

## SATURNIID AND SPHINGID CATERPILLARS: TWO WAYS TO EAT LEAVES<sup>1</sup>

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**Abstract.** We demonstrated allometric differences in relative head mass in different instars of 12 species of Saturniidae and 14 species of Sphingidae. The differences were related to the different ways in which individuals from the two families ate their respective host plants and to the different properties of the hosts that tended to be favored by each lepidopteran family.

The saturniids tended to have various simple cutting methods, while the sphingids tore and crushed the food, so that in the former, ingested food was in the form of relatively large uniformly sized pieces, and in the latter it was apparently well masticated. Saturniid mandibles were short and simple, while sphingid mandibles were long, toothed, and ridged in a variety of complex ways. The food of saturniids tended to consist of old, tough, tannin-rich leaves, while that of sphingids was softer, younger, and contained small toxic molecules. The generalists within each group tended to be similar to one another, while the specialists (which occurred more frequently among the sphingids) had very characteristic mandibles, each of unique design. One sphingid species feeding on a vine with characteristically very tough leaves had the "saturniid" design of mandibles. The features typical of the two groups of caterpillar are discussed in relation to feeding strategy, digestion, avoidance of plant "defenses," and rapidity of ingestion.

**Key words:** allometry; digestion; head size; ingestion; leaf toughness; Lepidoptera; lepidopteran mandibles; Saturniidae; Sphingidae.

### INTRODUCTION

Caterpillars of the families Saturniidae and Sphingidae are most species rich in the tropics, and where many species occur together they have few host-plant species in common (e.g., Janzen 1984). Plant species used by Sphingidae tend to be relatively deficient in phenolics but are likely to contain alkaloids and other small toxic molecules, while Saturniidae use host-plant species that are rich in phenolics and poor in alkaloids (e.g., Janzen and Waterman 1984). There are, however, exceptions and complications to this general picture: saturniid caterpillars often select older leaves and are usually found in the crowns of adult trees, treelets, or woody vines, while sphingids are less particular about plant age and commonly feed on younger leaves. They may even eat herbs and other small plants. In addition, saturniids are relatively more polyphagous than sphingids (Janzen 1984). A variety of physical and chemical features of leaves influences what species of host plant is fed upon by a species of caterpillar. Here we examine

the contrasting mandibular morphology in these two moth families and the potential roles of mandibular morphology in processing leaves of different types.

### MATERIALS AND METHODS

All caterpillars except *Manduca sexta* were collected in the dry forests of Santa Rosa National Park, northwestern Costa Rica (Janzen 1984). They were fixed in boiling water and preserved in 70% ethanol.

Relative sizes of mandibles, heads, and headless bodies were measured by taking the dry mass of each after removal of food from the gut lumen. Insect species examined and numbers of each are shown in Table 1. More extensive studies were undertaken with different instars of the saturniids *Othorene purpurascens* and *Rothschildia lebeau* and the sphingids *Pachylia ficus* and *Manduca dilucida*. Mandibles of selected species were measured with an eyepiece micrometer on a Wild stereomicroscope and drawn at appropriate magnifications with a camera lucida.

Gut contents of selected species were removed and sampled by random selection from suspensions in water. The samples were mounted on slides for examination,

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TABLE 1. Species analyzed. Unless stated, instars are IV or V.

Satumiidae	Number	Known food plants eaten by individuals examined
<i>Rothschildia lebeau</i>		
instar I	14	<i>Zulania guidonia</i> <i>Casearia corymbosa</i> <i>Spondias mombin</i> <i>Exostema mexicana</i>
II	10	
III	12	
IV	12	
V	12	
<i>Othorene purpurascens</i>		
I	5	<i>Manilkara chicle</i>
II	3	
III	2	
IV	5	
V	5	
<i>Hylesia lineata</i>		
II		<i>Casearia corymbosa</i>
V		
<i>Arsenura armida</i>	5	<i>Bombacopsis quinatum</i>
<i>Periphoba arcae</i>	2	<i>Spondias mombin</i>
<i>Eacles imperialis</i>	3	<i>Spondias mombin</i>
<i>Syssphinx molina</i>	4	<i>Pithecellobium saman</i> <i>Cassia grandis</i>
<i>Syssphinx colla</i>	5	<i>Pithecellobium saman</i>
<i>Automeris zugana</i>	4	<i>Annona purpurea</i>
<i>Citheronia lobesis</i>	5	<i>Spondias mombin</i>
<i>Automeris io</i>		<i>Crescentia alata</i>
<i>Caio championi</i>	5	<i>Bombacopsis quinatum</i>
<b>Sphingidae</b>		
<i>Eupyrrhoglossum sagra</i>		<i>Chomelia spinosa</i>
<i>Eumorpha satellita</i>	3	<i>Cissus sicyoides</i>
<i>Pachylia ficus</i>	2	
instar II	2	<i>Chlorophora tinctoria</i> <i>Ficus cotinifolia</i>
III	2	
IV	2	
V	2	
<i>Manduca rustica</i>	2	<i>Amphilophilum paniculatum</i>
<i>Manduca florestan</i>		<i>Cydista heterophylla</i>
<i>Manduca lanuginosa</i>	2	<i>Cydista heterophylla</i>
<i>Protambulyx strigilis</i>		<i>Spondias mombin</i>
<i>Pachylioides resumens</i>	3	<i>Forsteronia spicata</i>
<i>Aelopus fadus</i>	1	<i>Genipa americana</i>
<i>Enyo ocypete</i>	2	<i>Tetracera volubilis</i>
<i>Erinnyis ello</i>	1	<i>Sebastiania confusum</i>
<i>Manduca sexta</i>		
instar		
I	8	
II		
III	5	<i>Solanum tuberosum</i>
IV	5	
V	8	
<i>Manduca dilucida</i>		
instar		
II	1	<i>Tabebuia ochracea</i> <i>Sapranthus palanga</i>
III	1	
IV	1	
V	2	
<i>Cocytius duponchel</i>	1	
<i>Perigonia lusca</i>	1	<i>Calycophyllum candidissimum</i>

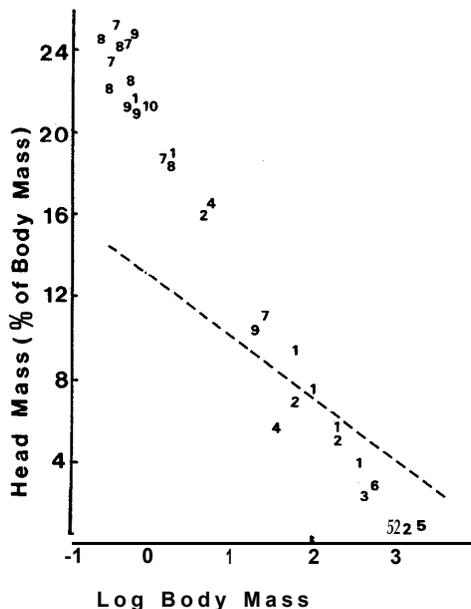


FIG. 1. The relationship between head mass as a percentage of headless body mass and headless body mass for various species of Satumiidae ( $r = -0.95$ ,  $y = 20.5 - 6.3x$ ). 1 = *Hylesia lineata*; 2 = *Arsenura armida*; 3 = *Periphoba arcae*; 4 = *Automeris zugana*; 5 = *Eacles imperialis*; 6 = *Automeris io*; 7 = *Caio championi*; 8 = *Citheronia lobesis*; 9 = *Syssphinx colla*; 10 = *Syssphinx molina*. --- the regression line for Sphingidae.

and 50 adjacent particles were drawn with a camera lucida. Areas and perimeters were measured using a digitizer and IBM PC.

## RESULTS

The relationship between relative head mass, expressed as a percentage of headless body mass, and headless body mass differs for the satumiid and sphingid caterpillars (Figs. 1-3). The slopes of the regressions for the two groups differ significantly ( $P < .001$ ,  $t$  test for parallelism), with the regression lines intersecting at a body mass of  $\approx 2$  mg. For caterpillars with masses  $< 10^2$  mg, the relative head mass was smaller for sphingids than for satumiids. For caterpillars  $> 10^2$  mg, relative head mass was greater for sphingids. A certain amount of variation in relative head mass was expected since body mass changes more than does head mass during an instar. The variation among sphingids appeared to be greater than that among satumiids (cf. Figs. 1 and 3).

For all species of both families taken together, mandible mass was closely correlated with head mass. The regressions for the two families were coincident. For the combined data,  $r^2 = 0.94$ ,  $y = -1.0 + 1.027x$ . The basic mandible shapes differed in the two families. Among satumiids all later instars had mandibles that were relatively short, with a broad base and no obvious teeth. Species that feed on many hosts (Janzen 1984) have the simplest mandibles (e.g., *Rothschildia lebeau*,

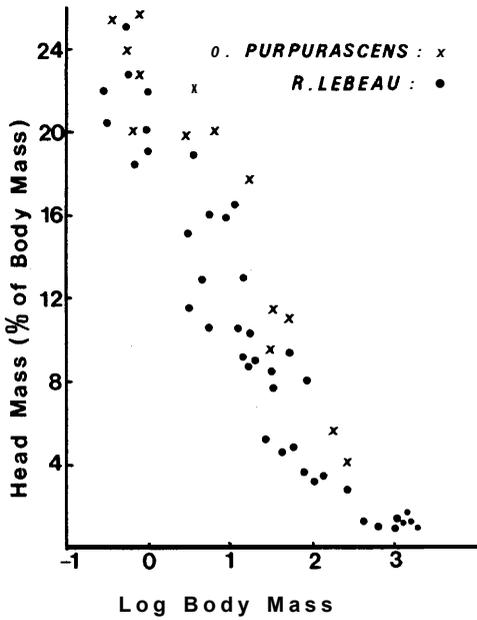


FIG. 2. The relationship between head mass as a percent of headless body mass and headless body mass in the saturniids *Rothschildia lebeau* and *Othorene purpurascens*. *R. lebeau* ( $r = -0.88$ ,  $y = 19.2 - 6.4x$ ); *O. purpurascens* ( $r = -0.80$ ,  $y = 22.5 - 6.6x$ ).

*Hylesia lineata*, and *Eacles imperialis*; Fig. 4), in which there are no strong grooves or ridges though there may be slight serrations on the very sharp and hard mandible edge. The apparently hard edge of one mandible works against a wide region on the inner face of the opposite mandible; this face becomes worn and roughened in contrast to the rest of the mandible. Increased wear thus tends to sharpen the edge of the blade. Presumably this rough surface aids purchase of the leaf

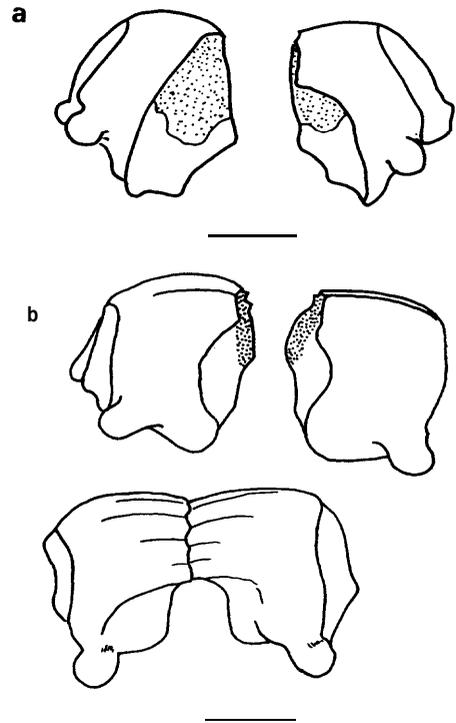


FIG. 4. Mandibles of (a) *Rothschildia lebeau* instar V ventral view slightly opened out and (b) *Eacles imperialis* instar V ventral view separated and in closed position. Scale line 1 mm.

during cutting. This general simplicity was characteristic of the Saturniidae, but there were variants. In *Arsenura armida*, for example, a relative specialist on *Bombacopsis quinatum*, the cutting edges were semi-circular blades with a short overlap. The outer mandible was stopped at a clear-cut ridge on the outer surface of the other, while the inner mandible fitted into an irregular groove on the inner surface of the other (Fig. 5a). In *Othorene purpurascens*, which feeds on *Manilkara chicle*, the mandibles were very globular in shape (Fig. 5b), with each having a double edge.

While in all cases there is some asymmetry in saturniid mandibles, at closure the left may overlap the right or vice versa, and in the species observed closure alternated between the two positions. Either way, the mechanisms for cutting appeared similar, with the sharp hard edge of one mandible fitting closely to the inner face of the other. The action appears to be of a simple snipping device or scissor action, or blade against an anvil. However, the first and second instars of saturniid caterpillars are usually of the more generalized caterpillar pattern (Snodgrass 1935) with a simple row of 4-8 teeth around the curved cutting edge (Fig. 6).

Sphingids had very different mandibles from those described above. There was much variation between species but a general pattern emerged. Mandibles were longer with narrower bases. Distally there were various grooves and teeth, *Manduca sexta* being the simplest.

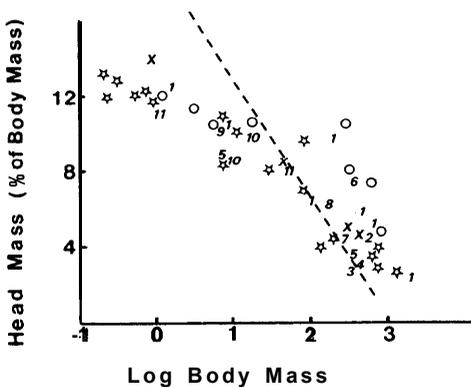


FIG. 3. The relationship between head mass as a percent of headless body mass and headless body mass in 12 sphingid species ( $r = -0.82$ ,  $y = 11.7 - 2.4x$ ). x = *Manduca dilucida*; o = *Pachylia ficus*; ☆ = *Manduca sexta*; 1 = *Pachyhoides resumens*; 2 = *Protambulyx strigilis*; 3 = *Eumorphia satelita*; 4 = *Eupyrhroglossum sagra*; 5 = *Enyo ocypete*; 6 = *Manduca florestan*; 7 = *Perigonia lusca*; 8 = *Erinnyis ello*; 9 = *Aellopos fadus*; 10 = *Manduca rustica*; 11 = *Manduca lanuginosa*. - - - the regression line for Saturniidae.

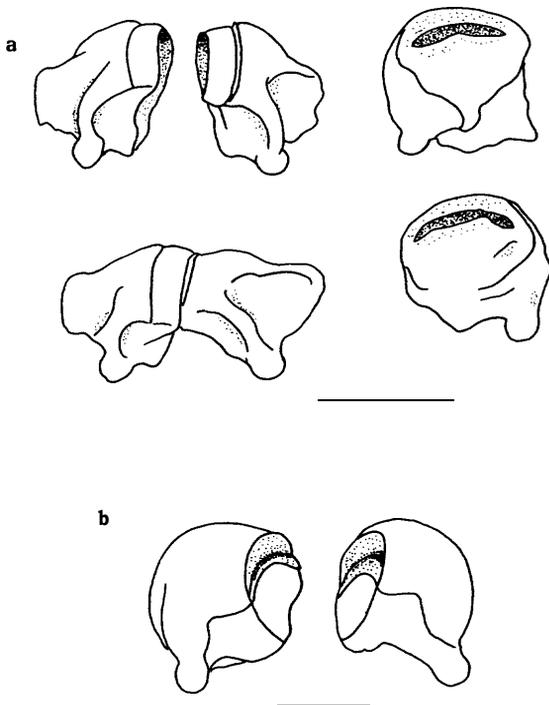


FIG. 5. Mandibles of (a) *Arsenura armida* instar V and (b) *Othorene purpurascens* instar V. Scale lines 1 mm in each case.

The most distal region of the mandible had 2-3 irregular rows of sharp-edged projections, while the inner face had a series of irregular ridges and grooves (Fig. 7). Other species displayed variations on this theme, with heavy and broad-based teeth forming a spiked club at the distal region and the inner faces being variously grooved and ridged. *Pachylia ficus* was one of the most extreme, and, like most, there was a dorsal region with a fine serrated edge (Fig. 8).

As with the satumiids, the closure could occur with left over right or right over left, usually alternating with successive bites. In either case the teeth covering the distal region of one mandible fit tightly into grooves on the inner face of the other. The action appeared to be one of crushing the blade fragment after it was cut or torn from the leaf. While sphingid mandibles had a basic similarity, the development of the parts varied: no two species had identical mandibles. Perhaps each species has a slightly different style of tearing and crushing related to the nature of its host leaves. Of the species examined, *Enyo ocypete* was the most extreme (Fig. 7), with the teeth and grooves so reduced as to more resemble the satumiid type.

The width of the mandibles (the distance across the base of the right mandible) in a number of different caterpillars of different species in different instars, was compared with the area of a sample of foliage particles taken from the gut of the same individual. Among satumiids the mandible width was directly related to the particle size bitten off and swallowed, with very

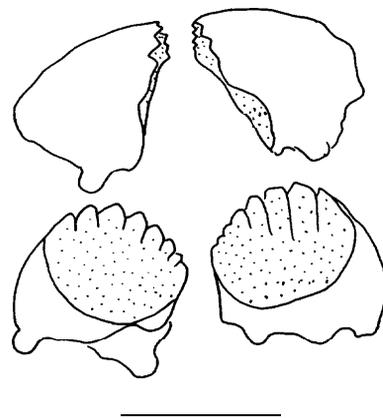


FIG. 6. Mandibles of *Rothschildia lebeau* instar I. Scale line 1 mm.

little variation (Fig. 9). In any individual on a single host plant the small standard deviation in particle size was notable while the overall pattern of size change with instar was quite consistent (Table 2). Also the pieces were of simple shape (Fig. 10), which resulted in relatively small perimeters. On the other hand, particles in sphingid guts were very small, were extremely variable and irregular in shape, and had relatively larger perimeters (Fig. 10; Table 3). In spite of the different food plants and the many species examined, the patterns found in the two families were consistently quite different.

#### DISCUSSION

The two groups of caterpillars processed leaf blades in two quite different ways. Satumiids simply snipped

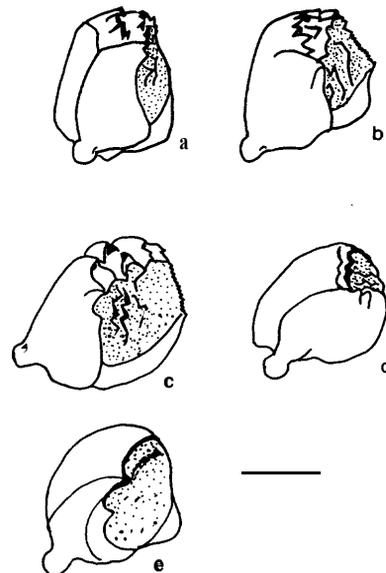


FIG. 7. Left mandibles of five sphingid species from various antero-ventral angles: (a) *Manduca lanuginosa* instar V, (b) *Cocytius duponchel* instar V, (c) *Pachylioides resumens* instar V, (d) *Protambulyx strigilis*, and (e) *Enyo ocypete*. Scale line 1 mm.

off pieces of the blade. This produced particle sizes that were closely correlated with mandible width and relatively invariant. Different species of saturniid caterpillars of the same **instar** snipped off pieces of leaves of **about** the same size (even though they were eating different species of leaves). If a single species of saturniid caterpillar, such as *Rothschildia Iebeau* or *Eacles imperialis*, fed on a number of different species of leaves, the same consistency among **instars** occurred. We feel that these insects should be viewed as having snipping rather than chewing mouthparts, since there appears to be no further mechanical processing of the food after it is bitten off. Such simple snipping behavior suggests a simple control mechanism; the entrance of the leaf to a certain point in the mouth causes a biting response, followed by swallowing.

The newly **eclosed** first-instar satumiids examined in this study eat the same tough and mature leaves as do the later **instar** larvae (e.g., Janzen 1984). Furthermore their hosts are almost all trees, many of which are evergreens with exceptionally thick and tough leaves (e.g., *Hymenaea courbaril*, *Manilkara chicle*, *Quercus oleoides*). As with the grass-feeding satumiids in the southwestern United States, the necessary power for biting through tough leaf tissue must come from large mandibular **adductor** muscles and heavily sclerotized

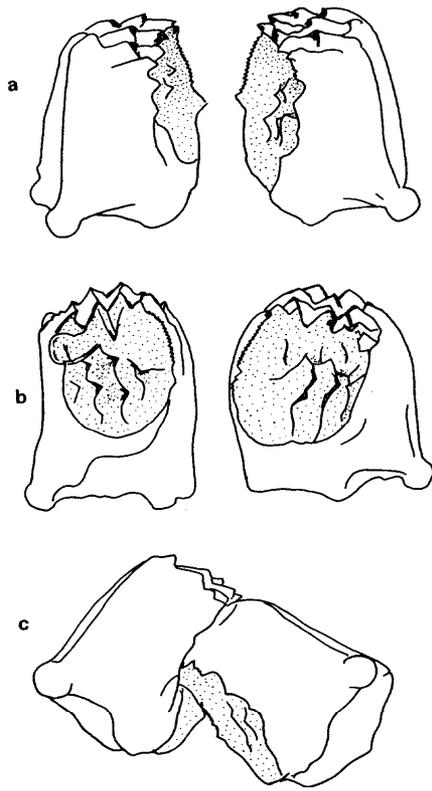


FIG. 8. Mandibles of *Pachylia ficus* instar V showing (a) antero-ventral view, (b) inner faces, and (c) mode of closure. Scale line 1.5 mm.

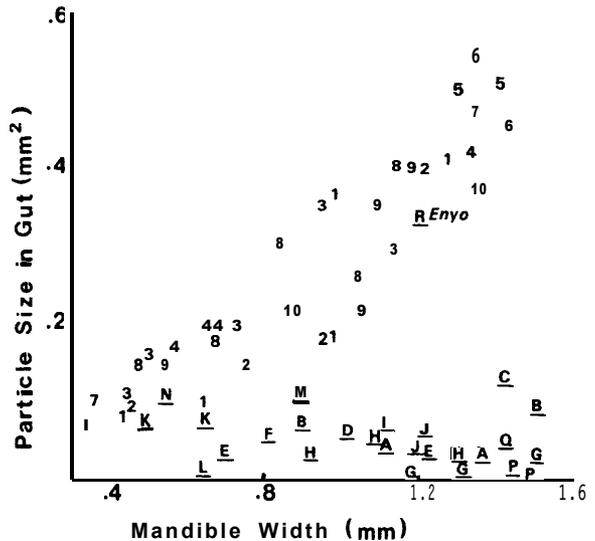


FIG. 9. Relationship between size of chewed food particles and mandible width. Numbers = saturniids; letters with underlining = sphingids. Saturniids ( $r = 0.88$ ,  $y = 0.07 + 0.38x$ ): 1 = *Othorene purpurascens* on *Manilkara chicle*; 2 = *Rothschildia lebeau* on *Casearia corymbosa*; 3 = *Rothschildia lebeau* on *Zuelania guidonia*; 4 = *Rothschildia lebeau* on *Spondias mombin*; 5 = *Sysspini molina* on *Pithecellobium saman*; 6 = *Arsenura armida* on *Bombacopsis quinatum*; 7 = *Hylesia lineata* on *Casearia corymbosa*; 8 = *Hylesia lineata* (food not recorded); 9 = *Rothschildia Iebeau* on *Exostema mexicanum*. Sphingidae: A = *Eupyrhroglossum sagra* on *Chomelia spinosa*; B = *Manduca rustica* on *Amphilophium paniculatum*; C = *Manduca florestan* on *Cydista heterophylla*; D = *Manduca lanuginosa* on *Cydista heterophylla*; E = *Pachyloides resumens* on *Forsteronia spicata*; F = *Perigonia lusca* on *Chlorophyllum candidissimum*; G = *Pachylia ficus* on *Chlorophora tinctoria*; H = *Manduca dilucida* on *Tabebuia ochracea*; I = *Cocytius duponchel* on *Annona reticulata*; J = *Erimmyis ello* on *Sebastiania confusum*; K = *Manduca dilucida* on *Sapranthus palanga*; L = *Pachylia ficus* on *Ficus cotintfolia*; M = *Eumorpha satellita* on *Cissus sicyoides*; N = *Manduca sexta* on *Solanum tuberosum*; P = *Pachylia ficus* (food not recorded); Q = *Pachyloides resumens* (food not recorded); R = *Enyo ocypte* on *Tetracera volubilis*.

mandibles (Bemays 1986). The consequence is that newly hatched larvae have an enormous relative head mass; while still in the egg, the head capsule appears to take up most of the egg volume. This may be why satumiids lay eggs that generally have 2-3 times the volume of the eggs of sphingids with the same adult body mass. Not only is the head mass relatively large, but the first-instar caterpillars are themselves relatively large (e.g., first-instar *E. imperialis* caterpillars prior to feeding are 5-7 mm long, with heads up to 2 mm wide).

The minimally processed simple leaf discs that are swallowed by satumiid caterpillars appear to pose a digestive challenge. The only plant tissue readily available for rapid digestion or removal of nutrients is that around margins of the leaf piece. A caterpillar has nothing analogous to the gizzard of a bird, and passage rates are measured in hours, which does not leave time for macrodegradation by microflora. The only tissue that

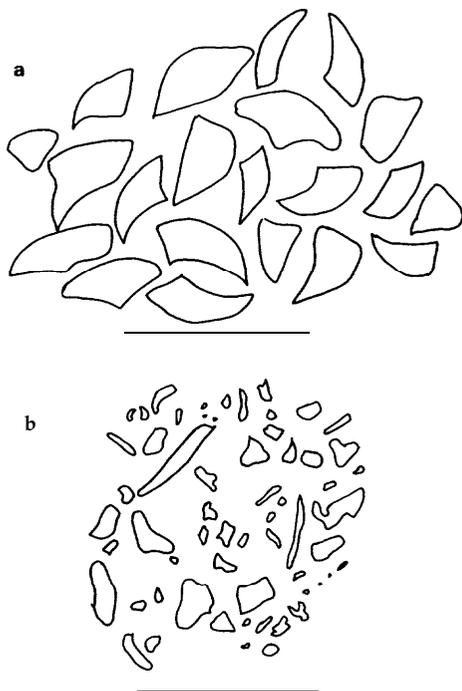


FIG. 10. Drawings of food particles from the midgut of (a) a satumiid, *Rothschildia lebeau* instar V (scale line 2 mm), and (b) a sphingid, *Pachylia ficus* instar V (scale line 1 mm).

was conspicuously removed from the discs was that around the disc margins. Indeed, the fecal pellets of saturniid larvae are simply tightly packed wads of almost morphologically intact leaf discs. This means that the larger the pieces snipped off, the lower the proportion of the food that is in a form such that its nutrients are rapidly available to the larva. This places a constraint on the size of the piece to be bitten off, which in our data is reflected in the relatively small heads of large saturniid larvae; during caterpillar development, the relative head mass changes from  $\approx 25\%$  of body mass to  $\approx 1\%$  of body mass. We predict that satumiid caterpillars will be found to spend proportionately large amounts of time cutting off and swallowing large amounts of leaf tissue. Whether this will also lead to disproportionate increase in gut transit time will depend on the relative yields from a small amount of processing of much tissue vs. a large amount of non-mechanical processing of less tissue. Many other families of caterpillars also feed on tough leaves. A preliminary survey (E. A. Bernays, *personal observation*) suggests that these, including grass specialists, also appear to have the simple mandibular shape, snipping action, and constant leaf-disc size described here for satumiids.

The sphingid caterpillar mandible shapes are very different from those of the satumiids. The varied and complex array of mandibular teeth and ridges grasp the sphingid's somewhat softer food and roughly tear it away (rather than cleanly snip it away). The inter-

locking jagged surfaces crunch the pieces into smaller pieces and puncture the cuticle. Because of their shape the mandibles produce something that is much closer to true chewing (mastication). However, we do not know if a sphingid bites more than once on any given leaf disc. Observation of the feeding process suggests a single bite per disc.

The particles in the sphingid caterpillar gut are extremely varied in size and shape, including some fibrous particles that have been tom off the leaf. Whole mounts of gut material show only a small proportion of the original leaf blade to be intact. Sphingid caterpillar fecal pellets are also a packed mass of extremely small and unrecognizable mushy tissue, and are easily distinguished from the wads of leaf discs defecated by satumiid caterpillars. The striking contrasts in variability of leaf particle area (Table 2) were probably even underestimated in this study; the sphingid guts contain a slurry of fine cellular plant material that was not measured or included in the particle-size analysis because it graded into the indeterminately minute. The mashed and pulverized nature of the sphingid gut contents could be partly created by digestive kneading,

TABLE 2. Representative examples of individual caterpillar's food particle areas and the coefficient of variation (cv) of those areas (Satumiidae).

Insect and instar	Food plant	Particle area (mm <sup>2</sup> ) <sup>c</sup>	Area v
<i>Hytesia lineata</i> II and V	<i>Casearia corymbosa</i>	.10	.19
		.49	.40
<i>Arsenura armida</i> V	<i>Bombacopsis quinatum</i>	.55	.70
		.53	.78
<i>Rothschildia lebeau</i>	<i>Casearia corymbosa</i>	.109	.46
		.143	.35
		.18	.23
		.42	.36
		.50	.57
	<i>Spondias mombin</i>	.06	.45
		.18	.38
		.22	.31
		.45	.52
		.45	.52
<i>Exostema mexicana</i>	.14	.28	
	.39	.23	
	.39	.51	
	.38	.38	
	.56	.67	
<i>Zulania guinonia</i>	.08	.40	
	.13	.34	
	.20	.37	
	.38	.30	
	.38	.30	
<i>Othorene purpurascens</i>	<i>Manilkara chicle</i>	.037	.10
		.081	.07
		.101	.07
		.179	.05
		.45	.11
<i>Syssphinx molina</i> V	<i>Pithecellobium saman</i>	.50	.44
		.45	.33
V	<i>Cassia grandis</i>	.45	.33

TABLE 3. Examples of individual caterpillar's food particle areas and the coefficient of variation (cv) of those areas (Sphingidae).

Insect and instar	Food plant	Particle area (mm <sup>2</sup> )	Area cv
<i>Manduca sexta</i> V	<i>Solanum tuberosum</i>	.081	1.03
<i>Protambulyx strigilis</i> IV	<i>Spondias mombin</i>	.053	1.19
<i>Eupyrhroglossum sagra</i> V	<i>Chomelia spinosa</i>	.044	1.58
<i>Eumorphia satelita</i> IV	<i>Cissus sicyoides</i>	.118	0.737
<i>Enyo ocypete</i> * V	<i>Tetracera volubilis</i>	.341	0.559
<i>Manduca florestan</i> V	<i>Cydista heterophylla</i>	.102	1.870
<i>Manduca rustica</i> V	<i>Amphilophilum paniculatum</i>	.165	1.0
<i>Manduca lanuginosa</i> V	<i>Cydista heterophylla</i>	.068	1.06
		.057	1.90
<i>Manduca dilucida</i> IV	<i>Tabebuia ochracea</i>	.04	1.3
III		.05	0.8
	<i>Sapranthus palanga</i>	.08	0.76
<i>Pachylioides resumens</i> IV	<i>Forsteronia spicata</i>	.045	0.98
V		.044	1.21
V		.049	1.17
V		.039	1.57
<i>Perigonia lusca</i> IV	<i>Calycophyllum candidissimum</i>	.082	0.97
<i>Pachylia ficus</i> V	<i>Chlorophora tinctoria</i>	.012	1.33
IV	<i>Ficus cotinifolia</i>	.011	1.23
III		.010	1.12
<i>Cocytius duponchel</i> IV	<i>Annona reticulata</i>	.065	1.36
<i>Erinnyis ello</i> IV	<i>Sebastiania confusum</i>	.076	1.12

\* This species has "satumiid type" mandibles.

since once a leaf disc has been ripped and broken, turbulent digestive movements can mechanically break it down further (as opposed to the small impact of such movements on intact leaf discs in a satumiid caterpillar gut).

The large sphingid caterpillars have relative head masses almost double those of large satumiid caterpillars. Sphingid digestion should not be hampered by increasing the initial bite size as the larva increases in size. We found that sphingid caterpillars with large heads produced particles just as small as did those with small heads. *Pachylia ficus*, the sphingid with the most complex mandibular teeth, had the smallest food particles in its gut, yet it had the largest relative head mass of any species.

Sphingid host leaves range from extremely flimsy to relatively tough (Janzen 1984). However, many, if not all, of the first instars of the sphingids examined here fed on very new leaves, leaves that were delicate and thin. Almost all sphingid hosts in the study area were deciduous and had relatively flimsy leaves. Finally, many species of sphingids feed on relatively herbaceous plants, which also have very flimsy leaves. Even the muscle mass in a very small head capsule can drive sphingid macelike mandibles to triturate such leaf blades. As sphingid larvae become larger, they incorporate both old and new leaves in their diets. It is striking that the sphingid larva that eats the toughest leaf blades, *Enyo ocypete* feeding on *Tetracera volubilis* (a nearly evergreen vine), has the most satumiid-like mandibles and leaf fragments in its gut. On the other hand, the sphingid that feeds on the greatest variety of leaf types, *Pachylia ficus* feeding on *Chlorophora tinctoria* (leaf blades like tissue paper), *Brosimum alicas-*

*trum* (tough evergreen leaf blades), and *Ficus* spp. (thick but fragile and nearly evergreen leaf blades), has the most massively destructive mandibles.

It is possible that the species differences in mandible shape simply indicate different ways to maximize the rate at which food can be ingested on the particular foliage utilized. Specialized mandible shapes may thus be more obvious in species with narrow host range, as appears to be the case. The virtue of rapid ingestion rate depends on the yet unknown selection for reduced time spent feeding, a pressure sometimes postulated to be imposed by visually hunting predators.

The sphingid method of feeding may represent a quite different method of circumventing plant chemical defenses than that which is used by the satumiid caterpillars. The sphingid way of processing leaves creates a soup in the gut, one in which the nutrients and the other chemicals are potentially in direct contact with each other and the caterpillar gut tissues (and free-ranging gut flora). The satumiid host plants are renowned for having foliage rich in phenolics including tannins (Janzen 1984, Janzen and Waterman 1984) and not conspicuous in the phytochemistry literature as producers of directly toxic small molecules. Sphingid host plants (e.g., Rubiaceae, Apocynaceae, Euphorbiaceae, Solanaceae, Bignoniaceae, Asclepiadaceae, Moraceae, Sapotaceae, Lauraceae), however, can easily be characterized as rich in toxic small molecules and are not famous for production of tannins (Janzen 1984). We hypothesize that the sphingid caterpillar feeding on a particular species of plant is explicitly resistant to the toxic chemicals in that plant, and therefore can thoroughly triturate the leaf so as to get the maximum amount of nutrient from it. If there are also phenolics

in the foliage, these will be present in such low amounts that they do not interfere with this mechanism, and may even contribute to the detoxification process by binding with toxic molecules.

Such a digestive mechanism implies that sphingids will be largely host specific, to one or a few closely related plants, which they are (Janzen 1984). By being tightly host specific, there is the opportunity for the evolution of colors, morphologies, and behaviors that are themselves extremely protective vis-a-vis the specific host plant. Saturniid caterpillars, on the other hand, being able to feed on plants with more varied or less species-specific "defenses" (as long as the defenses largely stay put within the untritured leaf discs), find themselves on a variety of backgrounds. This leads to a selective regime favoring individual defenses, such as urtication and its mimicry, that function in a wide variety of circumstances (Janzen 1984).

Thorough trituration of leaf fragments before the digestive process should lead to a greater amount of nutrient removal by the caterpillar per amount of leaf consumed, as compared with the saturniid digestive process with intact leaf discs as substrate. This may lead to either less leaf consumption or faster growth by the sphingid than by the saturniid caterpillar. Both topics are under examination with the species dis-

cussed here (D. H. Janzen, *personal observation*), but preliminary results strongly suggest that a sphingid caterpillar can accumulate dry mass almost twice as fast as can a saturniid caterpillar of the same size.

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