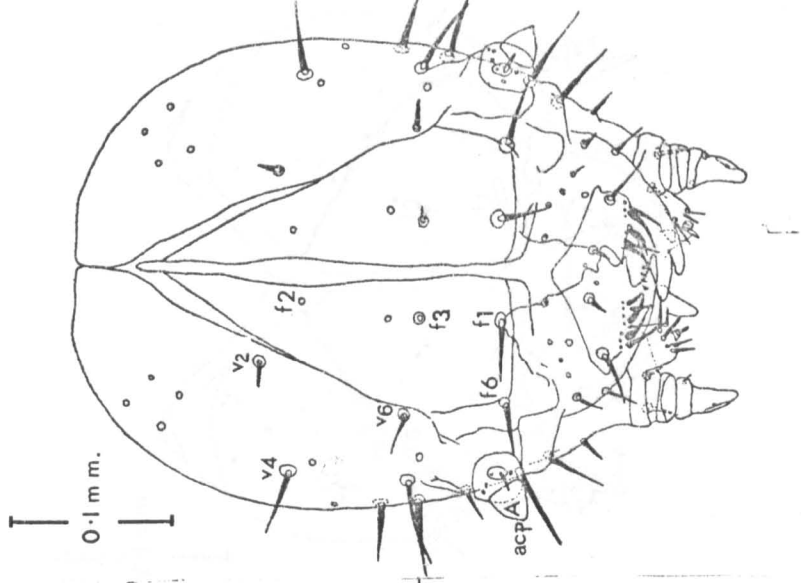


FIG. 49 *L. suturellus* Duft. Final instar

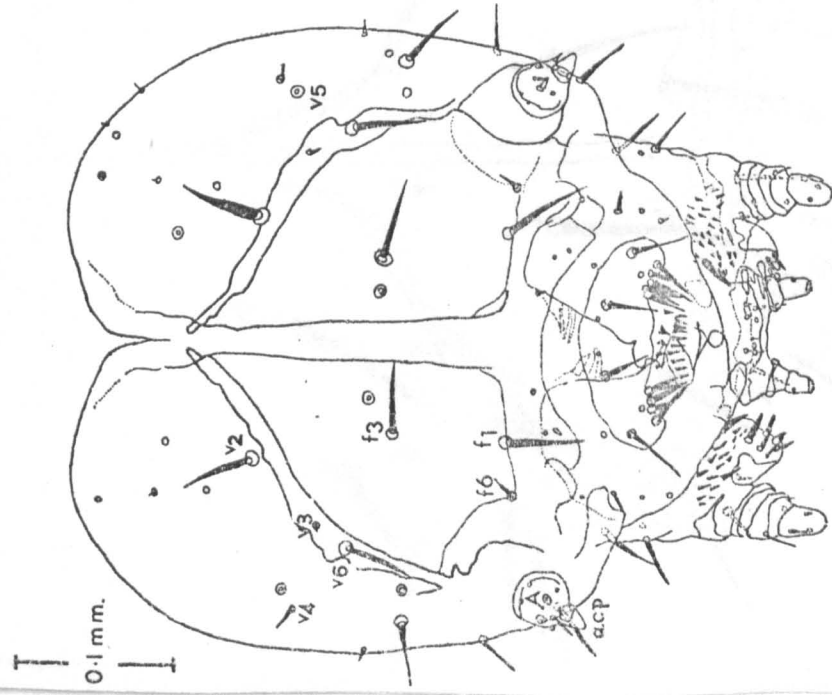


FIG. 50 *H. modeeri* (L.) Final instar

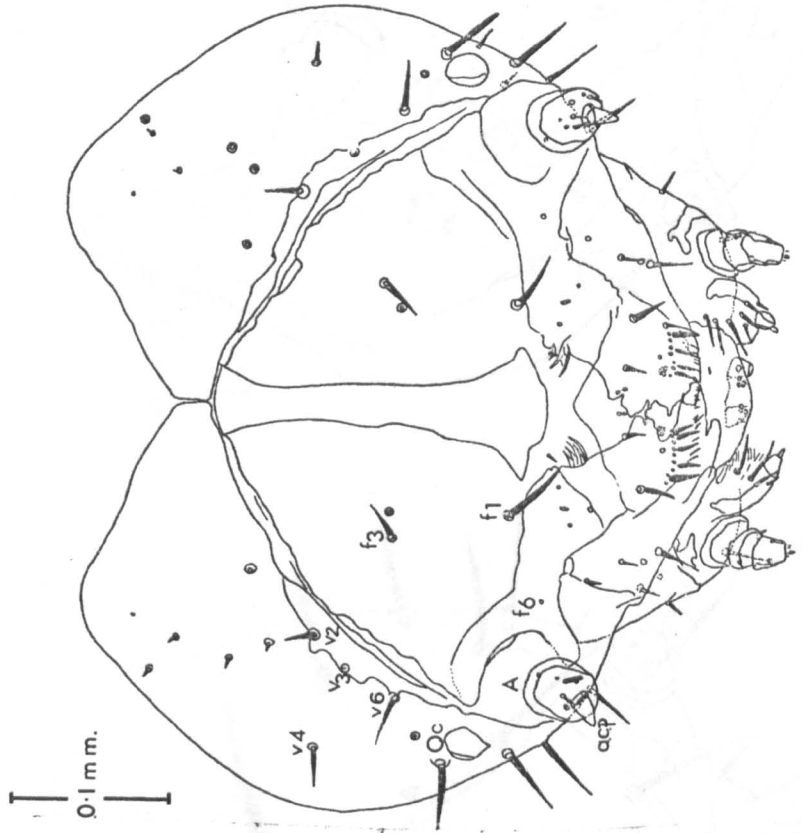


FIG. 51 *M. rustica* (L.) Final instar

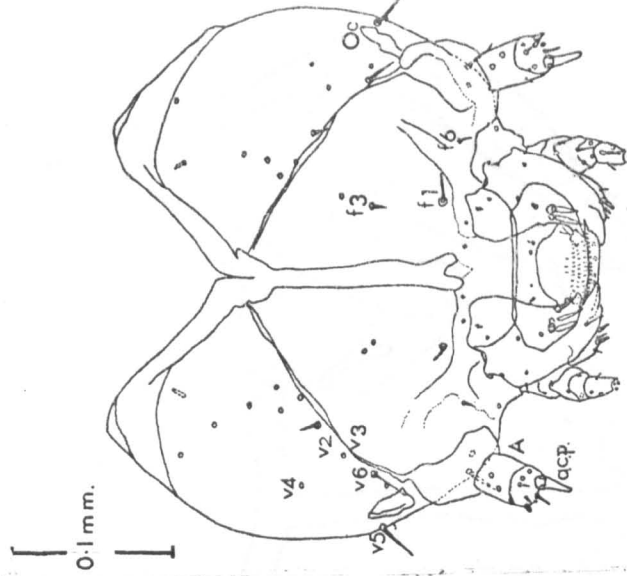


FIG. 52 *A. orbiculata* (Marsh.)  
Second instar

PSYLLIODES

SPHAERODERMA

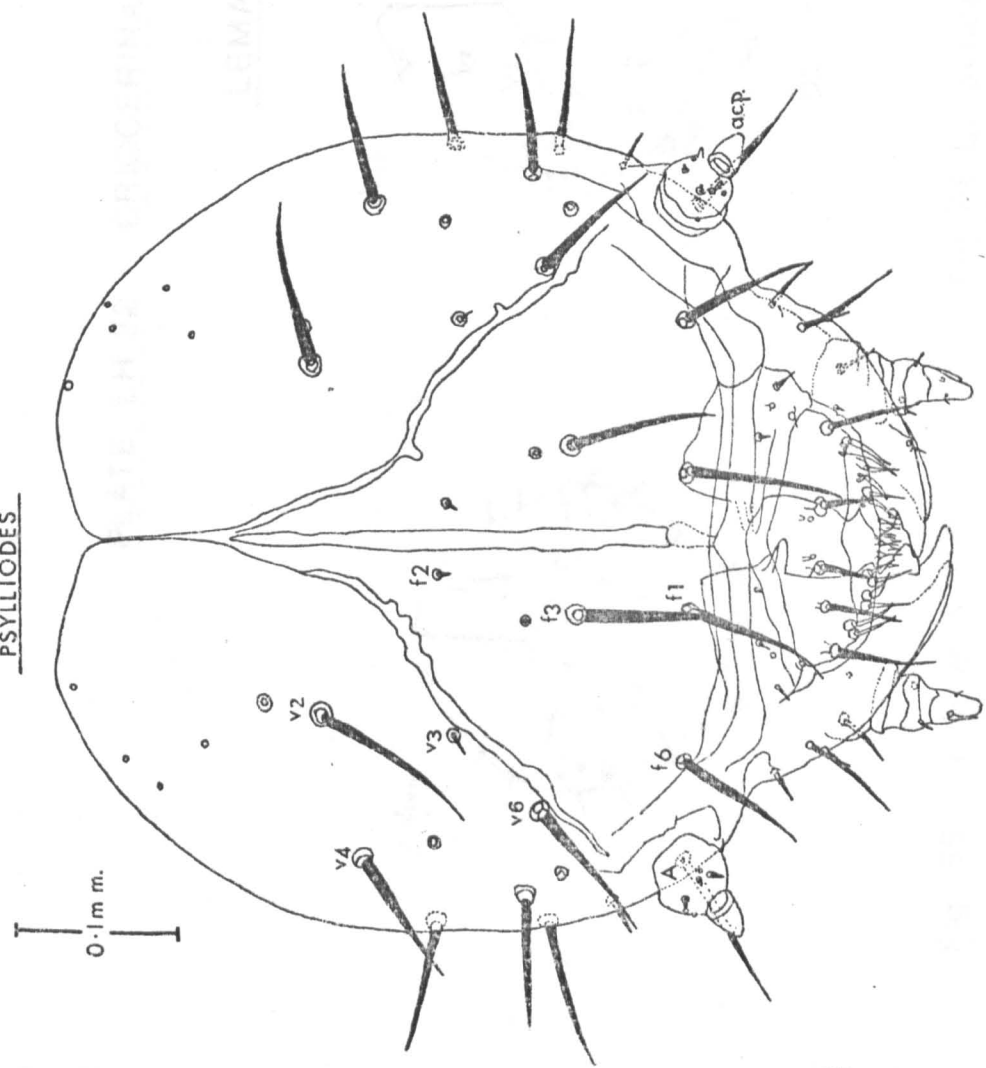


FIG. 53 *P. napi* (F) Final instar

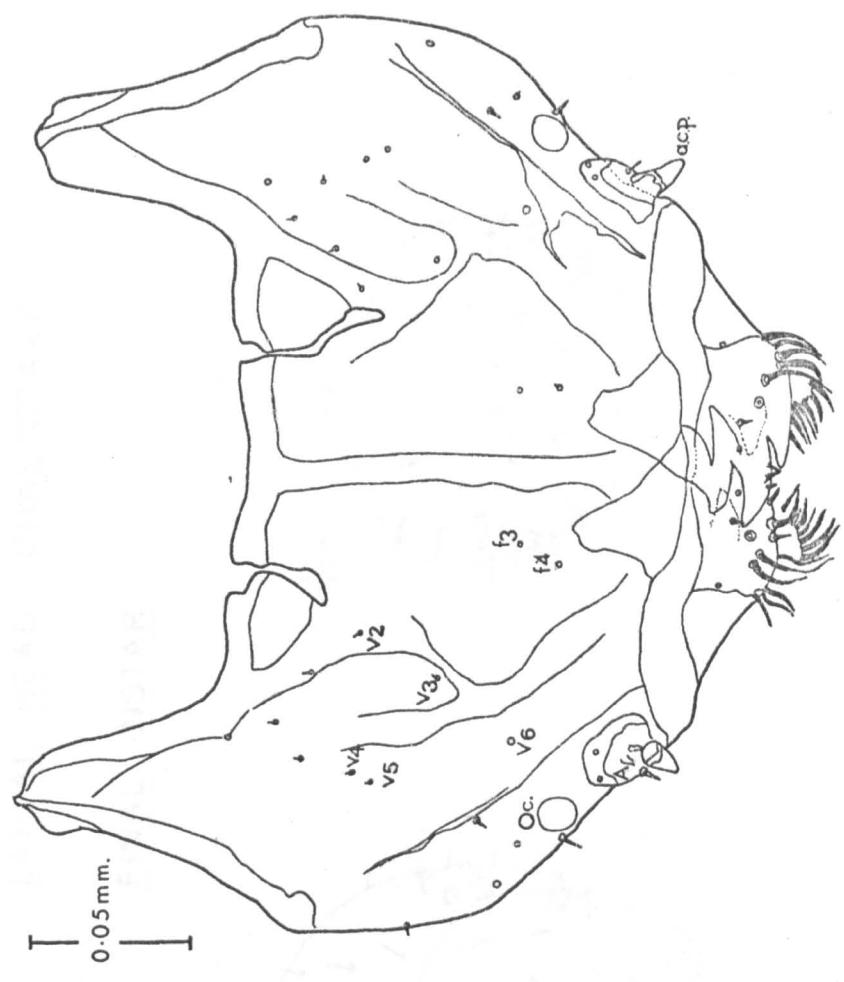


FIG. 54 *S. rubidum* Graells, First instar

LEMA

FINAL INSTAR

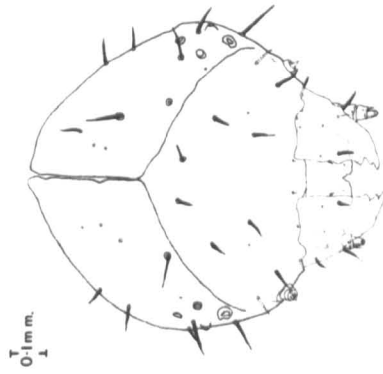


Fig. 55 *L. lichensis* Voet.

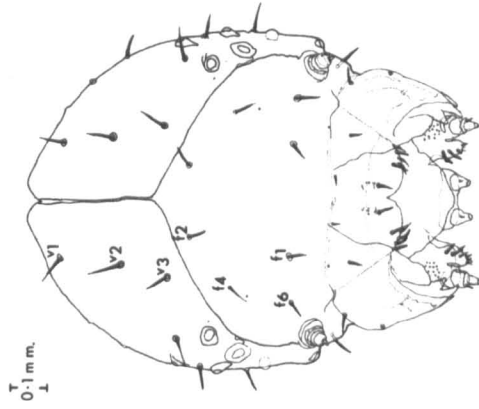


Fig. 56 *L. puncticollis* Curt.

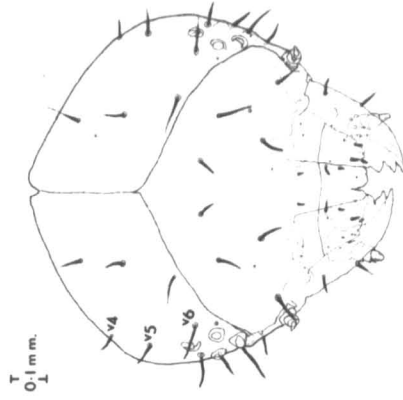


Fig. 57 *L. melanopa* (L.)



## LEMA

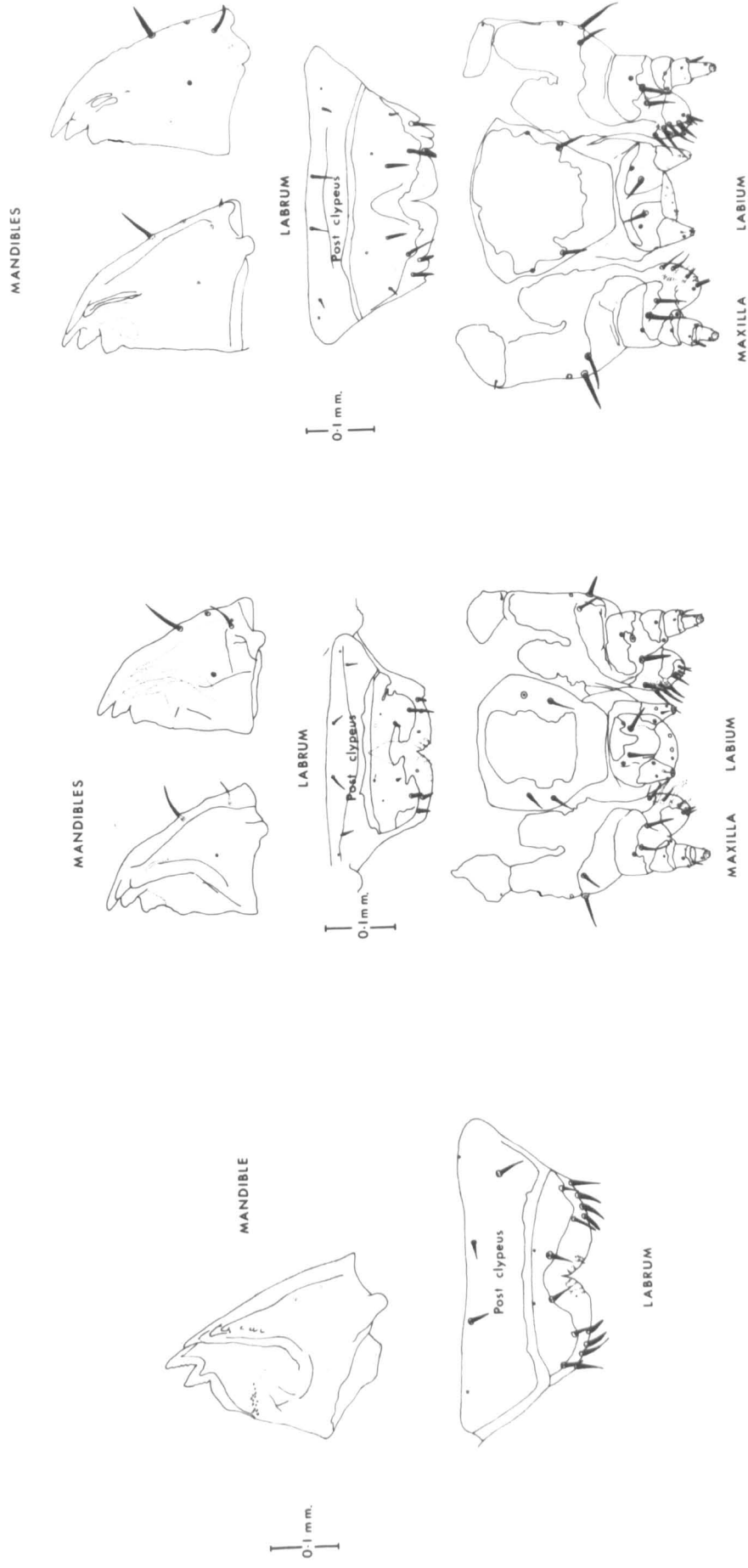


Fig. 58 L. puncticollis Curt.

Fig. 59 L.lichenis Voet.

Fig. 60 L. melanopa (L.)

PLATE LH 24 CRIOCERINAE

FIG. 61

LILIOCERIS L. illi (Scop.)

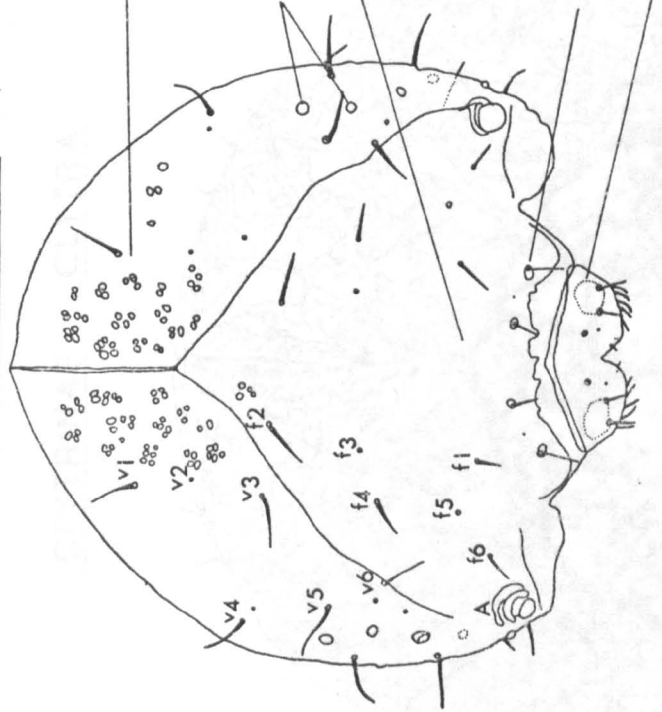
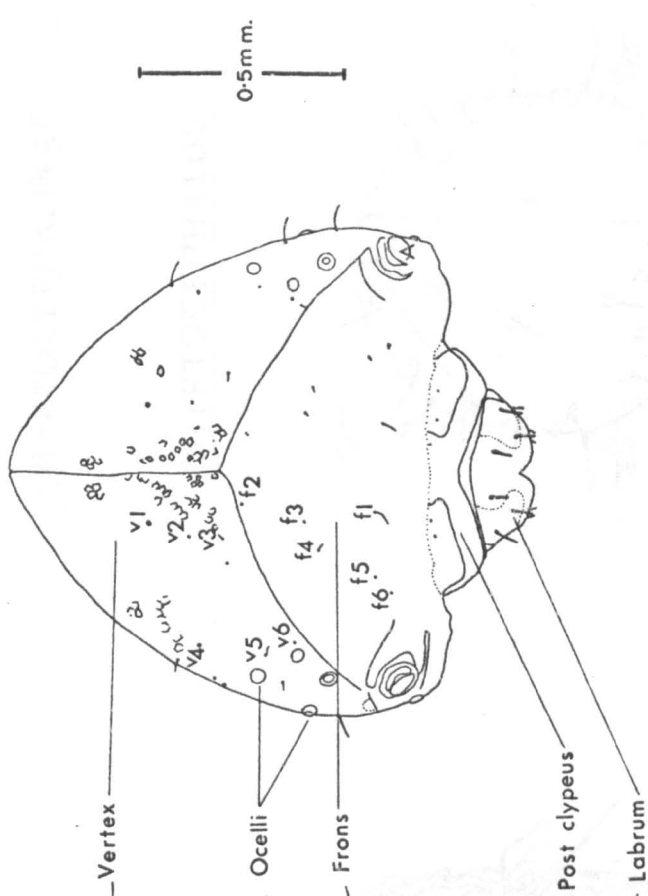


FIG. 62

CRIOCERIS C. asparagi (L.)



0.5mm.

(b) Maxillae & Labium



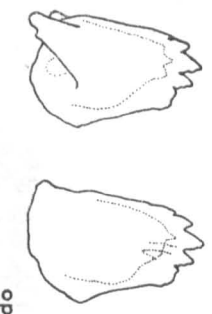
(c) Mandibles



(b) Maxillae & Labium



(c) Mandibles



CLYTRINAE      CLYTRA

CRYPTOCEPHALINAE

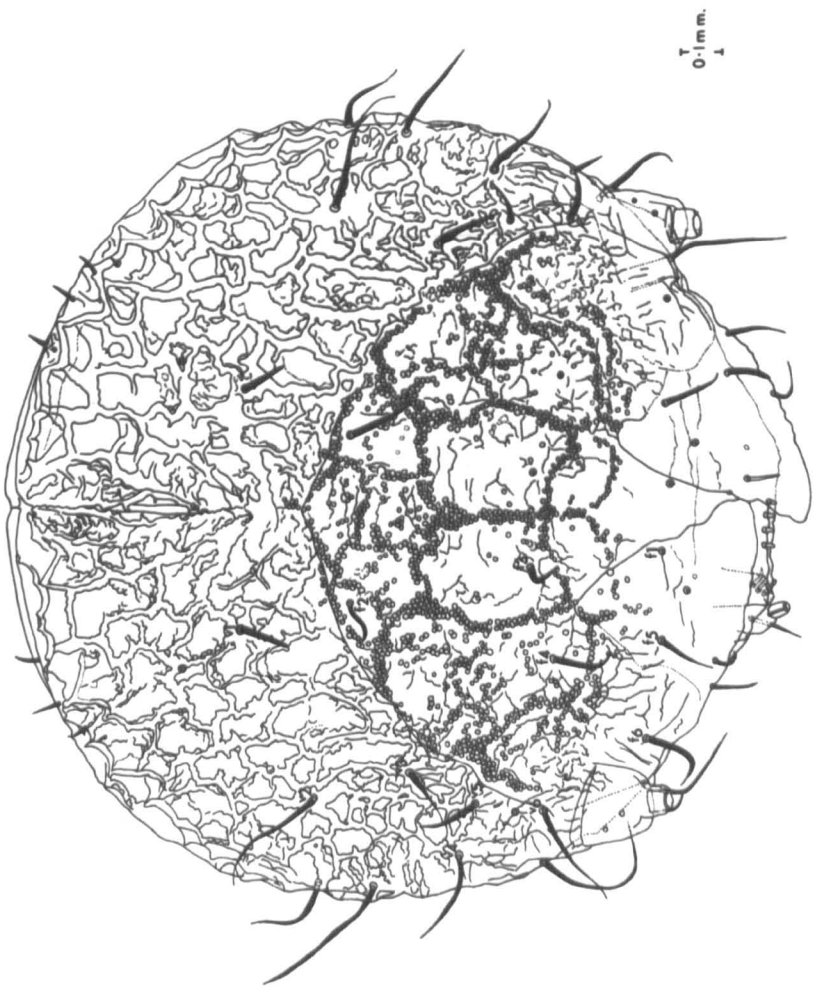


Fig. 63 *C. quadripunctata* (L.)

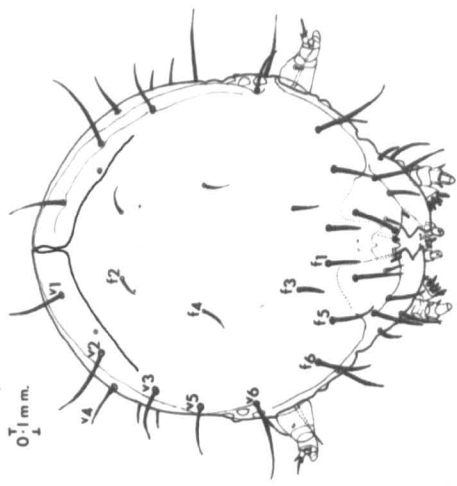
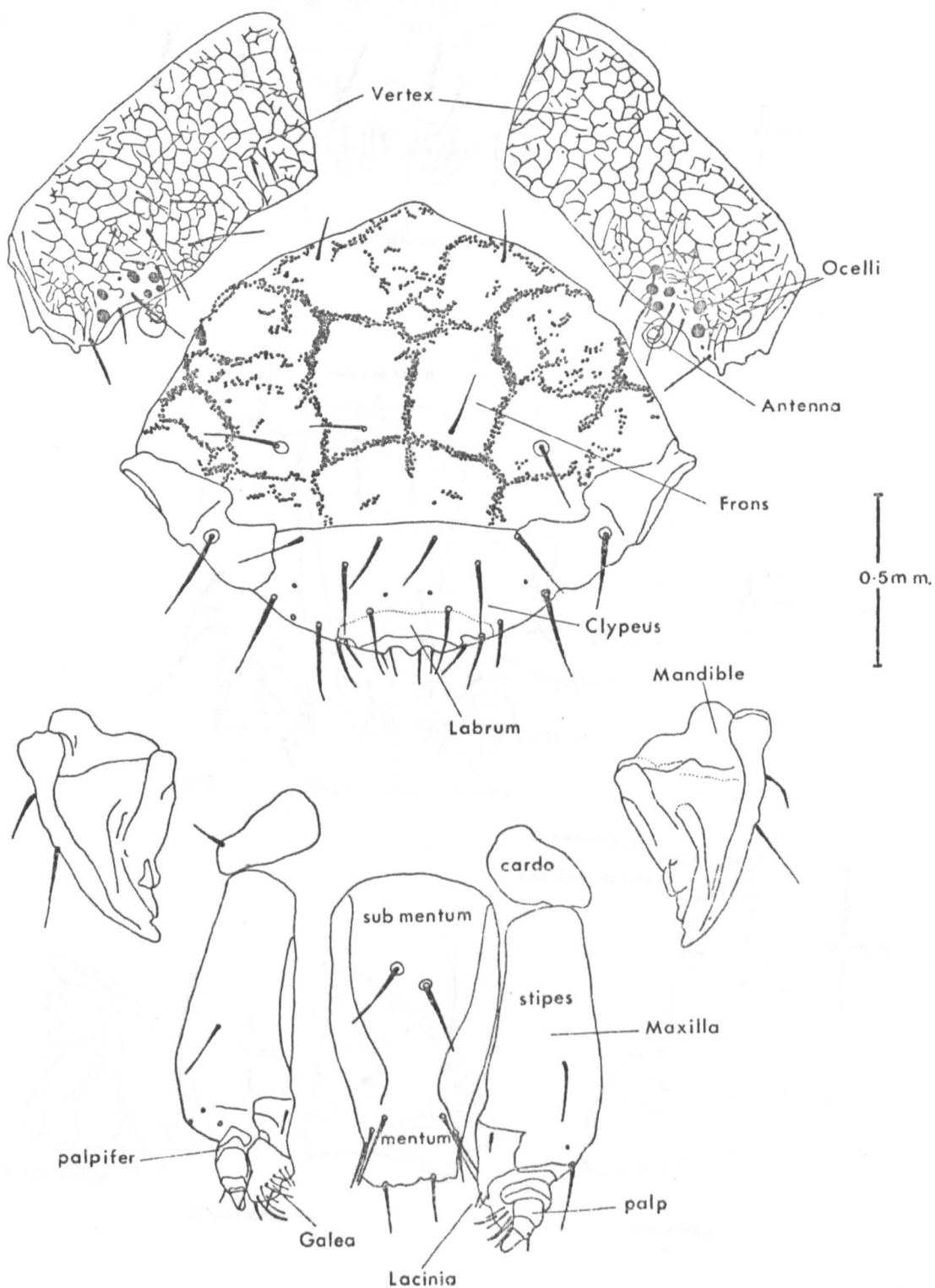


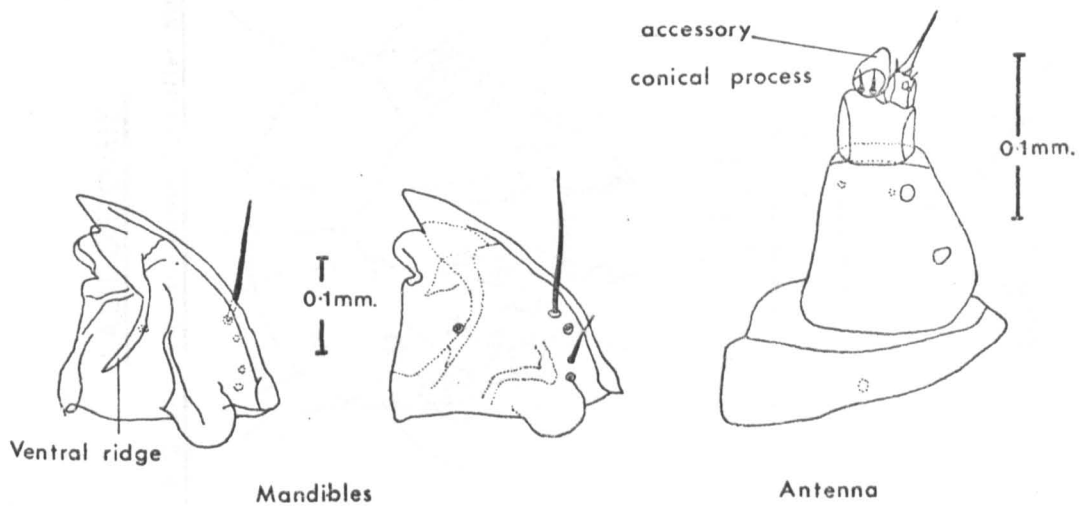
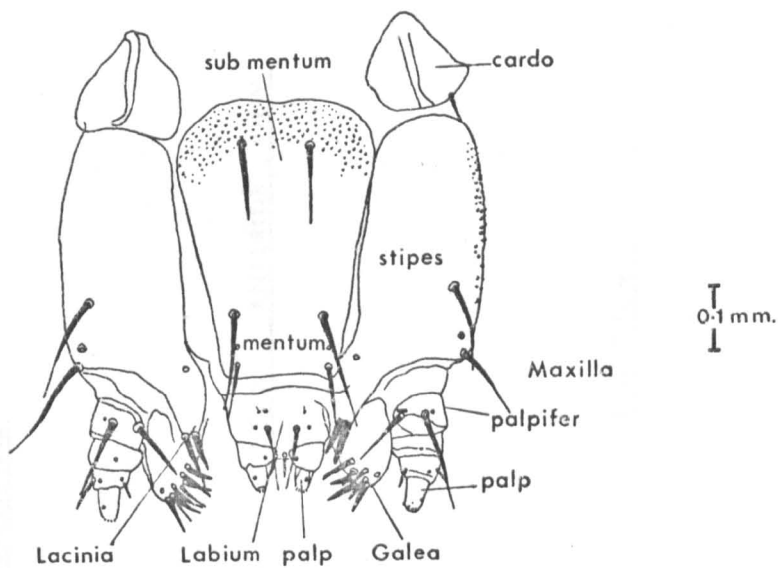
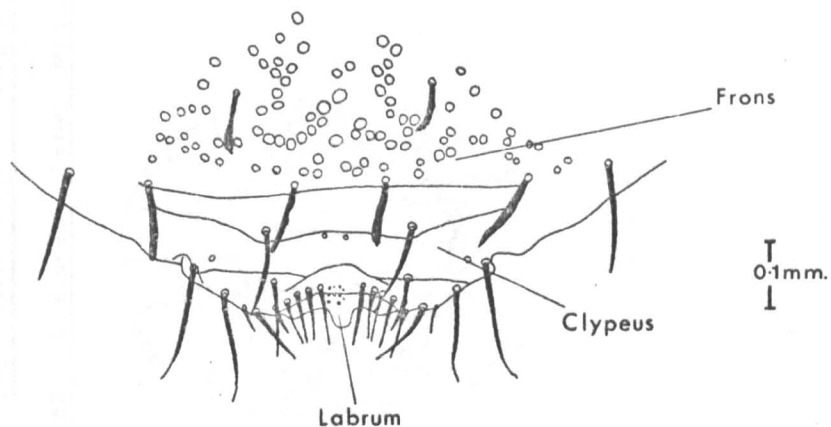
Fig. 64 *C. moraei* (L.)

CRYPTOCEPHALUS

PLATE LH 26    CLYTRINAE    LARVAL HEAD

FIG. 65    Clytra quadripunctata (L.)



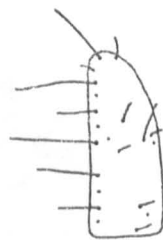


LABIDOSTOMIS

FIG. 67 L. tridentata (L.) (after Medvedev 1962)



HEAD ANTERIOR VIEW



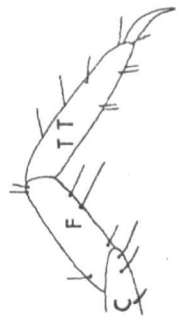
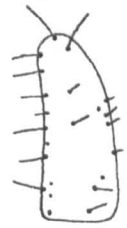
PRONOTUM



ANTERIOR LEG

GYNANDROPTHALMA

FIG. 68 G. cyanea (after Medvedev 1962)



PLATEUMARIS

MACROPLEA

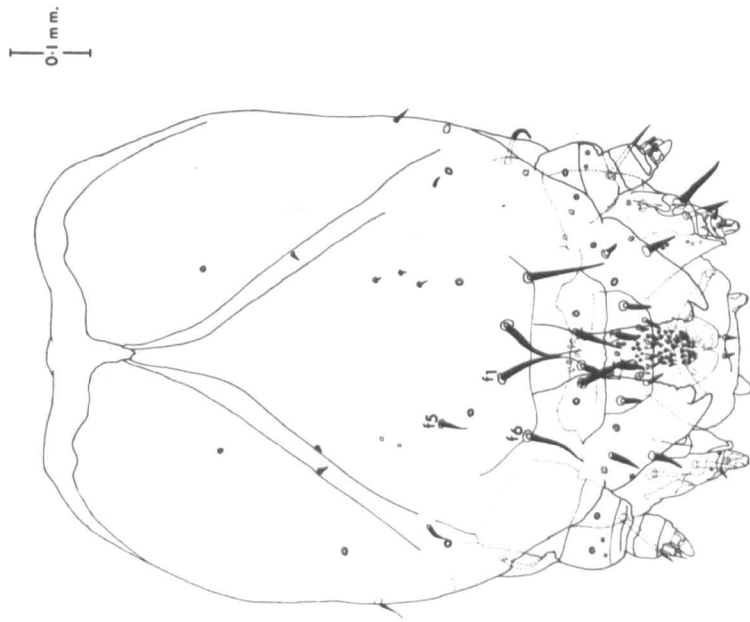


Fig. 69 *P. discolor* (Pz.) Final instar

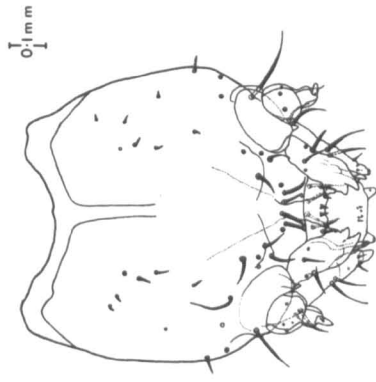


Fig.70 *M. appendiculata* (Pz.)

DONACIA

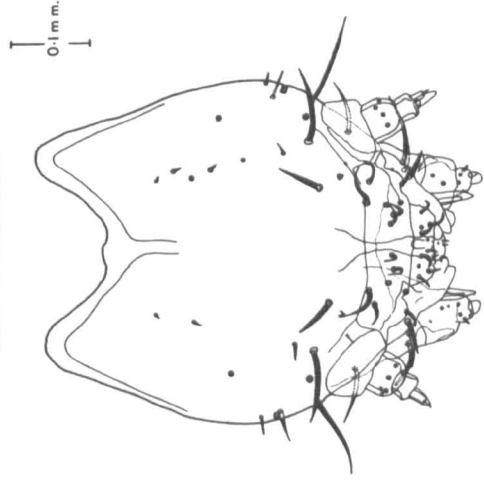


Fig.71 *D. cinerea* Hbst.

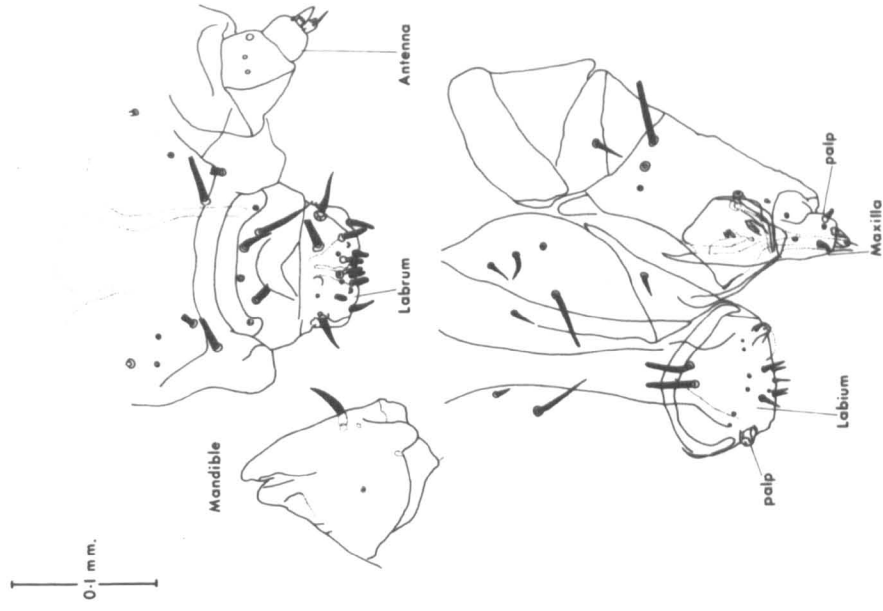


Fig.72 Mouthparts *D. cinerea* Hbst.

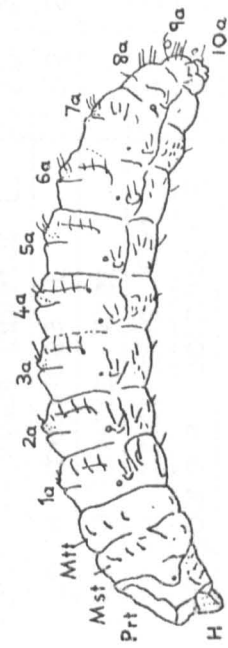


FIG. 73 LARVA - LATERAL VIEW

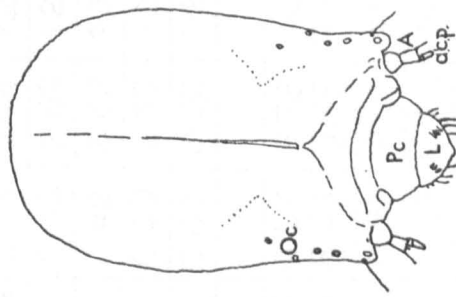


FIG. 74 HEAD DORSAL VIEW

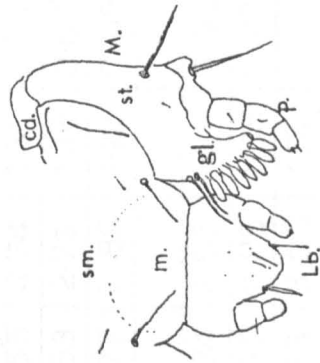


FIG. 75 MOUTHPARTS VENTRAL



a) VENTRAL



b) DORSAL

FIG. 76 RIGHT MANDIBLE



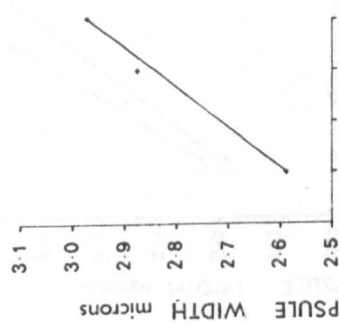
TABLE 4

SPECIES	$\bar{x}$ HCW. mm.	LOG. $\bar{x}$ HCW.	$\bar{x}$ HCW. mm.	LOG. $\bar{x}$ HCW.	G.R.	$\bar{x}$ HCW. mm.	LOG. $\bar{x}$ HCW.	G.R.	$\bar{x}$ HCW. mm.	LOG. $\bar{x}$ HCW.	G.R.	$\bar{x}$ HCW. mm.	LOG. $\bar{x}$ HCW.	G.R.
	1st. INSTAR	2nd INSTAR	3rd INSTAR	4th INSTAR		5th INSTAR								
Cassida flaveola Thunb.	0.44	2.65	0.56	2.75	1.27	0.67	2.83	1.20	0.87	2.94	1.29	1.07	3.03	1.23
Cassida viridis L.(English)	0.47	2.68	0.61	2.79	1.29	0.77	2.89	1.26	0.99	2.99	1.28	1.25	3.09	1.26
Cassida viridis L.(Spanish)	0.42	2.62	0.53	2.73	1.26	0.68	2.83	1.28	0.87	2.94	1.28	1.13	3.05	1.29
Cassida rubiginosa Müll.(Eng.)	0.47	2.67	0.55	2.74	1.17	0.68	2.83	1.24	0.85	2.93	1.25	1.04	3.02	1.22
Cassida rubiginosa Müll.(Sp.)	0.42	2.62	0.52	2.71	1.23	0.69	2.84	1.33	0.91	2.96	1.33	1.18	3.07	1.29
Cassida vittata Vill. (Sp.)	0.37	2.56	0.43	2.63	1.17	0.54	2.73	1.26	0.65	2.81	1.21	0.81	2.91	1.24
Cassida myrraea L.	0.44	2.64	0.55	2.74	1.25	0.74	2.87	1.34	0.93	2.97	1.27	1.24	3.09	1.32
Cryptocephalus parvulus Müll.	0.39	2.59	0.49	2.69	1.26	0.62	2.79	1.26	0.77	2.89	1.24			
Cryptocephalus pusillus F.	0.31	2.50	0.42	2.62	1.35	0.55	2.74	1.30	0.73	2.86	1.33			
Cryptocephalus labiatus L.	0.29	2.47	0.39	2.59	1.31	0.53	2.73	1.38	0.69	2.84	1.30			
Lema melanopa L.	0.52	2.71	0.63	2.80	1.21	0.77	2.89	1.22	0.95	2.98	1.23			
Lema lichenis Voet.														
Lema puncticollis Curt.	0.46	2.66	0.57	2.76	1.24	0.74	2.87	1.21	0.95	2.98	1.28			
Zeugophora subspinoso F.	0.39	2.59	0.52	2.72	1.33	0.70	2.85	1.35	0.93	2.97	1.33			
Sermyle halensis L.	0.53	2.72	0.81	2.91	1.54	1.23	3.09	1.51						
Phyllobrotica quadrimaculata L.	0.45	2.65	0.63	2.80	1.40	0.92	2.96	1.46						
Galerucella sagittariae Brit.C.	0.45	2.65	0.62	2.79	1.37	0.88	2.94	1.42						
Galerucella tenella L.	0.31	2.49	0.43	2.63	1.38	0.64	2.81	1.49						
Galerucella lineola F.	0.37	2.57	0.59	2.77	1.59	0.85	2.93	1.43						
Lochmaea capreae L.	0.43	2.63	0.63	2.80	1.46	0.89	2.95	1.41						
Lochmaea suturalis Th.	0.47	2.67	0.66	2.82	1.40	0.93	2.97	1.40						
Lochmaea crataegi Forst.	0.40	2.60	0.56	2.75	1.40	0.77	2.89	1.37						

TABLE 4 (cont.)

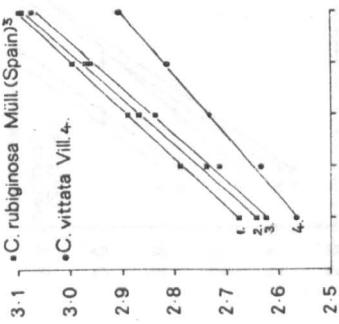
Chrysolina varians Schal.	0.58	2.76	0.75	2.88	1.29	0.99	2.99	1.33	1.28	3.11	1.28	
Chrysolina hyperici Forst.	0.47	2.67	0.66	2.82	1.40	0.93	2.97	1.41	1.28	3.11	1.37	
Chrysolina brunsvicensis Gr.	0.51	2.70	0.70	2.85	1.39	1.02	3.01	1.45	1.42	3.15	1.39	
Chrysolina fastuosa Scop.	0.61	2.78	0.85	2.93	1.39	1.17	3.07	1.37	1.54	3.19	1.32	
Chrysolina menthastri Suf.	0.67	2.83	0.98	2.99	1.31	1.42	3.15	1.45	2.03	3.31	1.43	
Chrysolina polita L.	0.74	2.87	0.98	2.99	1.33	1.37	3.14	1.39	1.84	3.26	1.35	
Chrysolina staphylea L.	0.80	2.90	1.08	3.03	1.36	1.55	3.19	1.43	2.15	3.33	1.39	
Timarcha tenebricosa F.	1.53	3.19	2.32	3.36	1.51	3.45	3.54	1.49				
Phytodecta olivacea Forst.	0.53	2.73	0.70	2.84	1.31	0.93	2.97	1.33	1.21	3.08	1.30	
Phytodecta pallida L.	0.75	2.88	0.95	2.98	1.27	1.23	3.09	1.28	1.53	3.18	1.25	
Gastroidea viridula De G.	0.53	2.73	0.84	2.93	1.58	1.26	3.10	1.49				
Gastroidea polygoni L.	0.53	2.72	0.82	2.91	1.54	1.16	3.06	1.42				
Phyllodecta vitellinae L.	0.48	2.68	0.67	2.82	1.39	1.01	3.00	1.51				
Phyllodecta laticollis Suf.	0.51	2.70	0.74	2.87	1.47	0.99	3.00	1.34				
Phyllodecta vulgatissima L.	0.46	2.67	0.69	2.84	1.48	1.03	3.01	1.50				
Phaedon tumidulus Germ.	0.53	2.72	0.78	2.89	1.47	1.10	3.04	1.41				
Phaedon cochleariae F.	0.45	2.65	0.68	2.83	1.51	0.99	2.99	1.45				
Phaedon armoraciae L.	0.47	2.67	0.70	2.85	1.49	1.03	3.01	1.46				
Hydrothassa marginella L.	0.40	2.60	0.60	2.78	1.52	0.86	2.93	1.42				
Prasocuris junci Brahm.	0.33	2.51	0.47	2.67	1.42	0.67	2.83	1.44				
Chrysomela populi L.	0.76	2.88	1.15	3.06	1.51	1.75	3.24	1.53				
Haltica lythri Aub.	0.42	2.62	0.65	2.81	1.56	0.98	2.99	1.52				
Haltica britteni Shp.	0.43	2.63	0.60	2.78	1.39	0.84	2.92	1.40				
Apteropeda orbiculata Marsh.	0.30	2.48	0.38	2.58	1.28	0.51	2.71	1.32				
Mantura rustica L.	0.23	2.35	0.32	2.51	1.42	0.48	2.68	1.49				
Hippuriphila modeeri L.	0.19	2.27	0.26	2.42	1.42	0.38	2.58	1.44				

77. ZEUGOPHORINAE  
*Zeugophora subspinosa* F.



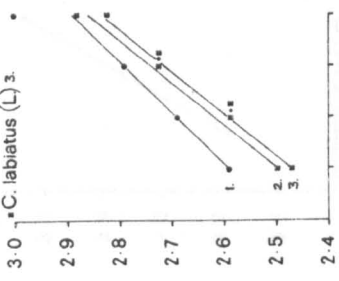
78. CASSIDINAE  
Cassida

- *C. viridis* L. 1.
- *C. murraea* L. 2.
- *C. rubiginosa* Müll (Spain) 3.
- *C. vittata* Vill 4.



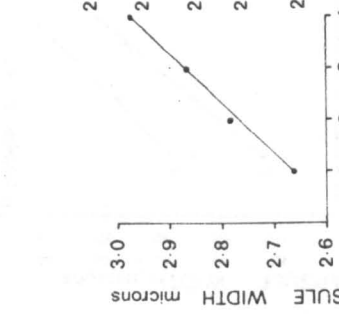
79. CRYPTOCEPHALINAE  
Cryptoccephalus

- *C. parvulus* Müll. 1.
- *C. pusillus* F. 2.
- *C. labiatus* (L.) 3.



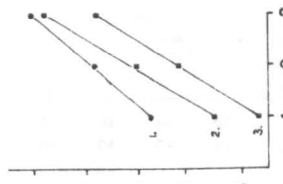
80. CRIOCERINAE  
Lema

- *L. puncticollis* Curt.



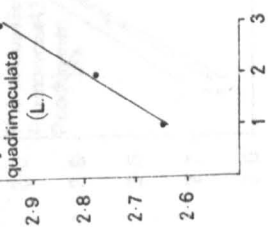
81. HALTICINAE

- *Apteropeda orbiculata* (Marsh) 1.
- *Mantura rustica* (L.) 2.
- *Hippuriphila modeeri* (L.) 3.



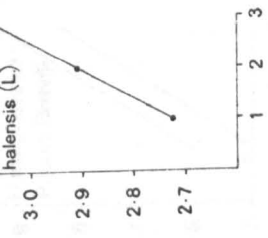
82.

GALERUCINAE  
*Phyllotreta quadrimaculata* (L)



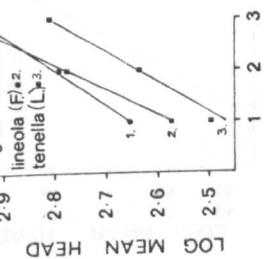
83.

GALERUCINAE  
*Semyla halensis* (L)



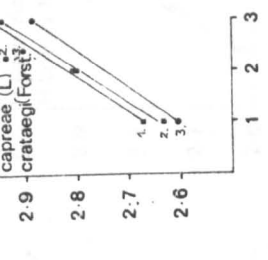
84.

Galerucella  
*sagittariae* BC<sup>1</sup>  
*lineola* (F.)<sup>2</sup>  
*tenella* (L.)<sup>3</sup>



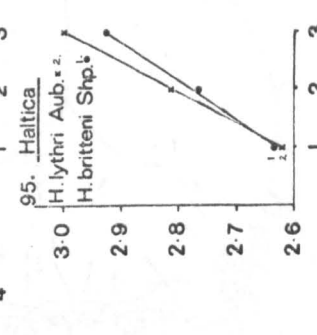
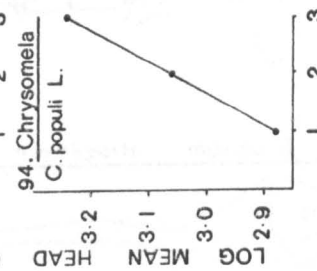
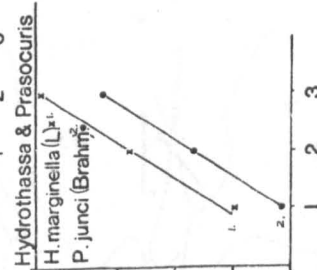
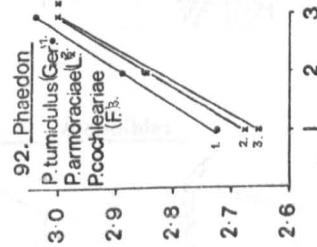
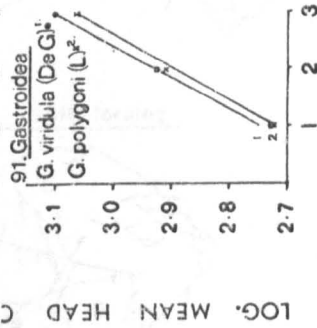
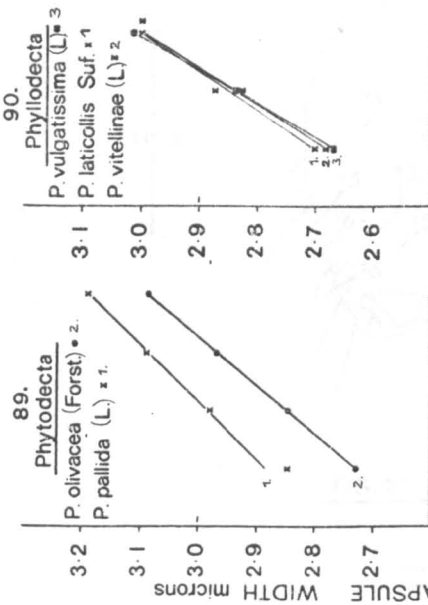
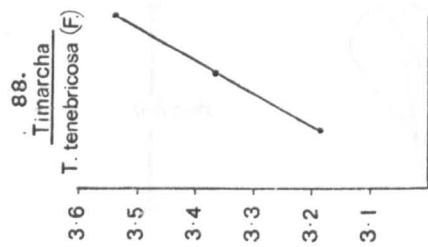
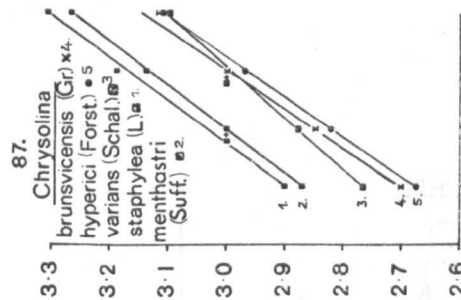
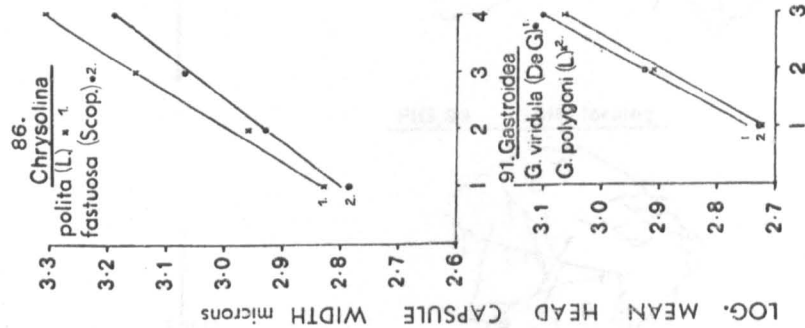
85.

Lochmaea  
*suturalis* (Th.)<sup>1</sup>  
*capreae* (L.)<sup>2</sup>  
*crataegi* (Forst.)<sup>3</sup>



LOG. MEAN HEAD CAPSULE WIDTH microns

INSTAR NUMBER



1 mm.

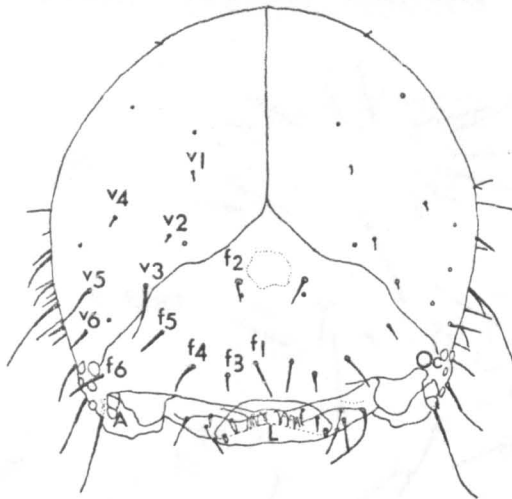


FIG. 96 Head chaetotaxy

FIG. 97 Mouthparts maxilla & labium

0.5 mm.

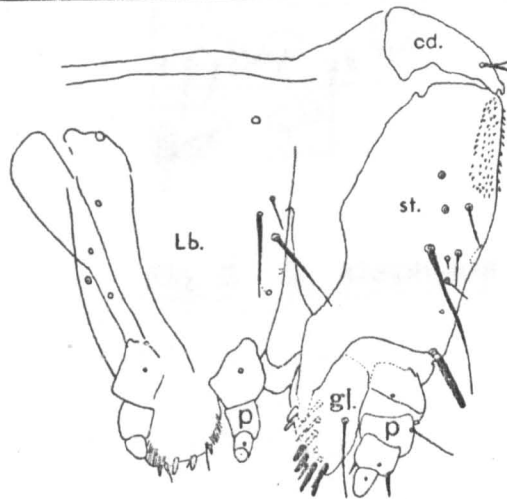


FIG. 98 Mandibles

1 mm.

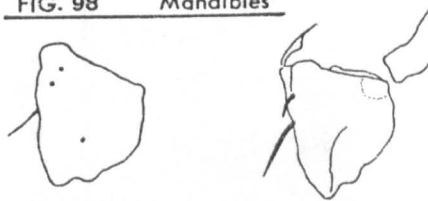


FIG. 99 Left foreleg

1 mm.



CHRYSOLINA FIRST INSTAR LARVAE

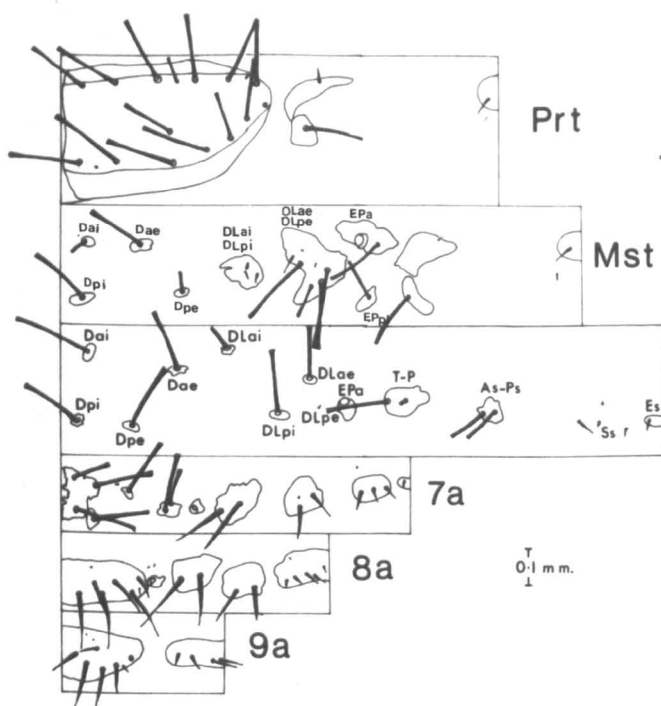


Fig. 1 *C. polita* (L.)

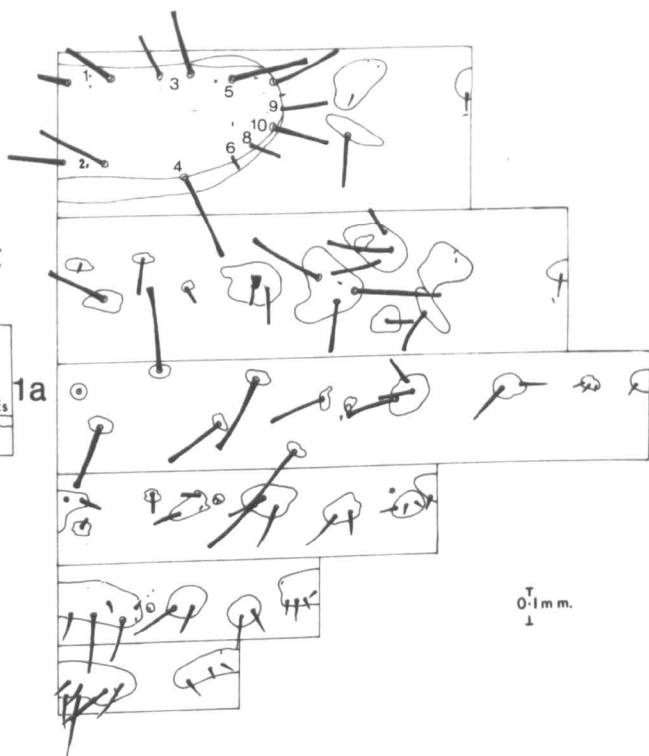


Fig. 2 *C. staphylea* (L.)

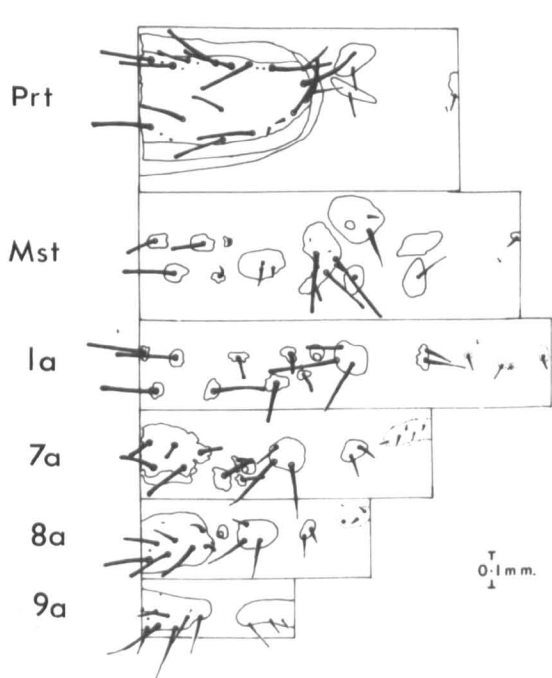


Fig. 3 *C. fastuosa* (Scop.)

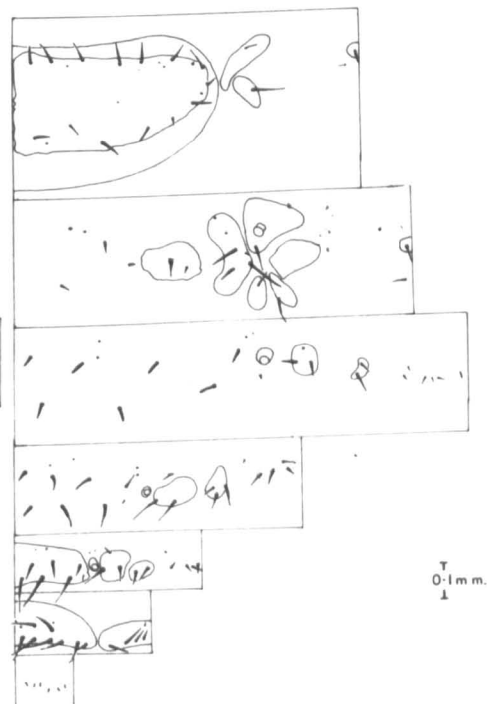


Fig. 4 *C. menthastri* (Suf.)

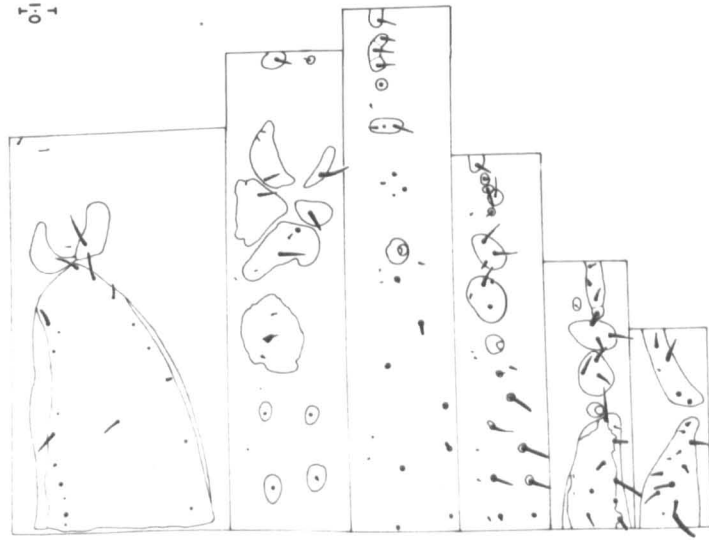


Fig. 5 *C. graminis* (L.)

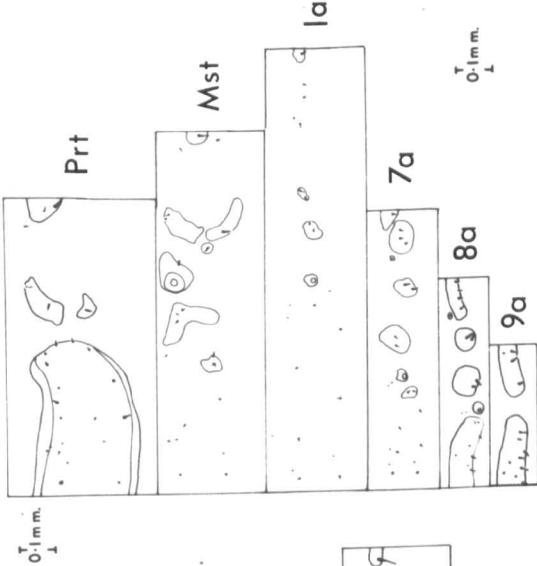


Fig. 6 *C. varians* (Schal.)

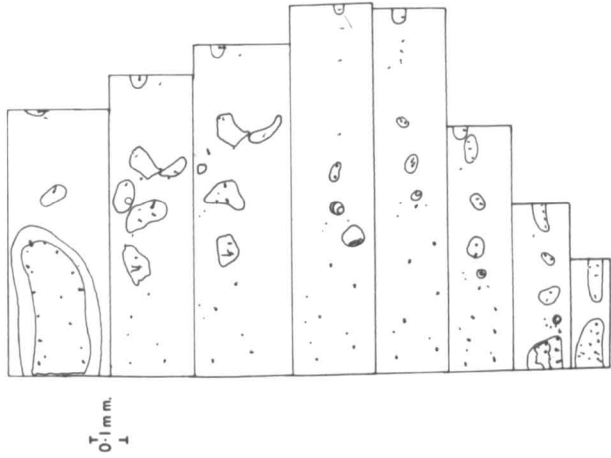


Fig. 7 *C. hyperici* (Forst.)

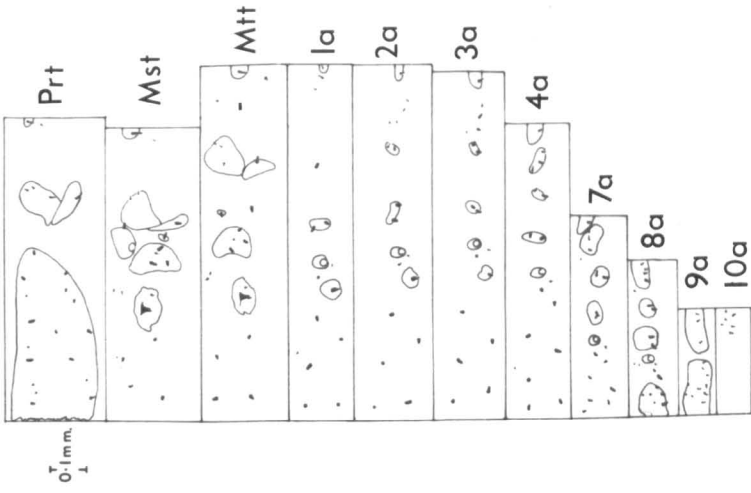


Fig. 8 *C. brunsvicensis* (Gr.)

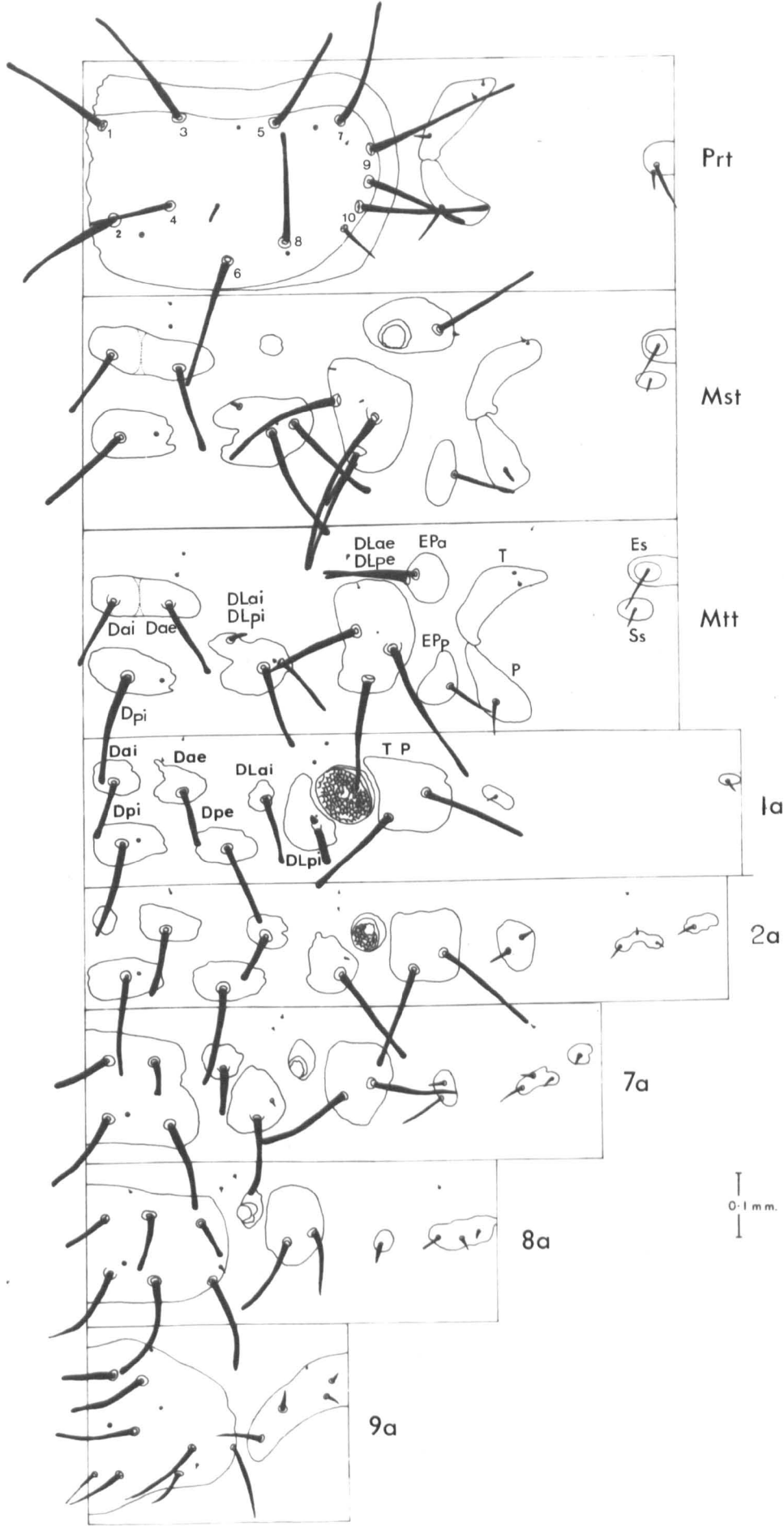
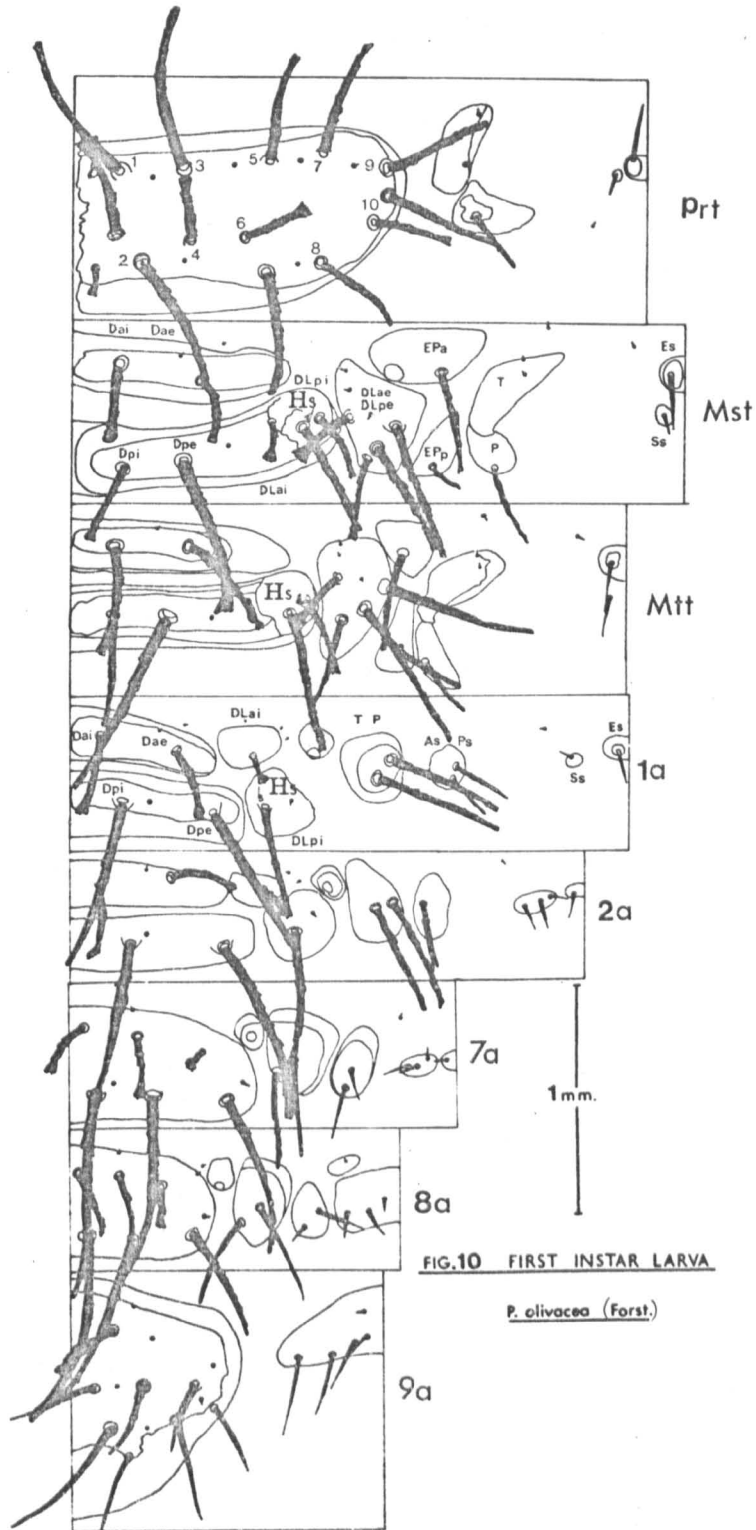


Fig. 9 *P. pallida* (L.)





FINAL INSTAR LARVAE

PHYTODECTA

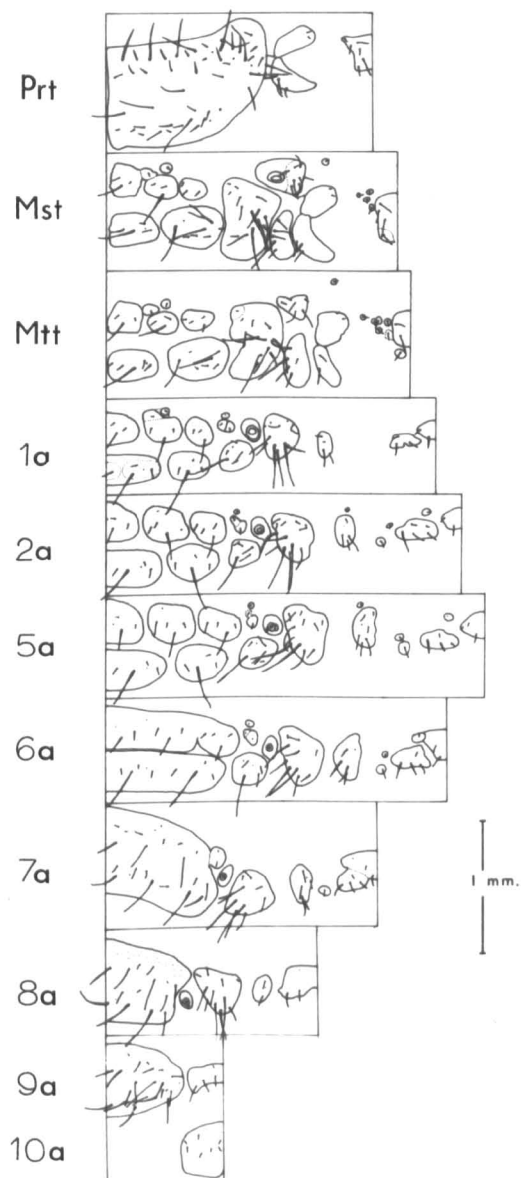


Fig.11a. *P. viminalis* (L.)

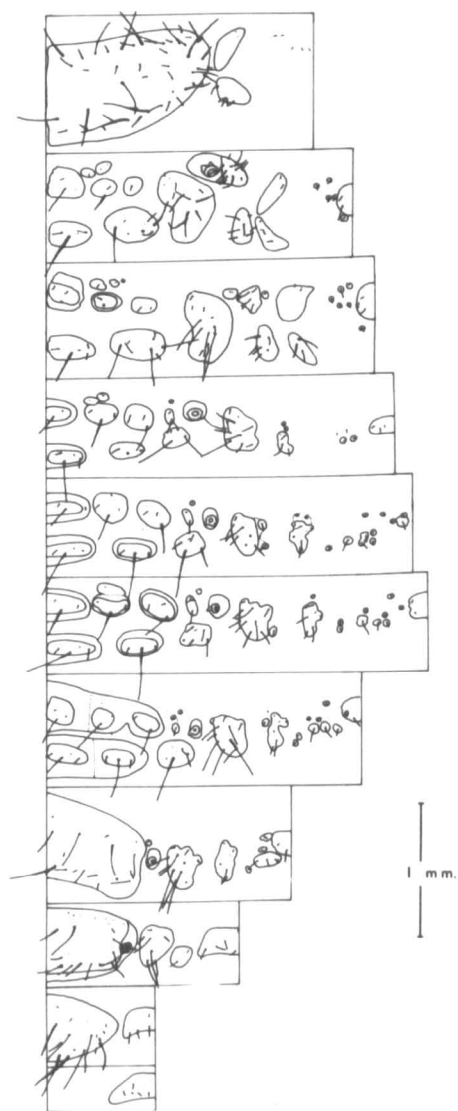


Fig. 11b. *P. rufipes* (De G.)

PLATE LB6

CHRYSOMELINAE

BODY CHAETOTAXY

FIRST INSTAR LARVAE

PHAEDON

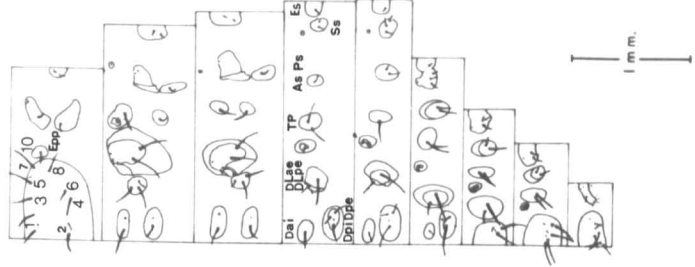
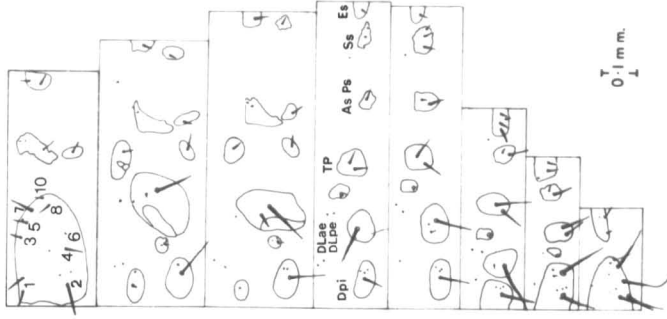
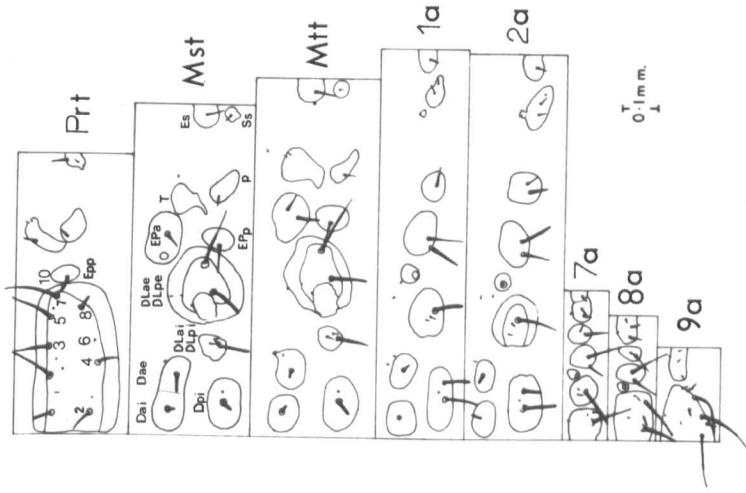
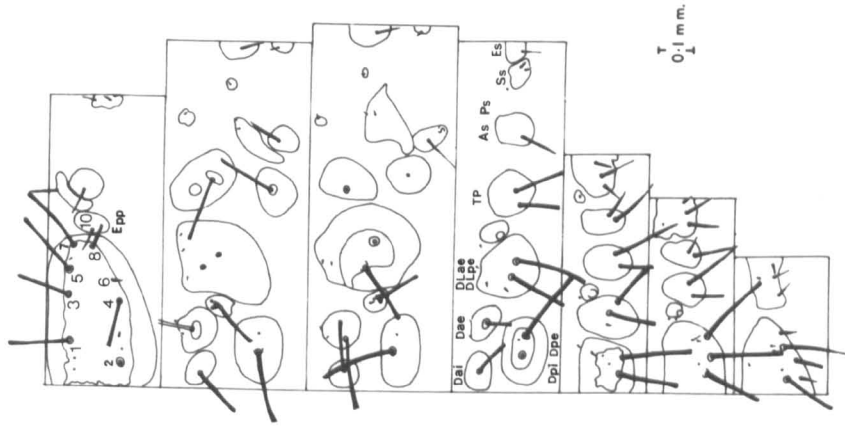
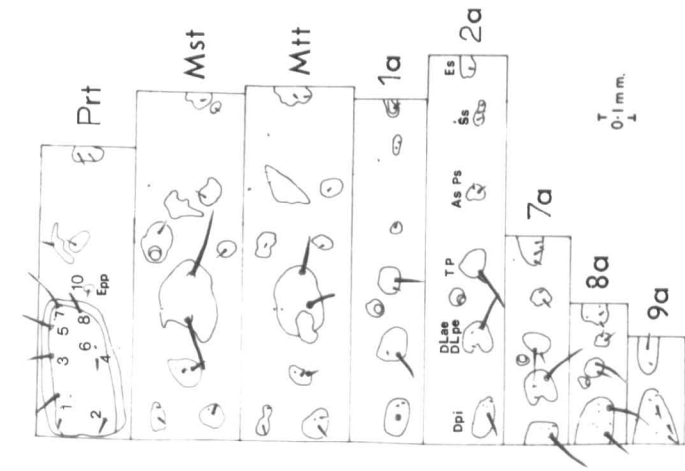


Fig.12 *P. cochleariae* (F.)

Fig.13 *P. tumidulus* (Germ.)

Fig.14 *P. armoraciae* (L.)

Fig.15 *H. marginella* (L.)  
Final instar

Fig.16 *H. aucta* (L.)  
Final instar

GASTROIDEA

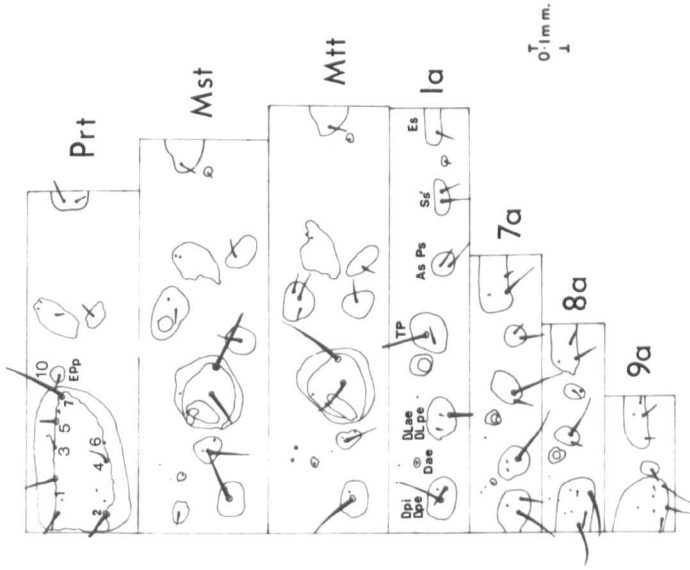
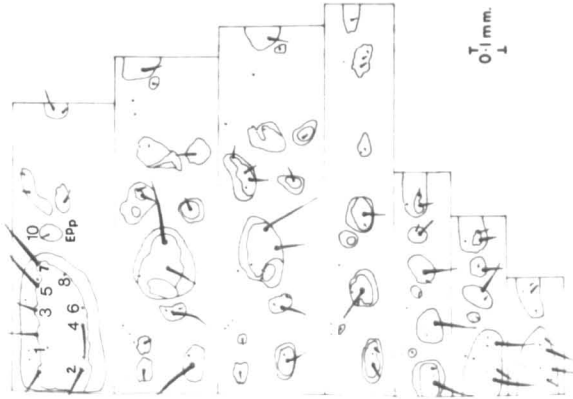


Fig.17 *G. polygona* (L.)

Fig.18 *G. viridula* (De G.)

PRASOCURIS

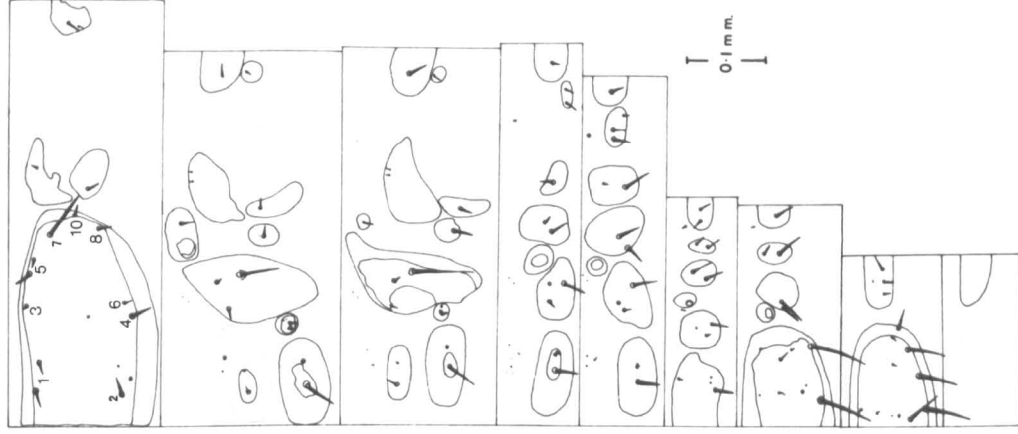


Fig.19 *P. junci* (Brahm.)

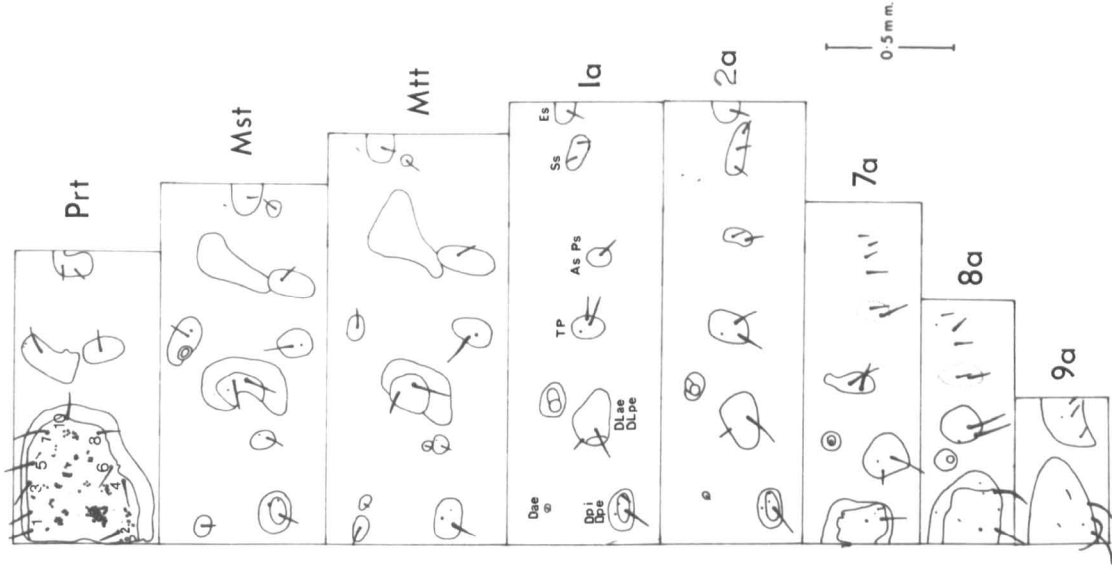


Fig.20 *P. phellandrii* (L.)

Final instar

PHYLLODECTA



FIG. 20d. *P. vulgatissima* (L.)

PLATE LB9  
PLAGIODERA

CHRYSOMELINAE

CHRYSOMELA

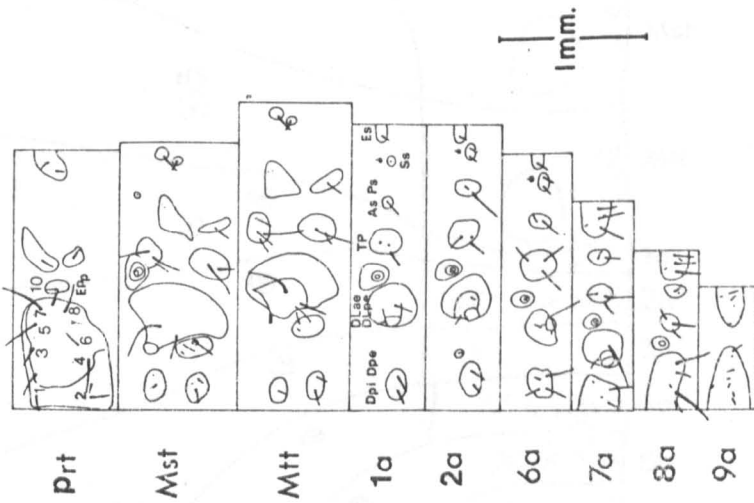


FIG. 21 *P. versicolora* (Laich.)  
Final instar

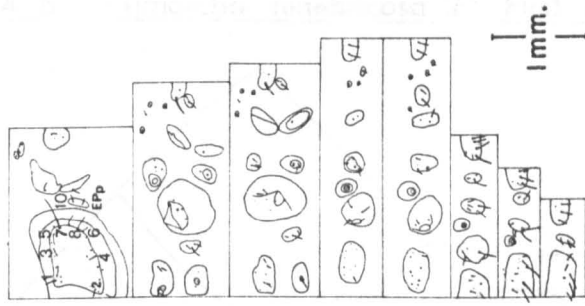


FIG. 22 *C. aenea* L. Final instar

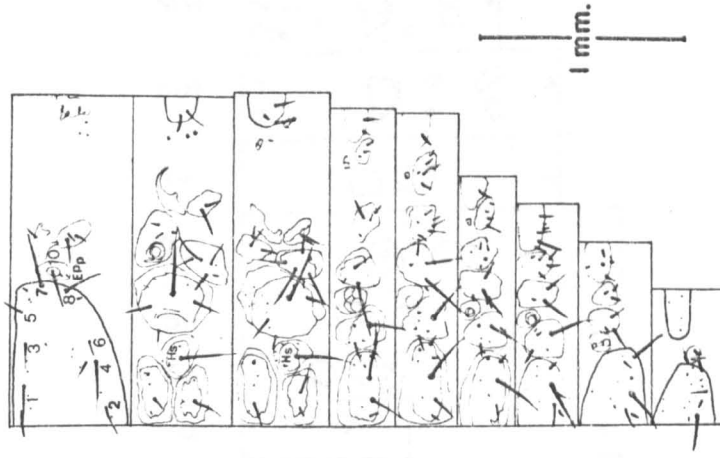


FIG. 23 *C. populi* L. First instar

Fig. 24 a *Leptinotarsa decemlineata* (Say.) Final instar larva

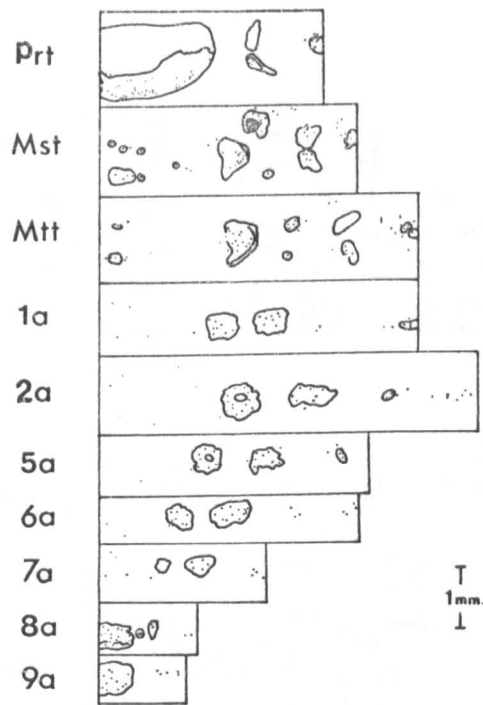
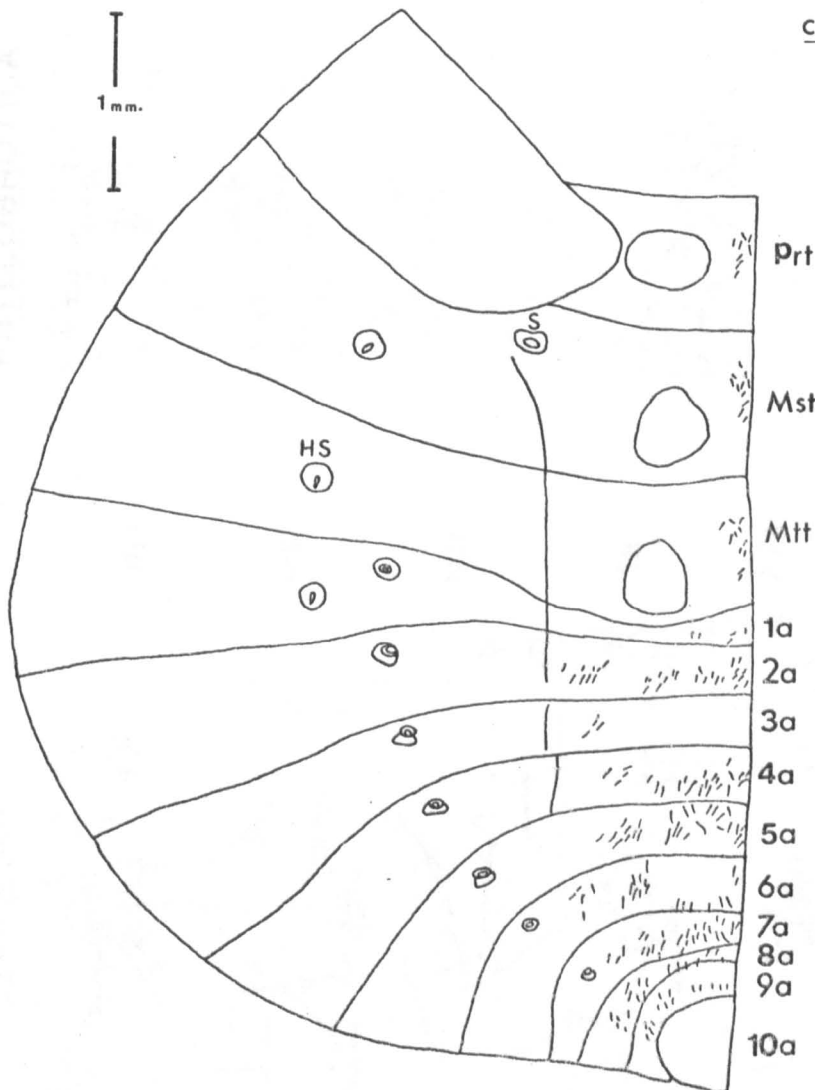


Fig. 24 b. *Timarcha tenebricosa* (F.) First instar larva



c. Hatching spines enlarged



SERMYLA

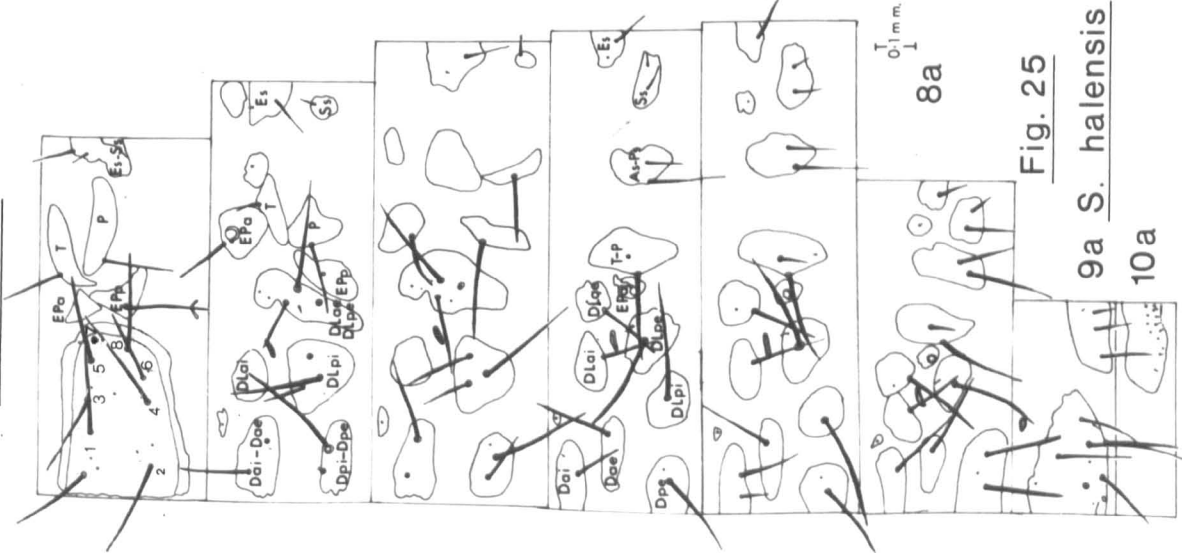


Fig. 25 *S. halensis* (L.)

PHYLLOBROTICA

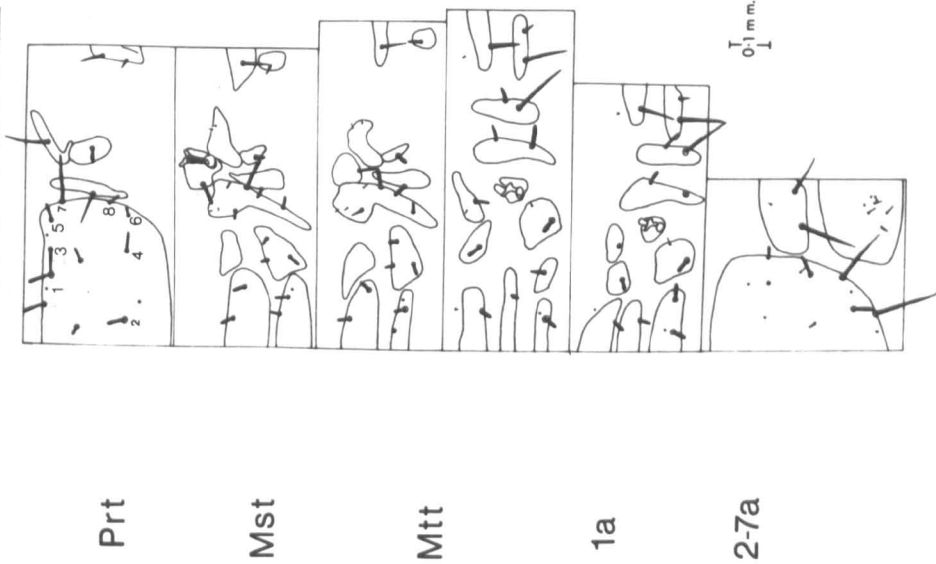


Fig. 26 *P. quadrimaculata* (L.)

LUPERUS

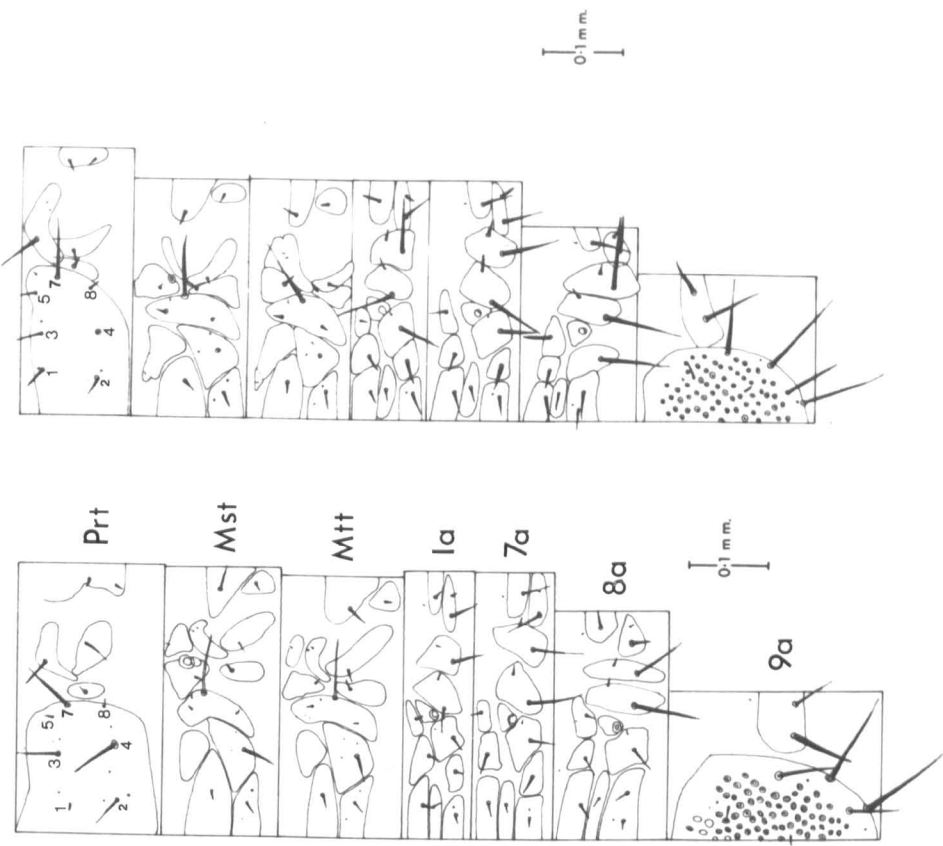
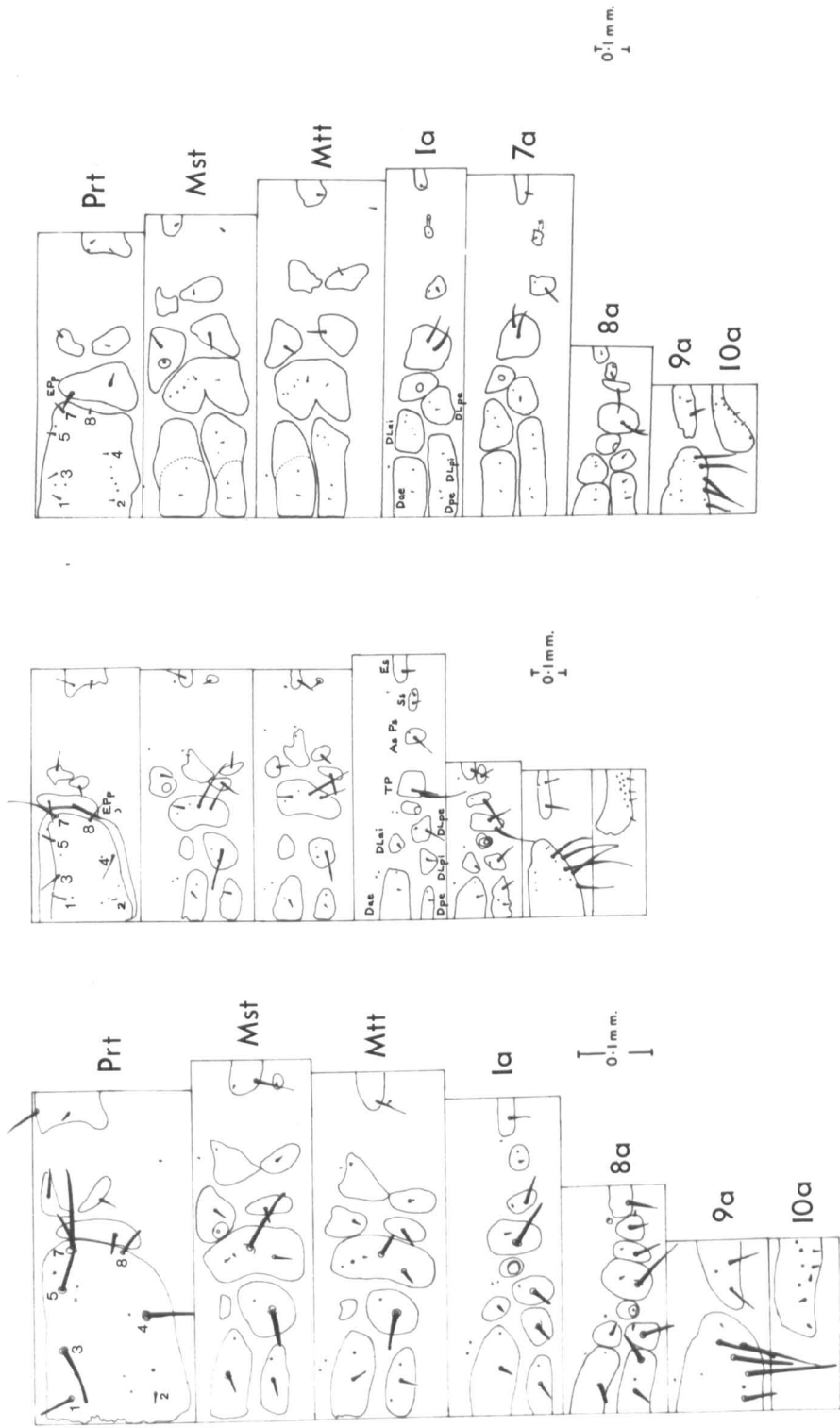


Fig. 27 *L. longicornis* F.

Fig. 28 *L. flavipes* L.



GALERUCELLA



AGELASTICA

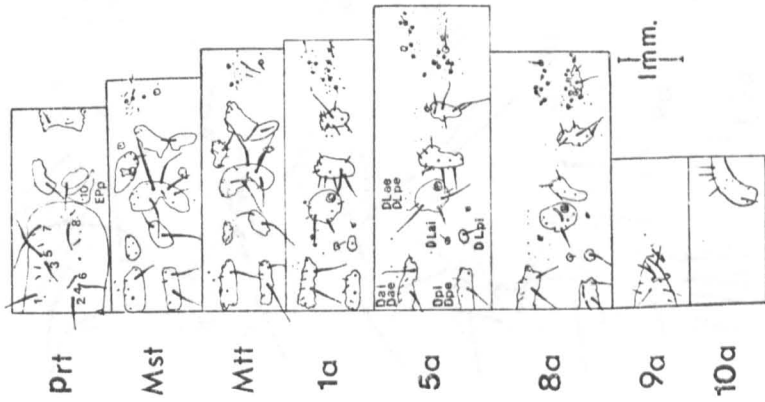


FIG. 32 A. alni (L.)

GALERUCA

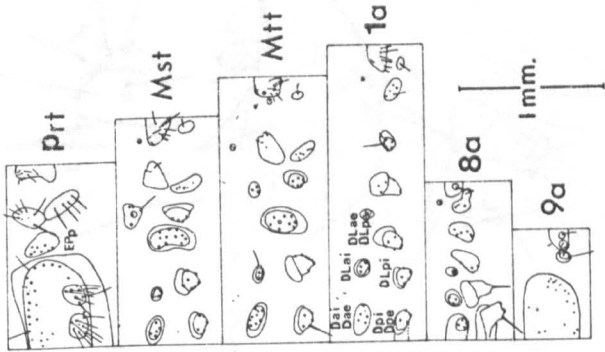


FIG. 33 G. tanacetii (L.)

GALERUCELLA

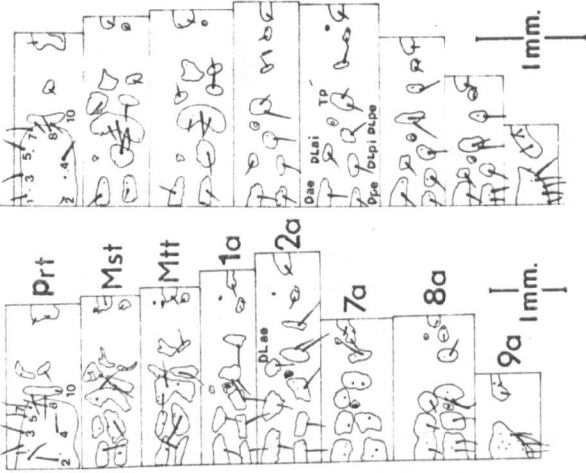
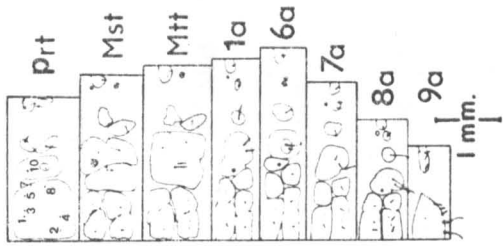
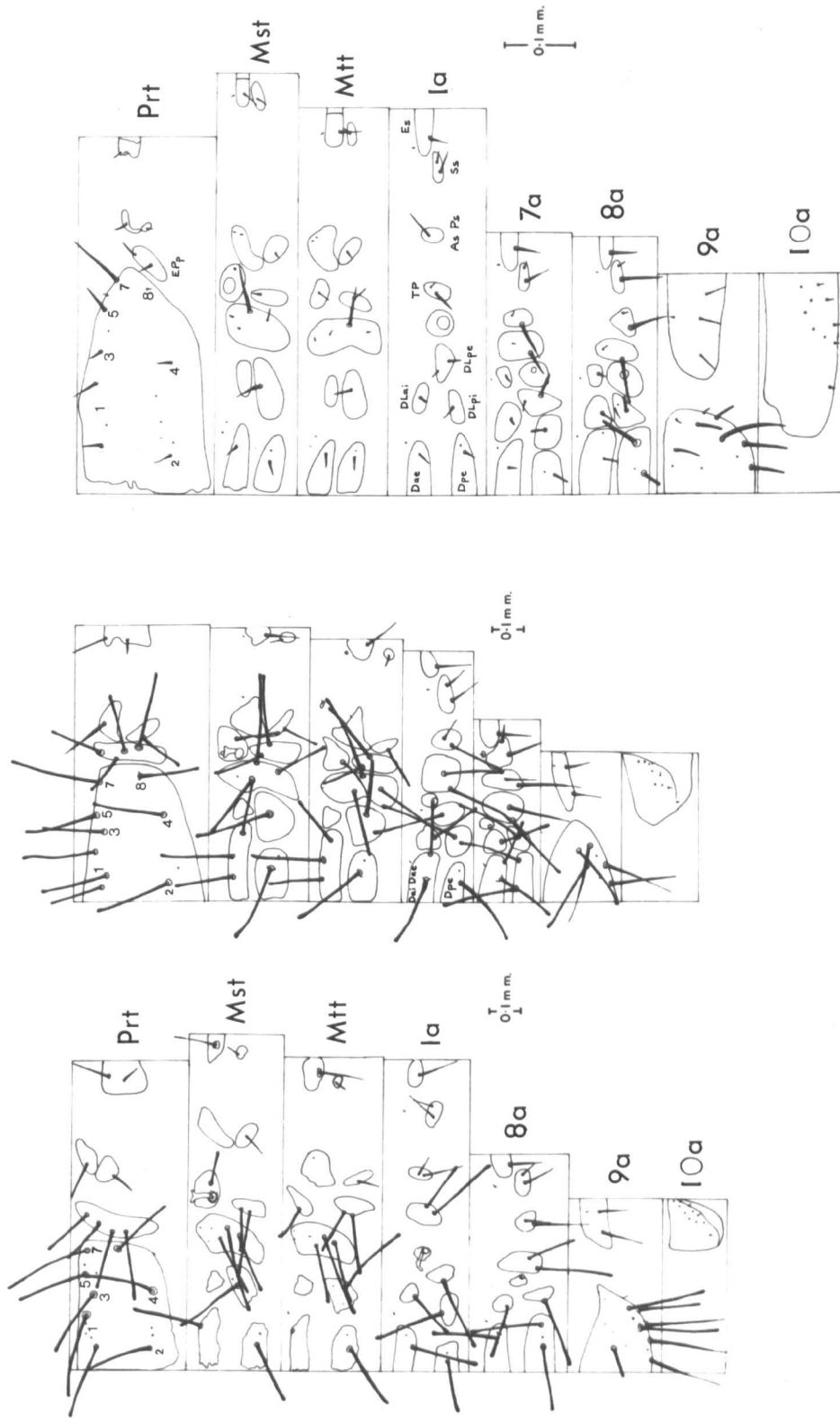


FIG. 34 G. viburni (Payk.)

FIG. 35 G. calmaridensis (L.)



LOCHMAEA



HALTICA

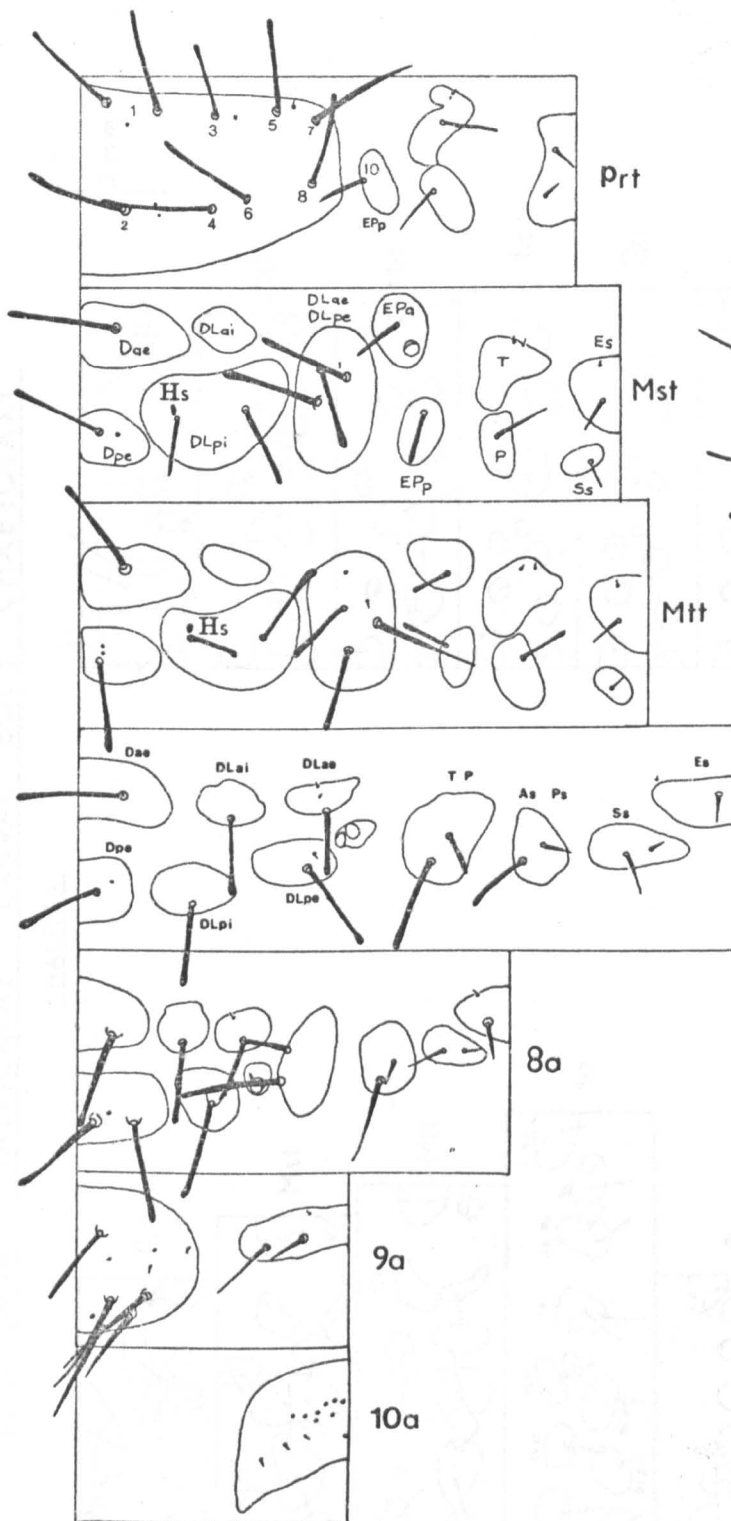


FIG. 40 *H. brittani* Shp. First instar

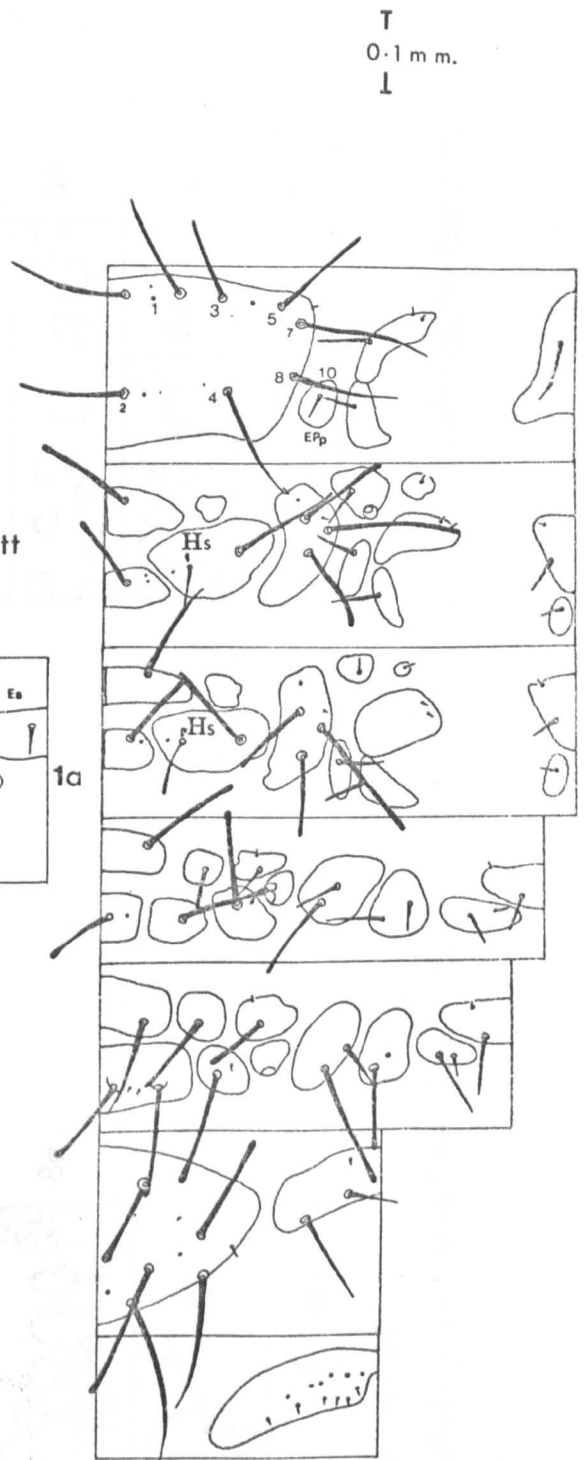


FIG. 41 *H. lythri* Aub. First instar

HALTICA

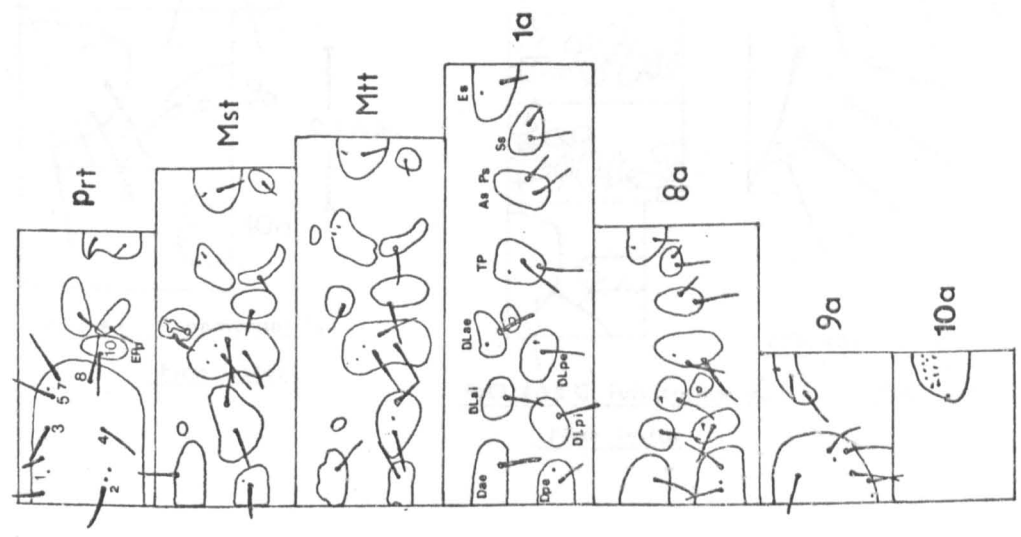


FIG. 42 *H. brevicollis* Foud. Final instar

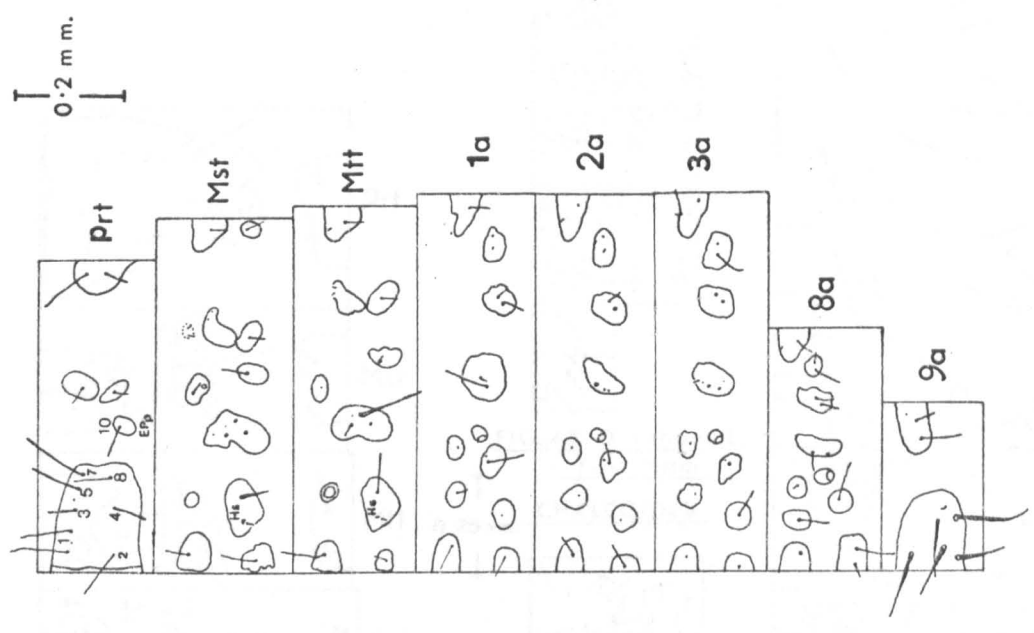


FIG. 43 *H. oleracea* (L.) First instar

HALTICINAE

PHYLLOTRETA

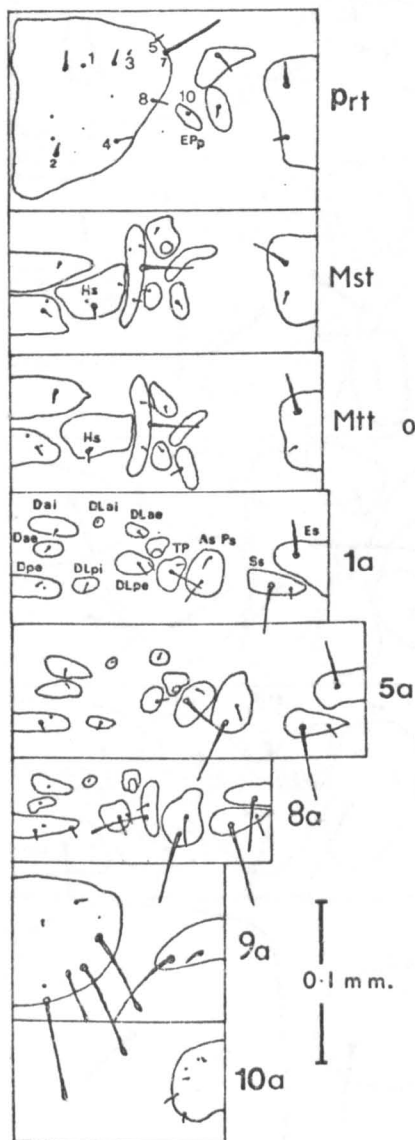


FIG. 44 *P. nemorum* (L.)  
First instar

DEROCREPIS

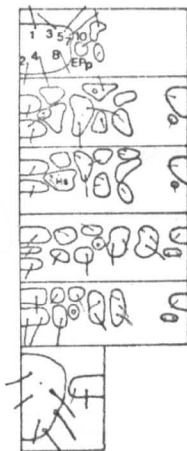


FIG. 45 *D. rufipes* (L.)

First instar

CHALCOIDES

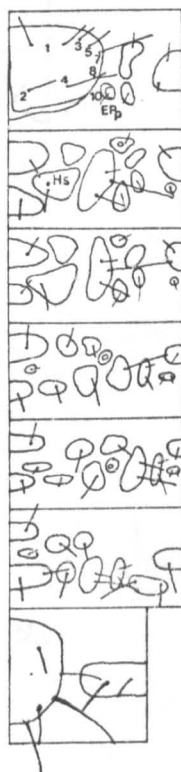


FIG. 46a *C. fulvicornis* (F.)  
First instar

LONGITARSUS

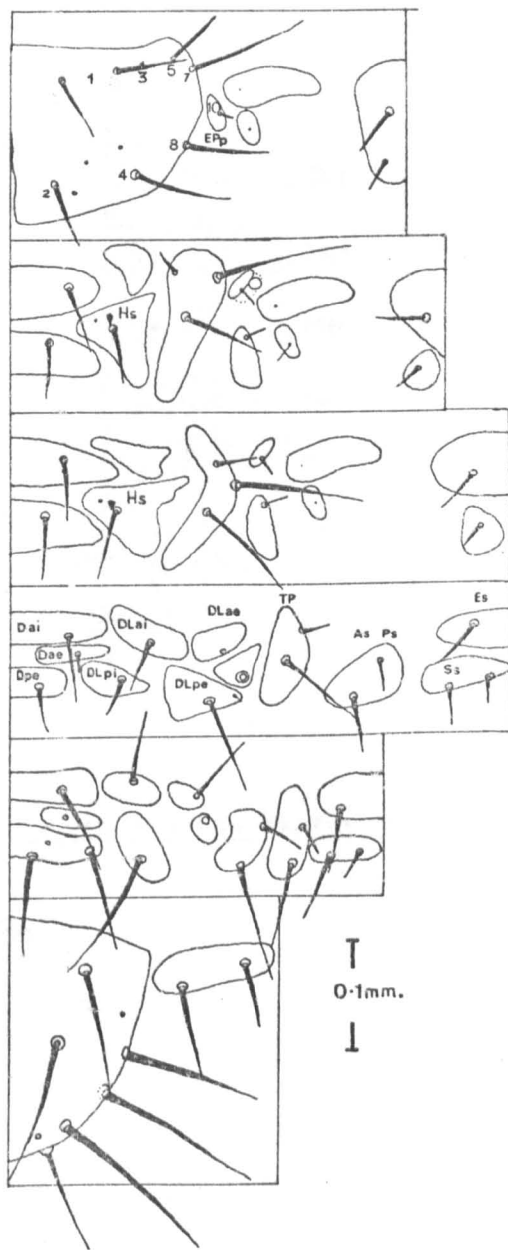


FIG. 46b. *L. melanocephalus* (De G.)  
First instar

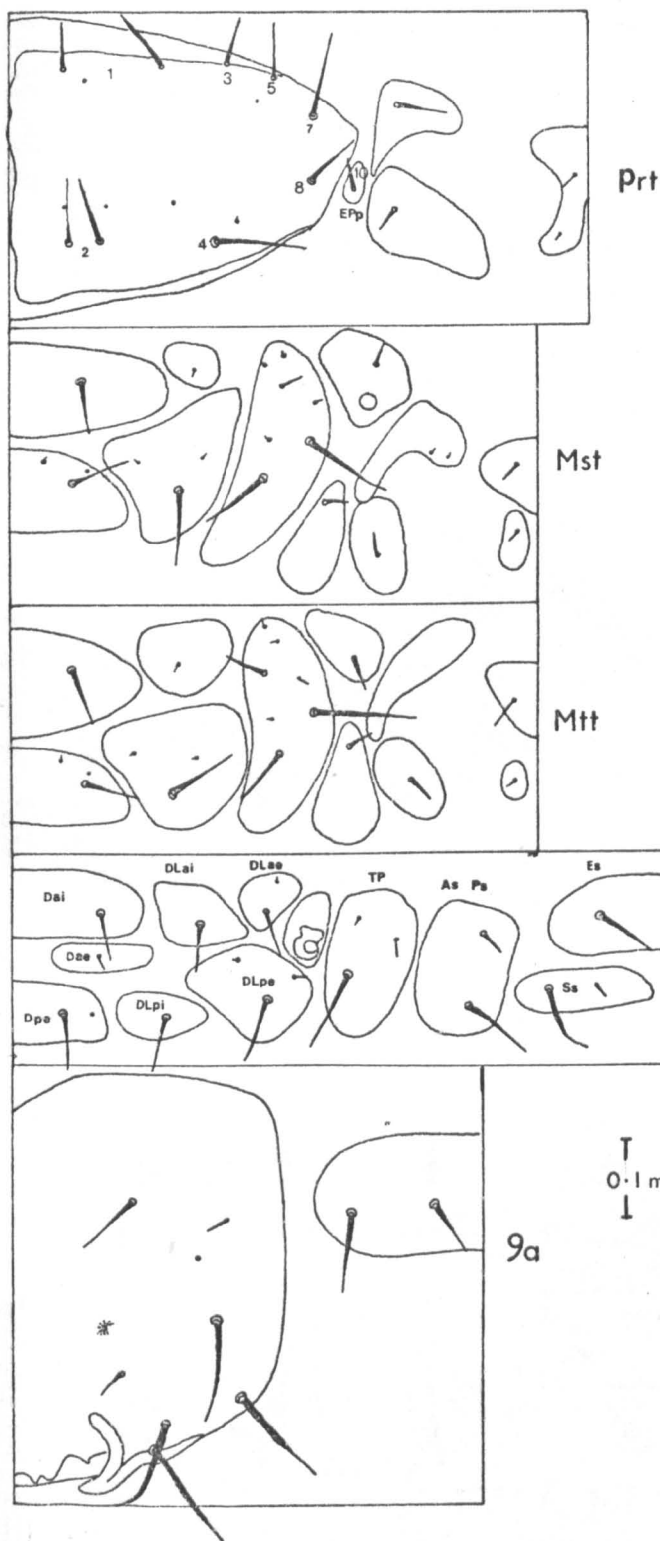


FIG.47 *P. napi* (F.) Final instar



FIG.48 *P. affinis* (Pk.) First instar

HERMAEOPHAGA



Fig. 49

*H. mercurialis* (F)

First instar

HIPPURIPHILA

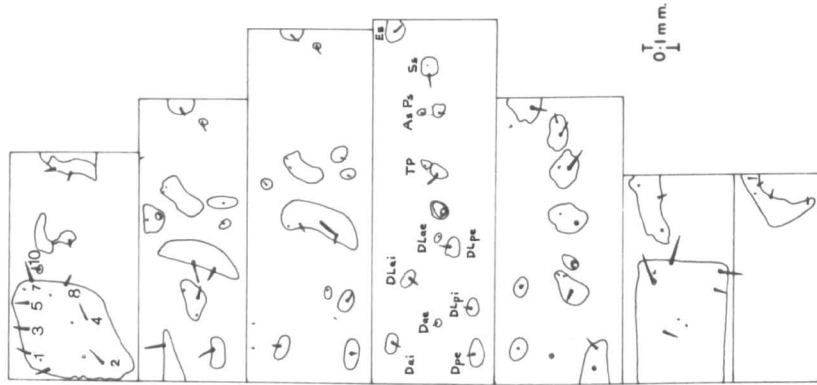


Fig.50 *H. modeeri* (L.)

Final instar

MANTURA

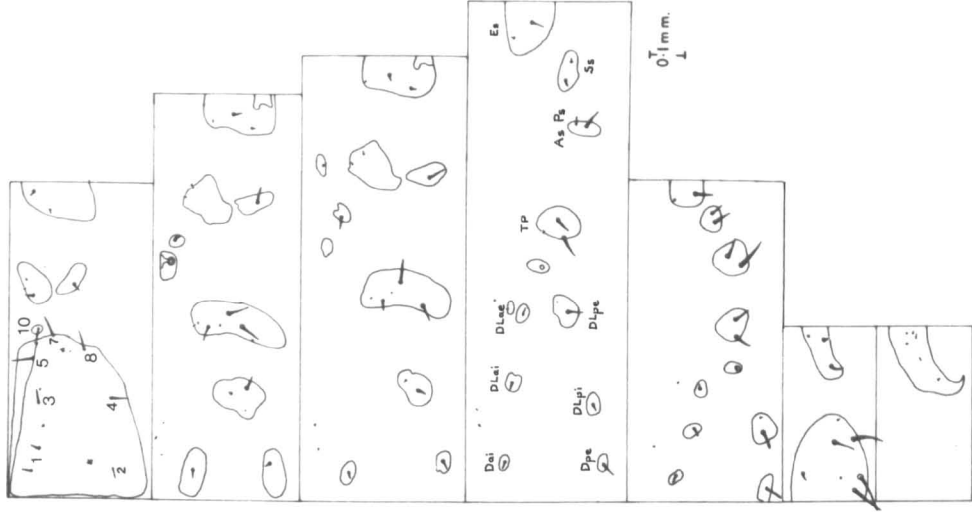


Fig.51 *M. rustica* (L.)

Final instar



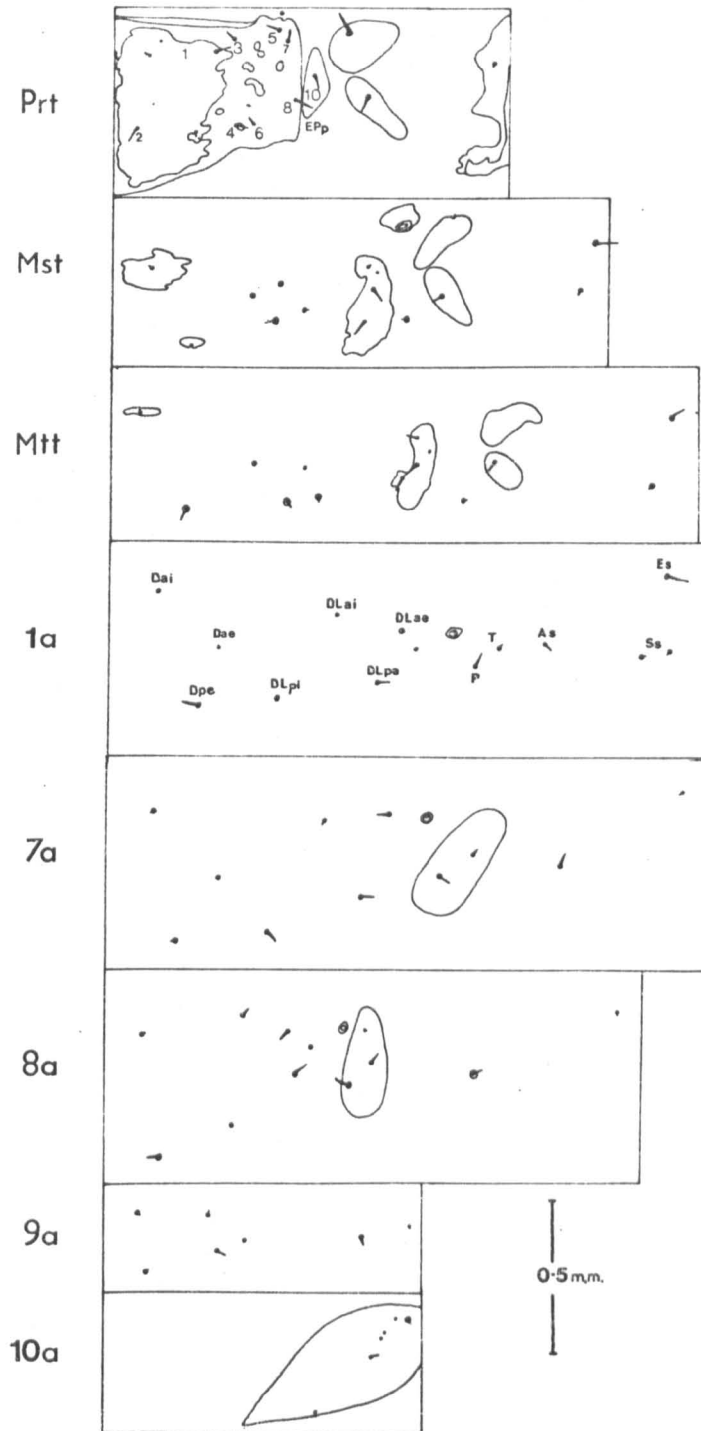


FIG. 52      FINAL INSTAR LARVA      *A. orbiculata* (Marsh.)

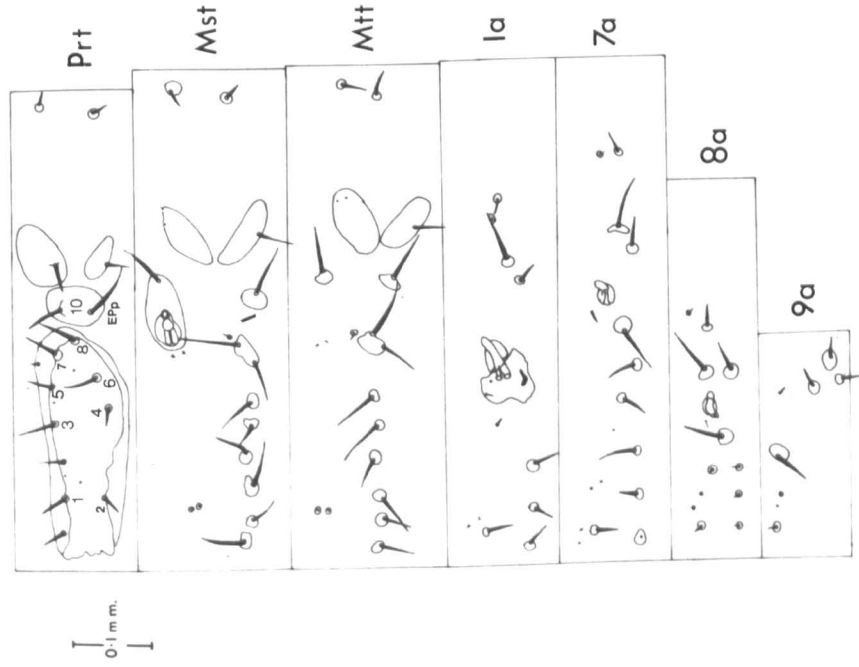


Fig. 53 *L. puncticollis* Curt.

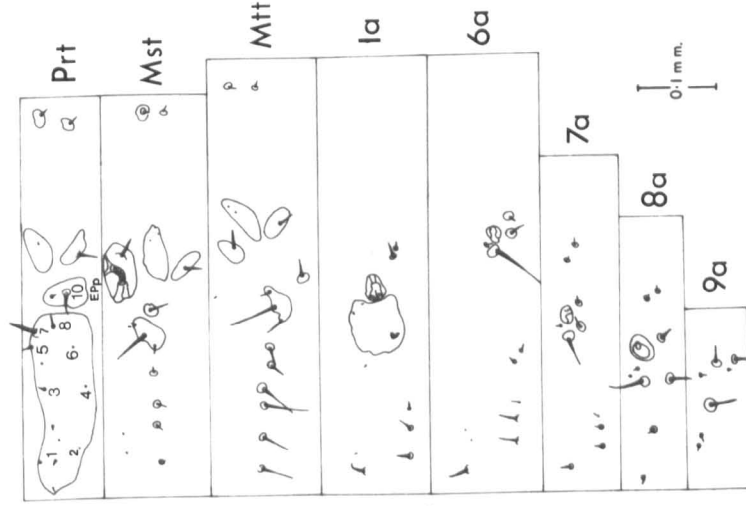


Fig. 54 *L. lichensis* Voet.

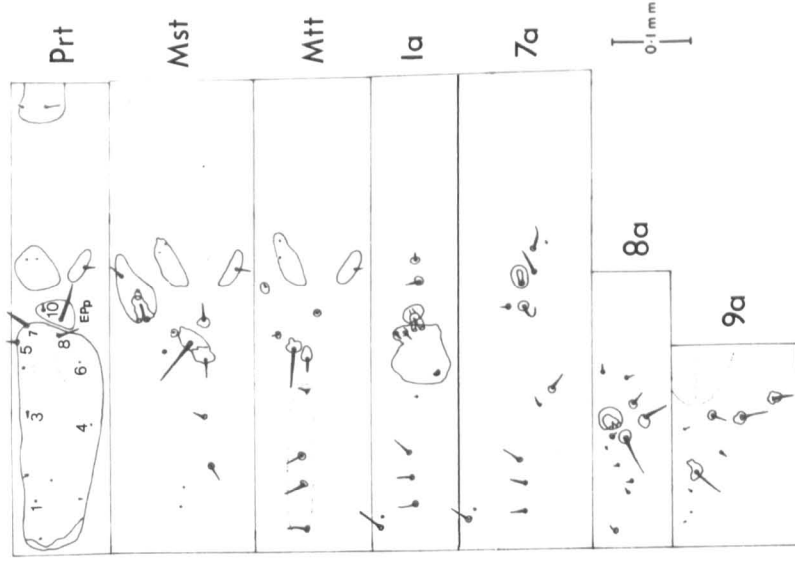


Fig. 55 *L. melanopa* (L.)

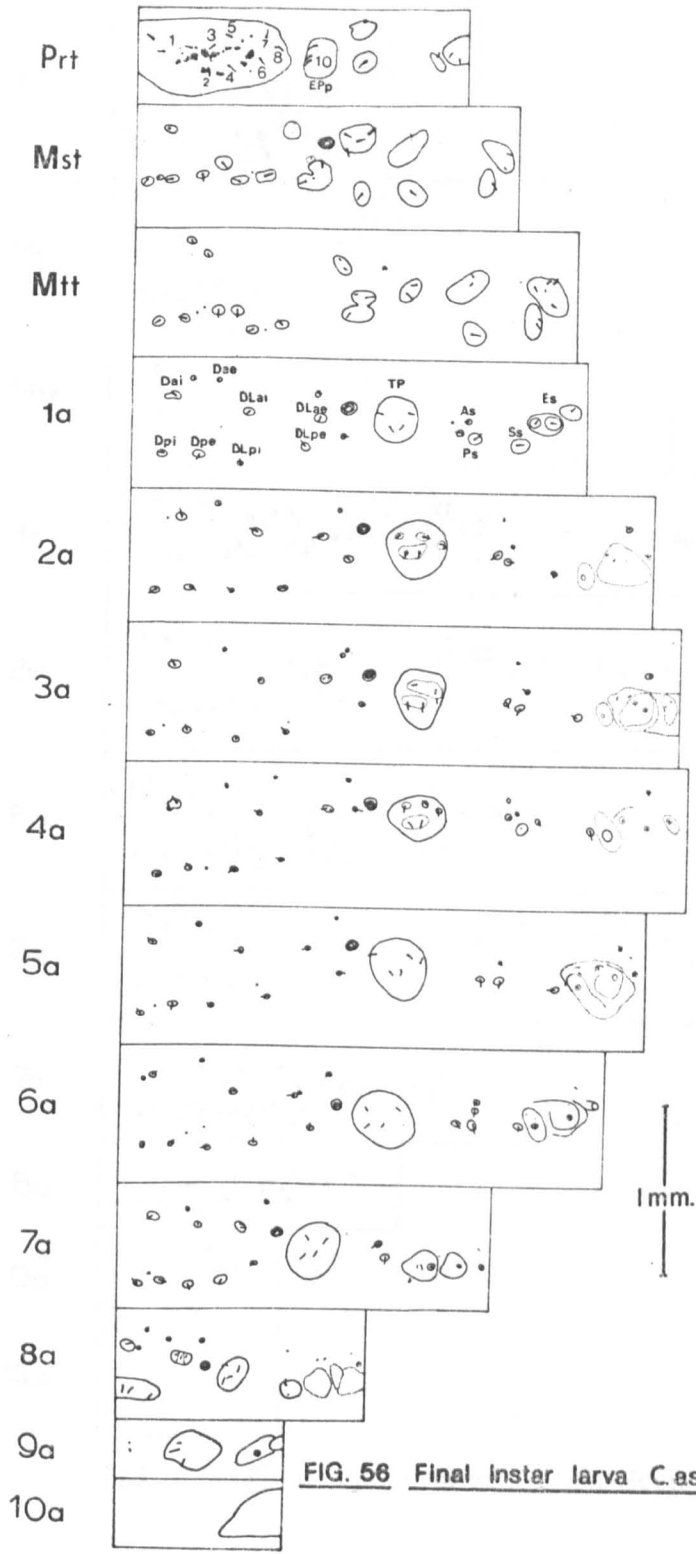


FIG. 56 Final instar larva *C. asparagi* (L.)

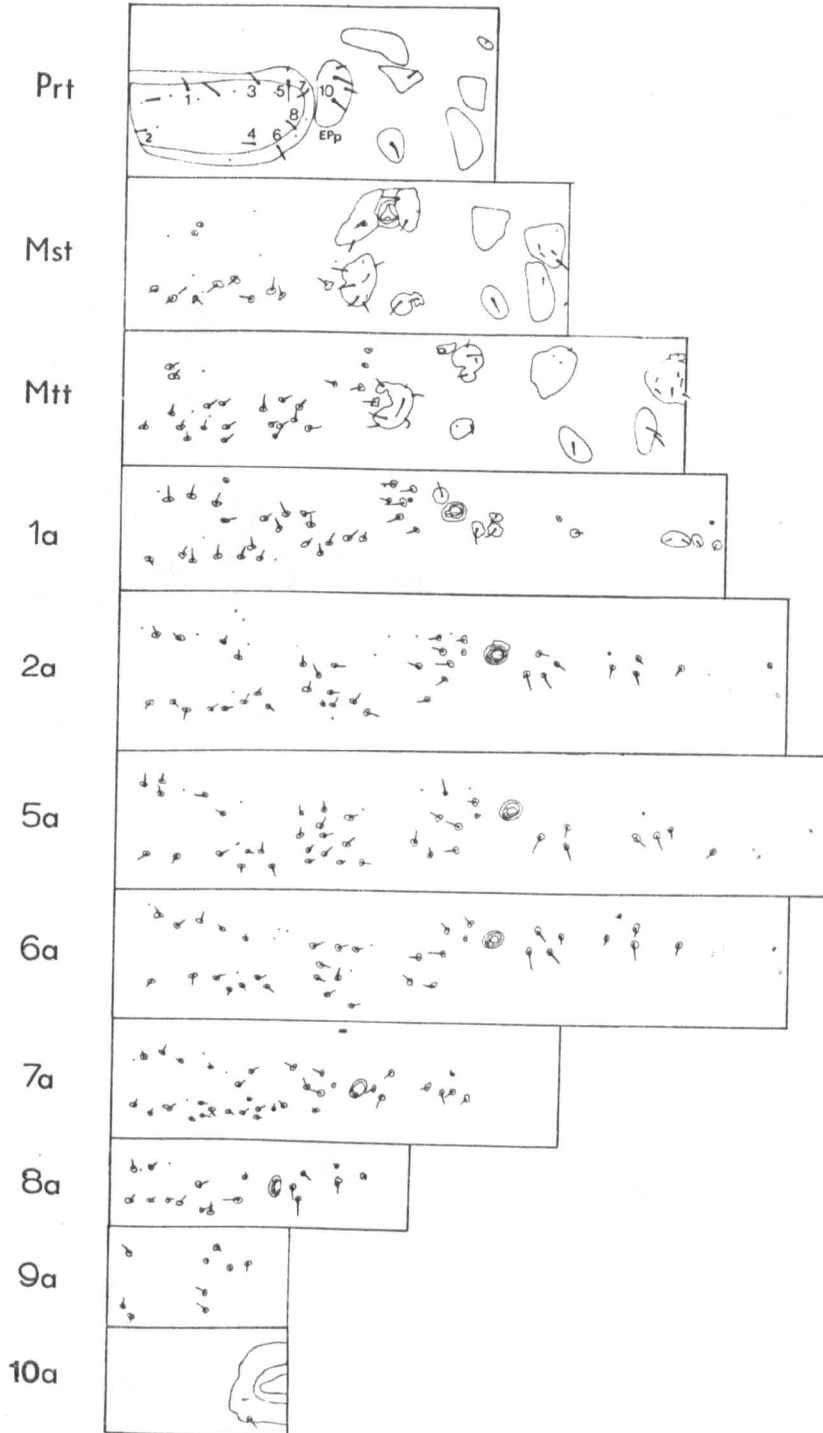


FIG. 57 Final Instar larva *L. lilli* (Scop)

CRYPTOCEPHALINAE

CRYPTOCEPHALUS

CLYTRINAE

CLYTRA

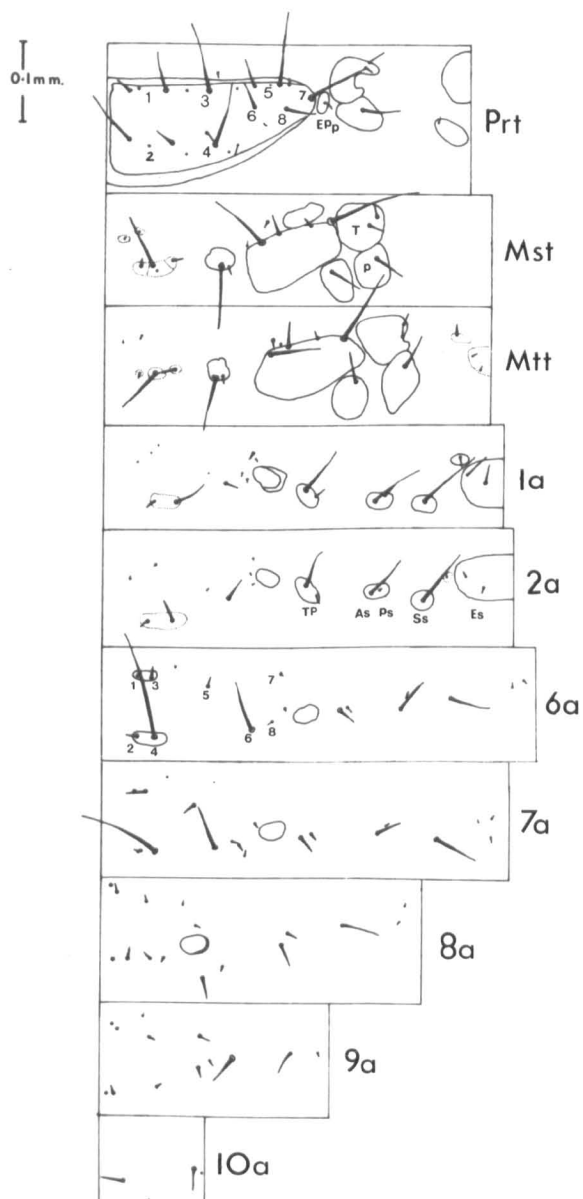


Fig. 58 *C. parvulus* Müll.

First instar

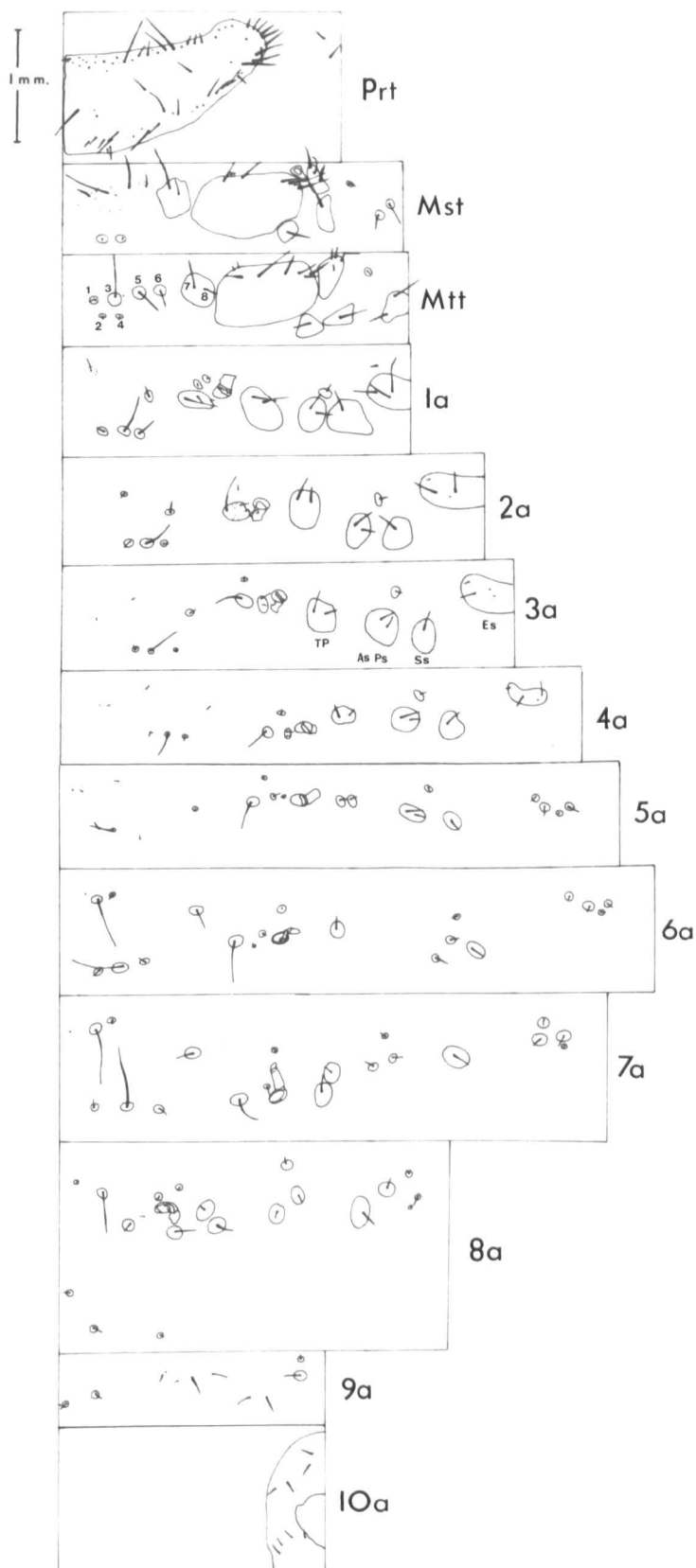


Fig. 59 *C. quadripunctata* (L.)

Final instar

PLATEUMARIS

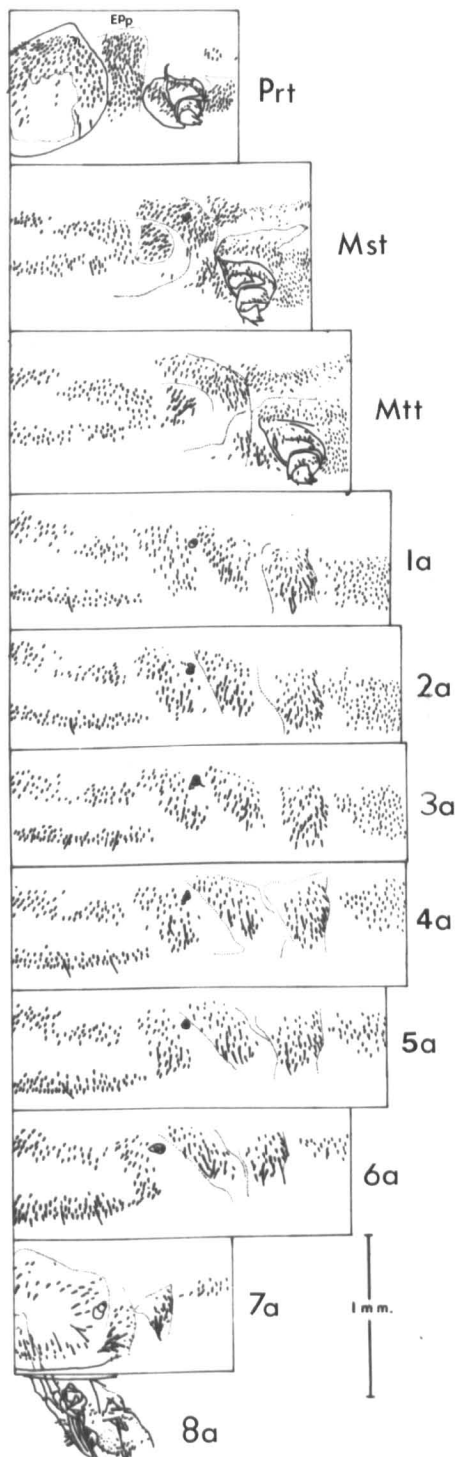


Fig. 60 *P. discolor* (Pz.)

MACROPLEA

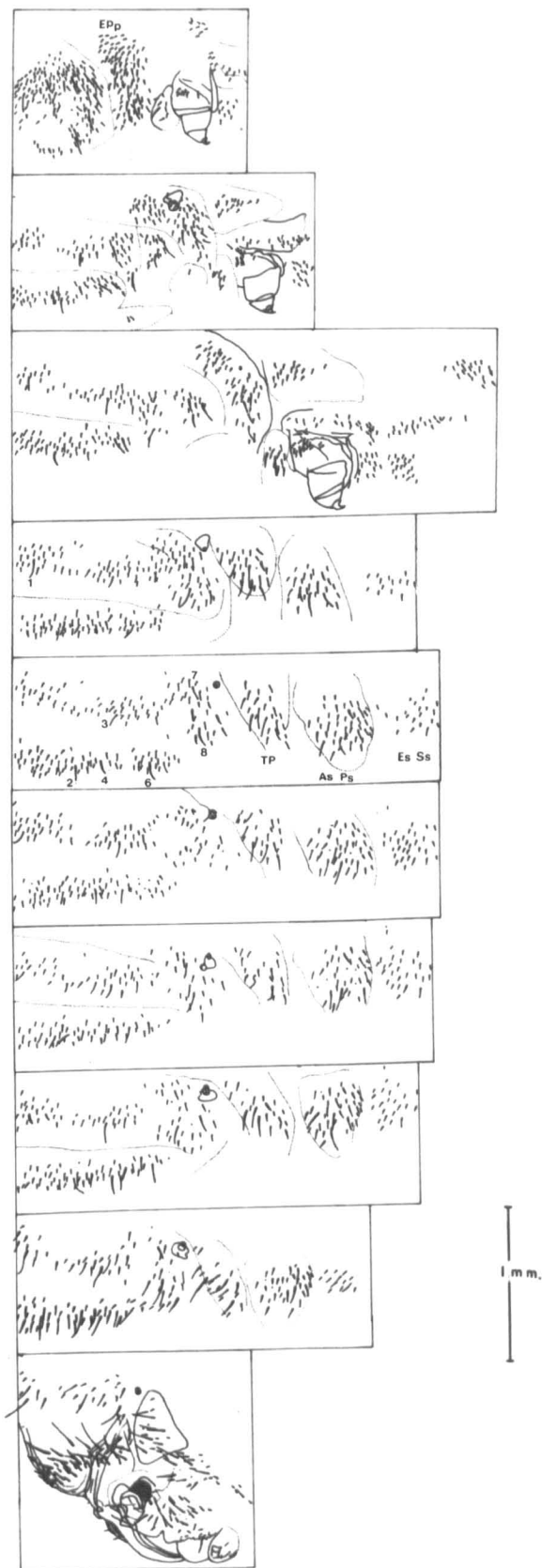


Fig. 61 *M. appendiculata* (Pz.)

FINAL INSTAR

DONACIA

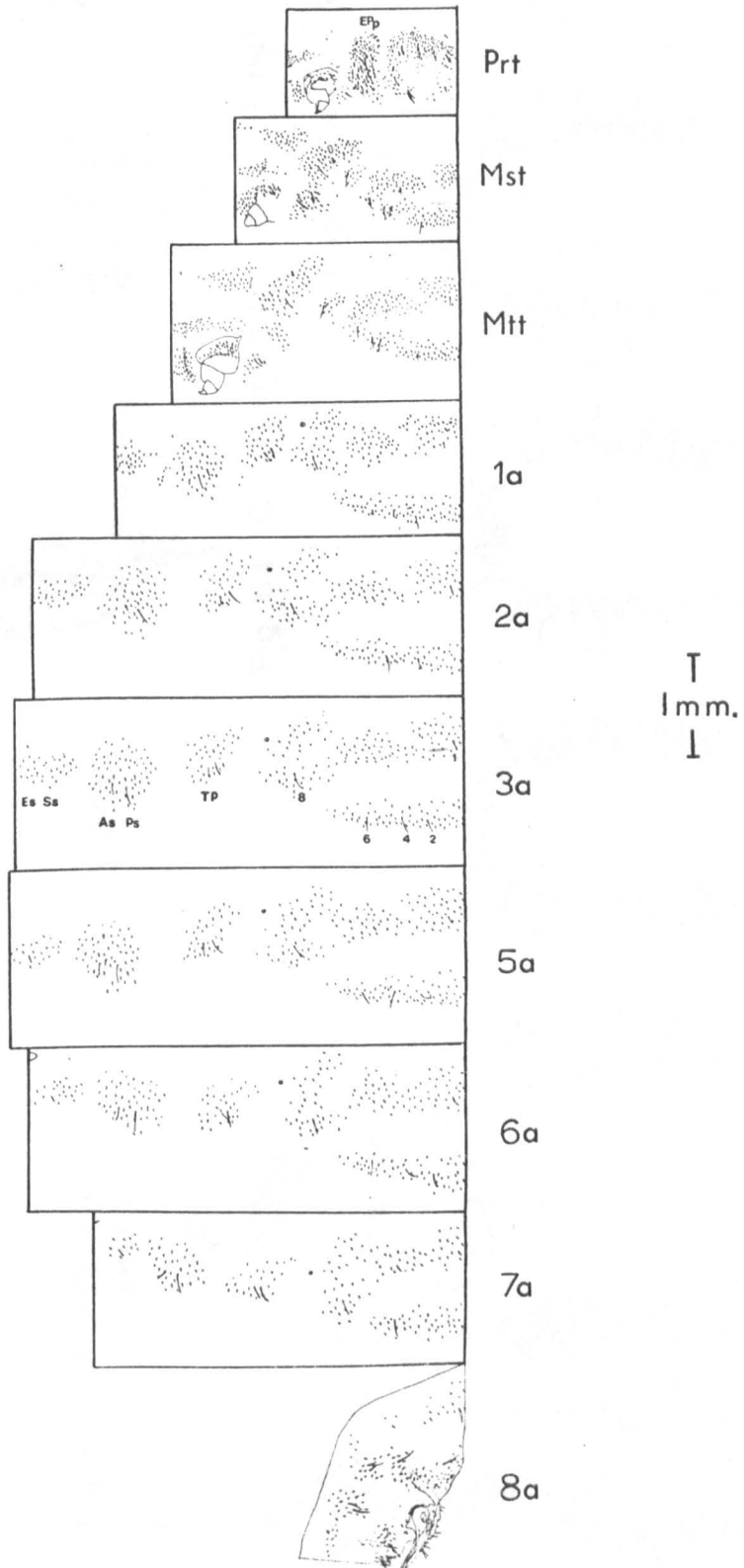
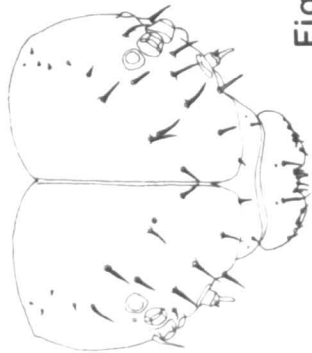


Fig. 62

D cinerea Hbst.

Final instar

a. Head Chaetotaxy



Dorsal view

PLATE LB 27  
C. rubiginosa Müll.

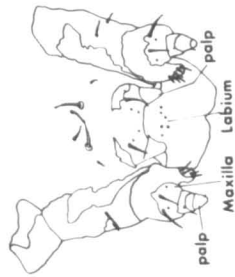


Fig. 63 b. Mouthparts

Ventral view

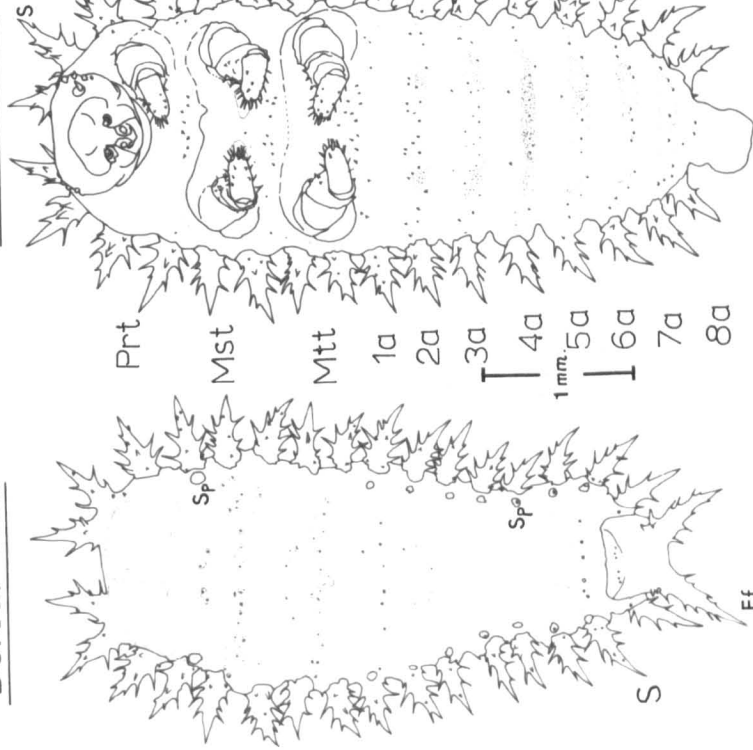
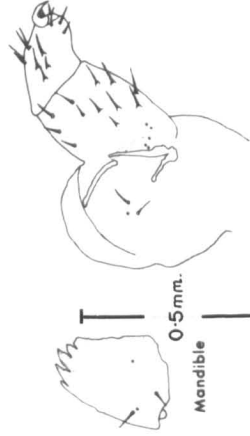


Fig. 65 C. flaveola Thunb. Third instar

CASSIDINAE  
Final instar



c. Left hindleg

CASSIDA LARVAE  
Lateral view

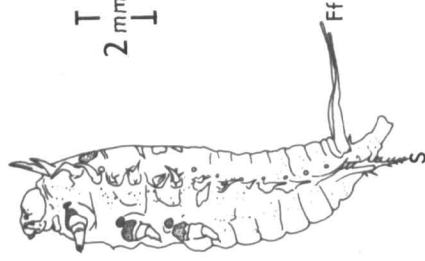
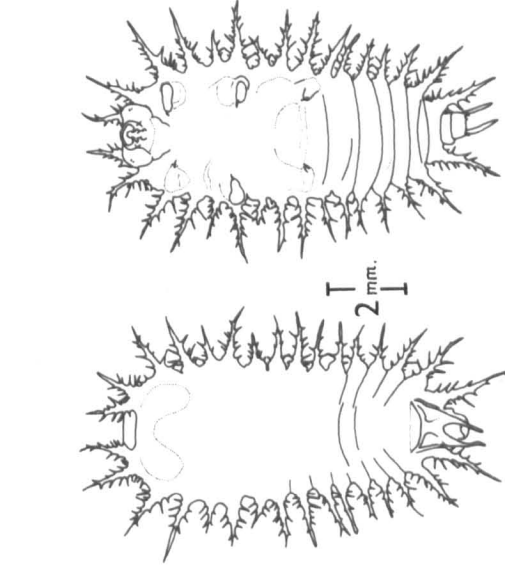


Fig. 64 C. rubiginosa Müll. Final instar

Dorsal view



Ventral view

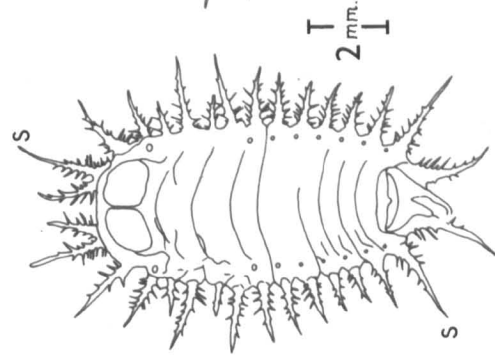


Fig. 66 C. viridis

L. Final instar

Fig. 67 C. murraea L. Final instar





Fig. 68 HEAD Dorsal view

Zeugophora flavicollis (Marsh.) FINAL INSTAR

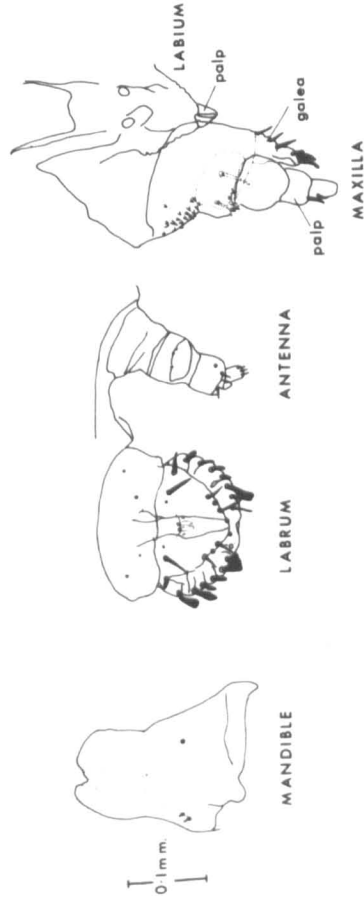


Fig. 69 Mouthparts

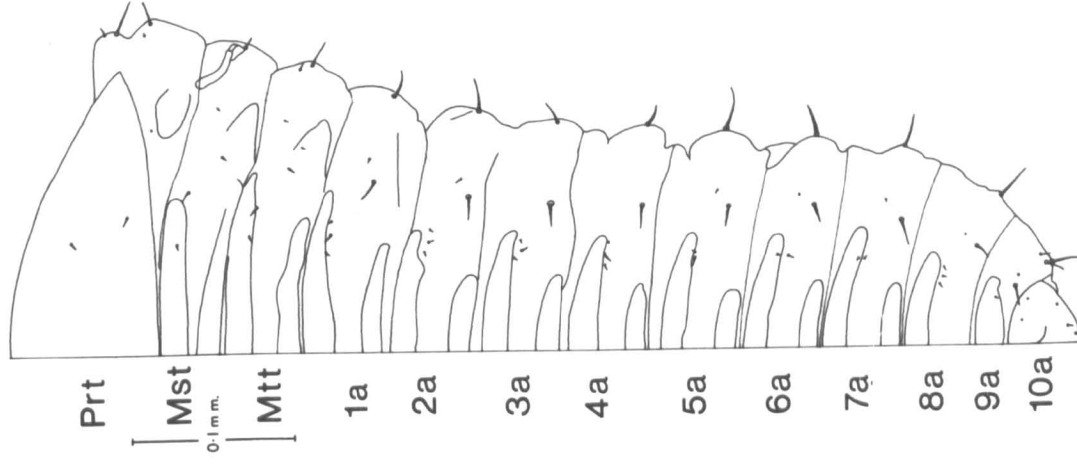


Fig. 70 Ventral view

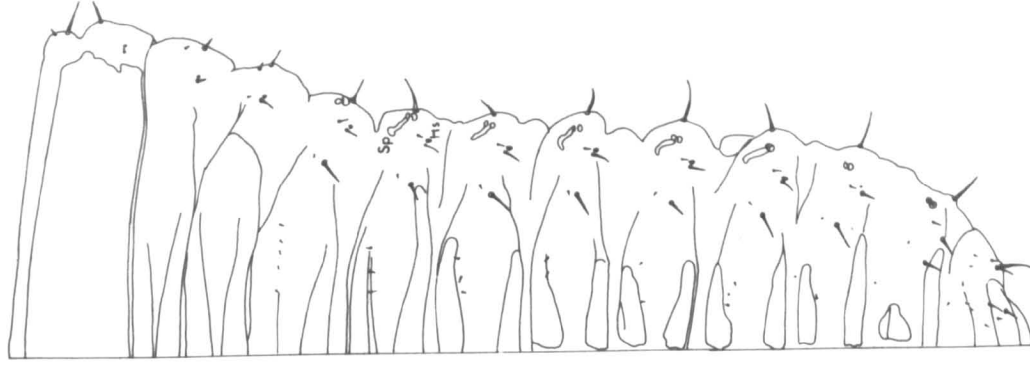


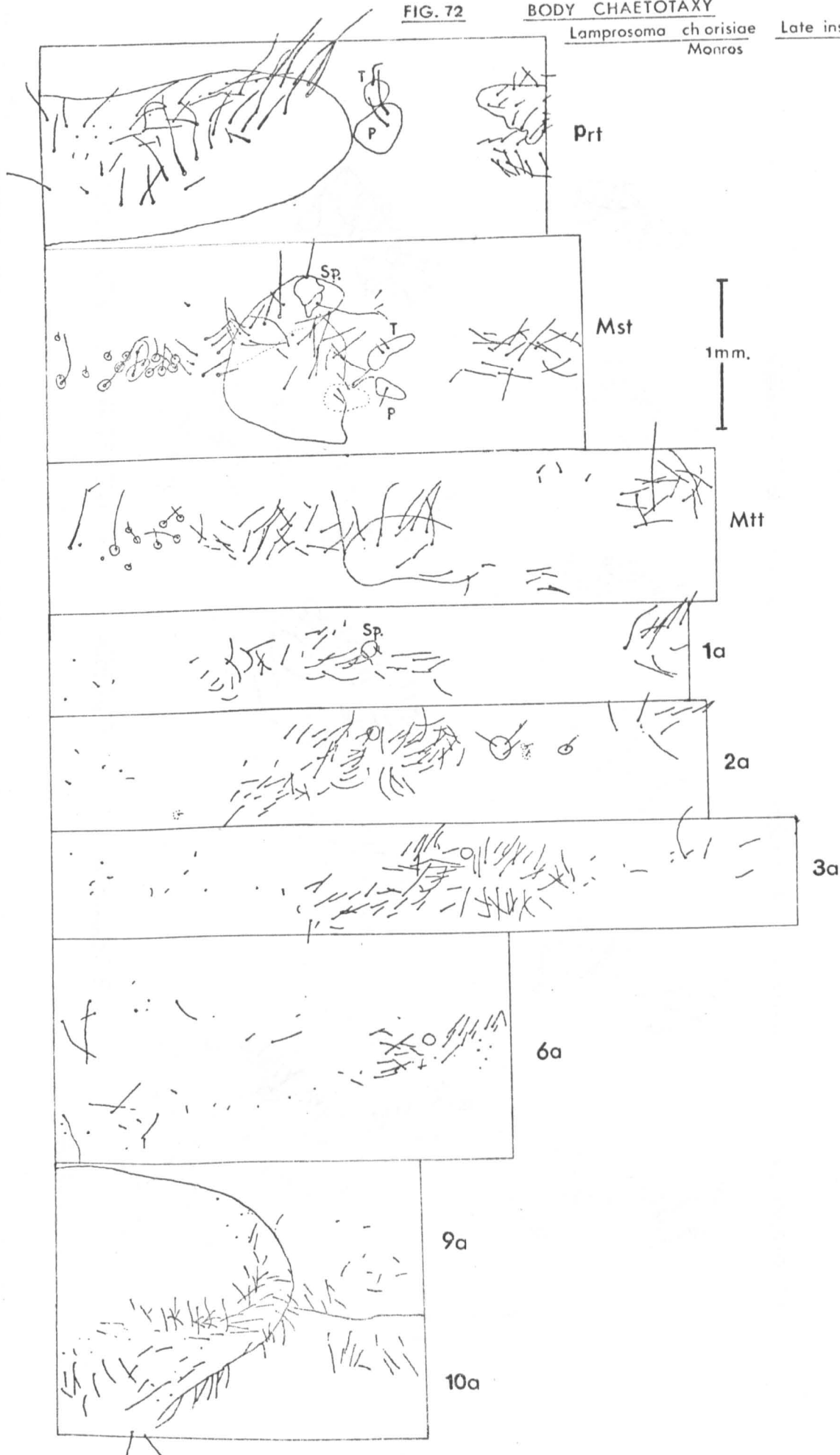
Fig. 71 Dorsal view

FIG. 72

BODY CHAETOTAXY

*Lamprosoma chorisiae*  
Monros

Late instar larva



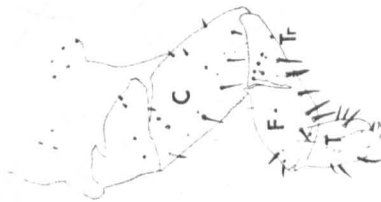
CHRYSEMELINAE

PLATE LL1

1. TIMARCHA



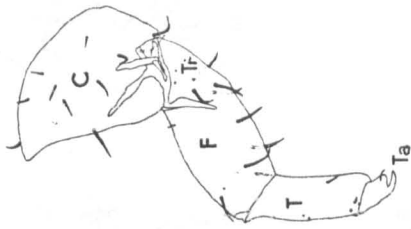
2. CHRYSOLINA



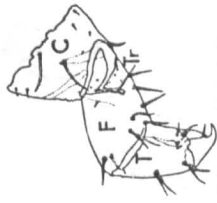
3. PHYTODECTA



4. LEPTINOTARSA



5. PHYLLODECTA



1 mm.



6. GASTROIDEA



7. PHAEDON



8. HYDROTHASSA



9. PRASOCURIS



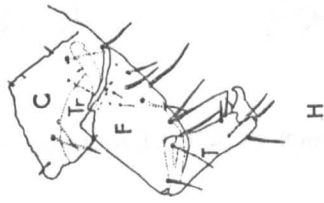
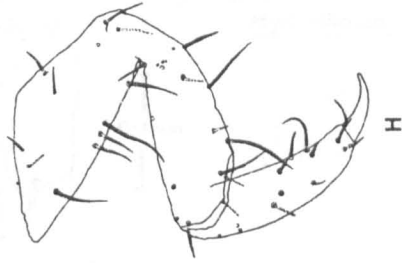
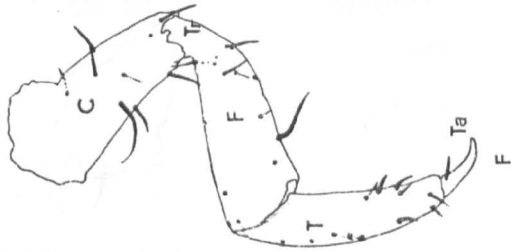
10. CHRYSOMELA



11. PLAGIODERA

CLYTRINAE & CRYPTOCEPHALINAE

12. CLYTRA



1 m m.

CRIOCERINAE

14. LEMA



CRIOCERINAE

GALERUCINAE



F

F FORE LEG

M MID "

H HIND "

15. LILIOCERIS

16. CRIOCERIS

17. PHYLLOBROTICA

Phyllodecta



FIG. 18 *P. vulgatissima* (L.)

Phaedon



FIG. 25 *P. armoraciae* (L.)

Timarcha



FIG. 32 *T. tenebricosa* (F.)

Phyllobrotica

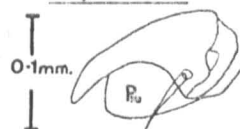


FIG. 35 *P. quadrimaculata* (L.)

Leptinotarsa



FIG. 19 *P. vitellinae* (L.)



FIG. 26 *P. cochleariae* (F.)

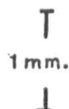


FIG. 33 *L. decemlineata* (Say)

Galeruca



FIG. 36 *G. tanacetii* (L.)

Lochmaea



FIG. 37 *L. crataegi* (Forst.)

Chrysolina



FIG. 20 *P. laticollis* (Suf.)



FIG. 27 *P. tumidulus* (Germ.)

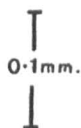


FIG. 34 *C. graminis* (L.)

Phytodecta



FIG. 21 *P. pallida* (L.)



Hydrothassa



FIG. 28 *H. marginella* (L.)

Prasocuris



FIG. 22 *P. versicolora* (Laich.)



FIG. 29 *P. junci* (Brahm.)

Chrysomela



FIG. 23 *C. populi* (L.)

Gastroidea



FIG. 30 *G. polygona* (L.)

Plagioderia



FIG. 24 *P. versicolora* (Laich.)



FIG. 31 *P. viridula* (DeG.)

Galerucella



FIG. 40 *G. viburni* (Pk.)

Haltica



FIG. 41 *H. lythri* (Aub.)

CHRYsolina

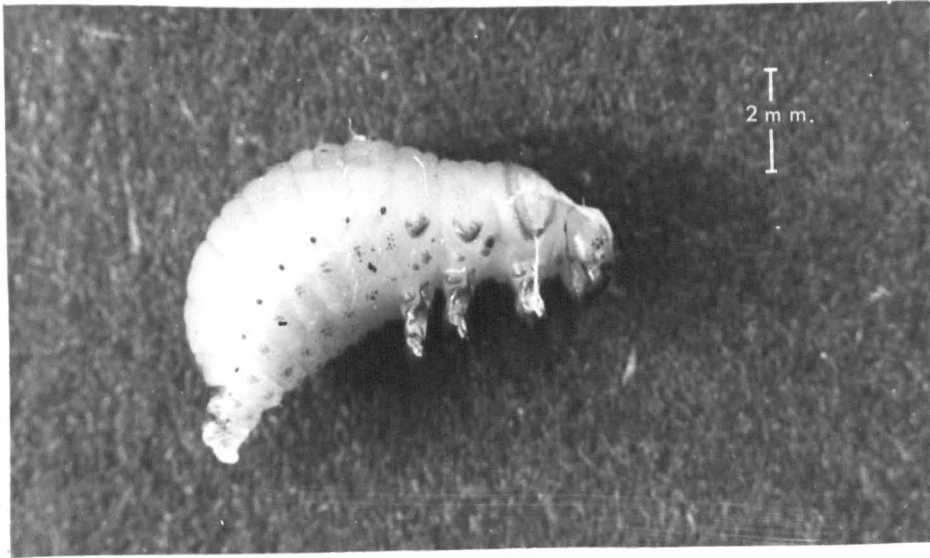


FIG. 1 C. staphylea (L.)



FIG. 2 C. polita (L.)

TIMARCHA



FIG. 3 T. tenebricosa (F.)

CHRYSOLINA



FIG. 4 C. brunsvicensis (Gr.)



FIG. 5 C. hyperici (Forst.)



FIG. 6 C. varians (Schal.)

CHRYSOLINA



FIG. 7 C. graminis (L.)



FIG. 8 C. menthastri (Suf.)



FIG. 9 C. fastuosa (Scop.)



PHYTODECTA



FIG. 10 P. olivacea Forst.

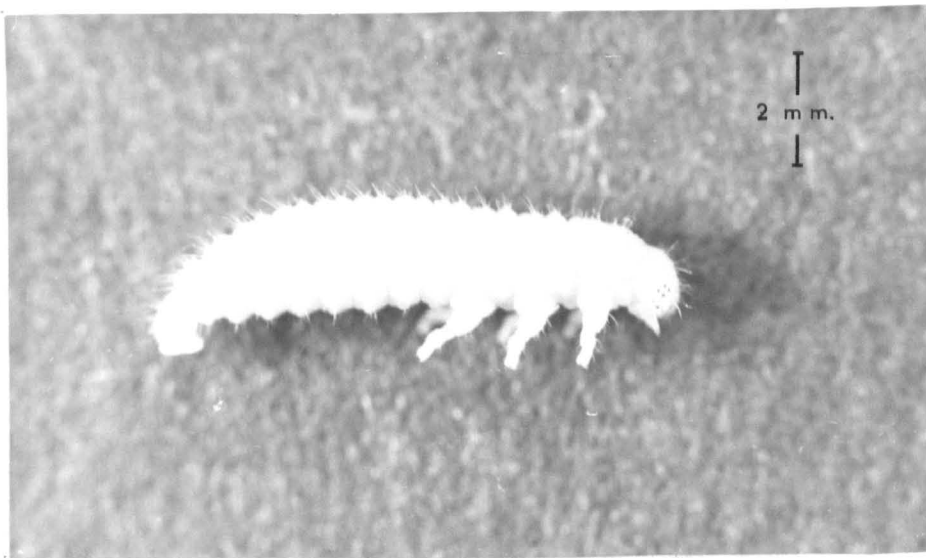


FIG. 11 P. pallida L.

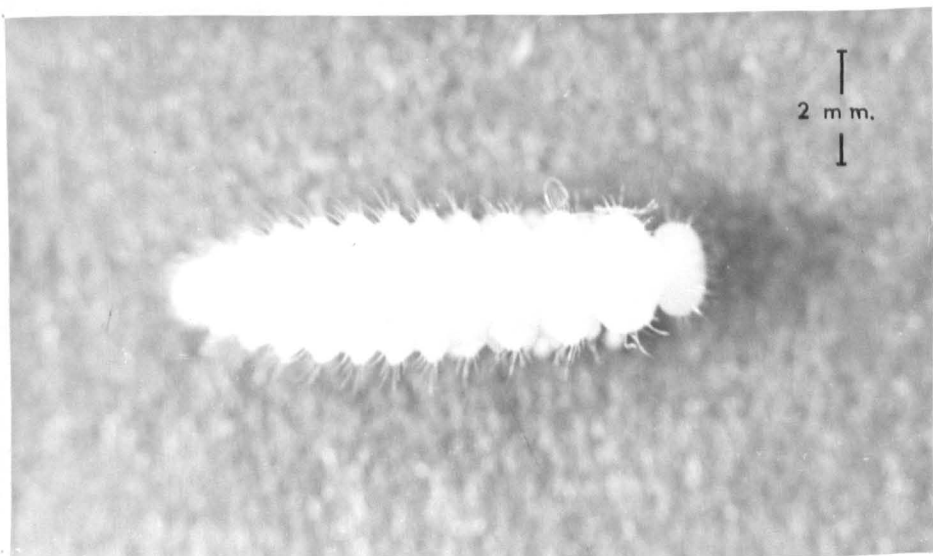


FIG. 12 P. pallida L. Dorsal view

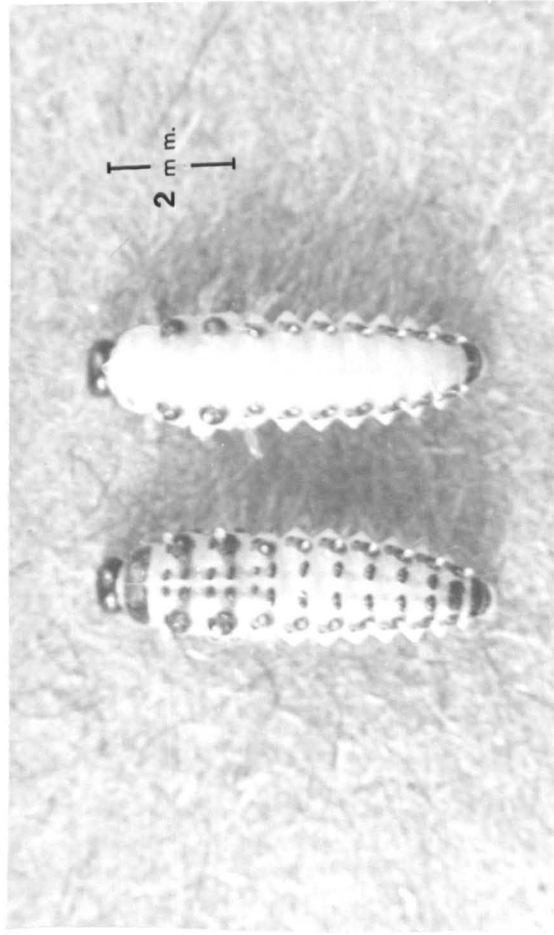


FIG. 13 The two forms of *P. laticollis* Suf. Dorsal view

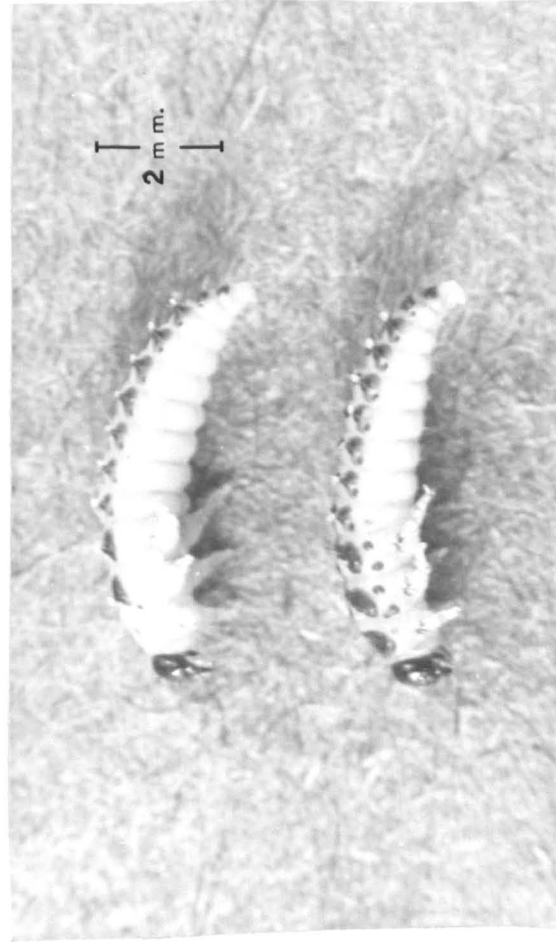


FIG. 14 "*P. laticollis* Suf. Lateral view



FIG. 15 *P. vitellinae* (L.)

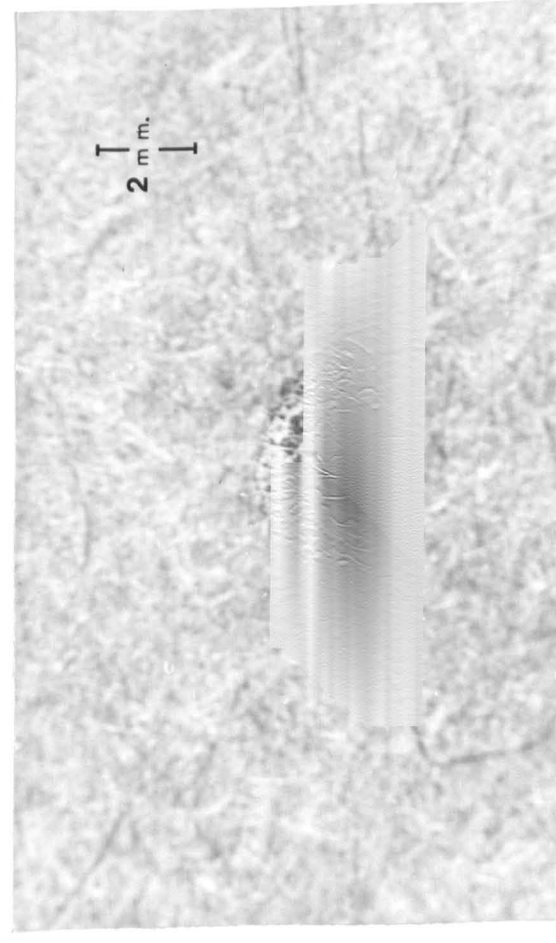


FIG. 16 *P. vulgatissima* (L.)

PHAEDON



FIG. 17 P. armoraciae (L.)



FIG. 18 P. cochleariae (F.)



FIG. 19 P. tumidulus (Germ.)

CHRYSEMELA

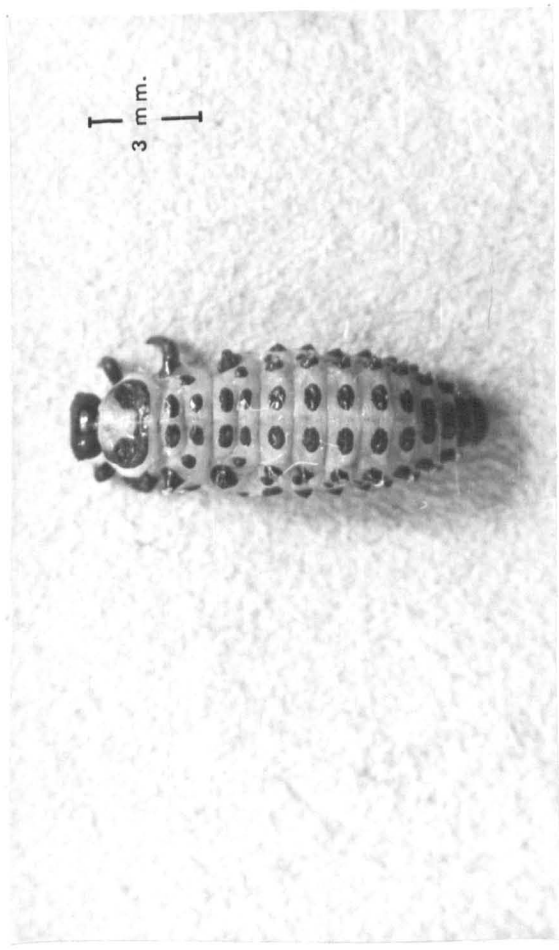


FIG. 20 C. populi L. Dorsal view



FIG. 22 G. viridula (De G.)



FIG. 21 C. populi L.



FIG. 23 G. polygani (L.)

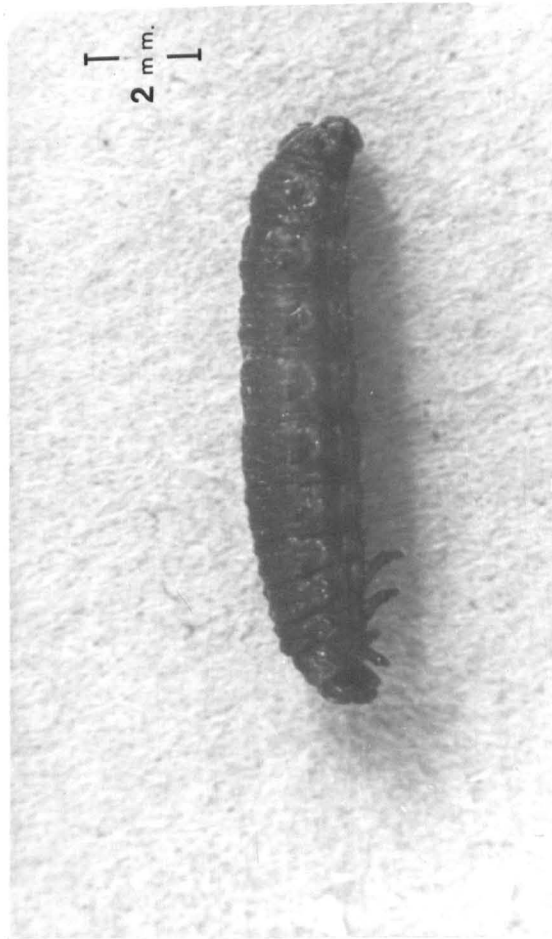


FIG. 24 *Agelastica alni* (L.)

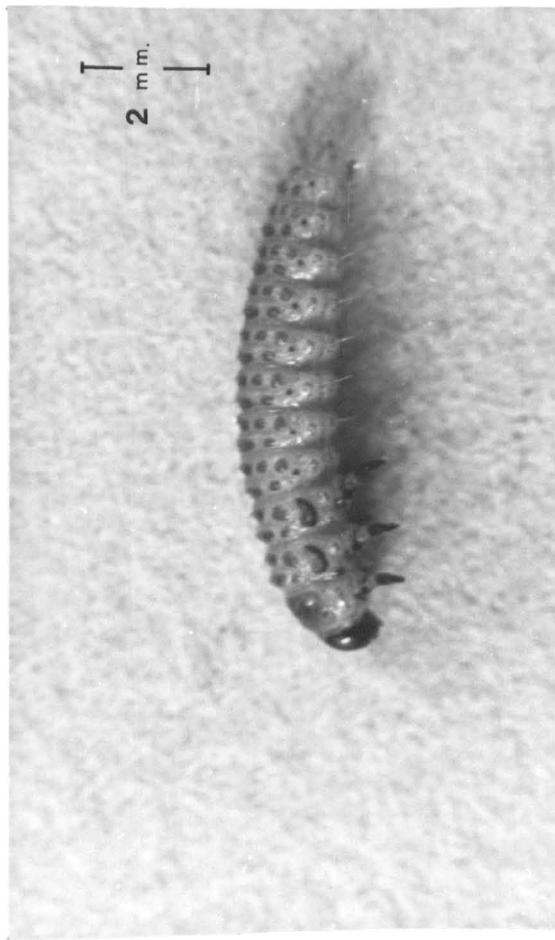


FIG. 26 *L. capreae* (L.)



FIG. 25 *Phyllobrotica quadrimaculata* (L.)



FIG. 27 *L. suturalis* (Th.)



GALERUCELLA



FIG. 28 *G. lineola* (F.)

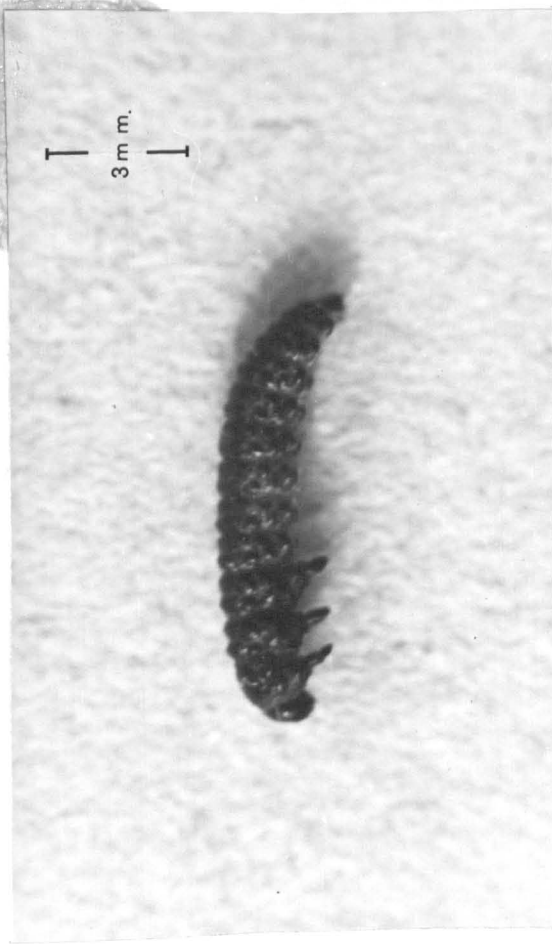


FIG. 30 *G. sagittariae* Brit. Cat.

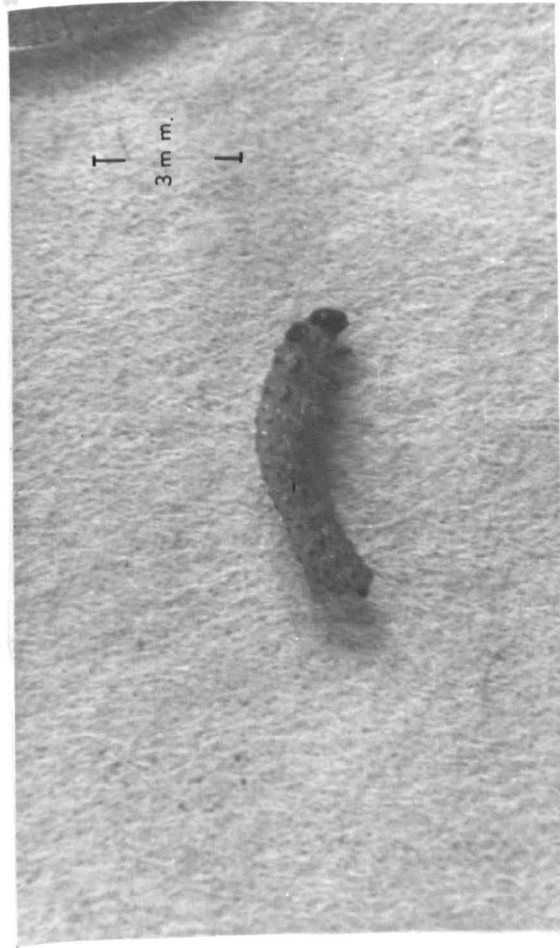


FIG. 29 *G. tenella* (L.)

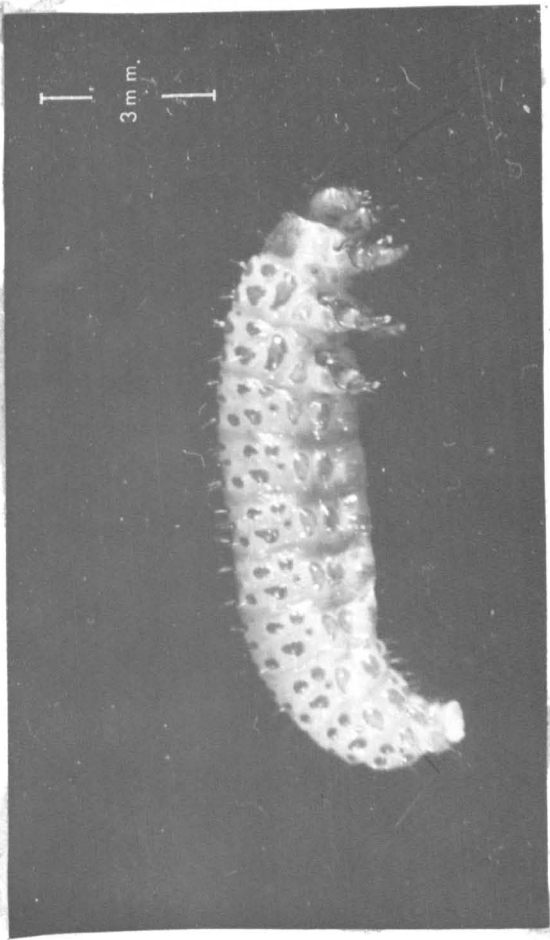


FIG. 31 *Sermyle halensis* (L.)

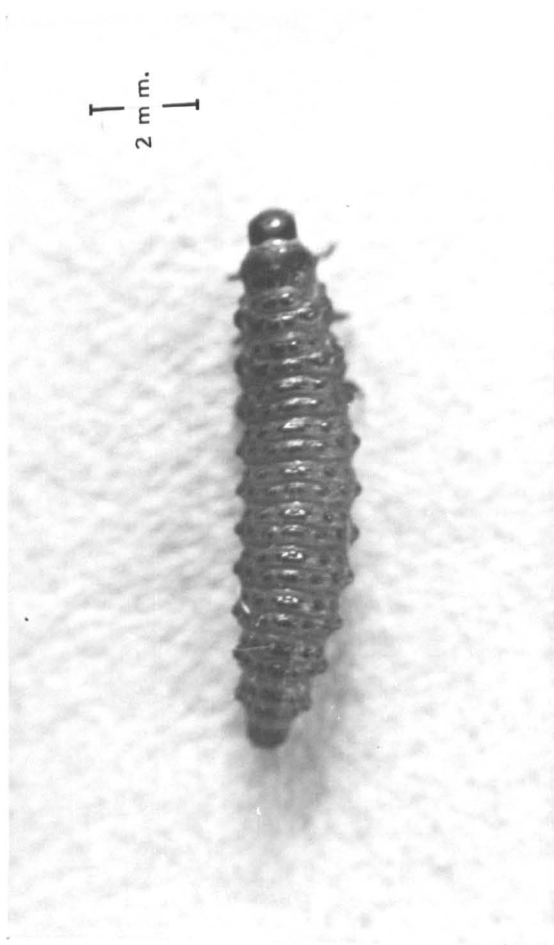


FIG. 32 *H. lythri*, Aub. Dorsal view

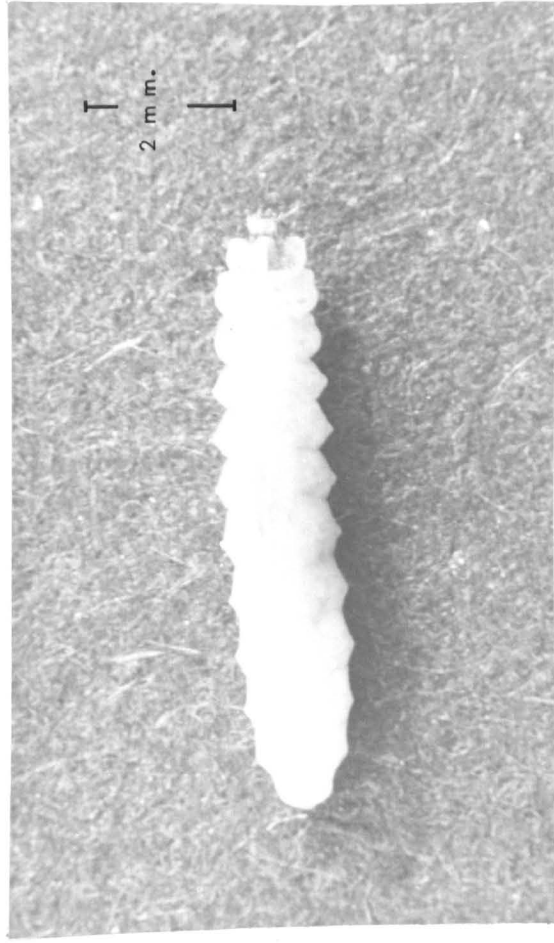


FIG. 34 *S. testaceum* (F.) Dorsal view

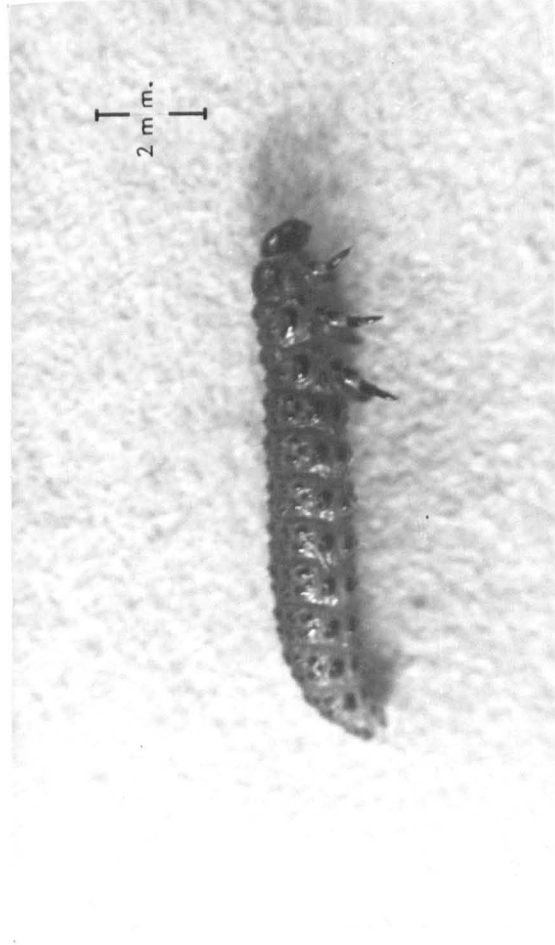


FIG. 33 *H. lythri*, Aub.



FIG. 35 *S. testaceum* (F.)

LEMA

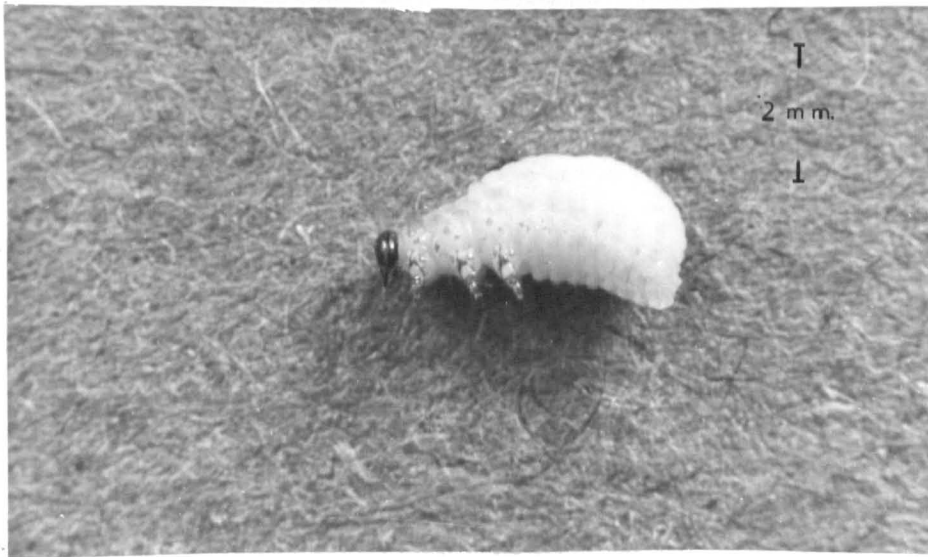


FIG. 36 L. puncticollis Curt.

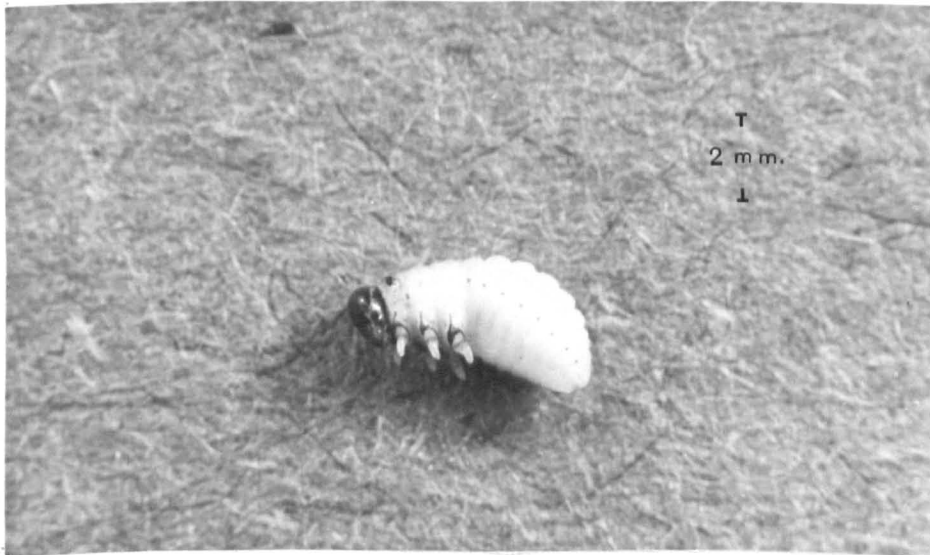


FIG. 37 L. melanopa (L.)

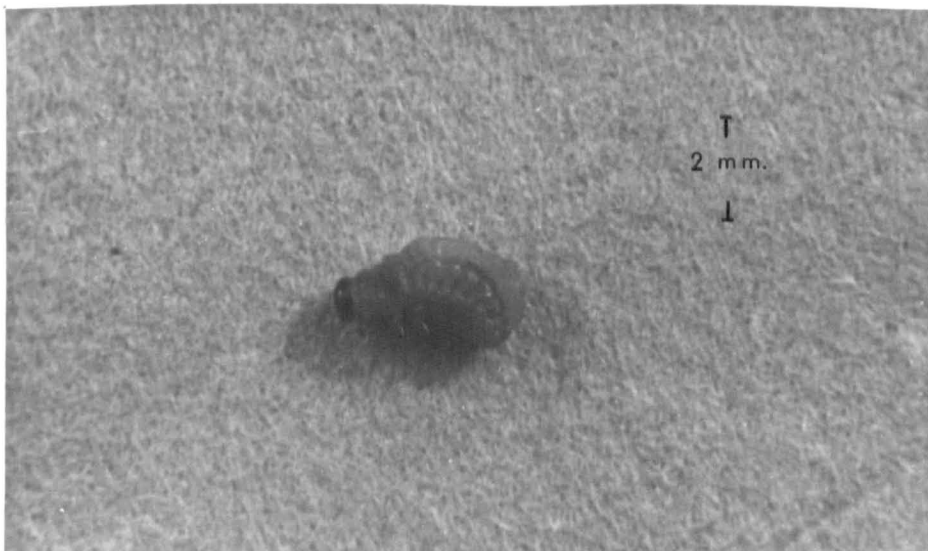


FIG. 38 L. lichensis Voet.



CRYPTOCEPHALUS

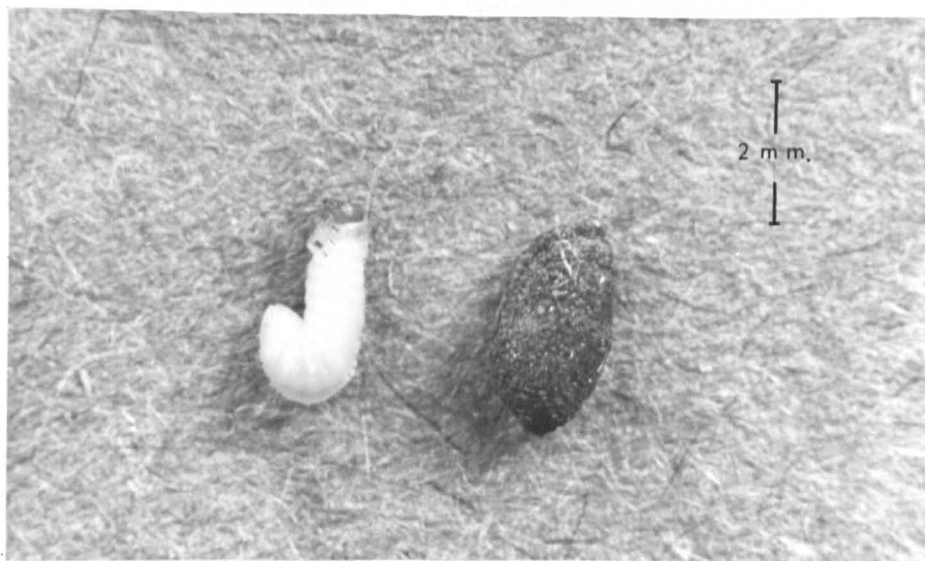


FIG. 39 C. pusillus F.

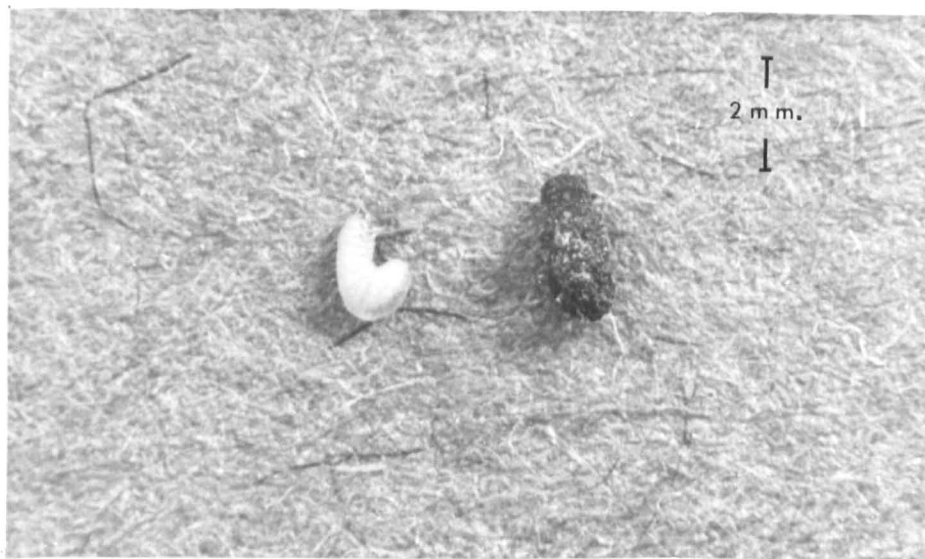


FIG. 40 C. parvulus Müll.

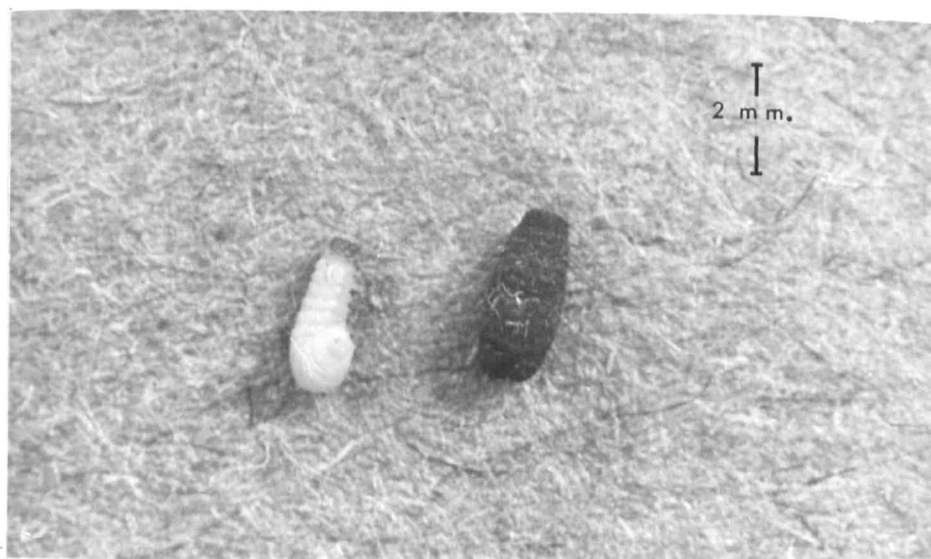


FIG. 41 C. labiatus (L.)

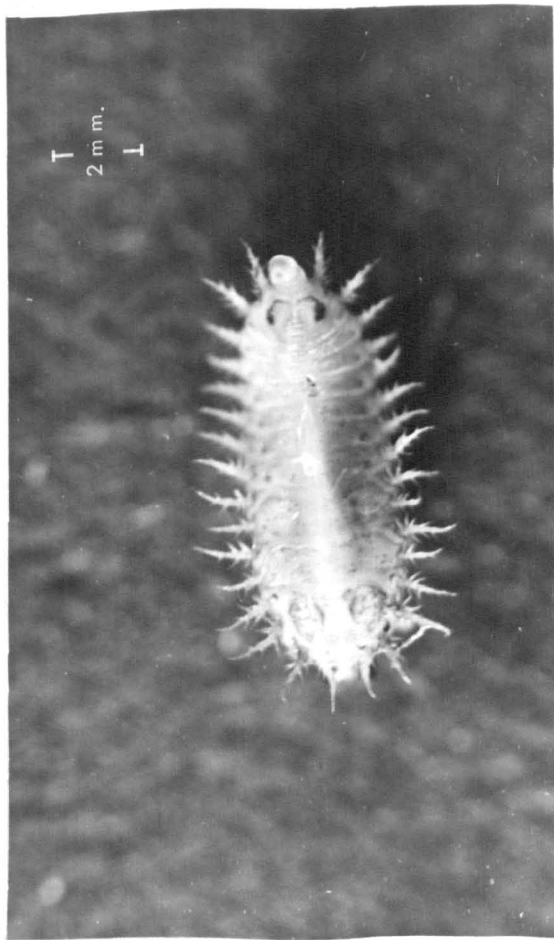


FIG. 42 C. rubiginosa Müll. Dorsal view

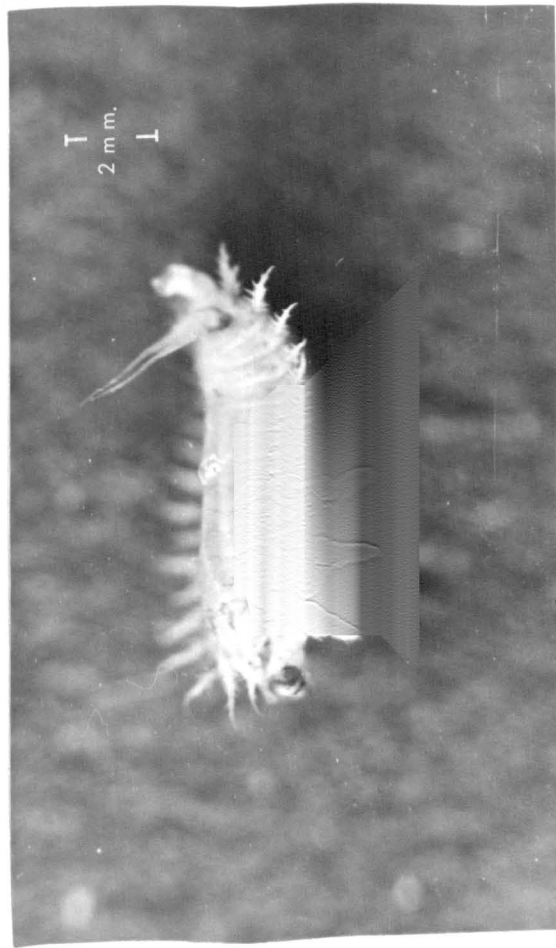


FIG. 43 C. rubiginosa Müll.



FIG. 44 C. viridis L. Dorsal view

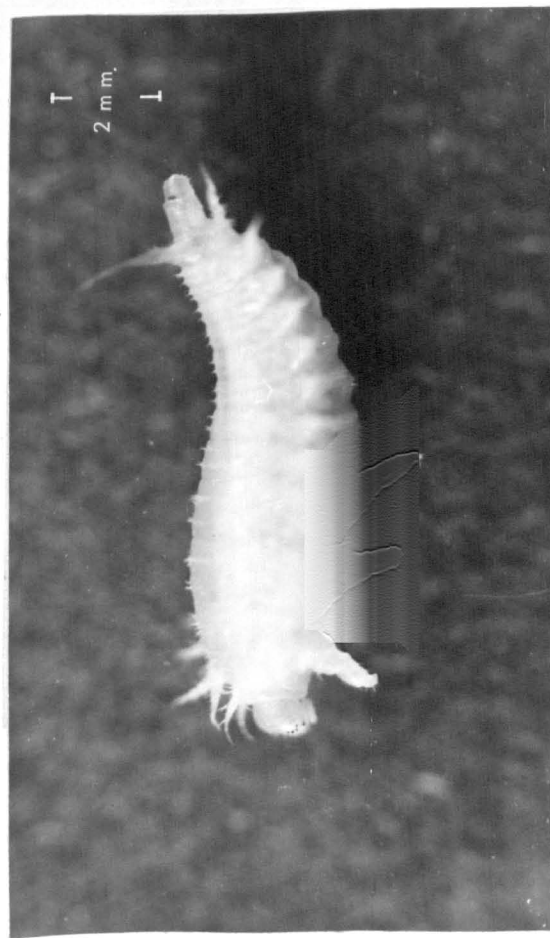


FIG. 45 C. viridis L.

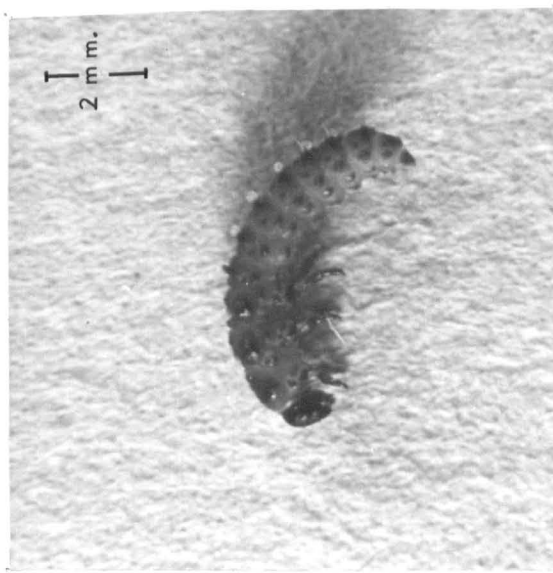


FIG. 46 FINAL INSTAR LARVA OF *Hydrothassa marginella* (L.)

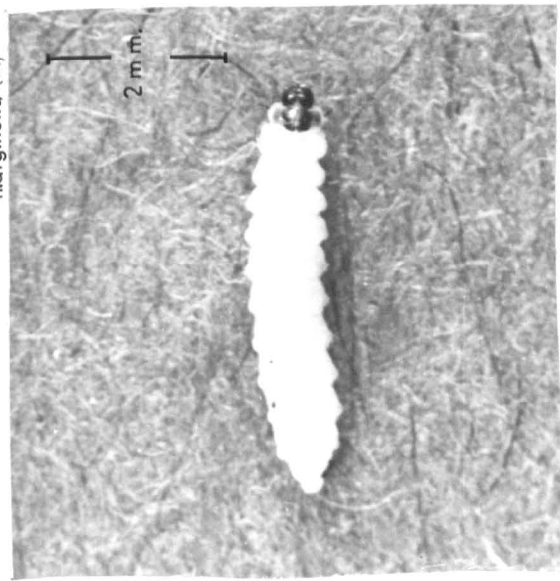


FIG. 47 FINAL INSTAR LARVA OF *Apteropoda orbiculata* (Marsh.)

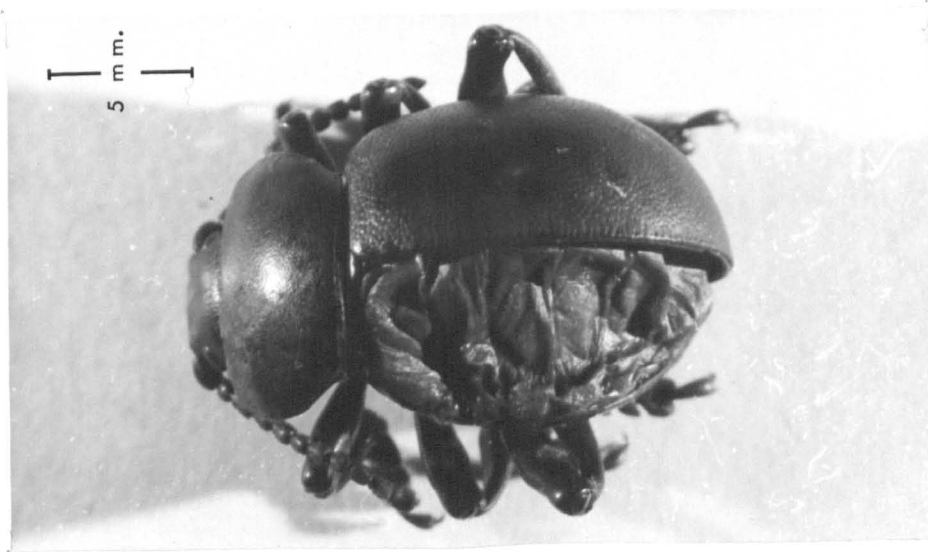


FIG. 48 ADULT ♂ OF *Timarcha tenebricosa* (F.) with the left elytron removed to show the missing hind wings

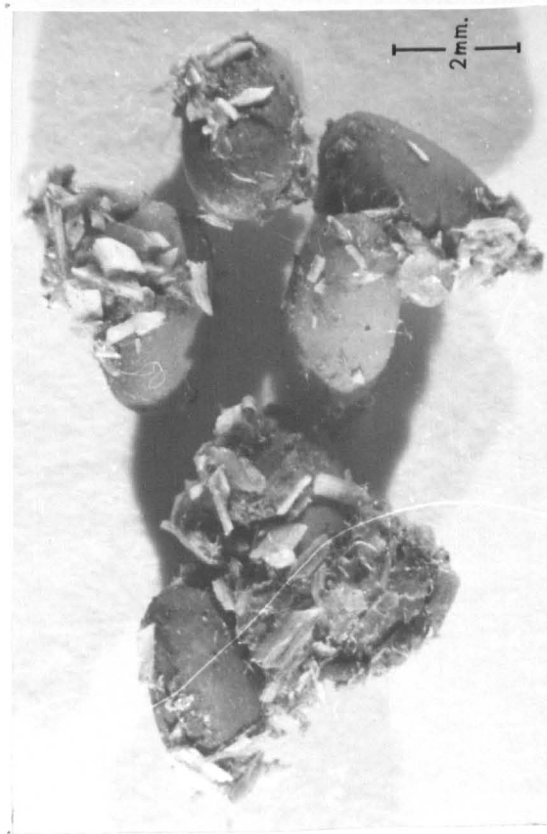


FIG. 49 EGGS OF *T. tenebricosa* (F.) showing adhering regurgitated food

# F. Subfamily relationships indicated by larval taxonomy.

(Tables 5 & 6      Plates L2-L4)

The larvae of chrysomelids are extremely variable morphologically and can be divided into several distinct groupings. Morphological similarities may occur in larvae living in the same habitats even though they are distantly related. This is shown by the leaf mining Zeugophora and Halticinae species. The presence of divergent modifications when the habits and environment are similar is evidence of a distant relationship of subfamilies. The Criocerinae and Cassidinae are both excrement bearers and exhibit divergent morphological characteristics. The abdominal fork of Cassidinae is absent in the Criocerinae and the dorsal position of the anus is not of similar origin. The anus is anatomically dorsal in the Criocerinae while in the Cassidinae it is terminal but becoming dorsal by upward bending of the tenth abdominal segment (Chen, 1940).

## Cassidinae.

The larval head of Cassida has the epicranial suture absent, a character possessed by no other subfamily. However, Cassida has the same ocellar number and basically the same head chaetotaxy as the Donaciinae. Hatching spines are absent in the first instar larvae of Donacia semicuprea and Cassida (Van Emden, 1925). The absence of a distinct arrangement of tubercles and setae in Cassida causes difficulties in relating them to other subfamilies using this character.

## Donaciinae.

The Donaciinae are distinct from other Chrysomelid larvae because the stipes is not connected to the mentum. However, the primary chaetotaxy of the first instar larvae is typically chrysomelid. In the prothorax groups I and VI are bisetose and IX and X are lateral to the pronotum as in the Galerucinae. The larvae of the Donaciinae show affinities to the Criocerinae as the abdominal chaetotaxy

TABLE 5 THE LARVAL CHARACTERS WITHIN THE SUBFAMILIES

SUBFAMILY	Number of Ocelli	Median suture	Epi cranial suture	Number of Antennal segments	Accessory conical process	Number of setae on Vertex	Number of setae on Frons	Number of setae on Gena	Number of maxillary palp segments	Lacinia	Number of labial palp segments	Number of setae on post-clypeus	Biforous spiracles	Penicillus on mandible	Number of instars
CASSIDINAE	5	+	—	2	+	5 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>5</sub> v <sub>6</sub>	6 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub> f <sub>6</sub>	4	2	+	1	2 4	—	—	5
DONACIINAE	5	—	+	3	+	6 v <sub>1</sub> —v <sub>6</sub>	6 f <sub>1</sub> —f <sub>6</sub>	4	2	+	1	6	+	—	?
ORSODACNINAE	5	—	+	2	+	?	?	1	3	—	2	?	—	—	?
ZEUGOPHORINAE	0,3	+	+	3	+	10 - 11 minute v <sub>1</sub> —v <sub>6</sub>	6	3	3	—	1	4	+	—	4
CRIOCERINAE	6	—	+	3	+	6 v <sub>1</sub> —v <sub>6</sub>	6 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub> f <sub>6</sub>	4-6	3	—, +	1	4-6	+	—	4
CLYTRINAE	6	—	+	2	—	6 v <sub>1</sub> —v <sub>6</sub>	6 f <sub>1</sub> —f <sub>6</sub>	4-5	3	+	2	4	—	—	?
CRYPTOCEPHALIN-AE	6	—	+	3	+	6 v <sub>1</sub> —v <sub>6</sub>	6 f <sub>1</sub> —f <sub>6</sub>	5	3	+	2	4	—	—	4
LAMPROSOMATIN-AE	6	—	+	2	—	6 v <sub>1</sub> —v <sub>6</sub>	6 f <sub>1</sub> —f <sub>6</sub>	15	3	+	2	4	—	—	?
CHRYSOMELINAE	6	+	+	3	+	3-7 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub> v <sub>7</sub>	3-5 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub> f <sub>6</sub>	4-7	3	—	1-2	4, 6, 8 15-23	—	—	4, 3
GALERUCINAE	0-1	+	+	1-2	+	2-5 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub>	3-4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub> f <sub>6</sub>	2-5	2-3	+	2	4, 6,	—	—, +	3
HALTICINAE	0-1	+	+	2	+	3-4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	3-4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub> f <sub>6</sub>	2-4	3	+	1-2	6,	—	+	3

\* reduced or absent

TABLE 6 LARVAL HATCHING SPINES WITHIN THE SUBFAMILIES

SUBFAMILY	PRESENT	ON THORACIC SEGMENTS	ON TUBERCLES	ON ABDOM. SEGMENTS	ON TUBERCLES
CASSIDINAE	—				
DONACIINAE	—				
CRIOCERINAE	+	—	—	1st	FUSED DLae-DLpe
ZEUGOPHORINAE	+	PRO, MESO & META		1st.—7th.	DLpe
• ORSODACNINAE	NO	SPECIMENS	AVAILABLE		
CLYTRINAE	NO	SPECIMENS	AVAILABLE		
CRYPTOCEPHALINAE	+	MESO & META	DLpi	—	—
LAMPROSOMATINAE	NO	SPECIMENS	AVAILABLE		
CHRYSOMELINAE	+	MESQ META	DLpi	—	—
		MESQ META	DLpi	1st	DLpi
GALERUCINAE	—				
HALTICINAE	+	MESO & META	DLpi	—	—

of Lema cyanella (L.) and Donacia simplex is similar and they also possess biforous spiracles (Paterson, 1931). The body tubercles are not clearly demarcated and in the later instars the primary chaetotaxy becomes obscured as the few long primary setae become interspersed with numerous minute secondary setae. This obscuring of the primary chaetotaxy does not occur in the Criocerinae but is comparable with that occurring in certain genera of the Chrysomelinae.

#### Orsodacninae.

The possession of an elongate head with the posterior part sunk into the prothorax and five pairs of ocelli are characters common to the larvae of the Donaciinae. The head morphology of the larvae of the Orsodacninae and Zeugophorinae is similar and the thoracic legs are absent in both subfamilies. These are probably characters related to the mining habit of the larvae.

#### Zeugophorinae.

The larvae of Z. flavicollis possess 3 pairs of ocelli and thus differ from the Orsodacninae and Donaciinae. Hatching spines are present along the lateral edge of the pro, meso and metathorax and first to seventh abdominal segments in the first instar larvae of Zeugophora subspinosa. Zeugophora larvae possess biforous spiracles as in Donaciinae and Criocerinae.

#### Criocerinae.

The Criocerinae are probably related to the Clytrinae and Cryptocephalinae because they all possess heads without a median suture and the ocellar number, antennal structure and head chaetotaxy are similar. Although the Criocerinae have similar setae on the vertex and frons their arrangement differs from that in the other two subfamilies. Also the lacinia may be absent and the labial palps have a single segment. The mouthpart structure, the submentum without the posterior pair of setae and the transverse tubercles bearing dorsal setae in the meso and metathorax are characters common

to the larvae of Cryptocephalus parvulus and Lema cyaneella (L.) (Paterson, 1931).

#### Clytrinae and Cryptocephalinae

The absence of the clypeal suture in the Clytrinae and Cryptocephalinae indicates a closer relationship between these than to the Criocerinae. This is supported by the identical arrangement of setae on the vertex and frons and the possession of a lacinia and two segmented labial palps in the Clytrinae and Cryptocephalinae. The chaetotaxy of tubercle Epp in the prothorax and the position of the hatching spines also differ. In the Criocerinae Epp is bi, tri or tetrasetate whereas it is unisetate in the Clytrinae and Cryptocephalinae. Hatching spines are located on tubercle DLpi in the meso and metathorax in Cryptocephalus in the Cryptocephalinae while in the Criocerinae they only occur on DLpi in the first abdominal segment. Tubercle EPa in the meso and metathorax is absent in the Clytrinae and Cryptocephalinae while it bears one to five setae in the Criocerinae. The claws of Criocerinae larvae usually have pulvilli while those of the Clytrinae and Cryptocephalinae lack pulvilli. The body is convex and covered by excrement in Lema in the Criocerinae and curved and case bearing in the Clytrinae and Cryptocephalinae.

#### Chrysomelinae, Galerucinae and Halticinae

The Chrysomelinae show certain affinities to the Criocerinae, possessing the same number of ocelli and lacking a lacinia. Also they rarely possess one segmented labial palps and the convex body of the larvae of some genera e.g. Chrysolina. However, Chrysomelinae larvae lack the biforous spiracles, pulvilli, ventral abdominal pseudopods and the dorsally situated anus of the Criocerinae larvae. Also Lema sp. lack the anal proleg and the primary chaetotaxy is not obscured after the first ecdysis as occurs in Chrysolina sp.



The Chrysomelinae are close to the Galerucinae and Halticinae. All three subfamilies possess the median and epicranial suture and the same setae on the vertex and frons of the head. The Chrysomelinae lack certain characters common to the other two subfamilies. They possess six ocelli whereas in the Galerucinae and Halticinae they are absent or one pair is present, a lacinia is absent whereas it is present in the Galerucinae and Halticinae, the antennae are three segmented whereas they are usually one-segmented in the Galerucinae and Halticinae and a penicillus is absent in the mandible whereas it is usually present in the Galerucinae and Halticinae. The similar position of  $f_1$  on the frons in the Galerucinae and Halticinae while it is interior in the Chrysomelinae is further evidence of the close relationship of the former two subfamilies. In the Chrysomelinae tubercle EPp in the prothorax when present is usually unisetate or rarely bisetose. This tubercle is always present in the Galerucinae and Halticinae, bearing one to five setae in the former and always one seta in the latter subfamily. Tubercle EPa in the meso and metathorax is also, uni, bi or trisetate in the Chrysomelinae while it is usually unisetate in the Galerucinae and always unisetate in the Halticinae. The position of the hatching spines also differs. In the Chrysomelinae there are two groups. In the first group hatching spines are located on tubercles DLpi of the meso and metathorax. In the second group they also occur on DLpi of the first abdominal segment. This indicates that the Chrysomelinae are possibly more closely related to the Halticinae than are the Galerucinae. Hatching spines are absent in the Galerucinae whereas in the Halticinae they are located in a similar position to those in the first group of the Chrysomelinae. The claw of the legs of Halticinae and Galerucinae possess pulvilli while they are absent in Chrysomelinae.

The presence or absence of hatching spines may be correlated with the shape of the egg. Hatching spines in the Chrysomelidae are

shown in Table 6 . The Galerucinae possess eggs which are hemispherical or nearly spherical whereas in the Chrysomelinae and Halticinae they are more elongate. The position of the hatching spines would mean that they could function easily against a straight surface but not against an arc.

In the present work the larvae of Chrysomelinae were easily separated from those of Galerucinae and Halticinae using ocelli number, antennal structure and the presence or absence of the lacinia and penicillus. However, Henriksen (1927) stated that there were no definite characters by which the larvae of these three subfamilies could be grouped in the same subfamilies as their adults and the larvae of these subfamilies should be treated collectively. On the contrary Boving (1927) easily distinguished the larvae of Chrysomelinae, Galerucinae and Halticinae using the number of antennal segments, ocelli number and the presence or absence of the coronal (= median epicranial) suture. He stated that if the tribes Diabroticini and Phyllobroticini are removed from the Galerucinae and placed in the subfamily Halticini near the tribes Systenini, Crepidoderini and Psylliodini, it is possible to separate the rest of the larvae into the same two subfamilies, Galerucinae and Halticinae as their adults. In the present work the larvae of Galerucinae and Halticinae are very similar and cannot be separated using Boving's characters alone. Indeed they all possess the median and epicranial sutures and ocelli number in both subfamilies varies from 0 - 1.

Galerucinae and Halticinae larvae were grouped under the tribe Trichostomata because of similarities in body chaetotaxy. However, Halticinae larvae differ from those of the Galerucinae as seta IX in the prothorax of Halticinae is located on the pronotum and the cardo of the maxilla bears a lateral seta (Paterson, 1931).

The presence of supraspiracular glands in Agelastica larvae suggests some connection with some Chrysomelinae larvae (Boving, 1927).

This is possible as the glands in both subfamilies are located on homologous tubercles. However, the arrangement of tubercles in the abdomen of Agelastica is similar to Sermyla halensis,<sup>and</sup> Phyllobrotica. Abdominal tubercle arrangement in Galerucella, Galeruca and Lochmaea is similar to that of the larvae of the tribe Halticini studied by Woods and Kenner (Boving, 1927).

## G. Generic Relationships indicated by Larval Taxonomy

### Donaciinae. (Table 7)

The head and body chaetotaxy of later instar larvae of the genera Plateumaris, Donacia and Macrolea are very similar and indicate a close relationship between these genera.

### Criocerinae. (Table 7)

The genera Lema, Crioceris and Lilioceris possess similar larval characters. The head chaetotaxy is constant but the setae on the vertex, gena, frons and post clypeus are stronger in Lilioceris than the other genera. Crioceris and Lilioceris may be related by the absence of the lacinia while it is present in Lema species. The body chaetotaxy is most similar in Crioceris and Lema, the tubercles being weakly chitinised and the setae reduced. In Lilioceris there are numerous well chitinised tubercles dorsally and dorsoventrally bearing well-developed setae. The tubercle EPp in the prothorax is bisetate in Lema, trisetate in Crioceris and tetrasetate in Lilioceris.

### Chrysomelinae.

Within the Chrysomelinae various distinct groupings can be made (Tables 8,9 ).

#### (a) Timarcha, Leptinotarsa, Chrysolina, Phytodecta group.

The genera in this group lack eversible glands on the fused DLae-DLpe tubercle of the meso and metathorax of first instar larvae and also on abdominal segments one to seven in later instars. However, small paired eversible glands occur dorsally in the abdomen of Chrysolina, Phytodecta and Leptinotarsa. In all instars of Chrysolina species they are located in the eighth abdominal segment, while in some Phytodecta species they occur between abdominal segments seven and eight. The first instar larvae possess hatching spines on tubercles DLpi of the meso and metathorax and first abdominal segment.

SYMBOLS USED IN THE FOLLOWING TABLES

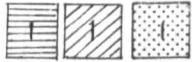
\* FINAL INSTAR LARVAE



TUBERCLE AND RESPECTIVE SETA ABSENT



AN UNFUSED TUBERCLE BEARING THE RESPECTIVE SETA



A FUSED TUBERCLE BEARING THE RESPECTIVE SETA



TUBERCLE PRESENT THE RESPECTIVE SETA ABSENT

TABLE 7

THE PRIMARY TUBERCLES AND SETAE OF  
DONACIINAE, CRIOCERINAE, CLYTRINAE AND

## CRYPTOCEPHALINAE LARVAE

TUBERCLE	Dai	Dpi	Dae	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1 I	2 II	3 III	4 IV	5 V	6 VI	7 VII	8 VIII	9 IX	10 X	11 XI	12 XII	13 XIII	14 XIV	15 XV	16 XVI
SPECIES																
DONACIINAE																
<i>Donacia cinerea</i> <sup>*</sup> Hbst.	1	1	1	1	1	1	1	1	10		1	1				
<i>Plateumaris discolor</i> <sup>*</sup> (Pz)	1	1	1	1	1	1	1	1	10		1	1				
<i>Macrolea appendiculata</i> (Pz) <sup>*</sup>	1	1	1	1	1	1	1	1	10		1	1				
CRIOCERINAE																
<i>Lema melanopa</i> (L)	3	1	1	1	1	1	1	1		2		1			1	1
<i>Lema lichensis</i> Voet.	3	1	1	1	1	1	1	1		2		1			1	1
<i>Lema puncticollis</i> <sup>*</sup> Curt.	3	1	1	1	1	1	1	1		2	1	1			1	1
<i>Crioceris asparagi</i> (L) <sup>*</sup>	3	1	1	1	1	1	1	1		3	1	1			2	1
<i>Lilioceris lili</i> (Scop.) <sup>*</sup>	3	1	1	1	1	1	1	1		4	1	1			4,5	2
CLYTRINAE																
<i>Clytra quadripunctata</i> (L) <sup>*</sup>	1	1	1	1	1	1	1	1		1	1	1			1	1
CRYPTOCEPHALINAE																
<i>Cryptocephalus parvulus</i> <sup>*</sup> Müll.	2	2	1	1	2	1	1	1		1	2	1				1
DONACIINAE																
<i>Donacia cinerea</i> <sup>*</sup> Hbst.	1	1	1	1		1	1	1	1	2	1	1			1	1
<i>Plateumaris discolor</i> <sup>*</sup> (Pz)	1	1	1	1		1	1	1	1	2	1	1			1	1
<i>Macrolea appendiculata</i> (Pz) <sup>*</sup>	1	1	1	1		1	1	1	1	2	1	1			1	1
CRIOCERINAE																
<i>Lema melanopa</i> (L)	1	1	1	1	1	1	1	1	1	1		1				
<i>Lema lichensis</i> Voet.	1	1	1	1	1	1	1	1	1	1		1			1	1
<i>Lema puncticollis</i> <sup>*</sup> Curt.	1	1	1	1	1	1	1	1	1	1		1			1	1
<i>Crioceris asparagi</i> (L) <sup>*</sup>	1	1	1	1	1	1	1	1	4	1		1			1	1
<i>Lilioceris lili</i> (Scop.) <sup>*</sup>	1	1	1	1	1	1	1	1	4	2		1			1	1
CLYTRINAE																
<i>Clytra quadripunctata</i> (L) <sup>*</sup>	1	1	1	1	1	1	1	1	6	1	3	1	1		1	1
CRYPTOCEPHALINAE																
<i>Cryptocephalus parvulus</i> <sup>*</sup> Müll.	1	1	1	1	1	1	1	1	4	1	2	1	1		1	1

PROTHORAX

MESO &amp; METATHORAX

TABLE 7. cont.

THE PRIMARY TUBERCLES AND SETAE OF  
DONACIINAE, CRIOCERINAE, CLYTRINAE AND  
CRYPTOCEPHALINAE LARVAE

[illegible]

TABLE 8 THE LARVAL CHARACTERS OF THE GENERA WITHIN THE CHRYSOMELINAE

GENUS	Number of setae on Frons	Number of setae on Vertex	Number of setae on Gena	Number of labial palp segments	Number of postclypeus setae	Position of hatching spines on thorax	Position of hatching spines on abdomen	Number of larval instars	Position of eversible glands	Tubercle EPP in prothorax
TIMARCHA	numerous, minute	numerous, minute	4 large, many minute	2	15-23	DLpi meso & meta thorax	DLpi 1st. abd. segment	3	—	+
CHRYSOLINA	5 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub>	4-7 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub> v <sub>7</sub> *	4-7	2	6	DLpi meso & meta thorax	DLpi 1st. abd. segment	4	Small pair on 9th. abd. segment	—
LEPTINOTARSA	5 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub>	6 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	6	2	8	DLpi meso & meta thorax	DLpi 1st. abd. segment	4	Small pair between abd. segs. 8 & 9	—
PHYTODECTA	5 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub>	5 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub>	5	2	6	DLpi meso & meta thorax	DLpi 1st. abd. segment	4	Small pair between abd. segs. 7 & 8	—
PHYLLODECTA	4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub>	4 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	4	2	4	DLpi meso & meta thorax	—	3	Pair on meso & meta thorax & abd. segs. 1-7	+
PHAEDON	4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub>	4 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	5	2	6	DLpi meso & meta thorax	—	3	—	+
GASTROIDEA	4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub>	4 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	5	2	6	DLpi meso & meta thorax	—	3	—	+
PRASOCURIS	4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub>	3 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub>	5	1	4, 6	DLpi meso & meta thorax	—	3	—	—
HYDROTHASSA	3-4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub>	3-4 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	5	2	4	DLpi meso & meta thorax	—	3	—	—, +
CHRYSOMELA	4-5 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub>	4-6 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	5	2	6	DLpi meso & meta thorax	—	3	—	+
PLAGIODERA	3 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub>	5 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub>	5	2	6	DLpi meso & meta thorax	—	3	—	+

\* Sometimes absent.



Of the genera Chrysolina, Phytodecta, Leptinotarsa and Timarcha only Timarcha possesses tubercle EPP in the prothorax but even here it is tending towards fusion with the pronotum. On the general shape of the head and head chaetotaxy Timarcha differs from all other genera in the Chrysomelinae. The body lacks distinct tubercles and bears numerous minute setae characteristic of the later instars in Chrysolina and Leptinotarsa. The claw in Timarcha lacks an inner tooth which is present in the other genera. Timarcha is probably allied to Chrysolina and Leptinotarsa as the larvae in these genera show the characters of a strongly convex body, the absent eversible glands on the thorax and abdomen and similar position of hatching spines. The genus Chrysolina is probably related to Leptinotarsa and Phytodecta as they all possess 5 frontal setae ( $f_1, f_2, f_3, f_4, f_6$ ) on the head. The pronotum in Chrysolina and Phytodecta bears setal groups one to eight, some of which are bisetose and thus 10-17 large setae may be present. The tubercle Dpe is usually present in the meso and metathorax. In Chrysolina Dpe occurs as a separate unisetate tubercle while it may be fused with either Dpi or DLpi in Phytodecta. In Timarcha this tubercle cannot be distinguished.

In the first abdominal segment tubercles Dai to Dpe are represented fully only in the genus Chrysolina and DLpe bearing seta VIII is usually reduced. The genus Phytodecta approaches this condition, only tubercle DLpi bearing seta vi is absent in P. viminalis and P. rufipes whereas in P. pallida and P. olivacea tubercles DLae and DLpe are absent. Tubercle DLai is always present in Chrysolina and Phytodecta.

(b) Phyllodecta, Phaedon, Gastrolidea, Prasocuris and Hydrothassa group.

The genera in this group all possess eversible glands on the fused DLae-DLpe tubercle of the meso and metathorax of first instar larvae and also on abdominal segments one to seven in later instars. The first instar larvae possess hatching spines only on

tubercle DLpi of the meso and metathorax. The tubercle EPp is usually present in the prothorax, the only exceptions being Prasocuris and Hydrothassa marginella. The genera Phyllodecta, Phaedon, Gastroidea, Prasocuris and Hydrothassa possess 4 frontal setae ( $f_1, f_3, f_4, f_6$ ). Phyllodecta, Phaedon, Gastroidea and some Hydrothassa species possess 4 vertex setae ( $v_1, v_3, v_4, v_6$ ) while in Prasocuris and some Hydrothassa species  $v_4$  is absent. The pronotum usually bearing setae I-VIII. Seta group 1 is usually bisetose, except in Phaedon tumidulus where it is unisetate. Seta VI is usually reduced except in Phaedon tumidulus, Hydrothassa aucta and Prasocuris phellandrii where it is well developed. Seta VIII is reduced in Gastroidea polygona and absent in G. viridula. Tubercle EPp has probably fused with the pronotum in Prasocuris and Hydrothassa marginella. In the meso and metathorax the tubercle Dpe is always absent. The tubercle Dae is present in the meso and metathorax of Phyllodecta, Phaedon and Gastroidea although in Phyllodecta and Phaedon cochleariae and armoraciae it is fused with Dai. The tubercle Dae is absent in Hydrothassa and Prasocuris. There is a reduction in the number of tubercles and setae in the dorsal and dorsolateral regions of the abdomen. The tubercles DLai and DLpi are always absent. In the first abdominal segment, only Phyllodecta, Phaedon tumidulus and armoraciae, Hydrothassa aucta and Prasocuris possess tubercle Dai. However, in the following abdominal segments in Phyllodecta tubercle Dai is absent. Tubercle Dai is absent in Phaedon cochleariae, Gastroidea, Hydrothassa marginella. Tubercle Dpi is always present but may be fused with Dpe as in Phyllodecta, Phaedon tumidulus and armoraciae, Gastroidea, Hydrothassa aucta. However, in Phaedon cochleariae, Hydrothassa marginella and Prasocuris tubercle Dpe is absent. Tubercle Dae is present only in Phaedon tumidulus, P. armoraciae and Gastroidea. In the first abdominal segment generic differences in the chaetotaxy of tubercle As-Ps occur. This tubercle is unisetate in the genera Phaedon, Hydrothassa, Prasocuris but usually bisetate or rarely tetrasetate in Gastroidea, Phyllodecta.

TABLE 9 THE PRIMARY TUBERCLES AND SETAE OF  
CHRYSEMELINAE LARVAE

A. ON THE PROTHORAX

TUBERCLE	Dai	Dpi	Dae	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1 I	2 II	3 III	4 IV	5 V	6 VI	7 VII	8 VIII	9 IX	10 X	11 XI	12 XII	13 XIII	14 XIV	15 XV	16 XVI
SPECIES																
<i>Chrysolina polita</i> (L.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>C. staphylea</i> (L.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>C. fastuosa</i> (Scop.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>C. menthastri</i> (Suf.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>C. graminis</i> (L.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>C. hyperici</i> (Forst.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>C. varians</i> (Schal.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>C. brunsvicensis</i> (Gr.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>Phytodecta pallida</i> (L.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>P. viminalis</i> (L.) *	1	1	1	1	1	1	1	1			1	1			1	1
<i>P. rufipes</i> (De G.) *	1	1	1	1	1	1	1	1			1	1			1	1
<i>P. olivacea</i> (Forst.)	1	1	1	1	1	1	1	1			1	1			1	1
<i>Phyllodecta vitellinae</i> (L.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>P. laticollis</i> Suf.	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>P. vulgatissima</i> (L.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>Phaedon tumidulus</i> (Germ.)	1	1	1	1	1	1	1	1		1	1	1			1	1
<i>P. armoraciae</i> (F.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>P. cochleariae</i> (F.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>Gastroidea polygoni</i> (L.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>G. viridula</i> (De G.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>Hydrothassa marginella</i> (L.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>H. aucta</i> (F.) *	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>Prasocuris junci</i> (Brahm.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>P. phellandrii</i> (L.) *	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>Chrysomela populi</i> L.	2	1	1	1	1	1	1	1		2	1	2			1	1
<i>C. aenea</i> L. *	2	1	1	1	1	1	1	1		2	1	1			1	1
<i>Plagioderma versicolora</i> (Laich.)	2	1	1	1	1	1	1	1		1	1	1			1	1

TABLE 9 cont.  
THE PRIMARY TUBERCLES AND SETAE OF  
CHRYSEMELINAE LARVAE

B. ON THE MESO & META THORAX

TUBERCLE	Dai	Dpi	Doe	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
SPECIES	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
<i>Chrysolina polita</i> (L.)	I	I	I	I		I	2-4		I	I		I			I	I
<i>C. staphylea</i> (L.)	I	I	I	I		I	2-4		3	I		I			I	I
<i>C. fastuosa</i> (Scop.)	I	I	I	I		I	2-4		2	I		I			I	I
<i>C. menthastri</i> (Suf.)	I	I	I	I		I	2-4		I	I		I			I	I
<i>C. graminis</i> (L.)	I	I	I	I		I	2-4		I	I		I			I	I
<i>C. hyperici</i> (Forst.)	I	I	I	I		I	I	I	I	I		I			I	I
<i>C. varians</i> (Schal.)	I	I	I	I		I	I	I	I	I		I			I	I
<i>C. brunsvicensis</i> (Gr.)	I	I	I	I		I	I	I	I	I		I			I	I
<i>Phytodecta pallida</i> (L.)	I	I	I	I		I	3	3-4	I	I		I			I	I
<i>P. viminalis</i> (L.) *	I	I	I	I		3	3	6	6	5		2-3			I	I
<i>P. rufipes</i> (De G.) *	I	I	I	I		3	3	6	6	5		5			I	I
<i>P. olivacea</i> (Forst.)	I	I	I	I		3	4		I	I		I			I	I
<i>Phyllodecta vitellinae</i> (L.)	I	I	I			I	I	I	I	I		I			I	I
<i>P. laticollis</i> Suf.	I	I	I			I	I	I	I	I		I			I	I
<i>P. vulgatissima</i> (L.)	I	I	I			I	I	I	I	I		I			I	I
<i>Phaedon tumidulus</i> (Germ.)	I	I	I			I	I	I	I	I		I			I	I
<i>P. armoraciae</i> (F.)	I	I	I			I	I	I	1-2	I		I			I	I
<i>P. cochleariae</i> (F.)	I	I	I			I	I	I	I	I		I			I	I
<i>Gastroidea polygoni</i> (L.)	I	I	I			I	I	I	2-3	I		I			I	I
<i>G. viridula</i> (De G.)	I	I	I			I	I	I	2-3	I		I			I	I
<i>Hydrothassa marginella</i> (L.)	I	I				I	I	I	I	I		I			I	I
<i>H. aucta</i> (F.) *	I	I				I	I	I	I	I		I			I	I
<i>Prasocuris junci</i> (Brahm.)	I	I				I	I	I	I	I		I			I	I
<i>P. phellandrii</i> (L.) *	I	I				I	I	I	I	I		I			I	I
<i>Chrysomela populi</i> L.	I	I				I	I	I	3	5		2			2	2 3
<i>C. aenea</i> L. *	I	I				I	I	I	3	5		I			I	2
<i>Plagioderma versicolora</i> (Laich.)	I	I				I	I	I	3	5		I			I	I

TABLE 9 cont.  
THE PRIMARY TUBERCLES AND SETAE OF  
CHRYSOMELINAE LARVAE

C. ON THE FIRST ABDOMINAL SEGMENT

TUBERCLE	Dai	Dpi	Dae	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1 I	2 II	3 III	4 IV	5 V	6 VI	7 VII	8 VIII	9 IX	10 X	11 XI	12 XII	13 XIII	14 XIV	15 XV	16 XVI
SPECIES																
<i>Chrysolina polita</i> (L.)	I	I	I	I	I	I	I	r			I	I	I	I	2-3	I
<i>C. staphylea</i> (L.)	I	I	I	I	I	I	I	r			3		I	I	3	I
<i>C. fastuosa</i> (Scop.)	I	I	I	I	I	I	I	I			3		I	I	2	I
<i>C. menthastri</i> (Suf.)	I	I	I	I	I	I	I	r			3		I	I	3	I
<i>C. graminis</i> (L.)	I	I	I	I	I	I	I	r			3		I	I		I
<i>C. hyperici</i> (Forst.)	I	I	I	I	I	I	I	r			I	I	I	I	3	I
<i>C. varians</i> (Schal.)	I	I	I	I	I	I	I	r			I	I	I	I	3	I
<i>C. brunsvicensis</i> (Gr.)	I	I	I	I	I	I	I	r			I	I	I	I	3	I
<i>Phytodecta pallida</i> L.	I	I	I	I	I	I					I	I			I	I
<i>P. viminalis</i> *	I	I	I	I	I		I	I			6		I	I	2	3
<i>P. rufipes</i> (De G.) *	I	I	I	I	I		I	I			6		I	I	I	I
<i>P. olivacea</i> (Forst.)	I	I	I	I	I	I					I	I	I	I	I	I
<i>Phyllodecta vitellinae</i> (L.)	I	I		I			I	I			I	I	I	I	2	I
<i>P. laticollis</i> Suf.	I	I		I			I	I			I	I	I	I	4	I
<i>P. vulgatissima</i> (L.)	I	I		I			I	I			I	I	I	I	2	I
<i>Phaedon tumidulus</i> (Germ.)	I	I	I	I			I	I			I	I	I		2	I
<i>P. armoraciae</i> (F.)	I	I	I	I			I	I			I	I	I		2	I
<i>P. cochleariae</i> (F.)		I					I	I			I	I	I		2	I
<i>Gastroidea polygona</i> (L.)		I	I	I			I	I			I	I	I	I	3	I
<i>G. viridula</i> (De G.)		I	I	I			I	I			I	I	I	I	3	I
<i>Hydrothassa marginella</i> (L.)		I					I	I			I	I	I		2	I
<i>H. aucta</i> (F.) *	I	I		I			I	I			I	I	I		2	I
<i>Prasocuris junci</i> (Brahm.)		I	I	I			I	I			I	I	I		2	I
<i>P. phellandrii</i> (L.) *		I	I	I			I	I			I	I	I		2	I
<i>Chrysomela populi</i> L.		I					I	I			I	I	I		3	2
<i>C. aenea</i> L. *		I		I			I	I			I	I	I		I	I
<i>Plagioderma versicolora</i> (Laich.)		I					I	I			I	I	I	2	2	I

(c) Chrysomela and Plagiodera group.

These genera possess eversible glands on the fused DLae-DLpe tubercle of the meso and metathorax of first instar larvae and also on abdominal segments one to seven in later instars. The first instar larvae possess hatching spines only on tubercle DLpi of the meso and metathorax. The genera Chrysomela and Plagiodera by the absence of seta  $f_2$  are probably more closely related to Phyllodecta, Phaedon, Gastroidea, Prasocuris and Hydrothassa rather than to Chrysolina, Leptinotarsa and Phytodecta. However Plagiodera has seta  $f_1$  and Chrysomela sometimes possesses an extra seta,  $f_5$ . They also differ from the other group (b) in usually possessing seta  $v_2$  and sometimes  $v_5$  on the head. The setal groups one to eight are present in the pronotum. In the meso and metathorax the tubercle Dpe is always absent. In lacking tubercle Dae in the meso and metathorax Chrysomela and Plagiodera are probably related to Hydrothassa and Prasocuris. However, in Hydrothassa and Prasocuris tubercle EPa in the meso and metathorax is unisetate whereas it is trisetate in Chrysomela and Plagiodera. There is a reduction in the number of tubercles and setae in the dorsal and dorsolateral regions of the abdomen. Tubercle Dai is absent in Chrysomela and Plagiodera. Tubercle Dpi is fused with Dpe in these genera. In the first abdominal segment tubercle As-Ps is unisetate in C. aenea and usually bisetate or rarely tetrasetate in C. populi and Plagiodera. The larvae of the Chrysomelinae were divided into two phylogenetically distinct groups. The genera Plagiodera, Chrysomela, Phyllodecta, Hydrothassa, Prasocuris, Phaedon and Gastroidea forming the Oligochaeten Larvengruppe and Chrysolina and Phytodecta forming the Polychaeten larvengruppe. The seta and tubercle nomenclature of Paterson (1931) was only applicable to the Oligochaeten Larvengruppe as in the later instars of the Polychaeten Larvengruppe one tubercle may bear many setae but a new system of nomenclature was not proposed (Hennig, 1938).

The division of the subfamily into two separate groups is probably valid. However, neither of the terms *Oligochaeten* or *Polychaeten* is correct, as there is no clear division between them, the number of setae often increasing in subsequent instars. The first instar larvae of the *Polychaeten* Larvengruppe bear fewer setae which can be homologised with those occurring in the *Oligochaeten* Larvengruppe.

A problem arises when tubercles fuse as the setae on them tend to vary in number, a problem also occurring in *Lepidoptera* larvae (Fracker, 1915). The homology of setae on these tubercles is impossible. However, a tubercle, bearing setae was thought to be homologous to all the setae on another homologous tubercle (Kimoto, 1962). Tubercles were considered to be important taxonomically as they are relatively large and varied little in first instar larvae. Studies on these were more accurate and more easily performed than those on larval setae. The *Oligochaeten* and *Polychaeten* Larvengruppe's of Hennig correspond to the Glanduliferous and nonglanduliferous taxonomic groups of Kimoto. However, the latter pair of terms is inappropriate as both *Chrysolina* and *Phytodecta* have glandulate larvae but fall into the nonglanduliferous taxonomic group of tribes. I consider *Chrysolina* and *Phytodecta* are closely related. However, these 2 taxonomic groups were further divided. The glanduliferous group into Generic group, *Phaedon* including *Phaedon*, *Phyllodecta* and *Gastroidea*, generic group *Chrysomela* including *Plagioderia* and *Chrysomela* and generic group *Prasocuris* including *Hydrothassa* and *Prasocuris*. The addition of secondary tubercles in second instar larvae of *Chrysomela* and *Plagioderia* may indicate a relationship between these genera. The relationship between the generic groups *Phaedon* and *Chrysomela* was considered to be much closer than that between the generic groups *Phaedon* and *Prasocuris*, the latter being regarded as a somewhat specialised taxonomic group. The nonglanduliferous group form two distinct generic groups *Chrysolina* and *Phytodecta* (Kimoto, 1962).

In the abdominal segments of Chrysomelinae larvae there are two basic tubercle arrangements. In Phytodecta and Chrysolina there are two transverse rows of primary dorsal tergal plates while in Phyllodecta, Prasocuris, Hydrothassa, Phaedon, Gastroidea, Plagiodera and Chrysomela there is only one. The terms seriate and uniseriate can be applied to these two groups. It could be considered that the seriate group has arisen from the uniseriate group by the transverse splitting into two of each tubercle. Thus the uniseriate group would be the most primitive of the two groups. However, it is more probable that the uniseriate group has arisen from the seriate group by the fusion of the anterior and posterior members of each pair of tubercles. This is confirmed by the primitive adult characters of Timarcha which is closely related to Chrysolina and Phytodecta (seriate group).

If all characters are considered the best possible division of the larvae of Chrysomelinae is into three groups. Timarcha is distinct from all other genera. Leptinotarsa, Chrysolina and Phytodecta can be included in the same group as they possess numerous common characters as can Phaedon, Phyllodecta, Gastroidea, Hydrothassa, Prasocuris, Chrysomela and Plagiodera. The larvae fall naturally into four tribes Timarchina including Timarcha, Chrysomelina including Chrysolina, Phaetonina including Phaedon, Gastroidea, Phyllodecta and Chrysomela and Prasocurina including Prasocuris and Hydrothassa. Prasocurina have tubercle EPp absent in the prothorax whereas it is present in the Phaetonina. However, the larvae of Hydrothassa aucta possesses EPp (Paterson, 1931). Gastroidea and Chrysomela belong to the Phaetonina while Phyllodecta, Phaedon, Hydrothassa and Prasocuris belong to the Prasocurina (Reitter, 1912).

Gastroidea was considered to be a connecting link between Phaedon tumidulus and Phyllodecta as the arrangement of tubercles in the meso and metathorax resembles that of Phaedon while the reduction of anterior dorsal setae in the abdomen is similar to Phyllodecta. The arrangement



of tubercles and setae in the meso and metathorax is similar to that of Phyllodecta and Phaedon cochleariae of the Phaetonina (Paterson, 1931).

It was considered that Phyllodecta and Phytodecta have many morphological differences and Phyllodecta shows many similarities to Gastroidea and Phaedon of the Phaetonina. Prasocuris and Hydrothassa should also be included in the Phaetonina (Hennig, 1938).

It is considered that the classification of Hennig (1938) in which the independence of Prasocurina from Phaetonina was not recognised is preferred. Prasocuris and Hydrothassa are closely related to Phaedon, showing similar larval chaetotaxy and cannot justifiably be separated.

Claw structure also differs between different genera. In Chrysolina, Phytodecta, and Chrysomela each claw possesses an obtuse inner tooth bearing a seta. This tooth is absent in the claws of Phaedon, Hydrothassa, Prasocuris, Phyllodecta.

### Galerucinae

Within the Galerucinae 3 groupings can be made using head and body chaetotaxy (Tables 10, 11 ).

#### (a) Galeruca, Agelastica group.

The larvae belonging to these genera usually have  $3 \begin{pmatrix} f & f & f \\ 1 & 3 & 6 \end{pmatrix}$  or  $4 \begin{pmatrix} f & f & f & f \\ 1 & 3 & 4 & 6 \end{pmatrix}$  frontal setae, four-five well developed vertex setae ( $v_2, v_3, v_4, v_5, v_6$ ) and five genal setae. They also possess one pair of ocelli but the penicillus is absent from the mandible. In the pronotum all of the tubercles Dai to DLpe and all of the setae one to eight are present. In the prothorax the tubercle EPp is usually unisetate. In the meso and metathorax the tubercles Dai is fused with Dae and Dpi fused with Dpe. The tubercle DLpi is usually bisetose or trisetose. In the abdominal segments two to seven the tubercle Dpi is present and fused with Dpe as are Dai and Dae. The tubercles DLae and DLpe are also fused and in

TABLE 10  
THE LARVAL CHARACTERS OF THE GENERA WITHIN THE GALERUCINAE

GENUS	Number of Ocelli	Number of setae on Frons	Number of setae on Vertex	Number of setae on Gena	Number of Antennal segments	Number of segments in maxillary palps	Number of segments in labial palps	Number of setae on post clypeus	Penicillus on mandible
GALERUCA	1	4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> 6	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> 6	5	1	3	2	6	-
AGELASTICA	1	3 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> 6	5 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> 6	5	2	3	2	4, 6	-
SERMYLA	0	4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> 6	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> 6	5	1	3	2	4	+
PHYLLOBROTICA	0	3 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> 6	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> 6	5	2	3	2	6	+
LUPERUS	0	4 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> 6	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> 6	5	1	3	2	6	+
GALERUCELLA	1	3 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> 6	2-4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> 6	2-4	1	3	2	6	+
LOCHMAEA	1	3 f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> 6	3-4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> 6	3	1	2, 3	2	6	- , +

r = reduced

\* = reduced or absent.

TABLE II THE PRIMARY TUBERCLES AND SETAE  
OF GALERUCINAE LARVAE

TUBERCLE	Dai	Dpi	Dae	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
SPECIES	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
<i>Galeruca tanacetii</i> (L.)*	1	1	1	1	1	1	1	1		8	9	4-6				6
<i>Agelastica alni</i> (L.)*	1	1	1	1	2	1	1	1		1	1	1			1	1
<i>Sermyla halensis</i> (L.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>Phyllobrotica quadrimaculata</i> (L.)	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>Luperus longicornis</i> F.	1	1	1	1	1		1	1		1	1	1			1	1
<i>L. flavipes</i> L.	1	1	1	1	1		1	1		1	1	1			1	1
<i>Galerucella viburni</i> (Pk.)*	2	1	1	1	1		1	1		3	1	1			1	1
<i>G. nymphaeae</i> (L.)*	1	1	1	1	1		1	1		2	1	1			1	1
<i>G. sagittariae</i> Brit. Cat.	1	1	1	1	1		1	1		2	1	1			1	1
<i>G. tenella</i> (L.)	1	1	1	1	1		1	1		2	1	1			1	1
<i>G. lineola</i> (F.)	1	1	1	1	1		1	1		2	1	1			1	1
<i>G. californiensis</i> (L.)	1	1	1	1	1		1	1		2	1	1			1	1
<i>Lochmaea crataegi</i> (Forst.)	2	1	1	1	1		1	1		2	1	1			1	1
<i>L. capreae</i> (L.)	2	1	1	1	1		1	1		4	1	1			1	1
<i>L. suturalis</i> (Th.)	3	1	1	1	1		1	1		3,4,5	1	1			1	1
<i>Galeruca tanacetii</i> (L.)*	1				2-5	7-9	10-11		3-6	6	1	5				1
<i>Agelastica alni</i> (L.)*	1					2			1	1		1			1	1
<i>Sermyla halensis</i> (L.)	1					3			1	1		1			1	1
<i>Phyllobrotica quadrimaculata</i> (L.)	1					3			1	1		1			1	1
<i>Luperus longicornis</i> F.			1	1		1			1	1		1			1	1
<i>L. flavipes</i> L.			1	1		1			1	1		1			1	1
<i>Galerucella viburni</i> (Pk.)*			1	1		1			1	1		1			1	1
<i>G. nymphaeae</i> (L.)*			1	1		1			1	1		1			1	1
<i>G. sagittariae</i> Brit. Cat.			1	1		1			1	1		1			1	1
<i>G. tenella</i> (L.)			1	1		1			1	1		1			1	1
<i>G. lineola</i> (F.)			1	1		1			1	1		1			1	1
<i>G. californiensis</i> (L.)			1	1		1			1	1		1			1	1
<i>Lochmaea crataegi</i> (Forst.)			1	1		1			1	1		1			1	1
<i>L. capreae</i> (L.)			1	1		1			1	2		1			1	1
<i>L. suturalis</i> (Th.)	2		1	1		1			1	2		1			1	1

PROTHORAX

MESO & METATHORAX

TABLE 11 cont.  
THE PRIMARY TUBERCLES AND SETAE

OF GALERUCINAE LARVAE

TUBERCLE	Dai	Dpi	Dae	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
SPECIES																
<i>Galeruca tanacetii</i> (L.)																
<i>Agelastica alni</i> (L.)																
<i>Sermyla halensis</i> (L.)																
<i>Phyllobrotica quadrimaculata</i> (L.)																
<i>Luperus longicornis</i> F.																
<i>L. flavipes</i> L.																
<i>Galerucella viburni</i> (Pk.)																
<i>G. nymphaeae</i> L.																
<i>G. sagittariae</i> Brit. Cat.																
<i>G. tenella</i> (L.)																
<i>G. lineola</i> (F.)																
<i>G. californiensis</i> (L.)																
<i>Lochmaea crataegi</i> (Forst.)																
<i>L. capreae</i> (L.)																
<i>L. suturalis</i> (Th.)																
<i>Galeruca tanacetii</i> (L.) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Agelastica alni</i> (L.) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>Sermyla halensis</i> (L.)	1		1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>Phyllobrotica quadrimaculata</i> (L.)	1		1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>Luperus longicornis</i> F.	1		1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>L. flavipes</i> L.	1		1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>Galerucella viburni</i> (Pk.) *			1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>G. nymphaeae</i> (L.) *			1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>G. sagittariae</i> Brit. Cat.			1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>G. tenella</i> (L.)			1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>G. lineola</i> (F.)			1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>G. californiensis</i> (L.)			1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>Lochmaea crataegi</i> (Forst.)			1	1	1	1	1	2	1	1	1	1	1	1	2	1
<i>L. capreae</i> (L.)			1	1	1	1	1	1	1	1	1	1	1	1	2	1
<i>L. suturalis</i> (Th.)	1		1	1	1	1	1	1	1	1	1	1	1	1	2	1

ABDOMINAL SEGMENTS 2-7

Agelastica tubercle Epa bearing the spiracle is also fused to these tubercles. In the larvae of Agelastica alni the openings of large glands occur on the tubercles DLae-DLpe-Epa in the abdominal segments one to seven. The larvae of Galeruca tanacetii are distinctive by possessing raised papillae or verucae bearing numerous setae on the body tubercles. Galeruca forms a well defined genus by the presence of these verucae in the larvae (Boving, 1927).

(b) Sermyla, Phyllobrotica, Luperus group.

The genus Sermyla is probably related to Galeruca of group (a) as the larvae possess four frontal setae ( $f_1, f_3, f_4, f_6$ ) and five well developed vertex setae ( $v_2, v_3, v_4, v_6$ ). In the larvae Sermyla, Phyllobrotica and Luperus ocelli are absent, the mandible possesses a penicillus and there are four genal setae. In Phyllobrotica there are three ( $f_1, f_3, f_6$ ) while in Luperus there are four frontal setae ( $f_1, f_2, f_3, f_6$ ). The vertex in both genera bears 4 ( $f_2, f_3, f_4, f_6$ ) setae, the seta  $v_2$  is reduced. In the pronotum all of the tubercles Dai to DLpe and all of the setae one to eight are present in Sermyla and Phyllobrotica. The setal group I is usually bisetose. However in Luperus it is unisetate and seta VI is absent.

In the genus Luperus the tubercles Dai and Dpi are absent but the tubercle Epp is unisetate. In Sermyla and Phyllobrotica tubercle Dai is fused with Dae and Dpi fused with Dpe in the meso and metathorax. The tubercle DLpi is usually bisetose or trisetose. In Luperus the tubercles Dai and Dpi are usually absent and DLpi is unisetate. In abdominal segments two to seven the tubercle Dpi is absent and Dai, Dae and Dpe occur as distinct separate tubercles. The tubercle DLae is also separate and DLpe is bisetose as distinct from the other genera where it is usually unisetate. The larvae of Sermyla halensis are distinct from those of Phyllobrotica and Luperus as they possess the apertures to secretory glands on all of the thoracic segments and in the abdominal segments one to nine. In the prothorax the apertures lie posterior to the

tubercle P while in the meso and metathorax and the abdominal segments they lie dorso-median to the tubercles DLai and DLpi. Phyllobrotica and Luperus longicornis differ from Sermyla as in these the tubercle Dae is fused across the mid-dorsal line similar to the tubercles Dai and Dpe. In Sermyla this fusion of the tubercle Dae across the mid-dorsal line does not occur.

(c) Galerucella, Lochmaea group.

The larvae in these genera possess one pair of ocelli, three frontal setae ( $f_1, f_3, f_6$ ), four setae on the vertex ( $v_2, v_3, v_4, v_6$ ) the seta  $v_3$  is usually reduced or absent and the seta  $v_4$  may also be reduced. A penicillus is always present in the mandible of Galerucella larvae whereas it may be absent in that of Lochmaeae larvae. In the pronotum seta VI is absent in Galerucella and Lochmaeae. The seta I is unisetate except in Galerucella viburni and the Lochmaea species. In Lochmaea suturalis the setal group 1 is trisetose. Tubercle EPp is bi, tri or tetrasetate in Galerucella and Lochmaea. In the meso and metathorax the tubercles Dai and Dpi are usually absent. However in Lochmaea suturalis Dai is fused with Dae and tubercle Dpi is absent. In this group the tubercle DLpi is always unisetate. In the abdominal segments two to seven the tubercles Dai and Dpi are usually absent except in Lochmaea suturalis where the tubercle Dai is fused with Dae. The tubercle DLae is usually absent except in Galerucella viburni, Lochmaea crataegi and the tubercle DLpe is usually unisetate except in L. crataegi where it is bisetose.

On tubercle arrangement the larvae of Galerucella can be separated into several species groups. The first includes G. viburni, the second G. nymphaea, G. sagittariae, and the third G. tenella, G. lineola, G. calvariensis. G. viburni is distinct from the others by possessing the tubercle DLae in the abdomen. G. lineola was included in the second group above by Boving (1927).

Lochmaea crataegi is similar to Galerucella viburni in possessing the tubercle DLae in the abdomen and a well developed penicillus in the mandible. In the other Lochmaea sp. these characters are absent. However, Boving (1927) considered the larvae of L. capreae were more closely related to G. vi burni than the latter species is to G. nymphaeae.

The larvae of the Galerucinae can be classified into three generic groups, using the characters previously discussed, the Galeruca,

Agelastica group, the Sermyla, Phyllobrotica, Luperus group and the

Galerucella, Lochmaea group. Takizawa (1971) divided the larvae of the Galerucinae into the glanduliferous and nonglanduliferous group. The glanduliferous group contains the Tribes Sermylini and Agelastisini. The nonglanduliferous group contains the Tribes Luperini, Galerucini and Oidini. This system agrees rather well with that of Wilcox (1965) based on male genital characters.

### Halticinae

#### a) A discussion of the morphological modifications associated with the leaf mining habit.

The general head and body structure within the subfamily Halticinae is probably dependent as much on the position of feeding as upon relationships between different genera and species. Only one British genus Haltica are external feeders whereas of the remaining 20 genera, 50% are leaf or stem miners and 50% are internal or external root feeders. Within the genera Psylliodes, Phyllotreta, Chaetocnema, Longitarsus and Aphthona both leaf and root feeding larvae occur.

Certain modifications in larval structure are concomitant with the habit of leaf mining. The externally feeding Haltica species possess a cylindrical body in which tubercles and setae are well developed. The mining larva is restricted within the mine cavity within the leaf tissues. The leaf tissues exert pressure on it and parallel with this a dorso-ventral flattening of the body occurs. (Hering 1951) The flatter the mine the more pronounced is this flattening. Body and head flattening is most pronounced in the epidermal miners, or sap feeders e.g. Sphaeroderma testaceum, S. rubidum, Apteropeda orbiculata, Dibolia, Mantura rustica, but also occurs in parenchymal miners where the mine is limited to either side of the leaf and is

only of shallow depth. Little or no dorso-ventral flattening occurs in Hippuriphila modeeri, Psylliodes napi, Phyllotreta nemorum and Aphthona coerulea. In Sphaeroderma, Apteropeda and Dibolia where increased resistance causes the larva difficulties in penetrating into the leaf the prothorax is broader than the remaining body segments and the body becomes wedge-shaped. In the dorsal and ventral areas other strongly chitinated plates may develop and increase the larva's pressure when it penetrates into the plant tissues. This is especially noticeable in Zeugophora subspinosa where paired dorsal and ventral plates occur on meso and metathorax and all abdominal segments. However in Halticinae it is restricted to the increase in size of tubercles on the meso and metathorax only. The necessity for an increase in protecting tubercles is probably linked with the frequent transfer from one mine to another.

Thickening and raising the body during normal movement in external feeders cannot be accomplished inside leaf mines. However, although legs may be reduced in the Halticinae leaf miners they are never absent as they are in Zeugophora and Orsodacne. This may indicate that leaf mining in the Halticinae is of a more recent origin than in the Zeugophorinae. The more pronounced constriction between the individual body segments in many miners, or the possession laterally of long setae as in Z. flavicollis and Z. subspinosa are modifications assisting movement in legless species.

The feeding action of the mining larva demands a horizontal setting of the head as opposed to the vertical setting of the external feeders. This is achieved by the longer dorsal portion of the head being withdrawn into the prothorax. The prothorax thus appears thicker and by becoming arched may cause problems in the epidermal miners which are in constant danger of their movements rupturing the epidermis of the leaf. Thus in epidermal miners or sap feeders the head is flat and



the horizontal position is achieved by the lower margin becoming longer and thus becoming less short in relation to the dorsal margin than in tissue feeders. The head is no longer withdrawn into the prothorax but only the rear edges are covered by the anterior margin of the prothorax. In the tissue feeders Psylliodes napi, Phyllotreta nemorum, Aphthona coerulea the head is oval, while in sap feeders it is wedge shaped with the sides extended and almost straight. This increases the strain upon all organs in this part of the head, especially in linear miners for example Apteropeda where the greater friction between the sides of the head and the leaf tissues has resulted in atrophy in certain organs.

The majority of mining larvae have the dorsal apodemata (chitinous plates extending into the centre of the head for muscle attachment) very different in structure from the external feeders. The Y-line defining the position of the endoskeletal ridges (tentorium) which unite to the rear of a single line is no longer developed. Instead the two apodemata tend to diverge to the rear and these two branches may be united by a chitinous bridge. Concurrently the apodemata are broader than in free living species but they do not extend so far inside the head. The sap feeders develop particularly strong lateral arms, suitable for supporting the dorsal angles of the head capsule, and a further branch may then arise from them, directed toward the rear angle.

The leaf mining Halticinae larvae have the ocelli absent but in Apteropeda and Mantura a large ocellus occurs behind the antennae. In Zeugophora flavicollis there are two dorsal and one lateral ocelli, whereas in Orsodache there are five ocelli in a line posterior to the antennae (Boving & Craighead, 1931).

A change in the position of the mandibles occurs from the vertical to a horizontal position. Since the central teeth of the mandible of an external feeder are the longest they would bore into the tissues of

the leaf but would no longer cut the cell, owing to the absence of pressure from the opposite teeth. Special modifications to the mandible are therefore necessary to enable them to fulfil their function. These changes occur from two different angles of which one applies particularly to parenchymal, the other to epidermal miners. In both cases the direction of development is towards a reduction in the number of teeth, since it is impossible to continue joint action with the corresponding teeth of the opposing mandible as occurred when the mandible was arranged vertically. In parenchymal miners the tendency is towards bringing the tips of the teeth more and more into a straight line with the inner margin. This occurs at the expense of the development of the median area of the mandible and the number of teeth. As the epidermal feeders live exclusively on flat epidermal cells and the head is markedly dorso-ventrally flattened the mandibles are quite thin, lamina-like blades. The teeth become increasingly atrophied while the median portion is greatly atrophied. This develops a fine serration so that these median parts work like a circular saw and cut up the cells.

Processes of modification also affect the mouthparts, the first and second maxillae merging in to the labium. The maxillae and labium together form a functional unit conveying pieces of bitten off tissue into the buccal cavity.

Mining larvae are never so deeply coloured as many of the externally feeding species. Endophagous larvae are invariably paler or almost colourless as light is essential for the development of pigment.

(b) Relationships indicated by Larval Taxonomy (Tables 12,13,14 )

The presence of seta  $f_2$  may indicate relationships between the different genera. The seta  $f_2$  is present in Hermaeophaga mercurialis, Psylliodes napi, Longitarsus suturellus and Phyllotreta nemorum which are root and leaf mining species and thus it is not an adaptation to

TABLE 12 THE LARVAL CHARACTERS OF THE GENERA WITHIN THE HALTICINAE

GENUS	Number of Ocelli	Number of setae on Frons	Number of setae on Vertex	Number of setae on Gena	Number of antennal segments	Number of segments of max palps	Number of segments of labial palps	Number of setae on post-clypeus	Penicillus on mandible
HALTICA	0	3 $f_1 f_3 f_6$	4 $v_2 v_3 v_4 v_6$	4	2	3	2	6	+
HERMAEOPHAGA	0	4 $f_1 f_2 f_3 f_6$	4 $v_2 v_3 v_4 v_6$	4	2	3	1	6	+
HIPPURIPHILA	0	3* $f_1 f_3 f_6$	4 $v_2^* v_3^* v_4^* v_6$	3	2	3	2	6	+
MANTURA	1	3* $f_1 f_3 f_6$	4 $v_2^* v_3^* v_4^* v_6$	4	2	3	1	6	+
APTEROPEDA	1	3* $f_1 f_3 f_6$	4 $v_2^* v_3^* v_4^* v_6$	2	2	3	1	6	+
PSYLLIODES	0	4 $f_1 f_2 f_3 f_6$	4 $v_2^* v_3^* v_4^* v_6$	4	2	3	2	6	+
LONGITARSUS	0	4* $f_1 f_2 f_3 f_6$	3 $v_2 v_3 v_4 v_6$	4	2	3	2	6	+

TABLE 13. THE PRIMARY TUBERCLES AND SETAE OF HALTICINAE LARVAE

TUBERCLE	Dai	Dpi	Dae	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
SPECIES	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
<i>Haltica lythri</i> Aub.	2	1	1	1	1		1	1		1	1	1			1	1
<i>H. britteni</i> Shp.	2	1	1	1	1	1	1	1		1	1	1			1	1
<i>H. oleracea</i> (L.)	2	1	1	1	1		1	1		1	1	1			1	1
<i>H. brevicollis</i> Foud.	2	1	1	1	1		1	1		1	1	1			1	1
<i>Psylliodes napi</i> (F.)	2	2	1	1	1		1	1		1	1	1			1	1
<i>P. affinis</i> (Pk.)	1	1	1	1	1		1	1		1	1	1			1	1
<i>Hippuriphila modeeri</i> (L.)	2	1	1	1	1		1	1		1	1	1			1	1
<i>Hermaphysa mercurialis</i> (F.)	2	1	1	1	1	r	1	1		1	1	1			1	1
<i>Mantura rustica</i> (L.)	2	1	1	1	1		1	1		1	1	1			1	1
<i>Apteropoda orbiculata</i> (Marsh.)	2	2	1	1	1	1	1	1		1	1	1			1	1
<i>Longitarsus melanocephalus</i> (DeG.)	2	1	1	1	1		1	1		1	1	1			1	1
<i>Crepidodera ferruginea</i> (Scop.)	2	1	1	1	1		1	1		1	1	1			1	1
<i>Derocrepis rufipes</i> (L.)	1	1	1	1	1		1	1		1	1	1			1	1
<i>Phyllotreta nemorum</i> (L.)	2	1	1	1	1		1	1		1	1	1			1	1
<i>Chaetocnema concinna</i> (Marsh.)	2	1	1	1	1	r	1	1		1	1	1			1	1
<i>Chalcoides fulvicornis</i> (F.)	2	1	1	1	1		1	1		1	1	1			1	1
<i>Haltica lythri</i> Aub.			1	1		2	3		1	1		1			1	1
<i>H. britteni</i> Shp.			1	1		2	3		1	1		1			1	1
<i>H. oleracea</i> (L.)			1	1		2	3		1	1		1			1	1
<i>H. brevicollis</i> Foud.			1	1		2	3		1	1		1			1	1
<i>Psylliodes napi</i> (F.)			1	1		1	3		1	1		1			1	1
<i>P. affinis</i> (Pk.)			1	1		1	3		1	1		1			1	1
<i>Hippuriphila modeeri</i> (L.)			1	1		1	3		1	1		1			1	1
<i>Hermaphysa mercurialis</i> (F.)			1	1		1	3		1	1		1			1	1
<i>Mantura rustica</i> (L.)			1	1		1	3		1	1		1			1	1
<i>Apteropoda orbiculata</i> (Marsh.)	1	1	1	1	1	1	3		1	1		1			1	1
<i>Longitarsus melanocephalus</i> (DeG.)			1	1		1	3		1	1		1			1	1
<i>Crepidodera ferruginea</i> (Scop.)			1	1		1	3		1	1		1			1	1
<i>Derocrepis rufipes</i> (L.)			1	1		1	3		1	1		1			1	1
<i>Phyllotreta nemorum</i> (L.)			1	1		1	3		1	1		1			1	1
<i>Chaetocnema concinna</i> (Marsh.)			1	1		1	3		1	1		1			1	1
<i>Chalcoides fulvicornis</i> (F.)			1	1		1	3		1	1		1			1	1

PROTHORAX

MESO &amp; METATHORAX

TABLE 13 cont. THE PRIMARY TUBERCLES AND SETAE OF HALTICINAE LARVAE

TUBERCLE	Dai	Dpi	Dae	Dpe	DLai	DLpi	DLae	DLpe	EPa	EPp	T	P	As	Ps	Es	Ss
SETA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
SPECIES	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
Haltica lythri Aub.			I	I	I	I	I	I			I	I	I	I	I	2
H. britteni Shp.			I	I	I	I	I	I			I	I	I	I	I	2
H. oleracea (L.)			I	I	I	I	I	I			I	I	I	I	I	2
H. brevicollis Foud.			I	I	I	I	I	I			I	I	I	I	I	2
Psylliodes napi (F.)	I		I	I	I	I	I	I			I	I	I	I	I	2
P. affinis (Pk.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Hippuriphila modeeri (L.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Hermaphroditus mercurialis (F.)			I	I	I	I	I	I			I	I	I	I	I	2
Mantura rustica (L.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Apteropoda orbiculata (Marsh.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Longitarsus melanocephalus (DeG.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Crepidodera ferruginea (Scop.)			I	I	I	I	I	I			I	I	I	I	I	2
Derocrepis rufipes (L.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Phyllotreta nemorum (L.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Chaetocnema concinna (Marsh.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Chalcoides fulvicornis (F.)	I		I	I	I	I	I	I			I	I	I	I	I	2
Haltica lythri Aub.																
H. britteni Shp.																
H. oleracea L.																
H. brevicollis Foud.																
Psylliodes napi F.																
P. affinis Pk.																
Hippuriphila modeeri L.																
Hermaphroditus mercurialis F.																
Mantura rustica L.																
Apteropoda orbiculata Marsh.																
Longitarsus melanocephalus DeG.																
Crepidodera ferruginea Scop.																
Derocrepis rufipes L.																
Phyllotreta nemorum L.																
Chaetocnema concinna Marsh.																
Chalcoides fulvicornis F.																

ABDOMINAL SEGMENTS 1-7

one particular habitat. The seta  $f_2$  is absent in Haltica, Hippuriphila modeeri, Mantura rustica, Apteropeda orbiculata, Sphaeroderma which are external, leaf or stem mining species. The setae  $f_1, f_3, f_6$  are present in Haltica, Longitarsus, Hermaeophaga, Apteropeda, Psylliodes and Hippuriphila.

The chaetotaxy of the pronotum is similar in the Haltica, Chaetocnema, Crepidodera, Hippuriphila, Hermaeophaga, Mantura, Phyllotreta and Chalcoides group and also in the Psylliodes, Longitarsus, <sup>and</sup> Derocrepis group.

In the meso and metathorax tubercle DLai is absent in Mantura rustica and Phyllotreta nemorum and also the tubercles Ss and Es are fused into a mid-ventral plate. Apart from these differences, the chaetotaxy of the thorax in all the genera is similar. Differences occur both between and within the genera in the presence of the hatching spines on the tubercle DLpi. Hatching spines are present in the genera Haltica, Hermaeophaga, Derocrepis, Chalcoides, Crepidodera, Phyllotreta, Longitarsus, Psylliodes affinis, which are external feeders, stem miners or root miners. They are absent in the genera Hippuriphila, Mantura, Sphaeroderma, Apteropeda, Aphthona coerulea, Psylliodes napi which are all leaf miners. The presence or absence of hatching spines in the Halticinae may be correlated with position in which the eggs are laid (Table 14 ). In some leaf miners for example Apteropeda orbiculata ova are actually laid within the tips of Plantago lanceolata leaves. In Mantura rustica they are deposited in pits on the underside of Rumex leaves, in Hippuriphila modeeri in the leaf axils and in Sphaeroderma on the leaf veins. The first instar larvae bite their way through the chorion adjacent to the leaf surface and mine directly into the leaf. Thus it is unnecessary for the larvae to hatch on to the leaf surface and hatching spines are absent. In the case of the externally feeding Haltica species the larvae must hatch from the egg onto the leaf surface to feed and develop. In root and stem feeders in which oviposition takes place in the soil near the roots of the host plant

TABLE 14

CORRELATION BETWEEN THE POSITION OF  
OVIPOSITION AND THE PRESENCE OF HATCHING  
SPINES IN HALTICINAE LARVAE

GENUS	SPECIES	WITH or WITHOUT HATCHING SPINES	POSITION OF OVIPOSITION	POSITION OF FEEDING
Haltica	lythri Aub.	+	LEAF SURFACE	LEAF SURFACE
Haltica	oleracea (L.)	+		
Haltica	britteni Shp.	+		
Hermaeophaga	mercurialis (F.)	+	IN SOIL	AT ROOTS
Chalcoides	fulvicornis (F.)	+		
Chalcoides	aurata (Marsh.)	+		
Chalcoides	aurea (Geof.)	+		
Crepidodera	ferruginea (Scop.)	+		STEM MINER
Crepidodera	transversa (Marsh.)	+		
Hippuriphila	modeeri (L.)	—	LEAF SURFACE	LEAF MINER
Mantura	rustica (L.)	—		
Sphaeroderma	testaceum (F.)	—		
Sphaeroderma	rubidum Graëlls.	—		
Apteropeda	orbiculata (Marsh.)	—	WITHIN LEAF	
Aphthona	coerulea (Geof.)	—	LEAF SURFACE	
Phyllotreta	nemorum (L.)	+		
Phyllotreta	undulata Kuts.	+	IN SOIL	AT ROOTS
Derocrepis	rufipes (L.)	+	IN SOIL	
Chaetocnema	concinna (Marsh.)	+	IN SOIL	AT ROOTS
Psylliodes	napi (F.)	—	LEAF SURFACE	LEAF MINER
Psylliodes	affinis (Pk.)	+	IN SOIL	AT ROOTS
Longitarsus	jacobaea Wat.	+		
Longitarsus	suturellus Duft.	+		
Longitarsus	melanocephalus (DeG)	+		

the larvae need to hatch and locate the host plant before feeding can occur. Thus hatching spines are indispensable to external, root and stem feeders.

On the abdominal chaetotaxy two groups can be made. The tubercle Dai is absent in Haltica, Hermaeophaga and Mantura whereas it is present in the second group comprising Psylliodes, Hippuriphila, Apteropeda, Longitarsus, Derocrepis, Phyllotreta and Chalcooides. Apart from this the abdominal chaetotaxy is remarkably constant within the genera. However, in the genera Hippuriphila, Mantura and Apteropeda the dorsal tubercles in the abdominal segments are not fused across the mid-dorsal line as in the other genera.

It is evident that all the genera of the Halticinae are extremely closely related and any differences which occur in the chaetotaxy may be correlated with the leaf or root mining habit. Thus it is impossible to justifiably divide the larvae of the Halticinae into generic groups.

(c) The Value of Larval Chaetotaxy.

Larval morphology and chaetotaxy are good characters at the tribal, specific and usually at the subfamily level. However, the larvae of the subfamilies Galerucinae and Halticinae cannot be separated using head or body chaetotaxy. Chaetotaxy is slightly variable intraspecifically in the later instars but the primary chaetotaxy of the first instars is usually constant.



9. LARVAL KEYSA. Subfamily Key

- Ia Head with distinct epicranial suture .....2a
- b Head without epicranial suture ..... Cassidinae  
(Body with lateral scoli and terminal fork)
- 2a Thoracic legs present .....4a
- b Thoracic legs absent .....3a
- 3a Labium with prementum and mentum separate, distinct;  
labial palps inserted well apart .....Orsodacninae
- b Labium with prementum and mentum fused,  
labial palps inserted close together .....Zeugophorinae
- 4a Head bearing 0,1 or 6 pairs of ocelli .....6a
- b Head bearing 5 pairs of ocelli .....5a
- 5a Larva C-shaped, posterior abdominal segments curved ventrally;  
without a pair of caudal spines; head large not partly or  
completely retracted into prothorax .....Lamprosomatinae
- b Larva not C-shaped, curved and usually tapering anteriorly  
and posteriorly from the middle of the body; with a pair of  
caudal spines; head small and partly or completely retracted  
into prothorax .....Donaciinae
- 6a Head bearing 6 pairs of ocelli .....7a
- b Head either without or bearing one pair of ocelli .....Galerucinae and  
Halticinae p.231
- 7a Head without median suture .....8a
- b Head with median suture .....Chrysomelinae p.230
- 8a Labial palps 2 segmented, tubercle EPp in prothorax unisetate .....9a
- b Labial palps 1 segmented, tubercle EPp in prothorax  
bearing 2-4 setae .....Griocerinae p.230
- 9a Antennae 3 segmented, 3rd segment bearing one long and  
2 short setae .....Cryptocephalinae
- b Antennae 2 segmented .....Clytrinae

## B. Generic and Specific Keys

### i. Criocerinae

- |    |  |       |                   |
|----|--|-------|-------------------|
| 1a | Tubercle EPp in prothorax bearing 3 or 4 setae | ..... | 2a                |
| b  | Tubercle EPp in prothorax bisetate             | ..... | <u>Lema</u>       |
| 2a | Tubercle EPp in prothorax tetrasetate          | ..... | <u>Lilioceris</u> |
| b  | Tubercle EPp in prothorax trisetate            | ..... | <u>Crioceris</u>  |

### ii. Chrysomelinae

- |    |  |       |                     |
|----|--|-------|---------------------|
| 1a | Post clypeus bearing 15-23 large setae. Abdomen with only 7 pairs of spiracles   | ..... | <u>Timarcha</u>     |
| b  | Post clypeus bearing at the most 3 pairs of setae. Abdomen with 8 pairs of spiracles   | ..... | 2a                  |
| 2a | Meso and metathorax without eversible glands   | ..... | 3a                  |
| b  | Meso and metathorax with eversible glands  | ..... | 5a                  |
| 3a | Tubercle EPa in 2nd abdominal segment at least 2/3 size of fused DLae-DLpe in meso and metathorax  | ..... | <u>Leptinotarsa</u> |
| b  | Tubercle EPa in 2nd abdominal segment at the most 1/5 size of fused DLae-DLpe in meso and metathorax   | ..... | 4a                  |
| 4a | Vertex of head never with setal conformation $v_1v_3v_4v_5v_6$ ; ratio of the number of tubercles dorsal to spiracles in meso and metathorax against number in 1st abdominal segment is 14/16, 12/14 or 12/16. Body strongly convex dorsally | ..... | <u>Chrysolina</u>   |
| b  | Vertex of head with setal conformation $v_1v_3v_4v_5v_6$ ; ratio of the number of tubercles dorsal to the spiracles in meso and metathorax against number in first abdominal segment is 3/6, 8/6 or 12/12. Body not strongly convex dorsally | ..... | <u>Phytodecta</u>   |

- 5a First abdominal segment differs from the following as tubercle  
Dai is present on the first segment ..... Phyllodecta
- b First abdominal segment identical with the remainder as tubercle  
Dai may be absent or present in all segments alike ..... 6a
- 6a Prothorax with tubercle EPp ..... 7a
- b Prothorax without tubercle EPp ..... I3a
- 7a Abdominal segments without tubercle Dai ..... 8a
- b Abdominal segments with tubercle Dai ..... IIa
- 8a Abdominal segments I-6 with tubercle Dae present but  
reduced ..... Gastroidea
- b Abdominal segments I-6 without tubercle Dae ..... 9a
- 9a Frons without seta  $f_I$  ..... Plagiodera
- b Frons with seta  $f_I$  ..... IOa
- IOa 9th abdominal segment with tubercle T-P separate  
and trisetate ..... Chrysomela
- b 9th abdominal segment with tubercle T-P not separate .. Phaedon  
cochleariae (F.)
- IIa Abdominal segments I-6 with tubercle Dae ..... I2a
- b Abdominal segments I-6 without tubercle Dae ..... Hydrothassa  
aucta (F.)
- I2a Seta I on pronotum bisetose; tubercle DLae-DLpe in  
the abdominal segments bearing I large seta ..... Phaedon  
armoraciae (L.)
- b Seta I on pronotum unisetate; tubercle DLae-DLpe in  
abdominal segments bearing 2 large setae ..... Phaedon  
tumidulus (Germ.)
- I3a Frons with seta  $f_I$  ..... Prasocuris
- b Frons without seta  $f_I$  ..... Hydrothassa  
marginella (L.)

### iii. Galerucinae - Malticinae

- Ia Abdominal segments I-6 with 3 transverse dorsal tubercles ..... 2a
- b Abdominal segments I-6 with 2 transverse dorsal tubercles ..... IIa
- 2a 3 transverse tubercles fused across the mid-dorsal line ..... 3a
- b Anterior and posterior tubercles fused, mid tubercles free ..... 4a
- 3a Dorsal fused tubercles on meso and metathorax bearing a  
total of 4 large setae each ..... Phyllobrotica  
Feeding openly on Scutellaria galericulata during quadrinaculata (L.)  
April, May, September and October

- 3b Dorsal fused tubercles on meso and metathorax bearing a total of 2 large setae each ..... Luperus  
(Root feeders during April, August, September and October.) & Derocrepis  
L. longicornis F.  
& D. rufipes (L.)
- 4a Frons bearing 4 large setae ( $f_1 f_3 f_4 f_6$ ); pronotum bearing 9 large setae; segmental pores present on abdominal segments I-9 ..... Sermyla  
Feeding openly on Galium verum in May and June ..... S. halensis (L.)
- b Frons bearing 3 large setae ( $f_1 f_3 f_6$ ); pronotum bearing 7 or 8 large setae; segmental pores absent on abdominal segments I-9 ..... 5a
- 5a Dorsal plate of 9th abdominal segment bearing numerous sensory pores ..... Luperus  
(Root feeders during April, August, September and October.) ..... L. flavipes (L.)
- b Dorsal plate of 9th abdominal segment without sensory pores ..... 6a
- 6a Seta  $f_2$  present on frons ..... 7a  
(Usually root feeders, rarely leaf miners )
- b Seta  $f_2$  absent on frons ..... 9a  
(Leaf miners )
- 7a Seta  $v_3$  present on vertex ..... Psylliodes  
b Seta  $v_3$  absent on vertex ..... 8a
- 8a Tubercles Es and Ss fused on meso and metathorax ..... Phyllotreta  
P. nemorum (L.)
- b Tubercles Es and Ss not fused on meso and metathorax... Longitarsus  
Chalcooides &  
Chaetoonema
- 9a Ocelli absent ..... Hippuriphila  
b Ocelli present ..... IOa
- IOa Tubercles Es and Ss reduced and not fused on the meso and metathorax ..... Apteropeda
- b Tubercles Es and Ss well developed and fused on the meso and metathorax .....;..... Mantura
- IIa Dorsal abdominal tubercles fused across mid-dorsal line .. I2a
- b Dorsal abdominal tubercles free ..... Galeruoa  
(Dorsal and epipleural tubercles distinctly G. tanacetii (L.)  
raised and bearing numerous setae.  
Feeding openly on Stellaria graminea, Tanacetum vulgare  
Thymus serpyllum and Succisa pratensis.

- I2a Meso and metathorax with a total of 6 tubercles dorsal  
to the spiracles ..... Galerucella  
Feeding openly on Polygonum and Rumex, May-September. G. sagittariae  
Feeding openly on Nuphar and Nymphaea ..... G. nymphaeae (L.)
- b Meso and metathorax with a total of 10 tubercles dorsal  
to the spiracles ..... I3a
- I3a Abdominal segments I-6 with a total of 8 tubercles  
dorsal to the spiracles ..... I4a
- b Abdominal segments I-6 with a total of 10 tubercles  
dorsal to the spiracles ..... I6a
- I4a Tubercle EPp in meso and metathorax unisetate ..... I5a
- b Tubercle EPp in meso and metathorax bisetate ..... Lochmaea  
Feeding openly on Salix, May-September ..... L. capreae (L.)  
Feeding openly on Calluna, May-September ..... L. suturalis (Thoms)
- I5a Abdominal segments 2-6 with the tubercle DLae anterior  
to the spiracle ..... Lochmaea  
Feeding within the fruits of Crataegus in May & June L. crataegi (Forst)
- b Abdominal segments 2-6 without the tubercle DLae  
anterior to the spiracle ..... Galerucella  
Feeding openly on Alnus, Corylus. ..... G. lineola (F.)  
Feeding openly on Filipendula ulmaria, Potentilla  
and Geum ..... G. tenella (L.)  
Feeding openly on Lythrum salicaria ..... G. californiensis (L.)
- I6a Abdominal segments I-8 with supra-spiracular glands.. Agelastica  
Feeding openly on Alnus in May, June, July ..... A. alni (L.)
- b Abdominal segments I-8 without supra-spiracular  
glands ..... Galerucella  
Feeding openly on Viburnum opulus and V. lantana  
during June and July ..... G. viburni (Payk.)  
Feeding openly on Corylus, Calluna, Epilobium etc..... Haltica  
Root feeders on Mercurialis perennis ..... Hermasophaga  
H. mercurialis  
Stem miners of Avena during August - May ..... Crepidodera  
C. ferruginea (Soop)

## 10. THE CHRYSOMELID PUPA.

### A. General structure.

All Chrysomelid pupae are exarate, varying in colour from white, cream, yellow, green, orange to black. The majority of species pupate within earthen cells in the ground, a few in a silken cocoon, larval cases or above ground and others in cocoons constructed from peritrophic linings and plant cells under water. A few tougher cuticled species pupate on the undersurface of leaves of the foodplant. The head is usually strongly deflexed and concealed beneath the large pronotum. The elytra and wings are curved onto the ventro-lateral surface of the body and the antennae pass around the projecting femora of the pro and mesothoracic legs. Spiracles are situated laterally in the mesothorax and usually in the first 5 abdominal segments. Chaetotaxy varies considerably from species to species, a few being glabrous and others multisetate. However, the majority of species have pupae bearing few setae which are usually arranged into a mid-dorsal pair, a dorso lateral group and a lateral group. The lateral group comprises a pair of setae located on a projecting lateral tubercle. A short, post-spiracular seta is usually present in the abdominal segments. Ventral setae are rarely present. The prothoracic setae are usually definitely arranged on either side of the large prothoracic plate and the cephalic setae arranged into a lateral row from the base of the antennae to the occiput. The setae are not usually borne on conspicuous deeply-pigmented tubercles but the base of each seta may be slightly raised. The last abdominal segment may bear single or paired stout spines (urogomphi). 2-5 setae are usually present at the apex of each femur and rarely setae are located on the tarsi and tibiae.

### B. Significance of the Pupal setae.

The pupal setae are probably protective rather than sensory, especially in those species which pupate within cells. Woods (1918) stated that the setae of pupae are formed by the same trichogen cells which formed the larval setae. They are not hollow sensory hairs like the larval setae but are solid and pointed. They are developed only on the dorsal side, or the anterior and posterior ends of the body so that their function could be to hold the pupa away from contact with the sides of the pupal cell since the pupa lies with the ventral aspect uppermost. The setae protect the delicate pupal integument from damage by friction against the comparatively rough walls of the cell.

The setae give little protection against predators and parasites. In those species in which pupation occurs on the leaves of the foodplant, the pupal integument has very small sparse setae.

The pupae of some species bear single or paired caudal spines or urogomphi. In the present study I did not investigate the pupation positions in the different species. Duffy (1953) showed that position of pupation, either head up, head down or horizontal in cerambycid species may have a bearing on the presence or absence of the urogomphi. The chief function of the well developed pupal urogomphi seems to be the protection of the posterior part of the body (which bears all the weight) from abrasion since apparently they are present only in pupae the larvae of which pupate head upward. Absence of urogomphi in species which pupate horizontally supports this view.

The pupae of Chrysomelidae, especially from the Chrysomelinae, Galerucinae and Halticinae have been fairly comprehensively studied by previous workers (Appendix Table 4). In the present study representative pupae from all subfamilies except the Orsodacninae, Lamprosomatinae and Zeugophorinae have been drawn and described.

### C. Pupal descriptions

#### 1. SUBFAMILY CASSIDINAE

##### GENUS Cassida

Colour varying from pale green, yellow, cream to grey brown.

Pupation occurring on the under surface of leaves of the foodplant. The old larval skins are retained at the apex of the abdomen, concealing the final 2 segments. Pupae dorso-ventrally flattened, the head concealed by the broad pronotum. Pronotum bearing 6 large anterior-spines which may have side branches and a variable number of smaller spines along the antero-lateral edge. Meso and metanotum without lateral spines or scoli. Abdominal segments 1-8 bearing lateral expansions or scoli with lateral spines. The scoli are progressively reduced in size from the first to the final segment and may be absent completely in segments 6 & 7 of most species. The scoli in segments 6-8 rarely possess side spines. Abdomen usually bearing 7 pairs of distinct spiracles. The 8th abdominal segment bearing laterally a pair of short scoli and sometimes apically a terminal fork. Setae absent.

#### C. viridis L. Plate P35 Fig. 48.

Pale green. Pronotum without dark patterning, bearing 52 small spines along the antero lateral edge. First abdominal spiracle distinct and usually surrounded by a small black area. Other spiracles indistinct as their peritremes are concolorous with the integument. Abdominal segments 6 & 7 without lateral scoli. Terminal fork absent.

#### C. murraea L. Plate P35, Fig. 47.

Pale green. Pronotum without dark patterning and bearing approximately 65 small spines along the antero-lateral edge. Otherwise similar to C. viridis but terminal fork reduced.



C. vittata Vill. Plate P35 Fig. 46.

Creamy. Pronotum with light brown patterning and bearing approximately 41 small spines along the antero-lateral edge. Reduced lateral scoli present on abdominal segments 6-8 but terminal fork absent. Abdomen bearing 7 distinct pairs of spiracles and each segment bearing 2 pale brown areas between mid-dorsal line and spiracle and a pale brown area mid-dorsally in segments 3-6.

Cassida rubiginosa Müll. Plate P34 Fig. 45.

Dirty white. Pronotum with pale brown patterning and bearing approximately 45 small spines along the antero-lateral edge. Lateral scoli absent on segment 6 and very reduced on 7th and 8th segments. Terminal fork present. Abdomen bearing 7 distinct pairs of spiracles and each segment with 2 darker brown areas between mid-dorsal line and spiracle.

Cassida flaveola Thunb. Plate 34 Fig. 44.

Creamy yellow. Pronotum with pale brown patterning and bearing approximately 29 small spines along the antero-lateral edge. Well developed lateral scoli present on segments 6-8 and a well developed terminal fork present. Abdomen bearing 7 distinct pairs of spiracles and each segment with 2 darker brown areas between mid-dorsal line and spiracle.

## II. SUBFAMILY DONACIINAE

Pupae white or creamy and without setae. Pupation occurring underwater within cocoons constructed by the final instar larvae. The cocoons have been shown to consist of a laminated substance apparently formed from layers of peritrophic membrane glued together, and embodying occasional interposed layers of material resembling plant cell walls.

GENUS Donacia

Donacia cinerea Hbst. Plate P31 Fig. 41.

Pupae white, without setae. Antennal and tarsal segments shorter and stouter than in Haemonia. Apex of tarsus of hindlegs reaching the 4th abdominal segment.

GENUS Haemonia (= Macroplea)

Haemonia appendiculata (Pz.) Plate P31 Fig. 40.

Pupae white without setae. Antennal and tarsal segments long, slender. Apex of tarsus of hindlegs reaching the 7th abdominal segment.

III. SUBFAMILY CRIOCERINAEGENUS Lema

Pupae white or yellow. Pupation occurring in soil within silken cocoons constructed by the final instar larvae. Setae absent.

Lema puncticollis Curt. Plate P30 Fig. 39.

Colour white. Thorax constricted at the mid-point. Apex of abdomen bearing a pair of urogomphi, the tips of which are inwardly curved. Abdomen bearing 4 distinct pairs of spiracles.

Lema melanopa (L.) Plate P29 Fig. 38.

Colour yellow. Thorax constricted near the base. Apex of abdomen bearing a pair of urogomphi, more slender and shorter than in L. puncticollis.

IV. SUBFAMILY CRYPTOCEPHALINAEGENUS Cryptocephalus

C. pusillus F. Plate P32 Fig. 42.

Colour creamy yellow. General form subcylindrical. Pupation occurring within the larval case of the final instar larva above the soil surface. Head bearing 2 pairs of setae on distinct raised papillae. Antennae filiform. Pronotum bearing numerous minute setae,

setae longer along the antero-lateral edge. Meso and metanotum bearing 2 pairs of small setae. Abdominal segments bearing 3 small setae on each side dorsal to lateral line. 5th segment with a small dorso-lateral papilla bearing a single seta. 6th and 7th segment bearing a dorso-lateral papilla larger than the papilla on the 5th segment and bearing 2 setae. 8th segment bearing a lateral unisetate papilla and apex with a pair of slender urogomphi without setae. Ventral setae absent and spiracles very indistinct.

#### v. SUBFAMILY CLYTRINAE

##### GENUS Clytra

C. quadripunctata (L.) Plate P33 Fig. 43.

Colour creamy white. General form sub-cylindrical. Pupation within the larval case of the final instar in the nest of the ant Formica rufa. Head without setae. Antennae serrate. Pronotum bearing numerous minute setae. Mesonotum bearing 3 pairs of minute setae. Metanotum bearing 2 pairs of small setae. Mesothoracic spiracle very large and distinct whereas the abdominal spiracles are indistinct. 1st abdominal segment without setae. 2-6 abdominal segments bearing a single minute dorsal, a post-spiracular seta may be present and 1 or 2 minute lateral setae. 7th abdominal segment bearing 2-3 minute dorsal setae on a small conical papilla, a pair of minute post-spiracular setae on a single papilla may be present and 2-3 minute lateral setae. 8th segment bearing dorsally 7 minute setae and 2 lateral setae borne on small conical papillae.

#### vi. SUBFAMILY CHRYSOMELINAE

Pupation usually occurring in earthen cells or rarely on the leaves of the foodplant. Last abdominal segment usually without urogomphi but single or paired urogomphi may be present. The majority of pupae show the typical arrangement of moderately long setae whereas

others may bear sparse minute setae or even numerous very long setae.

#### GENUS Timarcha

##### T. tenebricosa (F.) Plate P1 Fig. 1.

Colour orange-red, pupation within an earthen cell. Covered by numerous minute setae. Last abdominal segment bearing a single bilobed urogomph. Apex of femora without setae.

#### GENUS Chrysolina

Last abdominal segment bearing a single urogomph varying in shape from conical to truncate. Head bearing more than 3 pairs of setae. Pronotum bearing numerous short to moderately long setae. Mesonotum bearing 1-4 pairs of setae varying in length. Metanotum bearing 1 to numerous setae. Abdominal segments bearing numerous short to long setae dorsally. Apex of femora bearing 2-5 setae, tibiae and tarsi without setae. Pupation within an earthen cell.

##### C. staphylea (L.) Plate P5 Fig. 5.

Colour white. Head, bearing approximately 30 moderately long setae. Pronotum bearing numerous moderately long setae, longer along the lateral edge. Mesonotum bearing 2 pairs of setae. Metanotum bearing 3-6 setae on each side. Apex of femur bearing up to 3 pairs of long setae. Abdominal segments bearing dorsally about 15-30 setae on each half, laterally with 5-8 setae. Abdomen with 6 functional spiracles. Urogomph conical, bearing 9 dorsal setae. Ventral abdominal segments may bear up to 15 minute setae.

##### C. polita (L.) Plate P3 Fig. 4.

Colour white to cream. Head bearing approximately 16 moderately long setae. Pronotum bearing approximately 60 setae of variable length, somewhat longer laterally. Mesonotum and metanotum bearing 2 pairs of setae. Apex of femur bearing up to 4 setae. Abdominal segments bearing dorsally on each side about 9 setae of varying length and 4-6 longer

setae laterally. Urogomph more pointed than in C. staphylea bearing 10 dorsal setae. Ventral abdominal segments without setae.

C. menthastri (Suf.) Plate P2, Fig. 2; Plate P3, Fig.3.

Colour bright yellow. Head bearing approximately 20 moderately long setae. Pronotum bearing approximately 120 moderately long to long setae. Mesonotum bearing 2-4 setae on each side. Metanotum bearing 4-6 setae on each side. Apex of femur bearing up to 5 setae. Abdominal segments bearing dorsally about 20 long setae and laterally up to 8 setae on each side. Urogomph more truncate than in C. staphylea and C. polita and bearing dorsally about 14 large setae. Ventral abdominal segments without setae.

C. graminis (L.) Colour creamy white.

C. fastuosa (Scop.) Colour white.

C. varians (Schal.) Plate P6 Figs. 6 & 7.

Colour orange. Head bearing approximately 18 moderately long setae. Pronotum bearing about 64 moderately long setae, sometimes on dark raised papillae. Mesonotum bearing 4-5 minute to moderately long setae. Metanotum bearing few to numerous minute setae. Apex of femur bearing up to 2 setae. Abdominal segments bearing dorsally few to about 32 minute setae (a row along anterior edge of segment - not found in other Chrysolina sp.) and laterally 3-6 moderately long setae. Urogomph more truncate than in C. menthastri and bearing up to 8 dorsal setae. Ventral abdominal segments bearing 2 or 3 minute setae near lateral edge.

C. brunsvicensis (Gr.) Plate P7 Fig. 8 Plate PPI Fig.1

Colour yellow. Head bearing approximately 16 moderately long setae. Pronotum bearing about 64 moderately long setae, longer along lateral edge. Meso and metanotum bearing 1 pair of setae. Apex of femur bearing 1 minute seta. Abdominal segments bearing dorsally about 20-23 moderately long setae and 3 or 4 longer lateral setae. Urogomph similar in shape to C. varians, but bearing 4 dorsal setae. Ventral abdominal segments without setae.

C. hyperici (Forst.) Plate P8 Fig. 9.

Colour orange. Head bearing approximately 10 moderately long setae. Pronotum bearing about 46 moderately long setae. Meso and metanotum bearing 1 pair of setae. Apex of femur bearing 1 or 2 setae. Abdominal segments bearing about 12-16 moderately long dorsal setae and about 4 longer lateral setae. Urogomph less truncate than in C. varians and brunsvicensis and with only 2 dorsal setae. Ventral abdominal segments without setae.

GENUS Phytodecta

Pupation within earthen cells. Last abdominal segment bearing paired urogomph. Head usually bearing 14-20 setae. Pronotum bearing numerous moderately long to very long setae, longer along the lateral edge. Mesonotum bearing 9-45 setae variable in length. Metanotum bearing 18-66 setae variable in length. Abdominal segments bearing dorsally about 20-40 setae varying in length and randomly distributed, and 3-8 longer lateral setae. Apex of femur bearing 3 long setae. Outer edge of tibia near the apex bearing a single long seta and apex of tarsus usually bearing a long seta also.

P. pallida (L.) Plate P11 Fig. 12.

Colour pale green. Head bearing approximately 22 long setae. Pronotum bearing about 80 setae varying from short to very long. Mesonotum bearing 16 short to moderately long setae. Metanotum bearing 19 short to very long setae. Abdomen dorsally with about 20 short to moderately long setae and laterally with 4-5 long setae.

P. olivacea (Forst.) Plate P9 Fig. 10; Plate 10, Fig. 11

Colour white. Head bearing approximately 40 short to long setae. Pronotum bearing about 120 short to very long setae. Mesonotum bearing 20-45 short to long setae. Metanotum bearing 32-68 short to long setae. Apex of tarsus with seta very reduced. Abdominal segments bearing about 40 short to very long setae and laterally 5-7 long setae.

P. viminalis (L.) Plate P12 Fig. 13.

Colour cream. Head bearing about 12 long setae. Pronotum bearing about 68 very long setae. Mesonotum bearing about 9 short to long setae. Metanotum bearing about 19 short to long setae. Dorsal abdominal segments bearing about 16 short to long setae and laterally with 3-5 long setae.

GENUS Phyllodecta

Pupae white. Pupation within earthen cells. Last abdominal segment without urogomphi. Pronotum bearing 9-10 setae on each side, 6 along the antero-lateral edge and a posterior row of 3-4, the outer setae of which is sometimes reduced. Meso and metanotum bearing 1 pair of setae each. Head bearing 3 pairs of setae. 1st abdominal segment usually without setae laterally but with 1 pair dorsally. Following segments with a lateral tubercle bearing 2 setae. 8 pairs of rather conspicuous abdominal spiracles but those on the 8th segment are indistinct. Apex of femur bearing 2-3 setae.

P. vulgatissima (L.) Plate P14 Fig. 15.

Pronotum bearing 9 setae on each side, outer one of posterior row absent. Mesonotum with a single dark mid-dorsal tubercle bearing 2 setae. 1st abdominal segment with a lateral seta, 2 dorsal setae, the outer minute. 2-6 abdominal segments identical with first but with lateral tubercles bearing 2 setae, 7th abdominal segment as 1st but dorsal region on each side with a small dark tubercle bearing 2 setae.

P. vitellinae (L.) Plate P14 Fig. 16.

Pronotum bearing 10 setae on each side. Mesonotum bearing 2 setae on separate dark tubercles. 1st abdominal segment, 1 dorsal seta, and lateral seta absent. 2-6 abdominal segments, 1 dorsal seta, and 2 lateral setae. 6 & 7 abdominal segments 2 dorsal setae present.

P. cavifrons Th. (= laticollis Suf.) Plate P13 Fig. 14.

Pronotum bearing 10 setae on each side, outer seta of posterior row reduced. Mesonotum bearing 2 setae on separate dark tubercles. 1st abdominal segment; dorsal setae may be absent or one seta may be present but reduced, lateral setae absent 2-5 abdominal segments; 1 dorsal seta but sometimes a seta is present intero-dorsal to spiracle, 2 lateral setae. 6th abdominal segment, 1 dorsal seta but sometimes 2 setae are present intero-dorsal to spiracle. 7th abdominal segment bearing 2 dorsal setae.

#### GENUS Gastroidea

Pupae pale yellow or yellow, bearing brown setae. Pupation within earthen cells. Apex of femora bearing 2 setae. Head bearing 3 pairs setae. Last abdominal segment without urogomphi.

G. polygona (L.) Plate P16. Fig. 19.

Colour pale yellow. Pronotum bearing 9 setae on each side, 6 along antero-lateral edge and 3 in the posterior region. Meso and metanotum bearing a pair of setae each. 1st abdominal segment bearing 2 dorsal setae but these may be absent, laterals absent, 2-7th abdominal segments bearing 2 dorsal setae, a post spiracular seta and 2 lateral setae. 6 pairs of abdominal spiracles evident but peritreme of the 6th concolorous with the integument and therefore indistinct.

G. viridula (De G.) Plate P16. Fig. 20.

Colour yellow. Pronotum bearing 8 setae on each side, outer seta of posterior row absent. Mesonotum bearing 2 setae on a single mid-dorsal tubercle. Metanotal setae indistinct. 1st abdominal segment without setae. 2nd abdominal segment bearing 1 dorsal seta and 1 lateral seta. 3rd abdominal segment as 2nd but 2 lateral setae present. 4-7th abdominal segments as 3rd but a post spiracular seta also present.



GENUS Phaedon

Pupae yellow, bearing quite strongly developed brown setae. Pupation within earthen cells. Apex of final segment without urogomphi. Apex of femora bearing 2 setae.

P. cochleariae (F.) Plate P15 Fig. 17.

Pronotum bearing 9 setae on each side, 6 antero-laterally and 3 posteriorly. Mesonotum and Metanotum bearing 2 setae but also sometimes a smaller anterior pair. 1st abdominal segment bearing 2 dorsal setae, outer seta minute, 1 post spiracular and 1 or 2 lateral setae. Following abdominal segments as 1st but may have 2 post spiracular setae. 7th abdominal segment as previous segments but outer of 2 dorsals larger than in previous segments. 7 pairs of abdominal spiracles evident.

P. tumidulus (Germ.) Plate P15 Fig. 18.

Pronotum bearing 9 or 10 setae on each side, 6 or 7 antero-laterally and 3 posteriorly. Mesonotum bearing 2 setae. Metanotum bearing 2 pairs of setae, the anterior pair minute. 1st abdominal segment bearing 1 dorsal seta, 1 or 2 post spiracular setae and no laterals. 2nd-7th abdominal segments, bearing 2 dorsals, outer 1 minute, 1 or 2 spiracular setae and 2 laterals. 6 pairs of abdominal spiracles evident.

GENUS Hydrothassa

Pupae yellow with distinct setae. Pupation within earthen cells. Pronotum bearing 10 setae, 7 antero laterally and 3 posteriorly. Meso and metanotum bearing 2 setae each. Apex of femora bearing 2 or 3 setae. Abdominal segments bearing 1 or 2 dorsal setae, a post spiracular seta may be present and 2 lateral setae.

H. aucta (F.) Plate P17 Fig. 21.

Tubercles bearing setae in pronotum more distinct than in H. marginella, 1st abdominal segment bearing 1 dorsal seta. 2nd-6th abdominal segments bearing 1 dorsal seta and 2 lateral setae. 7th abdominal segment as 2-6 but bearing 1 or 2 dorsal setae.

H. marginella (L.) Plate P17 Fig. 22.

Setae on pronotum longer than in H. aucta but meso and metanotal setae shorter. 1st abdominal segment without setae. 2nd abdominal segment bearing 1 dorsal seta and no laterals. 3rd segment bearing 1 dorsal seta and 2 laterals. 4-7th abdominal segments bearing 2 dorsal, 1 post spiracular and 2 lateral setae. 7 pairs of abdominal spiracles can be distinguished.

GENUS Prasocuris

Pupae dirty white. Pupation on the underside of leaves. Head bearing 3 or 4 setae on each side. Pronotum bearing 12 small, plus 3 minute setae. Meso and metanotum bearing a pair of small setae, or mesonotum bearing 5-6 minute setae and metanotum with 4-5 minute setae. Post spiracular and lateral setae present on 1st abdominal segment. Apex of final segment without urogomphi.

P. junci (Brahm.) Plate P18 Fig. 23.

Meso and Metanotum bearing a pair of small setae. 1-6 abdominal segments bearing 1 or 2 dorsal, a post spiracular and 2 lateral setae, 6th abdominal segment sometimes bearing 2 post spiracular setae. 7th abdominal segment with a single dorsal tubercle bearing 2 setae. Apex of abdomen bearing 3 stout spines on each side.

P. phellandrii (L.) Plate P18 Fig. 24.

Mesonotum bearing 5-6, metanotum 4-5 minute setae on each side. 1-6 abdominal segments bearing 3-5 setae (1 large) between mid-dorsal line and spiracle, 1 or 2 post spiracular setae and 2 lateral setae. 7th abdominal segment without dorsal tubercle as in P. junci. Abdomen bearing 8 pairs of distinct spiracles.

GENUS Chrysomela

Colour white or cream, sometimes the integument bearing dark brown conspicuous tubercles but setae indistinct. Pupation on the underside of leaves.

C. populi L. Plate P19 Fig. 25.

White or cream, integument bearing a number of dark brown conspicuous tubercles but without regular chaetotaxy. Head with setae absent. Pronotum bearing 2 pairs of tubercles on each side. Mesonotum bearing a large fused mid-dorsal tubercle and 2 smaller tubercles anterior to a larger posterior tubercle. Metanotum bearing dorsally a small tubercle anterior to a larger tubercle and a single dorsolateral tubercle. There is usually a deeply pigmented area on each elytron and on the wing. The apex of the femur bearing 2 small setae. The first 6 abdominal segments are exposed and each bears 2 pairs of transversely arranged tubercles, the inner tubercles the larger. The posterior abdominal segments are concealed beneath the last larval skin and the dorsal integument is only weakly chitinised. Lateral tubercles usually bearing several short setae. Abdomen bearing 6 pairs of distinct spiracles.

C. aenea L. Plate P19 Fig. 26.

Colour cream, integument without dark brown tubercles. 6 abdominal

segments exposed. Lacking setae but sometimes with a dark area dorsal to spiracle in the abdominal segments.

#### GENUS Plagiodera

P. versicolora (Laich.) Plate P19 Fig. 27.

Colour creamy yellow. Pupation occurring on the underside of leaves. Head without setae. Pronotum bearing up to 7 minute setae on each side. Apex of femur bearing 2 setae. Abdominal segments bearing up to 3 small lateral setae. 6 abdominal segments exposed whereas the rest are concealed beneath the last larval skin. Abdominal segments 1-6 bearing a group of several minute brown spots dorsal to spiracles. Abdominal segments bearing 6 pairs of distinct spiracles.

#### vii. SUBFAMILY GALERUCINAE

Pupae white, cream, yellow, dark brown. Pupation usually occurring in earthen cells, rarely on the leaves of the foodplant. Head usually bearing <sup>3, rarely</sup> 4 pairs of setae, one pair located anteriorly on the frons. Apex of abdomen usually bearing one pair located anteriorly on the frons. Apex of abdomen usually bearing 2 distinct spines or urogomphi.

#### GENUS Galerucella

G. lineola (F.) Plate P24 Fig. 32.

Colour white. Pupation within earthen cells. Pronotum bearing 7 pairs of stout, black setae and sometimes 3 pairs of smaller setae. Mesonotum with a mid-dorsal tubercle bearing 2 setae and 1 or 2 setae ventral to this. Metanotum bearing 2 pairs of setae on raised bases, sometimes an outer smaller pair. 1-7 abdominal segments bearing a single large dorsal seta, 2 minute setae ventral to this and sometimes a minute seta anterior to the single dorsal seta. 1-2 large lateral setae also present. Abdomen bearing 7 pairs of distinct spiracles.

G. viburni (Pk.) Plate P23 Fig. 31.

Colour creamy white. Pupation within earthen cells. Head bearing 3-4 pairs of setae, <sup>(a pair interior to the ocellar setae may be present)</sup> Pronotum bearing 6 pairs of setae. Mesonotum usually bearing 3 pairs of setae, although 1 seta may be absent and usually the inner pair is borne on a small tubercle fused across the mid-dorsal line. Metanotum bearing 2 or 3 pairs of setae. Apex of femur bearing 2 setae. Abdominal segments 1-7 bearing a dorsal seta and one lateral seta. Apex of abdomen bearing 2 stout spines.

G. tenella (L.) Plate 25 Fig. 33.

Colour yellow. Pupation within earthen cells. Head bearing 3 pairs of setae. Pronotum bearing 7 pairs of setae but may also bear several smaller setae. Mesonotum bearing 2 pairs of setae, the inner 2 sometimes on a distinct tubercle fused across the mid-dorsal line. Metanotum bearing 2 pairs of setae. Apex of femur bearing 2 setae. 1-7th abdominal segments bearing a dorsal seta and a lateral seta. Apex of abdomen bearing 2 stout spines. Abdomen bearing 6 pairs of distinct spiracles.

G. sagittariae Brit. Cat. Plate P25 Fig. 34.

Colour dark brown, integument well chitinated. Pupation on the under surface of leaves of the foodplant. Head without setae. Pronotum bearing 3 pairs of minute setae along the antero-lateral edge. Meso and metanotum without setae. Abdominal segments bearing a single lateral seta, dorsal seta absent. Apex of abdomen bearing 2 pairs of spines, the anterior ventral pair are smaller than the apical pair.

GENUS Lochmaea

L. suturalis (Th.) Plate P26 Fig. 35

Colour creamy white. Pupation within earthen cells. Head bearing 5 pairs of setae, <sup>(including 2 anterior pairs on the frons)</sup> Pronotum bearing 6 pairs of setae on distinct

bases. Meso and metanotum bearing 2 pairs of setae each. Apex of femur bearing 2 setae. Abdominal segments 1-7 bearing 1 dorsal seta, sometimes 2 in 1st segment and one lateral seta. Apex of 8th abdominal segment bearing a pair of stout spines.

L. capreae (L.) Plate P27 Fig. 36.

Colour white. Pupation within earthen cells. Head bearing 5 or 6 pairs of setae. *(including 2 anterior pairs on the frons, a pair of setae may be present interior to the ocellar setae)* Pronotum bearing 6 pairs of setae on distinct bases.

Meso and metanotum bearing 2 pairs of setae with distinct bases. Apex of femur bearing 2 setae. Abdominal segments 1-7 bearing 1 dorsal and 1 lateral seta. Apex of 8th abdominal segment bearing 2 stout spines. Abdomen bearing 7 pairs of distinct spiracles.

GENUS Sermyla

S. halensis (L.) Plate PPI Fig. 1 Plate P22 Fig. 30

Colour yellow. Pupation within earthen cells. Head bearing 3 pairs of setae. Pronotum bearing 6 pairs of small setae. Meso and metanotum bearing 2 pairs of small setae each. Apex of femur bearing 2 setae. Abdominal segments 1-7 bearing 2 dorsal, 1 post spiracular and 1 lateral seta. Apex of 8th abdominal segment bearing a pair of stout spines.

GENUS Agelastica

A. alni (L.) Plate P20 Fig. 28

Colour white. Pupation within earthen cells. Pronotum damaged but bearing 5 pairs large setae along antero-lateral margin. Mesonotum bearing 3-4 setae on each side. Metanotum bearing 2 setae. 1st abdominal segment bearing 3 dorsal, 1 post-spiracular and 1 lateral seta. 2-7 abdominal segments bearing 3-4 dorsal, 1 post spiracular and usually 1, rarely 2 lateral setae. Apex of 8th abdominal segment bearing a distinct pair of stout spines or urogomphi. Abdomen bearing 6 pairs of distinct spiracles.

GENUS Galeruca

G. tanacetii (L.) Plate P21 Fig. 29.

Pupa yellow except for the distal ends of the antennae, mouth parts and legs which are tinged with black. Pupation within earthen cells. Head between the eyes bearing 3 pairs of setae and clypeus bearing transversely 4 setae. Pronotum bearing 9 pairs of setae, 6 pairs along the antero lateral edge and 3 pairs in a posterior row. Mesonotum bearing 1-2 setae on each side. Metanotum bearing 2 pairs of setae. Abdomen bearing 2 lateral series of yellow tubercles bearing short black setae, between which are black spiracles. A dorsal ridge extends across each abdominal segment. 1st abdominal segment bearing 1 dorsal seta. A lateral expansion bearing 1 or 2 setae, a tubercle posterior to spiracle bearing 2 setae. Abdominal segments 2-6 bearing 1 large dorsal seta, in addition 1-4 smaller setae arranged near the large seta, 1 large dorso lateral seta on a raised tubercle dorsal to spiracle, 1-7 setae on tubercle posterior to spiracle and 2-5 setae on a lateral tubercle. 7th abdominal segment bearing a large pair of dorsal setae and 3 smaller lateral setae. Apex of 8th abdominal segment bearing 3 pairs of stout setae. Abdomen bearing 7 pairs of distinct spiracles.

viii. SUBFAMILY HALTICINAE

Pupae yellow or white. Pupation within earthen cells.

GENUS Haltica

H. lythri Aub. Plate P28 Fig. 37.

(One of the ocellar setae is sometimes bisetose)

Colour orange. Head bearing  $3\text{ or }4$  pairs of setae. Pronotum bearing 8 pairs of setae but some may be absent. Meso and metanotum bearing 2 pairs of setae. Apex of femur bearing 3 setae. Abdominal segments 1-7 bearing 1 large dorsal seta, a minute seta anterior to these, 1 pre-spiracular seta, 1 post-spiracular seta, 1 minute and 1 large lateral seta. Apex of 8th segment bearing 2 stout urogomphi distinctly

larger in the female than the male. Abdomen bearing 6 pairs of distinct spiracles.

GENUS Hippuriphila

H. modeeri (L.)

Colour pale yellow. Head bearing 3 pairs of setae. Pronotum bearing 8 pairs of stout setae. Meso and metanotum bearing 2 pairs of setae each. Apex of femur bearing 3 setae. Abdominal segments bearing 2 dorsal, a large spiracular and 1 large lateral seta. Apex of 8th segment bearing 2 stout urogomphi.



LIST OF ABBREVIATIONS USED IN THE FOLLOWING PUPAL FIGURES

A	ANTENNA
IA	FIRST ABDOMINAL SEGMENT
I	I
8A	EIGHTH II II
E	COMPOUND EYE
Ex	EXUVIAE
F	FEMUR
H	HEAD
Mst	MESOTHORAX
Mtt	METATHORAX
Prt	PROTHORAX
S	SPIRACLE
Ta	TARSUS
Ti	TIBIA
TS	TERMINAL SPINE
W	WING

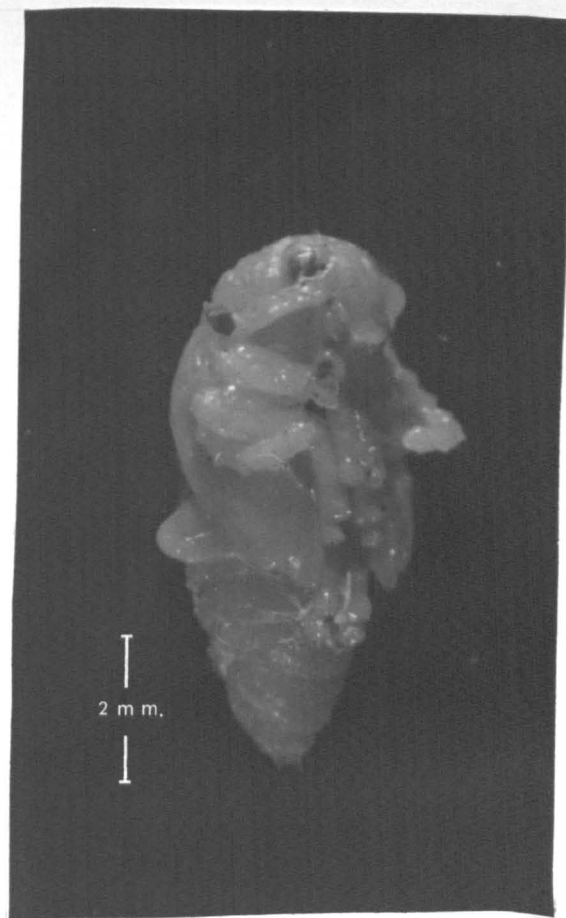
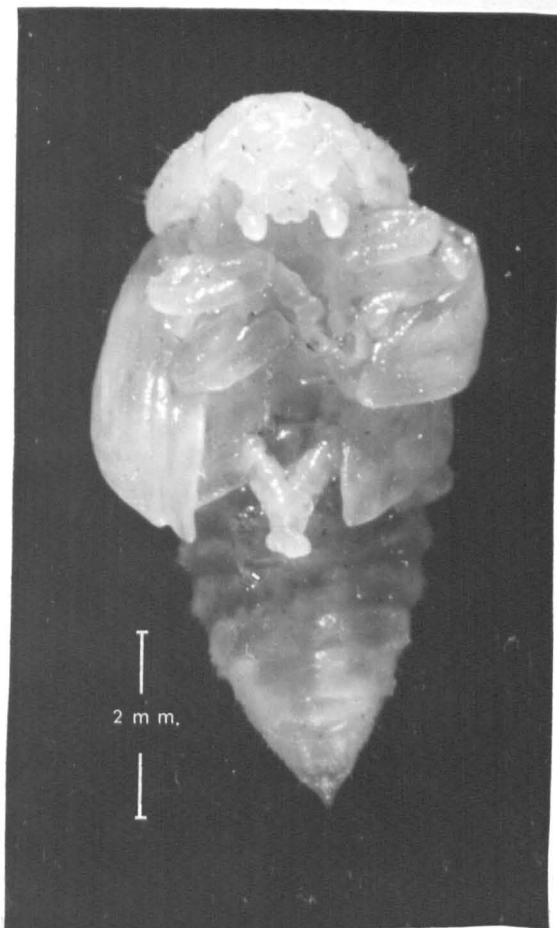


FIG. 1 PUPA OF *Chrysolina brunsvicensis* (Gr.)      FIG. 2 PUPA OF *Sermyla halensis* (L.)

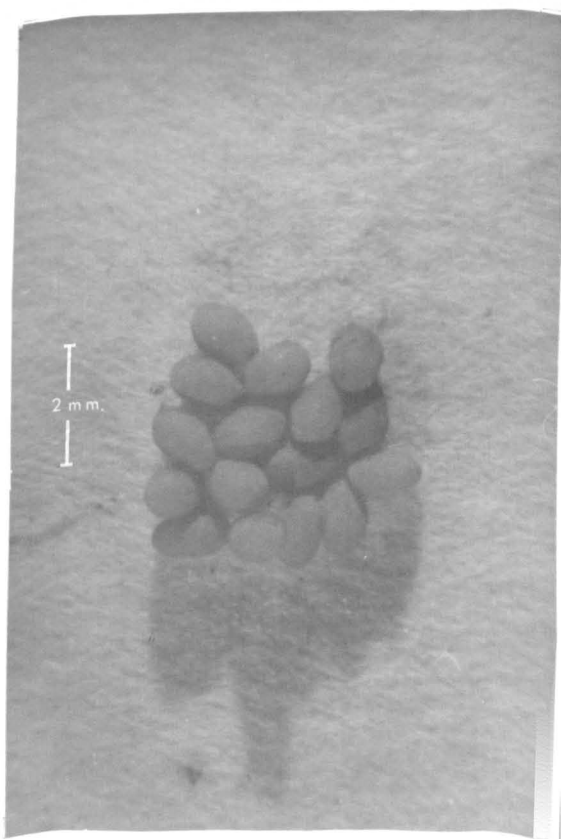
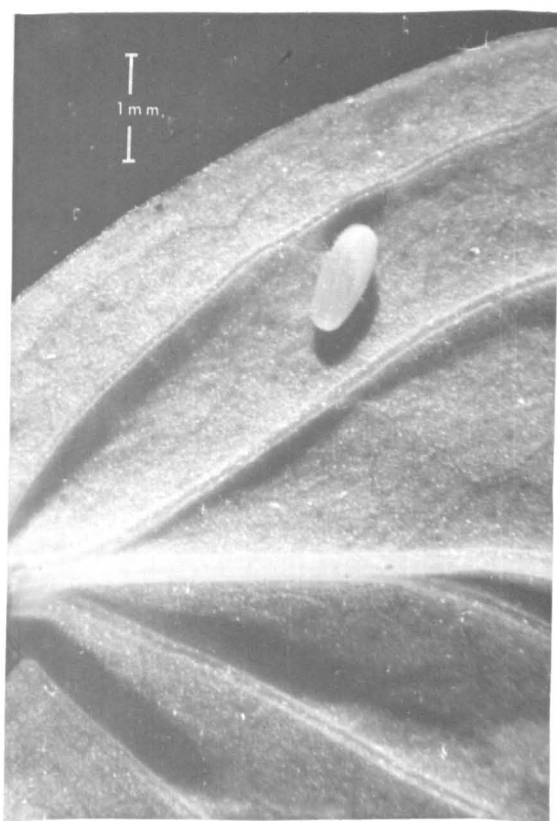
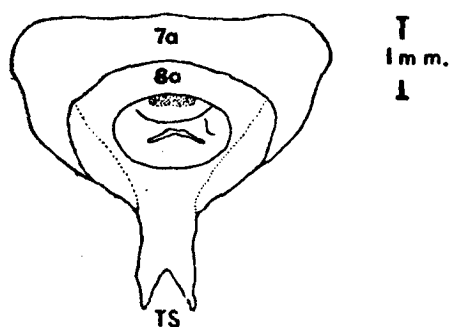


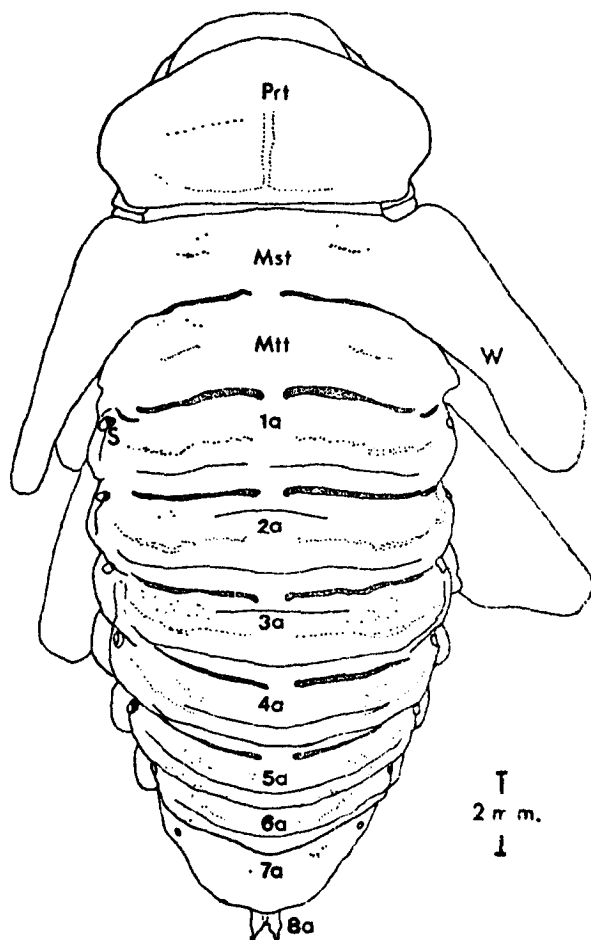
FIG. 3 EGG OF *Chrysolina brunsvicensis* (Gr.)      FIG. 4 EGG BATCH OF *Sermyla halensis* (L.)

FIG. 1 *Timarcha tenebricosa* (F.)

b. Ventral view of apex of male pupa



a. Dorsal view of male pupa



c. Ventral view of apex of female pupa

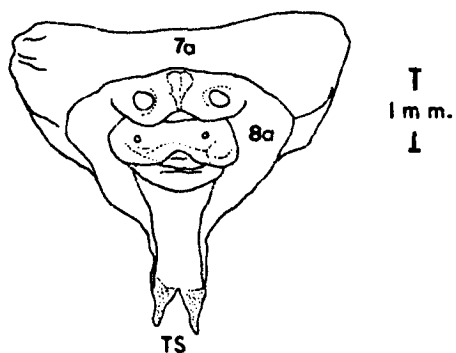
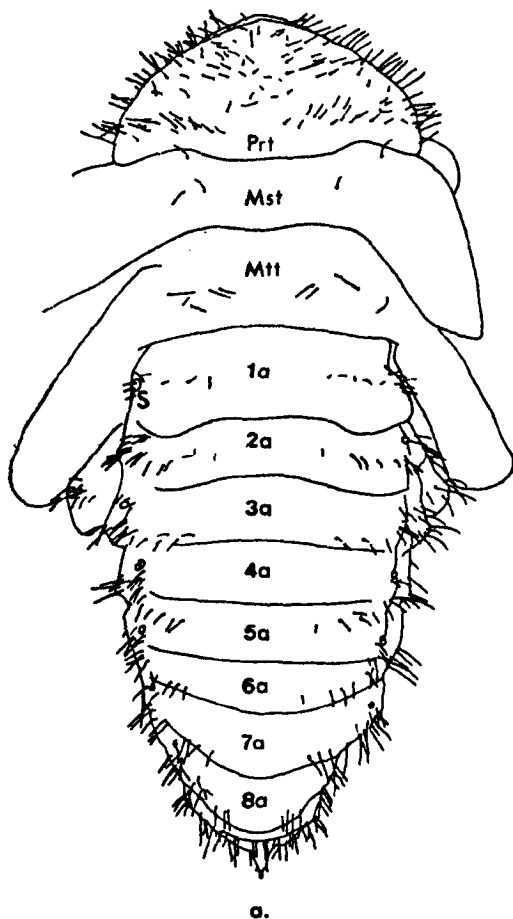


FIG. 2

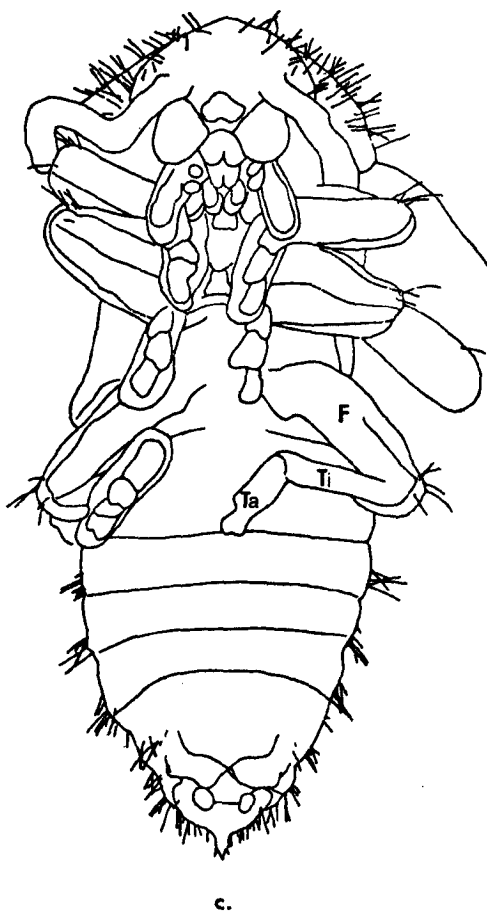
*Chrysolina menthastri* (Suf.) ♂

Dorsal view

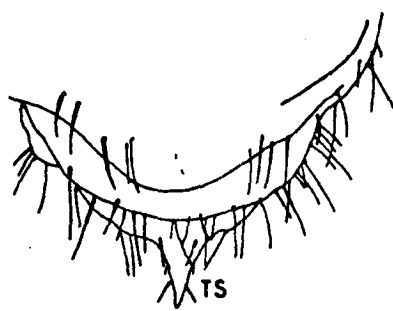


a.

Ventral view

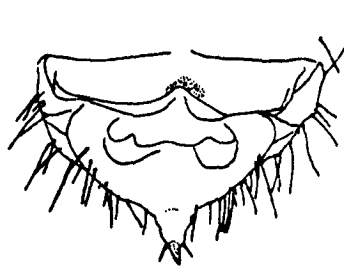


1 m m.



b.

Dorsal view Abd. segs. 9 & 10.



0.5 m m.

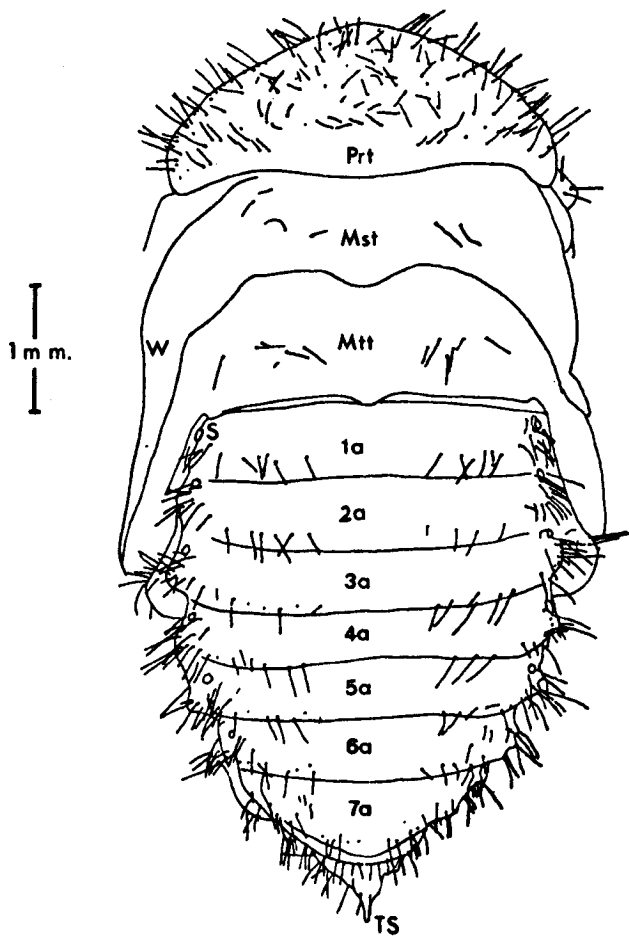
d.

Ventral view Abd. segs. 9 & 10.

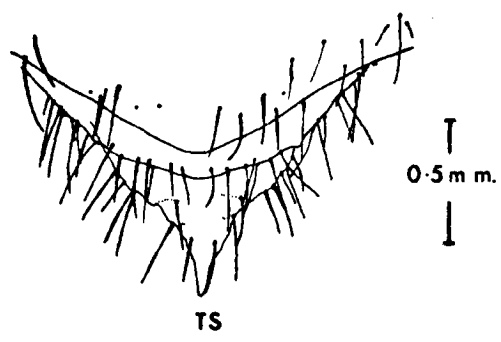
FIG. 3

Chrysolina menthastri (Suf.) ♀

a. Dorsal view



b. Dorsal view Abd. segs. 7 8 9 & 10



c. Ventral view Abd. segs. 9 & 10

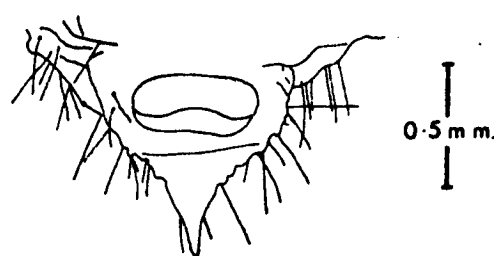
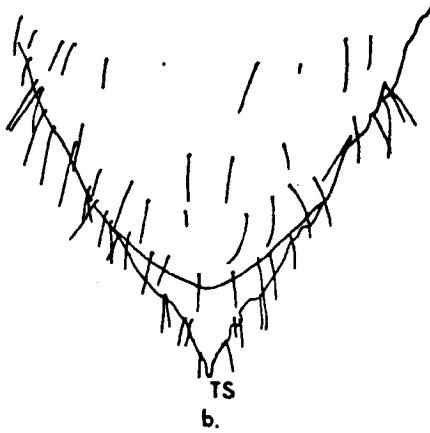
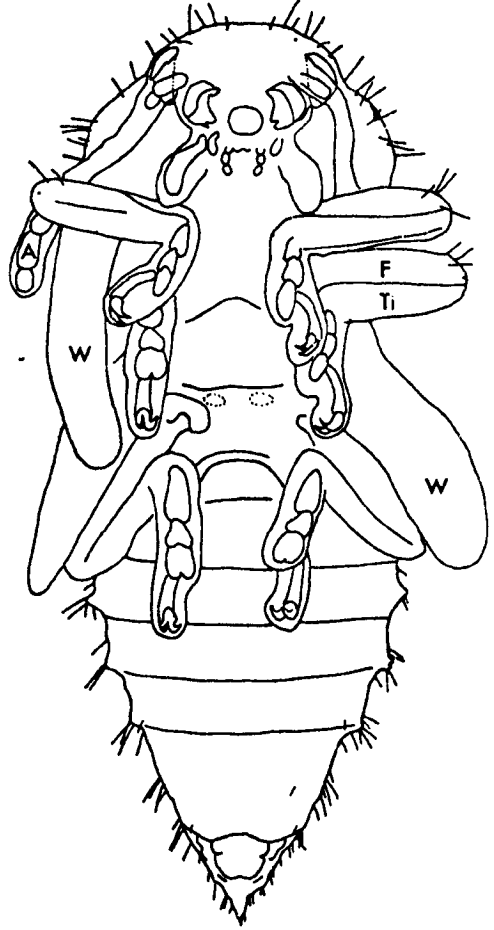
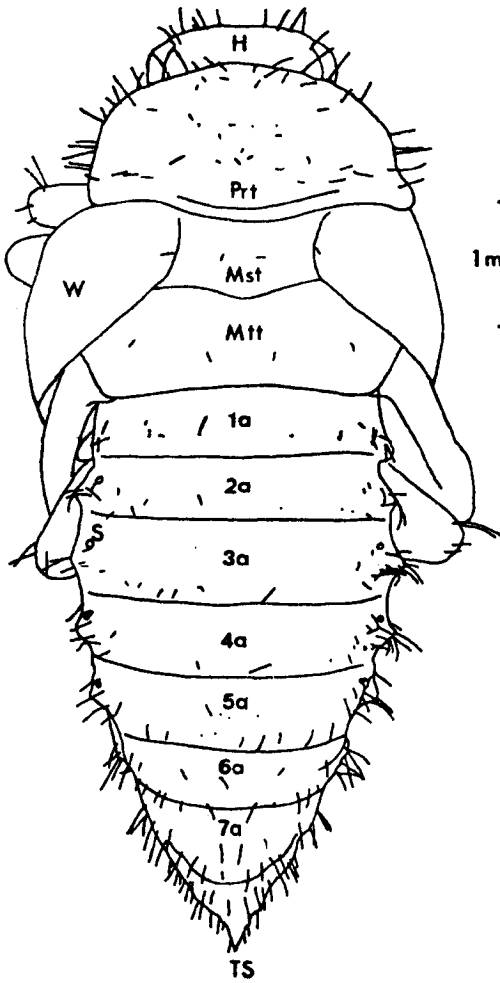


FIG. 4

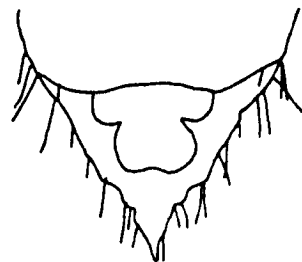
*Chrysolina polita* (L.)

a. Dorsal view

c. Ventral view



0.5mm.



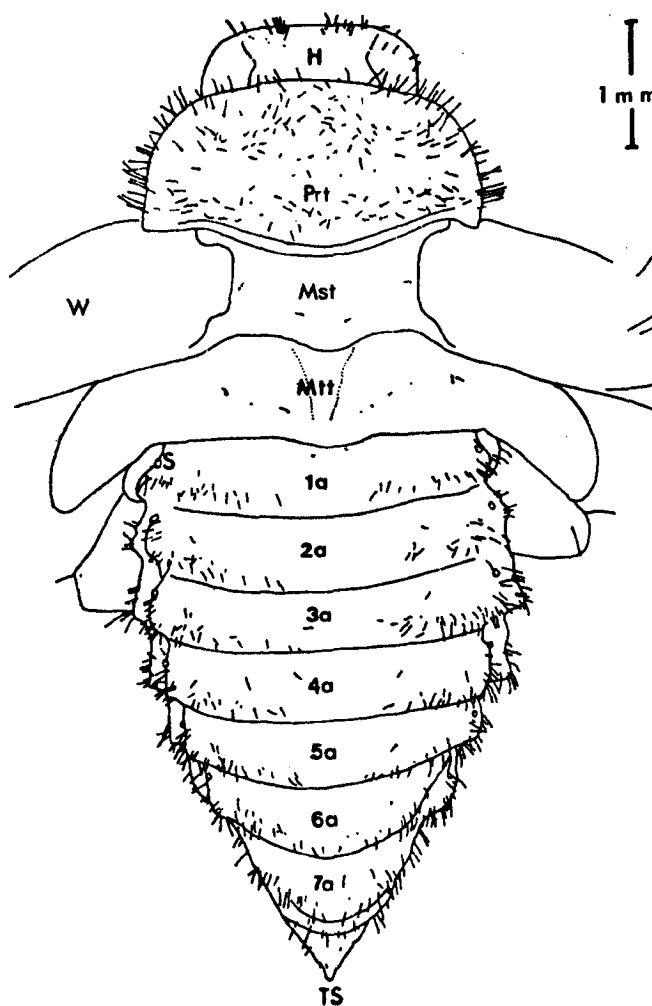
Abd. ssgs. 7, 8, 9 & 10.

Abd. ssgs. 9 & 10.

FIG. 5

*Chrysolina staphylea* (L.)

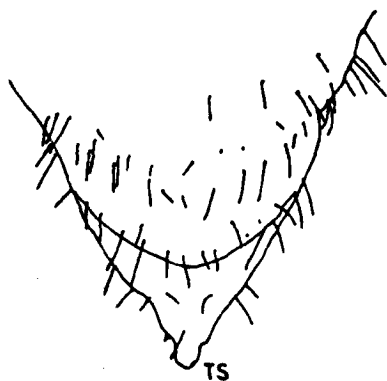
a. Dorsal view



c. Ventral view.



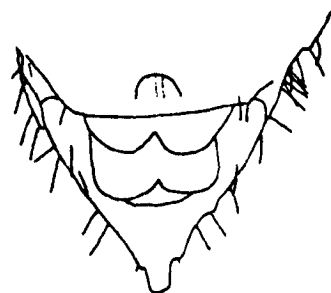
1 mm.



b.

Abd. segs. 7, 8, 9 & 10.

0.5 mm.



d.

Abd. segs. 9 & 10.

a. Dorsal view FIG. 6

*Chrysolina varians* (Schal) c. Ventral view

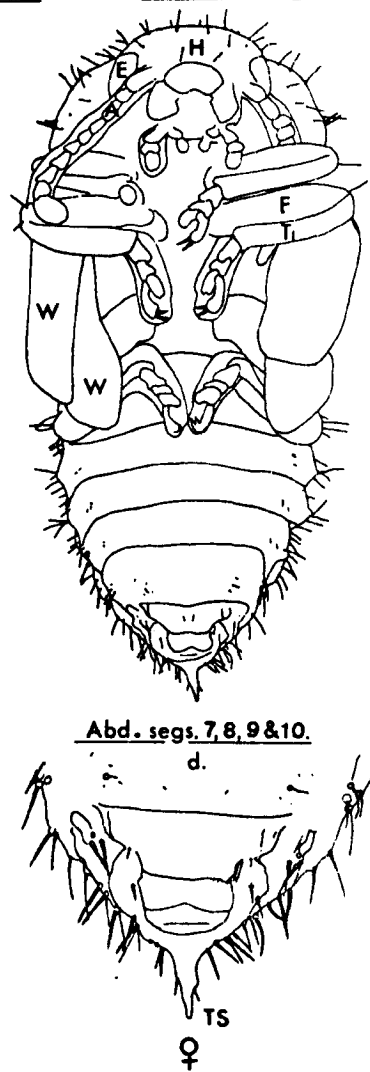
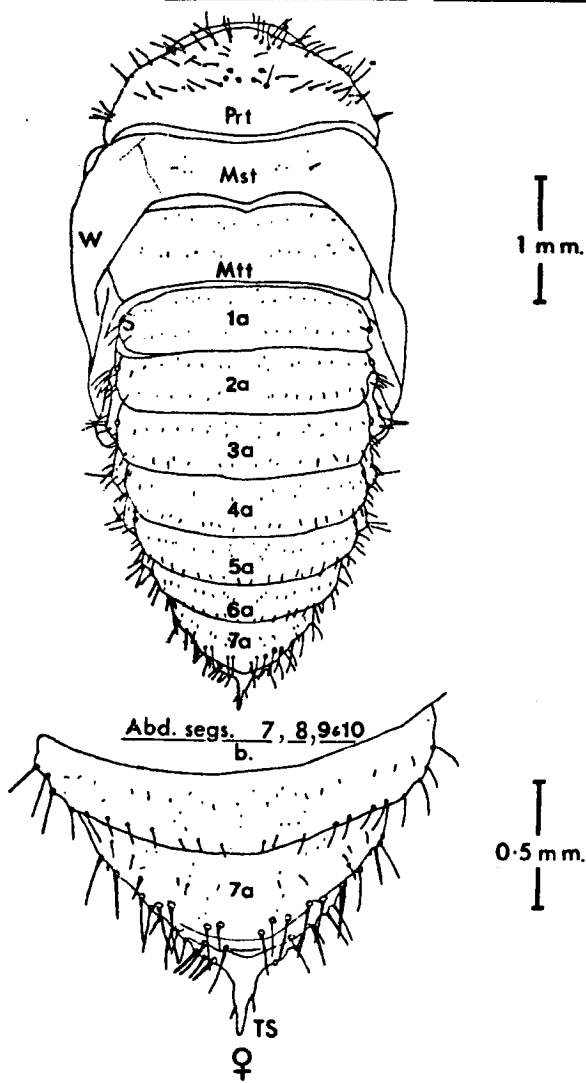
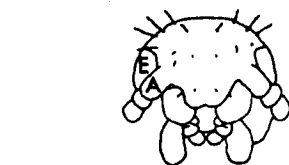
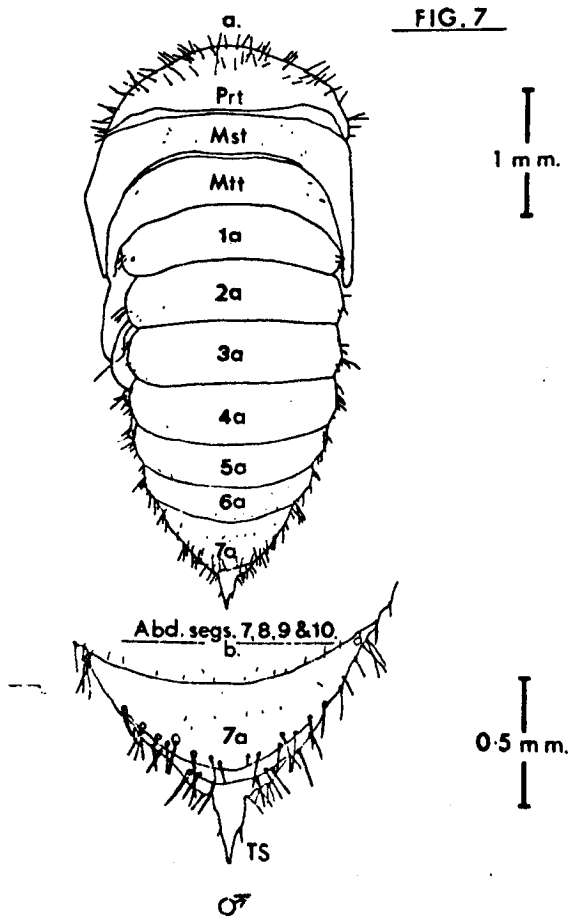


FIG. 7

c. Head-antero ventral view



Abd. segs. 7, 8, 9 & 10.  
d.

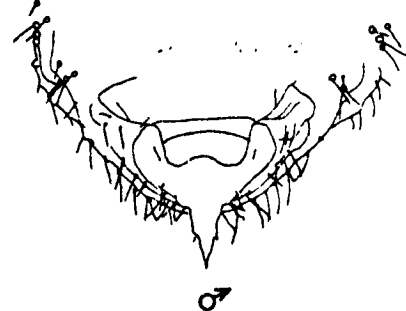
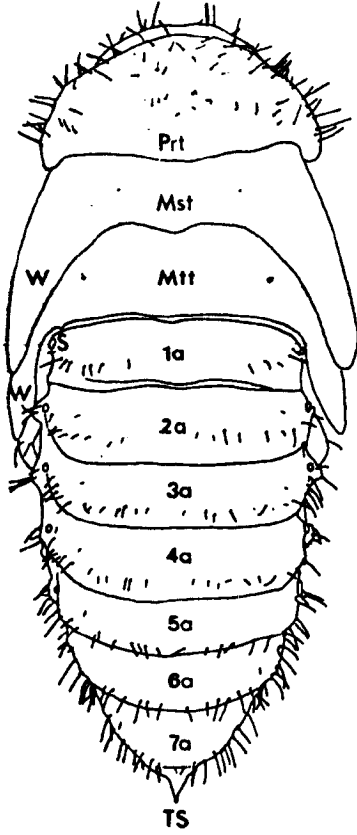




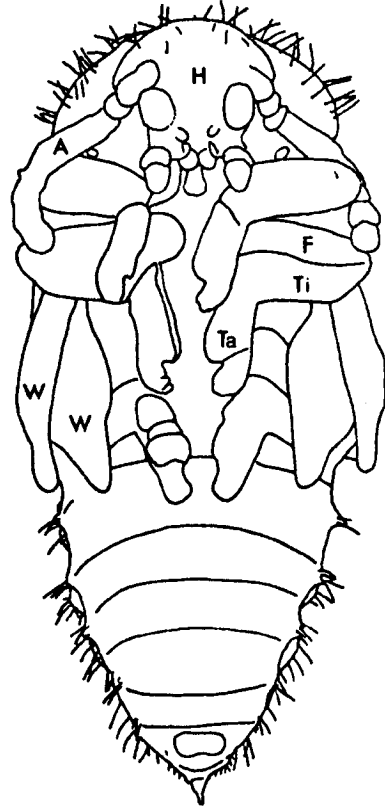
FIG.8

*Chrysolina brunsvicensis* (Gr.)

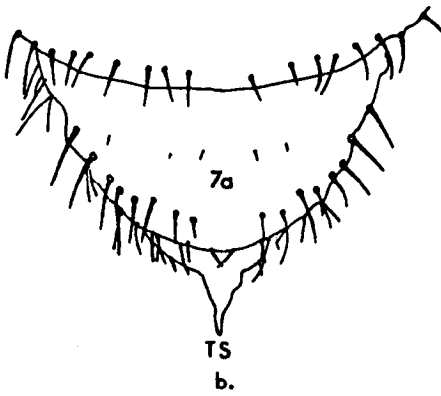
a. Dorsal view



c. Ventral view

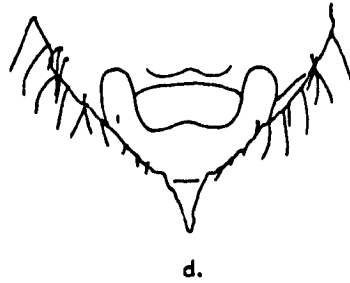


1 mm.



Abd. segs. 7, 8, 9 & 10.

0.5 mm.

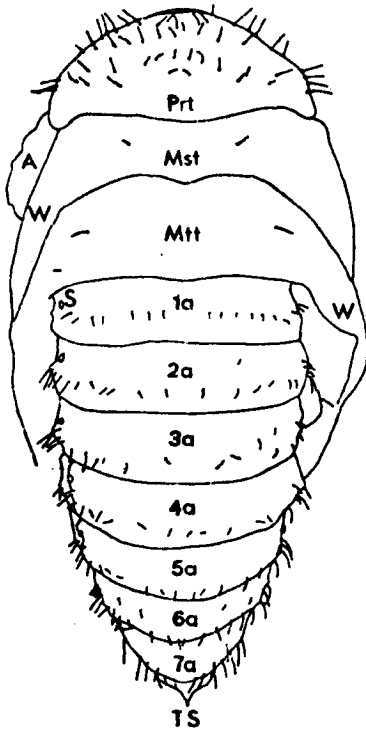


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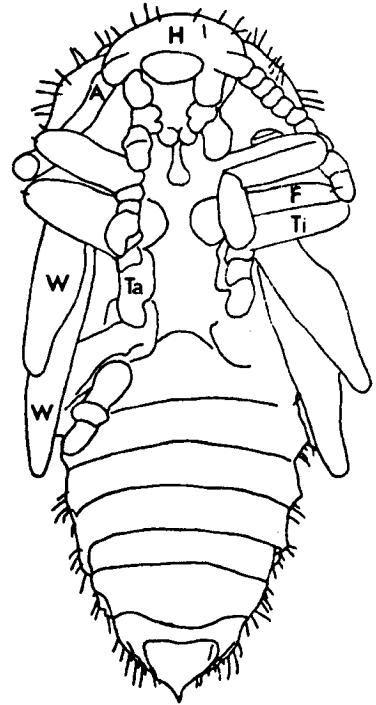
FIG. 9

Chrysolina hyperici (Forst.)

a. Dorsal view

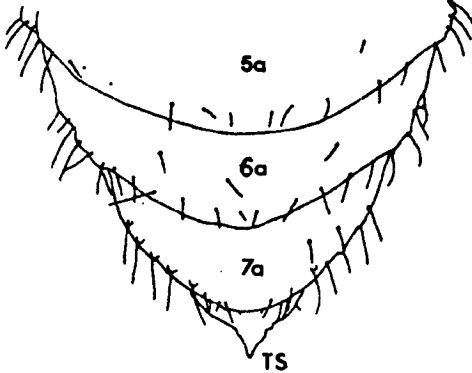


c. Ventral view



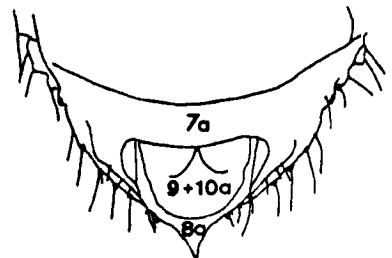
1 mm.

b.



Abd. segs. 5, 6, 7, 8, 9 & 10.

d.



Abd. segs. 7, 8, 9 & 10.

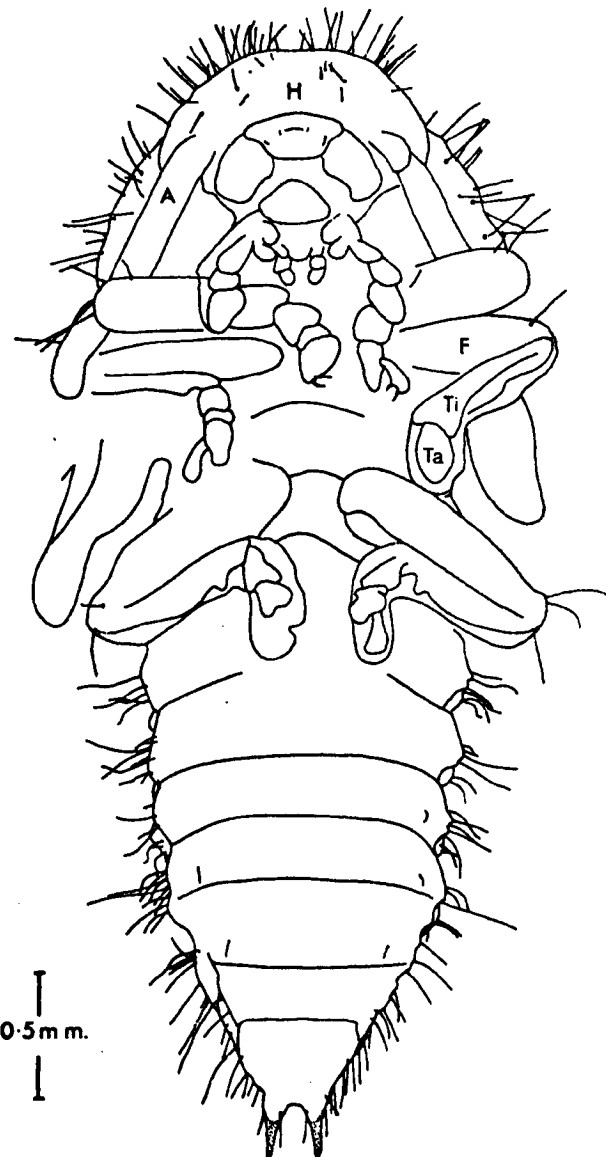
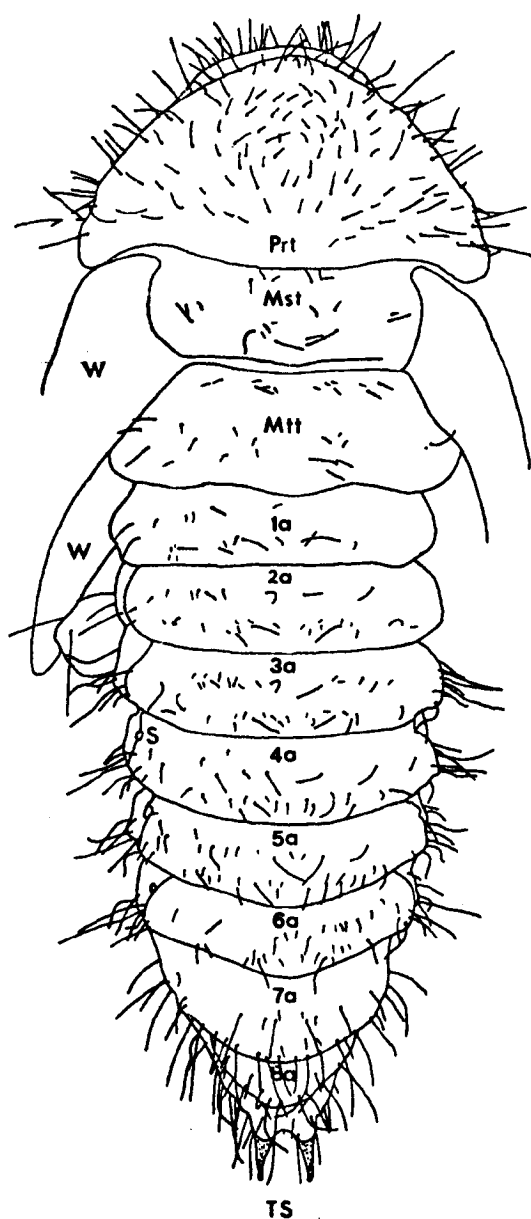
0.5 mm.

FIG. 10

*Phytodecta olivacea* (Forst.) ♂

a. Dorsal view

b. Ventral view



0.5 mm.

FIG. 11

*Phytodecta olivacea* (Forst.)

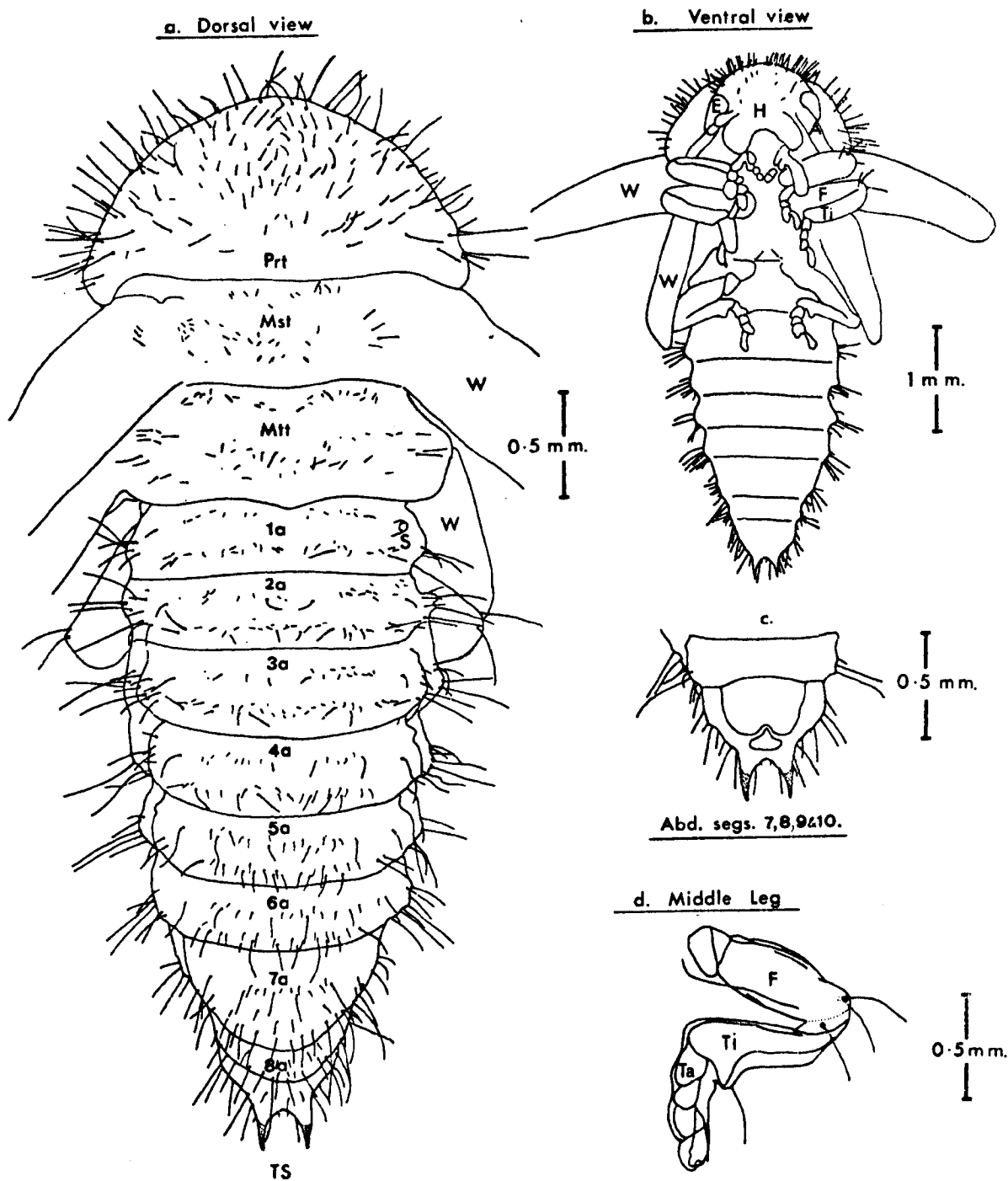
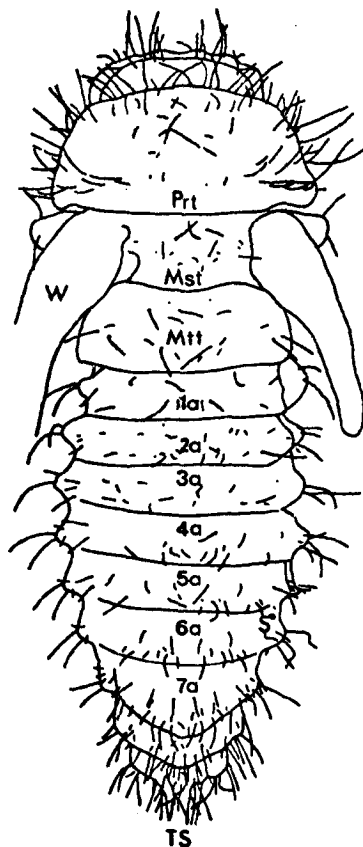
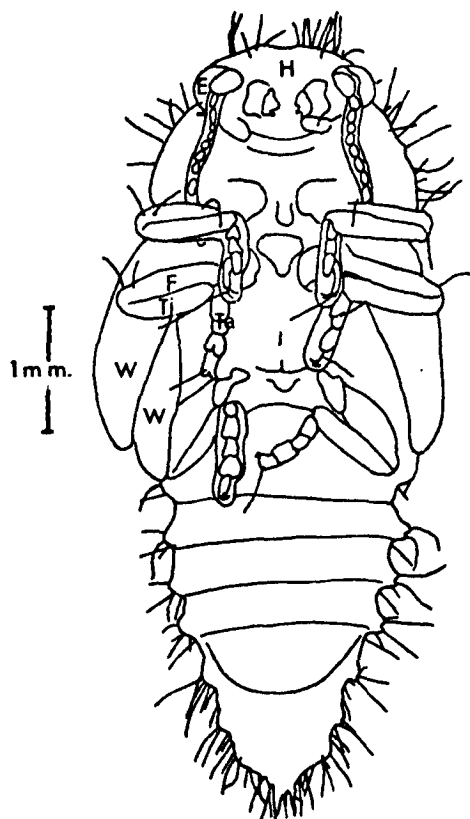


FIG. 12     Phytodecta pallida (L.)

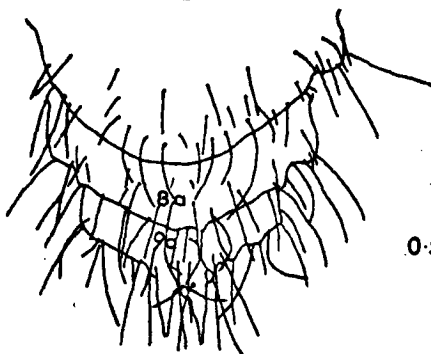
a. Dorsal view



c. Ventral view

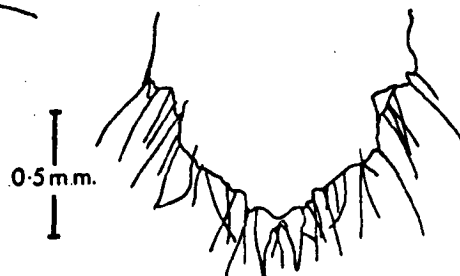


b.



Abd. segs. 7, 8, 9 & 10.

d.

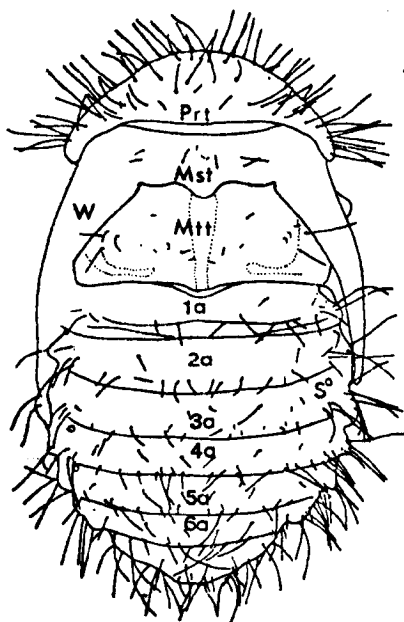


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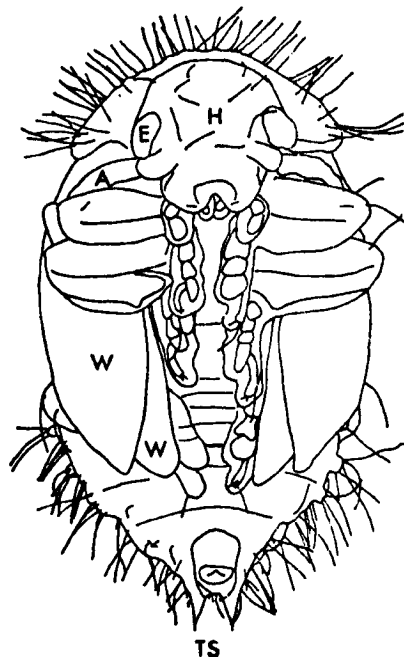
FIG. 13

*Phytodecta viminalis* (L.)

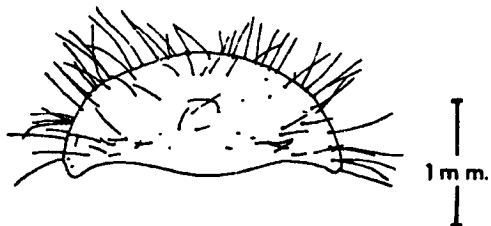
a. Dorsal view



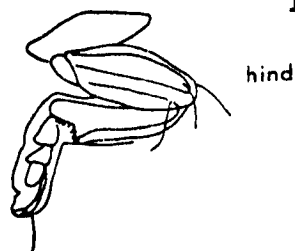
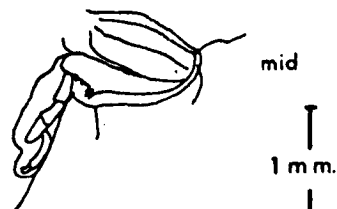
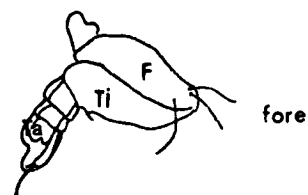
d. Ventral view



b. Pronotum



e. Legs



c. Abdominal segments 6, 7, 8, 9 & 10.

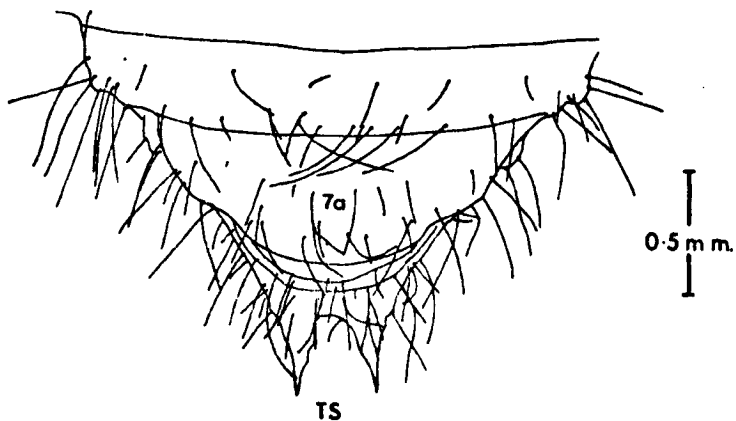
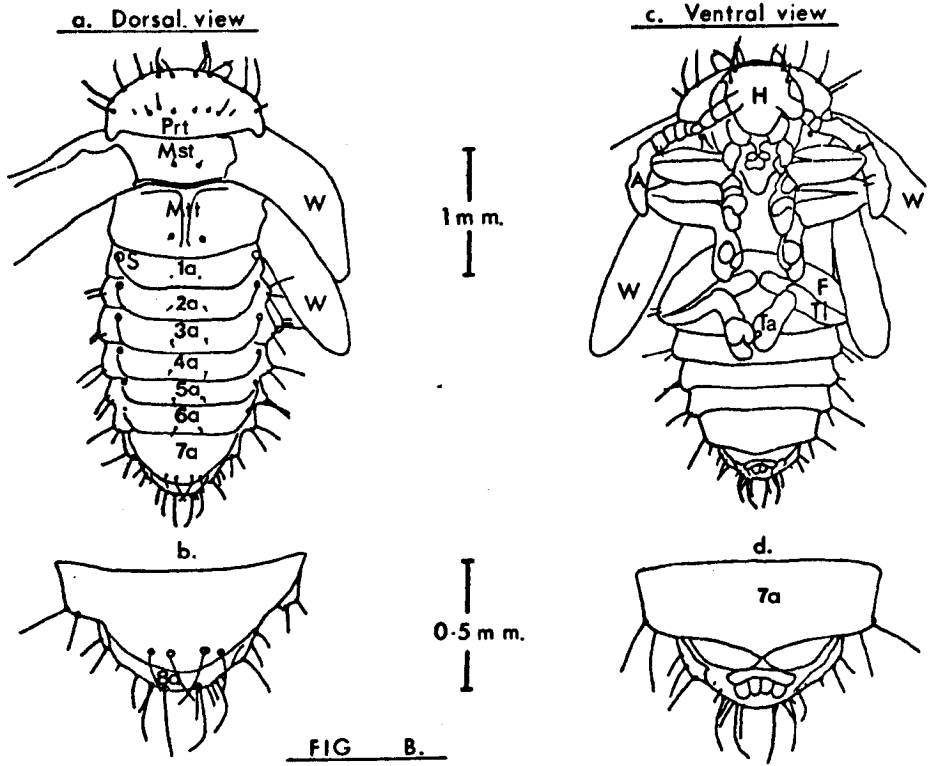


FIG. 14 *Phyllodecta laticollis* Suf.

A. Pupa of the light larval form



Pupa of the dark larval form

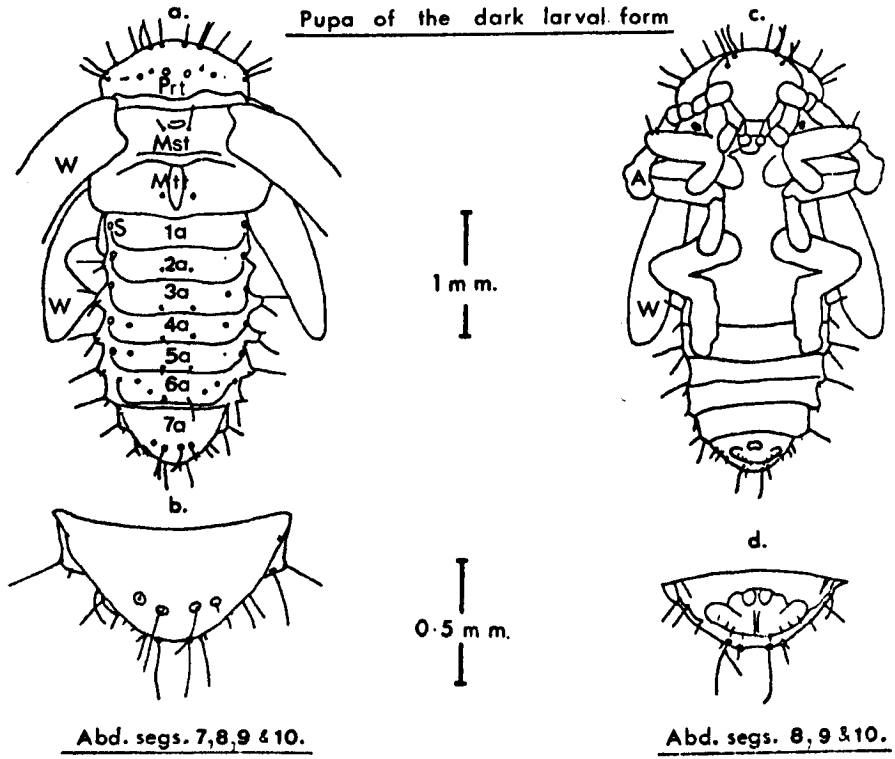
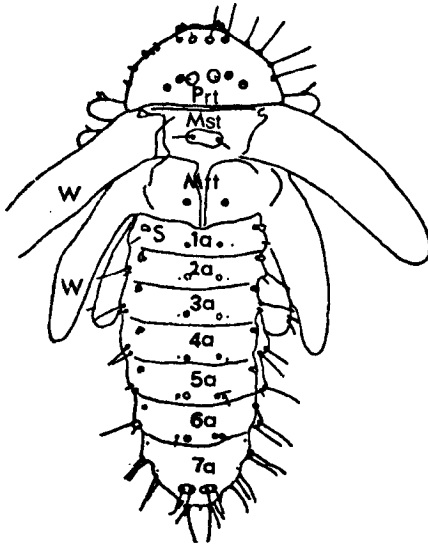


FIG. 15

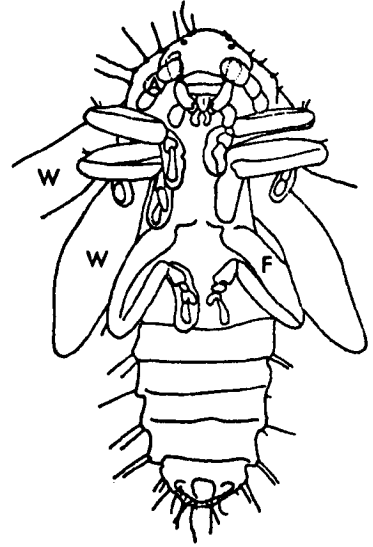
*Phyllodecta vulgotissima* (L.)

a. Dorsal view

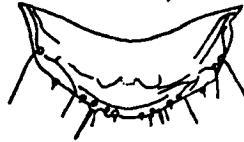
c. Ventral view



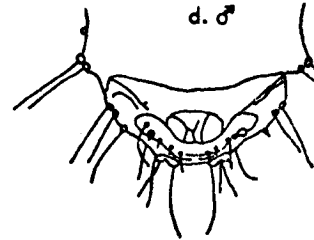
1 m m.



b. ♀



d. ♂



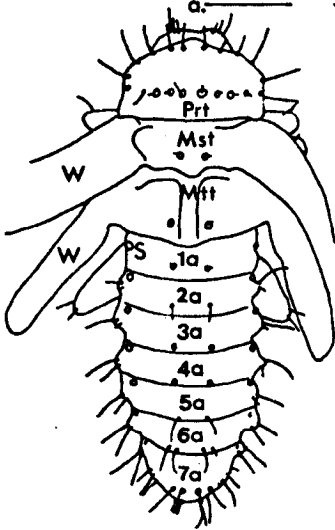
0.5 m m.

FIG. 16

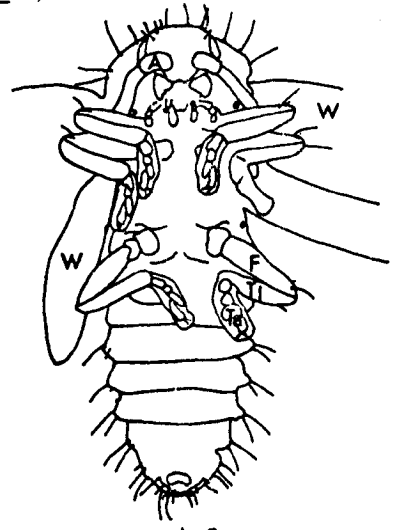
*Phyllodecta vitellinae* (L.)

a.

c.



1 m m.



b. ♀



d. ♂



0.5 m m.

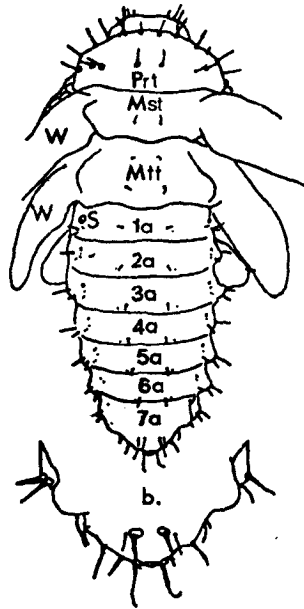
FIGS. b. & d. Abd. segs. 8, 9 & 10.



FIG. 17

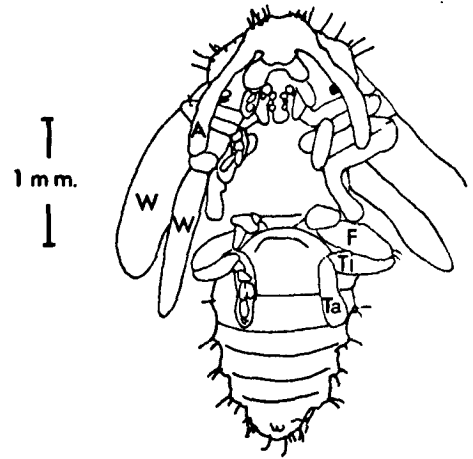
*Phaedon cochleariae* (F.)

a. Dorsal view



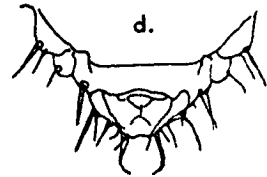
Abd. segs. 7, 8, 9 & 10.

c. Ventral view



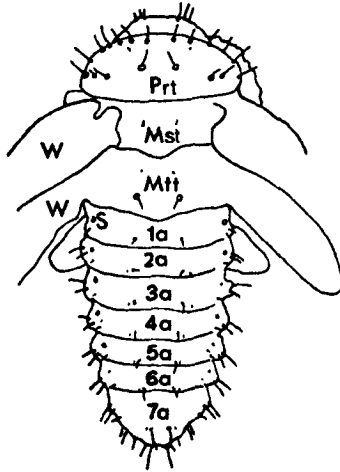
1 mm.

0.5 mm.



Abd. segs. 7, 8, 9 & 10.

FIG. 18 *Phaedon tumidulus* (Germ.)

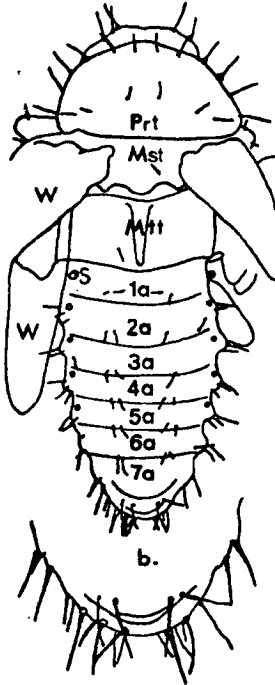


1 mm.

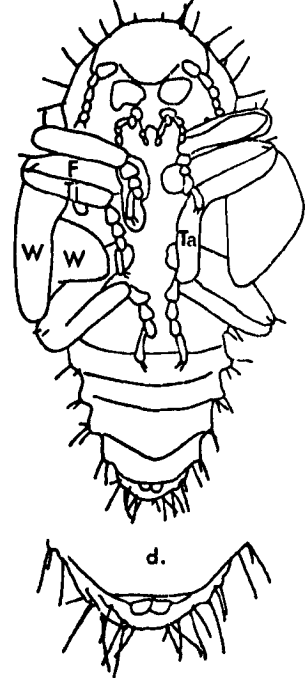
FIG. 19

*Gastroidea polygona* (L.)

a. Dorsal view



c. Ventral view



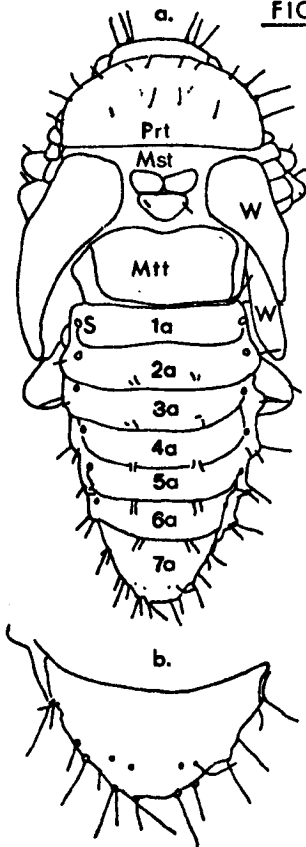
1 m.m.

0.5 m.m.

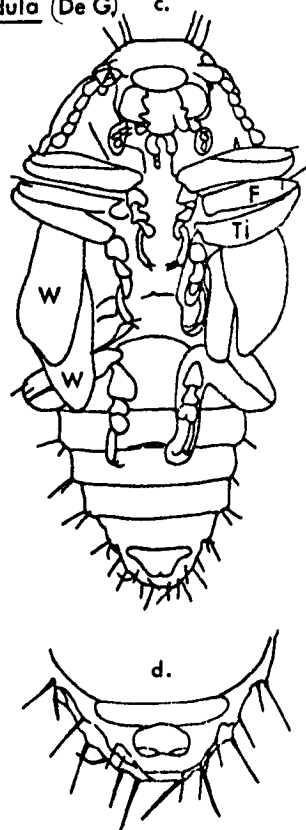
FIG. 20

*Gastroidea viridula* (De G.)

a.



c.



1 m.m.

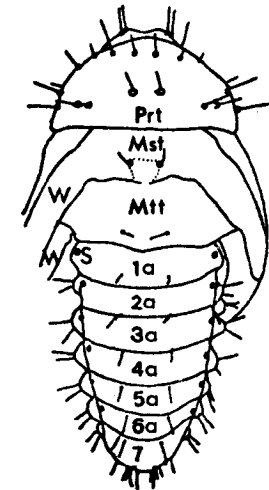
0.5 m.m.

FIGS. b. & d. Abd. segs. 7, 8, 9 & 10.

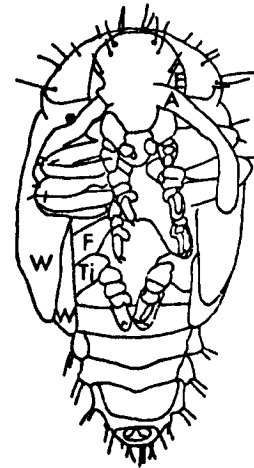
FIG. 21

*Hydrothassa aucta* (F.)

a. Dorsal view

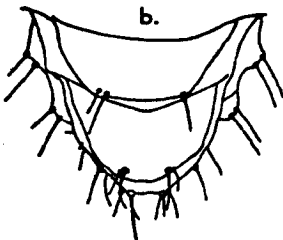


c. Ventral view



1 m m.

b.



0.5 m m.

d.

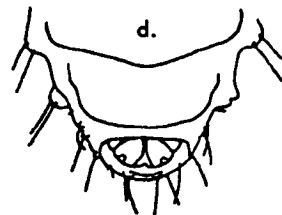
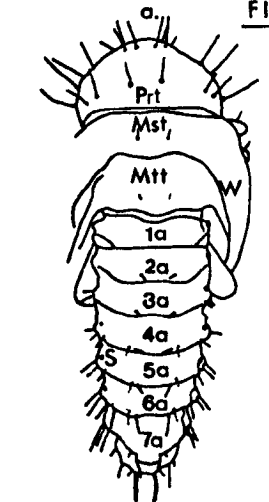
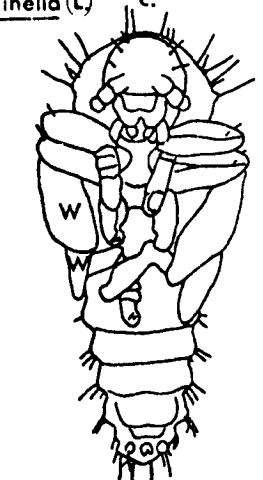


FIG. 22 *Hydrothassa marginella* (L.)

a.

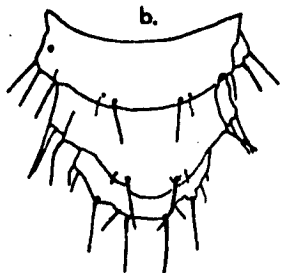


c.



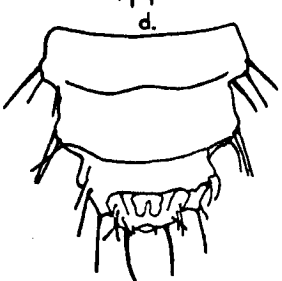
1 m m.

b.



0.5 m m.

d.



FIGS. b.&d. Abd. segs. 6, 7, 8, 9 & 10.

FIG. 23 *Prasocuris junci* (Brahm.)

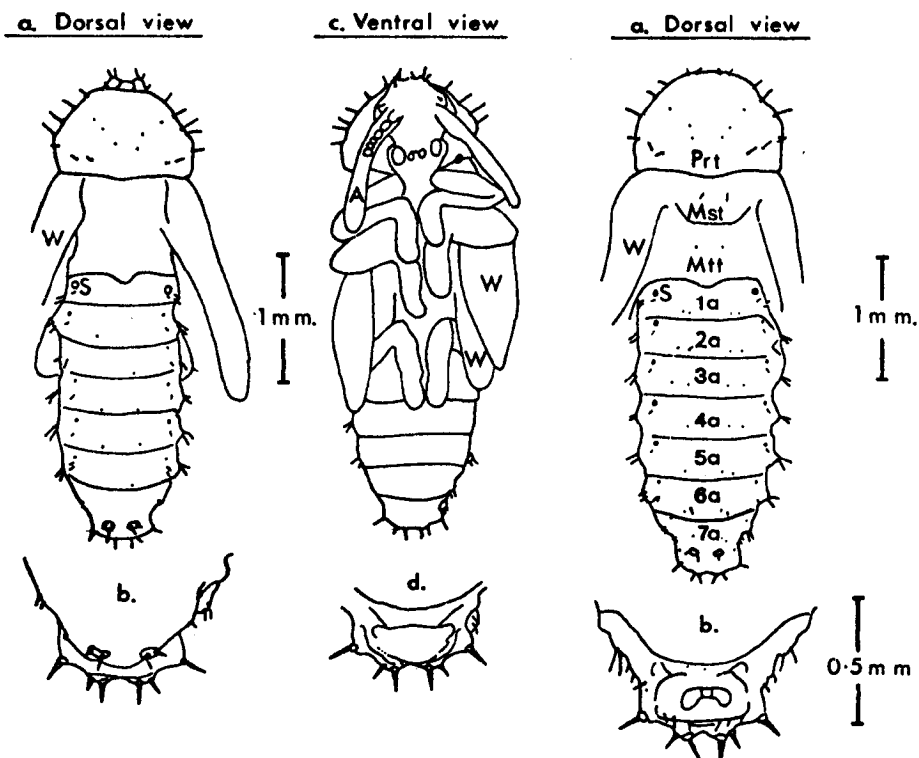
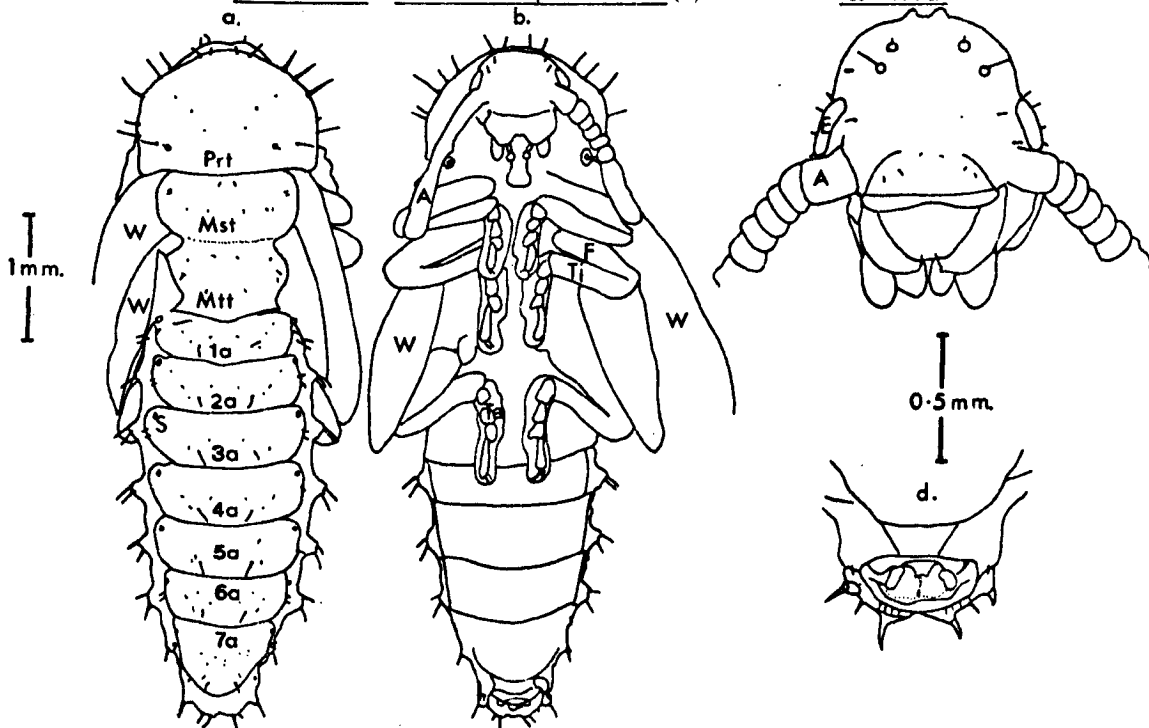


FIG. 24 *Prasocuris phellandrii* (L.)



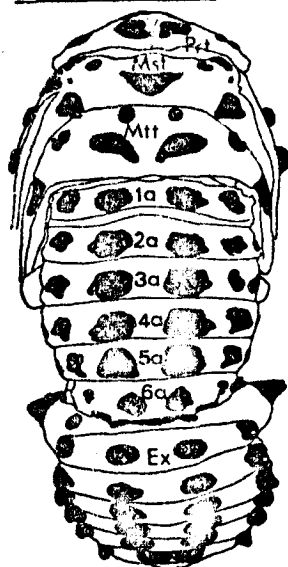
FIGS. b & d. Abd. segs. 7, 8, 9 & 10.

FIG. 25

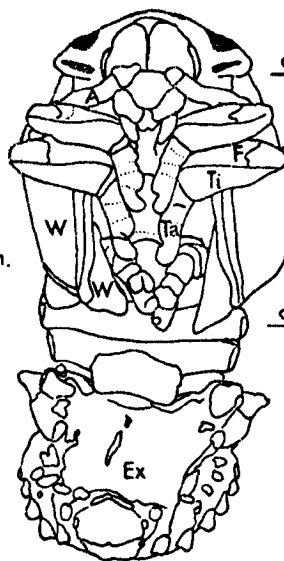
*Chrysomela populi* L.

a. Dorsal view

b. Ventral view



2 mm.



c. Dorsal view without exuvia



d. Ventral view without exuvia

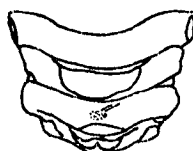


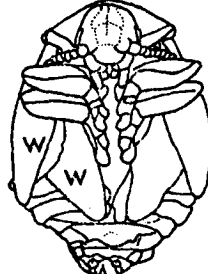
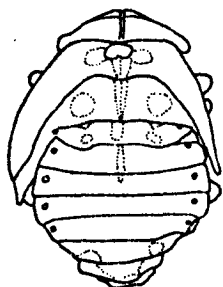
FIG. 26. *Chrysomela aenea* L.

a.

b.

Abd.

FIGS. b, c, d. segs. 6, 7, 8, 9 & 10.

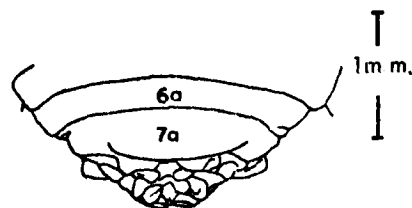
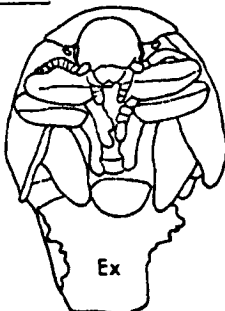
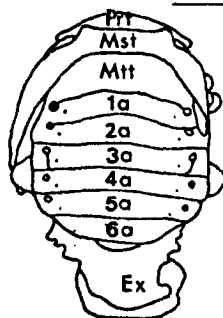


2 mm.

a. with exuvia

b.

c. Ventral view without exuvia

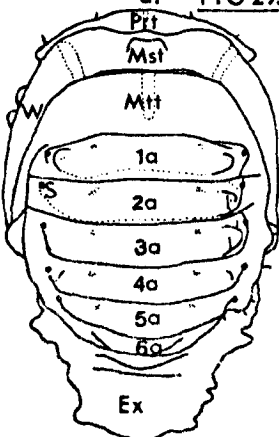


1 mm.

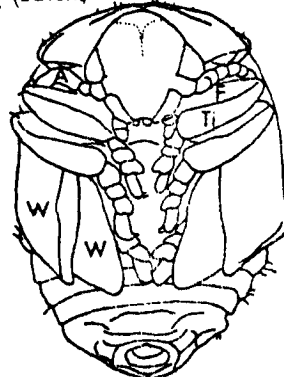
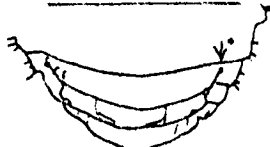
FIG. 27. *Plagioderia versicolora* (Laich.)

a.

c.



b. Dorsal view without exuvia



1 mm.

FIG.28 *Agelastica alni* (L.)

Dorsal view

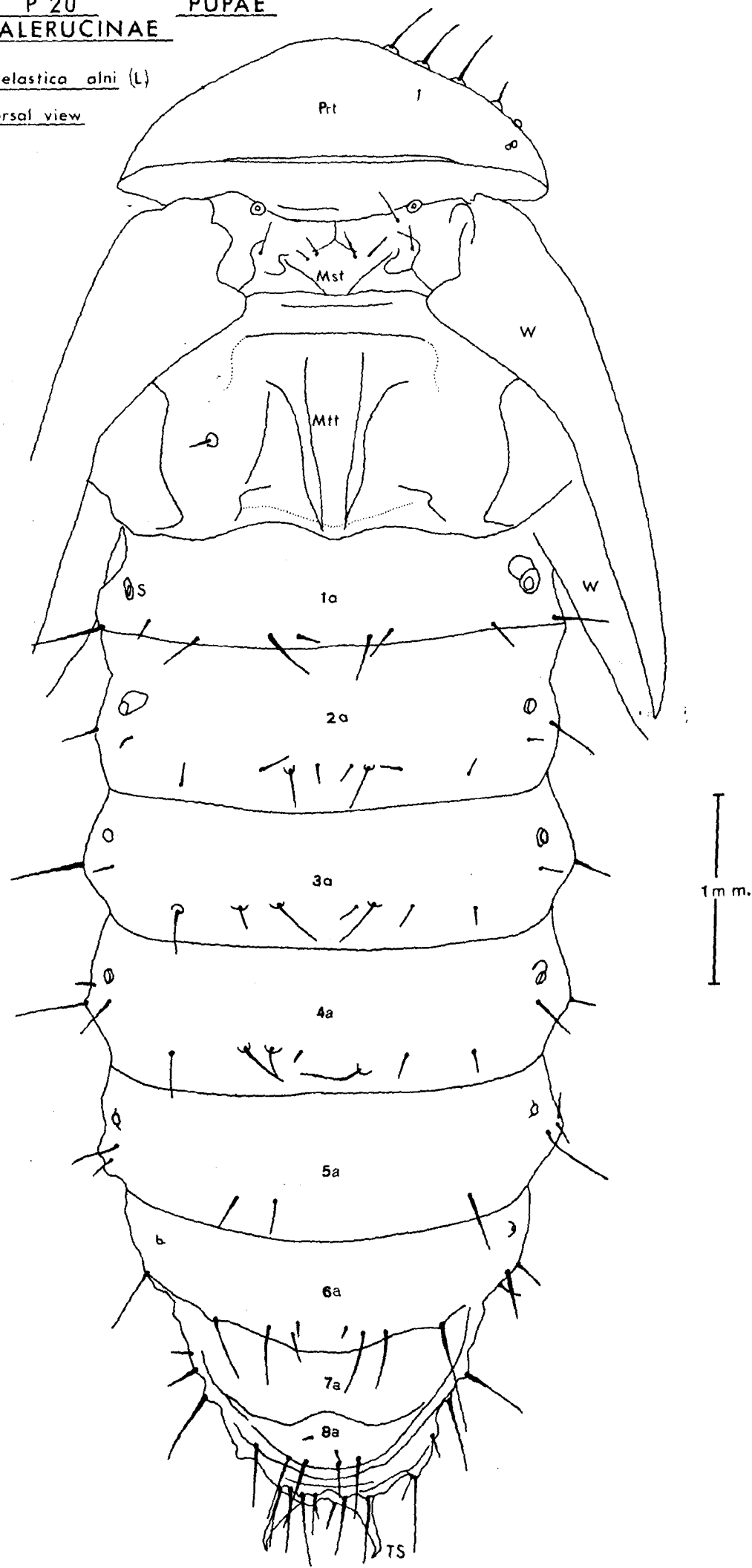


FIG. 29

*Galeruca tanacetii* (L.) Dorsal view

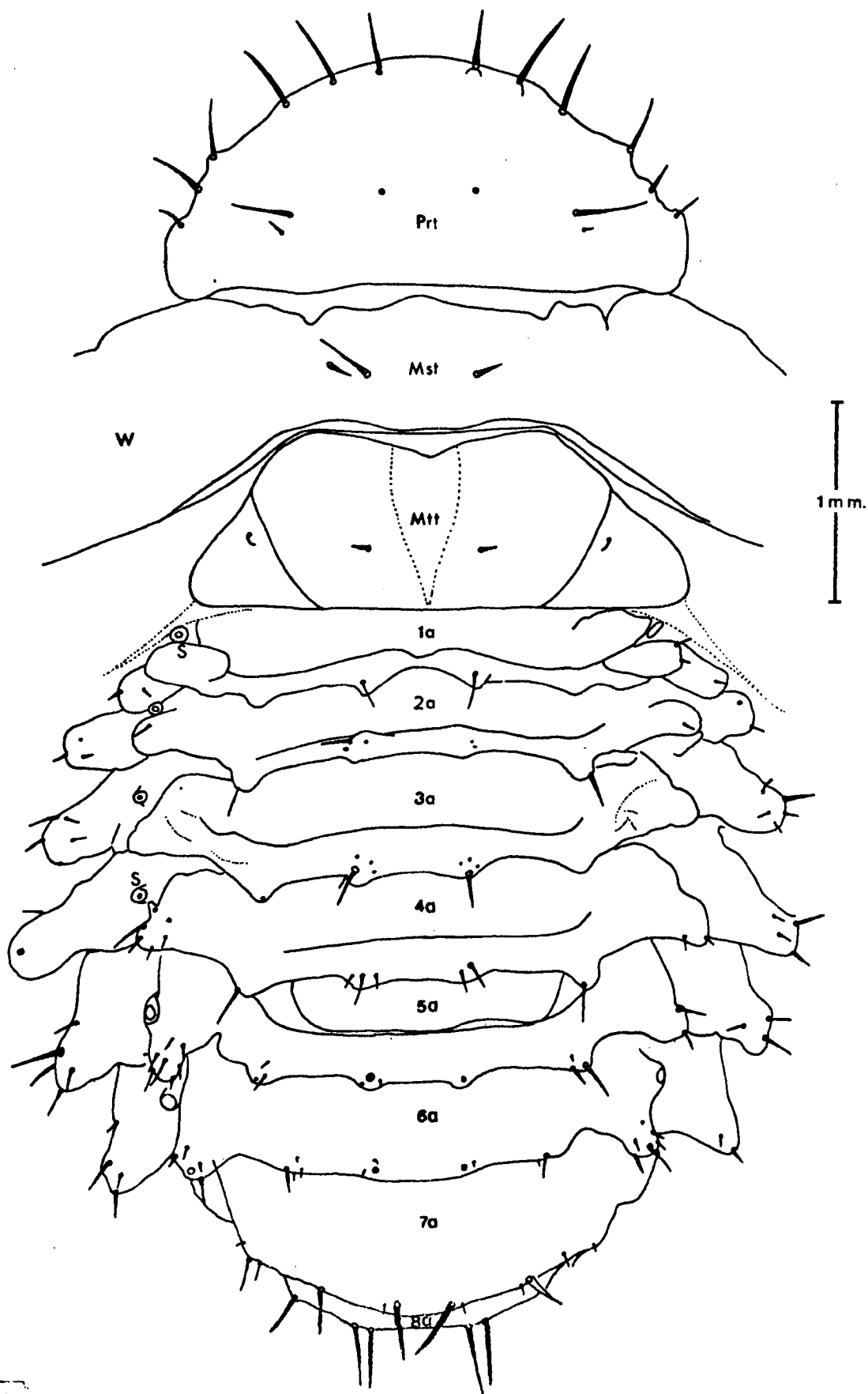
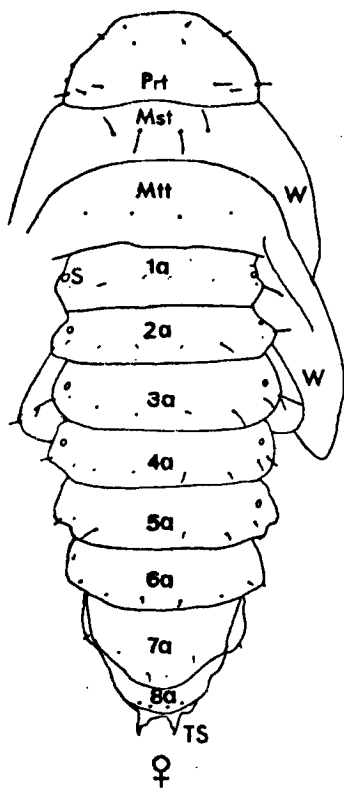
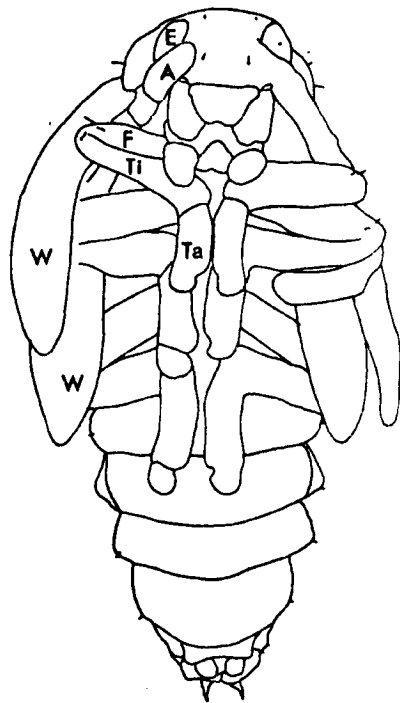


FIG. 30 *Sermyla halensis* (L.)

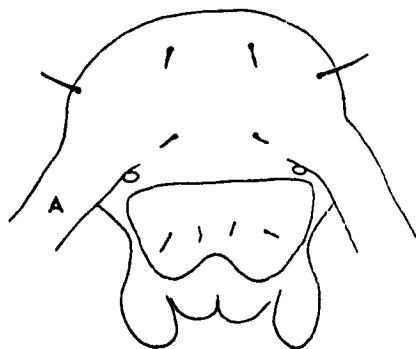
a. Dorsal view



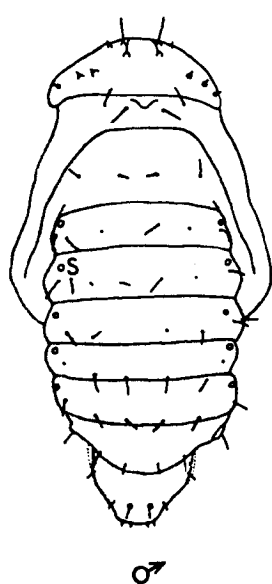
b. Ventral view



b. Head



a.



c. Ventral view Abd. segs. 7, 8, 9 & 10.

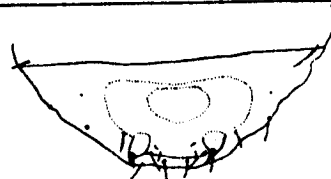
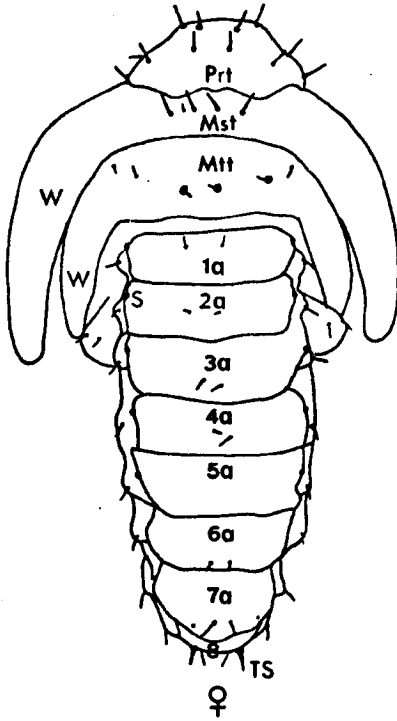




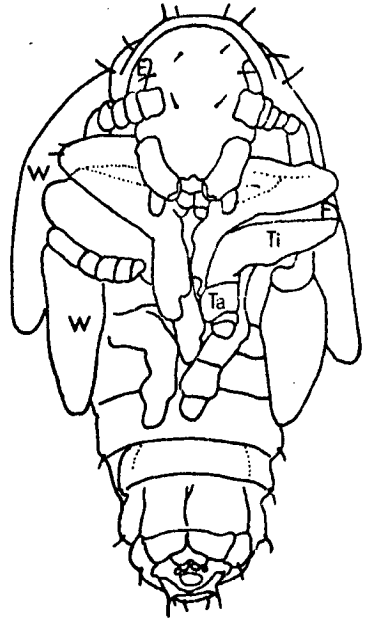
FIG. 31

*Galerucella viburni* (Pk)

a. Dorsal view

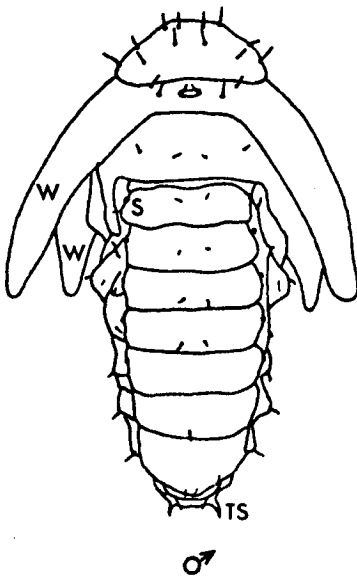


b. Ventral view



1mm.

a.



b.

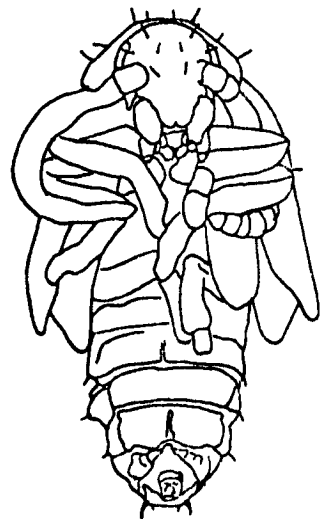


FIG. 32 *Galerucella lineola* (F.)

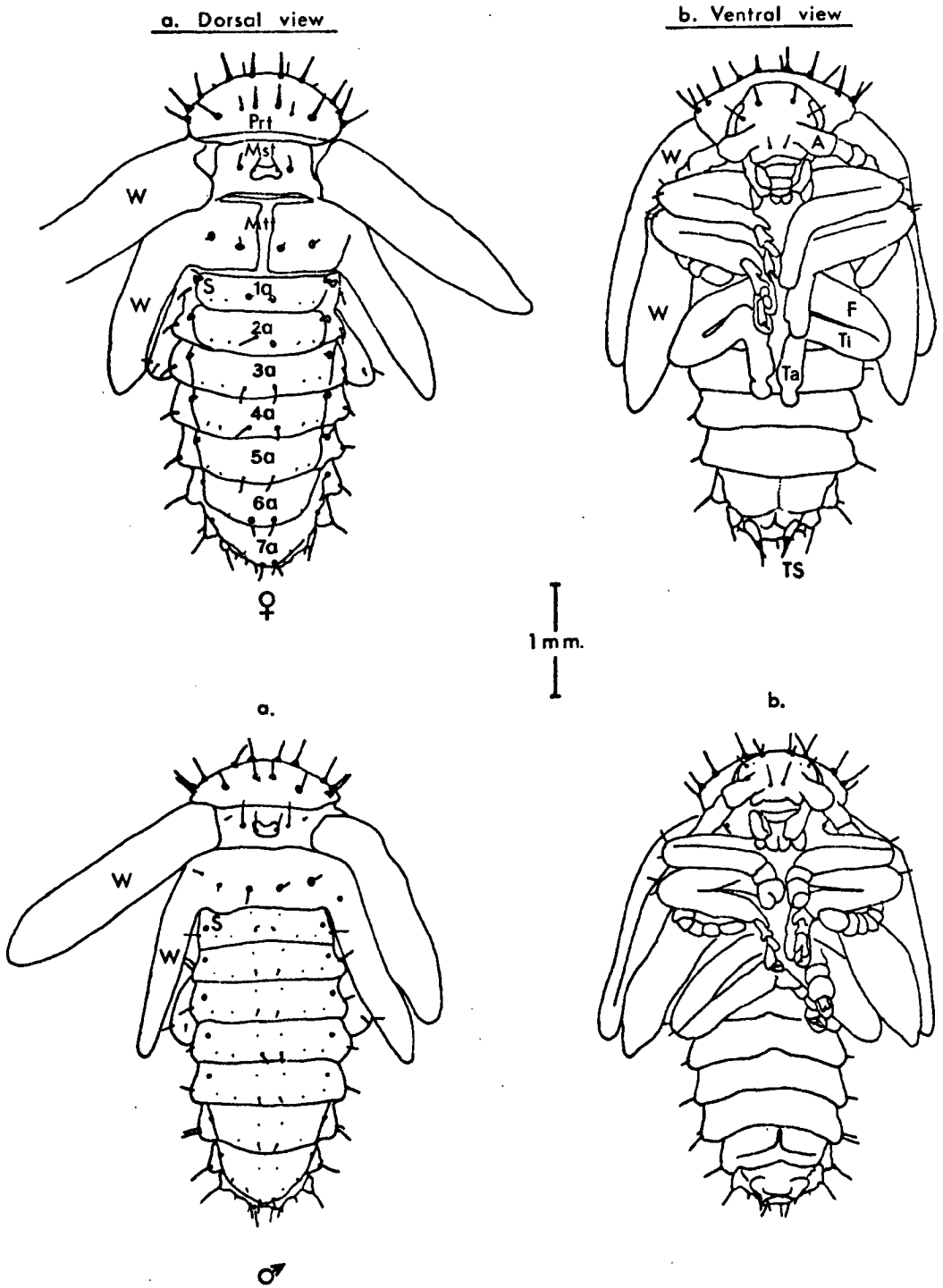
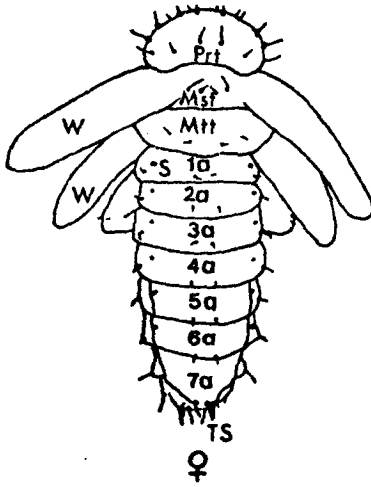


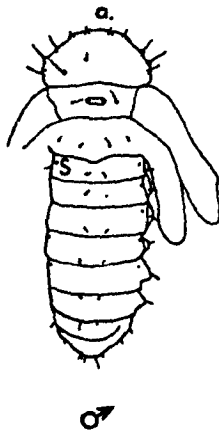
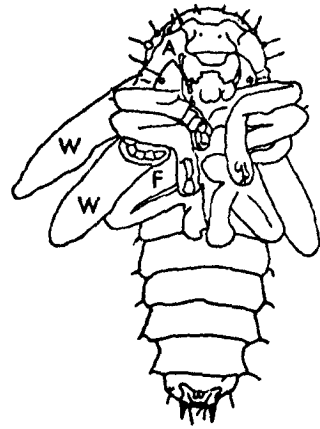
FIG. 33

*Galerucella tenella* (L.)

a. Dorsal view



b. Ventral view



1 mm.

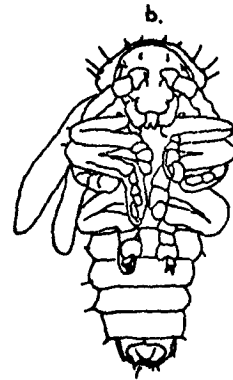
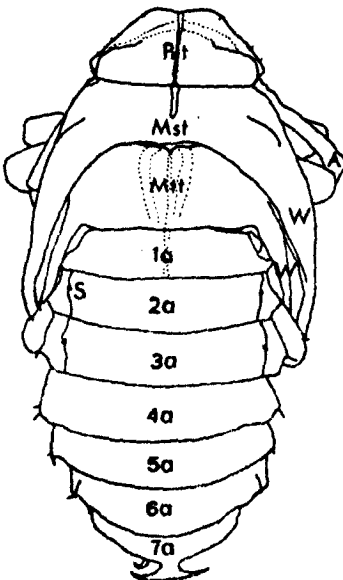


FIG. 34

*Galerucella sagittariae* Brit. Cat.

a.



b.

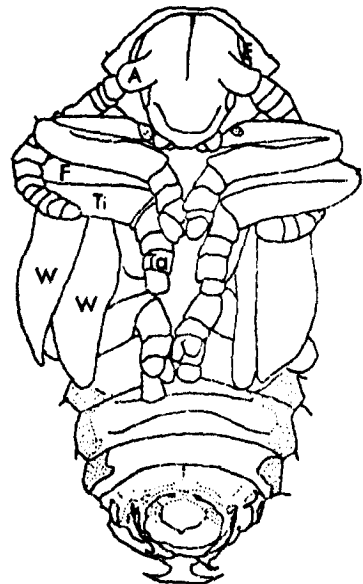
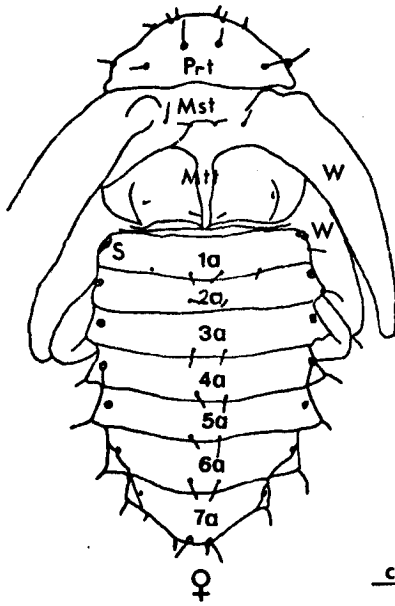


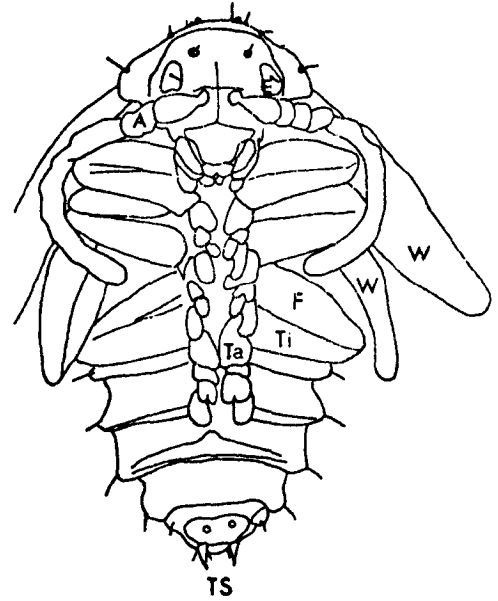
FIG. 35

*Lochmaea suturalis* (Th.)

a. Dorsal view

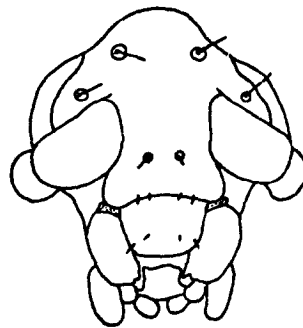


b. Ventral view



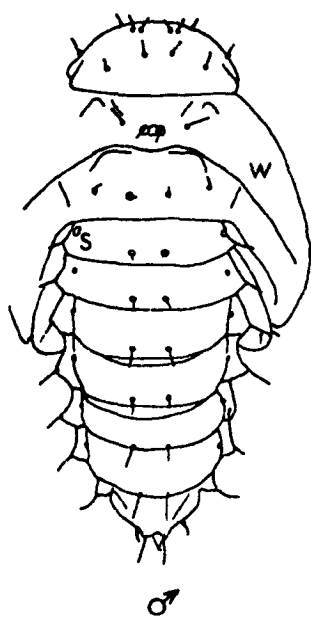
1 mm.

c. Head

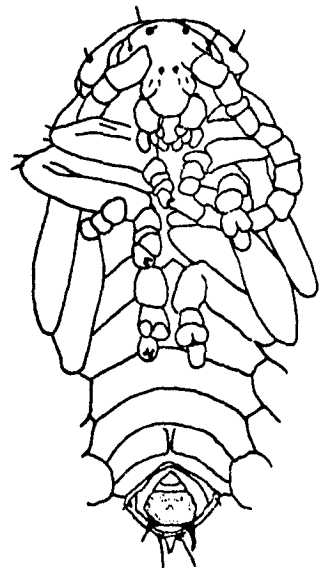


0.5 mm.

a.



b.



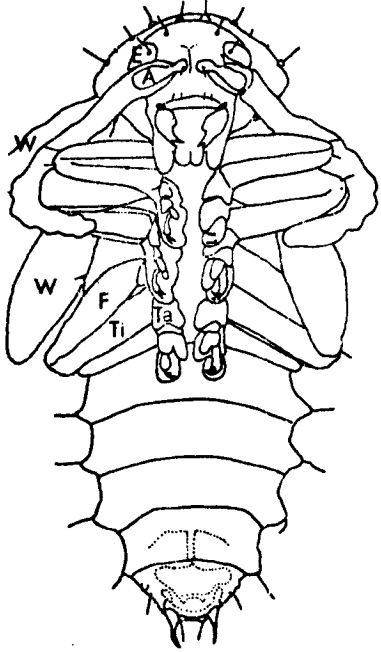
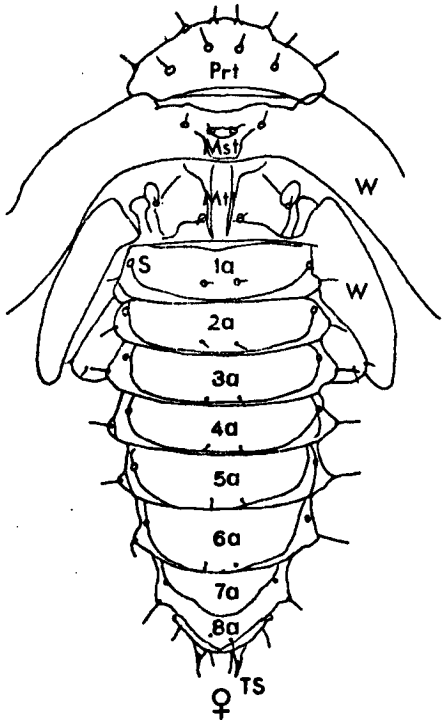
1 mm.

FIG. 36

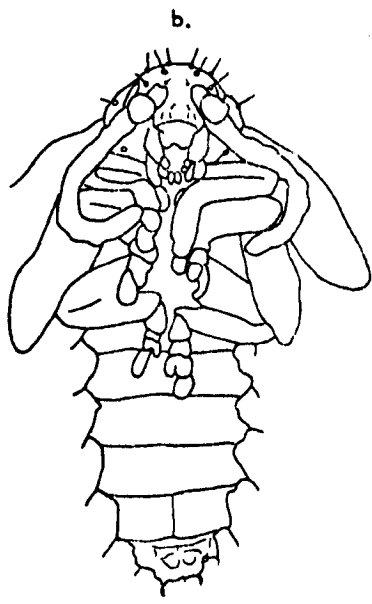
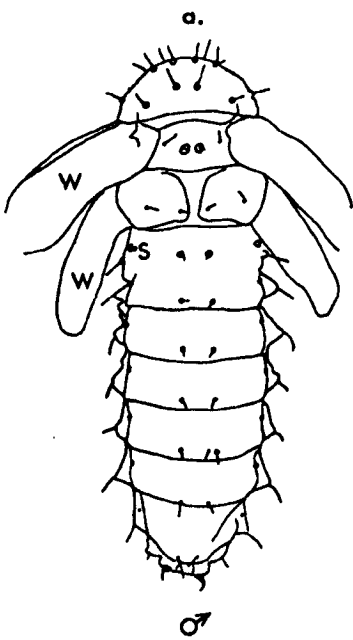
*Lochmaea capreae* (L.)

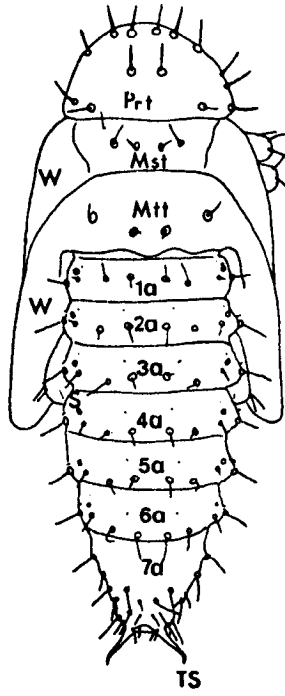
a. Dorsal view

b. Ventral view

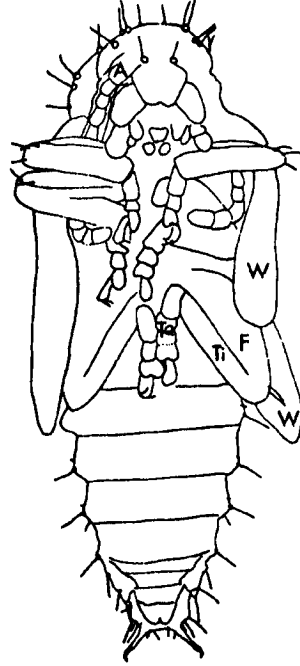


1 mm.

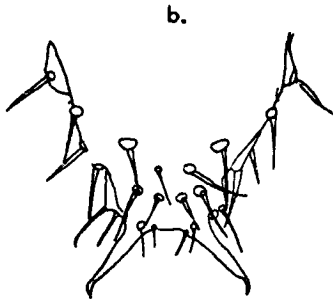




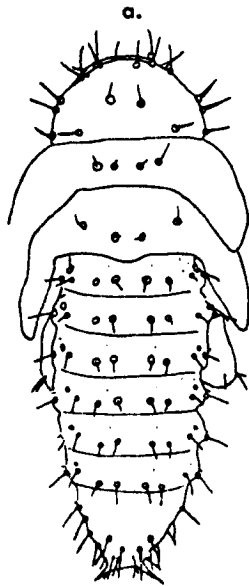
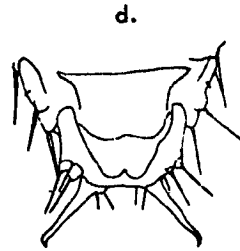
1 mm.



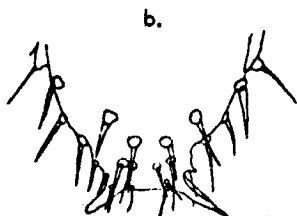
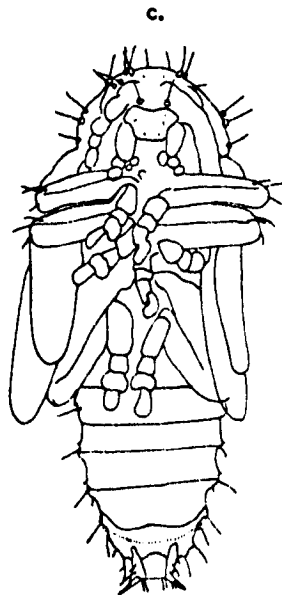
FIGS. b&d. Abd. segs. 7, 8, 9 & 10.



0.5 mm.



1 mm.



0.5 mm.

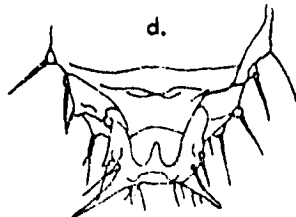
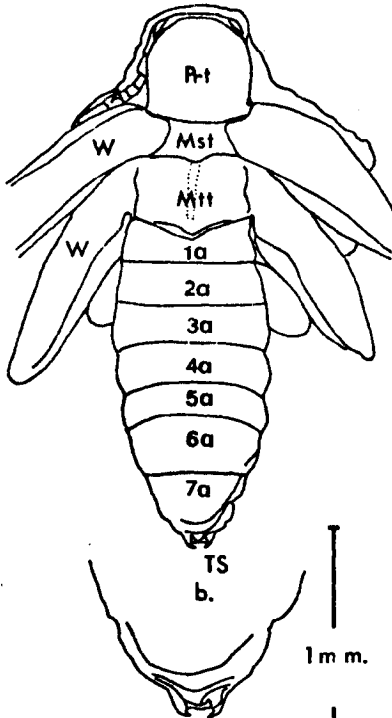


FIG. 38

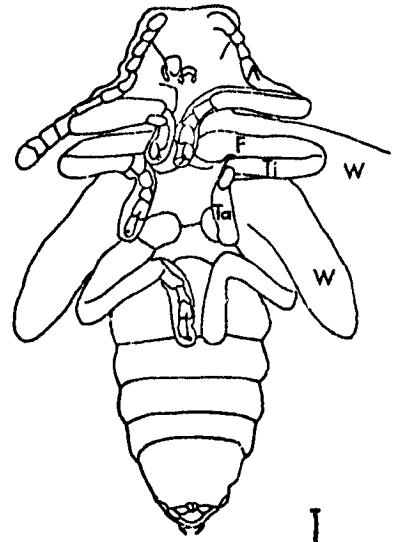
*Lema melanopa* (L.)

a. Dorsal view

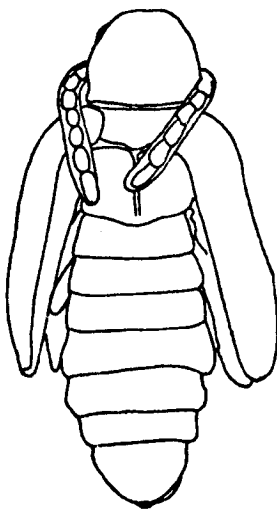


♀  
a.

c. Ventral view



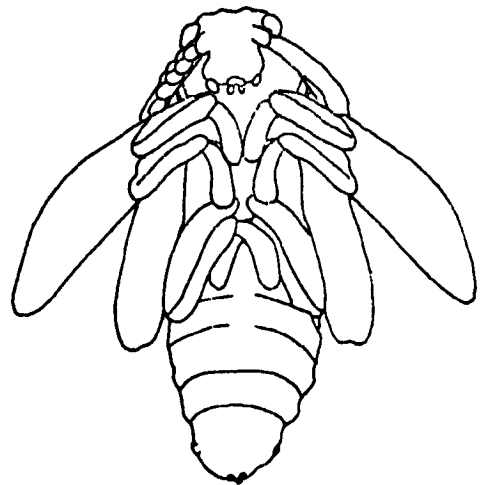
c.



b.

♂

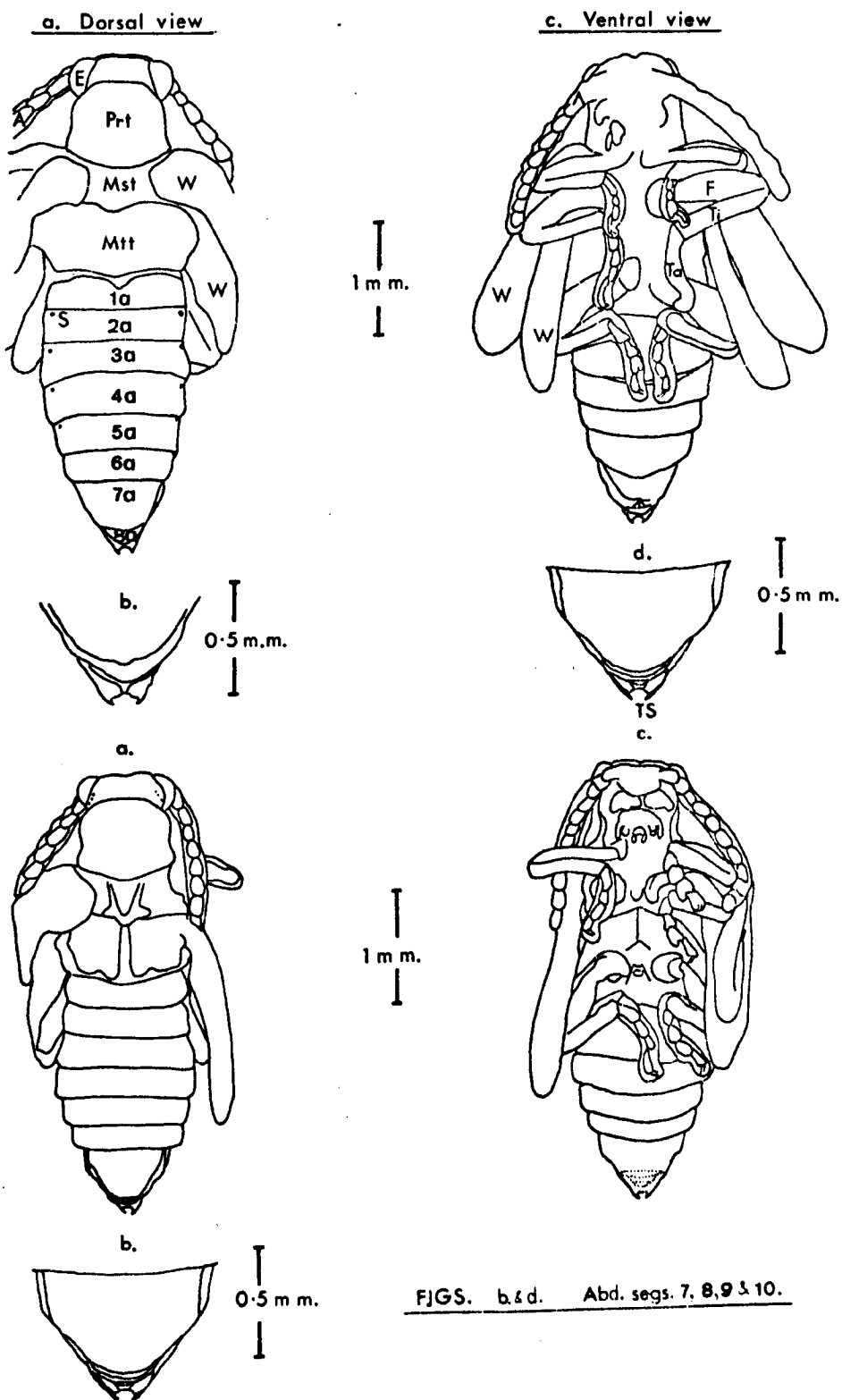
1 m m.



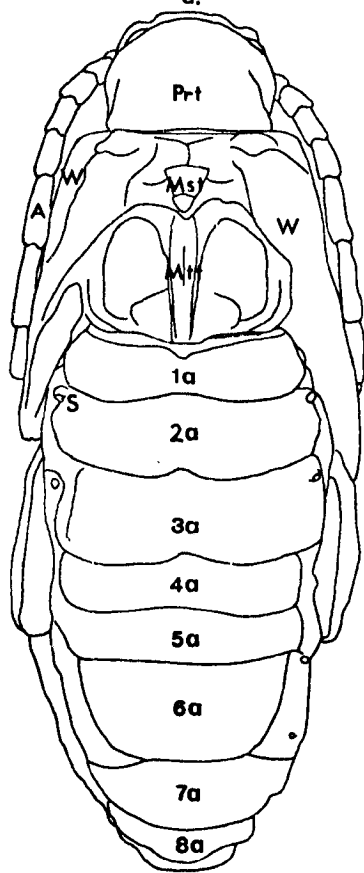
FIGS. b. & d. Abd. segs. 8, 9 & 10.

FIG. 39

*Lema puncticollis* Curt







1 m m.

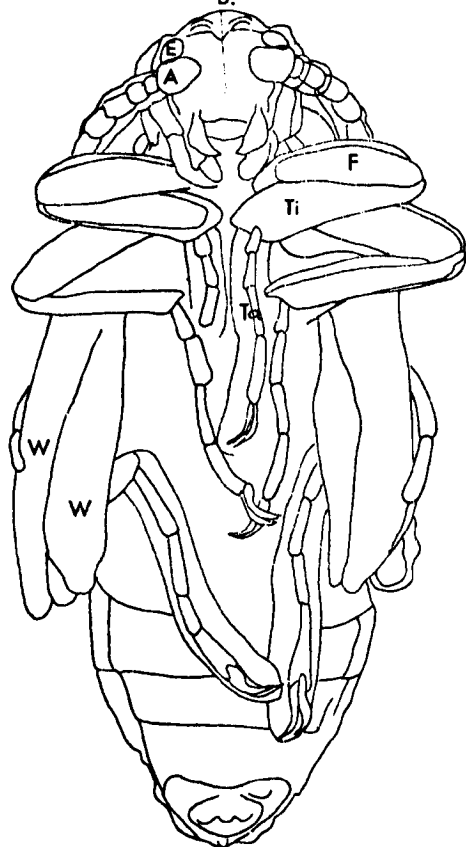
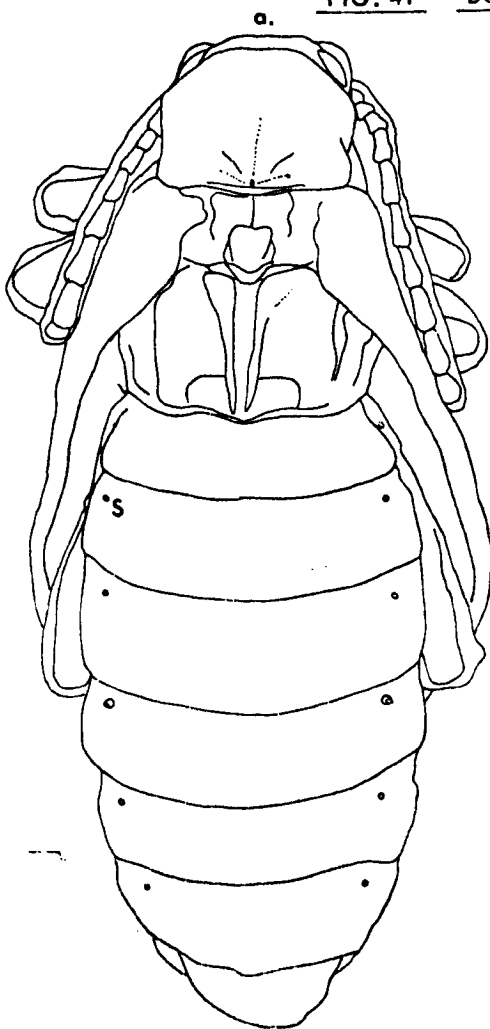


FIG. 41 *Donacia cinerea* Hbst.



1 m m.

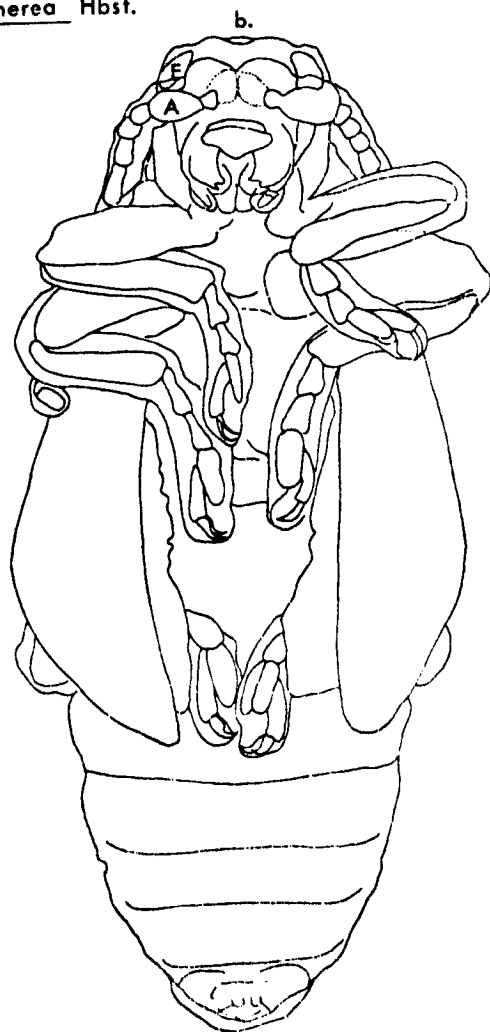
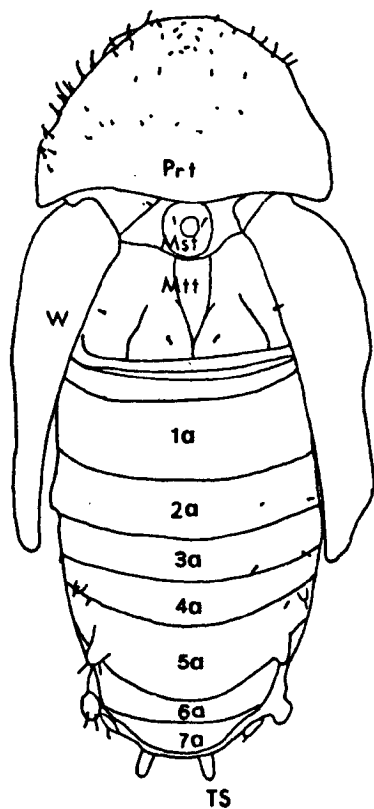


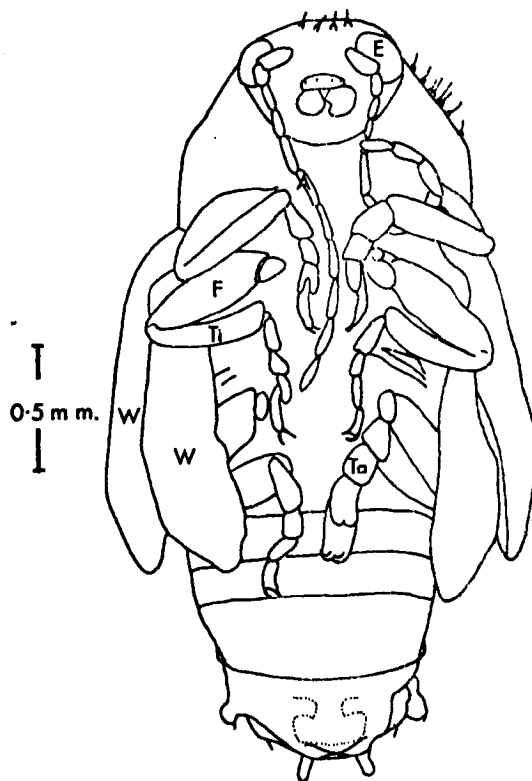
FIG. 42

*Cryptocephalus pusillus* F.

a. Dorsal view



b. Ventral view



c. Lateral view

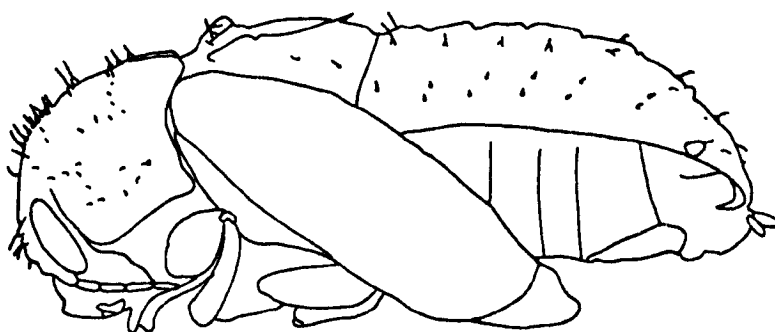
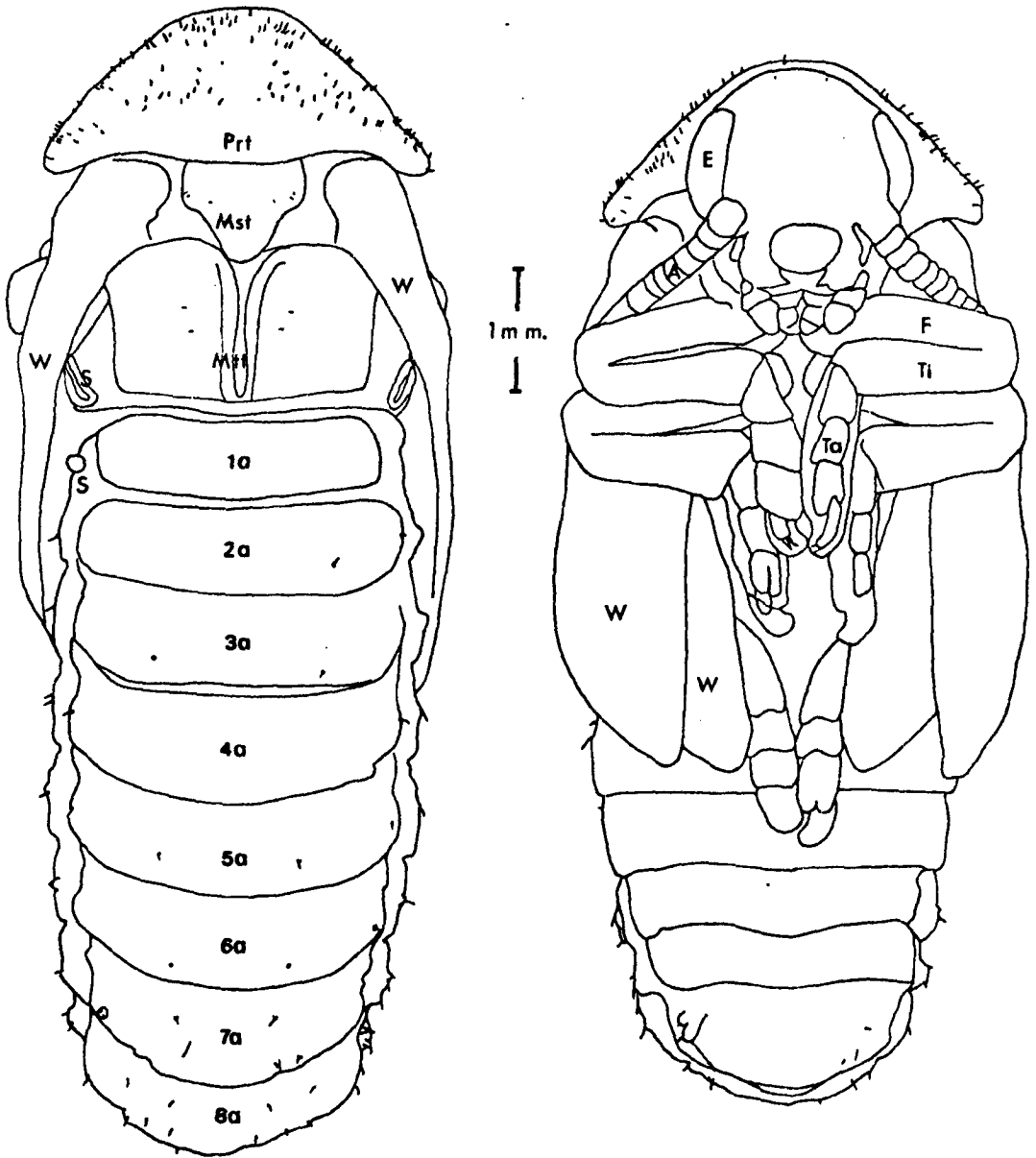


FIG. 43

*Clytra quadripunctata* (L.)

a. Dorsal view

b. Ventral view



c. Ventral view 8, 9 & 10th abdominal segments

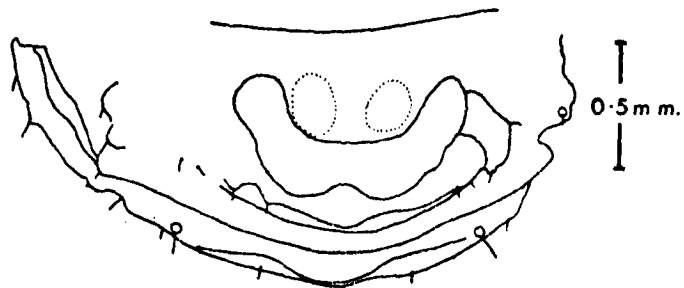


FIG. 44

*Cassida flaveola* Thunb.

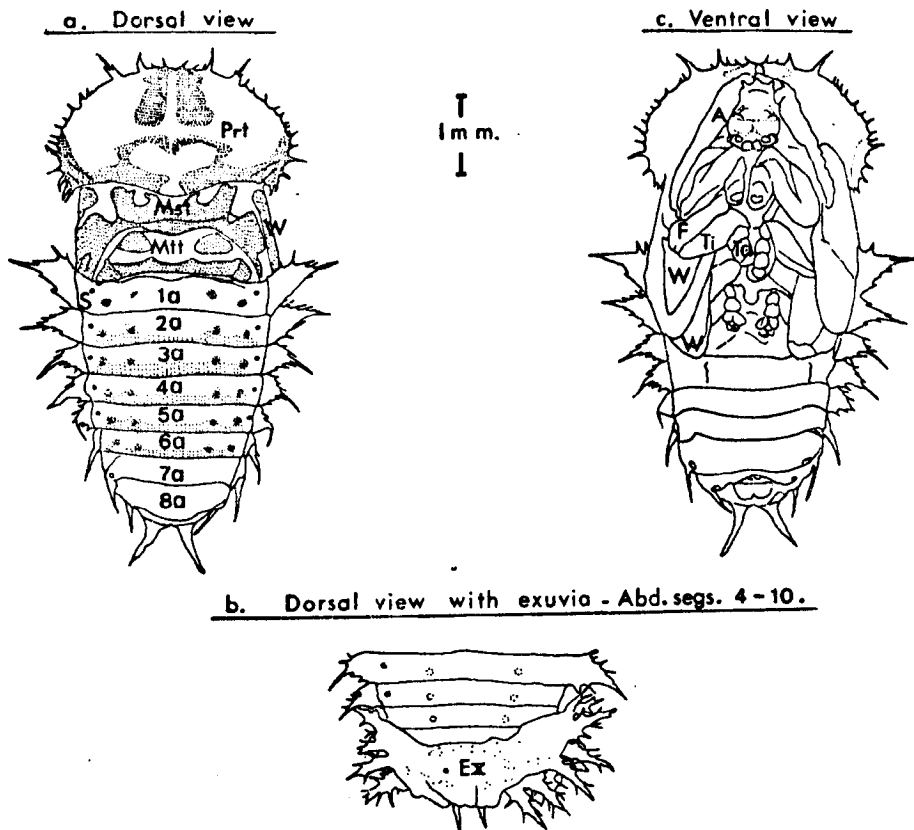


FIG. 45 *Cassida rubiginosa* Müll. Dorsal view

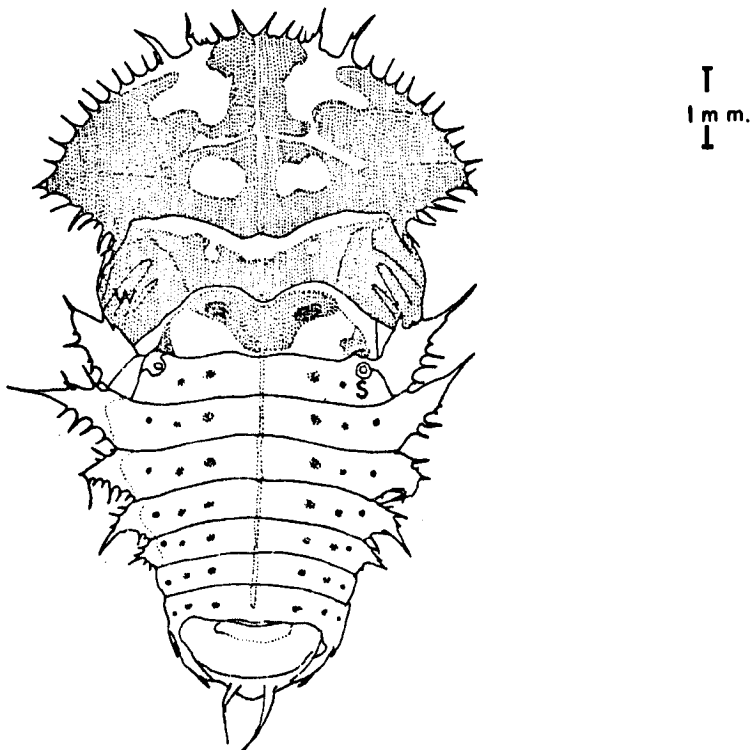
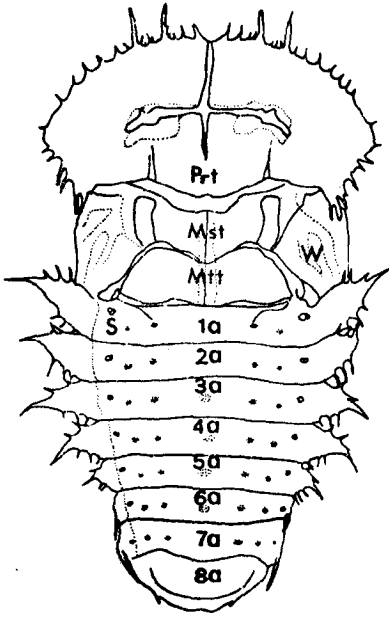


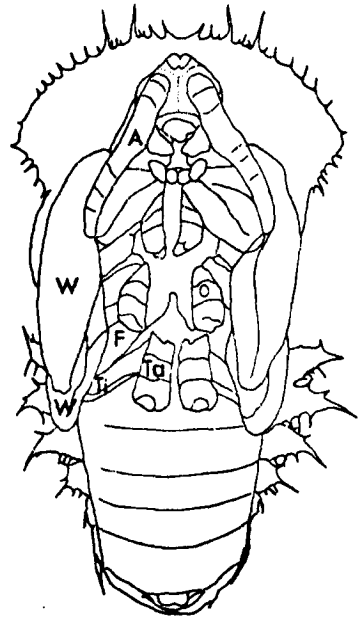
FIG. 46

*Cassida vittata* Vill.

a. Dorsal view

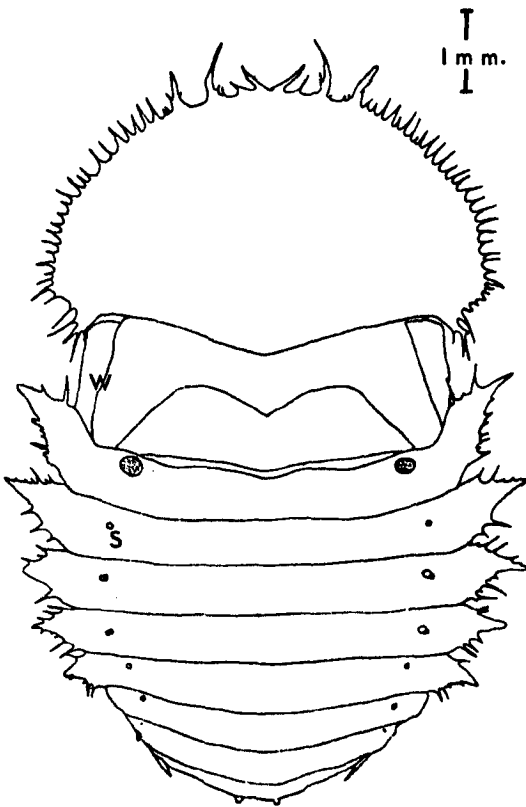


b. Ventral view



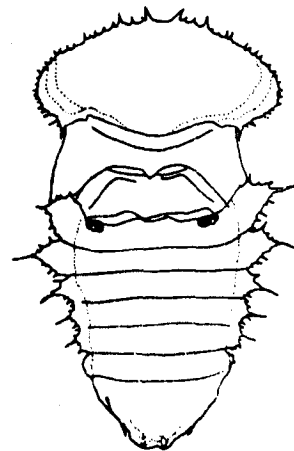
1 mm.

FIG. 47 *Cassida murraea* L. Dorsal view



1 mm.

FIG. 48 *Cassida viridis* L. Dorsal view



2 mm.

D. Subfamily and Generic Relationships shown by the pupae.

DONACIINAE - CRIOCERINAE

The absence of setae on the pupae of Donaciinae and Criocerinae indicates a probable relationship between these two subfamilies. The habit of cocoon spinning by the larvae is common to Donaciinae and Criocerinae.

ZEUGOPHORINAE

The pupae of Z. scutellaris is yellowish and the apex of the abdomen has a complex system of small plates and bears four pairs of large setae arranged symmetrically. The head bears 3 setae below each eye and there are numerous small setae on the body. Pupation occurred in a small spherical earthen cell (Grave, 1917).

CLYTRINAE - CRYPTOCEPHALINAE

The pupae of the Clytrinae and Cryptocephalinae are cylindrical, possessing numerous minute setae or spinules on the pronotum but with few setae dorsally on the abdomen. Pupation occurs within the larval cases.

CHRYSOMELINAE

The pupae of Chrysomelinae can be divided into three groups.

a) Timarcha, Chrysolina and Phytodecta group.

The pupae are red, orange, yellow or white and pupation occurs within earthen cells. In Timarcha the body is covered by numerous minute setae and the ninth abdominal segment bears a single bifid apical spine. In Chrysolina the body is also covered dorsally by numerous setae variable in length and terminated by a single apical spine. In Phytodecta setae are numerous but somewhat larger than in Chrysolina and the abdomen terminates in two apical spines. The tibiae and tarsi usually bear single setae which are absent in Chrysolina.

b) Phyllodecta, Gastroidea, Phaeton, Prasocuris and Hydrothassa  
group

The pupae are without the terminal abdominal spines of the former group. They possess fewer setae, the arrangement of which is uniform within the group. Pupae are white, cream or yellow, pupation occurring within earthen cells, the only exception being Prasocuris species which pupate on the leaves of their aquatic foodplants. Chaetotaxy of this latter group most resembles that of the Galerucinae and Halticinae.

c) Chrysomela, Plagioderia group.

Pupation occurs on the leaves of the foodplant. In these, setae are rare, especially Chrysomela but the dorsal tubercles are well developed and the integument is thick in C. populi. In Plagioderia versicolora the pronotum bears a few short setae and a few may occur laterally on the abdominal segments. Thus, Chrysomela and Plagioderia appear to be related by the similar pupal morphology and the habit of leaf pupation. However pupation on leaf surfaces may be necessary in those species which feed on plants sited in areas either near water or in areas liable to flooding. Chrysomela and Plagioderia both feed on Salix species near water. Similar pupal morphology arises from the habit of leaf pupation.

GALERUCINAE AND HALTICINAE

Chaetotaxy of the pupae of the Galerucinae and Halticinae is very similar and the pupae of both subfamilies possess a pair of terminal abdominal spines. The pupae are white or creamy yellow, with pupation occurring usually within earthen cells. In Galerucella sagittariae pupation occurs on the leaves of its aquatic foodplants and the integument is well chitinated bearing a few minute dorsal setae.

### The value of Pupal Chaetotaxy

Pupal morphology and chaetotaxy are good characters at the subfamily and tribal levels. However, it is difficult to separate certain genera and species using this character.

The number of setae on the head of the pupae may be a useful as a generic or specific character. Paterson (1931) considered that the pupae of Trichostomata (Galerucinae and Halticinae) only possess 3 pairs of setae on the head. Barstow and Gitting (1973) described only 3 pairs of setae on the pupal head of Altica bimarginata. However, Welch (1972) described 5 pairs of setae in Hermaeophaga, the anterior two pairs on the frons adhering closely to the clypeus and he considered that these may easily have been overlooked in other Chrysomelid pupae. In the present study these two pairs of setae are present only in Lochmaea capreae and L. suturalis. They are absent in Galerucella species. There may also sometimes be a pair of setae interior to the ocellar setae in L. capreae and Galerucella viburni. The ocellar setae are also sometimes bisetose as in Haltica lythri. Thus the observation made by Paterson (1931) is incorrect as there may be up to 6 <sup>pairs of</sup> setae on the head in Galerucinae and as Welch as indicated 5 <sup>pairs</sup> in Halticinae pupae (excluding the pair of microsetae in the clypeal region.)



11. SUBFAMILY, GENERIC & SPECIFIC KEY TO CHRYSOMELID PUPAE

- 1a. Pupae bearing lateral scoli ..... Cassidinae
- b. Pupae without lateral scoli ..... 2a
- 2a. Pupae without setae dorsally and laterally ..... 3a
- b. Pupae with setae if not dorsally then laterally ..... 5a
- 3a. Pupae with setae ventrally at abdominal apex ..... Zeugophora
- b. Pupae without setae ventrally at abdominal apex ..... 4a
- 4a. Apex of abdomen without small paired urogomphi ..... Donaciinae
- b. Apex of abdomen with small paired urogomphi ..... Criocerinae
- 5a. Pronotum bearing numerous minute setae and distinct abdominal spines absent ..... 6a
- b. Pronotum if bearing numerous setae then these usually moderately long and single or paired abdominal spines present ..... 7a
- 6a. Antennae filiform ..... Cryptocephalinae
- b. Antennae, , thickened ..... Clytrinae
- 7a. Setae numerous dorsally, usually long; single or paired apical abdominal spines present ..... Chrysomelinae part  
Timarcha, Chrysolina  
Phytodecta
- b. Setae fewer dorsally, moderately long; with or without apical spines or without dorsal setae, apical spines and integument thickened and usually bearing dark tubercles ..... 8a
- 8a. Without dorsal setae and apical spines absent..... Chrysomelinae part  
Chrysomela, Plagioderia
- b. Dorsally few moderately long setae present or dorsal setae minute. ... 9a
- 9a. Dorsally with few moderately long setae and apical spines absent ..... Chrysomelinae part  
Phyllodecta,  
Phaedon, Prasocuris,  
Hydrothassa, Gasteroidea

- b Dorsally with few moderately long setae and paired apical  
spines present or setae may be minute ..... IOa
- IO a Setae large ..... Galerucinae:
- Agelastica, Galeruca,  
Sermyla, Lochmaea,  
Galerucella viburni  
G. lineola  
G. tenella  
Halticinae
- b Setae minute ..... Galerucella sagittariae  
G. nymphaeae

## 12. THE BIOLOGY OF THE CHRYSOMELIDAE

### A. Introduction

The life history charts shown on plates B1-B15, Figs. 1-88, were compiled from information collected from several sources:-

- (1) sweeping throughout the year at Close House and other localities
- (2) suction trap catches at Close House (3) tussock sampling
- (4) dissections of adults for fully developed ova (5) laboratory experiments.

With the great variation in adult and larval habits and morphology it is not surprising that one would also find variations in the life cycles undergone by leaf beetles. There are 5 different types of cycles in Britain. I doubt that these cycles will be adhered to rigidly in different areas of a species geographic distribution. Daylength, temperature and humidity, major controlling factors in life cycles vary from region to region. Because Britain is the northern-most limit for several species it is likely that the life cycles for these species will be different from that on the continent. Variation in the growth habits of plants under different climatic conditions plays an important role.

CASSIDA



Fig. 1 *C. rubiginosa* Müll.



Fig. 2. *C. viridis* L.

DONACIINAE MACROPLEA



Fig. 3 *C. flaveola* Thunb.

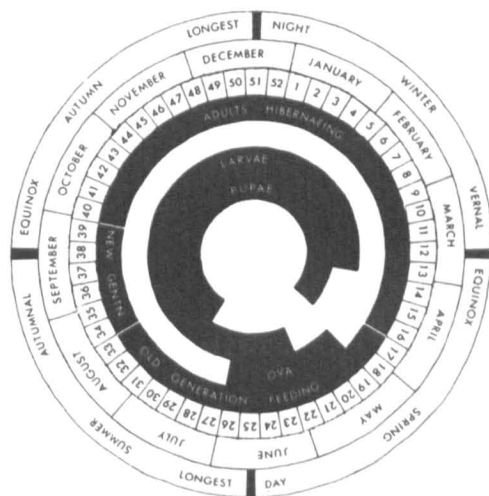


Fig. 4 *M. appendiculata* (Pz.)

DONACIINAE DONACIA



Fig. 5 *D. simplex* F.



Fig.6 *D. vulgaris* Zsch.

PLATEUMARIS



Fig. 7 *P. sericea* (L.)



Fig. 8 *P. discolor* (Pz.)

CRIOCERINAE LEMA



Fig. 9 *L. melanopa* (L.)



Fig. 10 *L. puncticollis* Curt.

LILIOCERIS

CRIOCERIS



Fig. 11 *L. lilii* (Scop.)



Fig. 12 *C. asparagi* (L.)

ORSODACNINAE

ZEUGOPHORINAE

ORSODACNE

ZEUGOPHORA



Fig. 13 *O. cerasi* (L.)



Fig. 14 *Z. subspinosa* (F.)

CRYPTOCEPHALINAE

CRYPTOCEPHALUS



Fig. 15 *C. pusillus* F.



Fig. 16 *C. labiatus* (L.)

CLYTRINAE

CLYTRA



Fig. 17 *C. parvulus* Müll.



Fig. 18 *C. quadripunctata* (L.)

TIMARCHA



Fig. 19 *T. tenebricosa* (F.)

CHRYSOLINA



Fig. 20 *C. menthastri* (Suf.)

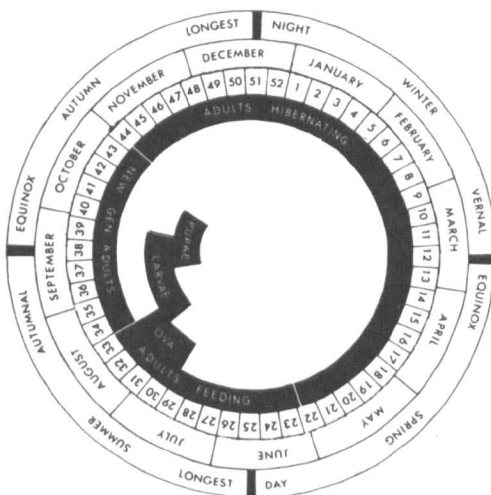


Fig. 21 *C. fastuosa* (Scop.)



Fig. 22 *C. graminis* (L.)



Fig. 23 *C. polita* (L.)



Fig. 24 *C. staphylea* (L.)

CHRYSOLINA



Fig. 25 *C. hyperici* (Forst.)



Fig. 26 *C. brunsvicensis* (Gr.)

PHYTODECTA



Fig. 27 *C. varians* (Schal.)



Fig. 28 *P. olivacea* (Forst.)



Fig. 29 *P. pallida* (L.)



Fig. 30 *P. viminalis* (L.)



PHAEDON



Fig. 31 *P. tumidulus* (Germ.)



Fig. 32 *P. armoraciae* (L.)

PHYLLODECTA



Fig. 33 *P. cochleariae* (F.)



Fig. 34 *P. vitellinae* (L.)



Fig. 35 *P. laticollis* Suf.



Fig. 36 *P. vulgatissima* (L.)

HYDROTHASSA



Fig. 37 *H. marginella* (L.)



Fig. 38 *H. aucta* (F.)

PRASOCURIS



Fig. 39 *P. phellandrii* (L.)

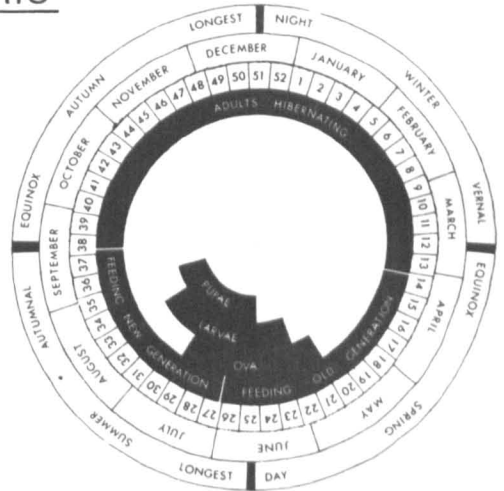


Fig. 40 *P. junci* (Brahm.)

GASTROIDEA



Fig. 41 *G. viridula* (De G.)



Fig. 42 *G. polygona* (L.)

CHRYSOMELA



Fig. 43 *C. populi* L.



Fig. 44 *C. aenea* L.

PLAGIODERA



Fig. 45 *P. versicolora* (Laich.)

LAMPROSOMA



Fig. 46 *L. concolor* (Stm.)

AGELASTICA



Fig. 47 *A. alni* (L.)

GALERUCA



Fig. 48 *G. tanacetii* (L.)

SERMYLA



Fig. 49 *S. halensis* (L.)

PHYLLOBROTICA



Fig. 50 *P. quadrimaculata* (L.)

LUPERUS



Fig. 51 *L. flavipes* L.

GALERUCELLA



Fig. 52 *G. viburni* (Pk.)

GALERUCELLA



Fig. 53 *G. sagittariae* Brit. Cat.



Fig. 54 *G. tenella* (L.)

LOCHMAEA



Fig. 55 *G. lineola* (F.)



Fig. 56 *L. crataegi* (Forst.)



Fig. 57 *L. capreae* (L.)



Fig. 58 *L. suturalis* (Th.)

HALTICA



Fig. 59 H. lythri Aub.



Fig. 60 H. britteni Shp.

HERMAEOPHAGA



Fig. 61 H. mercurialis (F.)

PODAGRICA



Fig. 63 P. fuscicornis (L.)

EPITRIX



Fig. 62 E. atropae Foud.

HIPPURIPHILA



Fig. 64 H. modeeri (L.)

MANTURA



Fig. 65 *M. rustica* (L.)

CREPIDODERA



Fig. 66 *C. ferruginea* (Scop.)

DEROCREPIS



Fig. 67 *D. rufipes* (L.)

CHALCOIDES



Fig. 68 *C. fulvicornis* (F.)

SPHAERODERMA



Fig. 69 *S. rubidum* Graells.



Fig. 70 *S. testaceum* (F.)



CHAETOCNEMA



Fig. 71 *C. concinna* (Marsh)



Fig. 72 *C. hortensis* (Geof.)

PSYLLIODES



Fig. 73 *P. affinis* (Pk.)



Fig. 74 *P. picina* (Marsh)



Fig. 75 *P. napi* (F.)



Fig. 76 *P. chrysocephala* (L.)



APTEROPEDA

BATOPHILA



Fig. 77 *A. orbiculata* (Marsh.)



Fig. 78 *B. rubi* (Pk.)

PHYLLOTRETA



Fig. 79 *P. nemorum* (L.)



Fig. 80 *P. undulata* Kuts.



Fig. 81 *P. nigripes* (F.)



Fig. 82 *P. cruciferae* (Goez.)



Fig. 83 *L. melanocephalus* (De G.)

Fig. 84 *L. suturellus* Duft.



Fig. 85 *L. parvulus* (Pk.)



Fig. 86 *L. jacobaeae* Wat.



Fig. 87 *L. luridus* (Scop.)



Fig. 88 *L. pratensis* (Pz.)

## B. BIOLOGY OF THE SUBFAMILIES

### SUBFAMILY CASSIDINAE

#### GENUS Cassida

C. rubiginosa Müll. Plate B1 Fig. 1.

Foodplants: Compositae      Cirsium arvense (L.)

Cirsium vulgare (Savi) Ten.

Centaurea nigra L.

Arctium sp.

Ova laid within brown oothecae at the underside of leaves of the foodplant. Oviposition in the field from the end of May until about 20th July.

#### Larvae.

Without hatching spines. Hatching occurring from about 7th June until about the end of July. There are 5 larval instars and fully grown larvae are present from about 7th July until the end of August. Pupae probably occur from mid July until mid September. Larvae in the later instars feed singly on the upper surface of Centaurea leaves.

#### Adults.

New generation adults emerge from 21st July until mid September. There is one generation/year and the adults overwinter, usually going into hibernation (in grass tussocks) at the end of September. Re-appearance of adults occurs about the beginning of April.

C. viridis L. Plate B1 Fig. 2. Biology studied by Engel (1932, 1935)

Foodplants: Labiatae      Mentha aquatica L.

Stachys palustris L.

Lycopus europaeus L.

#### Ova

Ova are laid within brown oothecae on the underside of leaves of Mentha. Each ootheca length about 5.18mm, width about 4.44mm may contain 1-10 ova ( $\bar{x} = 4$ ,  $n = 16$ ) which are elongate-oval & length 1.56mm & width 0.76mm ( $n = 2$ ).

Oviposition in the field occurs from the beginning of May until about 14th July. The female usually covers each ootheca with dark brown excretory material.

### Larvae

Hatching probably occurs from mid May until 21st July. There are 5 larval instars and fully grown larvae probably occur from mid June until about 21st August. Pupae occurring from about 21st June until the first week in September. Engel (1932, 1935) stated that the first instar larvae feed on the underside of the leaves, whereas later instar larvae feed upon the upper surfaces.

### Adults

New generation adults emerging from the end of June until mid September. It is probable that there is one generation/year and adults overwinter, reappearing the following spring.

C. flaveola Thunb. Plate B1 Fig. 3.

Foodplants: Caryophyllaceae     Stellaria graminea L.

Stellaria holostea L.

### Ova

Cream coloured, cylindrical, somewhat dorso-ventrally flattened,  $\times$  length 1.40mm  $\bar{x}$  width 0.75mm. Usually laid singly, rarely in pairs with the tips adjacent and covered by a thin yellow brown membrane on the underside of the leaves of Stellaria. Oviposition probably commences 14-21st May and continues until about 7th July.

### Larvae

Hatching commences at the end of May until mid July. There are 5 instars and fully grown larvae occur from the end of June until about 9th August. Pupation occurs from about 7th July and pupae may occur until mid August.

### Adults

New generation adults probably emerge about 21st July until the end of August. There is probably only one generation/year. The adults hibernate in tussocks, disappearing at the end of September and re-appearing about mid April the following year.

SUBFAMILY DONACIINAEGENUS MacropleaM. appendiculata (Panz.) Plate B1 Fig. 4.Foodplant: Potamogetonaceae      Potamogeton lucens L.<sup>1</sup>

Adults have been collected in the field on 22nd April, in June, July, August. Fully grown larvae and cocoons containing fully developed imagoes were collected in August. Two pale newly emerged adults were seen on the foodplant at the end of August. Again on 22nd September a cocoon containing a newly emerged imago was seen. It is probable that adults overwinter either within cocoons or above water reappearing during April the following year. Oviposition probably occurs from the end of April through May and hatching may occur in mid May. Larvae feed on the roots of the foodplant under water and are fully developed by the beginning of August. New generation adults emerge at the end of August until late September.

M. mutica (F.)Foodplants: Potamogetonaceae      Potamogeton pectinatus L.Zosteraceae      Zostera marina L.Biology probably similar to M. appendiculata Panz.GENUS DonaciaD. simplex F. Plate B1 Fig. 5.Foodplants: Sparganiaceae      SparganiumCyperaceae      CarexGramineae      Phragmites communis Trin.

Adults have been collected in the field from 25th April until 9th August. 2nd and final instar larvae were seen on 26th May. These final instar larvae had probably overwintered. Oviposition probably commences at the beginning of May and continues until the beginning of August. The larvae will probably be present from mid May until the following June. Pupae probably occur from the beginning of July, probably overwintering. Adults possibly occur in cocoons from the

end of August until mid June the following year. It is probable that this species overwinters as adults, larvae and pupae.

Donacia vulgaris Zsch. Plate B1 Fig. 6.

Foodplants: Nymphaeaceae Nuphar lutea L. Sm.

Nymphaea alba L.

Sparganiaceae Sparganium

Typhaceae Typha latifolia L.

Adults occur in the field from 16th May until August. Fully developed larvae were collected in cocoons on 14th June. It is probable that larvae overwinter. New generation adults probably emerge from these larvae at the beginning of July. The adults and pupae probably also overwinter. Ravizza (1973) showed that the adults overwinter within the cocoons in the Isleo-Provaglio swamps (Lombardia) Italy.

The female of Donacia palmata cuts a small hole in the leaf of Nymphaea advena from the upper surface and protrudes her abdomen through this to lay eggs in a circle on the underside. Each mass of 40-50 eggs consists of a double row covered by an opaque gelatinous substance. They are white, elongate and 1mm long and the chorion is without surface sculpturing. The eggs of D. cincticornis are laid in a row along the edge of a sedge leaf sheath (Mac Gillivray, 1903).

#### GENUS Plateumaris

P. discolor (Pz.) Plate B2 Fig. 8.

Foodplants: Cyperaceae Eriophorum

Carex

Adults occur in the field from 7th April until 22nd July, during August, October, November and December. It is probable that the adults overwinter. Oviposition probably occurs from mid May until the end of June and larvae from mid June until the beginning of the following year. A cocoon containing a pupa was found on 24th June. This had probably resulted from a larva which had overwintered. New generation adults probably emerge at the beginning of July or August.

P. sericea (L.) Plate B2 Fig. 7.

Foodplants: Nymphaeaceae Nuphar lutea (L) Sm.

Nymphaea alba L.

Typhaceae Typha latifolia L.

This probably has the same cycle as P. discolor and adults have been found in the field from 1st May until 14th July.

SUBFAMILY ORSODACNINAE

GENUS Orsodacne

Very little is known concerning the biology of these beetles but the larvae apparently live as miners in the leaf petioles of Rosaceae, Caprifoliaceae, Salicaceae etc. (Balachowsky and Mesnil, 1936). The larvae are similar to those of Donaciinae.

O. cerasi (L.) Plate B3 Fig. 13.

Foodplants.

Jolivet (1948) records this species feeding in the Spring on the flowers of cherry, plum, pear, Crataegus, Sorbus, Viburnum, Euonymus, Tamus. Adults have been observed in the field in England from 11th May until 1st July. Adults collected on 1st July at Forge Valley, Yorkshire and dissected showed developing ovaries. The oviposition period probably commences in the field in July. Adults have been collected usually from Heracleum sphondylium (Umbelliferae) flowers.

O. lineola (Pz.)

Adults have been collected in the field from 10th May until June from flowers of Heracleum sphondylium (Umbelliferae). A larva was dissected from the stomach of a Great Tit captured in the Forest of Dean on 1st January. It is possible therefore that larvae overwinter.



SUBFAMILY ZEUGOPHORINAEGENUS ZeugophoraZ. subspinosa (F.) Plate B3 Fig. 14.

Foodplants: Salicaceae Populus sp. usually P. tremulae (Aspen)

The adults cause netting of the leaves which become completely perforated by small holes and only the sclerotized veins remain intact.

Ova

Deposited singly below the upper epidermis of Aspen leaves, as many as 6 ova being laid per leaf. A small concavity is eaten out of the upper epidermis by the adult female, the egg deposited in this and covered by a secretion from the female. Black markings on the upper surface of the leaves indicate the position of the eggs. The eggs are yellow, oval  $\bar{x}$  length 0.61mm,  $\bar{x}$  width 0.31mm ( $n = 2$ ). Adults collected on 14th May started oviposition on 26th May.

Larvae

Larvae hatch using a row of hatching spines along the lateral margin of the thorax and abdomen. Hatching occurs from about 2nd June and larvae can be found until mid-July. The larvae do not emerge from the leaf but feed by mining the parenchyma causing characteristic black mines. When fully grown the larvae emerge from the leaves and drop to the ground, pupation occurring within an earthen cell. Pupae probably occur from about the beginning of July until the beginning of August and the new generation emerges about 12th August. In the field 2 eggs only are laid close together in one leaf. Both eggs usually hatched but one larva perishes as 2 larvae were never found in the same leaf. The majority of larvae seen in the field at the beginning of July 1975 were final instars with very few in the 3rd instar. From head capsule measurements there are probably four larval instars.

Adults

There is one generation/year and the adults overwinter. Adults

re-appear about 14th May and live until about 9th July. The oviposition period is relatively short from about the beginning to the end of June. New generation adults emerge about 12th August and feed until the beginning of September when the leaves are beginning to turn. They then move into their overwintering quarters.

SUBFAMILY CRIOCERINAE

GENUS Lema

L. melanopa (L.) Plate B2 Fig. 9.

Foodplants: Gramineae Avena sativa etc.

Ova

The eggs are fixed singly or in pairs, usually on the lower surface of the leaf blade of grasses by a film of adhesive substance. The majority are laid parallel to the leaf axis, near the median vein. They are yellow oval and  $\bar{x}$  length 0.943mm,  $\bar{x}$  width 0.435mm ( $n = 5$ ). The chorion is transparent and devoid of sculpturing. Incubation period at 19°C is 7-9 days during which the egg gradually darkens.

Larvae

The first instar larvae hatch using a pair of hatching spines or egg bursters on first abdominal segment. The larva is covered by a mucilaginous mixture of excrements. During development the larvae migrate towards the highest leaves of the plant and cause characteristic damage to the leaf blades. They eat small fragments of the upper epidermis in parallel lines 1mm wide, leaving the lower epidermis intact as a fine transparent membrane. There are 3 moults and thus 4 larval instars. Full development occurs in 12 days at 24°C, 21 days at 20°C (Balachowsky & Mesnil, 1936). When fully grown the larva penetrates the earth to about 4-5 cms. At the required depth it compresses the earth around it, its body bends and its anus is pressed against its buccal cavity. The larva lines its cell with a creamy viscous substance produced in the anterior dilated section of its body (i.e. its mesenteron is sacciform). The liquid is regurgitated in small quantities from the mouth and deposited on the partition wall where it coagulates very rapidly. The 6.7mm long cell is completed in 24 hours. The pupal period lasts 6 days at 26°C and 5 days at 30°C (Balachowsky & Mesnil, 1936).

### The Adults

New generation adults emerged at Close House about 24th July and feed until 20th September after which they move into grass tussocks and other hibernation sites. There is only one generation/year and the adults overwinter. The adults emerge from hibernation at the beginning of May and oviposition commences about 10th May. Development in the field thus takes about  $2\frac{1}{2}$  months. The damage is similar to that of the larvae but they completely perforate the leaf blades and the strips eaten are shorter than those eaten by the larvae.

### L. lichensis Voet.

Foodplants: Gramineae

### Ova

These are laid in ones or twos on the underside of grass leaf blades often in grooves eaten out by the adults or on the leaf stalk bases. The eggs are not always laid parallel with the leaf veins. Eggs yellow, oval & length 0.869mm, & width 0.427mm (n = 6).

### Larvae

Hatch using paired hatching spines on the first abdominal segment. They are fully grown by the end of June although final instar larvae were collected 9th August in the Forest of Dean, Gloucestershire. The larvae construct cocoons 2-3cms from the base of the upper surface of leaf stem or even in the ears of grain. The cocoon formed is hemispherical, maximum diameter of 6mm. Pupation occurs 15 days after the start of cocoon formation.

### Adults

New generation at Close House emerges 30th July and feed into October. They hibernate in grass tussocks and other sites. There is only one generation/year and the adults overwinter. The adults emerge from hibernation the beginning of May and oviposition commences mid-May. Development in the field thus takes about  $2\frac{1}{2}$  months.

L. puncticollis Curt. (L. cyanella (L.) ) Plate B2 Fig. 10.

Foodplants. Compositae Cirsium arvense (L.) Scop.

### Ova

The eggs are laid singly or in pairs on the upper and lower surfaces of thistle leaves. They are white, oblong oval  $\bar{x}$  length 1.041mm,  $\bar{x}$  width 0.462mm (n = 11). The incubation period at 19°C is 9 days.

### Larvae

Larvae hatch using a pair of 'egg bursters' on the first abdominal segment. The larvae usually feed on the upper surface of thistle leaves removing the upper epidermis but leaving the lower epidermis intact. The larval duration at 19°C was 16-17 days after which they move into the soil and construct silken cocoons similar to Lema melanopa L. Pupal duration at 19°C is 14 days and thus the development of egg to adult required 39 days at 19°C.

### Adults

New generation adults emerge at the beginning of August and it is likely there is a second generation as an adult collected on 5th August laid 21 eggs up to 20th August at 19°C. It could however have been an old generation adult with an exceptionally long longevity. Adults from the second generation emerged 13th September and it is likely they feed and move with adults of the first generation into their overwintering sites at the end of this month. Adults emerge from hibernation about 12th April and can be found in the field up to the end of June, no adults were collected in July. Oviposition may occur from about 12th May until the 26th June and thus development from egg to adult in the field requires 2½ months.

GENUS Crioceris

C. asparagi (L.) Plate B2 Fig. 12.

Foodplants Asparaginae Asparagus officinalis

A. Plumosus and wild Asparagus sp.

Ova

Greenish grey becoming progressively darker during incubation. Oblong oval, measuring 1.2-1.6mm long, about 0.46mm wide. The eggs are fixed by their extremities on the cladodes, stems or berries of the foodplant. Certain stems may have eggs deposited in a regular line. Incubation takes 3-8 days (Balachowsky & Mesnil, 1936).

Larvae

These remove the epidermis of the stems and leaves, causing discoloration and drying up of the aerial parts. The larvae are fully developed in 15-20 days (Balachowsky & Mesnil, 1936) after which they move into the ground and construct a pupal cell. Pupation occurs after 2-3 days and 3-4 days later new adults appear. In England fully grown larvae are found as early as 21st June.

Adults

Adults hibernate in old stems, under dead leaves or bark and re-appear towards the end of April in France (Balachowsky & Mesnil, 1936). According to Smith (1951) egg laying occurs in June and the life cycle is completed in about 1 month. The beetle has 2 or 3 overlapping generations a year, both adults and larvae occurring as late as October. The overwintering females emerge late in May, oviposition starts early in June and females of the first generation appear in July and August. After maturation which lasts about 4-6 days the females lay eggs and adults of the second generation emerge in August and September. Second generation females either remain sexually immature and hibernate or mature and oviposit, thus giving rise to the 3rd generation which hibernate. Overwintering beetles include adults of both the 2nd and 3rd generations. It is likely

in England that there are 2 generations only, as the foodplants die back in September.

#### GENUS Lilioceris

L. lillii (Scop.) Plate B2 Fig. 11.

##### Foodplants.

Principally the White Lily, Lilium candidum but also Fritillaria meleagris, Lilium auratum, L. giganteum, L. philippinense, L. regale, L. tigrinum, Nomocharis saluenensis, Polygonatum multiflorum (Wilson, 1943).

##### Ova

The eggs are stuck laterally on the leaves, singly or in irregular small groups. They are about 1mm long, changing from ruby red to brown immediately after oviposition. Incubation period 7-10 days.

##### Larvae

Larvae hatch using a pair of egg bursters on the first abdominal segment. They feed upon the leaves, stems, sepals and petals of the foodplant and are fully grown in 2 weeks. Fully grown larvae have been collected in England on 15th June. Pupation occurs in an earthen cell and at the end of 20-22 days adults emerge. In S.W. France the complete cycle require 47 days (Balachowsky & Mesnil 1936)

##### Adults

Adults hibernate and re-appear towards the end of March in France (Balachowsky & Mesnil 1936) towards mid-April in Germany (Hesse, 1932) or 20th May in England. Adults oviposit from 21st March in the Bordeaux region (Balachowsky & Mesnil 1936) and the 22nd March around Coulommiers (S et M) in France. In the latter case the egg laying period was considerable, oviposition occurring until 24th September and continued after a further hibernation from 18th March-12th April the following year. In England adults have been seen until 3rd September. It is probable there is a single generation/year.

SUBFAMILY CRYPTOCEPHALINAE

GENUS Cryptocephalus

C. labiatus (L.) Plate B3 Fig. 16.

Foodplant: Betulaceae Betula pendula Roth.

Ova

Eggs lime yellow, oval, pointed at one end,  $\bar{x}$  length 0.624mm,  $\bar{x}$  width 0.391mm ( $n = 88$ ). During oviposition the female retains each egg between the posterior tarsi, turning them around and depositing on each a regular layer of excrement. After this process they are dropped to the ground.  $\bar{x}$  length of egg case 1.233mm,  $\bar{x}$  width 0.712mm ( $n = 96$ ). The egg occupies half the length of the case and is situated at the broadest end of the egg case. The egg case has a thin walled cap at the anterior-end, which is possibly the point at which the head of the larva fits. Incubation period 17-22 days at 20°C. Oviposition probably occurs in the field from 6th July until 15th September.

Larvae

First instar larvae possess paired hatching spines on the meso and metathorax. They hatch within the egg case, making a small hole at the narrowed anterior end for the head. The larvae never abandon their cases but because of growth they need to enlarge them by adding new pieces made from excrement. The cases are more convex above than below, broader at the posterior end (for the curved abdomen) and tapering to the anterior end at which there is a hole for the head. There is a mid-ventral keel along which 2nd, 3rd and 4th instar cases can be split but this keel is absent in the first instar cases. Before moulting the larvae close the opening with an operculum composed of the same material as the case. Hatching probably occurs in the field from 6-10th September until the 1st October and 1st and 2nd instar larvae were overwintered under insectary conditions from 5th November 1973 until 24th April 1974. It is also possible in the



field that eggs could overwinter. The larvae resumed feeding upon Betula leaves in May and fully grown 4th instar larvae were present at 20°C in mid May. Before pupation the larvae close up their cases and turn to face the opposite end of the case. Pupation usually occurs attached to the bark of trees or on the ground and pupae are probably present from the beginning of June until mid-July. However, not all larvae pupated and it is possible there is a Summer diapause (as 4th instar larvae) during June, July, August and September.

#### Adults

New generation adults emerged at 20°C and a 16 hour day from 18th June until 22nd July. Emergence occurred by a small cap being displaced about 1.014mm from the anterior end. Adults have been observed in the field from 10th June until 15th September.

C. pusillus F. Plate B3 Fig. 15.

Foodplant: Betulaceae Betula pendula Roth.

#### Ova

Eggs similar to C. labiatus, but egg cases lighter brown,  $\bar{x}$  length of egg cases 1.268mm,  $\bar{x}$  width 0.724mm (n = 50). Incubation period at 20°C and 16hr. day 20-21 days. Oviposition in the field probably occurs from 7th July until 3rd September.

#### Larvae

Hatching probably occurring from the end of July until the end of September. Larvae kept at 20°C and 16hr. day were as 1st-4th instars when they were placed under insectary conditions 5th November 1973. The species overwintered as first to final instar larvae and resumed feeding about 24th April 1974 at 20°C. It is possible eggs also overwinter in the field. All larvae pupated between 7th May - mid June. Larvae are likely to occur in the field until the end of June and pupae until late July. Adults emerged by removing a small cap from the larval case about 1.248mm from the anterior end. Adults have been observed in the field from June until 5th September. At

20°C one adult emerged 30th May-4th June 1974 and contained fully developed ova by 24th June.

C. parvulus Müll. Plate B3 Fig. 17.

Foodplants Betulaceae Betula pendula Roth.

#### Ova

Lime green, oval, pointed at one end,  $\bar{x}$  length 0.755mm,  $\bar{x}$  width 0.476mm ( $n = 8$ ). Eggs covered by females excrement in the form of an egg case  $\bar{x}$  length 1.517mm  $\bar{x}$  width 0.952mm ( $n = 18$ ). Incubation period 17-22 days at 20°C and a 16 hr. day. Oviposition in the field probably occurring from the beginning of July until 18th September.

#### Larvae

Hatching probably occurring from the end of July until 3-4th October. Larvae reared at 20°C developed to 1st and 2nd instars up to 5th November 1973 after which they were overwintered under insectary conditions. Although larvae were reared at 20°C and a 16hr. day (in April 1974) they only developed to the 2nd and 3rd instar and were probably diapausing from the end of June until mid-September in this stage. The larvae feed upon the leaves of Betula but seemed to have a preference for the leaves which had turned brown and had a fungal infection.

#### Adults

New generation adults have been observed in the field in May until 18th September.

It can be seen that Cryptocephalus species overwinter as larvae and may complete their development the year following oviposition. However some species e.g. C. parvulus and C. labiatus probably require 2 years to achieve development to the adult.

SUBFAMILY CLYTRINAEGENUS Clytra

C. quadripunctata (L.) Plate B3 Fig. 18.

Biology studied by Donisthorpe (1902)

Foodplants

The newly emerged adults feed upon the tender shoots and young leaves of low bushes including Betula, Salix, Prunus and other fruit trees.

Ova

Elongate, oval, pale yellow, surface very finely striated, nearly smooth. Length 1mm, max. width 0.56mm. These are oval and surrounded by a collerette of small bracts which are made from the females excrement and deposited on the smooth chorion. During this process the eggs are retained in the abdominal depression and rotated by the hind tarsi. The eggs are dropped by the female from low vegetation onto the soil surface near the nests of the red ant Formica rufa L. The ants move the eggs into their ant hills possibly mistaking them for seeds or other plant debris. The incubation period is about 20 days.

Larva

The larva lives within a larval case which is enlarged after each moult. It feeds upon plant debris in the ant hill and can withdraw completely into its case when alarmed. At each moult the larva hooks its case onto a twig and places its head across the entrance sealing the case and thus protecting the soft parts within. Pupation occurs within the case but the entrance is completely closed up by the final instar larva. The newly emerged adult emerges from the pupal case and leaves the ant hill during May and June of the following year.

Adults

In England adults have been collected from 11th May until

10th June and again on 22nd August which possibly suggests a long oviposition period, as an adult collected in May started oviposition 30th May. According to Donisthorpe the cycle is yearly and as eggs take about 20 days to hatch first instar larvae would be expected to be found within the nests the 3rd week in June. The larvae would probably feed during the Summer, Autumn and Winter becoming fully developed the following Spring and giving rise to new generation adults in May.

SUBFAMILY CHRYSOMELINAEGENUS TimarchaT. tenebricosa (F.) Plate B4 Fig. 19.Foodplants: Rubiaceae Galium aparine L.Ova

The eggs are large,  $\bar{x}$  length 3.429mm,  $\bar{x}$  width 1.872mm ( $n = 14$ ) with the chorion finely microsculptured. They are orange to red brown when fertile but dark brown or black when infertile. Deposition usually occurring in batches of 4, 6 or 8 ova but also singly or in pairs. They are covered with regurgitated food material on the stems of the foodplant or at a shall depth in the soil. (Plate LP14 Fig 49)

Oviposition by 6 new generation females occurred from 7-8th August until 21-23 September and again from the beginning of May until the end of August the following year. (Figs. 89 & 90 ). This is compared with oviposition in the laboratory by 6 wild females collected in the Forest of Dean, 9th August 1972. The oviposition period occupies 5 months in the field. All ova laid undergo an obligatory diapause as the fully developed embryo within the egg. Diapause is probably predetermined by the females laying the ova as diapause occurs regardless of the external conditions to which they are subjected. Long day length treatment was ineffective in breaking diapause. The embryo required 42 days at 19°C to become fully developed whereas ova laid 10-13 June 1974 and kept under insectary conditions at Close House required 54-57 days. These latter eggs were dissected periodically to show their development (Table 15 ).

After becoming fully developed 30 days at 2°C caused hatching in 14 days on return to 20°C. 30 days at 0°C failed to cause hatching as did 30 days at -5°C. However 37.93% of larvae survived this period at -5°C. Eggs laid at Close House in Autumn 1973 had a 43.9% fertility. Eggs laid in Autumn of the first year will hatch the following Spring whereas the May-September ova of the next year will hatch the following Spring.

FIG. 89. OVIPOSITION UNDER LABORATORY CONDITIONS BY ADULTS OF TIMARCHA TENEBRICOSA (F) ♀

AND BY ♂♂ AT CLOSE HOUSE

OVIPOSITION IN LAB x—x—  
 OVIPOSITION AT CH. o—o—

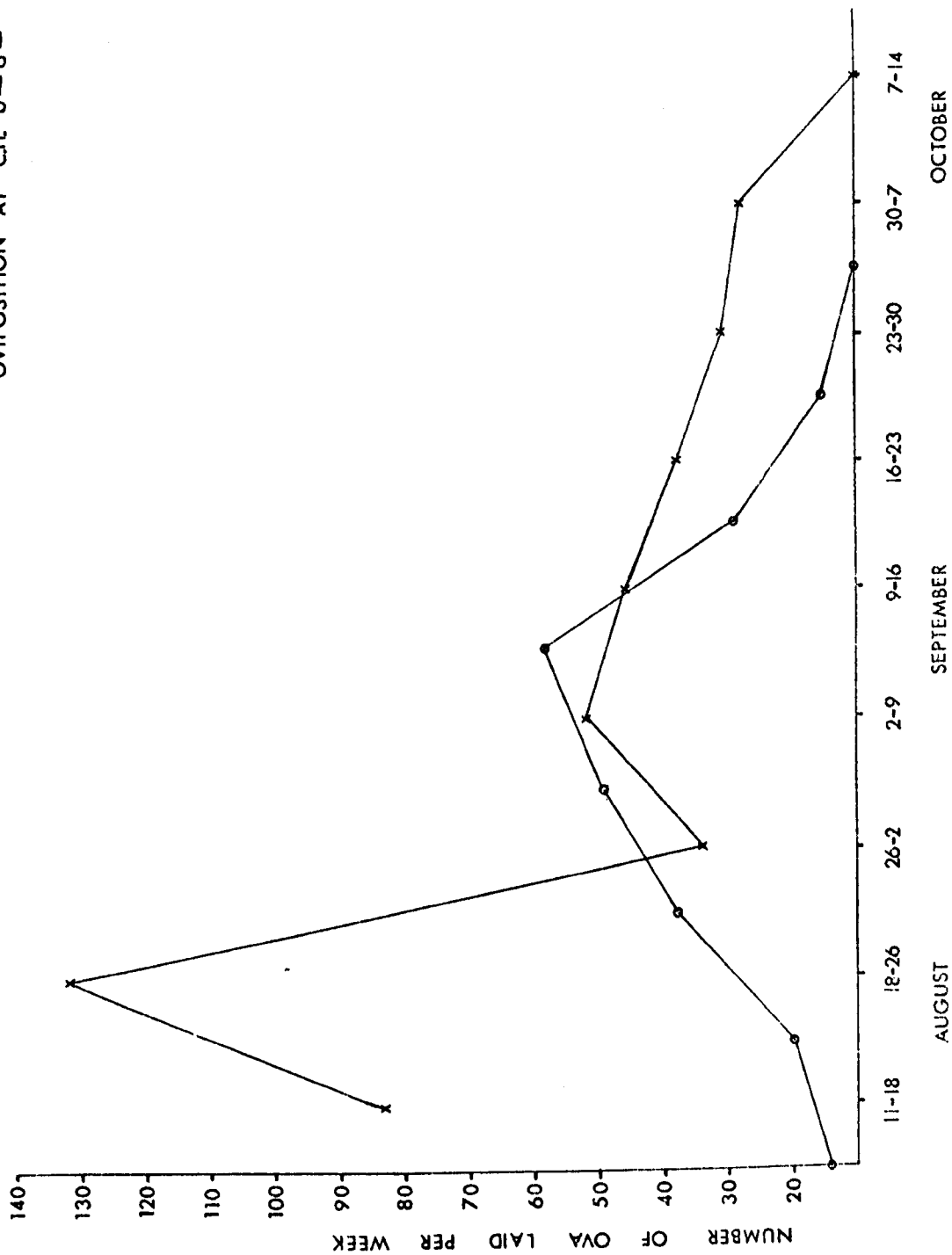


FIG. 90 OVIPOSITION BY 6 ADULT ♀ *T. tenebricosa* (reared under insectary conditions 1973) UNDER INSECTARY CONDITIONS 1974

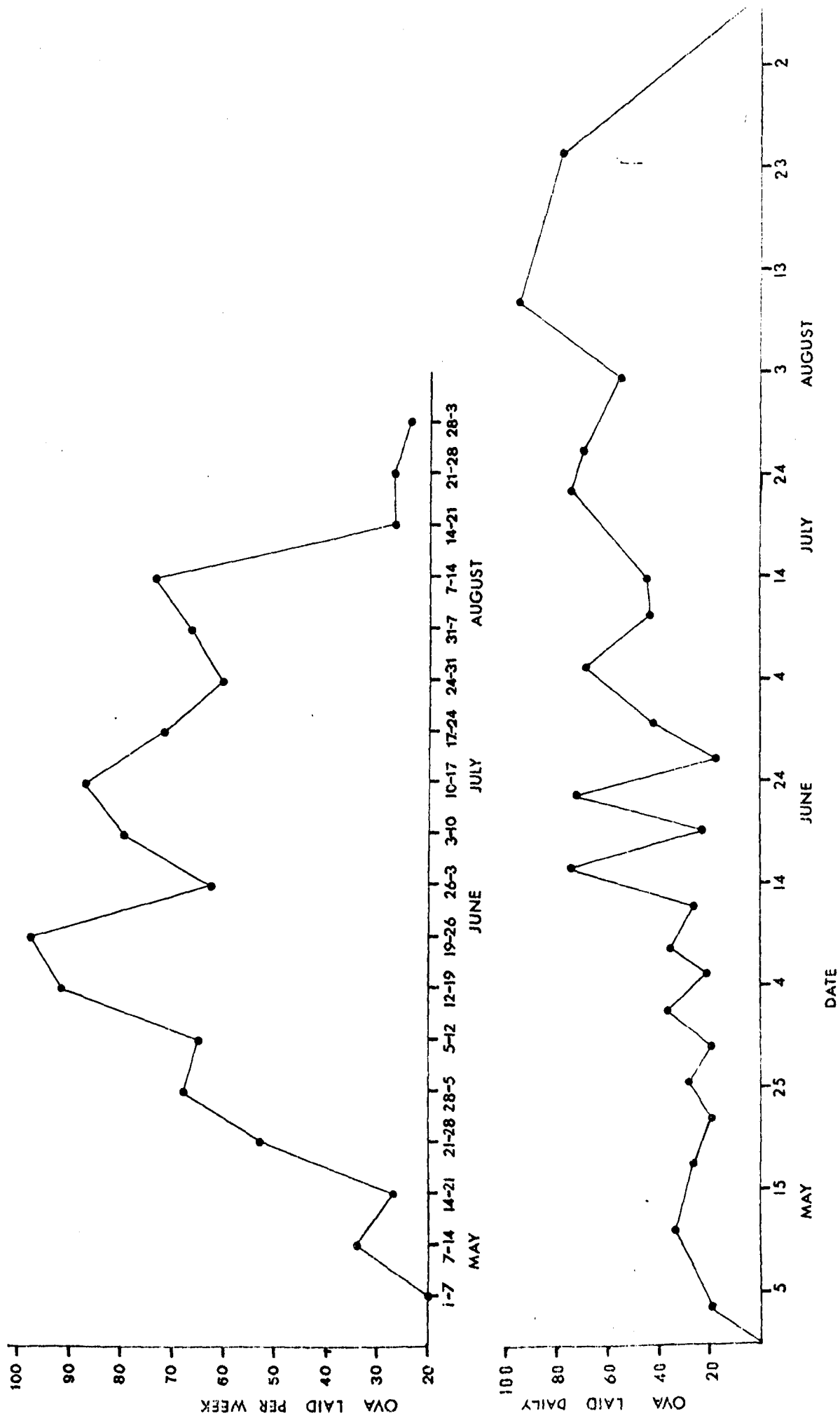


TABLE 15 EMBRYONIC DEVELOPMENT OF *T. tenebricosa* (F) UNDER INSECTARY CONDITIONS

DAYS AFTER OVIPOSITION	EMBRYONIC DEVELOPMENT
30	Very little development
40	12 ocelli visible as dark spots on the head
48	Ocelli, antennae, mandibles, labial palps, legs & spiracles visible
55	As for 48 days but spiracles darkened and body red brown



FIG.91 HATCHING OF *T. tenebricosa*(F)OVA (laid by insectary reared adults Autumn 1973) UNDER INSECTARY CONDITIONS 1974

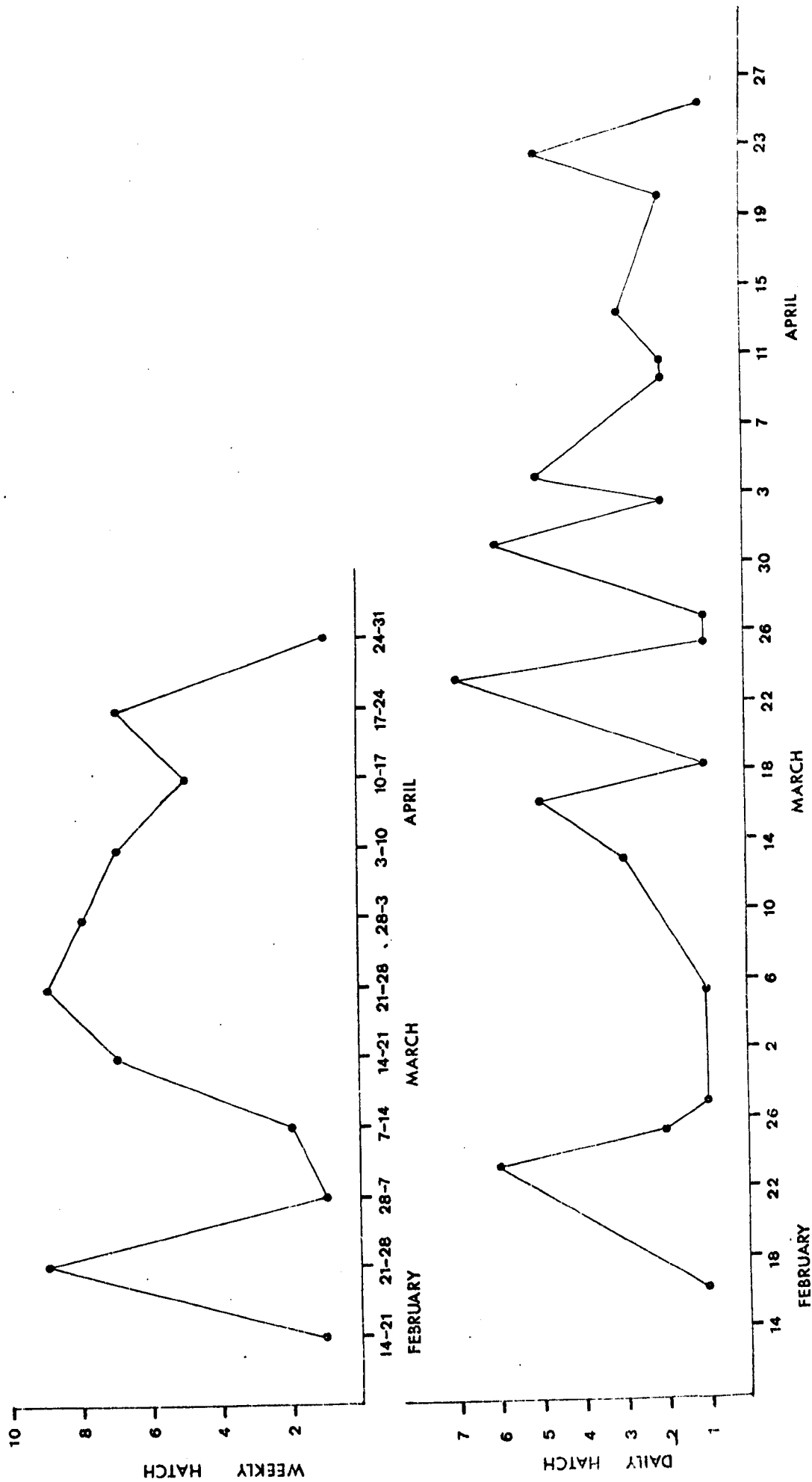
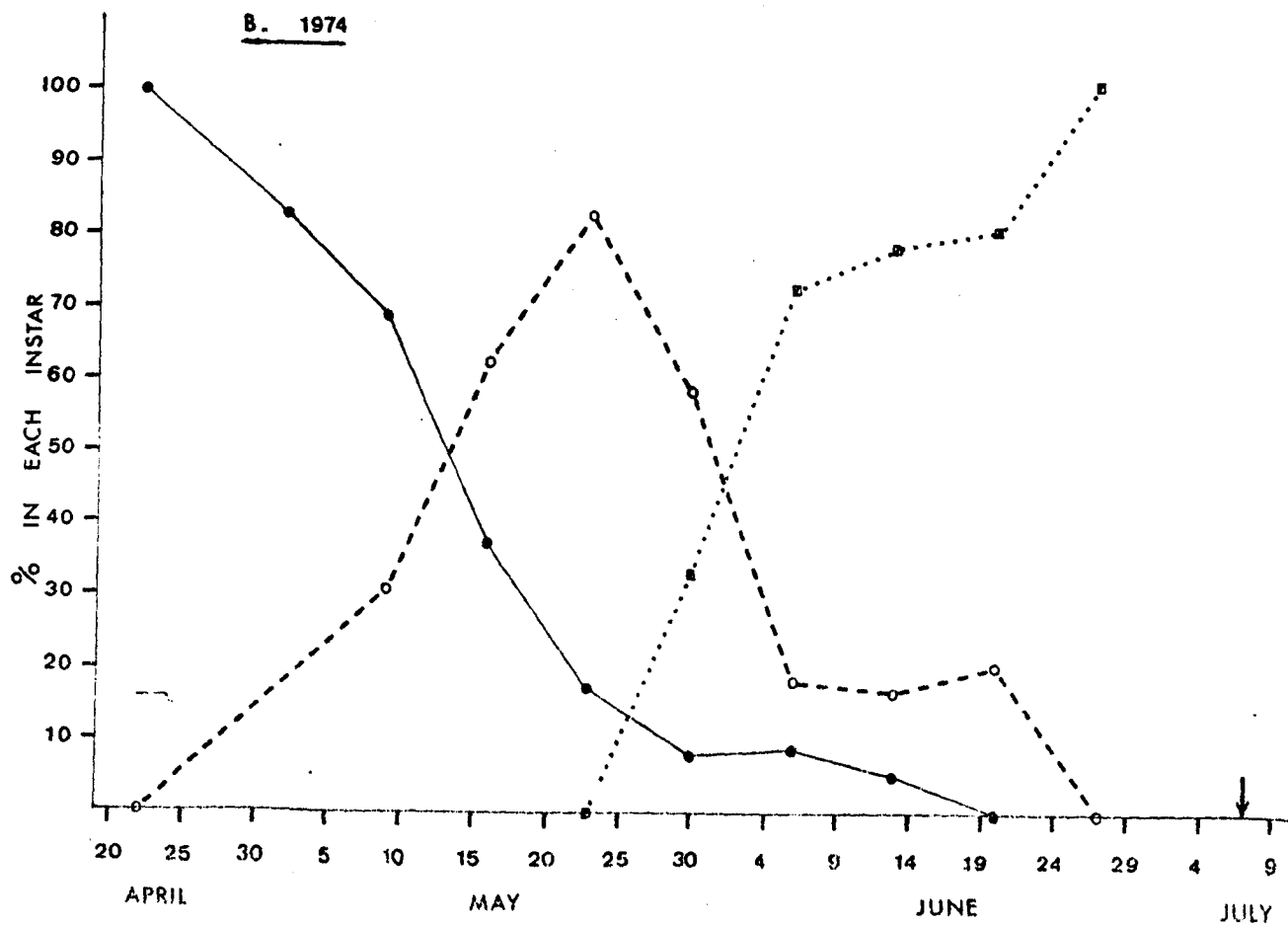
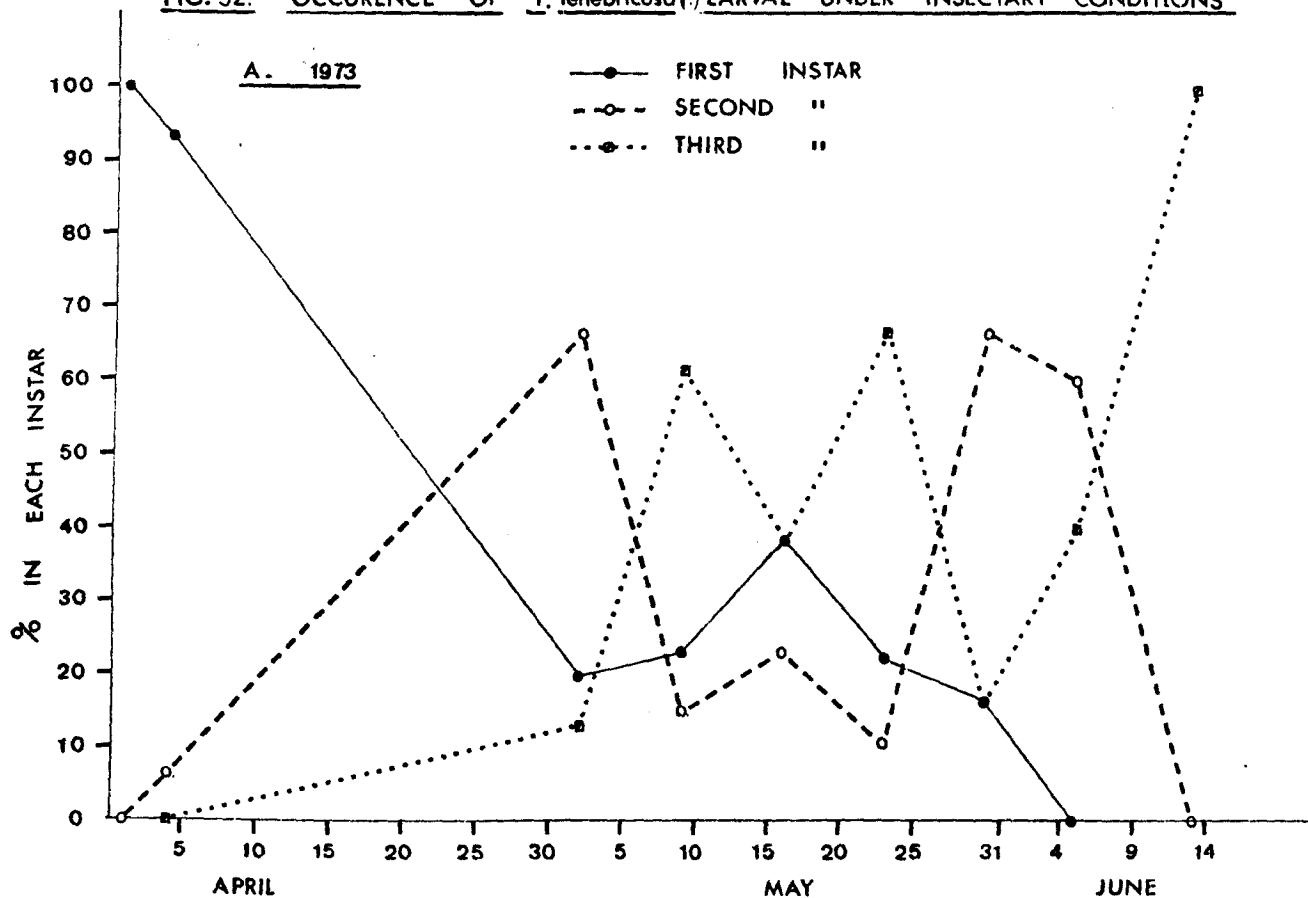


FIG. 92. OCCURENCE OF *T. tenebricosa*(F) LARVAE UNDER INSECTARY CONDITIONS



Ova from one generation will be present in the field in 3 years.

### Larvae

Hatching is caused by the previous distension of the egg by the intake of air by the larvae and the use of 3 pairs of hatching spines, situated respectively on the meso, metathorax and first abdominal segment. 2 spines on one side and not always the same are utilised to make a longitudinal slit in the dorsal face of the chorion. Hatching of Autumn eggs 1973 under insectary conditions occurred from about 14th February until late April 1974 (Fig. 91 ). It is probable that in the field the eggs laid at the beginning of May onwards will hatch about the same time as those laid in the Autumn and thus hatching of ova laid over a 5 month period will be concentrated over a 2½ month period.

The occurrence of larvae under insectary conditions during 1973 and 1974 are shown in Figs. 92A&B . Larvae occurred from about 14th February until 16-22nd July. Larvae commenced entering the soil to pupate from 2-9th May, the majority having entered by the end of June. There are 3 instars and larval development at 19°C required 33 days and 54 days at 16°C. Larvae present in the field during any year will consist of the progeny of 2 different generations of adults.

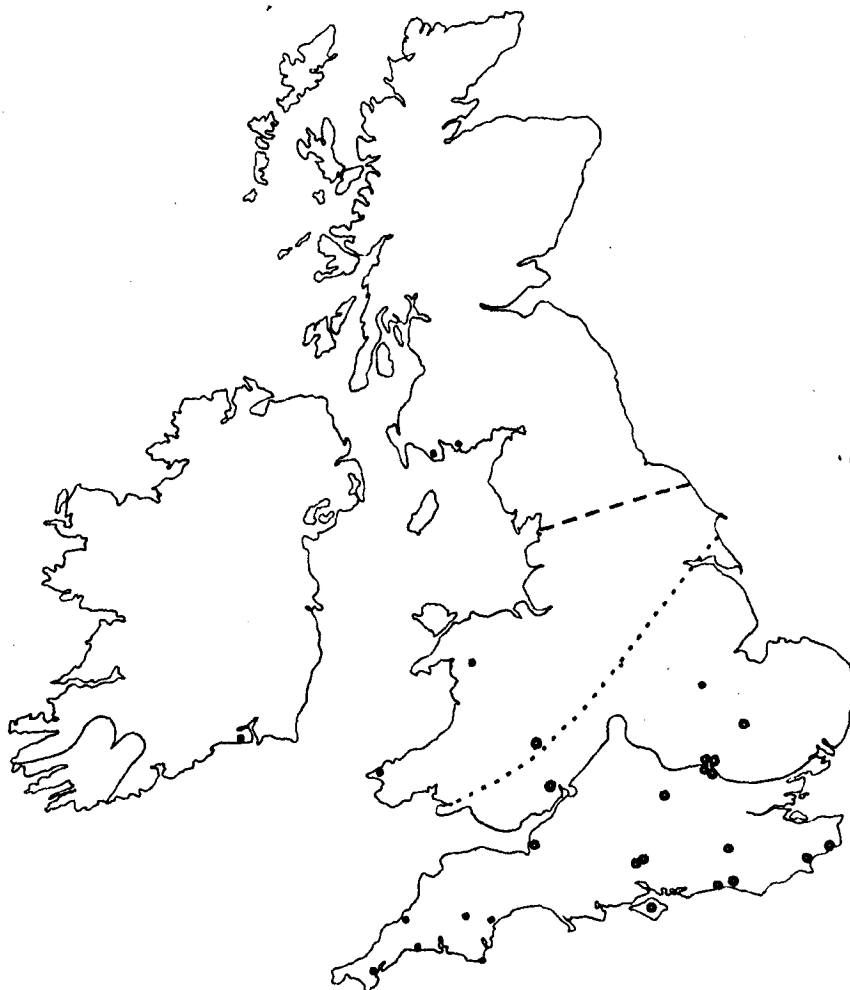
### Pupae

Pupation occurred within an earthen cell at a depth of 50-80mm. The first pupae occurred about 6-11th June until 3-13th September. The mean prepupal and pupal periods were 25.8 days and 21.0 days respectively. 4 adults after emergence from the pupa remained in their cells for a mean period of 8.6 days before appearing above ground (Tables 16a & b ).

### Adults

New generation adults emerged from about 6-9th July until 3-13th September. Adults emerging in 1973 were at least 1 month

FIG. 93. THE DISTRIBUTION OF *Timarcha tenebricosa* (F.) IN THE BRITISH ISLES



—— THE SOUTHERNMOST LIMIT OF THE LAST PLEISTOCENE GLACIER

---- 60°C JULY ISOTHERM

..... 62°C JULY ISOTHERM

• LOCALITIES ON CHALK, UPPER GREENSAND OR LIMESTONE

earlier than those in 1974 and started ovipositing at the beginning of August whereas those of 1974 did not show any ovariole development at the beginning of September. 6 new generation females laid a total of 205 ova during August and September of their first year and 1040 ova from the beginning of May until the beginning of September of their second year. The fecundity of these adults was 207.5 ova. The adults of one generation will give rise to larvae over 2 years. The 1973 adults survived from the beginning of July until September or a period of 14 months under insectary conditions. It is possible also that adults may overwinter for a second time and lay eggs the following year. Adults become inactive at the beginning of October and enter hibernation under dried vegetation etc., emerging the following Spring. Adults have been observed in the field from 18th March until the beginning of October. The sex ratio of 11 adults reared from eggs in 1973 was female: male 6 : 5 whereas for 13 adults reared in 1974 it was 8 : 5.

The life-cycle in Timarcha tenebricosa will consist of both annual and biennial components. Those eggs laid in Autumn (1st oviposition period) will take 11-12 months to develop to the adult whereas ova laid from May-September (2nd oviposition period) will take up to 15-16 months for development to the adult state.

#### Distribution (Fig. 93 )

By superimposing a map of the Pleistocene glaciations over the distribution map of this species one can see a fairly close correlation. Most records occur at or below the southerly most limit of the last glacier because north of this populations of this species will have been decimated. After the recession of the glacier, because this species is wingless there will have been very little dispersal from the south. A wingless adult is shown on Plate LPI4 Fig 48

GENUS CHRYSOLINAChrysolina hyperici (Forst.) Plate B5 Fig. 25Foodplants: Hypericaceae Hypericum tetrapterum Fr.Hypericum hirsutum L.Hypericum perforatum L.Ova

Red-orange or orange, elongate oval,  $\bar{x}$  length 1.166mm,  $\bar{x}$  width 0.487mm ( $n = 50$ ). Chorion clear, dull, with fine pentagonal or hexagonal microsculpture. The eggs are laid in ones and twos on the upper and lower leaf surfaces, usually only 1-2 per shoot. The eggs laid on the upper leaf surface are usually on the midrib. Eggs may also be laid on dried flower parts and on the top of the soil surface. Oviposition at Close House occurred from about 4-5th September until about 12th February the following year. The adults remain near the soil surface during the Autumn and Winter ovipositing on the younger procumbent perennial shoots. The eggs do not diapause but are inhibited from developing by the low ambient temperatures. However, hatching of ova laid 4-5th September occurred under insectary conditions 18-24th September but it was not shown if larvae can survive the Winter. Incubation times under various temperature regimes are shown in Table 17 .

Larvae

The larvae possess paired hatching spines on the meso and metathorax and also on the first abdominal segment. Hatching occurred from about 14th April until the 20th June at Close House. The larvae feed singly or two or three per shoot upon the leaves and stems of the foodplant. There are 4 instars and the occurrence of larvae at Close House is shown in Fig . 95 . Pupation occurs at a depth of 0-9cms in the soil. As fully grown larvae were not seen until 30th May it is probable that pupation occurs during the first week in June. 3rd instar larvae have been seen as late as 2nd July

TABLE 17 INCUBATION PERIODS OF Chrysolina OVA

SPECIES	TEMPERATURE °C	INCUBATION (days)	$\bar{x}$	n
C. hyperici (Forst.)	10	56 — 64.5	60.25	2
	13	24 — 27	25.5	2
	16	14 — 23	20.3	11
	19	6.5 — 15	10.5	18
	22	7.5		
	25	5 — 11	7.7	18
	30	9		
C. brunsvicensis (Gr.)	13	15 — 24	20.2	15
	16	13 — 19	16.4	6
	19	7 — 14	9.6	18
	25	5 — 8	6.6	7
	19	11 — 17	13.9	4
C. staphylea (L.)	25	11		
	16	12 — 14.5	13.25	2
C. menthastri (Suf.)	19	7 — 13	9.6	9

# OCCURENCE OF LARVAE AT CLOSE HOUSE

\* FIRST INSTAR  
 • SECOND "  
 ◊ THIRD "  
 - - - FOURTH "

FIG.94 Chrysolina brunsvicensis  
1973

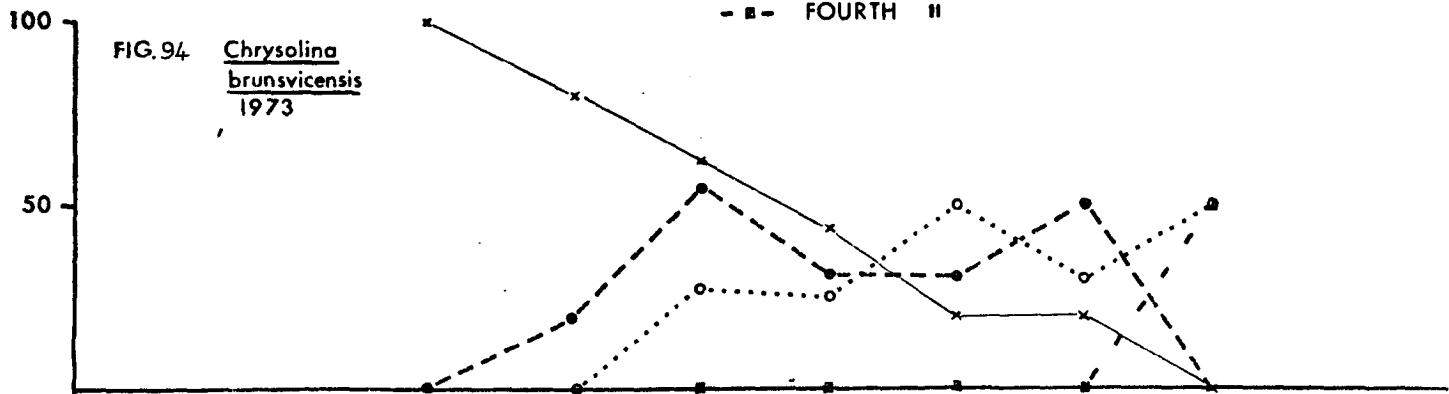


FIG.95 Chrysolina hyperici  
1973

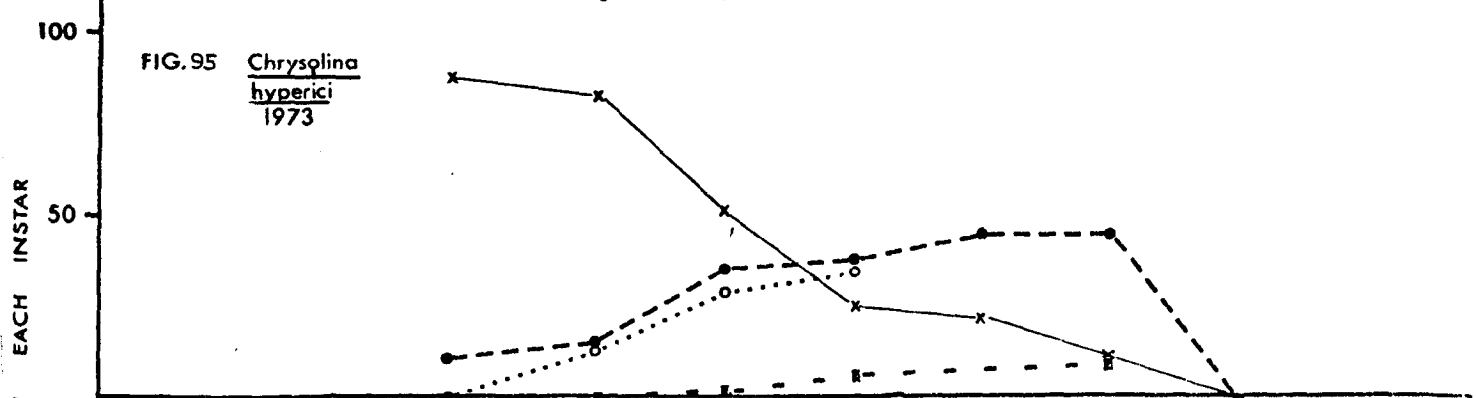


FIG.96 Phaedon tumidulus  
1974

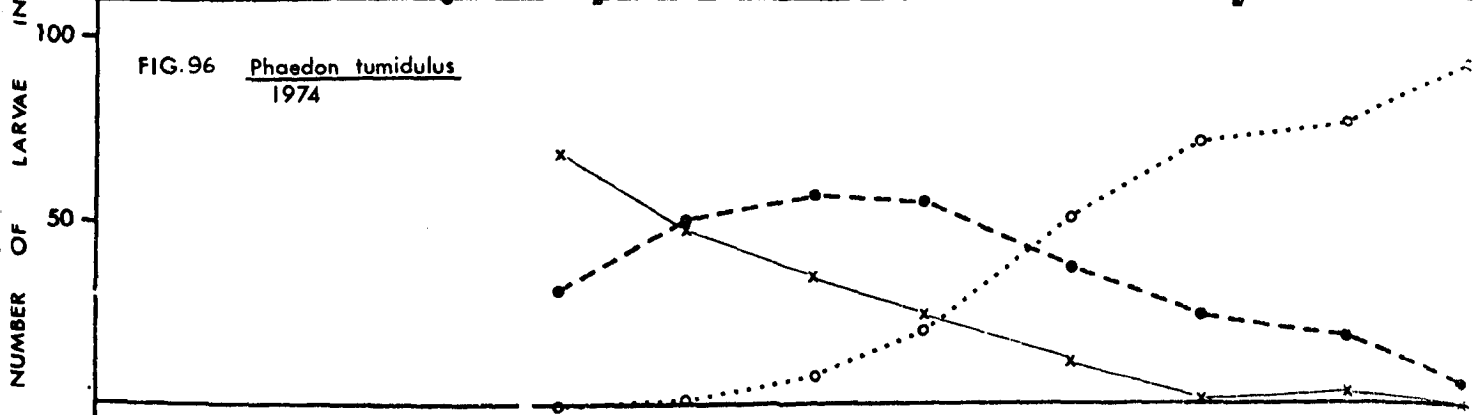


FIG.97. Apteropeda orbiculata  
1974

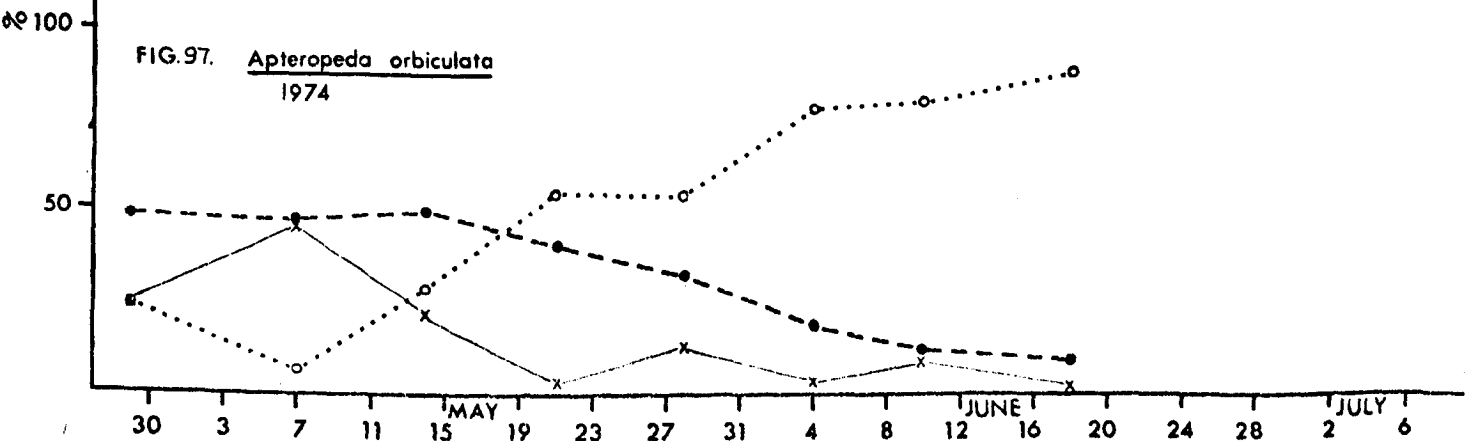




TABLE 18 POST EMBRYONIC DEVELOPMENT TIMES IN DAYS OF Chrysolina SPECIES

SPECIES	TEMP. °C	DURATION OF 1st INSTAR	DURATION OF 2nd INSTAR	DURATION OF 3rd INSTAR	DURATION OF 4th INSTAR	LARVAL DURATION	PUPAL DURATION	TOTAL TIME TO ADULT EMERGENCE
<i>Chrysolina varians</i> (Schal.)	16	12	10—14	—	—	44	11—13	55—57
	19	7	9—10	7	7	30—31	5—6	35—37
	25	—	8—10	4—6	—	—	—	—
<i>Chrysolina brunsvicensis</i> (Gr.)	16	7—9	6—7			49—57	18—19	67—76
	19	7—11				28—31	8—9	36—40
	25	—				23—24	6—7	29—31
<i>Chrysolina hyperici</i> (Forst.)	16					49—62	12—15	61—77
	19					26—38	8—10	34—48
	25					12—24	12—13	24—37
	30					28	—	—
<i>Chrysolina staphylea</i> (L.)	16	11	13	13	16	53	17	70
	19	6—9	6—10	6—10	8—14	26—43	12	38—55
	30	3—5	3—5	4—5	—	—	—	—
<i>Chrysolina menthastris</i> (Suf.)	19	4—7	5—8	5—8	9—14	23—37	10	33—47



TABLE 20      FECUNDITY , LONGEVITY & DURATION OF OVIPOSITION ( Days ) IN Chrysolina & Phyllodecta

Chrysolina brunsvicensis (Gr.)

19°C & 16hrs light/Day	♀ 1	♀ 2	♀ 3	♀ 4	♀ 5	♀ 6	♀ 7	♀ 8	$\bar{x}$
FECUNDITY	295	273	104	217	306	128	108	134	195
OVIPOSITION PERIOD	90	65	58	67	92	57	19	36	60
LONGEVITY days	290	350	145	213	290	187	110	290	234

19°C & 0 hrs light/Day	♀ 1	♀ 2	$\bar{x}$	INSECTARY		♀ 1	♀ 2	$\bar{x}$
FECUNDITY	304	535	419	FECUNDITY		228	97	162
OVIPOSITION PERIOD	79	46	62	OVIPOSITION PERIOD		65	82	73
LONGEVITY days	98	186	142	LONGEVITY days		73	144	108

Chrysolina staphylea (L.)

19°C & 0 hrs light/Day	♀ 1	♀ 2	♀ 3	♀ 4	♀ 5	♀ 6	♀ 7	♀ 8	$\bar{x}$
FECUNDITY	151	33	158	21	57	134	9	72	79
OVIPOSITION PERIOD	46	19	41	9	23	55	5	29	28
LONGEVITY days	76	37	58	38	58	114	12	45	54

Phyllodecta vulgatissima (L.)

19°C & 0 hrs light/Day	♀ 1	♀ 2	♀ 3	$\bar{x}$
FECUNDITY	109	254	127	163
OVIPOSITION PERIOD	13	27	21	20
LONGEVITY days	26	55	52	44

and thus pupae may probably occur until mid-August. Development of larvae at various temperatures are shown in Table 18 .

### Adults.

One adult was captured at Close House 27th May 1974 but it is probable that this overwintered. New generation adults started emerging from 10th June and continued emerging until 14th August 1974. The adults feed upon the leaves and flowers of Hypericum tetrapterum Fr. but the ovaries of the females did not start developing until 3rd September. Adults collected in the field 20th June 1973 at 19°C and a 16 hr. day showed no ovariole development when dissected 26th November. It is probable that C. hyperici is a short day insect and long daylength inhibits the development of the ovaries. Adults at 19°C and darkness laid ova from 18th October until 13th April 1972 but the majority of adults die before February in the field. Measurements of mean fecundity, longevity and oviposition period are shown in Table 19 .

### Chrysolina brunscivensis (Gr.) Plate B5 Fig. 26.

Foodplants: Hypericaceae Hypericum tetrapterum Fr.

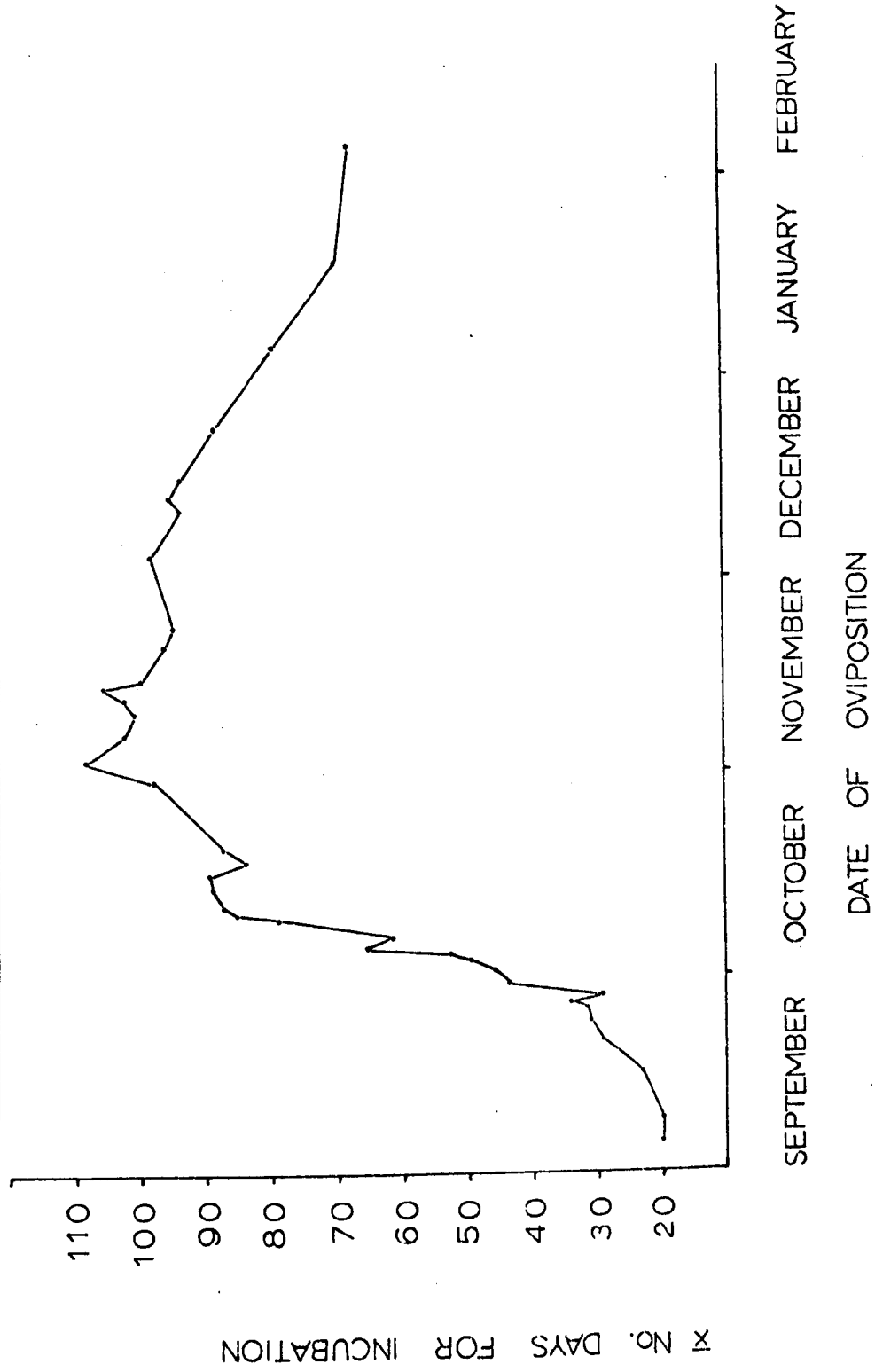
Hypericum hirsutum L.

Hypericum perforatum L.

### Ova Plate PI Fig. 3

Red-orange, elongate oval,  $\bar{x}$  length 1.177mm,  $\bar{x}$  width 0.491mm (n = 50). Chorion clear smooth and shiny with distinct pentagonal surface sculpturing more distinct than in C. hyperici. Eggs laid singly or sometimes in pairs on the upper and lower surfaces of leaves of the foodplant, chiefly on the apical leaves and shoots. Oviposition under insectary conditions at Close House occurred from 4-5 September until 12th February but it is likely that in the field the oviposition period will be longer. The adults remain near the soil surface during the Autumn and Winter, ovipositing on the younger procumbent perennial shoots. The eggs do not

FIG.98 TO SHOW THE EFFECT OF THE DATE OF OVIPOSITION OF *Chrysolina brunsvicensis*  
ON THE DURATION OF INCUBATION UNDER INSECTARY CONDITIONS



diapause but are inhibited from developing by the low ambient temperatures. However, hatching of ova laid 4th September - 12th February, occurred under insectary conditions 18th September - 17th April 1974. (Fig. 98 ) Incubation times under various temperature regimes are shown in Table 17 .

### Larvae

The larvae possess paired hatching spines on the meso and metathorax also on abdominal segments 1, 2, 3, 4, and sometimes 5. In the field at Close House hatching occurred about 15th May and continued until 20th June 1973. The larvae feed upon the leaves and stems of Hypericum being found singly or in two's or three's per shoot. There are 4 instars and the occurrence of larvae at Close House is shown in Fig. 94. . Pupation occurs at a depth of 0-12 cms in the soil. Fully grown larvae were not seen until about 30th May and second and third instar larvae were last seen 7th July. It is probable that the pupal stage lasts from about 7th June until mid-August. Development of larvae at various temperatures is shown in Table 18 .

### Adults

One adult was captured at Castle Morton Common 7th May 1973 but it is probable that this overwintered. New generation adults probably emerge from the end of June until the end of August. Adults are commonly seen in the field during September up to late October feeding upon the leaves of Hypericum. It is probable that C. brunsvicensis is a short day insect, long day length inhibiting the development of the ovaries. Adults at 19°C and darkness laid ova from 26th September until 1st January 1972. Measurements of mean fecundity, longevity and oviposition period are shown in Table 20 .

Chrysolina varians (Schall.) Plate B5 Fig. 27.

<u>Foodplants</u>	Hypericaceae	<u>Hypericum hirsutum</u> L.
		<u>Hypericum pulchrum</u> L.
		<u>Hypericum perforatum</u> L.
		<u>Hypericum tetrapterum</u> Fr.

Ova and Larvae

Red, chorion very thin, incubation time about 24 hours. Usually fully developed larvae are deposited surrounded by a thin chorion, the larvae emerging from the vagina head first. Larvae deposited singly or in pairs on the leaves of Hypericum. First instar larvae occur in the field as early as 3rd June until 31st July. Thus larvi-position occupies 2 months. There are 4 instars. Final instar larvae occur at the end of July probably up to the end of August as 2nd instar larvae were seen on the 6th August. Larvae in the field were found on the undersides of leaves or on the dried flower heads of Hypericum which they greatly resemble. Pupae probably occur the first week in August until about mid-September. Pupation occurs at a depth of 0-6cms in soil.

Adults.

The pupal stage at 16°C lasts 11-13 days with the prepupal stage about 5 days. Thus adults from mature larvae at the end of July will emerge from about mid August and from the later larvae about mid-September. Adults reared from larvae collected 31st July and kept at a high temperature but shortening day length did not bear larvae until the following year. There is only one generation/year and the adults overwinter. Adults re-appear at the beginning of May and the pre-larviposition period is about 1 month. There is probably a mixing of the old and new generations in the field and adults may go into hibernation for a second time at the end of September. Larval and pupal development at various temperatures is shown in Table 18 , and adult longevity and fecundity in Table 19 .

Chrysolina polita (L.) Plate B4 Fig. 23.Foodplants: Labiatae Glechoma hederacea L.Mentha aquatica L.Mentha arvensis L.Ballota nigra L.Lycopus europaeus L.Origanum vulgare L.Ova

Pale orange, chorion with distinct hexagonal microsculpture, elongate, oval  $\bar{x}$  length 1.776mm,  $\bar{x}$  width 0.724mm (n = 46). Eggs laid in batches of from 16-30 ova on the undersides of leaves of the foodplant. Incubation at 19°C lasts 8-10 days. Oviposition in the field occurs from about 7th June until the middle of July.

Larvae

Paired hatching spines are present on the meso and metathorax and on the first abdominal segment. First instar larvae occur at Close House as early as 23rd June and in another locality as late as 5th August. There are 4 larval instars. Fully grown larvae from the beginning until the end of August. Pupae probably occur from mid-August until mid-September.

Adults

New generation adults emerge from the end of August until the end of September in the field. They go into hibernation as late as 7th October and re-appear as early as 3rd April the following Spring. Adults overwinter in grass tussocks and under moss and there is one generation a year.

Chrysolina staphylea (L.) Plate B4 Fig. 24.Foodplants: Ranunculaceae Ranunculus repens L.Ova

Deep red brown becoming paler prior to hatching. Elongate, oval,  $\bar{x}$  length 1.653mm,  $\bar{x}$  width 0.832mm (n = 28).



Laid singly or in two's usually on the underside of Ranunculus leaves, sometimes on the upper surface or on the leaf petiole. Incubation period at 25°C 11 days, at 19°C 14 days. Oviposition probably occurs from about the beginning of May until mid June after which the adults die off.

### Larvae

Possess paired hatching spines on the meso and metathorax and first abdominal segment. Hatching probably occurs about mid May and larvae are fully developed by mid June. Pupation occurs from about 18th June, pupae probably occurring until about 21st August. The larvae feed in ones, two's or three's on the undersurface of Ranunculus leaves.

### Adults

The new generation adults start emerging from 2nd July at Close House and go into hibernation as late as 25th October. The adults overwinter in grass tussocks and there is one generation a year. Larval and pupal development at various temperatures is shown in Table 18 , and adult longevity and fecundity in Table 20 .

Chrysolina fastuosa (Scop.) Plate B4 Fig. 21.

Foodplants: Labiatae Galeopsis tetrahit L.

### Stachys

### Ova

Creamy white, chorion with distinct hexagonal microsculpturing. Elongate, oval,  $\bar{x}$  length 1.555mm,  $\bar{x}$  width 0.632mm ( $n = 57$ ). Laid without preference on the upper and lower surfaces of leaves of Galeopsis tetrahit usually 1, 2, or 3 per leaf. Incubation at 25°C requires 6-7 days. Majority of ova laid at about  $\frac{1}{8}$ " from the leaf edge and usually inclined at an angle but occasionally were almost parallel to the surface of the leaf. Oviposition in the field occurs from about the end of July until the 18th August.

### Larvae

Possess paired hatching spines on the meso and metathorax and 1st abdominal segment and hatch by making 1 or 2 slits in the side of the egg. Hatching occurs about 13-14th August and full grown 4th instar larvae enter the soil to pupate by about 11th September. Larvae feed at night, eating small holes in the leaves and hiding in the seed capsules during the day. The last larvae enter the soil by the end of September. Pupae possibly occur from 18th September and new generation adults emerge the end of September. According to Dobson (1924) larvae and adults can overwinter and in the present work adults were overwintered at 5°C and darkness in the laboratory.

### Adults

Dobson (1924) suggests that adults do not lay ova the year following their emergence from the pupa but hibernate a second time and then lay ova the following Autumn. New generation adults emerged from hibernation the first year on 4th June, paired throughout July, and disappeared into the earth by 14th September without laying ova. The following year adults were present in the field on 17th June and commenced oviposition 31st July.

Chrysolina menthastri (Suffr.) Plate B4 Fig. 20.

Foodplants: Labiatae Mentha aquatica L.

M. rotundifolia (L.)

### Ova

Creamy white turning yellow in about a day. Elongate oval with rounded ends,  $\bar{x}$  length 1.751mm,  $\bar{x}$  width 0.740mm ( $n = 47$ ). Laid in one's, two's or three's or in a double row quite regularly on the undersides of leaves of the foodplant. Incubation required at 16°C, 12.5 days, at 19°C, 9.5 days. Oviposition in the field probably occurs from about 3rd June until 9th July.

### Larvae

Possess paired hatching spines on the meso and metathorax and 1st abdominal segment. Hatching probably occurs about 13th June and fully grown 4th instar larvae have been seen as late as 23rd October feeding on Mentha. According to Van Emden (1951) larvae hibernate in the 4th instar which lasts 5-8 months, emerge the following mid April feed for 8-10 days and then pupate. Pupae were noticed on 2nd and 6th June in the field and it is probable that new generation adults emerge about 21st May. Old generation adults may survive the Winter and may survive several years living through 2 or even 3 mating periods. This explains their being seen as early as 24th April in the field. Adults have been seen as late as 18th October on the foodplants, after which they go into hibernation.

Chrysolina graminis (L.) Plate B4 Fig. 22.

Foodplants:    Compositae    Tanacetum vulgare L.

                 Labiatae        Mentha aquatica L.

### Ova

Creamy white, elongate, oval, with the chorion bearing distinct hexagonal microsculpturing. Laid in groups of 5-6 and are usually attached by their slightly flattened posterior extremity. Incubation

required about 7-8 days (Paterson, 1931). Oviposition possibly commences about mid-May as first instar larvae were collected at York at the beginning of June. Adults collected at Wicken Fen early in July oviposited in the laboratory and thus the oviposition period in the field is about 7-8 weeks.

### Larvae

Hatching commences at the beginning of June, fully grown 4th instar larvae occurring at the end of June. Larvae are probably present in the field up to the end of July. Paterson (1931) quotes the duration in days of each instar from 1st-4th as 12, 7, 7, 18 respectively, the prepupal stage 9-14 days and the pupal stage 10-11 days,

giving a total development time of about 65 days.

### Adults

New generation adults probably emerge in the field the final week in July until about the end of August. They go into hibernation in September and thus there is only one generation/year.

### GENUS Phytodecta

P. pallida (L.) Plate B5 Fig. 29.

<u>Foodplants:</u>	Corylaceae	<u>Corylus avellana</u> L.
	Salicaceae	<u>Salix lapponum</u> L.
	Rosaceae	<u>Sorbus aucuparia</u> L.

### Larvae

The adults are ovo-viviparous producing fully developed first instar larvae, rather than eggs. Larval deposition occurs from about 21st May until 18th June i.e. is of about 4 weeks duration. Each adult bears larvae for about 10 days, depositing one or two larvae on the under surface of each leaf. There are 4 larval instars and the duration of each at 20°C was 2, 4, 9 and 5 days respectively, the prepupal and pupal periods lasted 7 days each. The total development time from larval deposition to adult emergence was about 34 days at 20°C and about 23 days at 25°C. Fully developed larvae were found in the field as early as 17th June and it is probable they are present until the end of June. Pupae are probably present from about the end of June.

### Adults

The new generation adults probably emerge towards the end of July, feed until about mid August and go into hibernation at the end of this month. Re-appearance of adults occurs about the beginning of May the following year and these feed in the field until about 22nd June. They then stop feeding, enter the ground and diapause. The old generation adults may survive hibernation for a second time and bear larvae again the following year.

Phytodecta olivacea (Forst.) Plate B5 Fig. 28.

Foodplants: Papilionaceae Sarothamnus scoparius (L.) Wimm. ex Koch

### Ova

This is a potentially ovo-viviparous species. This involves the retention of eggs until the larvae are fully developed and the hatching of the larvae almost immediately after oviposition. Well developed embryos within the chorion were rarely seen in the ovarioles. However, normally the eggs took about 5 days to hatch at 19°C. The white ova are usually laid singly on the leaves and stems of the foodplant. Oviposition probably commences about mid May but it is arguable how long this continues. Waloff & Richards (1958) stated that oviposition occurs until early July, whereas Donia (1958) indicates that this continues until the end of August. Adults and all instars of larvae were collected near Monmouth 9th August. The adults continued oviposition in the laboratory until mid August. Thus it appears that the oviposition period continues until mid August.

### Larvae

Hatching probably occurs about 20th May and the larvae pass through 4 instars and are fully grown in about 1 month. Pupae probably occur towards the end of June. Larvae occur in the field until the end of August and thus pupae occur until mid September. There are 4 larval instars.

### Adults

The new generation adults emerge from about mid July until mid September feeding for about 2 weeks and then without maturing re-enter the litter. The adults are re-entering the litter from the end of July until the end of September. However, according to Waloff & Richards (1958) the old generation adults also re-enter the litter after oviposition in early July whereas Donia (1958) states that this does not occur until August or September. Thus adults are entering diapause over a very extended period from July until October. High temperature fails to prevent diapause and long

day treatment prevents it only in a minority of individuals. According to Donia (1958) the true diapause apparently lasts until January or February when it is usually followed by a period of quiescence (hibernation). The population of adults which re-appear towards the end of April consists of a few old generation adults and majority of new generation beetles. Soon after leaving the litter, a small percentage of the beetles make a dispersal flight (Waloff & Richards, 1958). P. olivacea is a long lived species which often lives for two years and lays eggs continuously in two seasons separated by a period during which oviposition ceases.

Phytodecta viminalis (L.) & Phytodecta rufipes (DeG.) Plate B5 Fig. 30.

Foodplants: Salicaceae     Salix capreae

Populus tremulae

These are both viviparous species bearing fully developed first instar larvae. Larval deposition probably commences at the beginning of May and continues for about one month. The larvae feed upon the foliage of Salix and Populus sp. becoming fully developed from 21st May until 21st June. Pupation occurs in the soil from the end of May until the end of June.

#### Adults

New generation adults probably emerge from mid June until mid July and feed into August. There is one generation/year and it is probable that adults of old and new generations enter the ground to diapause from July to August, hibernating until the following Spring.

GENUS Phaedon

P. tumidulus (Germ.) Plate B6 Fig. 31.

Foodplants: Umbelliferae Anthriscus sylvestris (L.) Hoffm.

Heracleum sphondylium L.

Aegopodium podagraria L.

Ova

Yellow, elongate, oval. Laid in one's and two's on the undersides of leaves of the foodplant. Oviposition at Close House occurs from about mid May until the end of June. Incubation required 8-9 days at 19°C.

Larvae

Possess paired hatching spines on the meso and metathorax. Hatching occurs about 21st May until about 7th July. Fully grown (Fig.96) 3rd instar larvae occur at Close House as early as 3rd June and these enter the soil about 7th June. The larvae feed in groups, many larvae being present on the under surface of one leaf. The later larvae are fully grown by 29th August. Pupae probably occur from about mid June until mid September.

Adults

New generation adults emerge at Close House from about 22nd July until mid September, feed up and go into hibernation in the soil or grass tussocks as late as the 25th October. At Close House the old generation adults disappeared by about the beginning of July and thus there is no mixing of old and new generations. The adults re-appear in the Spring as early as 27th March.

Phaedon cochleariae (F.) Plate B6 Fig. 33.

Foodplants: Cruciferae Rorippa nasturtium-aquaticum (L.) Hayek.

Sisymbrium allaria (L.) Scop.

Cochlearia officinalis L.

### Ova

Bright yellow, elongate oval, chorion colourless,  $\times$  length 1.39mm  $\times$  width 0.52mm ( $n = 6$ ). Laid singly within small cavities eaten by females in the lower epidermis of leaves of the foodplant. Oviposition probably occurs from about the beginning of June until the beginning of August.

### Larvae, Pupae & Adults

Hatching probably occurs in mid June and continues until about 10th August. Larvae are thus present in the field from mid June until the end of August. Pupae probably occur from mid July until mid September, giving rise to new generation adults by the end of July. It is unlikely that first instar larvae collected in the field on 7th August resulted from ova laid by this new generation. Thus it is probable that there is one generation/year and that adults of the new generation overwinter, going into hibernation as late as 25th October. It is doubtful if old generation adults overwinter a second time. Adults re-appear in the field as early as 24th March. Hamnett (1944) reported that the beetle has 3 generations a year. Under field conditions, Roebuck (1927) and Smith (1951) described 2 overlapping generations a year. However, it is not clear from their descriptions whether the females of the first generation die after laying or hibernate along with the second generation. According to Roebuck (1927) females of the first generation emerge between the 15th June and 30th July, while those of the second generation emerge between the 27th July and 10th September, hibernate and come out again in the Spring for oviposition in May and June. Balachowsky & Mesnil (1936) stated that this species has 2 overlapping generations a year, the females of the 2nd generation hibernating in the immature state and laying in the next Spring. According to the latter authors a 3rd generation may be produced in warmer climates. Thus under field conditions the females of the first generation lay eggs in one season,



at the end of which they either die or possibly hibernate with the second generation females. Donia (1958) showed that females died after oviposition and there were a large number of generations/year at 24°C and 16 hr. day illumination.

Phaedon armoraciae (L.) Plate B6 Fig. 32.

Foodplants: Scrophulariaceae Veronica beccabunga L.

V. scutellata L.

Ceratophyllaceae Ceratophyllum demersum L.

Rorippa nasturtium-aquaticum (L.) Hayek.

Boraginaceae Myosotis repens auct.

### Ova

Yellow, elongate oval, laid singly in small cavities eaten by the females in the stems (internodes) leaf bases and mostly near the apex of the shoot of Veronica beccabunga. Eggs sometimes covered with thin brown layer in depression. Oviposition in the field probably occurs from about mid May until mid July.  $\bar{x}$  length 0.984mm,  $\bar{x}$  width 0.49mm (n = 9). Incubation required 7-8 days at 19°C.

### Larvae

Hatching of larvae occurs about the end of May and fully grown third instar larvae have been seen in the field on the 30th June. The last larvae are seen in the field from the middle to the end of August. Pupae probably occur about the 7th July until mid September.

### Adults

New generation adults emerge in the field from the end of July until the end of September and may occur until the beginning of December after which they hibernate. There is one generation/year and the adults have been overwintered at 5°C. Re-appearance of adults in the field occurs about 12th April.

GENUS PhyllodectaP. vitellinae (L.) Plate B6 Fig. 34.Foodplants: Salicaceae SalixPopulus tremulaeOva

White or cream, elongate oval, laid in batches on the under surface of leaves,  $\bar{x}$  length 1.04mm,  $\bar{x}$  width 0.44mm (n = 20). Duration of oviposition from the beginning of May until about 12th August i.e. 10-11 weeks.

Larvae

Hatching probably occurs about 10th May and fully grown third instar larvae have been seen during this month until the beginning of September. Pupae probably occur from about 7th June until mid September.

Adults

New generation adults probably emerge at the end of July up to the end of September. There is one generation/year and the adults go into hibernation in October. Overwintering probably occurs under bark etc. The adults re-appearing the following year about mid April.

P. laticollis Suf. Plate B6 Fig. 35.Foodplants: Salicaceae Populus tremulaeOva

White, elongate oval, laid in batches on the underside of leaves of Populus. Oviposition in the field probably commences about mid May and may continue until September as 2 fully developed larvae were seen in the field on 29th November.

Larvae

Hatching probably occurs at the end of May until the beginning of July and fully developed third instar larvae occur from mid June until the end of July. Pupation probably occurs towards the end of

June and pupae may be present until mid August.

### Adults

New generation adults emerge from about mid July until the end of August. The old generation adults probably die during July. The new adults may oviposit, as final instar larvae have been seen in the field at the end of November. It is probable that the new generation adults go into hibernation during October and re-appear at the beginning of April the following year.

P. vulgatissima (L.) Plate B6 Fig. 36

Foodplants Salicaceae Salix

### Ova

White or cream, elongate oval,  $\bar{x}$  length 0.99mm,  $\bar{x}$  width 0.46mm ( $n = 40$ ). Laid in batches of 6 ova on the undersides of leaves of Salix but ova usually not in regular batches but up to 11 ova may be laid in close proximity to each other. Probably a similar cycle to P. cavifrons. The new generation adults may oviposit the year of emergence from the pupae to produce a second generation, as first to final instar larvae were seen in the field on 23rd August. However, it may be that the old adults have a very long oviposition period. New generation adults probably emerge at the end of July and larvae are present in the field until mid September.

## GENUS Gastroidea

G. polygoni (L.) Plate B7 Fig. 42.

Foodplants: Polygonaceae Polygonum aviculare L.

### Ova

Yellow, elongate oval, laid in batches on the leaves and stems of the foodplant. At Close House oviposition takes place in the field from about mid-May until the end of August. Incubation required 5-7 days at 19°C.

Larvae

Hatching occurred from 20th May until 4th September and fully grown third instar larvae were present from 11th June until 21st September. Pupae probably occur from about 7th June until 7th October.

Adults

New generation adults emerge about the end of June and continually up to mid or late October. The old generation adults may have a very long oviposition period or the new generation adults may oviposit and give rise to a second generation the year of emergence from the pupa. There may be 1 or 2 generations/year, the adults overwintering and re-appearing in early April the following year.

G. viridula (DeG.) Plate B7 Fig. 41.

Foodplants: Polygonaceae Rumex obtusifolius L.

Ova

Yellow, elongate oval, laid in batches on the undersurface of Rumex leaves. Oviposition occurs at the end of April until about 7th August.

Larvae

Feed in large numbers on the undersides of the leaves. Hatching occurs from the beginning of May until mid August and fully grown third instar larvae are present in the field from about 21st May until the beginning of September. Pupation occurs from the end of May until mid September. The larval duration including the feeding period and prepupal period is 23 days at 16°C and the pupal duration 9 days at 16°C.

Adults

New generation adults probably emerge in mid June continually up to the end of September. The number of generation/year in the field is uncertain but probably there is at least 2 and the old generation adults may have a long oviposition period of 3½ months.

4-5 generations were reared at 19°C from May until late October. Adults go into hibernation in October re-appearing about 7th April the following year.

#### GENUS Hydrothassa

H. marginella (L.) Plate B7 Fig. 37.

Foodplants: Ranunculaceae      Ranunculus repens L.

Ranunculus acris L.

#### Ova

Yellow, elongate oval, chorion colourless, smooth.  $\bar{x}$  length 1.09mm,  $\bar{x}$  width 0.40mm (n = 22). Laid singly or in groups of 1-3 within petioles of the younger leaves. Incubation period 13 days at 20°C, 7-8 days at 25°C. Oviposition occurring in the field from about mid May until the end of June.

#### Larvae

Feeding in groups on the underside of Ranunculus leaves. Hatching occurring in the field from the end of May until about mid July. There are three instars and larvae are fully grown in 14 days at 20°C. Fully grown larvae occurring in the field from mid June until the beginning of August. Pupation occurring from about 21st June until mid August. The pupal period is 7-8 days at 20°C.

#### Adults

New generation adults emerging from the beginning of July until mid August. It is probable that there is a second generation in the field and 2 generations were cultured in the laboratory. Adults go into hibernation during October, re-appearing about 13th April the following year.

H. aucta (F.) Plate B7 Fig. 38.

Foodplants: Ranunculaceae      Ranunculus repens

Biology similar to H. marginella (L.)

GENUS Prasocuris

P. junci (Brahm.) Plate B7 Fig. 40.

Foodplants: Scrophulariaceae Veronica beccabunga L.

Gramineae Catabrosa aquatica (L.) Beauv.

Ova

Laid within holes eaten by the female in the stem and leaves of the foodplant. Oviposition probably occurring from mid May until about 21st July. Incubation of about 10 days at 20°C.

Larvae

Hatching in the field from 27th May until the beginning of August. Fully grown third instar larvae occurring from 8th June until mid-August and pupae probably from 14th June to the first week in September.

Adults

New generation adults emerge from about 21st June up to mid-September. There is probably one generation/year and the adults overwinter emerging the following year as early as 2nd April.

Prasocuris phellandrii (L.) Plate B7 Fig. 39

Foodplants: Umbelliferae Oenanthe aquatica (L.) Poir.

Biology probably similar to P. junci there being one generation/year and the adults overwintering. Fully grown larvae and pupae have been seen in the field on 8th July. Adults occur in the field from 12th April until 17th September. Larvae feeding inside the stems and pupation occurring in the stems of the foodplants.

GENUS Plagiodera

P. versicolora (Laich.) Plate B8 Fig. 45.

Foodplants: Salicaceae Salix fragilis L.

Ova

Pale yellow, about 1.7mm long and 0.7mm wide, slightly broader at the base which is attached to the leaf. The eggs are laid upright

in irregular masses containing from 2-30, usually 8-15 ova.

Oviposition occurs on either face of the leaf with the majority on the lower surface. Oviposition probably commences in mid May and continues until the end of July. Incubation period about 10 days.

### Larvae

These skeletonize the foliage and are usually found in groups or rows moving across the surface of the leaf as they feed. Hatching occurring from about the end of May until the first week in August. There are three instars and fully developed larvae are present about 21st June until mid August. Pupae probably occur on the leaves from the end of June until the end of August.

### Adults

New generation adults start emerging about mid July to mid September. The old generation adults may survive until about 10th August. In England there is probably only one generation/year and winter is passed as adults under the bark of the willows, in debris and tufts of grass at the base of the trees. They re-appear at the end of April the following year. According to Hood (1940) this species has 3 generations and possibly a partial 4th generation at Melrose Highlands, Massachusetts.

## GENUS Chrysomela

C. populi L. Plate B8 Fig. 43.

Foodplants: Salicaceae Salix repens L.

Salix atrocinerea Brot.

Populus tremulae L.

Populus canescens (Alt.) Sm.

### Ova

Creamy white to deep yellowish brown, rounded at the end, chorion smooth  $\bar{x}$  length 1.957mm,  $\bar{x}$  width 0.844mm (n = 10). They are laid on the under surface of the leaves in groups of about 20. Oviposition

probably from 7th May until 7th July. Incubation required 8-9 days at 19°C.

### Larvae

Hatching commencing about 17th May, continuing until about 20th July. There are 3 instars and larvae may be fully grown by 7th June. Later larvae become fully developed by mid August. Pupation probably occurs about mid June and pupae may occur until the end of August.

### Adults

New generation adults emerge at the end of June continuing until mid September. There is one generation/year, the adults overwintering and re-appearing towards the end of April the following year. However Loi (1970) described three generations/year in Toscana, Italy.

C. tremulae. Biology studied by Bromley (1947) at Oxford.

Foodplants: Salicaceae - as C. populi

### Ova

Dirty white after laying, changing through light brown to reddish purple before hatching. Cylindrical, length 1.25mm, width 0.75mm, ends rounded. Loosely attached to the underside of leaves in groups of about 25. Biology otherwise similar to C. populi (Bromley 1947).

C. aenea L. Plate B8 Fig. 44

Foodplants: Betulaceae Alnus glutinosa (L.) Gaertn.

Biology probably similar to other Chrysomela sp.



SUBFAMILY LAMPROSOMATINAE

GENUS Lamprosoma

L. concolor (Stm.) Plate B3 Fig. 46

Little is known concerning the biology of this species. Adults have been collected from 29th May, through June, none in July but again in August and September. They have been taken in water nets in October, November and December. The adults probably overwinter, re-appearing in May and ovipositing during June. Larvae probably occur from mid June through July and new generation adults possibly emerge in August.

Several authors have indicated that the mature larva of Lamprosoma is the overwintering stage. Monros (1949) showed that L. chorisiae hibernates over 6 months as the fully grown larva, pupating at the end of September and the new generation adults emerge at the end of October. Kolbe (1897) demonstrated that in L. concolor hibernation is also undertaken in the larval stage. The adult fed upon the leaves of Astrantia and Aegopodium (Umbelliferae), whereas the larva was polyphagous and fed nocturnally on the stem and leaves of different plants on the ground, usually preferring the petioles. This work was substantiated by the observations of Kasap and Crowson (1976) who collected a fully grown larva of Oomorplus concolor (Sturm) from Hedera at Morroch Bay, Scotland on 11th September 1974. The larva fed nocturnally on the fresh green stems of Hedera helix L. (Araliaceae).

SUBFAMILY GALERUCINAEGENUS GalerucellaG. viburni (Pk.) Plate B9 Fig. 52Foodplants: CaprifoliaceaeViburnum sp. including V. opulus, V. lantana and  
V. tinus.Ova The biology is described by Zorin (1931)  
(Zorin 1931)

The eggs are spherical opaque white with the chorion finely reticulate. They are laid at the extremities of stems of small diameter on different Viburnum sp. The females hollow out small dimples 1mm x 1mm on the lower surface of the stems and introduce a single egg into each depression. The egg is then covered by excrement and mucous which solidify in the air. The oviposition period extends from about mid July until about the end of September or into October. The egg is the overwintering stage and it is very probably diapausing as otherwise it would hatch normally under the Summer temperatures to which it is exposed.

Larvae

Although first instar larvae were not studied it is very probable that hatching spines are absent as in all other Galerucinae and the larvae hatch using their mandibles to bite their way out. Hatching occurs from about the beginning of May when the first leaves are appearing until about 7th June. The larvae become widely dispersed on the foodplant and eat numerous perforations in the leaves. The size of the perforations varies according to the larval instar and often the leaves may be reduced to the principal veins.

<sup>(1931)</sup>  
Zorin describes the 5th stadia larva but this is unusual as all other Galerucinae studied have 2 moults and 3 instars. The duration of larval life varies from 25-35 days according to the climate. In England final instar larvae have been collected as early as 25th May and as late as 7th July. When fully grown the larvae drop to the

ground and penetrate to 3-5cms depth. Pupation occurs within an earthen cocoon which is rough externally but smooth on the internal face. The pupal stage lasts about 10 days and adults of the new generation appear from the 30th June. The period from hatching to adult emergence is about 8-10 weeks.

### Adults

The damage caused by the adults is often more important than that of the larvae. They feed upon the stem and leaves, eating the foliar parenchyma between the veins and making a multitude of irregular holes in the leaves. The adults pair about 3-4 days after emergence. In England adults have been collected from 30th June until 29th October.

G. sagittariae Brit.Cat. Plate B10 Fig. 53.

<u>Foodplants:</u>	Alismataceae	<u>Sagittaria</u>
	Polygonaceae	<u>Polygonum amphibium</u> L.
		<u>Rumex crispus</u> L. etc.
		<u>R. hydrolapathum</u> Huds.

### Ova

Colour pale yellow, slightly orange. Subcircular of about 0.75mm diameter and with the chorion finely reticulate. Ova laid in batches of 7-25 ova on the upper and lower surfaces of leaves of the foodplant. They are laid adjacent to one another in 2, 3 or 4 rows. In England eggs are found as early as 5th May (28th May at Close House) and as late as the end of July. The oviposition period extends over 3 months during which time the same female may lay many batches.

### Larvae

Hatching spines are absent and the first instar larvae bite their way out usually through the dorsal face. Hatching at Close House occurred as early as 18th June and fully grown third instar larvae

were seen as late as 20th September. Pupation occurred from 16th July until about the end of September, and thus larval development at Close House required 4 weeks. When fully grown the larvae attach themselves to the underside of the leaves by the final abdominal segment, there may be up to 4 larvae per leaf. Following the larval-pupal moult the pupa becomes attached to the cast larval skin by paired crotchets on the ventral surface of abdominal segments 8 and 9.

### Adults

Adults of the new generation emerged from pupae at Close House from 30th July following the disappearance of the majority of the old generation adults. Thus the duration of the pupal period at Close House is about 2 weeks and the period egg to adult is 2 months. Emergence of the new generation occurs until about the beginning of October, none of the new adults developing ova but going into hibernation with undeveloped ovaries. At Close House there is only 1 generation/year.

Galerucella tenella (L.) Plate B10 Fig. 54.

Foodplants: Rosaceae Filipendula ulmaria (L.) Maxim.,

F. vulgaris Moench.

Geum rivale L.

G. urbanum L.

Potentilla anserina L.

Fragaria sp.

Ova Biology studied by Petrov (1925)

The eggs are slightly oval 0.5 x 0.4mm., the chorion reticulated and of a rose salmon colour. They are laid singly or in small batches of up to 18 eggs on the 2 faces of leaves of the foodplant, the petiole and even on the veins. In England the first eggs are seen about 22nd May and hatch in 6-9 days at 19°C.

### Larvae

Hatching spines are absent and the first instar larvae bite their way out, usually through the dorsal face. The larvae feed on the underside of the leaves, removing the lower epidermis and parenchyma but leaving the veins and upper epidermis intact. The first larvae are seen about the 7th June and the larvae become fully developed in 3-4 weeks, during which there are 3 instars. Pupation occurs in an earthen cell at a shallow depth. From the laying of eggs to the emergence of the new generation occupies about 63 days. The last date that final instar larvae were found was on the 9th August.

### Adults

Adults of the new generation emerge at the beginning of August and feed until the beginning of September. They then move into their hibernation sites under dry leaves. Re-appearance of the adults occurs as early as 21st April, start oviposition at the end of May and die towards the end of June. The oviposition period is about 1 month. It is probable that there is only one generation/year.

Galerucella lineola (F.) Plate B10 Fig. 55.

<u>Foodplants:</u>	Betulaceae	<u>Alnus glutinosa</u> (L.) Gaertn.
	Corylaceae	<u>Corylus avellana</u> L.

### Ova

The eggs which are globular, white with a dark spot on the upper surface are laid in small batches on the underside of the leaves. Oviposition in the field commences at the beginning of June and continues until the end of July.

### Larvae

Hatching spines are absent and the first instar larvae bite their way out, usually through the dorsal face. The larvae feed on the lower epidermis of the leaves. First instar larvae are found in the field the first week in June and from the later eggs at the beginning

of August. The larvae are fully developed after 3-4 weeks and 3 instars were found in the field at the end of June. Final instar larvae were also seen 9th August. Pupation occurs within an earthen cell and the new generation adults emerge about 17th August.

### Adults

New generation adults emerge about 17th August and feed until the end of September. They then move into their overwintering sites. There is probably only one generation/year. Re-appearance of the adults in the Spring commences from about 12th April.

### GENUS Lochmaea

L. crataegi (Forst.) Plate B10 Fig. 56.

Foodplants: Rosaceae Crataegus monogyna Jacq.

### Ova

The eggs are laid singly on the leaves and flowers of hawthorn towards the end of May.

### Larvae

Hatching spines are absent and thus the larvae bite their way through the chorion. First instar larvae were collected in the field on the 3rd June and final instars on the 4th August. The larvae mine the pith of the fruits and when fully grown escape via the point of attachment of the flower parts. The larvae either make their entry into the fruit via this point or may bore directly through the wall of the ovary. This can be deduced as fruits containing larvae had holes whereas others in which larvae had been feeding sometimes did not. The presence of larvae in the fruit can be detected externally because the pericarp of the fruits which is normally green or red becomes partly and finally completely brown and soft. No seed develops in infected fruit. Larval duration is approximately 2 months and when fully grown the larvae drop to the ground. Pupation occurs within an earthen cell.

### Adults

Adults of the new generation emerge about mid August and feed upon the leaves of the foodplant until September. It is possible that the adults overwinter and there is one generation/year. Re-appearance of adults in the Spring commences from about 16th April and these survive until mid June. The oviposition period probably extends from mid May until mid June.

L. capreae (L.) Plate B10 Fig. 57.

Foodplants: Salicaceae Salix cinerea subsp. atrocinerea  
(Brot.) Silva & Sobrinho

### Ova

The eggs are small, yellow, spherical measuring about 0.6mm diameter. They are laid singly, in two's or three's on the under-surface of the leaves. The incubation period is about 14 days.

### Larvae

Hatching spines absent and the larvae use their mandibles to cut through the chorion. Oviposition commences at the beginning of June and continues until the end of July. First instar larvae were collected in the field 28th July, 5th September. Second instar larvae 28th July, 13th and 23rd August, 5th September, third or final instars 28th July, 3rd, 13th and 23rd August and 5th September. When fully grown the larvae penetrate into the ground and pupate within an earthen cell.

### Adults

New generation adults emerge about mid August and it is likely that all instars of larvae collected in the field 5th September resulted from eggs laid by these new adults. However, new generation adults reared from larvae collected 28th July did not produce a further generation in the laboratory. Adults feed on the foliage until 26th September after which they move into their overwintering sites. It is probable there is one generation/year. The adults emerge from hibernation about mid-April.

L. suturalis (Th.) Plate B10 Fig. 58.Foodplants: Ericaceae Calluna vulgaris (L.) Hull.EricaOva

Spherical, yellow brown, chorion with distinct circular irregular microsculpturing  $\bar{x}$  length 0.94mm,  $\bar{x}$  width 0.82mm. (n = 15). Laid on the stems and leaves of the foodplant in ones, two's or three's. Oviposition commences about 12th May and continues until about 15th July. Incubation required 10-11 days at 20°C.

Larvae

Hatching spines absent, the larvae biting through the chorion with their mandibles. Hatching occurs from about 14th June and the larvae feed upon the foliage and stems of the foodplants. Final instar larvae occur as early as 20th July up to the end of August. Full development of the larvae required 4-5 weeks, pupation occurring within earthen cells.

Adults

New generation adults emerge about the 7th August and do not oviposit. They feed upon the foliage and have been found in the field as late as 13th November. There is probably only one generation/year. The adults overwinter and re-appear as early as 26th March the following year.

GENUS GalerucaGaleruca tanacetii (L.) Plate B9 Fig. 48.Foodplants: Compositae Tanacetum vulgare L.Achillea millefolium L.Centaurea nigraCaryophyllaceae Stellaria graminea L.CerastiumLabiatae Thymus serpyllum L.Dipsaceae Scabiosa succisa L.



Cruciferae     Cardamine pratensis L.

Sinapis arvensis L.

### Ova

The eggs are laid from about mid-September until the end of November. Approximately 70 orange ova are laid within large oothecae about 8mm long deposited on grass and dessicated flower stems. The oothecae are soft and yellowish orange at deposition but quickly become hard and dark brown. Thus, this species overwinters as diapausing eggs on vegetation which remains standing during the Winter. It is assumed that the eggs diapause at a very early embryonic stage as eggs collected in December on dissection showed no development.

### Larvae

Hatching of the eggs occurs at the end of April or beginning of May and the larvae are fully grown by the end of May. Pupation occurs within an earthen cell formed from silken threads and soil particles. Pupation may occur at the end of May and new generation adults emerge as early as 12th June in England. The pupation period is about 11 days.

### Adults

Prevett (1953) considered the possibility of a second generation as 3 months elapse between emergence of the new generation adults and oviposition. Siew and Donia (1958) showed that the adults aestivate within grass tussocks during June, July and August. Galeruca is a short day insect and aestivation is reduced by photoperiods longer than 14 hours operating during the adult life. The effect is modified by temperature, the critical photoperiod being shorter at high temperatures i.e. the effects of long days are reinforced by high temperature. <sup>(Siew 1966)</sup> Donia (1958) divided the reproductive cycle of Galeruca into the following stages. The adults before aestivation feed for about 8-16 days, (June 7th-June 23rd).

- (1) The pre-maturation period lasting 56-80 days (June 23rd-21st August)

The females remain immature and are very rarely seen feeding.

- (ii) The maturation period lasting about 28 days (21st August - 21st September). Sexually mature females characterised by distended abdomens appear in the field, feeding and copulating.
- (iii) The oviposition period lasting about 28 days after which the females die. It is possible that some adults may survive the winter as they have been collected in April and May.

Adult aestivation during hot dry summers occurs in several beetles but it is curious to find this situation in an insect of a temperate country where the Spring and Summer are the seasons normally favoured for breeding. It is rendered possible because there is an egg diapause, Galeruca being unusual in having 2 periods of arrested development in the life cycle.

#### GENUS Agelastica

Agelastica alni (L.) Plate B9 Fig. 47.

Foodplants: Betulaceae Alder - Alnus glutinosa (L.) Gaertn.  
Corylaceae Hazel - Corylus avellana L.

#### Ova

The bright yellow eggs are laid in batches fixed vertically on the veins of the leaves. Oviposition occurs from about mid May until the end of June, the abdomens of the females during this period becoming distended.

#### Larvae

Hatching occurs at the end of May the larvae feeding on the lower epidermis and parenchyma but leaving the principal, secondary veins and upper epidermis intact. The foliage becomes skeletonised and russet red. The larva becomes fully developed in about 20-28 days, drops to the ground and pupates at a shallow depth.

### Adults

New generation adults emerge about the beginning of July into August. The adults feed little making irregular holes in the leaves and disappear at the beginning or mid-Summer. Oglobin (1936) states that A.alni may have a second generation if conditions are favourable and then the second generation adults hibernate. According to Beaumont (1944) this species is univoltine in the Northern hemisphere there being a very long obligatory adult diapause or Summer aestivation from July or August, followed by Winter hibernation from August to April. The adults re-appear in April and feed upon the young Alder shoots and leaves for about 10-20 days, later maturing and ovipositing.

### GENUS Phyllobrotica

Phyllobrotica quadrimaculata (L.) Plate B9 Fig. 50.

Foodplants: Labiatae      Scutellaria galericulata

### Ova

Laid singly or in groups of up to 10 on the leaves and stems of the foodplant, but also in soil. They are hemispherical, orange-yellow, chorion with very distinct sculpturing. The incubation period at 25°C was 26 days, at 19°C 32 days. The majority of ova kept at 19°C and darkness and 19°C and a 16 hour day hatched normally. However, one batch of 25 ova laid 16-20th August 1973 at 19°C and 16 hour day failed to hatch after 60 days. They were cold treated at 2°C for 4 months and then returned to 19°C. An 88% hatch (88% fertility) occurred between 3rd-16th April 1974. This suggests that in the field eggs may hatch the year of laying or a percentage may diapause at an early embryonic stage, pass the winter and hatch the following Spring. Oviposition in the laboratory occurred between 5th August and 11th September but it is likely that oviposition may occur from July in the field.

### Larvae

Hatching spines are absent, the larvae emerge by eating a small

hole in the chorion. Duration of the first instar at 16°C, 19°C and 25°C was 20, 14-15 and 13 days respectively. Larvae died at 30°C. Duration of the second instar at 19°C was 16-20 days. Third instar larvae reared at 19°C and 16 hour day, stopped feeding, moved into the earth, became inactive but did not pupate. They moved into the soil 10th October but had not pupated by 7th December. It was assumed they were diapausing and were placed under external conditions. 2 from 4 larvae survived the Winter and commenced feeding in May 1975. The fully fed larvae entered the soil but failed to pupate. It is probable in the field larvae diapause in the 3rd instar.

#### Adults

Adults have been collected in the field from 21st June - 20th September. The new generation adults emerge before 21st June.

#### GENUS Sermyla

Sermyla halensis (L.) Plate B9 Fig. 49.

Foodplants: Rubiaceae Galium mollugo L.

Galium aparine L.

#### Ova (Plate PPI Fig. 4)

Laid in batches of 9-29 ova at the roots of the foodplants from about 27th July - 7th November. They are oval, yellow, chorion with distinct sculpturing, length 1.25mm, width 1.00mm. The long and extremely variable developmental period of the eggs both in the outdoor insectary and at a constant temperature of 19°C suggests the presence of a diapause. Hatching of the eggs under various temperature regimes are shown in Table 21<sup>8</sup> Figs. 99&100. The shortest time before termination of diapause was 88 days at 10°C. It is probable that a low temperature is necessary during the diapause phase. The post diapause phase or development to hatching takes a minimum of 9-10 days at 19°C or 15 days at 16°C. The diapause phase is passed by at least the beginning of December in the field as eggs collected

TABLE 16 THE PUPATION OF *T. tenebricosa* (F) UNDER INSECTARY CONDITIONS a.1973 b.1974

	ENTERED SOIL	DATE OF PUPATION	PRE-PUPAL PERIOD	ADULTS IN CELLS	PUPAL PERIOD	ADULTS ABOVE SOIL
CELL 1	9-16.5.73	6-11.6.73	21-33 DAYS	29.6-2.7.73	23-27 DAYS	6-9.7.73
CELL 2	30.5-5.6.73	24-25.6.73	25-32 DAYS	13-16.7.73	19-22 DAYS	20-23.7.73
CELL 3	6-11.6.73	29.6-2.7.73	20-27 DAYS	20-23.7.73	21-24 DAYS	30.7.73
CELL 4	13-19.6.73	10-11.7.73	21-28 DAYS	25-27.7.73	15-17 DAYS	3.8.73
		15-22.7.74				14.8-39.74.

a.

b.

a.	Number adults emerging	Date
	1	6-9.7.73
	2	10-11.7.73
	1	11-13.7.73
	2	13-16.7.73
	2	20-23.7.73
	1	30.7.73
	1	30-31.7.73
	1	3.8.73
	11	69.7-3.8.73

Sex ratio 5♂ : 6♀

b.	Number adults emerging	Date
	10	14.8-3.9.74
	1	3-13.9.74

Sex ratio 5♂ : 8♀

TABLE 21 TO SHOW THE EFFECT OF VARIOUS TEMPERATURES ON THE HATCHING OF *S.halensis* OVA

DAYS TEMPERATURE	AT EACH TEMPERATURE °C	̄ DAYS TO HATCH	NUMBER OF BATCHES
2°	5° 19°		
29	31 23	83	1
2°	10° 5° 19°		
30	31 38 12	111	1

10°	19° 16°		
88	14 —	102	1
85	— 24	109	1
19°	8° 19°		
41	42 26	109	1

DAYS AT EACH TEMPERATURE °C	̄ DAYS TO HATCH	NUMBER OF BATCHES
AT 16°C CONSTANTLY	131	2
AT 19°C CONSTANTLY	109	15
AT 25°C CONSTANTLY	NO HATCH AND NO DEVELOPMENT	2

DAYS AT EACH TEMPERATURE °C	̄ DAYS TO HATCH	NUMBER OF BATCHES
15° 2° 16°		
7 63 37	107	1
21 42 72	135	2
21 49 48	118	3
21 56 43	120	4
21 63 41	125	1
44 42 20	106	1

FIG 99 TO SHOW THE EFFECT OF VARYING DAYS PRETREATMENT AT 19°C FOLLOWED BY VARYING PERIODS OF COLD TREATMENT AT 2°C ON THE DAYS TO HATCH AFTER LAYING OF *Sermyla halensis* OVA

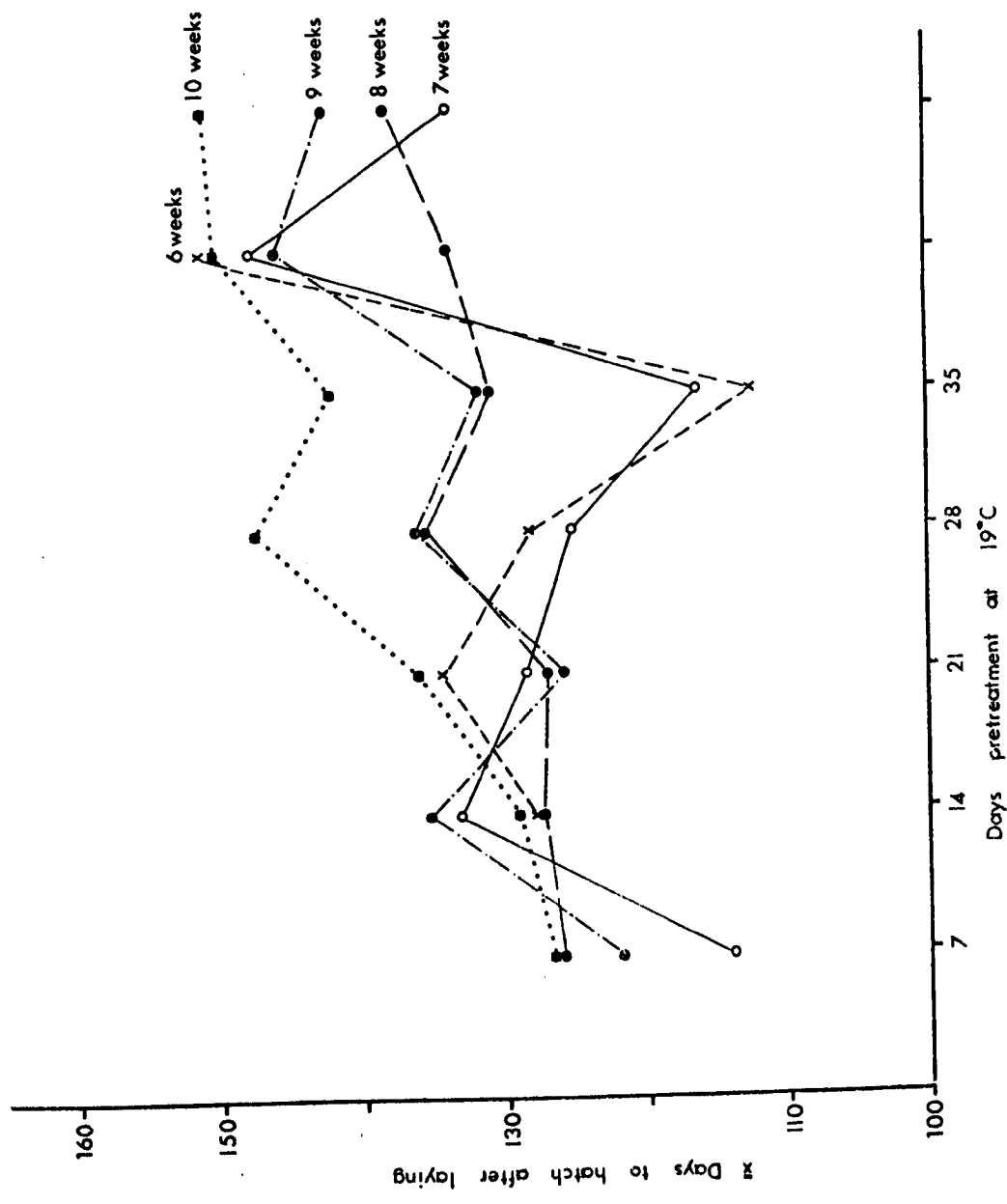


FIG 100. TO SHOW THE EFFECT OF VARYING DAYS PRETREATMENT AT 19°C FOLLOWED BY VARYING PERIODS OF COLD TREATMENT AT 2°C ON THE  $\bar{x}$  DAYS TO HATCH AFTER COLD TREATMENT OF *Sermyla halensis* OVA

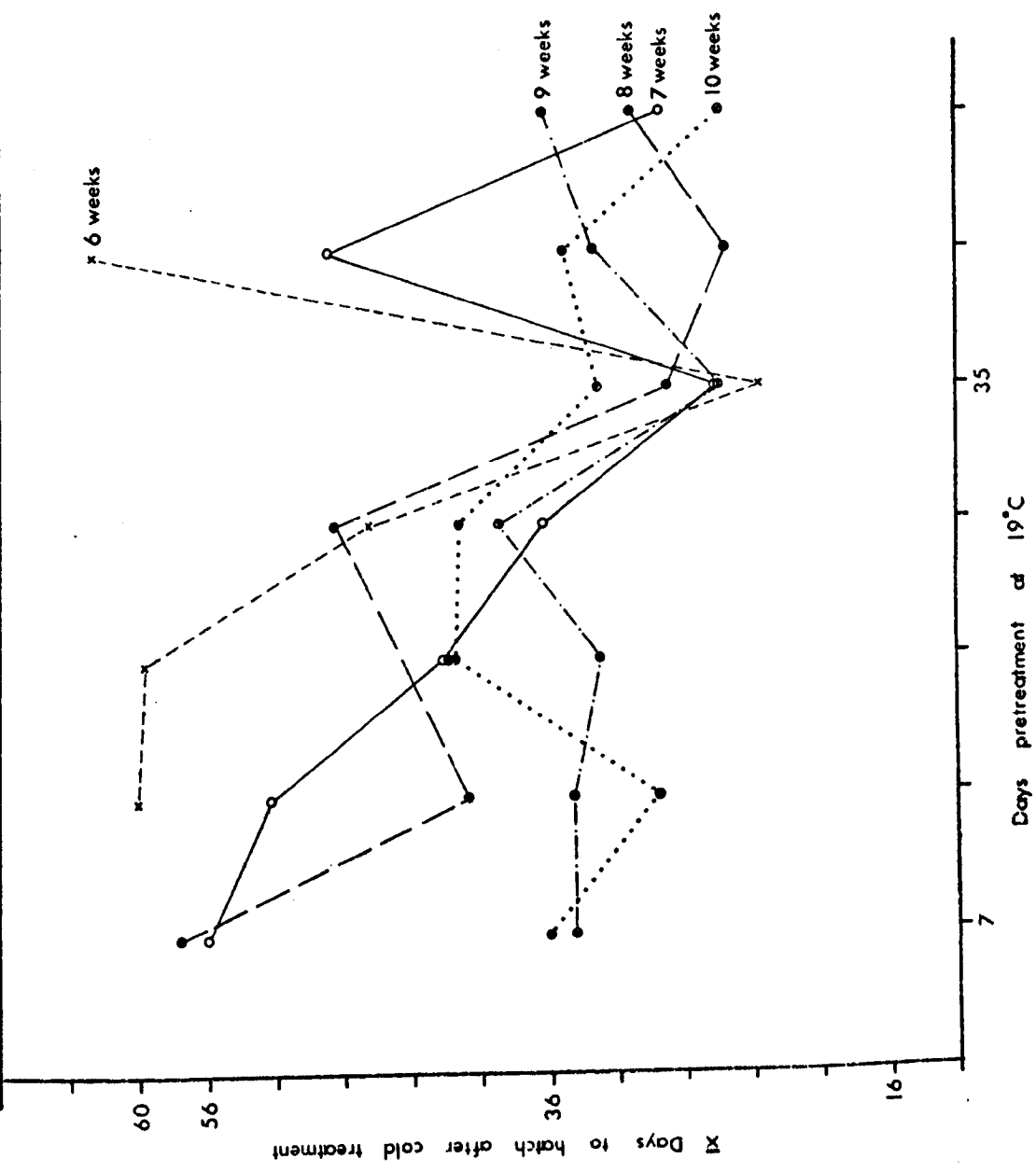




FIG. 101

HATCHING OF WILD *Sermyle halensis* OVA COLLECTED 3rd DECEMBER 1973 UNDER CONSTANT TEMPERATURE

--● 19°C  
 ---○ 16°C

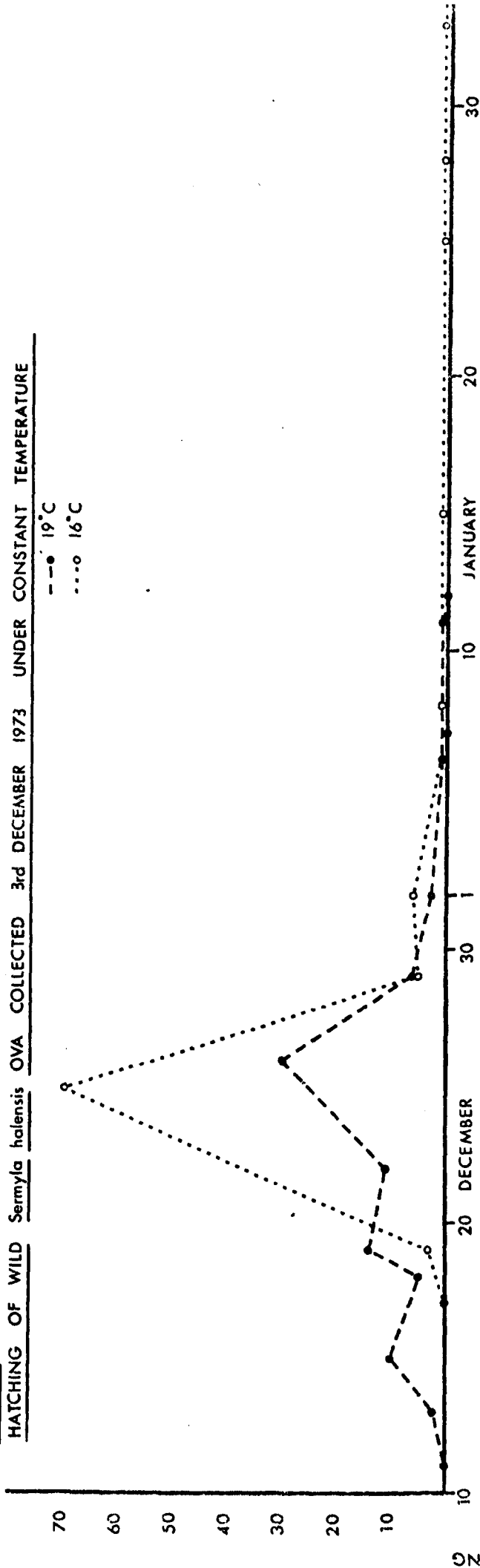
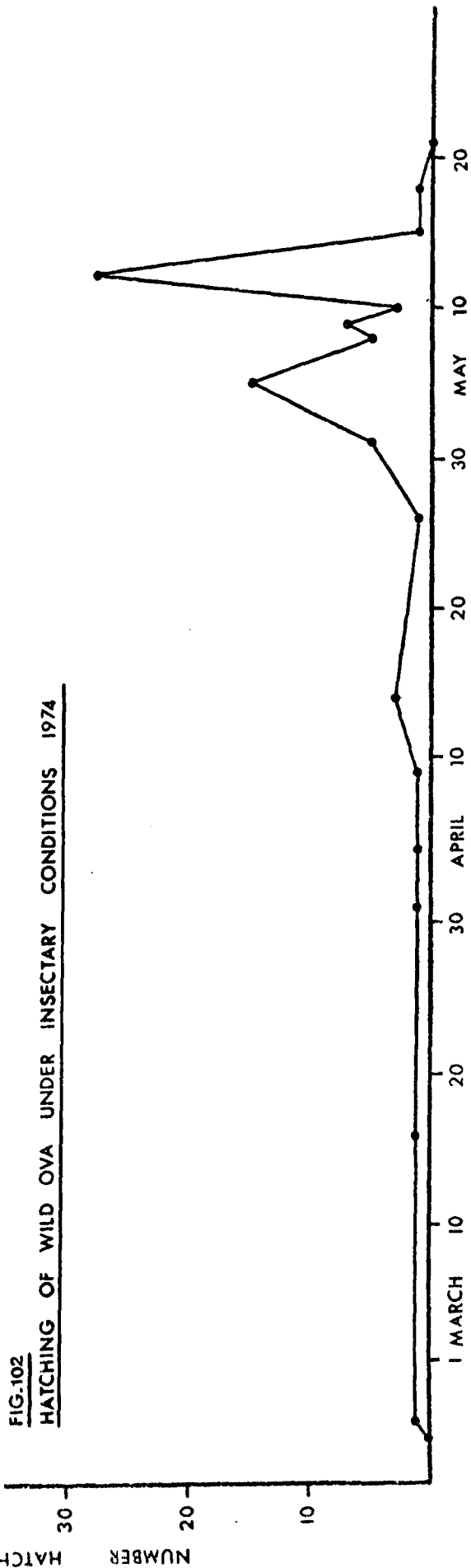


FIG. 102

HATCHING OF WILD OVA UNDER INSECTARY CONDITIONS 1974



HATCHING OF *Sermyle halensis* (L.) OVA LAID IN SOIL CONTAINED IN PLANT POTS KEPT UNDER INSECTARY

CONDITIONS AT CLOSE HOUSE

- ..... OVA LAID 29 Aug - 7 Sept 1973
- OVA LAID 7 - 21 Sept
- - - - OVA LAID 21 Sept - 7 Oct
- - - - OVA LAID 7 Oct - 7 Nov

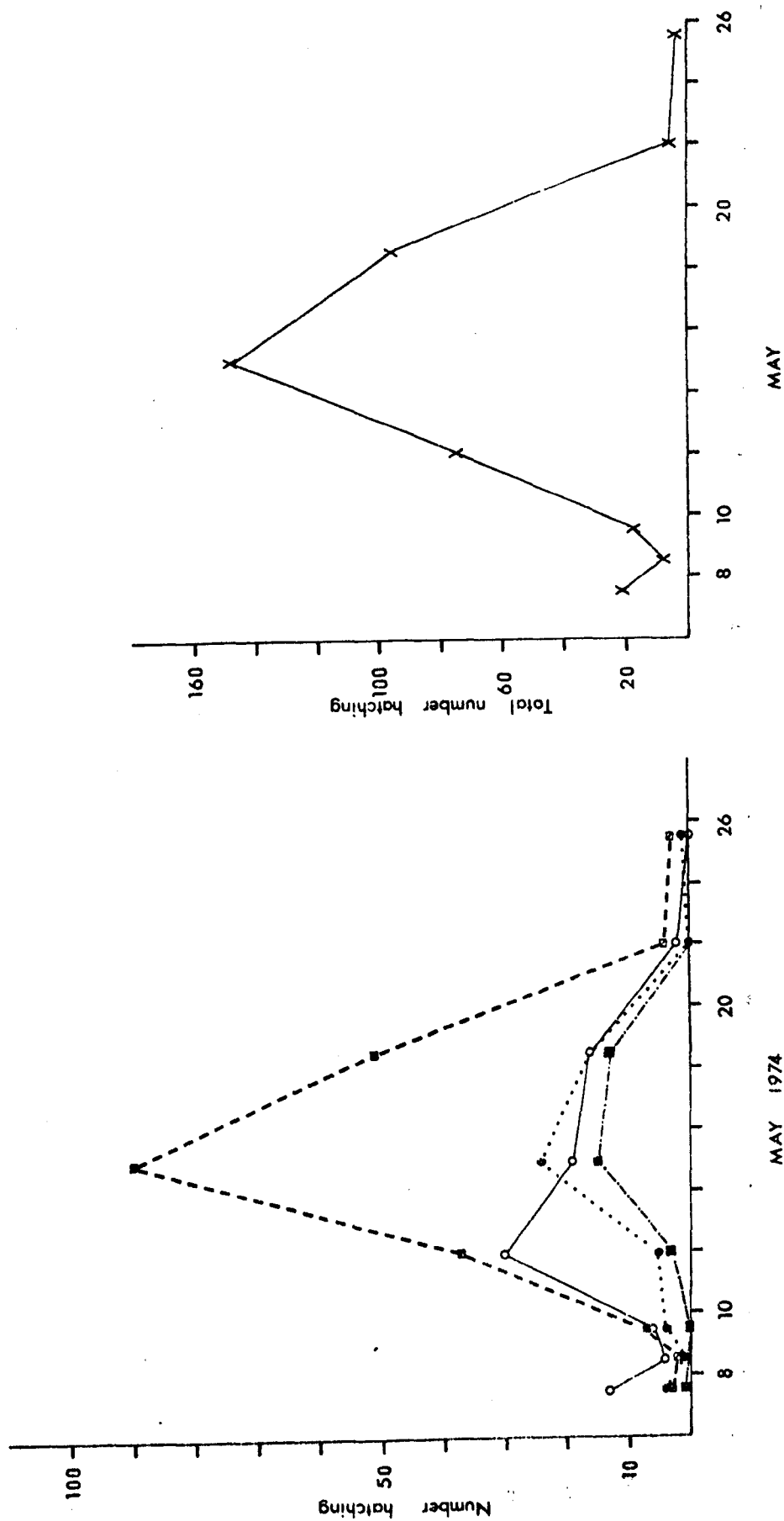


FIG.104

NUMBER OF NEWLY HATCHED LARVAE OF *Sermyle halensis* L AT CLOSE HOUSE

----- 1973

—— 1974

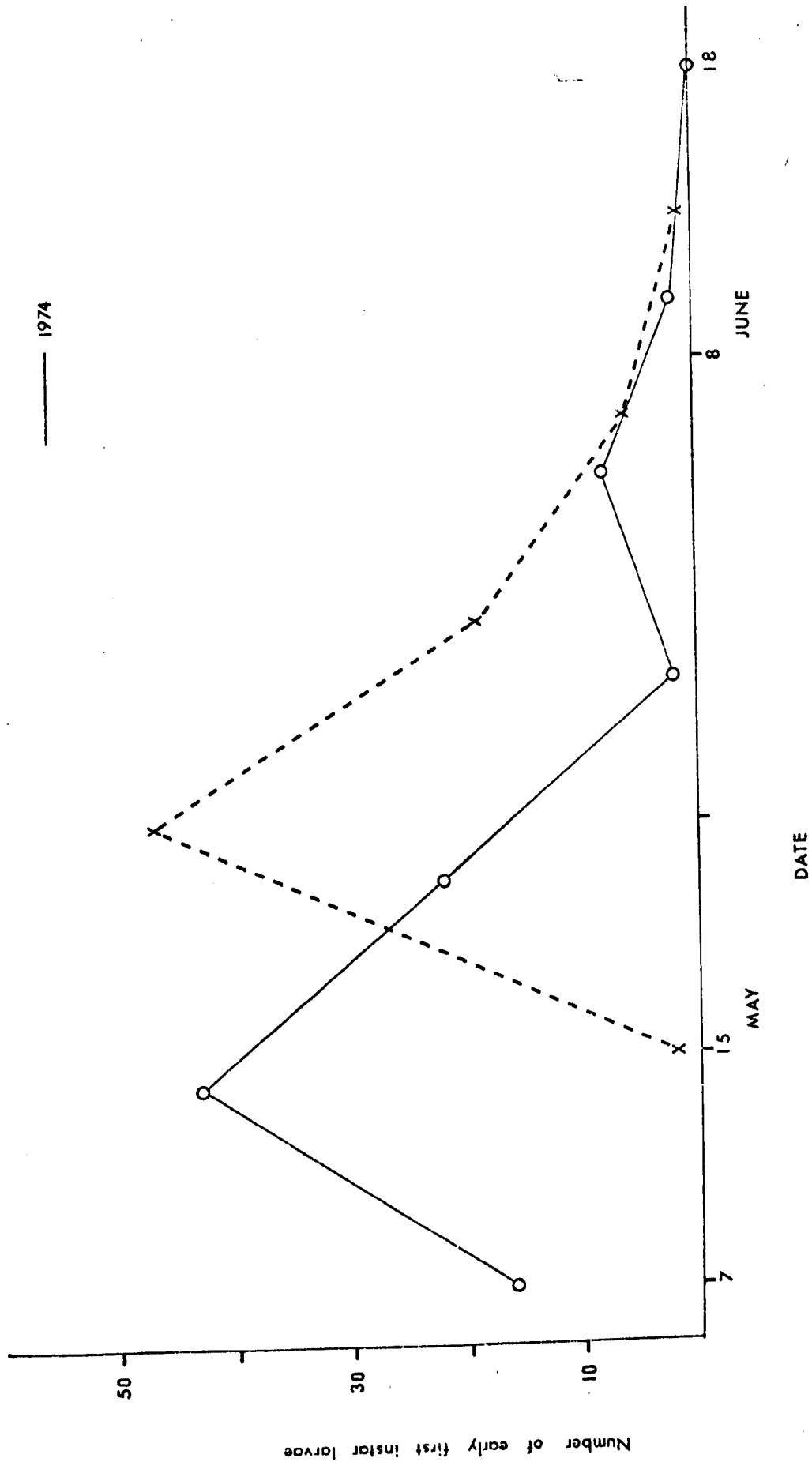
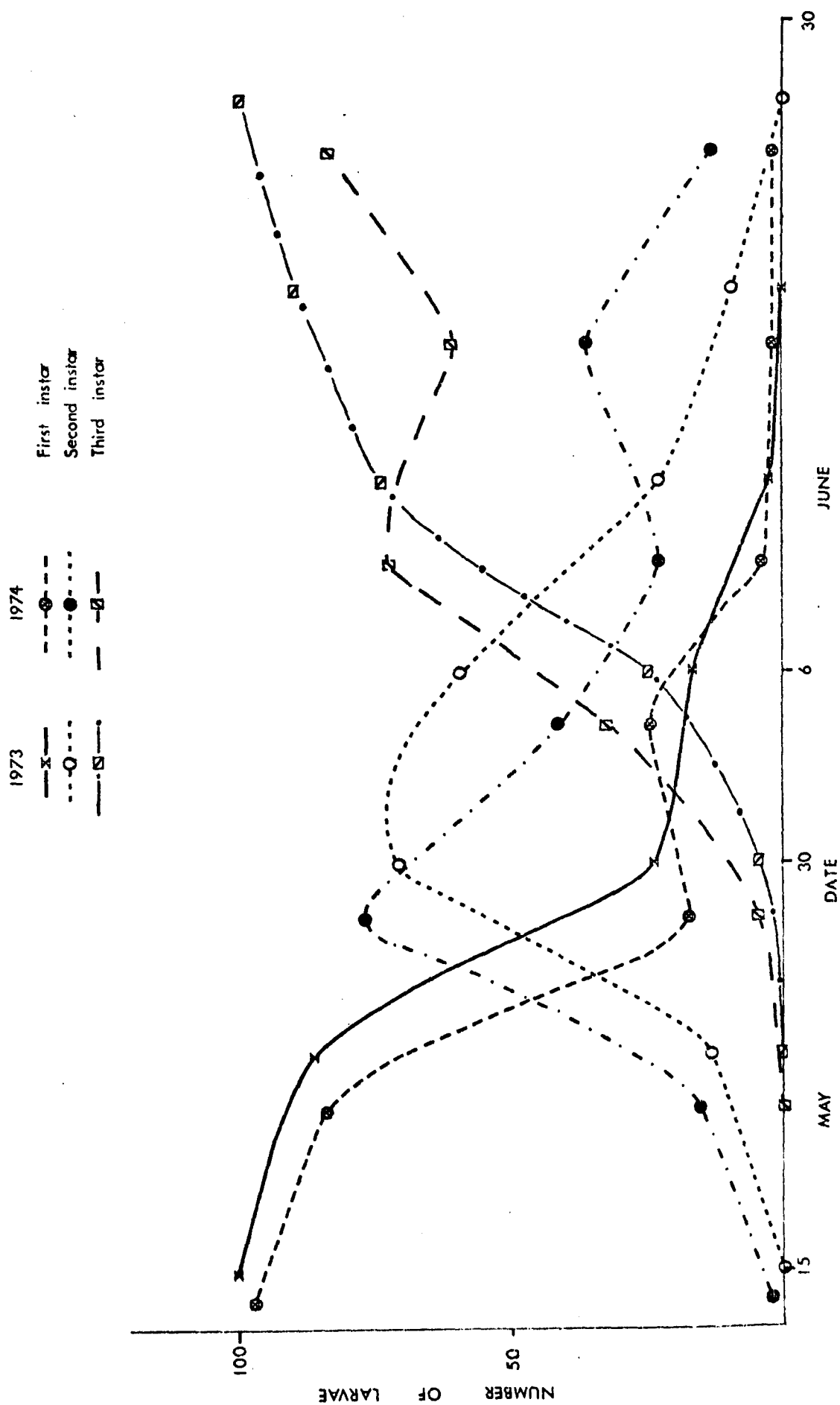


FIG. 105

OCCURRENCE OF *Sermyle halensis* LARVAE AT CLOSE HOUSE



then when placed at 16°C and 19°C hatched normally after about 10 days (Fig.101 ). This is comparable with laboratory results as the mean temperature for September, October and November from 1966 to 1974 was 9.50°C.

Eggs laid under insectary conditions had a spread of hatching of 21 days and the mean development time varied between 208 and 255 days, Fig.103. Eggs laid over a 10 week period hatched over 3 weeks and thus diapause tended to concentrate hatching. Egg diapause occurs at a very early embryonic stage as eggs laid under insectary conditions 29th August - 7th September and 7-21st September and dissected 13th November showed no development.

### Larvae

The larvae do not possess hatching spines and hatch by biting a small hole in the chorion. Hatching in the field commenced on 7th May 1973 and on 15th May 1974 and continued in both years until mid June (Fig.104 ). The larvae have 3 instars and feed upon the foliage and stems of Galium mollugo up to the end of June. The occurrence of the larvae at Close House during 1973 and 1974 is shown in Fig.105 . Fully grown larvae collected 13th June went into soil to pupate 13-15th June. These were kept at 19°C. Adults emerged 17th-20th July, i.e. the prepupal and pupal stages lasted 34-37 days. Fully grown larvae collected 27th June immediately went into soil to pupate. These were kept at 19°C and adults emerged 31st July - 8th August. Thus the prepupal and pupal stages lasted 34-42 days. The first adults of S. halensis in the field were seen at the bases of the foodplant on 22nd July. Thus in the field as final instar larvae occur as early as 20th May it can be assumed that a few larvae will have entered the soil by this time. The prepupal and pupal period in the field can therefore be assumed to be 20th May-22nd July or approximately 64 days. As final instar larvae were present as late as 26th June then larvae are still entering the soil

TABLE 22

LONGEVITY FECUNDITY & OVIPOSITION CHARACTERISTICS OF *Sermyle halensis* L.

ADULTS CULTURED AT 19°C &amp; 16 hrs light/Day

19°C & 16 hrs. light/Day	♀ 1	♀ 2	♀ 3	♀ 4	♀ 5	♀ 6	♀ 7	♀ 8	♀ 9	♀ 10	$\bar{x}$
No. BATCHES	13	7	16	15	19	6	5	17	17	7	12.2
$\bar{x}$ No. EGGS/BATCH	24.2	21.4	13.7	18.9	23.3	21	27	23	23.9	21.1	21.7
$\bar{x}$ No. DAYS BETWEEN	4.2	4.7	3.9	3.5	3.5	4.5	4.1	4.4	3.4	4	4
OVIPOSITION PERIOD	53.5	26	54	46	62.5	22	16	68	52	23.5	42.3
FECUNDITY	315	150	220	283	443	126	135	392	406	148	262
LONGEVITY days	73	48	80	67.5	84.5	27.5	36	88.5	75.5	31	61.3

ADULTS COLLECTED AT CLOSE HOUSE 16th OCTOBER 1972

19°C & 16 hrs light/Day	♀ 1	♀ 2	♀ 3	♀ 4	♀ 5	♀ 6	♀ 7	♀ 8	♀ 9	♀ 10	$\bar{x}$
No. BATCHES	10	4	8	12	9	5	4	9	8	12	8.1
$\bar{x}$ No. EGGS/BATCH	20.6	18.7	22.9	27.8	20.3	18.4	21.7	16.1	19.5	20.2	18.6
$\bar{x}$ No. DAYS BETWEEN	3.9	7	4.4	3.5	3.6	3	3	3.6	4.3	2.7	3.9
OVIPOSITION PERIOD	36	23	32	41	30	13	10	30	31	31	27.7
FECUNDITY	206	75	183	334	183	92	87	145	156	242	170
LONGEVITY days	37	33	37	45	34	21	22	45	44	46	36.4

ADULTS COLLECTED AT CLOSE HOUSE 16th AUGUST 1973

19°C & 16 hrs light/Day	♀ 1	♀ 2	♀ 3	♀ 4	♀ 5	♀ 6	♀ 7	♀ 8	♀ 9	♀ 10	$\bar{x}$
No. BATCHES	17	10	11	12	8	15	4	19	11	11	11.8
$\bar{x}$ No. EGGS/BATCH	22.3	17.8	23.4	22.5	25.7	21.3	24.2	19.8	21.7	23.4	22.2
$\bar{x}$ No. DAYS BETWEEN	4.8	8	4.3	4.4	4.8	4.1	5.5	4	4	3.4	4.7
OVIPOSITION PERIOD	70.5	51.5	35	48	31	59	17	73	35	17	43.7
FECUNDITY	379	178	258	270	206	319	97	376	239	258	258

at this time. Thus adults are expected to be emerging from pupae until at least 28th August, and adult emergence in the field will extend over a 5-6 week period depending on the environmental conditions.

### Adults

The pre-oviposition period in the laboratory at 19°C was about 10 days whereas in the field it is of about 3 weeks duration. Mean egg batch size, egg batch number, fecundity, longevity, oviposition period are shown in Table 22 .

## GENUS Luperus

Luperus flavipes L. Plate B9 Fig. 51

Foodplants: Betula and Salix species

### Ova

Small, oval, pale yellow with the chorion distinctly microsculptured. Deposited in small batches in the ground. Oviposition probably occurs in the field at Close House from 4th June - 8th July as females dissected during this period contained fully developed ova. The incubation period in the laboratory at 19°C was 28 days however at Close House the mean monthly temperature for June and July 1974 was 11.0 and 12.7 respectively. Hatching probably occurs at the earliest by the end of July.

### Larvae

Hatching spines are absent and the larvae bite their way through the chorion. The larvae possibly feed within the roots of Salix and Betula spp. but I was unable to culture this species in the laboratory or find larvae within Betula roots in the field.

### Adults

Feed upon the foliage of the foodplants. At Close House 1974 adults emerged on 21st May and survived until 8th July, whereas in other localities they have been seen as late as 9th August. The

pre-oviposition period was 14 days and the oviposition period lasted about 34 days. Emergence of the new generation adults was not observed and it is probable that winter is passed in the larval or pupal stages. The species is unlikely to overwinter as adults because no adults were observed on the foodplants in Autumn, no records exist of their being collected in grass tussocks during the winter, and their late emergence in the Spring as compared with the other common Close House Galerucid Galerucella sagittariae which overwinters as adults.

Luperus longicornis F. Plate B9 Fig. 52.

Foodplants: Salix and Betula spp.

#### Ova

Yellow orange, oval but one end more pointed than the other.  $\bar{x}$  length 0.59mm,  $\bar{x}$  width 0.35mm (n = 43). Chorion distinctly microsculptured. Laid in the soil. Incubation period in the laboratory at 19°C was 36 days. Oviposition period in the field probably similar to L. flavipes.

#### Larvae

Hatching occurs by the larvae eating a small hole in the chorion. They probably feed within the roots of Salix and Betula spp.

#### Adults

These have been observed in the field feeding on the foliage of the foodplant (more commonly in June and July) from May until 4th September and oviposition occurred in the laboratory at the end of June and beginning of July. It is probable this species has one generation a year and a similar cycle to L. flavipes L.



SUBFAMILY HALTICINAEGENUS Haltica

H. lythri Aub. Plate B11 Fig. 59.

Foodplants: Onagraceae Epilobium hirsutum L.

Ova

Incubation required 9 days at 20°C. Oviposition in the field occurs from the end of May until the beginning of August.

Larvae

Larvae possess paired hatching spines on the meso and metathoracic segments. The larvae feed externally upon the apical leaves of the foodplant. Hatching probably occurs about 7th June until 7th August. There are 3 larval instars, fully grown larvae occurring from the end of June until the end of August. Pupation occurs in the soil and pupae probably occur from 14th July until mid-September.

Adults

Adults occur in the field from 1st April until 24th September. New generation adults probably emerge at the end of July until late September. It is probable there is one generation/year and the adults overwinter. However Balcells (1951) recorded three generations in Spain in the subspecies *ampelophaga*.

H. britteni Shp. Plate B11 Fig. 60.

Foodplants: Ericaceae Calluna vulgaris (L.) Hull.

EricaOva

Orange with the chorion covered with a very thin layer showing distinct hexagonal sculpturing. The chorion beneath this layer is smooth and shiny. Oval, slightly broader at one end than the other  $\bar{x}$  length 1.107mm,  $\bar{x}$  width 0.57mm ( $n = 3$ ). Ova laid singly or in two's - four's at the bases of shoots, in stem axils, on flowers where they are very well concealed. Incubation required 11 days at 19°C, 5-8 days at 25°C. Oviposition probably occurs at the beginning

of April and continues until the beginning of May.

### Larvae

Hatching probably occurs at the end of April until the end of May. There are 3 instars, the larvae feeding upon the leaves and stems of Calluna and becoming fully developed by the end of May. Pupation probably occurs about 7th June and pupae may occur until 7th July.

### Adults

New generation adults emerge about mid June until about 21st July, feed and go into hibernation after 30th September. There is probably only one generation/year. Adults have been seen in copula as early as 11th March the following year.

### H. oleracea (L.)

Foodplants: Onagraceae Chamaenerion angustifolium (L.) Scop.

Adults occurred in the field from 6th May until 21st September. Oviposition probably commences at the beginning of June until mid July as fully grown larvae were collected 30th June and adults dissected 20th June and 4th July contained fully developed ova. Larvae become fully developed in the field from the end of June until the beginning of August. Pupation occurs from about mid July and pupae probably occur until mid September. Newly emerged new generation adults were collected on 7th September but probably emergence occurs during August. There is one generation annually, the adults overwintering.

### GENUS Hermaeophaga

H. mercurialis (F.) Plate B11 Fig. 61.

Foodplant: Euphorbiaceae Mercurialis perennis L.

### Ova

White or creamy yellow.  $\bar{x}$  width 0.45mm,  $\bar{x}$  length 0.96mm. Laid singly or in small groups in the soil at the roots of the foodplant.

Incubation required 7-10 days at 19°C. The oviposition period probably extends from the beginning of May until mid June.

### Larvae

Larvae possess paired hatching spines on the meso and metathorax. Hatching probably occurs about 21st May and larvae feed upon the roots of Mercurialis becoming fully grown in about 27 days. Fully grown larvae probably occur from mid June until the end of July. There are 3 larval instars (Welch, 1972). Pupae occur from the end of June until mid August.

### Adults

The new generation adults probably emerge about mid July.

The old generation probably dies out towards the end of June. There is one generation annually, the adults overwintering from October and appearing about 11th April the following year.

## GENUS Derocrepis

D. rufipes (L.) Plate B12 Fig. 67.

Foodplants: Papilionaceae Vicia  
Lathyrus

### Ova

Cream to pale yellow, oval,  $\bar{x}$  length 0.79mm,  $\bar{x}$  width 0.36mm (n = 21). Incubation requiring 16-17 days at 20°C. Oviposition occurring in the field from 14th May until mid June. The ova are laid upon the leaves and stems of the foodplant.

### Larvae

Larvae possess paired hatching spines on the meso and metathorax. Larvae are probably root feeders on various Papilionaceae. They probably occur from the beginning of June, becoming fully developed by the end of Summer.

Adults

New generation adults probably emerge the following Spring. The adults have been collected in the field from 29th April into July. They have not been collected during the Winter.

GENUS Podagrica

P. fuscicornis (L.) Plate B11 Fig. 63.

Biology studied by Manolache and Dobreanu in Rumania (1938), Heeger (1858) and Van Emden (1929).

Foodplants: Malvaceae Malva  
Althaea

Ova

Oval, chorion with irregular polygonal microsculpturing,  $\bar{x}$  length 0.960mm,  $\bar{x}$  width 0.380mm. Yellow immediately after laying but becoming paler towards the extremities during incubation. Oviposition occurring in Rumania over 6 weeks from the 3rd week in April or beginning of May until mid-June. Ova are present until the end of June. Incubation required 9 days at 25-26°C.

Larvae

1st instar larvae possess paired hatching spines on the meso and metathoracic segments. Hatching occurs the second week in May and pupation occurs about 7th June. The larvae have 4 instars and feed upon the superficial parts of the roots of Althaea officinalis and A. rosea but do not reach the root axil centre.

Adults

New generation adults emerge about the 21st June and start ovipositing 5th July. The second new generation adults emerge about the 30th September and these adults overwinter in stems of Althaea or beneath dry leaves. The adults re-appear from hibernation during the second week of April, pairing the 3rd week in April and beginning of May. The observations of Heeger and Van Emden differ markedly. Heeger (1858) stated that the fully developed larva penetrates the lignified parts of the roots of Malva where it hibernates.

Larval development is terminated at the end of March or beginning of April and the adults appear in May. Van Emden (1929) observed that larvae are fully developed in November and are found deep in the root tissues. At the end of Autumn they probably penetrate deeply into the earth as in April they have been found at a depth of 45-50cms. In the laboratory pupae were obtained from May and adults emerged about 15 days later.

In England adults have been collected in July and August and of the related species P. fuscipes on 23rd June. It is probable that the species shows the cycle indicated by Heeger and Van Emden.

#### GENUS Crepidodera

C. ferruginea (Scop) Plate B12 Fig. 66.

Foodplants: Gramineae  
Compositae

#### Ova

The eggs are elongate oval, chorion with distinct hexagonal sculpturing.  $\bar{x}$  length 0.64mm,  $\bar{x}$  width 0.32mm (n = 5). They are honey yellow immediately after deposition becoming rusty brown prior to hatching. They are laid in batches or singly in soil among grass roots at a depth of less than 1cm. Incubation requiring 16 days at 19°C. Oviposition occurring at Close House from 16th July until 12th September, but ova present in the field until about 7th October.

#### Larvae

Hatching occurs about 7th August until late September. The larvae excavate a gallery through the coleoptile and foliar sheaths to reach the centre of the stem of Gramineae. They are localised in the lowest parts of the stem, in a zone where the tissues are still unpigmented. After having lived for about a week in the axis of the hypocotyl the larva moves towards the roots or node of rooting. If it cannot pierce this node it leaves the plant and penetrates the stem at a higher level. The length of stem attached from the rooting

zone is less than 1-2 cms. The larva abandons the plant when the heart dessicates or decays. Duration of first instar 21-26 days at 19°C, 28 days at 17.6°C. Blunck (1932) showed an arrest of growth of variable duration during the inter moult in the laboratory. By the beginning of Spring the larva is not fully developed. It leaves the stem where it has hibernated and invades new stems. Fully developed larvae have been seen in the field from 24th April until 17th May but probably occur into June. Pupation occurs in the earth, probably commencing about mid-May and is of 2-3 weeks duration. In April the larvae cause similar symptoms to Oscinella frit (in Winter cereals) as the central leaf turns yellow and finally dries up. However, with C. ferruginea a second central leaf frequently withers also.

#### Adults

Newly emerged adults have been seen at Close House as early as 7th June but emergence continues into July. These adults survived until 12th September. The adults feed upon the foliage of various plant families including Compositae.

#### C. transversa (Marsh.)

Foodplants: Gramineae  
Compositae

#### Ova

Elongate oval, yellow brown, chorion with distinct pentagonal sculpturing.  $\bar{x}$  length 0.87mm,  $\bar{x}$  width 0.43mm ( $n = 12$ ).

Probably the same cycle as C. ferruginea, the adults occurring from 8th June until 2nd September in the field. The adults feed upon Cirsium in the laboratory and oviposited 9th August. The larvae however did not accept any part of the Cirsium plants offered to them.

GENUS Epitrix

E. atropae Foud. Plate B11 Fig. 62.

Biology studied by Newton (1929).

Foodplants: Solanaceae     Atropa belladonna L.

Hyoscyamus niger L.

Datura stramonium L.

Ova

Eggs are laid singly or in groups in the soil at 1-3cms depth.

The eggs are elongate oval, yellowish white, length 0.4mm, width 0.2mm.

Oviposition commencing 28th April and continuing until mid June.

Ova laid 11th May, 10-11th June, 4th July required incubation periods of 28, 24, and 14-15 days respectively.

Larvae

Hatching commences about 8th June and continues until about 20th July. The larvae feed upon the roots of Atropa becoming fully developed in about 21 days. Fully grown larvae occur by the end of June until mid August. Pupation occurring about 16th July and pupae occur until the end of August. Duration of prepupal and pupal stages 15-17 and 11 days respectively.

Adults

New generation adults emerging about the beginning to the end of August feed upon the foliage of Atropa until about 21st September after which they hibernate. There is one generation annually, the adults re-appearing in April.

E. pubescens (Koch.)

Foodplants: Solanaceae     Atropa belladonna L.

Solanum nigrum L.

S. dulcamara L.

This species probably has a similar cycle to E. atropae. In England adults occur in the field from the end of May until late August.

According to Balachowsky and Mesnil the eggs are laid in the soil during the Summer and the larvae feed on the roots of Atropa.

#### GENUS Batophila

B. rubi (Pk.) Plate B14 Fig. 78.

Foodplants: Rosaceae Rubus

The adults hibernate in the superficial part of the ground re-appearing in the Spring from 15th April and surviving until July. Oviposition probably occurs in May as females dissected 12th May all contained fully developed ova. The larvae are probably root feeders on Rubus sp. New generation adults probably emerge at the end of July and have been seen in the field until 4th September feeding upon the foliage of Rubus. There is probably only one generation annually.

B. aerata (Marsh)

Foodplants: Rosaceae Rubus idaeus etc  
Potentilla

This species probably has a similar biology to B. rubi Payk.

#### GENUS Mantura

M. rustica (L.) Plate B12 Fig. 65

Foodplants: Polygonaceae Rumex obtusifolius L.

#### Ova

Laid singly in small holes eaten by the females in the lower epidermis of Rumex leaves. Incubation requiring about 6 days at 19°C. At Close House adults contained fully developed ova from 28th May - 22nd July 1974. The oviposition period is about 8 weeks in the field.

#### Larvae

Hatching occurs about 14th June and continues until late July. Fully developed 3rd instar larvae are present from about 10th July until late August and pupae from about mid July - 7th September. The larvae mine the leaves of Rumex.



Adults

New generation adults emerged at Close House from 16th July - mid September 1974. These feed upon the leaves of Rumex, going into hibernation at the end of September. There is one generation annually, the adults re-appearing from 12th March.

GENUS Hippuriphila

H. modeeri (L.) Plate B11 Fig. 64.

Foodplants:      Equisetum arvense

Ova

Oval, pale yellow becoming orange later,  $\bar{x}$  length 0.717mm,  $\bar{x}$  width 0.28mm ( $n = 18$ ). The eggs are laid beneath the bracts at the internodes of the stem of Equisetum. Incubation required 7 days at 20°C. At Close House oviposition occurred from 25th May until 2nd July. The oviposition period is about 5 weeks.

Larvae

Hatching occurs about the beginning of June, the larvae mining the younger stems of Equisetum. There are 3 larval instars and fully developed larvae occur in the field from the end of June until about 7th August. Pupae probably occur from 7th July until the end of August.

Adults

New generation adults emerged from the beginning of August until the beginning of September. They feed until about the end of September and go into hibernation as late as 22nd November.. There is one generation annually. Adults re-appear the following year as early as 16th March usually at the beginning of May.

GENUS ChalcoidesC. fulvicornis (F.) Plate B12 Fig. 68.Foodplants: Salix atrocinerea Brot.Salix fragilis L.Ova

Pale yellow,  $\bar{x}$  length 0.62mm,  $\bar{x}$  width 0.29mm, (n = 11). Laid in small batches in soil. Oviposition occurring from 21st May until 25th June.

Larvae

Hatching occurs at the end of May or the beginning of June, the larvae feeding upon the roots of Salix sp. Larvae are probably fully developed in about 4 weeks and pupation occurs at the end of June.

Adults

New generation adults have been seen in the field from 9th July until 20th August. They feed on the foliage of Salix spp. entering hibernation at the end of September. They re-appear the following year about 7th May. There is one generation annually.

C. aurata (Marsh.)Foodplants: Salicaceae Salix atrocinerea Brot.Populus nigra L.Ova

Pale yellow, slightly darker than aurea, oval,  $\bar{x}$  length 0.66mm,  $\bar{x}$  width 0.31mm, (n = 6). They are laid in ones and two's in the soil. It is probable that the life cycle is the same as in C. fulvicornis as adults have been seen in the field from 7th May until October.

C. aurea (Geof.)

Foodplants: Salicaceae      Populus nigra L.

Ova

Creamy white, oval,  $\bar{x}$  length 0.78mm,  $\bar{x}$  width 0.30mm (n = 30).

They are laid in batches of up to 10 (24 in 1 batch) in the soil.

It is probable that the life cycle is the same as in C. fulvicornis as adults have been seen in the field from 6th May until 28th September.

GENUS Apteropeda

A. orbiculata (Marsh.) Plate B14 Fig. 77.

Foodplants: Plantaginaceae      Plantago lanceolata L.

Labiatae      Teucrium scorodonia L.

Compositae      Centaurea nigra L.

Ova

Laid singly within the leaf tips of Plantago lanceolata L.

Oviposition at Close House occurs from about the beginning of April until 11th June.

Larvae

Hatching spines absent. Hatching occurs about 14th April until 25th June at Close House (Fig. 97). There are 3 larval instars, the larvae feeding within the leaves and leaf petioles beneath the epidermis, making linear mines. Final instar larvae occurred from 29th April until 25th June 1974. Pupation occurs in the soil and pupae probably occur from mid May until mid July to the end of August.

Adults

New generation adults emerge about 25th June until mid August. Adults have been collected in the field until 19th September after which they enter hibernation, to re-appear about the beginning of April the following year. There is one generation annually. The larvae feed principally in the leaves of Plantago lanceolata. The first and second instars are upper or lower epidermal miners whereas the 3rd instar larvae eat the mesophyll and palisade tissue between

the upper and lower epidermis.

#### GENUS Sphaeroderma

S. testaceum(F.) Plate B12 Fig. 70

Foodplants: Compositae Cirsium vulgare (Savil) Ten.

Cirsium arvense (L.) Scop.

#### Ova

White elongate, oval, slightly flattened dorso-ventrally, the chorion distinctly microsculptured.  $\bar{x}$  length 0.822mm,  $\times$  width 0.40mm ( $n = 18$ ). The eggs are laid singly on the underside of both old and new Cirsium leaves (very rarely on the upper surface) and not usually adjacent to a main leaf vein. Rarely eggs may be laid on the primary and secondary veins. Number of eggs laid per leaf varied from 1-12 ( $\bar{x} = 4$ ,  $n = 55$ ). Incubation required 10-12 days at 19°C.

Oviposition period in the field from 22nd July until 25th October or 3 months.

#### Larvae

The first instar larvae do not possess hatching spines and mine straight into the leaf feeding in the early stages beneath the lower epidermis. Hatching probably commences about 5th August although first instar larvae were not observed in the field until 1st October, and continues until about 8th January the following year. Fully grown 3rd instar larvae were collected from 1st October until 27th March. The third instar larvae completely remove the mesophyll and palisade layers between the upper and lower epidermis of the leaves. Fully grown larvae at 19°C failed to pupate and it is probable that they diapause in this state during the winter. Pupation probably occurs from March until 21st July.

#### Adults

New generation adults probably start emerging at the beginning of April as one adult was collected from a grass tussock 3rd April.

A newly emerged adult was found as late as 21st July at Close House. Adults survived in the field from the appearance on Cirsium at the beginning of May until the end of October, and it is unlikely that any survive the Winter. There is one generation annually.

S. rubidum Graells. Plate B12 Fig. 69.

Foodplants:	<u>Centaurea nigra</u> L.
Compositae	<u>Cirsium vulgare</u> (Savi) Ten.
	<u>Cirsium arvense</u> (L.) Scop.

### Ova

Creamy white, ellipsoidal, length 0.65mm, width 0.37mm (Balachowsky 1963). Laid singly on the underside of Centaurea nigra L. leaves. Oviposition in the field occurring from 22nd July to the end of October.

### Larvae

First instar larvae without hatching spines. They hatch biting through the chorion adjacent to the leaf, mining directly into the leaf from the egg. They may mine directly into a primary or secondary vein. The larvae feed by mining below the lower epidermis causing irregular sinuous galleries. Later instars eat the entire leaf tissue between the upper and lower epidermis of the leaves. Hatching in the field probably occurs at the end of July continuing until mid November and larvae are fully developed in one month at 19°C. Fully developed larvae occur from the end of August and a few probably occur in the leaves during the Winter months. The majority however penetrate into the soil to about 3cms before December, pupating the following Spring. Pupae occur from April until 21st July. However Balachowsky (1963) stated that the overwintering stage is the pupa.

### Adults

Emergence of new generation adults on the foodplants occurs about June and these survive until late October. There is one generation annually and it is unlikely that adults overwinter.

Biology studied by Gomez-Clemente (1941) in Spain. The adults appeared from 15th April until the end of May. They leave the

Artichoke plants at the end of May and aestivate beneath vegetation debris, returning to the plants at the beginning of September. They oviposited from 20th September - 1st October, the first larvae appearing about 19th October. The larvae are fully grown from 10th November - 10th December and penetrate into the soil during this period. Pupation occurred the following Spring.

#### GENUS Chaetocnema

C. concinna (Marsh.) Plate B13 Fig. 71

<u>Foodplants:</u>	Chenopodiaceae	<u>Chenopodium</u>
	Polygonaceae	<u>Rumex obtusifolius</u> L.

#### Ova

Pale brown, oval, chorion with distinct microsculpturing,  $\bar{x}$  length 0.627mm,  $\bar{x}$  width 0.272mm. Laid in the soil at the base of the host plants. Incubation required 7-8 days at 19°C. Oviposition in the field probably occurring from 14th May until 16th July and incubation requiring 15-28 days under field conditions.

#### Larvae

Hatching probably occurs at the beginning of June and according to Newton (1929) fully grown larvae and prepupae occurred from 4th July - 7th August. Larval development takes about 4 weeks the larvae making fine galleries in the roots of the hostplants. Pupae occur in the field from 7th July until the beginning of September.

#### Adults

Adult captures in a suction trap and by sweeping are compared in Fig. 107. New generation adults emerge at the end of July or the beginning of August. At Close House 1974 newly emerged adults appeared 5th August until 3rd September. The adults feed upon the foliage going into hibernation in grass tussocks during October and November. Adults re-appear about 2nd April the following year and probably survive until the end of July. There is one generation annually.

FIG.106

OCCURENCE OF *Phyllotreta undulata* Kuts. AT CLOSE HOUSE

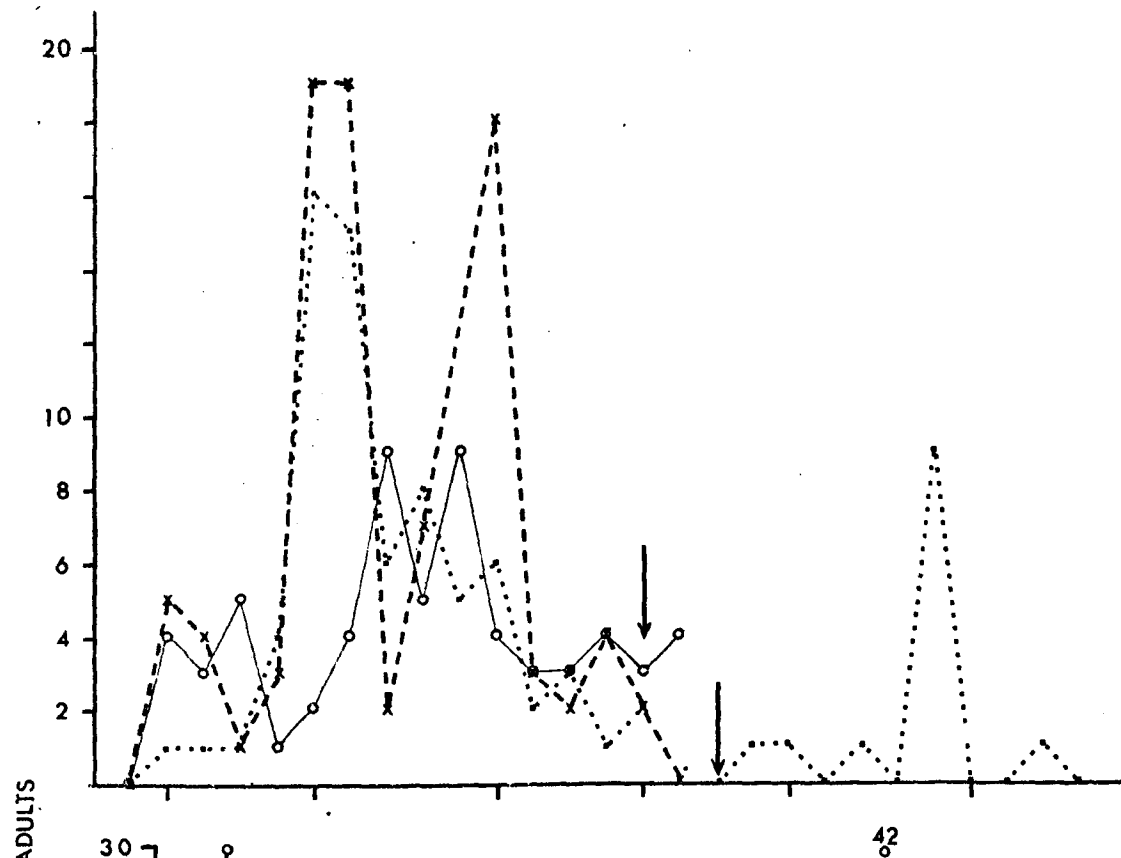
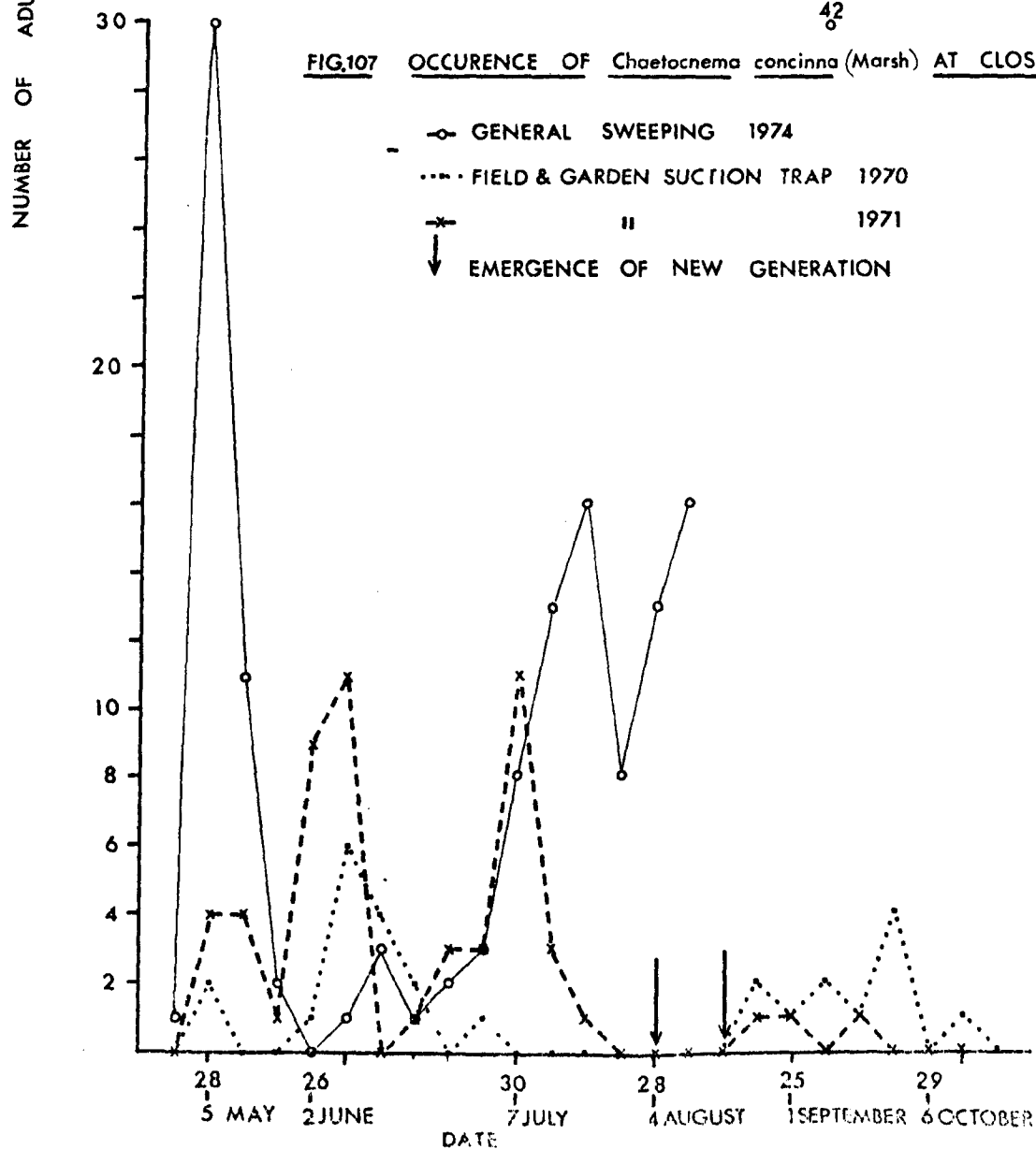


FIG.107 OCCURENCE OF *Chaetocnema concinna* (Marsh) AT CLOSE HOUSE



C. hortensis (Geof.) (= aridella Payk.) Plate B13 Fig. 72.

Foodplants: Gramineae

The eggs were not described. Adults occur in Britain from 22nd April until 2nd October and adults dissected 15th June and 2nd July contained fully developed ova. Newton (1929) stated that the larvae mine the pith of the first internode of Barley stems becoming fully grown during the first and second weeks of July. Prepupae occurred in the field 10-17th July and pupae 15-22nd July. The prepupal and pupal stages lasted 6-8 and 18-21 days respectively. The first adult occurred in its pupal cell 4th August. It is probable therefore that new generation adults emerge at the beginning of August, going into hibernation in late September and that there is one generation annually.

#### GENUS Phyllotreta

P. undulata Kuts. Plate B14 Fig. 80.

Foodplants: Cruciferae Brassica rapa L.

B. oleracea L.

B. nigra L. Koch.

Raphanus sativus L.

Rheum

#### Ova

Pale cream, elongate oval. Length 0.3mm, width 0.15mm. Chorion finely microsculptured. Laid in the soil at the roots of the foodplants. Oviposition in the field commenced about 4th June and continued until 30th July at Close House 1974. Newton (1928) stated that egg laying commenced about 3rd May, incubation required 10-11 days and the ova hatched 10-11th May. The larval feeding period lasted 13-16 days and the prepupal plus pupal period lasted 16-18 days. Pupae and prepupae occurred in the field on 6th August. The larvae feed in the roots of the foodplants.



### Adults

Adult captures in a suction trap and by sweeping are compared in Fig. 106. At Close House 1974 newly emerged adults appeared from 30th July and in previous years occurred in the field until 22nd November. There is one generation annually, the adults hibernating and re-appearing 29th April the following year.

P. nemorum (L.) Plate B14 Fig. 79.

Foodplants: Cruciferae Brassica rapa L.

B. oleracea L.

B. nigra (L.) Koch.

Raphanus sativus L.

Sinapis arvensis L.

Sinapis alba L.

### Ova

Pale yellow, oval. Laid singly or in small groups on the underside of Raphanus leaves usually on or near the principal veins and at the junction of veins and the mid rib. Incubations required 10-13 days at 19°C. Oviposition occurred from 31st May until the end of June.

### Larvae

Hatching occurs from about 14th June until mid July. According to Newton (1928) eggs laid 31st May - 2nd June hatched 21st June, thus requiring an incubation period of 19-21 days. The larval period was 15-17 days and the prepupal plus pupal period lasted 21 days. Fully grown larvae and pupae occurred in the field 29th June and pupae were present on 19th July. New generation adults emerged 28-30th July. The larvae feed by mining the leaves forming sinuous galleries 1-2cms long and widening out at the apices. Larvae occurred at Close House from 14th June until 21st July and pupae from 29th June - mid August. The fully grown larvae pupates in the soil at a depth of 1-2cms.

### Adults

At Close House 1974 new generation adults appeared 5th and 14th August but probably emerge until the end of the month. There is one generation annually, the adults entering hibernation in grass and under leaves etc., as late as 25th October. Adults re-appear the following year from 29th March and survive until about 23rd July.

P. cruciferae (Goez.) Plate B14 Fig. 82.

Foodplants: Cruciferae

Egg similar to undulata.

Biology studied by Newton (1928). Oviposition in the soil from about 7th May until mid July. During the first and second weeks in July eggs, and first and second instar larvae occurred. The larvae feed upon the roots of the foodplants. Pupae and prepupae only, were present the first 2 weeks in August and the last pupae were seen during the last week in August. The larval feeding period, prepupal and pupal period lasted 28, 7-10 and 14-20 days respectively. New generation adults emerged about 21st August. There is one generation annually and adults hibernate from September onward re-appearing the end of April the following year.

P. nigripes (F.) Plate B14 Fig. 81.

Foodplants: Cruciferae

Resedaceae Reseda lutea L.

Biology studied by Newton (1928).

Eggs laid 20th April commenced hatching 10th May, incubation requiring 14-24 days. Those laid 10-11th May hatched from 2-4th June. Ova occurred from mid May until the first week in July. The larvae feed on the roots of the foodplants and were fully developed in about 32 days. Larvae occurred from 10th May until 7th August. The prepupal and pupal periods lasted 21 days and pupae occurred from 21st June until the end of August. New generation adults emerged

about 21st July. There is one generation annually, the adults entering hibernation during October and re-appearing about 13th April the following year. It is probable that other species within the genus have a similar cycle to these species. There is one generation annually, the adults overwintering and the larvae feeding during the Summer months at the roots of Crucifers.

#### GENUS Psylliodes

P. napi (F.) Plate B13 Fig. 75.

Foodplants: Cruciferae Rorippa nasturtium-aquaticum (L.) Hayek.

#### Ova

Oval.  $\bar{x}$  length 0.72mm,  $\bar{x}$  width 0.34mm ( $n = 18$ ). Chorion very thin and colourless containing a yellow developing embryo. Eggs laid usually in three's and four's on the leaves and roots of the foodplant. Incubation required 12-13 days at 19°C. Oviposition in the field probably occurs from mid April until the end of May.

#### Larvae

Hatching probably occurs about the end of April until mid June. The larvae mined the leaves and stems of the foodplant and were fully developed in 3 weeks at 19°C. Larvae are probably fully grown by the end of May in the field and pupae probably occur from 7th June until about 7th August.

#### Adults

New generation adults probably emerge mid July continuing up to late August and newly emerged specimens were collected on 3rd and 5th August. There is one generation annually and the adults overwinter entering hibernation before October. Re-appearance of adults the following year commences about 28th March.

P. chrysocephala (L.) Plate B13 Fig. 76.

Foodplants: Cruciferae Brassica rapa L.

B. oleracea L.

B. napus L.

B. nigra (L.) Koch.

Raphanus sativus L.

### Ova

Ovoid, length 0.9 - 0.96mm, width 0.4 - 0.43mm. Pale orange with the chorion bearing fine polygonal microsculpturing. They are laid singly or in batches of 2-6 or even 16 in the soil. Oviposition probably starts about the 7th August and continues during the Winter until the end of March when the majority of adults have died.

Newton (1929) stated that eggs laid 14th February under laboratory conditions hatched in 22-24 days, whereas under field conditions

they did not hatch until May or after 75 days. Balachowsky (1963) showed that egg laying continues until early May.

### Larvae

According to Dobson (1959) the larvae possess paired hatching spines on the meso and metathorax. Hatching probably occurs from about 21st August and larvae are present until mid May the following year. After hatching the larve bore into the tender stems of the hypocotyl at ground level and mine within the stem. Borner and Blunck (1920) observed 2nd instar larvae in February and fully grown larvae appeared by the end of March. Pupae are probably present from 7th October until the end of June the following year.

### Adults

New generation adults emerge from about the end of May until the beginning of July. The adults after emergence feed for 8-10 days and then according to Bonnemaison and Jourdeuil (1954) enter a period of diapause. They resumed activity at the beginning of August and disperse by flight on to the seedlings of Winter Crucifers. Borner and Blunck (1920) observed the adults on

Rapistrum perenne in August becoming more frequent on Charlock in September, while in October it appeared in numbers on young Winter rape. The adults were found on these plants during Winter but at the end of February large numbers appeared from their Winter quarters.

Borner and Blunck (1920) concluded that there is one generation annually in N. Germany and this probably is the situation in Britain. The egg laying period continuing for 6 months of the year leads to the appearance of different stage larvae at the same time, leading one to conclude that there may be 2 generations annually. The adults of the summer brood may have arisen from the later eggs of the overwintering beetles or from those beetles which have overwintered as larvae emerging as adults about May.

P. affinis (Pk.) Plate B13 Fig. 73.

Foodplants: Solanaceae Solanum dulcamara L.

#### Ova

Yellow, elongate oval, length 0.6 - 0.7mm, surface of chorion finely microsculptured. Laid singly or in small groups in the soil near the hostplant at a depth of 1-2cm. Incubation requiring 8-10 days. Oviposition occurring during June.

#### Larvae

Hatching commencing about mid June and fully grown larvae and pupae occurred at the end of July. On August 11th few larvae remained but pupae predominated. The last pupae were found in early September. The larvae mine the roots, galleries usually being superficial but often they go down into the root.

#### Adults

New generation adults emerged from 9th July until the beginning of October. The adults feed on the foliage and enter hibernation in October. There is one generation annually. Adults re-appear the following year about 30th April.

P. picina (Marsh.) Plate B13 Fig. 74.

It is probable that this species has a similar cycle to P. napi and P. affinis. Adults occurred in grass tussocks at Close House 28th February and 13th April. Adults were collected by sweeping from 16th May until 18th September. A newly emerged new generation adult was collected on 6th September. It is probable that the larvae develop during July and August.

#### GENUS Longitarsus

L. luridus (Scop.) Plate B15 Fig. 87.

Foodplants: Compositae Cirsium arvense (L.) Scop.

The adults feed upon the foliage of Cirsium and occurred in the field from 8th March until late October. The majority of the overwintered generation probably die before mid June. Oviposition by this overwintered generation commences about 30th April continuing until 13th June as adults dissected over this period contained fully developed ova. The larvae probably hatch during May feeding at the roots of Cirsium. A newly emerged new generation adult was collected at Close House on 14th August. Emergence of the new generation occurred during August and September. Adults of this new generation dissected during September contained fully developed ova and thus there are 2 egg laying periods during the year, one in spring and the other in autumn. It is probable that the majority of ova laid will hatch in September or October but it is possible ova could overwinter. Larvae may overwinter in the early instars developing into pupae and adults the following Spring. It is probable that some of the new generation adults overwinter without ovipositing because adults have been collected during December, January and February.

L. pratensis (Pz.) Plate B15 Fig. 88.

Foodplants: Plantaginaceae Plantago lanceolata L.

The adults feed upon the foliage of Plantago and occurred in the field from the end of April and during May. Adults dissected 29th April and 7th May contained fully developed ova. Thus there is a Spring oviposition period. The larvae probably feed at the roots of Plantago during May and June. A newly emerged new generation adult was collected 9th July but the majority of the new generation probably emerge during August. Adults of the old generation were not collected during June. New generation adults dissected 6th and 12th September contained fully developed ova and there is an Autumn oviposition period as in L. luridus. It is probable that eggs and early instar larvae overwinter. The adults may also overwinter, as adults were collected on 1st December.

L. melanocephalus (DeG.) Plate B15 Fig. 83.

Foodplants: Plantaginaceae Plantago lanceolata L.

The adults feed upon the foliage of Plantago and occurred in the field from 22nd April until early October. Oviposition occurs during April and May as adults dissected on 22nd April, 5th and 7th May contained fully developed ova. The majority of the overwintered generation die out by mid June. The larvae probably feed at the roots of Plantago during May and June. Emergence of new generation adults probably occurs from the end of July and during August but no evidence of an Autumn oviposition period was observed in this species. The new generation adults feed during September entering hibernation from early October. Adults were collected in grass tussocks during February.

L. suturellus Duft. Plate B15 Fig. 84.

Foodplants: Compositae Senecio vulgaris L.

The adults feed upon the foliage of Senecio and occurred in the field from the 3rd March until 30th September. Adults dissected 28th April - 10th June contained fully developed ova. Thus there is a Spring oviposition period. The overwintered adults die out by mid June. Incubation required 8-9 days at 19°C, so that hatching in the field probably occurs after mid-May. Larvae were collected feeding on the roots of Senecio at Close House from 13th June until 4th July and pupae were found 11th July. Newly emerged new generation adults were collected 5th, 8th, 16th August and 3rd September. No evidence of an Autumn oviposition period was indicated. The new generation adults feed during September, entering hibernation during October.

L. jacobaeae Wat. Plate B15 Fig. 86.

Foodplants: Compositae Senecio aquaticus Hill.

The adults feed upon the foliage of Senecio and occur in the field from 7th July and during August and September. Newton (1933) studied its biology. The eggs are elongate and with the ends rounded, length 0.66mm, width 0.30mm. They are yellow but darken before hatching, the chorion bearing numerous polygonal pits. They are laid in the soil and the young larva bites its way out. Oviposition commenced from mid August and probably continues until late September. Eggs laid in late Summer hatched in about one month, or less at 19°C, later ones do not hatch until the following Spring so that both eggs and larvae overwinter. Larvae occurred from 19-21st September and were fully developed from the beginning of June the following year. The larvae feed on the roots of Senecio. Pupae occurred from 7th June until the end of July. New generation adults probably appear as early as 7th July but the majority emerge at the end of July and during August the number reaching a maximum in late August. The



adults survive into the Winter months as they have been collected during November and December. In L. jacobaeae there is an Autumn oviposition period only.

#### GENUS Aphthona

##### A. euphorbiae (Schrank.)

Foodplants: Linaceae Linum sp. (Balachowsky & Mesnil, 1936)

Euphorbiaceae Euphorbia cyparissias L.

##### Ova

Oval, yellowish white, length 0.49 - 0.52mm, width 0.28 - 0.33mm. They are laid singly or in small groups of 2-4 up to a depth of 5cm in soil in the proximity of roots. Under field conditions incubation required 9-25 days. Early instar larvae usually feed within the roots whereas final instar larvae feed externally on the peripheral root tissues.

##### Adults

New generation adults emerge about mid July, feeding on the foliage until mid October when they enter hibernation. There is one generation annually, adults re-appearing in Spring the following year.

##### A. coerulea (Geoff.) (= nonstriata Goeze)

Foodplants: Iridaceae Iris pseudacorus L.

##### Ova

Pale yellow, broader at one end than the other.  $\bar{x}$  length 0.54mm,  $\bar{x}$  width 0.343mm ( $n = 16$ ). Laid singly or in twos or threes on the upper and lower surfaces of Iris leaves. The oviposition period is probably about mid May to mid June as adults dissected on 22nd May and 15th June contained fully developed ova. Hatching probably occurs at the end of May.

##### Larvae

The larvae mine the leaves causing white elongate feeding marks on the leaves usually near leaf extremities. Pupation probably occurs towards the end of June.

Adults

New generation adults emerge at the end of July and during August. They feed on the leaves of Iris until the end of September, causing similar symptoms to those of the larvae. There is one generation annually, the adults entering hibernation during October. Adults emerge from hibernation the following year from 31st March and survive until early July.

GENUS DiboliaD. cynoglossi (Koch.)

<u>Foodplants:</u>	Labiatae	<u>Mentha</u>
		<u>Salvia</u>
		<u>Stachys</u>
		<u>Ballota</u>
		<u>Galeopsis tetrahit</u>

Little is known concerning the biology of Dibolia sp. Balachowsky & Mesnil (1936) stated that the larvae are leaf miners.

The biology of D. borealis Chevr. studied by Reed (1927) in Ithaca, U.S.A. may be comparable with that of D. cynoglossi.

a Adults appeared about 10th May, oviposition commencing 17th May and continuing for 6 weeks. During oviposition the female eats out a small area from the upper leaf surface leaving the lower epidermis and some of the spongy cells. A single egg is inserted together with some excreta. Incubation required 8-10 days and no unhatched ova occurred after 1st July. The larva upon hatching mines directly into the leaf without appearing on the surface. The larvae feed by mining the leaves of Plantago major. The larval, prepupal and pupal periods lasted 14, 5-9 and 9-12 days respectively. The complete cycle took 45 days and there is one generation annually. New generation adults emerge mid-July. The adults overwinter, appearing in May the following year and the majority are dead by mid July.

### C. RELATIONSHIPS INDICATED BY THE BIOLOGY.

It is probable that the biology at the northern most limit of a species will be different from that at the southern most limit. Not only will the number of annual generations differ but probably also the stage in which overwintering occurs.

In the Cassidinae, genus Cassida there is usually one generation annually. The larvae are found in June and July and the new generation adults emerge in August. The larvae feed externally on the leaves of Compositae etc. usually removing the lower epidermis only. The eggs are laid singly or in groups within oothecae and there are five larval instars. Pupation occurs on the leaves and the adults overwinter. The biology of Cassida resembles in many respects that of Criocerinae,

Chrysomelinae, some Galerucinae and some Halticinae. Matis (1972) showed that as many as five types of life cycle are undergone by the Cassidinae of Central Asia.

In the Orsodacninae there is probably one generation annually.

The larvae are probably found from June until April the following year.

The larvae feed as miners in the leaf petioles of Rosaceae etc.

(Bakachowsky & Mesnil, 1936) being fully grown before winter and probably pupating in the Spring. It is unlikely that the adults overwinter. The biology is similar to that of Donaciinae, Clytrinae, Cryptocephalinae, some Galerucinae and some Halticinae species.

In the Donaciinae there is probably one generation annually and the larvae are found from June until May the following year. It is probable that the adults also overwinter. Eggs are laid in groups on the submerged leaves of the aquatic foodplants and pupation occurs within cocoons spun by the larvae. The larvae feed externally or internally on the rhizomes of the foodplants.

In the Zeugophorinae there is one generation annually. The larvae are leaf miners of Populus in May, June and July. The ova are laid singly below the upper epidermis of the leaves. There are 4 larval instars. The new generation adults emerge in August and overwinter.

Pupation occurs within earthen cells. The biology of Zeugophora is similar in many respects to Criocerinae, Cassidinae, Chrysomelinae, Galerucinae and Halticinae.

From the cast skins in the mines it was thought that the larvae of Zeugophora scutellaris had three instars. This species actually overwintered as fully developed larvae in earthen cells (Strickland, 1920).

There is usually one generation annually in the Criocerinae. However in Crioceris asparagi two or three generations have been recorded. Criocerinae larvae are found during May, June and July feeding externally on the leaves of Gramineae etc. Pupation occurs in the soil, in Lema within cocoons spun by the larvae. The adults overwinter and eggs are laid singly or in small groups.

In the Cryptocephalinae, there is one generation every one or two years. The eggs are laid singly from July until September, covered by the females excrement and dropped to the ground. Hatching occurs in September and the larvae overwinter. Some larvae may achieve full development and pupate the year following hatching, whereas others diapause during the Summer of the first year, overwinter again and become adults the following year. The larvae feed externally on leaves of Betula etc. They live within cases which are periodically enlarged and in which pupation occurs.

In the Clytrinae there is probably one generation every one or two years. Oviposition occurs in May and June and hatching occurs at the end of June. In Clytra the eggs are covered by a collerette of small bracts made from the females excrement and they are dropped singly to the ground (Donisthorpe, 1902). In Labidostomis the eggs are laid in groups on the leaves of Betula, each attached by a pedicel to a common point (Jollivet, 1952). The larvae of Clytra probably develop usually within the nests of the red ant Formica rufa group.

They live within cases in which pupation occurs. It can be seen that the biology of the Clytrinae and Cryptocephalinae is very similar in many respects.

The larvae of Clytrinae and Cryptocephalinae achieve full development after two or three summers (Rosenhauer, 1852). The larvae of Cryptocephalinae feed on dry leaves in turf but at a certain stage move onto bushes searching for fresh leaves (Chapuis & Candeze, 1853). The three species studied definitely fed on leaves which were turning brown and even had fungal growths as well as on fresh leaves. The larvae of Clyt ra quadripunctata are thought to feed on plant material in ants nests (Donisthorpe, 1902). However, the larvae of Clyt ra longimana completed their development on Trifolium montanum (Chapuis & Candeze, 1853).

The Chrysomelinae show various types of developmental cycle.

Timarcha tenebricosa has a very long oviposition period from May until late August. The adults overwinter and may survive for over twelve months. The ova laid during this period diapause as the fully developed embryo until Spring of the following year when hatching occurs. The larvae develop during May, June and July and new generation adults emerge in August. The adults may oviposit until October. Larvae present in the field during any year will consist of the progeny of two different generations of adults. The cycle will consist of both annual and biennial components. Oviposition occurs in small groups of two to eight ova which are covered by regurgitated food material. The larvae have three instars and pupation occurs in earthen cells.

Four different cycles occur in Chrysolina. The larvae in this genus have four instars and pupation occurs in earthen cells.

In C. hyperici and C. brunswicensis the eggs are laid singly from October until January. These are inhibited from developing by low winter temperatures and usually hatch in April. Larvae feed during April, May and June. The new generation adults emerge in June and

there is a reproductive diapause during the Summer months. It is possible that the adults may survive the winter.

In Japan the following Chrysolina species overwintered in the egg stage, C. angusticollis (Mots.), C. aurichalcea (Mots.), C. exanthematica (Wiedeman, 1821), C. watanabei Takizawa, and C. yezoensis (Matsumura) and C. pirka Takizawa was shown to be viviparous (Takizawa, 1971). It is probable that C. orichalcea (Mull.) also overwinters in the egg stage in England as a fully grown larva was collected on Anthriscus sylvestris in mid June, and first to third instars were also collected in early May. No adults were observed whereas adults of C. polita which had overwintered were collected. However the adult may emerge and oviposit earlier in the year than other species.

C. varians is an ovoviviparous species laying almost fully developed embryos singly or in pairs during June and July. The new generation adults emerge in August and overwinter.

The adults of C. polita, C. staphylea and C. graminis overwinter, ovipositing singly in batches during May and June and there is one generation annually.

C. fastuosa adults oviposit in August and the larvae feed in August and September. Adults overwinter but do not oviposit for two years as they apparently diapause during the year following emergence (Dobson, 1924).

C. menthastri adults oviposit during June and July. The larvae hibernate in the fourth instar and pupate in Spring of the following year. The old generation adults may survive the Winter and live several years passing through two or even three mating periods (Van Emden, 1951).

The genus Phytodecta contains P. viminalis, P. rufipes and P. pallida which are all ovoviviparous and the potentially ovoviviparous P. olivacea. The larvae have four instars and pupate in earthen cells. There is an adult diapause during June and July, the adults resume feeding in August

and both the old and new generation adults hibernate together. Thus adults may oviposit in one or two years and there is one generation per year. In most respects Phytodecta and Chrysolina have similar biology. However the habit of the egg overwintering relates Timarcha and Chrysolina. Timarcha differs from Chrysolina and Phytodecta as it has three larval instars and has no adult diapause during the summer.

The larvae of Leptinotarsa have four instars and are related to those of Phytodecta and Chrysolina which also have the same number of instars. They also pupate in the ground as do the other genera, (Kimoto, 1957).

The genera Phaedon, Phyllodecta, Gastroidea, Hydrothassa, Prasocuris, Plagioderia, Chrysomela have basically the same type of life cycle. The adults overwinter, oviposit during May, June and July and the new generation adults emerge in July. There are three larval instars and probably only one generation annually.

The adults of Phyllodecta, Gastroidea, Plagioderia and Chrysomela oviposit in batches on the under surface of leaves of the foodplant. Pupation in Phyllodecta and Gastroidea occurs in earthen cells while in Plagioderia and Chrysomela it occurs on the foodplant.

Oviposition behaviour in Phaedon varies from species to species. All of the species lay eggs singly. The adults of P. tumidulus lay eggs on the leaf surface whereas P. armoraciae and P. cochleariae adults oviposit within small cavities eaten by the female in the lower epidermis of the leaves and also in the stems of the foodplant. This habit of laying eggs within the foodplant has been carried even further in Hydrothassa marginella where adults lay eggs in small groups within the hollow leaf petioles of Ranunculus. In the genus Prasocuris, P. junci oviposits singly within cavities eaten by the female in the stem and leaves of Veronica. The larvae of P. phellandrii have been found feeding within the stems of Oenanthe aquatica. Phaedon, and Hydrothassa pupate

within earthen cells whereas Prasocuris phellandrii pupates on the foodplant or even in the stems. The biology of Phaedon, Hydrothassa and Prasocuris is very similar. The larvae of Chrysomelinae were divided into two biological groups on the position of pupation. The Chrysomela, Plagioderia, Prasocuris and Hydrothassa group moult twice and pupate on the host plant, while the Gastrolidea, Phaedon and Phyllodecta group moult twice and pupate under the ground (Kimoto, 1957). However this is incorrect as in the present work Hydrothassa aucta and H. marginella pupated within earthen cells and it is considered should not be included in the second group.

In the Galerucinae various developmental cycles are shown. All species have three larval instars and usually pupate within earthen cells.

The species Galerucella viburni, Galeruca tanacetii, Sermyla halensis, Phyllobrotica quadrimaculata overwinter as diapausing ova. In G. viburni the eggs are laid singly from July until September in Viburnum stems. Hatching occurs in May and the new generation adults emerge in July. The ova of G. tanacetii are laid in large numbers within oothecae from mid September until late November on dried vegetation. They hatch at the beginning of May and new generation adults emerge about mid-June. They diapause in grass tussocks during the Summer months. Agelastica alni resembles G. tanacetii in this respect as it also has an adult summer diapause (Prevett, 1953; Donia, 1958). The adults of Sermyla halensis lay eggs in batches from the end of July until the beginning of November at the roots of Galium. True diapause is terminated by the beginning of December but larvae do not hatch until the beginning of May the following year. They feed during May and June on the foliage and new generation adults emerge at the end of July. The egg diapause occurs to a lesser extent in Phyllobrotica quadrimaculata. Oviposition occurs in batches and the majority of ova hatch in September. The larvae feed on the foliage of



Scutellaria galericulata and some may become fully grown before Winter. This species overwinters as eggs and larvae, pupation probably occurring the following Spring. Adults probably oviposit from July and September. In many respects Sermyla resembles Phyllobrotica in its biology.

The genus Luperus resembles Phyllobrotica as larvae overwinter, feeding at the roots of plants and they pupate the following Spring. Oviposition occurs in batches in June and July.

The larva of Luperus circumfusus feeds at the roots of Spartium junceum L. during the winter and pupates at the end of March (Laboissiere, 1934).

Galerucella sagittariae, G. tenella, G. lineola and Lochmaea sp. have very similar developmental cycles. Their larvae usually feed externally on the foliage of their foodplants. However in L. crataegi the larvae feed internally on the pulp of Rosaceae fruits. Pupation usually occurs within earthen cells but in the case of G. sagittariae it occurs on the underside of leaves of the foodplants. There is usually one generation annually and the adults overwinter. The adults of Galerucella lay eggs in batches whereas those of Lochmaea lay them singly or in twos and threes.

In the Halticinae there are three larval instars and pupation occurs within earthen cells. The type of cycle shown does vary between genera.

In the first type shown by the majority of genera, adults overwinter and there is one generation annually. The larvae of Haltica are external foliage feeders but this is rare in the Halticinae. The genera Hermaeophaga, Derocrepis, Epitrix, Chalcoides, Chaetocnema (C. concinna), Phyllotreta (P. undulata etc), Longitarsus (L. suturellus etc.) Aphthona (A. euphorbiae) have root feeding larvae and show this type of cycle. The leaf and stem miners, Mantura rustica, Hippuriphila modeeri, Apteropeda orbiculata, Chaetocnema hortensis, Phyllotreta nemorum, Phyllodes napi, Aphthona coerulea also show this type of cycle.

The larvae of Podagrica fuscicornis, Crepidodera ferruginea, Sphaeroderma testaceum and rubidum, Psylliodes chrysocephala, Longitarsus luridus and L. jacobaeae overwinter and thus show some relationship with Luperus in the Galericinae. The larvae of Podagrica and Longitarsus are root feeders whereas Crepidodera ferruginea and Psylliodes chrysocephala feed within stems. Sphaeroderma larvae are leaf miners of Compositae.

Within the genus Longitarsus three different cycles are found. The adults of Longitarsus suturellus and L. melanocephalus oviposit in Spring and early Summer and show the first type of cycle. L. luridus and pratensis have both Spring and Autumn oviposition periods and the larvae overwinter. The adults of L. jacobaeae have an Autumn oviposition period only and the larvae also overwinter.

On the type of developmental cycle shown the subfamilies Criocerinae, Chrysomelinae, Galerucinae and Halticinae are probably related. The Galerucinae are in some respects related to the Chrysomelinae in that overwintering in the egg stage is found in both of the subfamilies. However the habit of larvae overwintering is common to the Galerucinae and the Halticinae whereas larvae never overwinter in the Chrysomelinae or Criocerinae.

The Donaciinae and Orsodacninae are related by their larvae overwintering as are Clytrinae and Cryptocephalinae.

The oviposition cycles of Coleoptera have been classified into four types (Dick, 1937). The adults of Timarcha tenebricosa, Chrysolina hyperici and Chrysolina brunsvicensis can be included in Dick's type (2) as they live for a long time often over a year and produce eggs continuously over a long period. In the case of T. tenebricosa oviposition occurs from Spring to early Autumn, whereas in the two Chrysolina sp. it occurs over the Winter. The majority of Chrysomelids can be included in type (3) in which egg laying occurs in batches at short intervals in one season. However

Phytodecta pallida, P. olivacea, Chrysolina menthastris and Psylliodes chrysocephala can be included in type (4) as they oviposit continuously in two or more seasons, each oviposition period being separated by a period during which oviposition ceases. T. tenebricosa could possibly be included in this type also as oviposition may occur in Autumn of the year of emergence and again from Spring to Autumn of the following year. A period of hibernation separates the two egg laying periods.

Biological characters such as egg and pupal coloration, larval instar number, oviposition behaviour are less likely to be influenced by environmental conditions than the stage in which overwintering occurs, number of annual generations and the presence of an adult Summer diapause.

#### D. RELATIONSHIPS INDICATED BY THE FOODPLANTS

The foodplant refers to the plant eaten by the adult but not necessarily upon which the larvae can achieve full development. In the latter case the term host plant is preferable. Most records are observations of adults in the field on the different plant species and thus deal with the foodplants. Errors do occur as adults may be seen on plants on which they do not feed and laboratory experiments are necessary to indicate the correct foodplant and host plant range for each species.

To be able to indicate which are the primitive and more specialised subfamilies of the Chrysomelidae it is necessary to make a list of the families of plants on which each feed (Table 23 ). Then it is necessary to show which are the most primitive families in the plant kingdom and try to indicate their relationships to each other. The genealogical tree of the plant kingdom was worked out by Mez (1924) using serum diagnosis. The protein relationship of plants most closely affect the natural relationships of plant families, since it is known that the bearers of heredity are certain nuclear or cytoplasmic protein bodies. Information obtained was largely supported by leaf miners which are dependent on protein for their food. The genealogical tree agrees on most points with the relationships as determined by morphological and cytological investigations.

The position of Monocotyledons in the plant system has been disputed on many occasions but they are probably a primitive group. However the mining species of Monocotyledons are not all primitive and the majority of them transferred to these plants in recent times and evolved from forms which lived on Dicotyledons (Hering, 1951). Fig. 108 shows the genealogical tree worked out by Mez and the Chrysomelid subfamilies feeding upon each plant family.

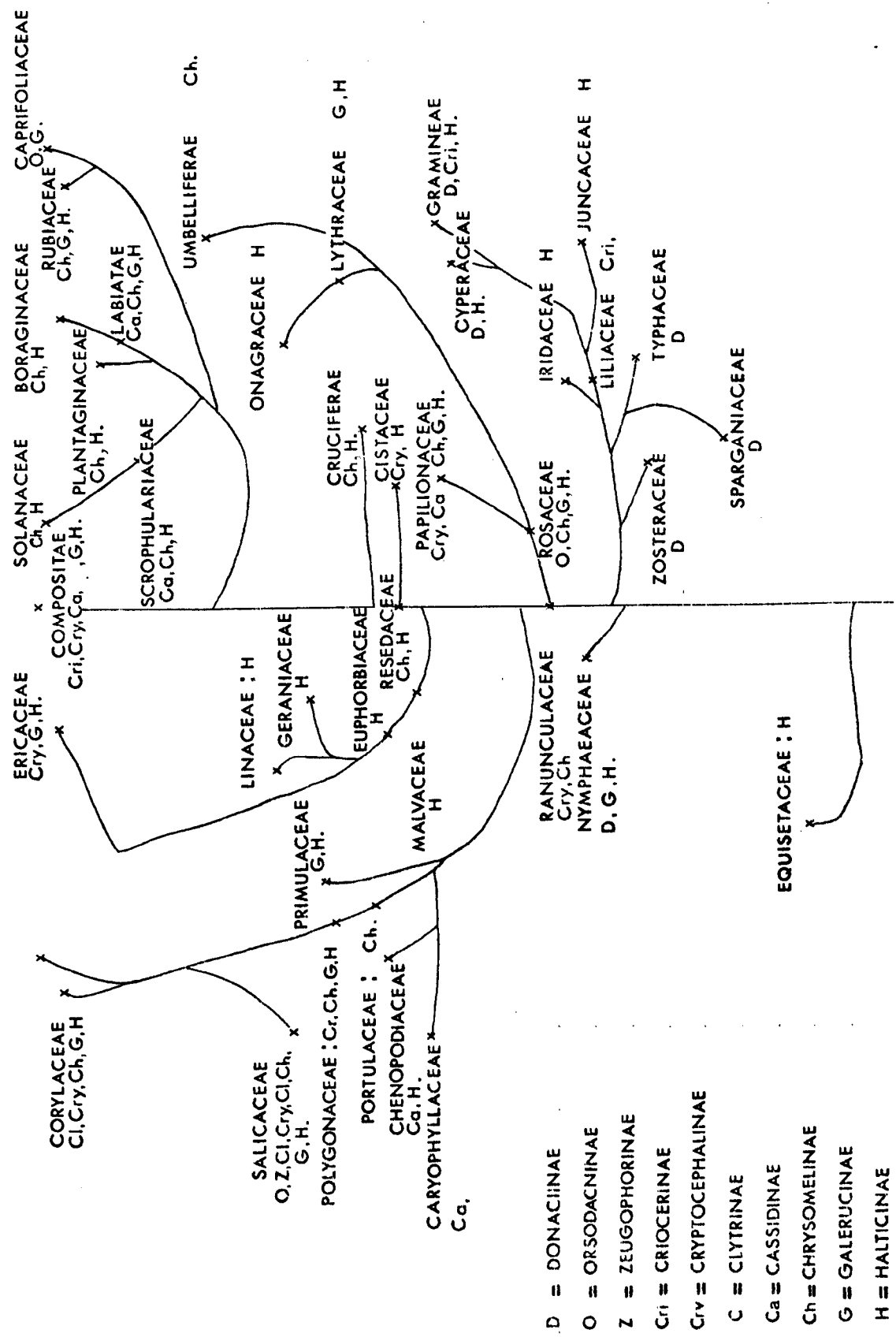
**TABLE 23**  
**CHRYSEMELID SUB FAMILIES AND THE PLANT FAMILIES**  
**ON WHICH THEY FEED**

CHRYSEMELIDAE SUB FAMILY	MONOCOTYLEDON FAMILY	DICOTYLEDON FAMILY
DONACIINAE	ALISMATACEAE TYPHACEAE SPARGANIACEAE POTAMOGETONACEAE RUPPIACEAE ZOSTERACEAE CYPERACEAE GRAMINEAE	NYMPHAEACEAE HALORAGACEAE
ORSODACNINAE		ROSACEAE CAPRIFOLIACEAE SALICACEAE
ZEUGOPHORINAE		BETULACEAE SALICACEAE
CRIOCERINAE	LILIACEAE GRAMINEAE	COMPOSITAE
CLYTRINAE		BETULACEAE SALICACEAE CORYLACEAE
CRYPTOCEPHALINAE		RANUNCULACEAE CISTACEAE HYPERICACEAE PAPILIONACEAE COMPOSITAE ERICACEAE POLYGONACEAE BETULACEAE CORYLACEAE SALICACEAE
CASSIDINAE		CRUCIFERAE CARYOPHYLLACEAE PAPILIONACEAE CALLITRICHACEAE COMPOSITAE SCROPHULARIACEAE LABIATAE CHENOPODIACEAE

TABLE 23(continued)

CHRYSEMELIDAE SUB FAMILY	MONOCOTYLEDON FAMILY	DICOTYLEDON FAMILY
CHRYSEMELINAE	JUNCAGINACEAE	RANUNCULACEAE CRUCIFERAE RESEDACEAE PORTULACEAE HYPERICACEAE PAPILIONACEAE ROSACEAE CALLITRICHACEAE CERATOPHYLLACEAE BORAGINACEAE UMBELLIFERAE ARALIACEAE RUBIACEAE SOLANACEAE SCROPHULARIACEAE LABIATAE PLANTAGINACEAE POLYGONACEAE SALICACEAE
GALERUCINAE	HYDROCHARITACEAE	NYMPHAEACEAE HYPERICACEAE PAPILIONACEAE ROSACEAE LYTHRACEAE CAPRIFOLIACEAE RUBIACEAE ERICACEAE PRIMULACEAE LABIATAE POLYGONACEAE BETULACEAE CORYLACEAE SALICACEAE COMPOSITAE
HALTICINAE	IRIDACEAE JUNCACEAE CYPERACEAE GRAMINEAE	CRUCIFERAE CISTACEAE HYPERICACEAE MALVACEAE LINACEAE GERANIACEAE PAPILIONACEAE ROSACEAE LYTHRACEAE ONAGRACEAE COMPOSITAE ERICACEAE PRIMULACEAE BORAGINACEAE SOLANACEAE SCROPHURIACEAE LABIATAE PLANTAGINACEAE CHENOPODIACEAE POLYGONACEAE EUPHORBIACEAE CORYLACEAE SALICACEAE

FIG.108 THE GENEALOGICAL TREE OF THE PLANT FAMILIES (After Mez 1924) AND THE CHRYSOMELID SUBFAMILIES FEEDING ON THEM.



- D = DONACIINAE
- O = ORSODACNINAE
- Z = ZEUGOPHORINAE
- Cri = CRIOCERINAE
- Cry = CRYPTOCEPHALINAE
- C = CLYTRINAE
- Ca = CASSIDINAE
- Ch = CHRYSOMELINAE
- G = GALERUCINAE
- H = HALTICINAE

The subfamilies Donaciinae and Criocerinae feed largely upon the primitive Monocotyledons but the only family which they have in common is the Gramineae. The Donaciinae also feed on the Nymphaeaceae which is considered to be a primitive family. In the Criocerinae Lema puncticollis Curt. feeds upon Compositae but has probably transferred to these from Monocotyledons. It would appear that Donaciinae and Criocerinae are related.

The Orsodacninae and Zeugophorinae feed upon various tree families, The Orsodacninae feed upon Rosaceae, Salicaceae and Caprifoliaceae whereas Zeugophorinae feed upon the Salicaceae and Betulaceae. They are probably related. The Clytrinae feed upon the tree families Betulaceae, Salicaceae and Corylaceae. The Cryptocephalinae also feeds upon these three tree families but also upon seven other Dicotyledon families from the relatively primitive Ranunculaceae to the highly specialised Compositae.

The Cassidinae feed upon eight Dicotyledon families but have only two in common with Cryptocephalinae, the Papilionaceae and the Compositae. These two subfamilies do not appear to be closely related.

The Chrysomelinae feed upon the Juncaginaceae of the Monocotyledons and a wide range of nineteen families of Dicotyledons from the primitive Ranunculaceae to the specialised Solanaceae. However they do not feed upon the Compositae.

The Galerucinae feed upon the Hydrocharitaceae of the Monocotyledons and fourteen families of Dicotyledons from the primitive Nymphaeaceae to the specialised Compositae. They have seven families in common with the Chrysomelinae, the Hypericaceae, Papilionaceae, Rosaceae, Rubiaceae, Labiatae, Polygonaceae, Salicaceae. The Halticinae feed upon the primitive Equisetaceae and four Monocotyledon families. The Dicotyledon foodplants cover twenty three families including the specialised Compositae. They have eleven families in common with the Chrysomelinae, the Cruciferae, Hypericaceae, Papilionaceae, Rosaceae,



Solanaceae, Scrophulariaceae, Boraginaceae, Labiatae, Plantaginaceae, Polygonaceae and Salicaceae and eleven families in common with the Galerucinae, the Hypericaceae, Papilionaceae, Rosaceae, Lythraceae, Compositae, Ericaceae, Primulaceae, Labiatae, Polygonaceae, Corylaceae, Salicaceae. The Halticinae would appear to be related to the Chrysomelinae and Galerucinae but probably more to the Galerucinae as they both feed upon the specialised Compositae. The large number of food plant families upon which the Halticinae feed may indicate that it is the most specialised and recent subfamily being able to utilise many ecosystems.

It cannot be deduced that the occurrence of certain Chrysomelid species on primitive plant families is an indication that the species themselves are primitive as they have not adapted their feeding habits parallel with the development of the plant family concerned, but only commenced feeding on it later. This is well illustrated by the Halticid, Hippuriphila modeeri a specialised Chrysomelid feeding upon the primitive plant Equisetum arvense.

Special terms are used to differentiate the type of feeding by each species. Monophagy is the feeding by a species on a single species or several species within the same genus. When a species feeds on a number of genera belonging to the same family or on genera belonging to different but closely related families the term Oligophagy is used. In Polyphagy many different plants from widely varying families are eaten.

In the Donaciinae as in the Criocerinae most species exhibit Oligophagy. However two cases of monophagy occur in Criocerinae that of Crioceris asparagi on Asparagus sp. and Lema puncticollis on thistles. The genera Crioceris and Lilloceris are probably the closer related as they both feed on Liliaceae.

In the Clytrinae monophagy and oligophagy occur. The genera Clytra, Labidostomis and Gynandrophthalma are probably related as

they feed on tree families Salicaceae, Betulaceae and Corylaceae, three closely related families.

In the Cryptocephalinae genus Cryptocephalus polyphagy is the commonest followed by monophagy. Several species groups can be delimited on the plant families eaten. C. aureolus and C. cristula feed on Hieraceum in the family Compositae. C. pusillus, C. frontalis, C. punctiger and C. parvulus feed on Salicaceae, Betulaceae and Corylaceae.

In the Chrysomelinae all types occur. In the genus Chrysolina various groupings can be made. C. hyperici, C. varians and C. brunsvicensis are monophagous feeding upon Hypericum sp. whilst C. polita, C. fastuosa, C. menthastri and C. graminis are oligophagous usually feeding upon Labiatae.

The genera Phytodecta, Phyllodecta, Chrysomela and Plagiodera may be related as all feed upon Salicaceae. In Phytodecta, P. olivacea is monophagous feeding upon Papilionaceae, P. viminalis and P. rufipes oligophagous feed on Salicaceae whilst P. pallida is polyphagous feeding upon Salicaceae, Corylaceae and Rosaceae. Phyllodecta species are all oligophagous and restricted to Salix and Populus of the Salicaceae. Plagiodera is monophagous feeding solely upon Salix of the Salicaceae. Chrysomela populi and tremulae are oligophagous feeding upon Salix and Populus of the Salicaceae whereas C. aenea is monophagous and feeds on Alnus of the Betulaceae. In Phaedon two groups occur P. tumidulus and cochleariae are oligophagous, tumidulus feeding upon Umbelliferae whilst cochleariae is restricted to Cruciferae some of which may be aquatic. P. armoraciae is polyphagous and feeds upon aquatic or semi-aquatic Scrophulariaceae, Ceratophyllaceae and Boraginaceae. In Hydrothassa monophagy is the rule and H. aucta, marginella and hannoverana feed upon Ranunculaceae. Monophagy is usual in Prasocuris, P. junci feeds upon aquatic Scrophulariaceae and may be related to Phaedon armoraciae whereas P. phellandrii feeds upon aquatic Umbelliferae.

In the Galerucinae all types occur even within one genus e.g. in Galerucella. G. viburni is monophagous feeding upon Viburnum of the Caprifoliaceae, G. tenella and G. lineola oligophagous the former feeding upon Rosaceae, the latter upon Betulaceae and Corylaceae. G. sagittariae is polyphagous feeding upon Polygonaceae of the Dicotyledons and Sagittaria sagittifolia L. of the Alismataceae of the Monocotyledons. In Lochmaea oligophagy and monophagy occur. L. crataegi is oligophagous and feeds upon Rosaceae whereas L. capreae and L. suturalis are monophagous, the former feeding upon Salix sp. of Salicaceae and the latter on Calluna of Ericaceae. Galeruca tanacetii is polyphagous as it feeds on Compositae, Caryophyllaceae, Labiatae, Dipsaceae and Cruciferae. Agelastica alni is oligophagous and feeds upon Betulaceae and Corylaceae. Phyllobrotica and Sermyla are both monophagous, the former feeds upon Scutellaria galericulata of the Labiatae whilst Sermyla feeds upon Galium of the Rubiaceae. The genus Luperus contains species which are monophagous or oligophagous. L. flavipes and rufipes are oligophagous and feed on Betulaceae and Salicaceae whereas L. circumfusus is monophagous and feeds on Sarothamnus scoparius (L.) of the Papilionaceae.

In the Halticinae polyphagy is rare but oligophagy and monophagy are common. Monophagy occurs in the genera Hermaeophaga, Batophila, Mantura, Hippuriphila. The Halticinae feed upon primitive plants such as Equisetum, members of the Gramineae of the Monocotyledons, members of the tree family Salicaceae and the most specialised of all plant families, the Compositae. Each genus is usually restricted to one plant family and very few genera feed on the same family as another genus. Thus it is difficult to make relationships between the genera. Dibolia and Apteropeda are probably closely related as they both feed upon Plantaginaceae, as are Mantura and Chaetocnema which feed on Polygonaceae.

The major problem in determining which species, genera and subfamilies of Chrysomelidae are the most primitive from their feeding habits is deciding which is the more primitive, monophagy or oligophagy. Generally in insects polyphagy represents the more primitive type of food selection (Hering, 1951; Takahashi, 1971) and many phytophagous insects were presumably polyphagous at the beginning of their phytophagy. Many polyphagous or oligophagous species of Thysanoptera and Hemiptera have separated into monophagous races, and from these monophagous species must have been derived through isolation and mutation (Takahashi, 1971). This view that monophagy only developed via oligophagy from an earlier polyphagy is supported by examples of oligophagy still found in parasitic fungi. These can only be explained by the species which today are able to produce two generations on plant families far removed from each other and in no way related, being formerly polyphagous. If the transfer to the other family was a secondary development the species concerned would have chosen a more closely related family. There is little doubt that polyphagy is the primitive and monophagy the derived more specialised form of food selection (Hering, 1951). However, many monophagous or oligophagous insects show a distinct tendency to increase their foodplants, becoming polyphagous, and polyphagy must have originated secondarily from monophagy. Polyphagy and monophagy seem to have alternated in the course of evolution, with monophagous species generally younger in age and distributed in more restricted areas (Takahashi, 1971).

### 13. SYNTHESIS OF TAXONOMIC RESULTS

Subfamily and tribal groupings have been constructed using key characters ( Tables 24-28 ).

#### I. Subfamily Groupings ( Table 24 )

##### A. The Orsodaeninae, Donaciinae, Zeugophorinae Group.

This group corresponds to the division Eupoda of Chapuis (1874) less the Criocerinae. The Orsodaeninae are probably the most primitive of these subfamilies and resemble the Cerambycidae by possessing stem mining larvae and a wing with an enlarged anal cell formed from the cubital and the first 2 anal veins. In all three subfamilies the aedeagi have a lateral lobe and the spermatheca has a distinct cornu, nodulus, collum and ramus. Orsodaeninae and Donaciinae adults lack coiling in the spermathecal duct, have cross vein r-m in the wing and lack a lateral tuberosity in the pronotum. Their larvae usually overwinter. The adults of the Orsodaeninae possess bifid claws similar to the appendiculate claws of the Zeugophorinae adults. Orsodaeninae and Zeugophorinae adults lack the anterior edge to the pronotum usually present in Donaciinae. Their larvae are without thoracic legs and feed as miners of trees. Crowson (1955), described the larva of Megalopus belonging to the Megalopodinae which is represented in Britain only by the rather anomalous genus Zeugophora. The Megalopus larva is straight, Cerambycid-like in shape with distinct short thoracic legs and differing also from Zeugophora in having a fully developed labium. Crowson (1955) considered that the Megalopodinae show relationships with the Clytrinae. Hatching spines are present in the larvae of the Zeugophorinae whereas they are absent in those of the Donaciinae. Biforous spiracles occur in Donaciinae and Zeugophorinae larvae.

##### B. Criocerinae.

This subfamily was included in the Eupoda of Chapuis but received separate family status by Chen (1940). Crowson (1955), also used the Criocerinae, subfamily status. Criocerinae and Donaciinae adults have an uncoiled spermathecal duct, cross vein r-m and only one anal cell in the wing. Criocerinae differ from Donaciinae by lacking a lateral lobe in the aedeagus and by possessing a ring-like spiculum gastrale consisting of 4 arms. Criocerinae and Donaciinae pupae are glabrous and pupation occurs in

TABLE 24 TAXONOMIC AND BIOLOGICAL CHARACTERS IN THE SUBFAMILIES OF THE CHRYSOMELIDAE

SUB FAMILY	ADULT										LARVA							PUPA	BIOLOGY				
	AEDEAGUS			SPERMATHECA			HIND WING				LARVA							PUPA	BIOLOGY				
	Lateral lobe in aedeagus	Spiculum dorsolaterally flattened in aedeagus	Tegmen dorsolaterally flattened	Median lobe apex with setae	Nodus dilated	Collum long coiled	Spermathecal duct coiled	Brachypterous or Apterous	Number of Anal cells	Cross veins in anterior	Number of Larval instars	Number of Ocelli pairs	Median suture	Epi-cranial suture	Clypeal suture	Lacinia	Hatching spines	Dorsal setae in Pupae	Larvae over Winter	Adults over Winter	Ova over Winter	Egg Dia-pause	Adult Summer Dia-pause
ORSODACNINAE	+	+	-	-	-	-	-	-	1	+	?	5	+	+	+	-	?	?	+	-	-	-	-
	+	+	-	-	-	-	-	-	0 1	+	?	5	+	+	+	+	-	-	+	+	-	-	-
ZEUGOPHORINAE	+	+	-	-	-	-	+	-	1	-	4	0,3	+	+	+	-	+	-	-	+	-	-	-
CRIOGERINAE	-	+	-	-	-	+	-	-	1 1	-	4	6	-	+	+	+	+	-	-	+	-	-	-
CRYPTOCEPHALINAE	-	+	+	+	-	-	+	-	2	-	4	6	-	+	-	+	+	+	+	-	-	-	-
CLYTRINAE	-	+	+	+	-	-	+	-	2	-	?	6	-	+	-	+	?	+	+	-	-	-	-
LAMPROSOMATINAE	-	-	+	+	-	+	+	Brachypterous	0	-	?	6	-	+	-	+	?	?	-	+	-	-	-
CHRYSOMELINAE	+	+	-	-	-	+	-	Apterous	1 1 1	-	3, 4	6	+	+	+	-	+	+	-	+	+	+	+
GALERUCINAE	-	+	-	-	+	-	-	-	1 1 1	-	3	0,1	+	+	+	+	-	+	+	+	+	+	+
HALTICINAE	-	+	-	-	+	+	+	B & A	1 1	-	3	0 1	+	+	+	+	+	+	+	+	+	-	-
CASSIDINAE	-	-	+	-	-	-	-	+	2	-	5	5	+	-	+	+	-	+	-	+	-	-	-

cocoons spun by the final instar larvae. Their adults and larvae feed on Monocotyledons. Criocerinae larvae differ from those of the Donaciinae as in the former, the median suture is absent, 6 pairs of ocelli and abdominal hatching spines are present and the claws have pulvilli. The larvae of Criocerinae do not overwinter whereas they can in the Donaciinae but both possess biforous spiracles.

The larvae of Criocerinae and Cryptocephalinae-Clytrinae have 4 instars, the median suture absent, 6 pairs of ocelli and similar head and body chaetotaxy. The clypeal suture is absent in Clytrinae-Cryptocephalinae larvae but is present in the Criocerinae. Hatching spines occur on the first abdominal segment in Criocerinae but on the meso and metathorax in Cryptocephalinae. The habit of Criocerinae larvae covering themselves dorsally with excrement may be analogous with that of Clytrinae and Cryptocephalinae larvae concealing themselves within excremental cases. The process of concealment has developed further in the Clytrinae and Cryptocephalinae. The larvae overwinter and usually have a summer diapause in the Clytrinae and Cryptocephalinae whereas in the Criocerinae the adults overwinter and the larvae do not have a summer diapause. In the adults of Clytrinae and Cryptocephalinae the spiculum gastrale is Y-shaped, the spermathecal duct coiled, the wings have 2 anal cells and cross vein r-m is present whereas in Criocerinae adults there is only one anal cell and cross vein r-m may be absent. The pupae of Clytrinae and Cryptocephalinae bear numerous setae and pupation occurs in the larval cases.

The adults of the Criocerinae and Chrysomelinae are similar in having the lateral lobe absent in the aedeagus, an uncoiled spermathecal duct, an elongated, coiled collum in the spermatheca, one anal cell present and cu-an usually absent in the wing. Chrysomelinae larvae may have 4 instars, be strongly convex dorsally, possess 6 pairs of ocelli, have abdominal hatching spines and do not overwinter. The adult is the usual overwintering stage in both subfamilies.

### C. The Clytrinae-Cryptocephalinae group

The group corresponds to the Camptostomes of Chapuis (1874). The adults have an aedeagus with the lateral lobe absent, a Y-shaped spiculum gastrale, a coiled spermathecal duct and the wings have 2 anal cells and cross veins r-m and cu-an are absent. The larvae have the median and clypeo-labral sutures absent, 6 pairs of ocelli and similar head and body chaetotaxy. Their abdomens are curved ventrally and they live and pupate in excremental cases. There are four larval instars in the Cryptocephalinae. Both subfamilies overwinter in the larval stage and there may be a summer larval diapause. The adults appear in mid-summer, ovipositing singly, covering the eggs with excreta and letting them fall to the ground.

### D. The Lamprosomatinae

The Lamprosomatinae were included with the Chrysomelids and the Galerucides in the Cycliques of Chapuis (1874). They most resemble the Chrysomelinae in their spermathecal form and external adult morphology. However, the male genitalia is without a spiculum gastrale whereas it is usually present in the Chrysomelinae. The C-shaped larvae are case bearing, lack the median suture, possess vertex setae ( $v_I - v_6$ ), frons setae ( $f_I - f_6$ ), have similar clypeal and labral chaetotaxy and are the overwintering stage as in the Clytrinae and Cryptocephalinae. However, they only possess 5 pairs of ocelli whilst those of the Clytrinae and Cryptocephalinae have 6 pairs. Kasap and Crowson (1976) also use the visible paramentum between the mentum and stipes in Lamprosomatinae larvae to separate them from Clytrinae and Cryptocephalinae in which the paramentum is not externally visible. Crowson (1955) considers the Lamprosomatinae as Cryptocephaline forms secondarily adapted to a Clytrine habit. The aedeagus has a median lobe with a setate apex, the tegmen is Y-shaped and is dorso-ventrally flattened. However, in the Lamprosomatinae, the abdomen is not constricted in the middle. From adult characters Kasap and Crowson (1976) consider the closest links are with the Sphaerocharinae. They can be separated from the Camptosomata by the absence of any connation of the last 2 ventrites, the presence of sternal longitudinal muscles in the ventrite 4. The Lamprosomatinae also show the most complete and probably most primitive wing venation in the Camptosomata, almost identical with that of Megascelis and many Eumolpinae (Kasap and Crowson 1976).

### E. The Chrysomelinae

This subfamily was grouped with the Lamprosomides and Galerucoides in the Cycliques of Chapuis (1874) and with the Lamprosomatinae (Jacoby 1908) Chen (1940), included the Chrysomelinae with the Galerucinae and Halticinae in a separate family the Chrysomelidae. The adults of these groups possess



similar wing venation with one anal cell, with or without cross vein r-m, male genitalia with the lateral lobe absent, the spiculum gastrale usually present, an uncoiled spermathecal duct and sometimes appendiculate claws. The adult is the usual overwintering stage in the three subfamilies and there are usually three larval instars. The larvae of the Chrysomelinae differ from those of the Galerucinae-Halticinae group by possessing 6 pairs of ocelli, instead of 0-I, 3 distinct antennal segments, instead of I-2, and lack a lacinia and a penicillus. Chrysomelinae pupae differ in that if they bear a few long setae, the paired apical spines are absent. Those of the Galerucinae-Halticinae possess a few long dorsal setae and paired apical spines. The nodulus of the spermathecae is undilated in the Chrysomelinae whereas it is usually dilated in the other two subfamilies. The position of the antennal insertion is an important character separating the adults of the Galerucinae and Halticinae from the Chrysomelinae. Chen (1940), was probably incorrect in considering that this character to be of secondary importance.

#### F. The Galerucinae-Halticinae group.

The separation of these from the Chrysomelinae by Jacoby (1908) forming the Trichostomata is considered to be valid. The Galerucinae of Crowson (1955), corresponds to Jacoby's Trichostomes and the subfamilies Galerucinae and Halticinae. The difficulty of making any clear separation between the Galerucinae and Halticinae has long been recognised, particularly in relation to the larvae (Crowson 1955). The larvae share the common ocellar number of 0-I, the lacinia is present, there is usually a penicillus in the mandible, the claws have pulvilli and the head and body chaetotaxy is similar. The larvae cannot be separated into their respective subfamilies. Their pupae are usually white or cream and have few moderately long setae and paired terminal spines, while pupation usually occurs in the ground. The adults have similar wing venation with one anal cell and cross veins r-m and cu-an present or absent. The spermathecal structure is similar with the nodulus dilated and the spermathecal duct uncoiled.

#### G. The Cassidinae.

The Cassidinae and Hispinae form the Cryptostomes of Chapuis (1874). The subfamily Hispinae of Crowson (1955), corresponds exactly to the old group Cryptostomes and to the subfamilies Hispinae and Cassidinae of the commonly accepted classification. Crowson, considered that although typical Hispines look quite unlike typical Cassidines, the two groups are

connected by an almost perfect series of transitional forms in adult structure and it seems doubtful whether they can be distinguished in the larval stage either. Chen (1940), gave them the family status of Cassididae and stated that their head orientation, wing venation and male genitalia were similar to the Eumolpidae. Later, Chen (1973), included the families Cassididae and Hispididae in a new superfamily, the Cassidoidea using head, antennal, abdominal and tarsal characters.

Their larvae have 5 instars, are without the epicranial suture, possess lateral scoli and a terminal fork and always pupate on the foodplant. These differences separate them from all the other subfamilies. Their pupae have lateral scoli similar to the larvae. Their adults have wings with 2 anal cells and cross veins r-m and cu-an absent as in the Clytrinae-Cryptocephalinae. They resemble the last two subfamilies in the position of the attachment of the tegmen to the median lobe, in the dorso-ventral flattening of the tegmen and the long coiled spermathecal duct. The spiculum gastrale is absent<sup>as</sup> in the Lamprosomatinae and in some Chrysomelinae and Galerucinae. The adult is always the overwintering stage as in the Criocerinae, Chrysomelinae, Galerucinae and Malticinae. The Cassidinae are the only British subfamily which lay their eggs singly or in groups within brown oothecae.

## 2. Generic Groupings

### A. Within the Donaciinae

#### (i) Donacia-Plateumaris (Table 25)

The apex of the lateral lobe of the aedeagus is usually bilobed and the wings possess an anal cell and cross vein cu-an. Tarsal segment 5 is not longer than I-4 combined and the elytral apices are untoothed.

#### (ii) Macrolea

The apex of the lateral lobe of the aedeagus is rounded and the wings are without the anal cell and the cross vein cu-an. Tarsal segment 5 is longer than I-4 combined and the elytral apices are toothed.

### B. Within the Criocerinae (Table 25)

#### (i) Lilioceris-Crioceris

The larvae with seta  $f_3$  present on the frons, the laolinia absent,

TABLE 25 TAXONOMIC AND BIOLOGICAL CHARACTERS IN THE GENERA OF THE DONACIINAE, CRIOCERINAE AND CLYTRINAE

DONACIINAE

GENUS	Apex of lateral lobe	Anal Cell	Cross vein cu-an	Elytral apices toothed	Tarsal segment 5 longer than 1-4 combined
DONACIA	bilobed	+	+	-	-
PLATEUMARIS	bilobed	+	+	-	-
MACROPLEA	rounded	-	-	+	+

CRIOCERINAE

GENUS	Claws	Frons with setae f <sub>3</sub>	Lacinia	Tubercle EPP on prothorax	Tubercle EPA in meso & meta thorax	Tubercle Es & Ss in abdomen	Feeding upon
LEMA	connate	-	+	bi setate	uni setate	-	Graminaceae Composite
CRIOCERIS	simple	+	-	tri setate	tetra setate	+	Liliaceae
LILIOCERIS	simple	+	-	tetra setate	tetra setate	+	Liliaceae

CLYTRINAE

GENUS	Apex of Median lobe setate	Apex of m.l. much broader than proximally	Sperm aithecal duct coiled	Larval head with sulcat ions	Eggs laid singly & dropped to the ground
CLYTRA	+	+	-	+	+
LABIDOSTOMIS	-	-	+	-	-
GYNANDROPHTHALMA	-	-	+	-	-

3-4 setae present on tubercle EPp of the prothorax, tubercle EPa tetrasetate in the meso and metathorax and tubercles Es and Ss present in the abdomen. The adults possess free, simple claws. Feeding upon Liliaceae in the adult and larval stages.

(ii) Lema

The larvae are without seta  $f_3$  on the frons, the lacinia always present, 2 setae present on tubercle EPp of the prothorax, tubercle EPa unisetate in the meso and metathorax and tubercles Es and Ss absent in the abdomen. The adults possess connate claws. Feeding upon Gramineae and Compositae in the adult and larval stages. Crowson (1955) stated that the lacinia is absent in the larvae of Lema.

C. Within the Clytrinae (Table 25 )

(i) Labidostomis-Gynandrophthalma

The apex of the median lobe of the aedeagus is without setae and is not much broader than the proximal part. The spermathecal duct is coiled. The eggs in Labidostomis are attached in groups by pedicels to the leaves of the foodplant.

(ii) Clytra

The apex of the median lobe of the aedeagus bears setae and is much broader than the proximal part. The spermathecal duct is uncoiled. The eggs are covered by excremental bracts and dropped singly to the ground.

D. Generic groupings within the Chrysomelinae (Table 26 ).

(i) Timarcha

The first instar larvae are without distinct dorsal tubercles and have hatching spines on the meso, metathorax and first abdominal segment. There are 3 larval instars and the head bears numerous minute setae. The post clypeus also bears numerous large setae. The larval claws are without an inner tooth and no glands are present in the later abdominal segments. Meso and metathoracic and abdominal eversible glands are absent. There are only 7 pairs of abdominal

TABLE 26 TAXONOMIC AND BIOLOGICAL CHARACTERS IN THE GENERA OF THE CHRYSOMELINAE

GENUS	ADULT					LARVA										PUPA					BIOLOGY						
	AEDEAGUS	SPERMATHECA	WING	Claws appendiculate	Sperm. - Hinds wings	Cross vein r-m	Dorsal tubercles in 1st instar	Hatching spines in 1st abdominal seg.	Number of Larval instars	Number of pairs of abdominal spiracles	Setae on Frons	Setae on Vertex	Setae on Post clypeus	Claws with inner tooth	Eversible glands in thorax & abdomen	Glands in final abdominal segs.	Tubercles Epp in prothorax	Pupa tion on food plant	Pupal colour	Setae	Spines at apex of abdomen	Number of setae on femoral apices	Eggs over winter	Egg colour	Eggs laid within plant tissue	Ovo-viviparity	Adult Summer diapause
TIMARCHA	Spiculum gastrale	+	-	+	-	-	-	+	3	7	many minute	many minute	15-23	-	-	-	+	-	Red	many minute	+	0	Diapause single	Red	-	-	-
LEPTINOTARSA	U	-	+	+	+	+	+	+	4	8	f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	6 v <sub>1</sub> -v <sub>6</sub>	3 prs	+	-	Between segs. 8-9	-	-	Yellow	many long	+		-	Yellow	-	-	+
CHUKYSOLINA	Y or V	-	-	+	+	+	+	+	4	8	f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	4-7 v <sub>1</sub> -v <sub>7</sub>	3 prs	+	-	Between segs. 8-9	-	-	Orange Yellow White	many long	+	2-5	+	Red Orange Brown White	-	+	-
PHYTODECTA	V	-	+	-	+	+	+	+	4	8	f <sub>1</sub> f <sub>2</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	5 v <sub>1</sub> v <sub>2</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	3 prs	+	-	Between segs. 7-8	-	-	Green White	many long	+	2-5	-	White	-	+	+
PHYLLODECTA	Y	-	+	+	+	-	+	-	3	8	f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	4 v <sub>1</sub> v <sub>2</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	2 prs	-	+	-	+	-	White	few short	-	2-3	-	White	-	-	-
GASTROIDEA	-	-	-	+	+	-	+	-	3	8	f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	4 v <sub>1</sub> v <sub>2</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	3 prs	-	+	-	+	-	Yellow	few short	-	2-3	-	Yellow	-	-	-
PHAEDON	Y	-	-	+	+	-	+	-	3	8	f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	4 v <sub>1</sub> v <sub>2</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	3 prs	-	+	-	+	-	Yellow	few short	-	2-3	-	Yellow	+	-	-
HYDROTE-ASSA	V	-	-	+	+	-	+	-	3	8	f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	3, 4 v <sub>1</sub> v <sub>2</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	2 prs	-	+	-	+	-	Yellow	few short	-	2-3	-	Yellow	+	-	-
BRASOCURIS	V	-	-	+	+	-	+	-	3	8	f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	3 v <sub>1</sub> v <sub>2</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	2, 3 prs	-	+	-	-	+	Yellow	few short	-	2-3	-	Yellow	+	-	-
CHRYSOMELA	U	-	-	+	+	-	+	-	3	8	f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> f <sub>5</sub> f <sub>6</sub>	4-6 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>5</sub> v <sub>6</sub>	3 prs	+	+	-	+	+	Cream or White block	very few minute	-	2	-	Pale Yellow	-	-	-
QUAGIODERA	U	-	-	+	+	-	+	-	3	8	f <sub>3</sub> f <sub>4</sub> f <sub>6</sub>	3 v <sub>1</sub> v <sub>2</sub> v <sub>3</sub> v <sub>4</sub> v <sub>6</sub>	3 prs	-	+	-	+	+	Cream	very few minute	-	2	-	Pale Yellow	-	-	-

spiracles and the tubercle EPp is present on the prothorax. The pupae are pale red and bearing numerous minute setae and an apical bifid spine but no setae are present at the femoral apices. Pupation occurs in the ground. The adults have a lateral lobe in the aedeagus and wings are absent. Both adults and eggs overwinter. The eggs diapause as the fully developed embryo and hatch in the spring. The adults have a very long oviposition period, ovipositing in two seasons, which are not separated by a diapause. Timarcha is probably related to the following group.

(ii) The Chrysolina, Leptinotarsa and Phytodecta group

The first instar larvae have distinct dorsal tubercles and hatching spines on the tubercle DLpi in the meso, metathorax and the first abdominal segment. There are 4 larval instars. The head bears 5 setae ( $f_1 f_2 f_3 f_4 f_6$ ) on the frons, 4-7 setae ( $v_1 v_2 v_3 v_4 v_5 v_6 v_7$ ) on the vertex and 6 setae on the post clypeus. The larval claws have an inner basal tooth. Paired glands are present in abdominal segment 9 or between abdominal segments 7 and 8. Meso, metathoracic and abdominal eversible glands are absent. There are 8 pairs of abdominal spiracles and the tubercle EPp is absent in the prothorax. The pupae are orange, yellow, or white and bear numerous large setae and single or paired apical spines. The femoral apices bear 2-5 large setae. Pupation occurs in the ground. The adults are without a lateral lobe in the aedeagus and have wings with the cross vein r-m present. The adult is the usual overwintering stage although in some Chrysolina species the egg overwinters but is not diapausing. Phytodecta adults have very long oviposition periods being able to oviposit in 2 seasons and a diapause occurs between the 2 periods. Phytodecta adults and also some Chrysolina adults are without spermathecae, this being associated with ovoviviparity.

(iii) The Phyllodecta, Phaedon, Gastroidea, Hydrothassa and  
Prasocuris group

The first instar larvae have distinct dorsal tubercles and bear hatching spines on the tubercle DLpi in the meso and metathorax. There are 3 larval instars. The head usually has 4 setae on the frons ( $f_1$   $f_3$   $f_4$   $f_6$ ) seta  $f_2$  absent, 3-4 setae on the vertex ( $v_1$   $v_3$   $v_4$   $v_6$ ) seta  $v_5$  absent and 4-6 setae on the post-clypeus. The larval claws have the inner tooth absent. Paired glands are absent in the final abdominal segments but meso, metathoracic and abdominal eversible glands are present. There are 8 pairs of abdominal spiracles and tubercle EPp is usually present in the prothorax. The pupae are yellow or white, bear few moderately long setae but are without apical spines and the femoral apices bearing 2-3 setae. Pupation usually occurs in the ground. The adults lack a lateral lobe in the aedeagus and have wings without the cross vein r-m. The adult is always the overwintering stage and there is neither an egg diapause or an adult summer diapause. The adults lay eggs singly or in batches over a 2-3 month period and probably do not oviposit in the second year. The habit of laying eggs singly occurs in Phaedon, Hydrothassa and Prasocuris.

The classification by Weise (1915-1916) in which Phyllodecta is included with Phytodecta in the tribe Phyllodectinal because the claws of the adults are appendiculate is not valid as there are many more important adult, larval and pupal differences between these two genera. Paterson (1931) and Kimoto (1957) grouped Hydrothassa and Prasocuris separately on larval taxonomy and biology. However, the genera Hydrothassa and Prasocuris should be placed in the same generic group as Phaedon, Phyllodecta and Gastroidea. The setae on the frons and vertex of Prasocuris larvae are identical with those of Phaedon larvae while those of Hydrothassa larvae are identical with Gastroidea and Phyllodecta larvae. The presence of four setae on the post-clypeus

of Prasocuris and Hydrothassa larvae indicates a closer relationship to Phyllodecta which also bears two post clypeal setae. The pupal chaetotaxy is similar in all these genera although the pupae of Hydrothassa are yellow as in Gastroidea and Phaedon whilst they are white in Phyllodecta. The habit of oviposition within the foodplant is common to the adults of Hydrothassa, Prasocuris and some Phaedon species. The eggs are yellow in Hydrothassa, Prasocuris, Phaedon and Gastroidea whilst in Phyllodecta they are white. Pupation occurs within earthen cells although according to Kimoto (1957) pupation in Hydrothassa and Prasocuris occurs on the leaves of the foodplant. However, in this study Hydrothassa marginella and H. aucta pupated within earthen cells and not on the foodplant whilst Prasocuris phellandrii pupates within the stems of its aquatic foodplant. Paterson (1931) also included Chrysomela in the generic group (iii) on larval body chaetotaxy. While it is admitted that there are larval similarities and the adult wing venation and male genitalia are similar there are important differences which are considered sufficient to justify the exclusion of Chrysomela.

#### (iv) The Chrysomela, Plagioderia group

The first instar larvae have distinct dorsal tubercles and bear hatching spines on the tubercle DLpi in the meso and metathorax. There are 3 larval instars. On the head the frons bears 3-5 setae ( $f_1$   $f_3$   $f_4$   $f_5$   $f_6$ ;  $f_1$  &  $f_5$  may be absent), the vertex bears 4-6 setae ( $v_1$  -  $v_6$ , seta  $v_2$  always present, seta  $v_5$  often absent), and the post clypeus bears 6 setae. The claws of Chrysomela larvae possess an inner tooth which is absent from the larval claws of Plagioderia. Paired glands are absent from the final abdominal segments and meso and metathoracic and abdominal eversible glands are present. There are 8 pairs of abdominal spiracles and tubercle EPp is always present in the prothorax. The pupae are white or cream with the integument thickened or bearing dark brown tubercles but few minute setae.



Femoral apices bear 2 setae but apical abdominal spines are absent. Pupation occurs on the leaves of the foodplant. The adults are without a lateral lobe in the aedeagus and cross veins r-m and cu-an are absent in the wings. The spiculum gastrale is U-shaped and consists of a single piece. The adult is always the overwintering stage and an egg diapause does not occur. However, there may be an adult summer diapause in Chrysomela. The adults lay eggs in batches of about 20 in early summer and new generation adults emerge in August. The larvae feed upon Salix and Populus.

E. Generic groups within the Galerucinae (Table 27 )

(i) The Galeruca, Agelastica group

The head of the larvae bears 1 pair of ocelli, the frons bears 3 ( $f_1 f_3 f_6$ ) or 4 setae ( $f_1 f_3 f_4 f_6$ ) the vertex bears 4-5 setae ( $v_2 v_3 v_4 v_5 v_6$ ), and the gena bears 5 setae while the penicillus is absent from the mandible. The fused tubercles DLae - DLpe in the meso and metathorax bear 5 or more setae. Tubercles Dal and Dae in the abdomen are fused as are the tubercles Dpi and Dpe. The pupa bears 3 pairs of dorsal setae in the abdomen. Pupation within earthen cells. In the male genitalia of the adults the spiculum gastrale is absent and the base of the tegmen is unhooked. In the wings the vein r-m is present and the claws in Galeruca are bifid whereas in Agelastica they are appendiculate. Eggs are laid in batches, those of Galeruca in an ootheca. In Galeruca there is a winter egg diapause and an adult summer diapause before oviposition commences in late summer. In Agelastica the adults overwinter, oviposit during the early summer and diapause during late summer.

It is considered that there are sufficient common adult, larval and pupal differences from other genera to justify the inclusion of Galeruca and Agelastica in a separate tribe.

TABLE 27 TAXONOMIC AND BIOLOGICAL CHARACTERS IN THE GENERA OF THE GALERICINAE

GENUS	ADULTS				LARVAE												PUPA	BIOLOGY				
	Spiculum gastrale	Hook at base of tegmen	Cross vein r-m	Claws	Number of Ocelli pairs	Setae on Frons	Setae on Vertex	Setae on Gena	Setae on Post-clypeus	Penicillus	Segmental glandular pores	Tubercle on abdomen	Tubercle on abdomen	Tubercle on abdomen	Tubercle on prothorax	Tubercle on mesothorax & metathorax	Dorsal setae on pupae	Eggs laid singly	Winter egg diapause	Larvae over winter	Adults over winter	Adults Summer diapause
GALERUCA	-	-	+	Bifid	1	4 f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> 6	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	5	8	-	-	+	+	+	8	5	3	-	+	-	-	+
AGELASTICA	-	-	+	Appendiculate	1	3 f <sub>1</sub> f <sub>3</sub> f <sub>6</sub>	5 v <sub>2</sub> -v <sub>6</sub>	5	4-6	-	+	+	+	+	1	5	3	-	-	-	-	+
SERMYLA	+	-	-	Appendiculate	0	4 f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> 6	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	5	6	+	+	+	-	-	1	3	1	-	+	-	-	-
PHYLLOBROTICA	+	-	-	Appendiculate	0	3 f <sub>1</sub> f <sub>3</sub> f <sub>6</sub>	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	5	8	+	-	+	-	-	1	3	-	-	+	+	-	-
LUPERUS	+	-	-	Appendiculate	0	4 f <sub>1</sub> f <sub>3</sub> f <sub>4</sub> 6	4 v <sub>2</sub> v <sub>3</sub> v <sub>4</sub>	5	8	+	-	+	-	-	1	3	-	-	-	+	-	-
GALERUCELLA	-	+	+	Bifid	1	3 f <sub>1</sub> f <sub>3</sub> f <sub>6</sub>	2-4 v <sub>2</sub> *v <sub>3</sub> v <sub>4</sub> v <sub>6</sub>	2-4	8	+	-	-	-	-	2-3	3	1	+	+	-	-	+
LOCHMAEA	-	+	+	Bifid	1	3 f <sub>1</sub> f <sub>3</sub> f <sub>6</sub>	3-4 v <sub>2</sub> *v <sub>3</sub> v <sub>4</sub> v <sub>6</sub>	3	8	+	-	-	-	+	2-5	3	1	+	+	-	-	+

r = reduced

\* = reduced or absent.

(ii) The Sermyla, Phyllobrotica and Luperus group

The head of the larvae is without ocelli, the frons usually bearing 3 setae ( $f_1 f_3 f_6$ ) except in Sermyla which bears 4 setae ( $f_1 f_3 f_4 f_6$ ), the vertex bears 4 setae ( $v_2 v_3 v_4 v_6$ ) and the gena bears 5 setae while the penicillus is present in the mandible. The fused tubercle DLae - DLpe in the meso and metathorax bears 3 setae. The tubercle Dai is present in the abdomen but is not fused with Dae, the tubercle Dpi is absent, while the tubercle DLpe is unisetate. The pupae bear one pair of dorsal setae in the abdomen. Pupation occurs within earthen cells. In the male genitalia of the adults the spiculum gastrale is present and the base of the tegmen is unhooked. In the wings the cross vein r-m is absent and the claws appendiculate. Eggs are laid in batches in the ground. The adults do not overwinter but in Sermyla and to a lesser extent in Phyllobrotica the eggs diapause over the winter.

In Sermyla and Phyllobrotica diapause occurs at a very early embryonic stage although it may not be obligatory because some of the Phyllobrotica ova hatched without diapausing. Thus it is probable that Phyllobrotica larvae from non diapausing eggs overwinter in the field. However in S. halensis an obligatory diapause occurred in all ova. These eggs overwinter and hatch the following spring. Diapause is terminated at the beginning of December but the eggs are prevented from hatching by the low ambient temperature.

In Phyllobrotica and Luperus the larvae overwinter. There is no adult diapause.

(iii) The Galerucella-Lochmaea group

The head of the larvae bears one pair of ocelli, the frons bears 3 setae ( $f_1 f_3 f_6$ ), the vertex bears 2-4 setae ( $v_2 v_3 v_4 v_6$ ) some of which are reduced or absent and the gena bears 4-5 setae while the penicillus may be present or absent from the mandible. The fused

tubercles DLae-DLpe in the meso and metathorax bear 3 setae and tubercle Dai is absent from the abdomen except in L. suturalis where it is present and fused with the tubercle Dae. Tubercle Dpi is absent and the tubercle DLpe is unisetate, except in L. crataegi where it is bisetate. The pupae bear one pair of dorsal setae in the abdomen. Pupation usually occurs within earthen cells although in G. sagittariae and G. nymphaeae leaf pupation occurs. In the male genitalia of the adults the spiculum gastrale is absent and the base of the tegmen is hooked. In the wings the cross vein r-m is reduced and the claws are bifid. Eggs of Galerucella are usually laid in batches whereas in Lochmaea they are laid singly or in twos or threes. The adult is the usual overwintering stage. However, in G. viburni, adults do not overwinter but there is an egg diapause, the eggs being laid in autumn in Viburnum stems.

Laboissiere (1934) divided the Galerucinae into two tribes, the Galerucini and the Luperini on the position of the antennal insertion and the disposition of the anterior epimeres. The Galerucini included the subtribes Galerucina and Coelomerina in which the claws are bifid. In the Galerucina including Galeruca, the apices of the anterior epimeres are contiguous whereas in the Coelomerina including Lochmaea and Galerucella they are distant. The Luperini contained the subtribe Luperina containing the genera Agelastica, Sermyla, Phyllobrotica and Luperus. From this classification it is apparent that Agelastica and Galeruca are not closely related. If the similarities in larval and pupal morphology as well as adult wing venation and male genitalia are taken into account it is considered that Agelastica is undoubtedly more closely related to Galeruca than to the Sermyla, Phyllobrotica and Luperus group.

F. Generic groups within the Halticinae (Table 28 )

The constancy of characters between the genera within the Halticinae makes it difficult to separate the subfamily into generic groups.

Joy (1932) divided this subfamily into 2 tribes, the Halticini and Aphthonini using the presence or absence of an impressed line or fovea at the base of the pronotum in the adult. However, if larval morphology and the adult wing venation, male genitalia and spermathecae are compared then this division is not valid. Certain genera such as Haltica from the Halticini and Psylliodes from the Aphthonini have similar venation.

(i) Sphaeroderma, Crepidodera

In the adults the cross vein r-m is strongly developed in the wing and the fused collum and ramus is uncoiled in the spermatheca. The larvae overwinter and the adults both feed on Compositae.

B = BRACHYPTEROUS      S = SIMPLE      A = APPENDICULATE.

TABLE 28 TAXONOMIC AND BIOLOGICAL CHARACTERS IN THE GENERA OF THE HALTICINAE

	HIND WINGS	RADIAL TRIANGLE	ANAL CELL	CROSS VEIN r-m	COLLUM COILED	BASAL IMPRESSED LINE OR FOVEA ON THORAX	HATCHING LEAF SPINES	LEAF MINERS	SETA f <sub>2</sub> ON FRONS	OVER WINTER AS ADULTS	OVER WINTER AS LARVAE	ADULT CLAWS
EPITRIX	+	-	-	-	-	+	+	-	-	+	-	S
PODAGRICA	B	-	-	-	-	+	+	-	-	-	+	A
MANTURA	+	+	-	+	+	+	-	+	-	+	-	S
HERMAEOPHAGA	B	-	-	-	-	+	+	-	+	+	-	A
HALTICA	+	+	+	+	+	+	+	-	-	+	-	A
HIPPIURIPHILA	+	+	-	+	+	+	-	+	-	+	-	S
OCHROSIS	+	-	-	-	+	+	?	?	?	?	?	A
CREPIDODERA	+	+	+	+	-	+	+	-	+	-	+	A
DEROCREPIS	B	-	-	-	-	+	+	-	+	?	-	A
CHALCOIDES	+	+	+	+	-	-	+	-	+	+	-	A
PSYLLIODES	+	+	+	+	+	-	+	+	+	+	+	S
MNIOPHILA	-	-	-	-	-	-	?	?	?	?	?	S
SPHAERODERMA	+	+	+	+	-	-	-	+	-	-	+	A
CHAETOCNEMA	+	+	+	+	+	-	+	-	+	+	-	S
LONGITARSUS	+	+	-	-	+	-	+	-	+	+	+	S
APTEROPEDA	-	-	-	-	-	-	-	+	-	+	-	S
BATOPHILA	-	-	-	-	+	-	?	-	?	+	-	A
PHYLLOTRETA	+	+	+	+	-	-	+	+	+	+	-	S
DIBOLIA	+	+	-	+	-	-	?	+	?	+	-	A
LYTHRARIA	+	-	-	-	+	-	?	?	?	?	?	S
APHTHONA	+	+	-	-	-	-	-	+	+	+	-	S

## DISCUSSION

This study of the adult, larval, pupal and biological characters of representative species from many of the genera and all of the subfamilies of the British Chrysomelidae shows that no significant changes are required in the present classification. However, the genera Hydrothassa and Prasocuris should be placed in the same generic group as Phaedon, Phyllodecta and Gastroidea. In these genera the adult, larval, pupal and biological characters complement each other. The Galerucinae should be divided into three tribes, the first including Galeruca and Agelastica, the second Sermyla, Phyllobrotica and Luperus and the third Galerucella and Lochmaea. The adult, larval, pupal and to a lesser extent the biological characters complement each other within these three tribes of the Galerucinae.

British chrysomelid beetles may overwinter as adults, larvae or ova. In addition many have adults with a summer reproductive diapause. A very few aestivate as adults for example Galeruca tanacetii although it is unusual to find aestivation in temperate insects where both the Spring and Summer are favourable breeding seasons. It is probable that the genus Galeruca evolved in regions where the summers were hot and dry. This is substantiated by the Southern European, Asian and North African distribution of the genus.

Galeruca is unusual in the British Chrysomelidae in having two periods of arrested development in the life cycle. Galeruca is a short day insect and aestivation is induced by photoperiods longer than 14 hours operating during the adult life. The effect is modified by temperature and the critical photoperiod is shorter at high temperatures. The effects of long days are reinforced by high temperature as, in examples of autumn diapause, the effects of short days are often reinforced by low temperatures (Siew, 1965, 1966). The same type of Winter egg diapause occurs in Galeruca tanacetii, Sermyla

halensis and Galerucella viburni. This type of egg diapause is not restricted to the Coleoptera but has also been reported in Chesias legatella in the Lepidoptera (Wall, 1974). Winter egg diapause occurs in representatives of the three tribes of the Galerucinae and taxonomic characters are better indicators of true relationships. Taxonomic characters are not influenced by environmental conditions and the growth habit of the foodplants as are biological characters.

The influence of environmental conditions upon biology is well illustrated by the potentially ovoviviparous Phytodecta viminalis and P. olivacea. In Southern England P. viminalis is ovoviviparous depositing groups of very small orange larvae (Williams, 1914). In Germany the adults lay reddish, cylindrical eggs which hatch on the first day (Cornelius, 1857). It is concluded that P. viminalis can under different conditions, be either viviparous or oviparous.

It is significant that no spermatheca occurs in the four British species of the genus Phytodecta and thus spermathecal disappearance is associated with ovoviviparity. A spermatheca is present in the oviparous P. scutellaris Baly and P. rubripennis Baly from Japan. The adults of P. viminalis do not lay a second batch of larvae and mate frequently which suggest that there is probably no need for an organ of sperm retention (Williams, 1914). In P. olivacea the spermatozoa are stored in the sperm chamber at the top of the pedicel of the fully formed egg and migrate upwards to the next egg immediately before ovulation, (Donia, 1958). It is probable that viviparity is associated with insects from the Northern hemisphere or those living at high altitudes where the summers are short. Phytodecta species are chiefly confined to the colder areas of the Northern hemisphere where the period for maximum growth is somewhat shorter than elsewhere. Certain species of the related genus Chrysolina also lack a spermatheca. Amongst these are C. varians, C. hyperici and C. brunsvicensis.



However, although only C. varians is ovoviviparous it is probable that C. hyperici and C. brunsvicensis which are oviparous in Britain are potentially viviparous under colder conditions. C. varians is distributed over the northern and temperate parts of Eurasia and may be found up to 2,000 metres. Both the foodplant, Hypericum spp. and the adults are very resistant to low temperatures and are able to maintain their place in the mixed glacial fauna and flora. The complete development of the species is rapid and takes 27 days including the larval and pupal periods which last 20 and 7 days respectively. However, in C. hyperici complete development including egg incubation and post embryonic development required 66 days (Rethfeldt, 1924). Thus viviparity would confer a distinct advantage over ovoviviparity in those species in which there is the possibility of a second generation in favourable years. However, in this study, the adults of P. pallida and C. varians did not produce a second generation. C. hyperici and C. brunsvicensis both Chrysomelids of the Northern hemisphere are adapted in other ways to survive low temperature winter conditions and short summers. Their adults have a summer reproductive diapause but rarely overwinter. Reproductive diapause probably serves as a safety mechanism preventing egg laying and hatching during the late autumn. It prevents egg laying until the environmental temperatures fall to the normal winter levels. However, their overwintering eggs are resistant to low temperatures and hatch in early April. The very early hatch confers an advantage upon these two species comparable with that of viviparous species. Similarly the eggs of Timarcha tenebricosa hatch very early in the Spring after an obligatory diapause. The adults have a very long oviposition period from May until the end of September and hibernate over the Winter. They are able to oviposit in two seasons separated by hibernation. The eggs develop normally to the fully developed embryo in about 50 days and then enter diapause. The species overwinters as an adult or as a diapausing ovum. Chrysolina

fastuosa is also adapted to survive in Northerly latitudes. Egg laying occurs in late summer and development is rapid. The adults have a very long reproductive diapause and do not produce eggs until their second year.

Many Coleoptera reproduce during more than one season. In Leptinotarsa the oocytes are continually formed and resorbed during hibernation (De Wilde, 1954). This continuation of oogenesis is probably characteristic of species in which the adult is capable of reproducing in more than one season and is found frequently in the Chrysomelidae. In P. olivacea the new generation females emerge from the pupal stage in the summer with undeveloped ovaries. After feeding for approximately two weeks they diapause. The true diapause lasts until January or February and is followed by a period of low temperature quiescence. Usually immature females emerge again late in the spring with the rise in temperature. After the first season of oviposition the females enter diapause for the second and last time in late Summer and emerge again next Spring to start the second oviposition cycle. More work is needed to improve our understanding of diapause in the adults of Chrysomelid beetles. The factors initiating diapause are seldom known and diapause often appears to be obligate. Most Chrysomelids oviposit in only one season and the new generation adults do not oviposit the same year but enter a reproductive diapause. Most of these are long day insects which oviposit in the Spring and early Summer whilst a few such as Galeruca tanacetii, Sermyla halensis, Galerucella viburni, Chrysolina hyperici, C. brunsvicensis and Psylliodes chrysocephala are short day insects which oviposit in the Autumn and Winter. The females of many Chrysomelid species for example Timarcha are fertilized before hibernation and egg laying begins very soon after emergence in the Spring.

The stage in which overwintering occurs may differ even in the same species. In Rumania Podagrica fuscicornis L. overwinters as

adults whilst in Germany it is the larvae of this species which overwinter within the roots of *Malva* (Van Emden, 1929).

The habitat of the host plant may also influence other biological characters for example the position of pupation. Leaf pupation has evolved in many species which feed on aquatic plants or on plants living in areas liable to flooding where the pupae would perish in waterlogged soil. Thus leaf pupation occurs in Cassida spp. some of which feed on Mentha and Inula, in Chrysomela and Plagiodera which feed on Salix spp. near water and in G. sagittariae and G. nymphaeae which feed on the aquatic plants Polygonum aquaticum, Sagittaria and Nymphaea.

In this study the adult, larval and pupal morphological characters tend to indicate the same relationship both at subfamily and tribal levels. Biological characters such as viviparity, winter egg diapause, summer adult diapause and reproductive cycles are less reliable indicators of such relationships as they are influenced by environmental conditions. Instar number is the only biological character which has been found to be a reliable character.

14. SUMMARY

1. The adult characters of aedeagus, spermatheca, wing venation and claw structure are described. Keys are produced to the subfamilies, genera and species excluding the genera Longitarsus and Haltica.
2. The aedeagus can be used to separate species but its variability within genera prevents its use as a generic character. The shape and size are constant, the apex proving to be the most useful character. In genera possessing species with similar apices, size can be used. The presence or absence of the lateral lobe can be used to group subfamilies. Cryptocephalus species can be grouped using the shape of the apex of the median lobe.
3. The spermatheca is useful at the subfamily level and its shape is usually constant within a genus. Thus it can be used to separate genera. However, it is not as good a specific character as the shape of the apex of the median lobe. Chrysolina species can be grouped using the shape of the spermatheca.
4. Wing venation is a very good character at the subfamily level and also good at the tribal level. It is not a good specific character.
5. Although claw structure is not a good character for indicating relationships at the subfamily level, it is sometimes useful in forming generic groups. It is of little use as a specific character because it is so constant intra-genericly.
6. Head and body larval chaetotaxy is described for representatives from all of the subfamilies. Both are good characters at the subfamily, tribal and specific levels. Chaetotaxy is slightly variable intraspecifically in the later instars but the primary chaetotaxy is usually constant. A subfamily key and generic keys to the Criocerinae, Chrysomellinae and Galerucinae-Halticinae are produced.

7. The pupal chaetotaxy is described for representatives of 8 of the 11 subfamilies found in Britain. Chaetotaxy is useful at the subfamily and tribal levels. However it is difficult to separate certain genera and species using this character. Pupal colour can be used to make generic groupings, e.g. within the Chrysomelinae. A subfamily key to the pupae is made.
8. The biology of representatives from all the subfamilies is described. The biology to a slight extent supports generic groupings based upon adult, larval and pupal characters. The foodplant range can only rarely be used to indicate subfamily relationships. The more recent subfamilies feed upon a wider host range and yet their species are probably more host specific.

## APPENDICES

TABLE 1. Previous Taxonomic works on the Aedeagus of the British species  
of the Chrysomelidae,

<u>Subfamily/Genera studied</u>	<u>Author</u>	<u>Useful Characters</u>
Not stated	Baly 1879	
Galerucinae/ <u>Galerucella</u>	Weise 1889	Not a detailed work
Halticinae/ <u>Longitarsus</u>	Tomlin & Sharpe 1911	Not entirely reliable
Chrysomelinae/ <u>Phaedon</u>		
Galerucinae/ <u>Galerucella</u>	Joy 1932	
Halticinae/ <u>Haltica</u>		
Criocerinae/ <u>Crioceris asparagi</u> L.		Dorsal and lateral views
Chrysomelinae/ <u>Leptinotarsa decemlineata</u> Say.	Powell 1941	Good as includes other parts of aedeagus
" <u>Plagioderma versicolora</u> Laich		
" <u>Gastroidea polygoni</u> L.		
Galerucinae/ <u>Galerucella</u>	Hincks 1950	Good dorsal and lateral views but no scale
Halticinae/ <u>Chaetocnema</u>		Good ventral and lateral views but no scale
<u>Mantura</u>		
<u>Podagrica</u>	Heikertinger 1951	
<u>Batophila</u>		
<u>Crepidodera</u>		
Halticinae/ <u>Haltica</u>	Kevan 1962	Median Depression or furrow Sulcation of ventral face Good dorsal and ventral views and measurements
Halticinae/ <u>Longitarsus</u>	Strand 1962	Photographs
Halticinae/ <u>Longitarsus</u>	Mohr 1962	Drawings appeared to Kevin 1969 as more waisted than newly extracted specimens
Halticinae/ <u>Longitarsus</u>	Kevan 1967	Central channel or medio-dorsal depression in median lobe & size useful Good dorsal views of median lobe and scale
All subfamilies	Freude, Harde & Lohse 1966	Good dorsal and lateral views of median lobe.

TABLE 2. Previous Taxonomic works on the spermatheca of the  
British Chrysomelidae.

<u>Subfamily/Genera &amp; Species Studied</u>	<u>Reference</u>
Donaciinae <u>Donacia semicuprea</u> Panz.	Spett & Lewitt 1927
Halticinae <u>Phyllotreta cruciferae</u> (Goez.)	Varma 1955
Donaciinae <u>Donacia clavipes</u>	
Criocerinae <u>Crioceris asparagi</u>	
Cryptocephalinae <u>Cryptocephalus aureolus</u>	Donia 1958
Chrysomelinae <u>Chrysolina menthastri</u>	
<u>Gastroidea polygoni</u>	
<u>Phaedon cochleariae</u>	
<u>Chrysomela populi</u>	
<u>Phyllodecta vitellinae</u>	
<u>Timarcha tenebricosa</u>	
Galerucinae <u>Galeruca tanacetii</u>	
<u>Lochmaea suturalis</u>	
Halticinae <u>Longitarsus jacobaeae</u>	
<u>Haltica palustris</u>	
Cassidinae <u>Cassida viridis</u> L.	
Halticinae <u>Haltica</u> (all species)	Kevan 1962
Halticinae <u>Longitarsus</u> (all species)	Kevan 1967
Halticinae <u>Longitarsus</u>	Allen 1967



TABLE 3. Previous taxonomic works on the larvae of British Chrysomelidae

Subfamily	Genus	Species	Reference	Keys and	
				General Description	Detailed Chaetotaxy
Donaciinae	<u>Donacia</u>	<u>simplex</u>	Paterson 1931		Head & Body (1st instar)
	<u>Donacia</u> & <u>Haemonia</u>		MacGillivray 1903	Generic Key	
	<u>Donacia</u> sp.		Peterson 1951	General description	
Criocerinae	<u>Crioceris</u>	<u>asparagi</u> (L.)	Peterson 1951	General description	
	"	"	Saisbury 1943	Generic Key to Crioceris & Lema	Head and Body (Final)
	"	"	Balachowsky & Mesnil 1936	Generic description	
	<u>Lema</u>	<u>cyaneella</u> (L.)	Paterson 1931	-	Head and Body (Final)
	"	<u>melanopa</u>	Balachowsky & Mesnil 1936	General description	
	"	<u>lichenensis</u>	"	General description	
	<u>Lilioceris</u>	<u>lilii</u>	"	General description	
Cryptocephalinae			Anderson 1936	Labium	
	<u>Cryptocephalus</u>	<u>biguttatus</u>	Medvedev 1965 & Oglobin.	Key to Species	Body
	"	<u>bipunctatus</u>			Body and Head
	"	<u>nitidulus</u>			Body
	"	<u>labiatus</u>			Body
	"	<u>sericeus</u>			Head
	"	<u>exiguus</u>			Head
	"	<u>moraei</u>			Head
	<u>Cryptocephalus</u>	<u>parvulus</u>	Paterson 1931		Head and Body (Final)
Lamprosomatinae	<u>Lamprosoma</u>	<u>cherisiae</u> (Not British)	Monros 1949		Head and Body
	<u>Oomorphus</u>	<u>concolor</u> (Sturm.)	Kasap & Crowson 1976		All.

TABLE 3 (continued)

Subfamily	Genus	Species	Reference	Keys and	
				General Description	Detailed Chaetotaxy
Clytrinae	<u>Clytra</u>	<u>quadripunctata</u>	Boving & Craighead 1931		Head and Body
	<u>Labidostomis</u>	<u>tridentata</u>	Medvedev 1962		Head and Pronotum
	<u>Gynandrophthalma</u>	sp.	" "		Head and Pronotum
Cassidinae	<u>Cassida</u>		Van Emden 1962	Key to all species General descriptions General description	
	<u>"</u>	<u>rubiginosa</u>	Palli 1959		
	<u>Cassida</u>		Peterson 1951		
	"	"	Paterson 1931		Head and Body (Final)
Chrysomelinae	"	"	"		"
	"	<u>viridis</u>	"		"
	"	<u>vibex</u>	"		"
	<u>Timarcha</u>	<u>tenebricosa</u>	Paterson 1931		Head and Body (Final)
	<u>Chrysolina</u>	<u>coriaria</u>	Buddeberg 1885		" (A11)
		<u>orichalcea</u>	Paterson 1931		" (A11)
		<u>hyperici</u>	"		" (A11)
		<u>varians</u>	"		" (A11)
		<u>graminis</u>	"		" (A11)
		<u>menthastri</u>	"		" (A11)
		<u>polita</u>	"		" (A11)
		<u>marginalis</u>	"		"
		<u>violacea</u>	Chapuis & Candeze 1853	General description	
		<u>sanguinolenta</u>	Hennig 1938	Key to Genera	Head and Body
	<u>Leptinotarsa</u>	<u>decemlineata</u>	Hennig 1938		Head and Body
	<u>Phytodecta</u>	<u>rufipes</u>	Peterson 1951	General description	
			( Chapuis & Candeze 1853	General description	
			( Rosenhauer 1882	General description	
			( Hennig 1938		Body Chaetotaxy

TABLE 3 (continued)

<u>Subfamily</u>	<u>Genus</u>	<u>Species</u>	<u>Reference</u>	Keys and <u>General Description</u>	<u>Detailed Chaetotaxy</u>
Chrysomelinae (continued)	<u>Phytodecta</u>	<u>viminalis</u>	Henriksen 1927	General description	Body Chaetotaxy
			Hennig 1938		
	<u>Phaedon</u>	<u>olivacea</u>	Letzner 1857	"	Head and Body (A+I) Body Chaetotaxy Head and Body (All) Body Chaetotaxy
		<u>pallida</u>	Weise 1893	"	
		<u>tumidulus</u>	Paterson 1931		
		<u>armoraciae</u>	Hennig 1938		
		<u>cochleariae</u>	"	"	
		"	"		
	<u>Gastroidea</u>	<u>polygoni (L.)</u>	Chapuis & Candeze 1853	General description	Head and Body (All)
			Paterson 1931		" (3rd instar)
	<u>Phyllodecta</u> "	<u>viridula (De G.)</u>	Johnson & Carrick 1950		"
			Paterson 1931		Pronotum
		<u>laticollis</u>	Hennig 1938		
		"	Henriksen 1927	General description	
			Hennig 1938	"	
<u>Hydrothassa</u>		<u>laticollis</u>	Paterson 1931		Head and Body (Final)
		<u>vitellinae</u>	"		" (All)
		"	"		
			Chapuis & Candeze 1853	General description	
		<u>marginella</u>	Paterson 1931		Head and Body (All)
		<u>aucta</u>	Chapuis & Candeze 1853	General description	Body (Final)
		"	Kaltenbach 1874		Body
		"	Hennig 1938		Head and Body
			Hennig 1938		
		<u>hannoverana</u>	Cornelius 1857	General description	

TABLE 3 (continued)

<u>Subfamily</u>	<u>Genus</u>	<u>Species</u>	<u>Reference</u>	<u>Keys and General descriptions</u>	<u>Detailed Chaetotaxy</u>
<u>Chrysomelinae</u> (continued)	<u>Prasocuris</u>	<u>phellandrii</u>	Paterson 1931		Head and Body (All)
		"	Hennig 1938		Pronotum and Abdomen
		<u>junci</u>	Paterson 1931		Head and Body (All)
		"	Hennig 1938		Abdomen
		<u>versicolora</u>	Henriksen 1927	General description	Abdomen
	<u>Plagiodera</u>	"	Hennig 1938		
		"	Hood 1940	General description	
		"	Paterson 1931	General description	
		"	Kimoto 1962		Head and Body (All)
		<u>populi</u>	Kimoto 1962		Head and Body (All)
	<u>Chrysomela</u>	<u>tremulae</u>	Paterson 1931		"
		"	Henriksen 1927	General description	
		"	Hennig 1938		Body (Final)
		<u>aenea</u>	Lipp 1935	General description	
		"	Hennig 1938		Body (Final)
		"	Kimoto 1962		Head and Body (Final)
<u>Galerucinae</u>	<u>Galeruca</u>		Anderson 1936		Labium
			Boving 1929	Key to Genera	
		<u>tanacetii</u>	Prevett 1953		Body (Final)
			Laboissiere 1934	General description	
			Boving 1929	General description	
	<u>Agelastica</u>	<u>alni</u>	Boving 1929	"	"
			Laboissiere 1934	"	"
			Boving 1929	"	"
	<u>Galerucella</u>	<u>viburni</u>	Laboissiere 1934	"	"
			Paterson 1931	"	"
				"	Head and Body (Final)

TABLE 3 (continued)

<u>Subfamily</u>	<u>Genus</u>	<u>Species</u>	<u>Reference</u>	<u>Keys and General descriptions</u>	<u>Detailed Chaetotaxy</u>
Galerucinae (continued)	<u>Galerucella</u>	<u>nymphæae</u>	Boving 1929	General description	
		"	Laboissiere 1934	" "	
		"	MacGillivray 1903	" "	
		"	Peterson 1951	" "	
		"	Paterson 1931		Head and Body (1st and 3rd) " (All)
		"	Servadei 1938		
		<u>sagittariae</u>	Paterson 1931		
		<u>lineola</u>	Boving 1929	General description	
		<u>calmariensis</u>	Cornelius 1867	" "	
		"	Paterson 1931		Head and Body (All)
	<u>Lochmaea</u>	"	Boving 1929	General description	
		<u>tenella</u>	Paterson 1931		Head and Body (All)
		<u>suturalis</u>	Paterson 1931		Head and Body (All)
		"	Laboissiere 1934	General description	
		<u>capreae</u>	Paterson 1931		
		"	Boving 1929	General description 1st	
		"	Laboissiere 1934	General description	
		<u>halensis</u>	Boving 1929	General description	
			Paterson 1931		Head and Body (All)
			Laboissiere 1934	General description	
	<u>Sermyla</u>	<u>quadrinaculata</u>	Boving 1927		Head and Body (Final)
			Laboissiere 1934	General description	
		<u>rufipes</u>	Paterson 1931		Head and Body (1st)
		<u>circumfusus</u>	Laboissiere 1934	General descr. Final	

Galerucinae :  
Glanduliferous  
group of Japan.

Takizawa 1971

Head and Body.

TABLE 3 (continued)

<u>Subfamily</u>	<u>Genus</u>	<u>Species</u>	<u>Reference</u>	<u>Keys and</u>	
				<u>General descriptions</u>	<u>Detailed Chaetotaxy</u>
<u>Halticinae</u>	<u>Haltica</u>	<u>oleracea</u>	Chapuis & Candèze 1853	General	
		<u>lythri</u>	Paterson 1931		Head and Body (All)
	<u>Haltica</u> sp. (Not British)		Woods 1918		Head and Body
	<u>Chalcoides</u>	<u>fulvicornis</u>	Paterson 1931		Head and Body (1st)
	<u>Hermæophaga</u>	<u>mercurialis</u>	Welch 1972		" (All)
	<u>Podagrica</u>	<u>fuscicornis</u> (L.)	Manolache & Dobresanu & Manolache 1938		Head and Body (All)
		<u>malvae</u>	" 1943		"
	<u>Crepidodera</u>	<u>ferruginea</u>	Blunck 1932		Head and Body (All)
	<u>Chaetocnema</u>	<u>aridula</u> (Gyll.)	" 1932		Body
		<u>aridella</u> Payk	" 1932		"
		"	Newton 1929		"
		<u>concinna</u>	"		"
	<u>Sphaeroderma</u>	<u>rubidum</u>	Grandi 1932		Head and Body (All)
	<u>Epitrix</u>	<u>atropae</u>	Newton 1929		Head and Body (1st)
	<u>Psylliodes</u>	<u>affinis</u> (Payk.)	Tolg 1915		Head and Body (Final)
		<u>attenuata</u>	Tolg 1912		"
		"	Newton 1929		Body (Final)
		<u>hyoscyami</u>	Newton 1934		Head and Body (Final)
		<u>napi</u>	Goureau 1864		
		<u>chrysocephala</u>	Kaufman 1941		
		"	Bonnemaison & Jourdhueil 1954		
		<u>cuprea</u>	Dobson 1960		Body (All)
		<u>nemorum</u>	Grandi 1932		Head and Body (Final)
	<u>Phyllotreta</u>		Blunck 1932		Body (Final)

TABLE 3 (continued)

Subfamily	Genus	Species	Reference	General descriptions	Detailed Chaetotaxy
Halticinae , (continued)	Phyllotreta	<u>memorum</u>	Grandi 1932		Head and Body (Final)
			Blunck 1932		Body (Final)
		"	Newton 1928	General description	
		<u>undulata</u>	" "	"	Anal Plate
		<u>cruciferae</u>	" "		Head and Body (All)
		<u>consobrina</u>	" "		Anal Plate
		<u>diademata</u>	" "		"
		<u>ochripes</u>	Borner & Blunck 1920		"
		<u>tetrastigma</u>	"		"
		<u>nodicornis</u>	"		"
		<u>atra</u>	"		"
		<u>vittula</u> Redt.	Harukawa & Tokunaga 1938		Head and Body (All)
		<u>sinuata</u> Redt.			
		<u>vittula</u> Redt.	Meyer 1934		Head and Body (All)
		<u>jacobaeae</u>	Newton 1933		Head and Body (Final)
		Longitarsus		<u>dorsalis</u>	" "
<u>succineus</u>	" "				Dorsal Plate
<u>gracilis</u>	" "				"
<u>parvulus</u>	Rhynehart 1932				Head and Body (All)
"	Principi 1941				"
<u>euphorbiae</u> (Sch.)	Manolache & Dobreanu 1957				Head and Body (All)
"	Principi 1941				"
<u>Aphthona</u>	Sanderson 1901				
	Boving & Craighead 1931				
	Peterson 1951				
<u>KEYS TO ALL SUBFAMILIES</u>			Oglobin & Medvedev 1971		

TABLE 4 Previous studies on the Pupae of the British Chrysomelidae

Subfamily	Genus	Species investigated	Reference
<u>Chrysomelinae</u>	<u>Phaedon</u>	<u>tumidulus</u> (Germ.)	Paterson 1930
	"	<u>armoraciae</u> (L.) *	" 1931
	"	<u>cochleariae</u> (F.)	" 1931
	<u>Gastroides</u>	<u>polygoni</u> (L.) *	" 1931
	"	"	Johnson & Carrick 1950
	"	"	Jolivet 1951
	"	<u>viridula</u> (DeG.)	Paterson 1931
	"	"	Jolivet 1951
	"	"	Paterson 1931
	"	"	" 1931
<u>Galerucinae</u>	<u>Phyllodecta</u>	<u>vitellinae</u> (L.)	Hood 1940
	<u>Chrysomela</u>	<u>populi</u> L. *	Paterson 1931
	<u>Plagiodera</u>	<u>versicolora</u> (Laich) *	" 1931
	<u>Prasocuris</u>	<u>phellandrii</u> (L.)	" 1931
	<u>Hydrothassa</u>	<u>marginella</u> (L.)	" 1931
	<u>Chrysolina</u>	<u>orichalcea</u> (Müll.)	" 1931
	"	<u>hyperici</u> *	" 1931
	"	<u>graminis</u>	" 1931
	"	<u>polita</u> *	" 1931
	<u>Lochnaea</u>	<u>capreae</u> (L.)	Paterson 1931
	<u>Galerucella</u>	<u>viburni</u> (Payk.)	" 1931
	"	<u>sagittariae</u> (Gyll.)	" 1931
	"	<u>calmariensis</u> (L.)	" 1931
	"	<u>tenella</u> (L.) *	" 1931
	<u>Sermyle</u>	<u>halensis</u> (L.)	" 1931
<u>Halticinae</u>	<u>Galeruca</u>	<u>tanacetii</u> (L.)	Prevett 1953
	<u>Epitrix</u>	<u>atropae</u> Foud.	Newton 1929
	<u>Podagrica</u>	<u>fuscicornis</u> (L.)	Manolache, Dobreanu & Manolache 1938
	<u>Haltica</u>	<u>lythri</u> Aube.	Paterson 1931
	<u>Psylliodes</u>	<u>affinis</u> *	Newton 1929
	"	<u>chrysocephala</u> (L.)	Kaufmann 1941b.
	"	"	Bonnemaison & Jourdheuil 1954
	"	<u>hyoscyami</u> (L.)	Newton 1934
	"	<u>attenuata</u> (Koch.)	Tolg 1912
	<u>Chaetocnema</u>	<u>aridella</u> *	Newton 1929
	"	<u>concinna</u> *	" 1929
	<u>Longitarsus</u>	<u>jacobaeae</u> Wat. *	" 1933
	"	<u>dorsalis</u> (F.) *	" 1933
	"	<u>gracilis</u> Kuts. *	" 1933
	"	<u>parvulus</u> (Payk.)	Rhynehart 1932
	<u>Hermaphaga</u>	<u>mercurialis</u>	Welch 1972



TABLE 4. (continued)

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