

DEVELOPMENTAL CHANGES AND WEAR OF LARVAL MANDIBLES IN *HETEROCAMPA GUTTIVITTA* AND *H. SUBROTATA* (NOTODONTIDAE)

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ABSTRACT. Detailed descriptions and scanning electron micrographs of worn and unworn larval mandibles and physical measurements of cuticle loss owing to wear within each instar were made for *Heterocampa guttivitta* (Walker) and *H. subrotata* (Harvey) (Notodontidae). First instar mandibles of both species lack a retinaculum and are used to skeletonize leaf tissue. The mandibles of later instars have a retinaculum and are more robust. The latter are used to cut through the leaf blade. The retinaculum of *H. subrotata* is bifurcate as opposed to the simple retinaculum of *H. guttivitta*. The teeth and retinaculum on the mandibles of instars two through five of both species are almost completely worn down during their short period of use; the length of mandibles is reduced by at least 20 percent during the final larval instar.

Additional key words: saddled prominent, systematics, morphology.

Mandibular characters of lepidopterous larvae have been used in many taxonomic keys (Gardner 1946a, 1946b, Beck 1960, Godfrey 1972, Brown & Dewhurst 1975) and in phylogenetic studies of various Notodontidae (Godfrey et al. 1989). However, relatively little research has focused on the functional morphology and feeding ecology of lepidopterous larval mandibles (Tragardh 1913, Bernays & Janzen 1988), and no study has accounted for wear of these structures. Thus, the reliability of some mandibular characters may be questionable. The purpose of this study was to document the ontogenetic changes of larval mandibles of *Heterocampa guttivitta* (Walker) and *H. subrotata* (Harvey) (Notodontidae) and to determine the extent of wear on the mandibles within each larval stadium of both species.

Heterocampa guttivitta, the saddled prominent, is an occasional pest in hardwood forests in the northeastern part of the United States. In the past it has caused reduction in yields in the sugar maple and lumber industries. *Heterocampa guttivitta* has five larval instars and overwinters in the pupal stage. In the northeast it has one generation per year, with the moth emerging in May-June (Forbes 1948). In central Illinois there are two generations per year, with the moths emerging May-June and July-August, based on collection records in the Illinois Natural History Survey (G. L. Godfrey pers. comm., Illinois Natural History Survey, Champaign, Illinois). The larvae have been reported feeding on *Acer* (Aceraceae), *Betula* (Betulaceae), *Carya* (Juglandaceae), *Castanea dentata* (Fagaceae), *Corylus* (Corylaceae), *Fagus* (Fagaceae), *Hamamelis virginiana* (Hamamelidaceae), *Juglans* (Juglandaceae), *Malus pumila* (Rosaceae), *Ostrya virginiana* (Corylaceae), *Populus* (Salicaceae), *Prunus* (Rosaceae), *Pyrus* (Rosaceae), *Quercus* (Fagaceae),

Rubus (Rosaceae), *Spiraea* (Rosaceae), *Ulmus* (Ulmaceae), and *Viburnum* (Caprifoliaceae) (Tietz 1972).

Heterocampa subrotata is the smallest *Heterocampa* species in North America. The "evenly green form" or variety "celtiphaga" (Forbes 1948) was used in this study. Larval hosts have been reported as *Acer*, *Betula*, *Carya*, *Cornus* (Cornaceae) and *Hamamelis virginiana* (Teitz 1972). *Heterocampa subrotata* also has five larval instars and overwinters as a pupa. It appears to have two generations in central Illinois, with adults emerging in May–June and July–August.

METHODS AND TECHNIQUES

Collecting and Rearing

To ascertain the feeding histories of the larvae used in this study, larvae were reared from eggs deposited by wild females. Three *Heterocampa guttivitta* and five *H. subrotata* females were collected at a UV-light trap in Trelease Woods, Champaign County, Illinois. One *H. guttivitta* was collected at a similar UV-light trap in Wolf Creek State Park, Shelby County, Illinois. All life stages of both *Heterocampa* species were maintained in an insectary and were exposed to ambient temperature and humidity during the summer of 1989 in Champaign, Illinois.

Voucher specimens of both study species are placed in the Illinois Natural History Survey Insect Collection, Champaign, Illinois. Voucher specimens include the pinned adult females from which eggs were obtained, as well as alcoholic specimens of the following: eggs just prior to hatch, intact larvae from each stadium, and head capsules from the exuviae of all five larval stadia. George L. Godfrey verified all species identifications.

Individual field-collected females were placed into one-ounce plastic diet cups with cardboard lids. Each cup contained a strip of brown paper towel which served as a resting spot for the moth and as a possible oviposition site.

Four cohorts of *Heterocampa guttivitta* and five cohorts of *H. subrotata* were reared. Each cohort consisted of approximately 45 individuals. To reduce mortality attributable to handling, fresh leaves and the diet cup containing unhatched eggs were placed into a rearing container. Rearing containers were plastic Solo (P550) cups with a depth of 5 cm, a top diameter of 8 cm, and a bottom diameter of 5 cm. The cups were fitted with clear plastic lids. Newly hatched first instar larvae were allowed to crawl onto the leaves. After one or two days of feeding, the leaves were cut so that each section had only one larva on it. Each leaf section with a single larva was placed in a separate rearing container with additional leaves. The addition of several leaves to a container

helped minimize the loss of leaf moisture. The larvae were reared individually in the described containers until reaching the prepupal stage.

An unknown percentage of larvae of both *Heterocampa* species in this study were infected with a cytoplasmic polyhedrosis virus (CPV) (J. V. Maddox pers. comm., Illinois Natural History Survey). Individuals in six of the eight cohorts reared for this study displayed symptoms consistent with those typical of CPV infections.

The CPV infection did not produce a high mortality in the larval cultures and was not diagnosed until most of the larvae had reached late third instar. Larvae were discarded and not used in this study if they displayed any symptoms consistent with a CPV infection. No attempt was made to histologically determine if larvae used were infected with CPV. The assumption was made that a CPV infection that produced no physically visible symptoms would have little or no effect on mandibular morphology or on the general nature of how mandibles wear with use.

Heterocampa guttivitta was reared on white oak (*Quercus alba* L., Fagaceae) and *Heterocampa subrotata* was reared on northern hackberry (*Celtis occidentalis* L., Ulmaceae). White oak foliage was replaced every third day or earlier if the existing foliage appeared to be dry. Northern hackberry was replaced every day or every other day depending on foliage condition. Dark green, mature leaves of northern hackberry and white oak were collected fresh each morning.

Prepupae were placed in half-pint cardboard ice cream containers (with no more than three individuals of the same species per container) that contained an approximately 2-cm layer of sand covered with approximately 4 cm of moist peat moss. Larval exuviae were carefully removed from the pupal chambers and stored in 70-percent ethanol until the mandibles could be dissected from the head capsule and measured.

Unworn mandibles were collected from newly molted larvae. It was difficult to obtain larvae that had not fed unless they were isolated from the foliage before ecdysis. This was done by carefully cutting a small section from the leaf that contained the silk mat and larva. The leaf section, silk mat, and any remaining exuvia were removed after the larva had completed molting and begun moving around the container. Larvae were not used if they had fed on the dry leaf sections after molting. However, a majority of the larvae did eat part of their exuviae. The assumption was made in this study that feeding on exuvia caused negligible wear; no effort was made to keep the larvae from feeding on it or to determine if any wear was produced by this type of feeding.

Newly molted larvae were held without foliage for 8–12 hours before

being preserved. Mandibles that were not allowed to harden in this manner were difficult to dissect without tearing or otherwise damaging them. Larvae were killed in boiling water and subsequently preserved in 70-percent ethanol until the head capsules could be measured and the mandibles dissected and measured. Both the left and right mandibles were removed from intact, preserved larvae as described by Godfrey (1972). If the mandibles were not completely sclerotized at the time of preservation, the abductor muscle was cut where it attached to the mandible, but the adductor muscle was removed with the mandible. Excess muscle tissue was removed before the mandibles were measured.

Mandibles from exuviae were used to represent the worn condition because they could be obtained in a non-destructive manner, and because they potentially demonstrate maximum wear. Head capsules were collected from the rearing containers with a small camel's-hair paint brush and placed directly into 70-percent ethanol until they could be measured and the mandibles could be removed and measured. Mandibles were removed from molted head capsules by severing any cuticular attachments and lifting out the mandibles with a curved dissecting tool. They were returned to 70-percent ethanol after being measured.

Scanning Electron Microscopy Preparation

Mandibles were washed in three changes of 70-percent ethanol and then sonicated in a 1:1 solution of Photo-Flo and 70-percent ethanol for 30 seconds. Seventy-percent ethanol was used in the sonicating fluid to keep the mandibles from floating or sticking to the sides of the container above the fluid line during sonication. Sonication times of over 30 seconds occasionally result in lost or damaged setae. After sonication, the mandibles were washed three to five times in 70-percent ethanol and were then dehydrated in a graded ethanol series: 85%, 95%, and three times in 100% (10 minutes in each concentration). The specimens were critical-point dried and attached to stubs using aluminum tape. The tape worked very well for attaching the small samples, which had a tendency to sink into liquid adhesives. However, aluminum tape produces a light-colored background, which may interfere with the viewing and photographing of the specimen. The specimens were coated three times with gold-palladium. Each coating was for 30 seconds at 30 mA. An AMRAY 1830 scanning electron microscope operating at 10 kV was used to view the specimens.

Statistical Analysis

Six to fifteen randomly chosen pairs of mandibles from each species, representing each stage of development (1st to 5th instar) and both

states of wear (unworn and worn) were measured in order to determine the extent of wear. Two measurements were taken of each mandible: the distance between the condyle and the adductor apodeme (CI) and the distance from the condyle to the tip of the second tooth (CT) (Figs. 1-2). Teeth were not discernible on worn mandibles from stadia three, four, and five. In those cases, the point most distad from a line connecting the condyle and the adductor apodeme was used in place of the second tooth (Figs. 1-2). CT and CI were taken for both right (R) and left (L) mandibles to produce four groups of measurements (RCT, LCT, RCI, and LCI) for each pair of mandibles. CI measurements were taken to ensure that changes in the length of the mandible (CT) were due to wear and not due to changes that resulted from sclerotization.

All measurements were taken at the highest practical magnification for each group (e.g., all first instar RCI and LCI for *H. subrotata* were taken at 120 \times) through a dissecting stereomicroscope with an ocular micrometer that had been calibrated with a stage micrometer.

Means and standard deviations for RCI, LCI, RCT, and LCT were calculated for each state of wear in each instar. An unpaired *t*-test was used to test for differences between means of unworn and worn mandibles. A paired *t*-test was used to test for differences between right and left mandibles from the same larva.

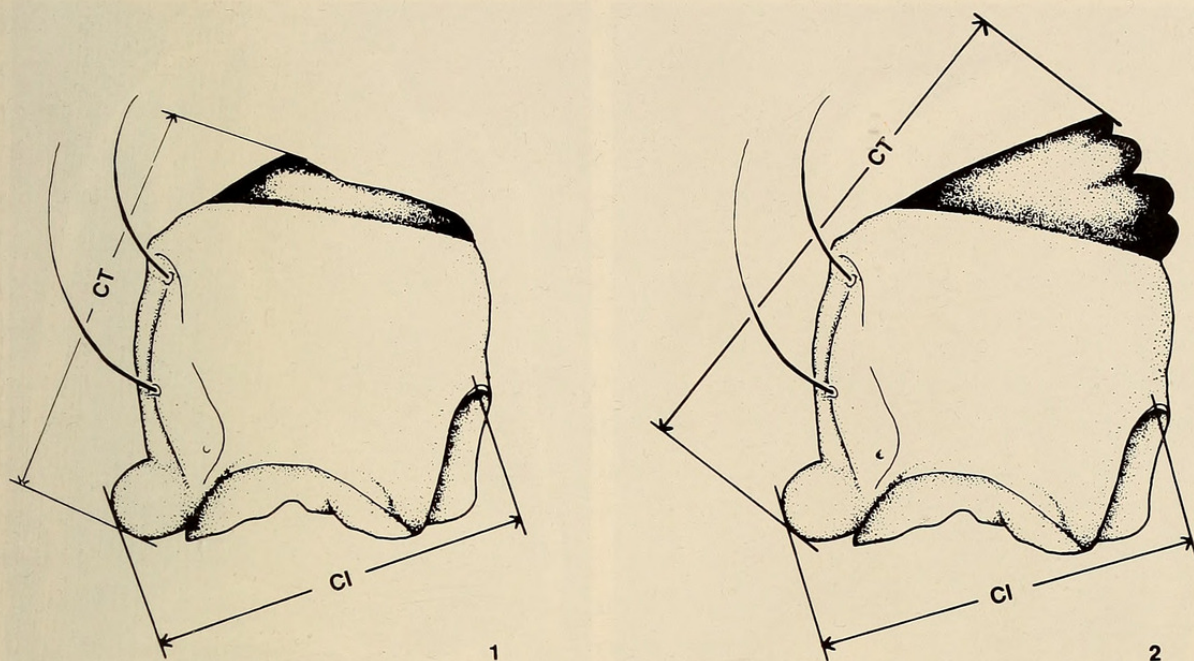
RESULTS

Mandible Descriptions

Notodontid mandibles are hollow structures with the distal (cutting) edge heavily sclerotized. They appear dark caramel brown in color under a dissecting stereomicroscope. The proximal end is open. There are two points of articulation on the mandible (Figs. 3-5). The condyle (C) articulates with the subgena and the acetabulum (A) (=socket) articulates with the lateral part of the clypeus.

There are four surfaces on the mandible: lateral, dorsal, ventral, and oral. These surfaces are defined with respect to the orientation of the mandible to the caterpillar. There is a textured area on the lateral surface, which is located in a slight depression. Two setae (M1 and M2) (Beck 1960) can be found in this area (Figs. 4-5).

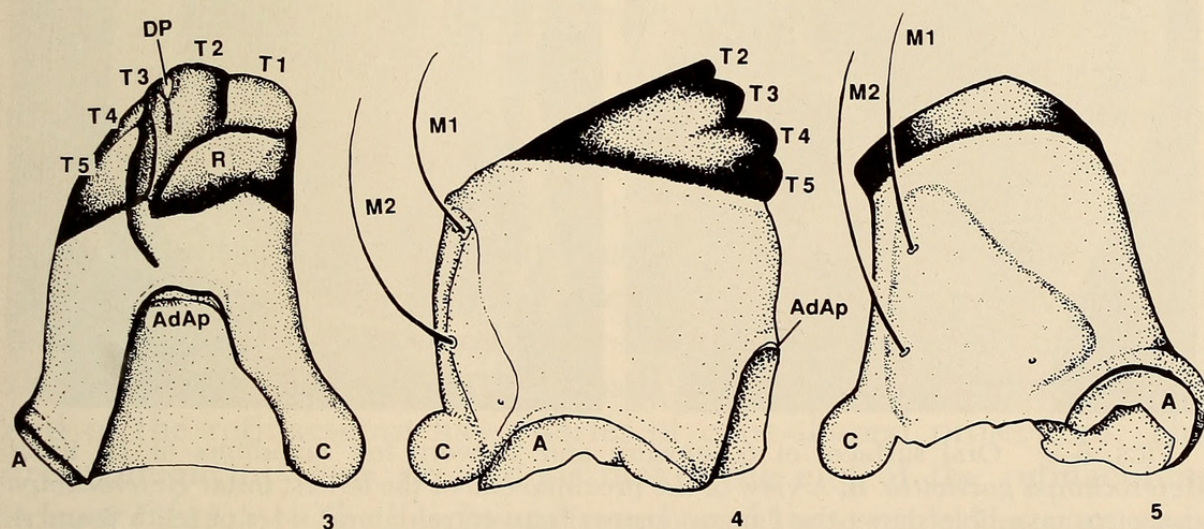
The oral (=inner or mesal) surface was the emphasis of this study. Leaf cutting occurs on the extreme distal edge of the mandible. This edge may be smooth or it may have a series of teeth (dentes). The teeth are numbered from the ventral to the dorsal surface with Arabic numerals (Fig. 3) (Godfrey 1972). A retinaculum (R) or inner ridge is usually present in notodontids (Fig. 3). The retinaculum is part of the heavily sclerotized distal end of the mandible.



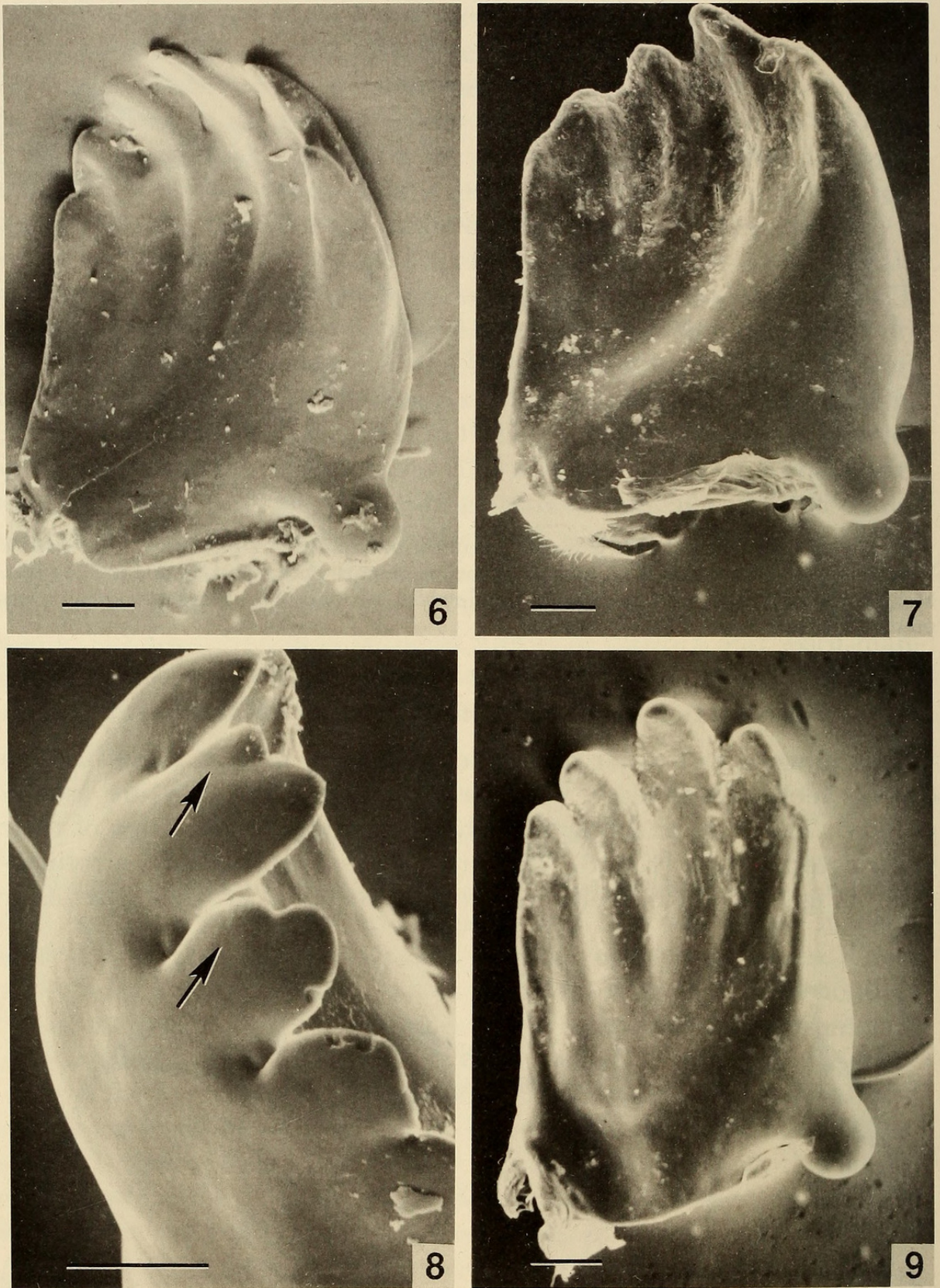
FIGS. 1-2. 1, Worn and 2, Unworn 3rd instar mandibles of *Heterocampa guttivitta*. Dorsal view of left mandible showing how measurements were taken for analysis of wear. Measurement CI was used to indicate absolute size of mandible. Measurement CT was used to measure wear-related changes.

Description of *Heterocampa guttivitta* Mandibles

The unworn first instar mandible is laterally flattened and has five distinct teeth. These teeth, with the exception of the fifth, are usually pointed. The third and fourth teeth have flanges on the bases of their ventrolateral edges (Fig. 8). The first instar mandible lacks a retinaculum (Figs. 6-8). The teeth are greatly shortened in worn first instar



FIGS. 3-5. Unworn 3rd instar mandible of *Heterocampa guttivitta*. Three views of the left mandible. 3, Oral surface; 4, Dorsal surface; and 5, Lateral surface. A = acetabulum (socket), AdAp = adductor apodeme, C = condyle, DP = distal pits, M1 and M2 = setae, R = retinaculum, T1, T2, T3, T4, and T5 = teeth.



FIGS. 6-9. Oral surfaces of 6, unworn and 7, worn left mandibles of 1st instar *Heterocampa guttivitta*. 8, A view of the proximal end of the left 1st instar *Heterocampa guttivitta* mandible shows the flanges (arrows) on ventral-lateral sides of teeth 3 and 4; 9, Oral surfaces of worn left mandibles of 1st instar *Heterocampa subrotata*. Micron bar = 20 microns.

mandibles, however, they are usually still discernable. Usually, the cuticle on much of the oral surface appears rough (Fig. 7). This roughness is probably a result of wear on the cuticle.

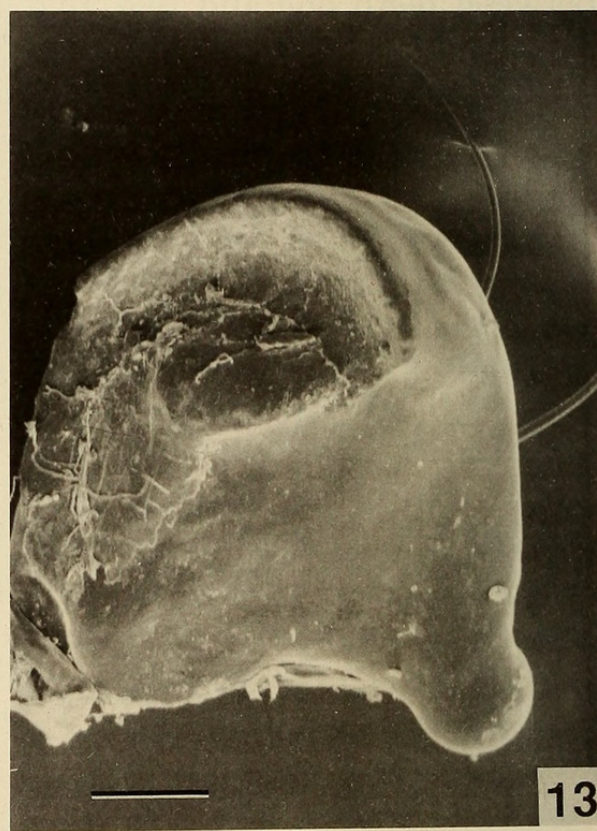
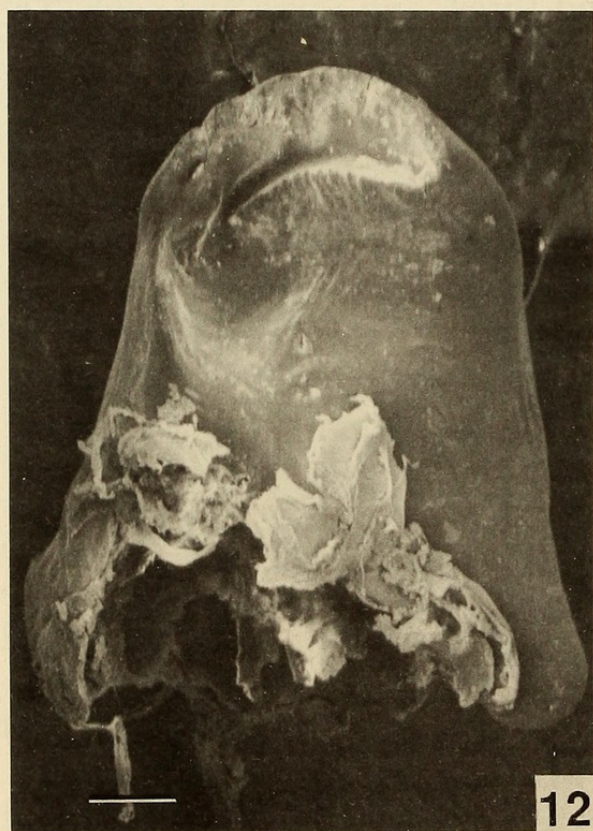
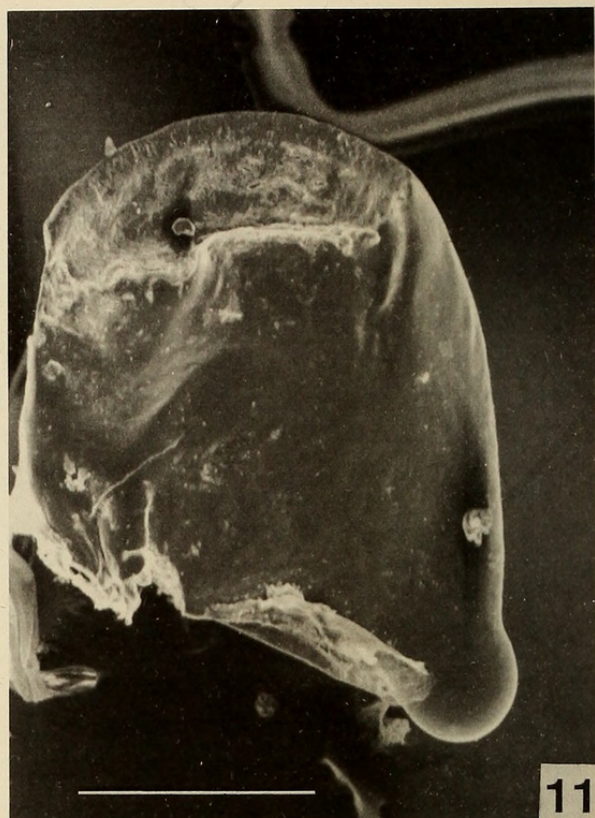
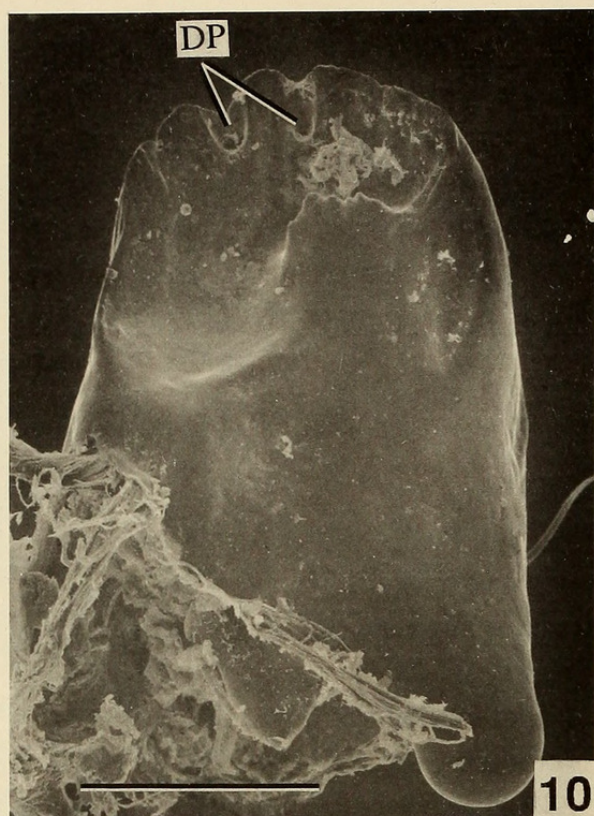
Second instar mandibles have five truncate teeth (Fig. 10). Teeth one and two are not very distinct from one another and often appear fused. The fifth tooth has a series of ridges on its inner surface. There are two distal pits (Fig. 10) on the mandible's oral surface that lie between teeth two and three, and three and four. The second instar mandible is laterally flattened, but the presence of a retinaculum makes it appear more robust than the first instar mandible. The retinaculum is a simple ridge with several dentes at the dorsal end. The retinaculum is worn smooth, often to the point that there is little or no concavity between it and the outer cutting edge (Fig. 11). The cutting edge wears to a smooth, continuous edge. Instars three through five appear to wear in a manner similar to that of the second instar.

The third instar mandible has four truncate teeth (Fig. 12). The first tooth is broad and smooth and may be the result of the fusion of two teeth. The fourth tooth is crenulate. In this instar, there are distal pits between teeth one and two, two and three, and three and four. The distal end of the mandible is curved at approximately a 90 degree angle, causing the cutting edge to be projected mediad. This angle makes the third instar mandible appear more robust than the second instar mandible. The retinaculum is a simple crenulate ridge.

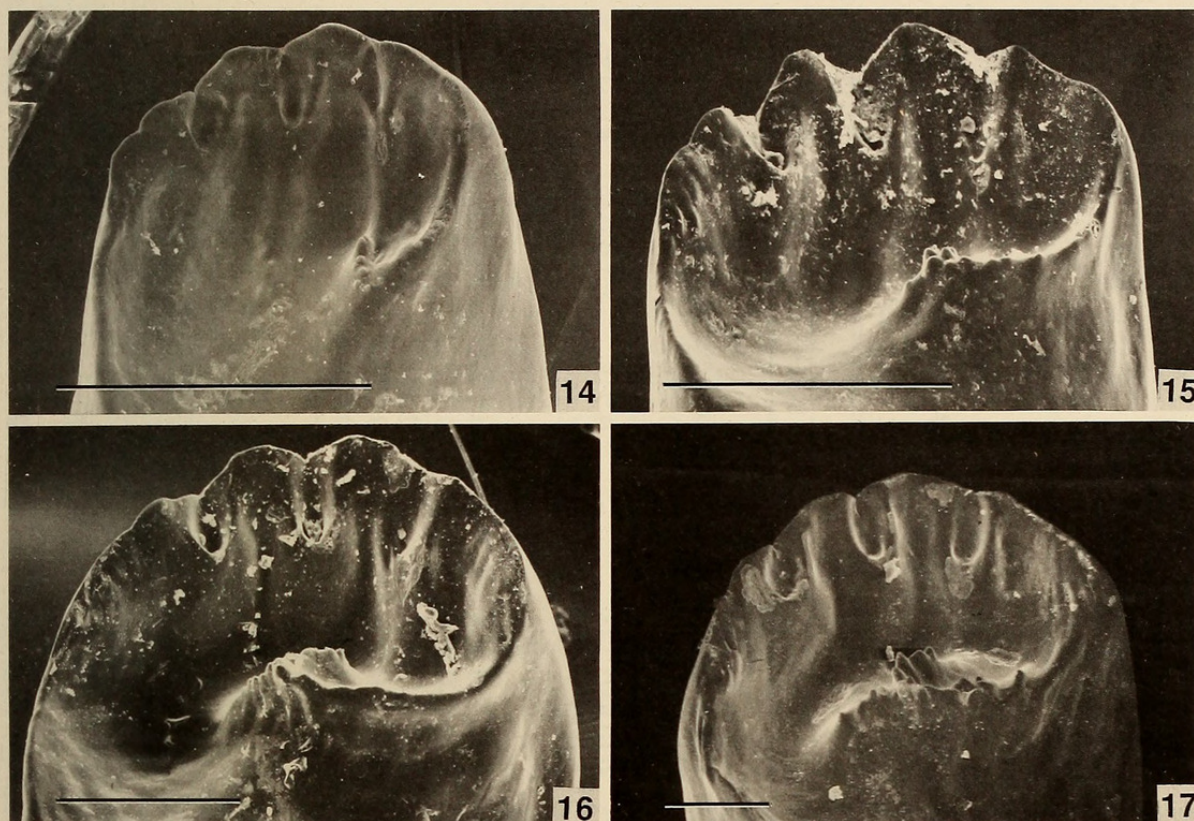
The fourth and fifth instar mandibles are very similar to those of the third instar, except that the distal teeth are not as distinctly separate. The crenae on the retinaculum of the fifth instar mandible are quite small and, in some cases, the retinaculum appears almost smooth.

Description of *Heterocampa subrotata* Mandibles

The unworn and worn mandibles of *H. subrotata* appear very similar to those of *H. guttivitta* with the following exceptions. *H. subrotata* mandibles are smaller than those of *H. guttivitta* (Table 1) and the retinaculum is strikingly different. The retinaculum of the second instar mandible is quite small and has a "hook" at the end. The surface of the retinaculum is irregular. Occasionally, there are cone-shaped projections located on the retinaculum (Fig. 14). There are five, short, rather pointed teeth on the third instar mandible (Fig. 15). The dorsal end of the retinaculum has a series of cone-shaped projections. The arrangement of these projections makes the end of the retinaculum appear bifurcate. The height and number of these projections are variable. However, the location of each projection in relation to the other projections appears to be fixed. The retinaculum of the fourth instar mandible ends in a definite bifurcation (Fig. 16). The branches of the



FIGS. 10-13. Oral surfaces of **10**, unworn and **11**, worn left mandibles of 2nd instar *Heterocampa guttivitta*. Distal pits (DP) are located between teeth two and three, and three and four of the unworn mandible. The concavity between the distal cutting edge and the retinaculum is greatly reduced in the worn mandible. Oral surface of 4th instar mandibles of **12**, *Heterocampa guttivitta* (unworn) and **13**, *H. subrotata* (worn). Micron bar = 100 microns.



FIGS. 14-17. Distal end of unworn mandibles of 14, 2nd instar; 15, 3rd instar; 16, 4th instar; and 17, 5th instar *Heterocampa subrotata*. Micron bar = 100 microns.

retinaculum and the retinaculum for a short distance before the bifurcation are crenate. Some of the crenae are fairly sharp. The fifth instar mandible (Fig. 17) differs from the fourth instar mandible in that its retinaculum is dentate its entire length and is more strongly bifurcate.

Right Mandible Versus Left Mandible

The results from the paired *t*-test showed that there was no statistically significant difference ($P > 0.10$) between RCT and LCT or between RCI and LCI for unworn or worn mandibles of *H. guttivitta* at the level of $P = 0.10$, except between the 5th instar RCI and LCI measurements for unworn ($P = 0.0669$) and worn ($P = 0.0422$) mandibles. There was no statistically significant difference ($P > 0.10$) between RCT and LCT or between RCI and LCI for unworn mandibles of *H. subrotata*. No significant difference ($P > 0.10$) for 6 out of 10 measurements was found between RCT and LCT or between RCI and LCI for worn mandibles of *H. subrotata*. The four exceptions were as follows: 1st instar RCT vs. LCT ($P = 0.0137$), 2nd instar RCI vs. LCI ($P = 0.0891$), 4th instar RCT vs. LCT ($P = 0.0380$), 5th instar RCI vs. LCI ($P = 0.0294$). No major morphological differences between the left and right mandibles were found (Dockter 1991). Therefore, only the

TABLE 1. The length of unworn and worn left mandibles of *Heterocampa guttivitta* and *H. subrotata*. The measurement (CT), in mm, is from the condyle to the tip of the second tooth (Fig. 1).

Species/instar	Unworn				Worn			
	Range	Mean	SD	n	Range	Mean ^a	SD	n
<i>H. guttivitta</i>								
1	0.160-0.171	0.165	0.003	8	0.140-0.165	0.156 ^b	0.008	12
2	0.314-0.342	0.330	0.011	9	0.257-0.296	0.276	0.011	12
3	0.473-0.593	0.546	0.034	11	0.410-0.490	0.447	0.021	12
4	0.792-0.940	0.858	0.037	12	0.618-0.774	0.715	0.040	13
5	1.340-1.541	1.419	0.052	11	1.039-1.206	1.128	0.066	6
<i>H. subrotata</i>								
1	0.143-0.160	0.153	0.007	6	0.134-0.154	0.145 ^c	0.006	12
2	0.239-0.285	0.266	0.012	12	0.217-0.245	0.230	0.010	12
3	0.376-0.439	0.404	0.019	12	0.302-0.371	0.348	0.018	15
4	0.592-0.661	0.631	0.020	12	0.479-0.557	0.526	0.023	15
5	0.938-1.039	0.985	0.039	12	0.748-0.896	0.796	0.051	11

^a All means for worn mandibles were significantly different from means for unworn mandibles at the level of 0.0001 unless otherwise noted.
^b Significantly different at 0.01 ($P = 0.0015$).
^c Significantly different at 0.05 ($P = 0.0284$).

TABLE 2. The width of left mandibles as measured from the condyle to the adductor apodeme (Fig. 1) for *Heterocampa guttivitta* and *H. subrotata*. The measurements (CI), in mm, of unworn and worn mandibles are combined for each instar of each species.

Species/instar	Range	Mean ^a	SD	n
<i>H. guttivitta</i>				
1	0.108–0.120	0.113 ^b	0.003	20
2	0.251–0.279	0.262	0.008	21
3	0.393–0.473	0.436	0.019	23
4	0.626–0.748	0.684	0.028	25
5	1.005–1.139	1.054	0.045	17
<i>H. subrotata</i>				
1	0.097–0.114	0.104	0.005	18
2	0.182–0.222	0.203 ^b	0.010	24
3	0.285–0.348	0.318	0.017	27
4	0.444–0.531	0.493 ^b	0.023	27
5	0.687–0.792	0.730	0.026	23

^a All means for worn mandibles were not significantly different from means for unworn mandibles at the level of 0.05 unless otherwise noted.
^b Significantly different at 0.05 but not at 0.01 (P = 0.0140, P = 0.0413, P = 0.0474, respectively).

left mandible was used for quantitative and qualitative descriptions in this paper (Tables 1–2).

Mandible Wear

First instar mandibles of both *Heterocampa* species were reduced in length by at least 5.2 to 5.5% (Table 3). The amount of wear increased in the second instar to 13.5 to 16.4% (Table 3). Mandible lengths of the final larval instar mandible are reduced by 19.2 to 20.5% (Table 3). The LCT length for larval mandibles from newly molted larvae of *H.*

TABLE 3. The percent of unworn mandible length that is lost during a larval instar for *Heterocampa guttivitta* and *H. subrotata*. Means from Table 1 were used to calculate percent length lost.

Species/instar	% length lost
<i>H. guttivitta</i>	
1	5.5
2	16.4
3	18.1
4	16.7
5	20.5
<i>H. subrotata</i>	
1	5.2
2	13.5
3	13.9
4	16.6
5	19.2

guttivitta was significantly longer ($P < 0.01$) than the LCT length of *H. guttivitta* mandibles taken from the exuviae (Table 1). Unworn LCT length of *H. subrotata* was also significantly longer ($P < 0.01$) than worn LCT length (Table 1). There was no statistically significant difference ($P < 0.01$) between unworn and worn LCI in *H. guttivitta* or in *H. subrotata* (Table 2). A worn mandible surface appears strikingly different from that of an unworn surface. At relatively low magnifications ($\times 300$), an unworn surface appears smooth in contrast to the rough surface of a worn mandible. High magnification of a worn mandible (Figs. 18–19) demonstrates that portions of the cuticle are flaked from the surface.

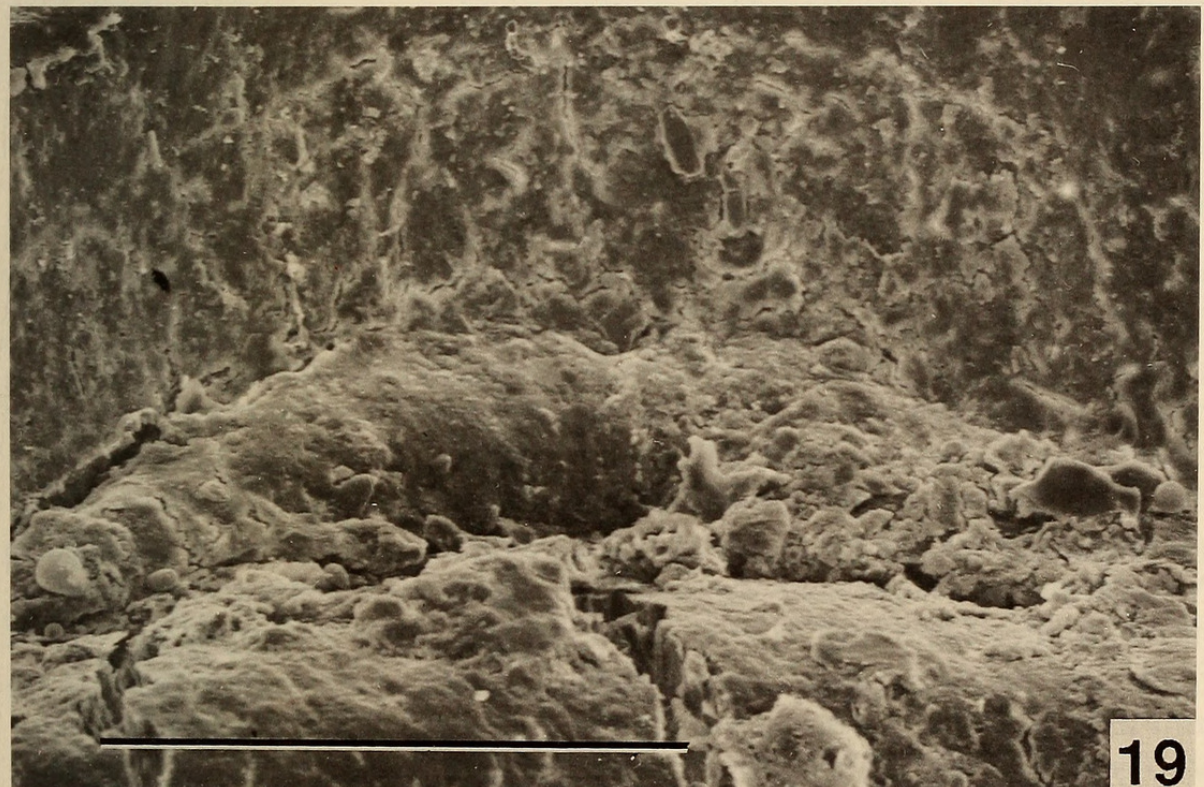
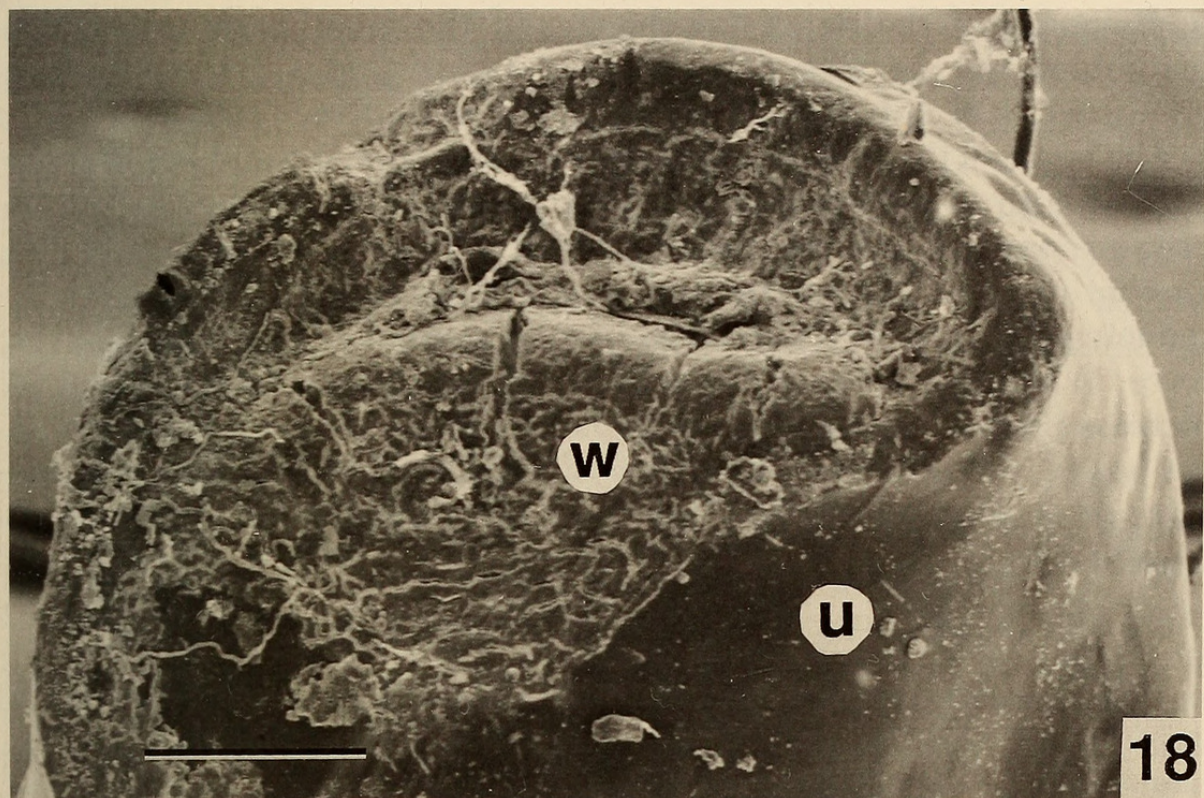
The absolute difference between the length (CT) of unworn and worn mandibles does not represent the actual amount of cuticle loss due to wear. The amounts of wear reported in this study are conservative because there is a bend between the proximal and distal ends of the mandible. It is not possible to compare amounts of wear between species or instars from the data collected in this study because the angle between the proximal and distal areas varies between instars, and especially between species. The difference between unworn LCT and worn LCT becomes more representative of actual cuticle loss as the angle between the proximal and distal areas increases.

DISCUSSION

Developmental and Behavioral Changes Within Species

The change from a shovel-shaped first instar mandible that has a sharply serrate distal margin but lacks a retinaculum, to a second instar mandible that is more robust at the mid- and proximal areas and bears a retinaculum, is associated with a change in feeding habits. This change occurs in both *Heterocampa guttivitta* and *H. subrotata*.

The following description of feeding behavior is based on observations made in the laboratory during the course of the present study. First instar larvae are leaf skeletonizers: they feed on the lower (occasionally upper) epidermis of the leaf while leaving the rest of the leaf tissue intact. The first instar uses the sharp serrations on the mandible to break through the epidermis. The head is quickly and forcefully tilted slightly to one side. This motion is repeated at the same spot on the leaf until the mandible penetrates the epidermis. Once the epidermis is broken a mandible is slid through the leaf tissue and the mandibles are closed to break off a piece of the leaf. Second instar larvae begin feeding on the leaf edge and bite through its entire thickness. During the early part of the second instar, larvae avoid the major veins, but toward the end of this instar, they eat through almost all veins except the midvein.



FIGS. 18-19. 18, Detail of distal end of worn 4th instar *Heterocampa guttivitta* left mandible. Note the difference between unworn (u) and worn (w) cuticle. 19, High magnification of worn area of same mandible. Micron bar = 100 microns.

A discussion of the structural changes of the mouthparts (especially mandibles) and the behavioral differences associated with them for two other species of notodontids can be found in Godfrey (1991).

The teeth on the cutting edge become more truncate and less sharply defined with successive instars in both species studied. The amount of pressure needed to break through the leaf tissue is a function of the amount of force exerted per unit area. Pressure can be increased by reducing the area over which the force is exerted or by increasing the force. When the larvae are small, a sharp tooth may be important to increase pressure so that the leaf tissue can be penetrated. As the larvae get larger, the muscles are capable of producing more force, and the extra pressure generated by a sharper more pointed edge may become unnecessary.

Developmental and Behavioral Changes Between Species

The ontogenetic development of the retinaculum in *H. subrotata* is quite different from that in *H. guttivitta*. The retinaculum on the mandibles of *H. subrotata* has a more intricate pattern than the retinaculum of *H. guttivitta*. *H. subrotata* feeds on a more succulent host (northern hackberry) than *H. guttivitta* (white oak). Bernays and Janzen (1988) found a correlation between host texture and mandible morphology. They found that sphingids, which tend to feed on rather succulent leaves, have mandibles that are "long, toothed, and ridged in a variety of complex ways," whereas saturniids have "short and simple" mandibles and feed on "old, tough tannin-rich leaves." The present study tends to support the findings of Bernays and Janzen (1988).

However, more work needs to be done in this area. It would be interesting to determine if the larvae *Nemoria arizonaria* Grote (Geometridae), which exhibit caterpillar morphs that feed on two very different tissues of the same host, also show a change in mandibular structure to best exploit the host tissue. Greene (1989), in his work with *N. arizonaria*, found that the catkin morph, which is a pollen feeder, has a smaller head and jaws (mandibles) than the twig morph, which feeds on "leathery" oak leaves. Bernays (1986) found that head mass and mandible mass were significantly greater in grass-feeding lepidopterous larvae which feed on a tougher diet. One might assume that cuticle production increases when the size of the head and jaw (mandible) increases. It may be that the same factors that control these changes in allometry may also trigger mandibular polymorphisms: if mandibular polymorphisms are in fact shown to exist.

An advantage of an intricate retinaculum is that it may allow the host tissue to be broken into smaller pieces than would be possible with a more simple retinaculum. Bernays and Janzen (1988) indicate that

the smaller the pieces produced by the biting process, the more nutrients that could be extracted from a given amount of tissue, because there is no further mechanical breakdown of food in the gut. However, Bernays (1991) in response to Barbehenn's (1989) study which found that bite size was not correlated with digestibility, concludes that handling time may be more important than bite size. Bernays (1991) states, "Tough leaves are efficiently handled by the snipping, scissor action, whereas the softer more flaccid leaves are more efficiently ingested by the tearing, crushing action".

Mandibular Characters in Systematics

Godfrey et al. (1989) used the presence or absence of teeth on the mandible's distal edge to make hypotheses about phylogenetic relationships among notodontids. However, before systematic (phylogenetic) decisions are made or characters are described with respect to mandibles, one must be certain that unworn mandibles are being examined, especially when a character is easily altered by wear. Nevertheless, for the purpose of identification of caterpillars, it is necessary to describe the most common form of the mandibles, which is often the worn condition in field-collected larvae.

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