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Mandible Form Relative to the Main Food Type in Ladybirds (Coleoptera: Coccinellidae)

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The Coccinellidae is an economically important family within the Coleoptera. Some members are phytophagous pests, but many are beneficial predators and valuable biocontrol agents. This study investigates the morphology of the mandibles of adult Coccinellidae in relation to diet. Using scanning electron microscopy on 86 species of Coccinellidae, it was found that the morphology of the mandibles was dictated by the general feeding method, and could only be used to indicate a phytophagous, mycophagous or carnivorous diet. Phytophagous Coccinellidae of the subfamily Epilachninae had mandibles with denticulate apical teeth and setae for feeding on leaf material. The mandibles of the mycophagous Psylloborini had secondary teeth on the ventral apical tooth for collecting fungal spores. The mandibles of carnivorous Coccinellidae and Scymninae had either a bifid or unidentate apex. The unidentate mandible seemed to be restricted to coccidophagous species. Many species also had a mandibular groove along which prey body juices were conducted. Although mandible morphology could be related to the overall feeding method, there was no relationship between specific diet or food taxon and mandible shape. Mandible shape does not appear to be especially restricting for changes in diet either in the ecological sense or over evolutionary time. Mandible morphology is of limited use in determining diet and host specificity in Coccinellidae that are being selected as potential biocontrol agents.

Keywords: mandible morphology, food type, Coccinellidae, biocontrol agents

INTRODUCTION

The Coccinellidae (Coleoptera) is an economically highly important family (Iablokoff-Khnzorian, 1982). Some species are phytophagous, causing damage to agricultural and forest plants (Hodek, 1973). Many others feed on agricultural pests, such as aphids, scale insects and phytophagous mites, and some, such as *Rodolia cardinalis* and *Cryptolaemus montrouzieri*, are major biocontrol agents (Hodek, 1973; Laing & Hamai, 1976; Majerus & Kearns, 1989). Other species are mycophagous (Ricci, 1982; Ricci & Stella, 1988).

Smith (1893) noted differences between the mouthparts, especially the mandibles, of *Coccinella 9-notata* (an aphid feeder) and *Epilachna borealis* (a herbivore). Similarly, Pradhan (1938) found differences between the mandibles of herbivorous and carnivorous Coccinellidae, with predaceous versus phytophagous species differing in the incisor apex and in molar regions.

Minelli and Pasqual (1977) examined 37 species of most tribes and concluded that there was no strong relationship between diet and mouthparts, despite Schilder and Schilder (1928) showing some specificity in food habits at the tribe level. This paper re-examines in detail this relationship between adult mandible morphology and diet in 86 species, with the specific aim of seeing whether the relationship can be used in biological control methodology.

MATERIALS AND METHODS

Adults used here were dissected from dry (pinned), wet (in 70% ethyl alcohol) or fresh specimens. Mostly dry specimens were used, being more readily available. A total of 86 species in 53 genera from 19 tribes and six subfamilies were examined (Table 1). Specimens contaminated with dust particles were centrifuged in clean alcohol for 60 s. The mandibles of the adults were dissected out of the heads of specimens and embedded in wax plates, using a Nikon dissecting microscope and fine forceps. Once specimens had been sputter coated, they were viewed in the scanning electron microscope.

RESULTS AND COMMENTS ON FEEDING

Epilachninae

Mandible morphology. The mandibles of the Epilachninae have been described previously by Butt (1951), Kovář (1973) and Pradhan (1938). The mandible can be divided into a distal incisor region, inner cutting edge and molar region. The incisor region has three or four large, apically round or blunt teeth, some of which are denticulate on the inner margin. From this typical incisor region (see also Figure 17 later), other mandibles can be derived, with a gradual reduction of accessory teeth and a strong shortening of apical teeth. This can be seen in *Afidenta alia*, where the teeth are shorter and show no secondary denticulation (Figure 1). *Cynegetis impunctata* also shows a shortening of the teeth and no secondary denticulation. *Chnootriba similis* has a reduced number of teeth (Figure 2). The inner cutting edge of the mandibles of the Epilachninae extends from the apical teeth to the molar region, and is serrated for about one-third of its length adjacent to the inner teeth. The molar region of the mandibles is rounded and has no basal or crushing tooth. On the ventral side of each mandible, there is a soft lobe (a prostheca) which is fringed with setae and is joined to the mandible at the base only.

Feeding. The Epilachninae feed on plants, with some species being important pests of crops, especially the Cucurbitaceae and Solanaceae (Booth *et al.*, 1990). There is some specificity in diet in different *Epilachna* species (Hodek, 1973).

Coccinellinae

Mandible morphology. The mandibles of the Coccinellinae are the typical carnivorous type described by Kovář (1973), Pradhan (1938), and Pandey *et al.* (1982). The distal incisor region of the mandibles is formed by two teeth, giving them a bifid apex. In the aphidophagous tribe, Coccinellini, these terminal teeth are split near the top. In most species, the ventral tooth is smaller than the dorsal one. This is also the case in the tribe Psylloborini, but the ventral tooth is also divided into a row of additional teeth.

The number of secondary teeth varies between species. *Vibidia 12-guttata* has four secondary teeth (Figure 3), while *Psyllobora 22-punctata* has three secondary teeth (Figure 4). In the tribe Tytthaspini, both the terminal teeth are of equal size, while in the Bulaeini the ventral tooth is slightly smaller. The inner cutting edge is smooth in the Coccinellini, but covered in minute, blunt teeth in the Tytthaspini, Bulaeini and Psylloborini. The molar region is formed by a basal tooth or molar projection. This consists of two teeth, one dorsal and one ventral, both of which point outwards. The dorsal basal tooth is usually larger but varies in shape from small and blunt

TABLE 1. Species of adult Coccinellidae whose mandibles were used for the scanning electron microscopy in this study

Species	Country of collection ^a	Food ^b
EPILACHNINAE		
<i>Epilachna annulata</i>	Zaire	Cucurbits, beans, solanaceous crops
<i>E. bifasciata</i>	South Africa	Cucurbits, beans, solanaceous crops
<i>E. chenoni</i>	Zaire	Cucurbits, beans, solanaceous crops
<i>E. hurta</i>	Rwanda	Cucurbits, beans, solanaceous crops
<i>E. lupina</i>	Zambia	Cucurbits, beans, solanaceous crops
<i>E. mirifica</i>	Zaire	Cucurbits, beans, solanaceous crops
<i>E. misella</i>	Zaire	Cucurbits, beans, solanaceous crops
<i>E. pavonia</i>	Madagascar	Cucurbits, beans, solanaceous crops
<i>E. reticulata</i> ^c	Ghana	Cucurbits, beans, solanaceous crops
<i>Chnootriba maderi</i>	Rwanda	Wheat, maize and other Gramineae
<i>C. similis</i> ^c	Kenya	Wheat, maize and other Gramineae
<i>Subcoccinella 24-punctata</i>	Germany	Clover, lucerne and vetches
<i>Afidenta alia</i> ^c	Uganda	Clover, lucerne and vetches
<i>Cynegetis impunctata</i>	Germany	Wheat and bilberry
COCCINELLINAE		
Bulaeini		
<i>Bulaea lichatoshovii</i>	Egypt	Pollen, occasionally plants, e.g. sugar beet, and fungal spores
Psylloborini		
<i>Psyllobora 22-punctata</i> ^c	Germany	Powdery mildews and spores
<i>P. variegata</i>	South Africa	Powdery mildews and spores
<i>Vibidia 12-guttata</i> ^c	Germany	Powdery mildews and spores
Tytthaspini		
<i>Tytthaspis 16-punctata</i> ^c	Germany	Fungi and occasionally pollen, Acari and Thysanoptera
Coccinellini		
<i>Adalia bipunctata</i>	USA	Mostly aphids, but occasionally other Homoptera and rarely other insects
<i>A. decempunctata</i>	Germany	Mostly aphids, but occasionally other Homoptera and rarely other insects
<i>Aiolocaria mirabilis</i>	Russia	Immature stages of Coleoptera
<i>Anatis ocellata</i>	Germany	Mostly aphids
<i>Aphidecta decempunctata</i>	Germany	Mostly aphids
<i>Calvia 14-guttata</i>	Germany	Pre-imaginal stages of Chrysomelidae
<i>Cheilomenes lunata</i>	South Africa	Mostly aphids
<i>C. propinqua</i>	South Africa	Mostly aphids
<i>C. sulphurea</i>	Madagascar	Mostly aphids
<i>Coccinella 5-punctata</i>	Germany	Mostly aphids
<i>C. 7-punctata</i>	Germany	Mostly aphids
<i>C. 14-punctata</i>	Germany	Mostly aphids
<i>C. 14-pustulata</i>	Former Yugoslavia	Mostly aphids
<i>Coleomegilla maculata</i>	Canada	Mostly aphids
<i>Declivitata hamata</i>	Zaire	Mostly aphids
<i>D. olivieri</i>	South Africa	Mostly aphids
<i>D. uncifera</i>	Zaire	Mostly aphids
<i>Dysis 4-lineata</i>	Mozambique	Mostly aphids
<i>Harmonia axyridis</i>	Japan	Mostly aphids
<i>Hippodamia 12-punctata</i>	Austria	Mostly aphids
<i>Liodalia flavomaculata</i>	South Africa	Mostly aphids
<i>Myrrha 18-guttata</i>	Germany	Mostly aphids
<i>Oenopia conglobata</i>	Jordan	Mostly aphids
<i>Pania luteopustulata</i>	China	Mostly aphids
<i>Propylea japonica</i>	China	Mostly aphids
<i>P. 14-punctata</i>	Germany	Mostly aphids
<i>Xanthadalia rufescens</i>	Zaire	Mostly aphids

TABLE 1. *Continued*

Species	Country of collection ^a	Food ^b
COCCIDULINAE		
Lithophilini		
<i>Mimolithophilus capensis</i>	South Africa	Unknown
<i>M. alobatus</i>	South Africa	Unknown
<i>Tetrabrachys graecus</i>	Ethiopia	Unknown
<i>T. tenebrosus</i>	Turkey	Unknown
Coccidulini		
<i>Epipleuria rufosuturalis</i>	South Africa	Coccidae (?)
<i>Rhizobius decoratus</i>	South Africa	Coccidae
<i>R. litura</i>	Corsica (France)	Coccidae
Exoplectrini		
<i>Aulis annexa</i>	Zaire	<i>Icerya</i> and relatives
Noviini		
<i>Rodolia cardinalis</i>	Australia	<i>Icerya</i> and relatives
<i>R. occidentalis</i>	Zaire	<i>Icerya</i> and relatives
STICHOLOTINAE		
Serangiini		
<i>Serangium giffardi</i> ^c	Kenya	Aleyrodidae
Sticholotini		
<i>Lotis neglecta</i>	South Africa	Diaspididae
<i>L. quadrivulneratus</i>	Unknown	Diaspididae
<i>Pharoscymnus 6-guttatus</i>	Sao Tome	Mostly aphids and coccids
<i>P. ovoideus</i> ^c	Crete	Mostly aphids and coccids
<i>Xanthorcus concinnus</i>	'Guinea'	Homoptera
<i>X. rufescens</i>	Chad	Homoptera
SCYMNINAE		
Stethorini		
<i>Stethorus arthropis</i> ^c	South Africa	Phytophagous mites
<i>S. punctillum</i>	USA	Phytophagous mites
<i>Cryptolaemus montrouzieri</i> ^c	Algeria	<i>Pseudococcus</i> mealybugs
<i>Midus 4-stillatus</i>	South Africa	Unknown
<i>Nephus binaevatus</i>	Unknown	Unknown
<i>Scymnus apetzi</i>	Former Yugoslavia	Coccids and aphids
<i>S. frontalis</i> ^c	Austria	Coccids and aphids
<i>S. rubromaculatus</i>	Germany	Coccids and aphids
Hyperaspini		
<i>Hyperaspis campestris</i>	Germany	Coccids
<i>H. felixi</i>	South Africa	Coccids
<i>H. senegalensis</i>	Zaire	Coccids
Ortalini		
<i>Ortalia ochraea</i>	Botswana	Psyllids, Flatidae larvae and <i>Pheidole</i> ants
Cryptognathini		
<i>Cryptognathus nodiceps</i> ^c	France	Aphids and coccids
Cranophorini		
<i>Cranophorus varius</i>	South Africa	Unknown
CHILOCORINAE		
Platynaspini		
<i>Platynaspis solieri</i> ^c	Zaire	Mainly aphids

TABLE 1. *Continued*

Species	Country of collection ^a	Food ^b
Chilocorini		
<i>Brumus nigrifrons</i>	São Tome	
<i>Chilocorus bipustulatus</i>	South Africa	Mainly Diaspididae
<i>C. infernalis</i>	Pakistan	Mainly Diaspididae
<i>C. nigritus</i> ^c	South Africa	Mainly Diaspididae
<i>C. schiodtei</i> ^c	Cameroon	Mainly Diaspididae
<i>C. wahlbergi</i>	Zaire	Mainly Diaspididae
<i>Exochomus flavipes</i>	South Africa	Pseudococcidae
<i>E. 4-pustulatus</i> ^c	Austria	Coccidae

^a This may not be the country of origin as some species have been translocated or have invaded new areas.

^b From various sources, including field observations and references listed in text. NB Some of these categories are broad while others may represent only a single, possibly even abnormal, feeding preference (see, for example, details of *C. nigritus* feeding behaviour).

^c Mandibles illustrated in this paper.

to large and pointed. The prostheca, which extends ventrally from the base of the mandible, is attached to the mandible along half its length. It is fringed with short setae. The prostheca is more developed in the Tythaspini species, *Tythaspis 16-punctata* (Figure 5; see also Figure 17 later). The setae are thick, long and evenly spaced.

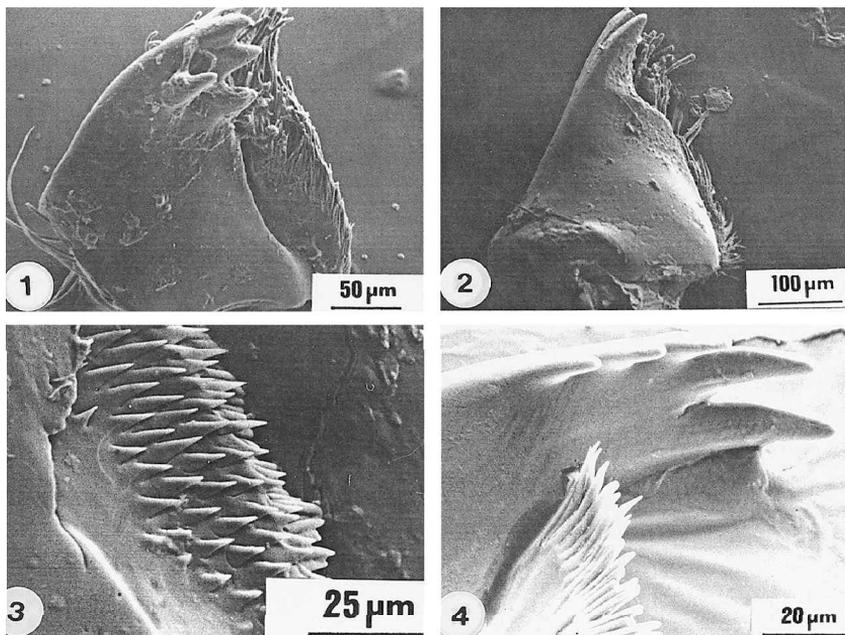


FIGURE 1. Dorsal view of left mandible of *A. alia* (Epilachninae), with dentition concentrated near the tip.

FIGURE 2. Dorsal view of left mandible of *C. similis* (Epilachninae), with dentition reduced to two apical teeth.

FIGURE 3. Dorsal view of the inner cutting edge of the left mandible of *V. 12-guttata* (Coccinellinae: Psylloborini) showing minute sharp teeth.

FIGURE 4. Ventral view of the tip of the right mandible of *P. punctata* (Coccinellinae: Psylloborini) showing two apical and three secondary teeth.

Feeding. Although *Aiolocaria* spp. and *Calvia* spp. specialize on feeding on immature Coleoptera, the mandibles of *Calvia 14-guttata* and *Aiolocaria mirabilis* examined here show no structural adaptations for feeding in this way. The comb-like prostheca of the mandibles of *T. 16-punctata* is probably used as a rake to collect spores of fungi or pollen grains by inserting the rake between the spore-bearing fungal hyphae or pollen-bearing stigmas and moving it upwards to detach the spores or pollen grains, which are then ingested. Ricci (1982) examined the stomach contents of *T. 16-punctata* and found fungal spores, Gramineae pollen, Acari and Thysanoptera. The most frequently found fungi were *Alternaria* sp. and *Cladosporium* sp.

Species within the tribe Psylloborini feed on lower fungi, especially Erysiphaceae (Hodek, 1973; Lawrence, 1989; Majerus & Kearns, 1989; Booth *et al.*, 1990). They can be clearly distinguished from the other three tribes of the Coccinellinae by their distinctly shaped mandibles. The secondary teeth on the ventral, apical tooth of the mandibles are used to rake spores or hyphae from the surface (Ricci, 1982; Lawrence, 1989; Booth *et al.*, 1990). These teeth were seen here in the Psylloborini, which have between three and four secondary teeth on the ventral tooth. Aphidophagous Coccinellini have both small dorsal and ventral teeth, and feed on the sucked body fluids and solid body parts of aphids (Hodek, 1973). Coccinellinae are polyphagous and are able to switch to different prey (Hodek, 1973). Although predaceous Coccinellinae are polyphagous, they show much specificity to ensure complete development (Hodek, 1973).

Coccidulinae

Mandible morphology. In the tribe Lithophilini, the four species *Tetrabrachys graecus*, *T. tenebrosus*, *Mimolithophilus alobatus* and *M. capensis* have two well-developed apical teeth of similar size (Figure 6). In *Aulis annexa* (tribe Exoplectrini), *Rhyzobius litura* and *Epipleuria rufosuturalis* (tribe Coccidulini) also have equal-sized apical teeth. In the tribe Noviini, the ventral tooth is less well developed than the dorsal one. The inner molar region is entirely smooth in all the Coccidulinae species, and the basal tooth of the molar region is of medium size. The prostheca is attached along half the length of the mandible.

Feeding. The well-developed mandibular teeth of *Mimolithophilus* spp., *Tetrabrachys* spp. and *A. annexa* are typical of predaceous species. These species all feed on Aphididae, Coccidae and Aleyrodidae (Hodek, 1973). Predatory coccinellids usually have two large teeth positioned side by side (Majerus, 1994). The presence of a molar region and basal tooth in these species also relates to their general predaceous behaviour.

Sticholotinae

Mandible morphology. The mandible of *Serangium giffardi* (tribe Serangiini) (Figure 7) is very distinct from the mandibles of all the other species in the subfamily. The incisor region is a single, long, sharp tooth with a distinct groove. The basal tooth is completely absent and the inner cutting edge is covered in small, sharp, tooth-like processes. The prostheca is very different from that of any other tribe, being attached along most of its length to the mandible and having no setae. In *Lotis neglecta*, *Pharoscygnus ovoideus* (Figure 8), *P. 6-guttatus* and *Xanthorcus concinnus*, the ventral apical tooth in the incisor region is smaller than the dorsal tooth. In *L. quadrivulneratus* the incisor region is formed by a single tooth, giving the mandible a unidentate apex. The tooth is relatively wide and short. The basal tooth is present in all the species but is reduced in *P. ovoideus* and *P. guttatus*. The prostheca is present in all the species in its normal form, i.e. a fringed lobe extending ventrally from the molar to the incisor region.

Feeding. The Sticholotinae are predatory and have well-developed mandibular teeth. The Sukunahikonini feed on Coccidae; the Sticholotini feed on Diaspididae. The Serangiini feed on Aleyrodidae (Sasaji, 1971; Hodek, 1973). The mandibles of Serangiini and Sukunahikonini (Sticholotinae) are very similar to each other in that their mandible is simple, with no distinct

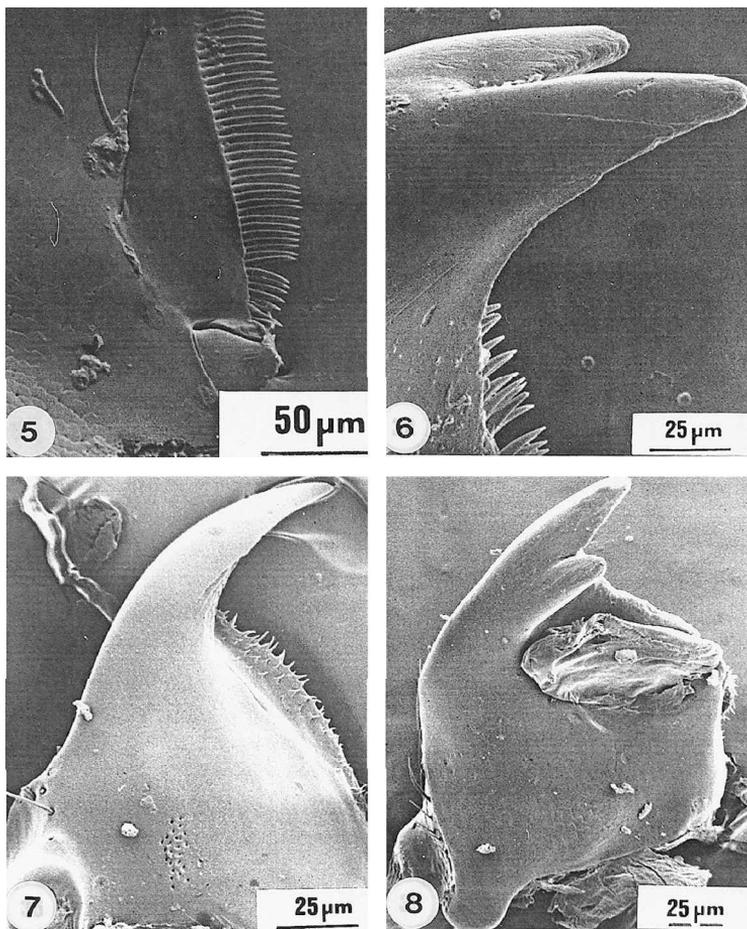


FIGURE 5. Ventral view of the right mandible of *T. 16-punctata* (Coccinellinae: Tytthaspini), showing the distinct comb-like prostheca.

FIGURE 6. Dorsal view of the bifid tip of *M. capensis* (Coccidulinae: Lithophilini).

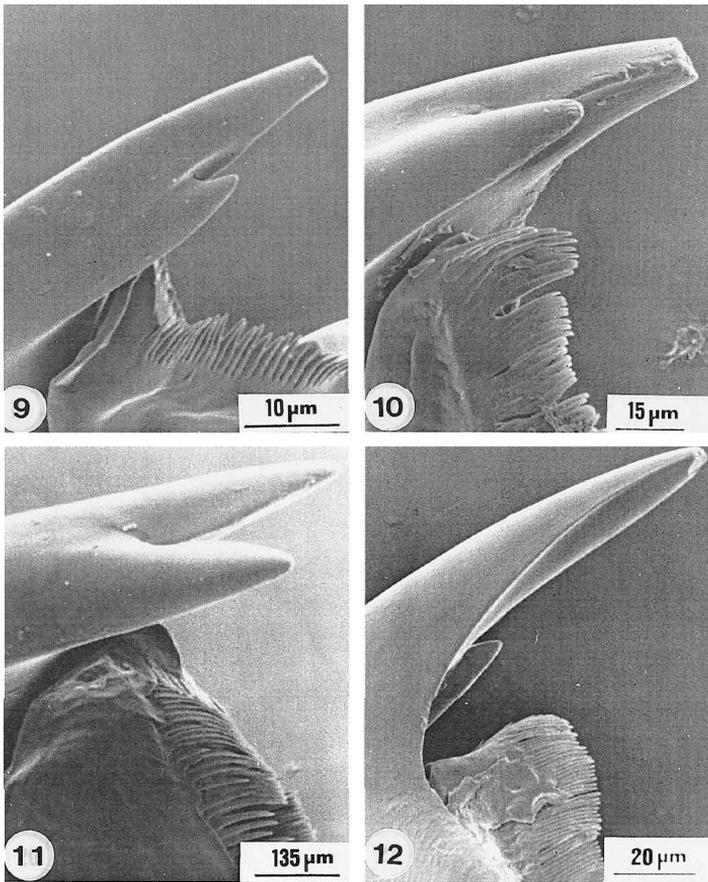
FIGURE 7. Dorsal view of the left mandible of *S. giffardi* (Sticholotinae, Serangiini).

FIGURE 8. Ventral view of right mandible of *P. ovoideus* (Sticholotinae: Sticholotini) showing the bifid tip with shorter ventral tooth.

tooth, an undivided tip and only an indistinct elevation at the inner side. The similarity of the mandibles relates more to similarity in feeding method rather than distinct dietary differences. Unlike most carnivorous Coccinellidae, the basal tooth is absent in *S. giffardi* for unknown reasons.

Scymninae

Mandible morphology. The mandibles of the Scymninae are of the general carnivorous type. The incisor is formed by two teeth giving the mandible a bifid apex. In the tribes Scymnini and Stethorini and the genus *Stethorus*, the ventral apical tooth is one quarter of the length of the dorsal tooth (Figure 9). In *C. montrouzieri* and *Nephus binaevatus*, the ventral tooth is one half of the length of the dorsal tooth (Figure 10). In the genus *Scymnus*, the ventral tooth varies from being the same length as the dorsal one in *S. apetzii*, to being slightly smaller, as in *S. frontalis*



- FIGURE 9. Ventral view of the tip of the right mandible of *S. arthiops* (Scymninae: Stethorini), showing the shorter ventral tooth.
- FIGURE 10. Ventral view of the tip of the right mandible of *C. montrouzieri* (Scymninae: Scymnini), showing the slightly smaller ventral tooth.
- FIGURE 11. Ventral view of the tip of the right mandible of *S. frontalis* (Scymninae: Scymnini), showing the slightly smaller ventral tooth.
- FIGURE 12. Dorsal view of the tip of the left mandible of *C. nodiceps* (Scymninae, Cryptognathini), showing the markedly smaller ventral tooth.

(Figure 11). The ventral apical tooth is also smaller in *Hyperaspis* sp. (tribe Hyperaspini), and is one half of the length of the dorsal tooth in *H. senegalensis*. The ventral tooth is also smaller in *Ortalia ochraea*. In *Cryptognathus nodiceps* (tribe Cryptognathini) the dorsal apical tooth is very long with a distinct groove (Figure 12). The ventral tooth is very reduced to resemble a secondary tooth on the dorsal tooth. All the species have a smooth inner cutting edge and a basal tooth on the molar region.

Feeding. All species are predatory, feeding on Coccidae, Margarodidae, Aleyrodidae, Aphididae or Acari. Many are beneficial in controlling agricultural pests and have been used in biocontrol projects (Booth *et al.*, 1990). Acariphagous species in the genus *Stethorus* feed by pre-digesting tissues of their prey, and the digestate is then conducted along grooves in the mandible and galea (Ricci & Stella, 1988). These species have a small ventral tooth, probably because they feed on digestate and do not chew their food. Adult acariphagous species attack all

stages of mites and sometimes chew and consume the exoskeleton as well (Putman, 1955). Coccidiphagous species such as *C. montrouzieri* and *Nephus* spp. generally feed on immobile or highly sedentary prey. If the prey is large, the coccinellid bites and sucks out the body juices and then consumes the empty 'skin' (Ricci & Stella, 1988). *Nephus* spp. and *C. montrouzieri* both have a ventral apical tooth of similar size and of similar proportions to the dorsal tooth, and they also have similar feeding behaviour. Aphid feeders, such as *Scymnus*, feed by injecting the prey with digestive juices and masticating and ingesting the exoskeleton (Ricci & Stella, 1988).

Chilocorinae

Mandible morphology. The tribe Platynaspini has a bifid apex to the mandibles formed from the two teeth (Figure 13). The ventral apical tooth is smaller than the dorsal one. The mandibular groove described by Ricci (1979) is also present. In all the species examined here, the incisor region is formed by a single tooth, giving the mandibles a unidentate apex. The mandibles are strongly curved and mandibular grooves are present in *Chilocorus* spp. The inner cutting edge is smooth and a basal tooth of the molar region is present. The prostheca is attached to the molar region along half of its length. Many species have a mandibular groove, e.g. *P. solieri* (Figure 13) and *Chilocorus schioedtei* (Figure 14). The only three species in this subfamily which have unidentate mandibular tips are *C. wahlbergi*, *Exochomus 4-pustulatus* (Figure 15) and *Brumus nigrifrons* (Figure 16).

Feeding. Species in this subfamily feed mainly on Aphididae and Coccidae. The bifid incisor region of the mandibles enables *Platynaspis* spp. (tribe Platynaspini) to seize hold of the prey before injecting it with digestive juices. The mandibular groove facilitates the uptake of digestate. The unidentate mandibles of *C. wahlbergi* may be used to lift the scale cover of the Coccidae (Balduf, 1935; Ricci & Stella, 1988), which may also be the function of the unidentate tip in *Brumus* spp. and *Exochomus* spp., which also feed on Coccidae (Balduf, 1935).

DISCUSSION

Comparison of Mandible Morphology and Diet

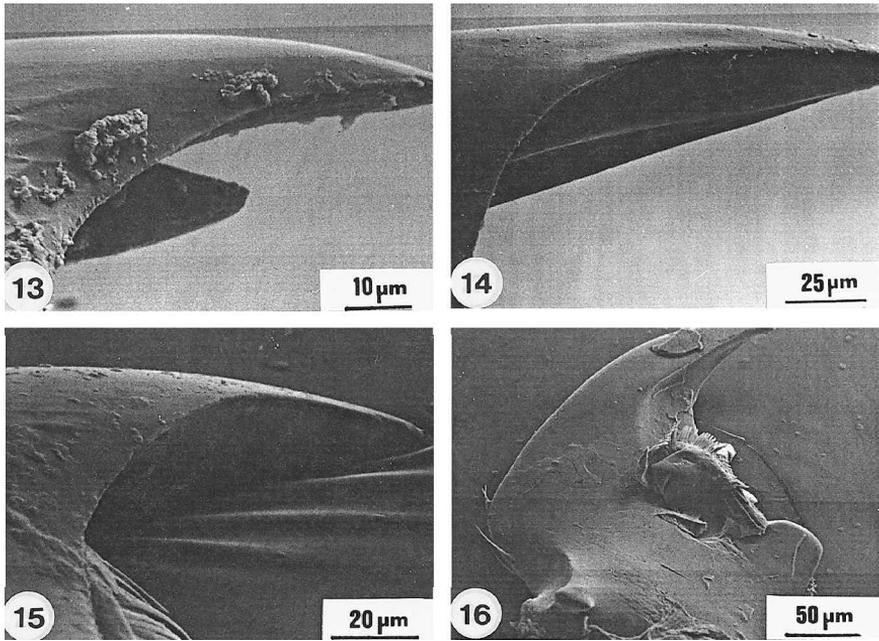
The major difference in mandible morphology within the Coccinellidae is between phytophages and predators. The phytophagous Coccinellidae (Epilachninae) have chewing-type, multidentate mandibles, which are used to scrape the surface of leaves to ingest the plant juices but not the solid plant material. The setal areas of the mouthparts then trap the plant juices.

Although the carnivorous coccinellid mandibles are the typical coleopteran biting type, ladybirds feed by piercing and sucking their prey, rather than crushing it. This is done using the bifid or unidentate tip, which pierces the prey rather than chewing it. The sharp tip enables species such as *Chilocorus nigritus* to feed on hard, mature female diaspid scales, thus making this species an effective biocontrol agent (Samways & Wilson, 1988).

The mandibular groove described by Ricci (1979), which is also present in the larvae of *Platynaspis* spp., *Stethorus punctillum*, *Scymnus subvillosus* and *Nephus includiens*, was also present in some of the adults in this study. The function of this groove is to introduce mesenteronic juices into the victim and then suck up the digested liquids (Ricci, 1979).

There are two types of carnivorous coccinellid mandibles: (1) with a bifid or (2) with a unidentate tip. The unidentate mandible is found among coccidiphagous coccinellids, and is an adaptation for lifting the scale cover by cutting it open in a tin-opener type of way (Samways & Wilson, 1988).

There seems to be no special morphological modification of the mandibles for feeding on pollen as many of the carnivorous species use pollen as an alternative food source when their normal prey is scarce. In the genus *Bulaea*, which is exclusively pollen feeding, the mandibles resemble that of an aphid- or coccid-feeding coccinellid, with a bifid tip and normal basal tooth. However, the mycophagous coccinellids seem to have two types of adaptation for feeding on



- FIGURE 13. Dorsal view of the tip of the left mandible of *Platynaspis solieri* (Chilocorinae: Platynaspini), showing the bifid tip and mandibular groove.
- FIGURE 14. Dorsal view of the tip of the left mandible of *C. schioedtei* (Chilocorinae: Chilocorini), showing the mandibular groove.
- FIGURE 15. Dorsal view of the unidentate tip of *E. 4-pustulatus* (Chilocorinae: Chilocorini).
- FIGURE 16. Ventral view of the right mandible of *B. nigrifrons* (Chilocorinae: Chilocorini), showing the unidentate tip.

fungi. In the tribe Psylloborini, secondary teeth on the ventral apical tooth are present which can be used for combing out the fungal spores. In the tribe Tythaspini, the adult mandibles have developed a comb-like prostheca which may be used to collect spores (Ricci, 1982; Ricci & Stella, 1988).

IMPLICATIONS FOR BIOCONTROL

Predator-prey relations of Coccinellidae have mostly been established by observing these beetles feeding. The presence of both predator and prey together on the same plant, although stimulating biocontrol interest, can nevertheless be misleading. Thompson (1951) pointed out that various species of Coccinellidae do not feed on all the host insects with which they seem to be physically associated. The feeding preferences of Coccinellidae can only be determined by a detailed experimental study of the food specificity of each species.

Although the predacious Coccinellidae accept a wide range of food, many species are quite specific or take food for only a limited period of time. They can, however, change to a substitute food of insect or plant origin. For example, many predacious species will use pollen or honeydew as a food substitute when insect prey is scarce. However, in most cases, the larvae do not develop or oviposition is prevented or reduced unless the essential food is taken (Hattingh & Samways, 1992); so although they may be polyphagous, there are specific foods that are essential (Hattingh & Samways, 1993).

This study shows that the shape of coccinellid mandibles can only be used generally to distinguish between phytophagous, mycophagous and carnivorous species (Figure 17). It is the

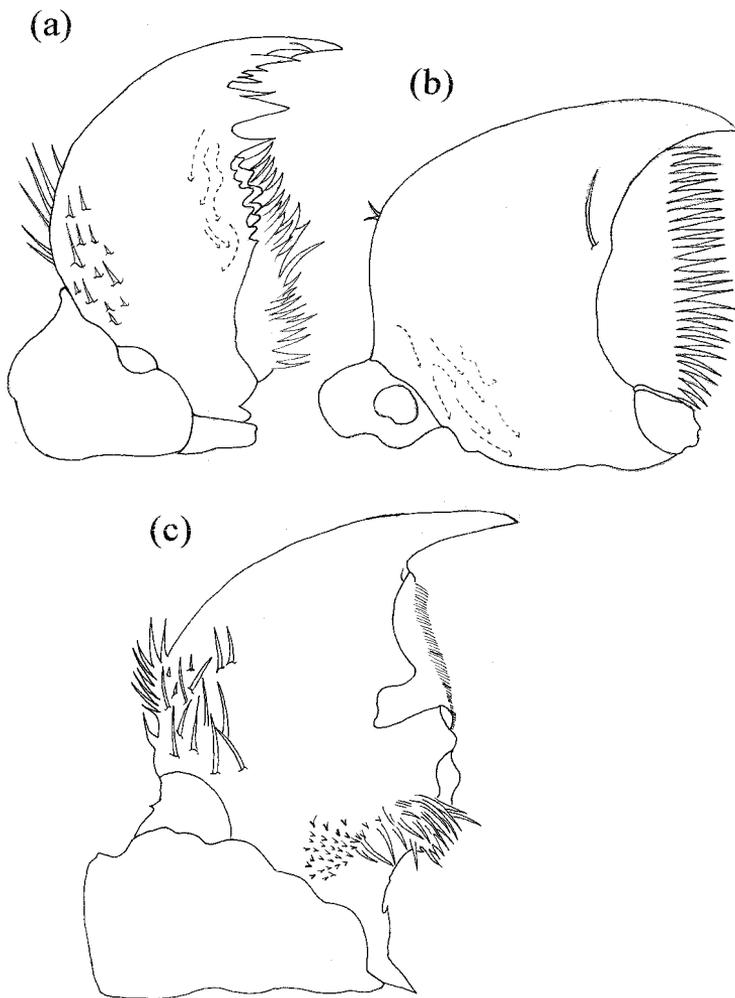


FIGURE 17. Mandibles of a (a) phytophagous species (*E. reticulata*), (b) mycophagous species (*T. 16-punctata*), and (c) carnivorous species (*C. nigrinus*).

method of feeding, rather than the specific diet or prey, which dictates the shape of the mandibles. For example, mandibles with a bifid tip may belong to an aphidophagous, a acariphagous or a coccophagous species because all use a piercing and sucking feeding method. Mandible morphology is therefore of limited use in selecting biocontrol agents.

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REFERENCES

- BALDUF, W.V. (1935) *The Bionomics of Entomophagous Coleoptera*. John S. Swift, New York.
- BOOTH, R.G., COX, M.L. & MADGE, R.B. (1990) *IIE Guides to Insects of Importance to Man: Coleoptera*. CAB International, Wallingford.
- BUTT, F.H. (1951) Feeding habits and mechanism of the Mexican Bean Beetle. *Cornell Experimental Station Memoirs* **306**, 2–32.
- HATTINGH, V. & SAMWAYS, M.J. (1992) Prey choice and substitution in *Chilocorus* spp. (Coleoptera: Coccinellidae). *Bulletin of Entomological Research* **82**, 327–334.
- HATTINGH, V. & SAMWAYS, M.J. (1993) Evaluation of artificial diets and two species of natural prey as laboratory food for *Chilocorus* spp. *Entomologia Experimentalis et Applicata* **69**, 13–20.
- HODEK, I. (1973) *Biology of Coccinellidae*. Junk, The Hague.
- IABLOKOFF-KHNZORIAN, S.M. (1982) *Les Coccinelles–Coleopteres–Coccinellidae*. Boubée, Paris.
- KOVÁR, I. (1973) Taxonomy and morphology of adults, in *Biology of Coccinellidae* (HODEK, I., Ed.) Junk, The Hague, pp. 15–35.
- LAING, J.E. & HAMAI, J. (1976) Biological control of insect pests and weeds by imported parasites, predators and pathogens, in *Theory and Practice of Biological Control* (HUFFAKER, C.B. & MESSENGER, P.S., Eds) Academic Press, New York, pp. 685–743.
- LAWRENCE, J.F. (1989) Mycophagy in the Coleoptera, in *Insect–Fungus Interactions* (WILDING, N., COLLINS, N.M., HAMMOND, P.M. & WEBBER, J.F., Eds) *Symposium of the Royal Entomological Society, London* **14**, pp. 2–23.
- MAJERUS, M.E.N. (1994) *Ladybirds*. Harper Collins, London.
- MAJERUS, M. & KEARNS, P. (1989) *Ladybirds*. Richmond Publishing, Slough.
- MINELLI, A. & PASQUAL, C. (1977) The mouthparts of ladybirds: structure and function. *Bolettino di zoologia* **44**, 183–187.
- PANDEY, U.K., SHANDILYA, R.S. & PANDEY, M. (1982) Comparative studies on the mouthparts of (Coleopterous) phytophagous (*Epilachna vigintipunctata* F.) and carnivorous (*Coccinella septempunctata* L.) beetles. *Indian Journal of Zoology* **22**, 97–103.
- PRADHAN, S. (1938) Neuromuscular study of the mouthparts of *Coccinella septempunctata* with comparison in carnivorous and herbivorous coccinellids. *Record of the Indian Museum* **40**, 341–358.
- PUTMAN, W.L. (1955) Bionomics of *Stethorus punctillum* Weise in Ontario. *The Canadian Entomologist* **87**, 9–33.
- RICCI, C. (1979) L'apparato boccale pungente succhiante della larva di *Platynaspis luteorubra* Goeze (Col. Coccinellidae). *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri' di Portici* **36**, 179–198.
- RICCI, C. (1982) Sulla costituzione e funzione delle mandibole delle larve di *Tythaspis sedecimpunctata* (L.) e *Tythaspis trineleata* (Weise). *Frustula Entomologica* **3**, 205–212.
- RICCI, C. & STELLA, J. (1988) Relationship between morphology and function in some Palaearctic Coccinellidae, in *Ecology and Effectiveness of Aphidophaga* (DIXON, A.F.G., Ed.) Academic Publishing, The Hague, pp. 21–25.
- SAMWAYS, M.J. (1984) Biology and economic value of the scale predator *Chilocorus nigritus* (F.) (Coccinellidae). *Bicontrol News and Information* **5**, 91–105.
- SAMWAYS, M.J. & WILSON, S.J. (1988) Aspects of the feeding behaviour of *Chilocorus nigritus* (F.) (Col., Coccinellidae) relative to its effectiveness as a biocontrol agent. *Journal of Applied Entomology* **106**, 177–182.
- SASAJI, H. (1971) Coccinellidae. *Fauna Japonica*. Academic Press, Tokyo.
- SCHILDER, F.A. & SCHILDER, M. (1928) Die nahrung der coccinelliden und ihre Beziehung zur verwandtschaft der Arten. *Arb. Biol. Reichs. Anst. Land-u. Forstw* **16**, 213–282.
- SMITH, J.B. (1893) Carnivorous and herbivorous insects. *Entomological News* **4**, 123–125.
- THOMPSON, W.R. (1951) The specificity of host relations in predacious insects. *The Canadian Entomologist* **83**, 262–269.