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Evolution of Insect Morphology in Relation to Plants [and Discussion]

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Evolution of insect morphology in relation to plants

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SUMMARY

This short review points out some of the major physical problems faced by insects feeding on plants, and some of the kinds of morphological adaptations that have been noted to date. Major emphasis is given to two factors: the nature of the plant surface, and the difficulty of dealing with hard or tough food. The surface provides a great variety of terrains that require specialization for maximizing tenacity and agility, especially for small insects. It is suggested that natural enemies may provide significant selection for the relevant morphologies. The difficulty of feeding upon certain plant tissues is shown to be overcome in different ways by different herbivore groups. In the case of tough leaves for example, grasshopper mandible adaptations appear to have evolved to maximize efficiency of processing. On the other hand, in the case of caterpillars, mandible adaptations for tough food appear to be minimizing handling time with a concomitant reduction in risk of predation. Convergent evolution is shown in both grasshoppers and caterpillars for dealing with leaves of similar design and an example is given of rapid evolution of mouthpart morphology in response to differences in host characteristics. These examples are used to indicate the risks of using such characters in establishing phylogenetic relationships. Finally, it is pointed out that plant chemical qualities and plant ecological factors can influence insect morphological features.

1. INTRODUCTION

Compared with Darwin's finches, selection pressure on insect herbivore morphology in relation to food has been almost ignored. There are comparative morphological studies on such structures as tongue length in bees but evolutionary approaches are relatively recent. Yet phytophagous insects provide a wealth of variety that reveals physical problems and the consequent selective pressures that plants provide: the evolution of morphological adaptations has certainly been as important as the much discussed chemical ones. As structures can now be studied quantitatively we have a new opportunity for the study of morphological character evolution.

Plant-feeding insects have been the subject of many theoretical and experimental studies and the examples given here will provide a first brief attempt to consider morphology. Plants present a series of potential problems that could influence the evolution of insect form, including superficial impediments to progress or attachment, impediments to reaching the food substrate, hardness, toughness or abrasiveness, nutritional deficiency or toxicological stress, and temporal or spatial challenges in plant distribution.

It is also unlikely that the animal adaptations to these problems would be the same without the additional influence of organisms in other trophic levels. For example, the morphological adaptations involved in host-specific crypsis show the relation between herbivore morphology, their hosts and their predators. The third trophic level is of particular importance in the case of host-related adaptations of small herbivores such as insects.

2. SURFACES

Surface features are significant for all insects, and tarsal claws are of general value for grasping at irregularities and maintaining a hold on the substrate. However, it might be expected that the variety of adaptations in tarsi will be greatest in small insects for whom the terrain is relatively more varied and conspicuous. Plant surface features have indeed posed considerable challenges for the herbivores that live, rest and feed upon them. Southwood (1973) drew attention to this fact in his description of the 'attachment hurdle' that herbivores had to overcome, and more recently several different elegant adaptations for attachment to particular types of leaf surface have been described. For example, Stork (1980) showed that in chrysomelid beetles, as in geckos, molecular adhesion from the thousands of minute setae on each tarsal pulvillus are responsible for an ability to walk on glabrous leaves. Individuals could hold on against a force of nearly 50 times their own body mass, so that whiplash of leaves in a gusty wind does not dislodge them. By contrast, Lee *et al.* (1986) showed that certain leafhoppers in the genus *Empoasca* can produce a miniature suction cup with each tarsal pulvillus which enables them to effectively hold onto smooth surfaces. On contact with the surface the pulvillus assumes a circular shape and fluid fills the area circumscribed. The fluid secretion

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and withdrawal is apparently under control and the system works very effectively on the preferred smooth host leaves, but is ineffective on hairy surfaces.

There are also adaptations for movement on hairy leaf surfaces. Southwood (1986) described special 'pseudoaroliae' on the tarsi of certain mirid bugs. Individuals are able to grasp hairs between this projection and the pretarsal claw, allowing a very effective grasp of the hair. A different development has been described for a specialist oak aphid, *Myzocallis schreiberi* (Kennedy 1986). Like other related aphids its tarsi have a pair of claws terminally and a pair of flexible spatulate empodia. These empodia are laid along and around surfaces and provide additional contact area, but in *M. schreiberi* the empodia are more flexible, allowing a good grasp on the hairs of the densely pubescent leaves of *Quercus ilex*. As a result it is much more effective at holding on than relatives that feed mainly on other, more glabrous oaks. Such mechanisms may be common among the many insect species that appear to prefer leaves with trichomes (Southwood 1986).

Moran (1986*b*) found a highly significant negative correlation between host trichome density and length of hind tarsi in *Uroleucon* species, with unrelated species groups from different geographical regions showing a similar relation. Moran suggests that short tarsi help prevent entanglement in trichomes whereas long ones provide a better grip on glabrous surfaces. By contrast, Eastop (1985) noted that aphids on hosts with sticky exudates had short tarsi; species described from the extremely resinous *Grindelia squarrosa* have no tarsi at all (Gillette 1911). Presumably 'walking on tip toe' reduces work and allows greater agility.

The ability to negotiate the surfaces of host plants with agility has value not just for feeding and ovipositing, but also for escaping from predators. For many herbivores the leaf surface is not just a feeding site and habitation, but the lifetime habitat where predators may be more abundant than prey. For example, the ability to jump away from a predator and successfully land without falling was an important component of survivorship of alfalfa aphids in the presence of their coccinellid predators (Bernays 1989). Moran (1986*a*) noted that in the aphid genus *Uroleucon*, the specialist species on goldenrod was also much better able to escape predation than was the generalist species. Indeed, it appears very likely that one of the benefits of a narrow host range is the possibility of developing specialized tarsal morphology that promotes agility on the host (Kennedy 1986), and thus efficient escape behaviours (Bernays 1989). In addition, herbivore fall-off rates can be 10% of the population per day, with the majority of those falling becoming prey for ground predators (Winder 1990). There must be intense selection pressure for competence on the host surface.

The nature of the surface is also important directly in feeding; the morphological challenges again relate to trichomes on the one hand and hard or ultrasmooth surfaces on the other. Hoffman & McEvoy (1985) found that the dense layer of simple lanate trichomes on the stems of certain host plants provided a problem to the spittle bug, *Philaenus spumarius*. When the length of the trichomes exceeded the length of the rostrum, the tip of the rostrum could not contact the leaf surface. Long rostra are an advantage on such plants, indeed the adult *P. spumarius* has a relatively long rostrum (1 mm), and it is the younger nymphs with shorter rostra whose feeding sites are limited. An analogous study on aphids specialized for feeding on *Tilia* spp. with dense stellate hairs showed that elongate rostra were essential and the successful species had them (Carter 1982). Moran's (1986*b*) morphometric study of the aphid genus *Uroleucon* showed that trichome density was correlated with the length of the terminal rostral segment, and it is likely that the adaptation is associated with a similar problem.

The difficulty in penetrating a smooth hard surface has not been addressed specifically although there is a suggestion that many details of mouthpart structures relate to this, and the ability of the tarsi to obtain a firm purchase is also likely to be important. Edge feeding is a behavioural approach to gaining entry for biting insects, but species that feed from the leaf surface can be expected to have a wide gape and needle-like incisor teeth: characteristics described by L. Casher (unpublished results) for first instar caterpillars feeding on the surface of very hard, smooth leaves of evergreen oaks.

Grasshoppers feeding on hard cylindrical leaves and stems appear to have very enlarged paraglossae on the labium. Chapman (1966) described the mouthparts of one such species, *Xenocheila zarudnyi* which feeds on *Ephedra*, where the paraglossae are cone-shaped and extend back to the front legs. In discussing these and similar structures that have evolved independently in several different grasshopper subfamilies, Chapman quotes suggestions that enlarged paraglossae act like the jaws of a brace, gripping the tip of the cylinder while the mandibles cut through it.

3. LEAF HARDNESS OR TOUGHNESS AND GRASSHOPPER MANDIBLES

The majority of grasshoppers feed on many plant species, with herbaceous plants predominating, but a large proportion have become grass specialists. Indeed the evolution of grasses, perhaps in response to vertebrate grazing pressure, has had a profound influence on the evolution of grasshopper mandible morphology. This has been known for a long time and the differences between the mandibles of forb (non-grass) feeders and grass feeders have been described in detail (see, for example, Iseley 1944; Chapman 1964). Unlike some of the holometabolous insect larvae, grasshoppers have a clearly distinguished distal incisor area and a separate molar area. The two mandibles are asymmetrical with the left mandible closing over the right to bring the molar areas together. The inner surface of the left incisor region and the outer surface of the right incisor region are of particularly hard cuticle (Gardiner & Khan 1979). In forb feeders the incisor edge bears several sharp cusps or teeth, and the molar region is also strongly toothed when unworn. In grass

Table 1. *Examples of grasshopper species from different taxa which all share the characteristic graminivorous mandibles and are host specialists on the Poaceae*

(Different numbers represent independent evolutionary origins. From Chapman (1964, 1988) and Bernays & Chapman (1978).)

Romaleidae	*Epiprora hilaris*	1
Acrididae		
Hemiacridinae	*Laxabilla smaragdina*	2
Tropidopolinae	*Tristia marginicosta*	3
Oxyinae	*Oxya japonica*	4
Catantopinae	*Tristia conops*	5
Cyrtacanthacridinae	*Nomadacris septemfasciata*	6
Leptysminae	*Stenacris fissicauda*	7
Acridinae	*Acrida conica*	8
Oedipodinae	*Locusta migratoria*	8
Gomphocerinae	*Chorthippus curtipennis*	8
Truxalinae	*Mesopsis gracilicornis*	8

Table 2. *Relative leaf toughness or hardness in plants with different growth form, with leaves of herbaceous dicots standardized to 1*

(Partly after Bernays & Hamai (1987).)

Plant type	*n*[a]	Relative toughness
palms: expanded fronds	8	9.8
woody plants: fully expanded leaves	89	6.3[b]
C4 grasses: all blades	34	6.2
C3 grasses: all blades	42	3.1
woody plants: new leaves	25	1.7[b]
herbaceous dicots: all leaves	166	1.0

[a] *n*, Number of species, each species figure based on 10–20 readings on apparently typical leaves.

[b] The ratio of old:new leaves of 3.7 is close to that of Raupp (1985) of approximately 4 for willow leaves.

specialists the incisor cusps tend to be chisel edged and the molar regions present ridges that appear to provide a grinding apparatus, reminiscent of the molar teeth in mammalian grazers (on a scale that is smaller by three orders of magnitude). Mixed feeders tend to have forbivorous mandibles, but of very stout construction. The interesting evolutionary factor here is the convergence of grass specialists on a common phenotype: the derivation of the graminivorous mandibles from the more generalized ones has probably occurred eight times (table 1).

Quantitative morphometric analyses were done by Patterson (1984) on overall dimensions. Forb feeders, in some subfamilies at least, have mandibles longer from hinge to distal cusps relative to the length of the hinge than do grass feeders, and the ratio of these values is clearly related to the proportion of forbs in the diet, at least in some groups. Maximum length of mandible, including incisor cusps, is achieved when 80% or more of the food is composed of herbaceous dicots. Grass specialists invariably have relatively short mandibles.

The benefits that accrue from the mandibular adaptations of graminivores are probably several. Firstly, the physical structure of grasses provides a difficult challenge for small herbivores in actually cutting through the many sclerophyllous parallel veins (Vincent 1982) which are responsible for the toughness (table 2), and the chisel-type incisor region is likely to be important for this task. Overall mandible shape differences will bring the occlusal surface nearest to the hinge in graminivorous forms, providing a mechanical advantage for the work needed as well as a stouter structure. The molar ridges are unlikely to be acting in precisely the same way as in grazing mammals owing to the differences in scale, and the fact that much ingestion of grasses in grasshoppers occurs without periods of grinding or chewing. However, a similar purpose may be served. It is possible that a single effective grinding action occurs when the piece of grass blade is grasped by the mandibles and passed back. Ab- and adaxial surfaces are sheared apart so that swallowed particles have a large exposure of parenchyma, potentially increasing the digestive area. Boys (1981) found that in a forb feeder 80% of ingested fragments had two epidermises, whereas in a grass feeder 80–100% of the fragments had only one epidermis. It should be noted that the grass specialist *Locusta migratoria* does pause and chew between successive bites, and that the chewing probably makes up about 10% of the meal time (Simpson *et al.* 1988). A very extreme case is the grasshopper *Microtylopteryx hebardi.* Its mandibles are similar to those of grass specialists and it feeds on extremely tough rainforest monocots, especially palms (see table 2): it has been observed to chew a cut particle of palm leaf up to twenty times before taking another bite (E. A. Bernays, unpublished results). Finally, the presence of silica in grasses may have had some influence on mandibular morphology: certainly the wear caused by feeding on grasses can be extreme (Chapman 1964), although perhaps the silica bodies in grass epidermis could be used in obtaining a purchase by the molar ridges.

In addition to form, it has been noted that grass-specialist grasshoppers have much larger mandibles and heads relative to body size compared with forb feeders, with mixed feeders being intermediate (Bernays 1986*a*). The log–log regressions of head mass against headless body mass have identical slopes but significantly different intercepts for the three types of feeders, with overall head sizes (as percent of headless body) being 23, 11 and 15% respectively (Bernays & Hamai 1987). Mandible and mandible adductor muscle mass together make up 49% of the total dry head mass with very little variation in relation to diet or to a variety of cryptic head shapes. The force needed to cut graminaceous tissue requires powerful muscles, and heads large enough to house them, and the conclusion must be that graminivores are well adapted for dealing with their food. The benefits probably relate both to improved handling and improved digestive processing, but the cost is large in terms of investment in head mass.

4. LEAF HARDNESS OR TOUGHNESS AND CATERPILLAR MANDIBLES

Unlike orthopterans, lepidopterous larvae have mandibles without a true molar area. In general the mandible is a simple structure with a row of simple incisor cusps. Various projections and teeth occur in different positions on the inner face, some of which are taxonomic characters of unknown function (Peterson 1962). Feeding habits are often not independent of taxonomy, adding a further difficulty in discerning adaptive value for particular morphological structures, but some contrasts can be made between species utilizing tough trees or grass leaves and those utilizing soft herbaceous plants. Unlike grasshoppers, a relatively small proportion have become strict graminivores,, whereas tree-feeding species are at least as abundant as herb feeders (Bernays & Barbehenn 1987).

The common observation that trees, shrubs and grasses have harder or tougher leaves than do herbaceous dicots has been quantified by Bernays & Hamai (1987) by using a penetrometer with a blade intended to represent the incisor edge of an insect mandible. Measured in arbitrary units, the ratios of toughness, with herbaceous plants as 1, are shown in table 2. Clearly the difficulty of biting through a leaf is dependent on several different factors, in particular the presence and arrangement of sclerophyllous tissues including lignified veins, and to a lesser extent, hard cuticles. Penetrometer measurements done with a pinpoint between veins allows independent measures of penetrability of upper and lower surfaces and L. Casher (unpublished results) found that in *Quercus agrifolia* the abaxial cuticle was harder than the adaxial.

Caterpillar species that have become grass specialists have, as in grasshoppers, relatively larger heads than those that feed on herbaceous dicots (Bernays 1986*a*). As grasses and other tough foliage is low in protein, the challenge is twofold.

1. An increased force must be developed, which, together with reduced contact area of mandible and leaf, will provide the necessary pressure (Wheater & Evans 1989). This requires adductor muscles with a large cross-sectional area.
2. More bites are needed to obtain enough food on the tough leaves, with the possibility that the increased work will cause an increase in muscle development.

The fact that greater positive allometric growth of the head occurred within a cohort of caterpillars of *Pseudaletia unipuncta* fed on tough grasses, compared with others on soft food, provides further evidence of the importance of head and mandible size.

All species examined that feed primarily on grasses and older tough leaves of woody plants have simplified mandibles in the later instars. Instead of the primitive row of sharp incisor cusps along the edges that loosely overlap (left over right and vice versa), there is a smooth incisor edge, usually devoid of cusps, and often with a groove or ridge of some kind into which the opposing incisor region fits. Instead of a cutting and tearing behaviour, the action is more akin to scissor or tin-snip action. Examples in table 3 show the convergence of this trait in several different families. Godfrey *et al.* (1989) examined 143 species of Notodontidae and the few species having incisor teeth are those specializing on very soft new leaves. Similarly, Bernays & Janzen (1988) examined 12 species of Saturniidae, all of which feed generally on mature tree leaves, and all had the incisorless mandible type, albeit each with characteristic details. Barbehenn (1989) found incisorless mandibles characteristic of 18 species of Hesperiidae that feed on grasses or trees. As with grasshoppers, the ratio of length of mandible to length of hinge is lowest for these tree-feeders and grass-feeders, resulting in a very stout structure. The convergence of the phenological characters is clearly indicative of an adaptive function, apparently related to the toughness or hardness of the foliage consumed.

Several authors have noted that many of the species with toothless snipping mandibles in late instars have well-developed teeth in the earlier instars. They feed between major veins and their problem is partly dealing with smaller veins, but more often with a hard cuticle. Indeed the teeth seem to be used in gouging out mesophyll between the veins, leaving the rest of the leaf intact. The change in morphology and the switch to a feeding habit in which whole leaf thickness is cut occurs at different instars depending on species (Hagen & Chabot 1986; Godfrey *et al.* 1989; L. Casher, unpublished results). On the other hand, some very small species of caterpillar that feed on tough tree leaves

Table 3. *Examples of species pairs within families where one has typical lepidopteran incisor teeth and the other has adopted the toothless snipping mandibles associated with their feeding on tough leaves of trees or grasses*

	food: new leaves or herbaceous	food: tree leaves or grasses	
family	Incisor teeth	No incisor teeth	reference
Notodontidae	*Crinodes besckiae*	*Cerura vinula*	1
Dioptidae	*Cyanotricha necyria*	*Phryganidia californica*	1, 2
Noctuidae	*Spodoptera littoralis*	*Spodoptera exempta*	3
Sphingidae	*Manduca rustica*	*Enyo ocypete*	4
Hesperiidae	*Pyrgus communis*	*Erynnis tristis*	5
Pyralidae	*Uresiphita reversalis*	*Chilo partellus*	6

[a] 1, Godfrey *et al.* (1989); 2, L. Casher (unpublished results); 3, Brown & Dewhurst (1975); 4, Bernays & Janzen (1988); 5, Barbehenn (1989); 6, E. A. Bernays (unpublished results).

remain skeletonizers and retain strongly toothed mandibles (L. Casher, unpublished results). The relation between leaf type, feeding behaviour and gross mandible morphology is very compelling, and in addition there is a suggestion that the snipping mandible is associated with toughness (fibres, sclerenchema, lignin) and very sharp teeth with cuticle hardness.

The cutting or snipping action of mandibles dealing with tough leaves results in rather standard ingested particle size for a particular size of mandible, which was considered a constraint on size by Bernays & Janzen (1988) because large particles might be inefficiently digested. Although there may be upper limits to ideal bite sizes for digestion in caterpillars, Barbehenn (1989) found that sizes were not correlated with digestibility levels, even though at larger bite sizes as few as 6% of leaf cells were physically damaged. In spite of the commonly held belief that folivores chew their food, most caterpillars (unlike grasshoppers) ingest unmacerated leaf tissue and can efficiently digest the nutrients therein (Harvey 1975; Hocking & Depner 1961; Rybicki 1957; Barbehenn 1989). This is achieved through a combination of high gut pH (Jones *et al.* 1989), presence of surfactants (Martin & Martin 1984) and efficient phospholipases that rapidly degrade cell membranes allowing rapid diffusion through the plasmodesmata, which have diameters of over 60 nm after disruption of the desmotubule (Barbehenn 1989). Furthermore, Barbehenn found that in two grass-feeding species, protein was quite efficiently removed even from C4 grasses where about half of the leaf protein is contained within the bundle sheath cells the walls of which are highly lignified. In fact, digestibility was equally good in the hesperiid with a food transit time of 8–20 h and noctuid caterpillar with a transit time of 2–4 h.

From this it would appear that incisor teeth, even though they result in leaf particles with relatively large circumference to area ratios (Bernays & Janzen 1988), have no role in assisting digestive processing by caterpillars, especially as species with and species without all have similar digestibilities of standard seedling wheat (Bernays & Barbehenn 1987).

Convergence can also be seen in mandibles of large caterpillar species that feed on soft flaccid leaves. There is considerable development of projections or teeth, not just on the edge of an incisor area but on the whole distal region and inner face of the mandibles; teeth of one mandible fit into depressions on the opposing mandible. Dorsally, where the two mandibles first meet during a bite, there is a serrate edge apparently for penetration of the leaf. This pattern, with many variants, can be seen in Sphingidae (Bernays & Janzen 1988) and in certain examples elsewhere (Godfrey *et al.* 1989). Interestingly, in the sphingids, at least one species, *Enyo ocypete*, has returned to the toothless snipping type and is a specialist on the very tough leaved *Tetracera volubilis* (table 3).

Bernays & Janzen (1988) contrasted the snipping mandibles of Saturniidae with the complex interlocking mandibles of Sphingidae and concluded that differences related to both handling and digestibility. In the light of Barbehenn's (1989) findings the emphasis should perhaps be on efficiency of handling. 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. Because both leaf types can be eaten by both caterpillar types, the concept of efficient handling becomes more subtle: rate of food intake may be under intense selection pressure if feeding increases the chances of predation. Certainly tough leaves take longer to ingest by caterpillars not specifically adapted than by those that are (Bernays 1986*a*; Devitt & Smith 1985), whereas feeding caterpillars are about 30% more vulnerable to predation by vespid wasps than are resting ones (E. A. Bernays, unpublished results), so that reduction in time spent feeding could provide a considerable selective advantage. In addition, the studies of Heinrich (1983) suggest that the act of feeding by caterpillars increases vulnerability to bird predation.

Wear is a potential problem for mandibulate insects feeding on hard, tough or abrasive material, and it is known to have a large impact on the form of grasshopper (Chapman 1964) and beetle (Raupp 1985) mandibles, increasing the time taken to eat a given quantity of leaf. Wear also occurs in caterpillar mandibles and measurements were made of the incisor:hinge ratio in newly molted fifth instar saturniid *Rothschildea lebeau* or on the exuviae. Big changes occur – a 10% reduction in incisor length – but interestingly the edge appears to be more or less maintained, indicating that the mandibles may be self sharpening, perhaps by having a softer cuticle on the inner face than on the outer face. This ability may be a feature of species feeding on tough leaves, and it has been noticed that the weakly toothed mandibles of third instar *Phryganidia californica* are quickly worn down to the smooth type (unpublished observations). Photographs published by Djamin & Pathak (1967) suggest that the stem borer, *Chilo suppressalis*, maintains toothed mandibles on low silica hosts but these become toothless snipping structures on high silica rice.

5. CHEMORECEPTORS

Number and arrangement of chemoreceptors is apparently related to host-specific behavioural adaptation in some groups. In the aphid genus *Uroleucon*, alatae of species on hosts that have a clumped distribution have significantly less extensive rhinaria on the antennae than those that utilize highly dispersed plant species (Moran 1986*b*), suggesting that host location needs will determine this aspect of aphid morphology. This idea is supported by the differences found in relation to aphid polyphenism: less mobility, as judged by lack of wings and shorter legs, is always associated with fewer antennal chemoreceptors.

Chapman (1982) undertook an extensive study of sensilla and found strong evidence of larger numbers being associated with broader host ranges. At higher taxonomic levels it is possible, as he suggests, that smaller numbers permit or promote narrow host range:

diets are markedly broader in the orthopteroid orders where sensillum numbers are extremely large. On the other hand, among grasshoppers, where specialized diets are clearly derived, it appears that narrow diet has led to a reduction in chemoreceptors. The subfamilies that are characteristically grass feeding all have fewer receptors, and there is evidence of considerable further reduction in all the specialists examined (Chapman & Thomas 1978). For example in the Gomphocerinae, where most species are graminivorous, the polyphagous species examined have larger numbers, whereas the extreme specialists have fewer (Chapman & Fraser 1989). Chapman (1982) suggests that the functional significance of the morphological specialization perhaps relates to the relative ease of determining appropriate food among specialists, because of labelled chemosensory lines for host-specific chemicals. However, information so far suggests that grass specialists select food plants on the basis of absence of deterrents instead of via grass-specific cues (Bernays & Chapman 1978), so the explanation may not be so simple.

6. INTERNAL MORPHOLOGY

There are few studies on what morphologies are under selection pressure internally. Chapman (1988) examined the guts of 170 species of grasshopper, in which there are six gastric caeca that typically have anterior and posterior arms. In grass feeders, however, the posterior arms were invariably reduced or absent. The average ratio of posterior arm length to anterior arm length was twice as high in forb feeders as in graminivores, and he suggested that this morphological difference may relate to reduced needs for detoxification of plant secondary metabolites in grass feeders.

In the examination of fifteen grasshopper species the foregut volume was also found to be significantly greater in polyphagous species than in graminivores (E. A. Bernays & Raubenheimer, unpublished results). The most extreme polyphagous forb feeder, *Taeniopoda eques*, had a full crop mass that was 50% of the total body mass, whereas at the other extreme in four of the grass specialists it was about 10%. Whether this relates to chemical composition is unknown, but other possibilities exist. From the few observations made so far, one could suggest that the grass feeders and other relative specialists are less exploratory than the polyphages and perhaps less likely to become separated from highly suitable food resources.

Plant material being commonly low in protein, insects could possibly conserve on protein by reducing investment in cuticle. This could be seen as one of the benefits accruing to soft bodied holometabolous larvae of caterpillars having a thin cuticle, in comparison with grasshoppers, in which nearly half of the dry body mass is proteinaceous cuticle (Bernays 1986*b*). Rees (1986) used similar reasoning when he found that leaf-feeding beetles and bugs had thinner cuticles than carnivorous ones.

Examination of internal organs will certainly reveal more: there are likely to be variations in relation to specific host chemistry, water content, symbiotes and lifestyle. Large structural differences exist at the ordinary level and there are well known adaptations for regulation of water content: it would be surprising if there were not an infinite variety of adaptations between and within species.

7. EVOLUTION AND CONCLUSIONS

The evolution of morphological adaptations is largely veiled in the past, and direct measures of any evolutionary change are rare. Natural rates of evolution of morphological traits in insects are thus virtually unknown. In a recent study Carroll & Boyd (1991) provide direct evidence of evolution by natural selection of beak length in *Jadera haematoloma* bugs over 20–50 years. This insect feeds on seeds contained within the fruits of various species of Sapindaceae, and its stylets must reach through the fruit to the seeds. In the southern U.S.A., recently introduced plants have been colonized by this bug which has formed host races with beak lengths either longer or shorter to suit large or small fruits. Measures of museum specimens have provided the evidence that ancestral populations were different and had the requisite variation to respond to novel selection pressures seen over decades. Directional selection for beak length has been uniformly rapid in three different host races; differences among the races in patterns of phenotypic change also imply differences in the genetic processes.

The examples of morphological adaptations given in this paper show quantitative changes that are probably achieved by allometric growth. In addition, the ontogenetic changes may partly reflect effects of experience, as in the case of hard foods that cause greater positive allometry in *Pseudaletia unipuncta* larvae. The development of snipping lepidopterous mandibles in species that start off with toothed incisor regions may also be influenced by the feeding regime, directly by wear, and perhaps indirectly by the effect of wear on subsequent patterns of cuticle deposition.

Adaptive morphology of insect structures related to host use is present wherever it is looked for. Because morphological characters seem to respond rapidly to selection, they may be limited in their use for inferring phylogenies. In addition, care is needed to interpret correlations found in relation to host characters, as these may arise through having clusters of related similar species. Thus phylogeny and host-related morphological adaptation need to be studied together (Felsenstein 1985). Finally, morphology is inextricably associated with behaviour and ecology, and in studying the adaptations of insect herbivores with plants, particular account must be taken of predators, and perhaps other mortality factors, that influence evolution of insects in relation to their host plants.

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Discussion

E. A. Jarzembowski (*Booth Museum of Natural History, Brighton, U.K.*). There has been much discussion recently on the functional morphology of flight in insects. *Rhyniella praecursor*, the earliest known insect (hexapod) was a flightless apterygote and lived in an arachnid-infested bog as described by Professor Chaloner (this symposium).

By analogy with living insects (e.g. *Podura*), would not the long pretarsi of this small wingless insect have enabled it to walk on the surface of water and thus avoid predation?

E. A. Bernays. This is an interesting idea but maybe walking on the surface had more importance for prevention of drowning!

S. B. Malcolm (*Department of Biology, Imperial College, Silwood Park, U.K.*). Professor Bernays suggests that natural enemies constrain the movement of cryptic insect herbivores and select indirectly for increased morphological feeding adaptations so that plant food can be ingested as effectively as possible. Do you think that aposematic insect herbivores are less constrained by the need for morphological feeding adaptations because they forage conspicuously? Perhaps aposematic generalists show less morphological feeding adaptation than aposematic specialists and both are less specialized morphologically than cryptic feeders.

E. A. Bernays. This would be a most interesting approach to testing my hypothesis. I cannot think of any studies to draw upon at this point but it is well worth investigation. Of course even aposematic species have their enemies so the pattern is probably not clear cut.