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Biology of some Aphthona spp (Col., Chrysomelidae) feeding on Euphorbia spp. (Euphorbiaceae), with special reference to Leafy Spurge (Euphorbia sp. near esula)

University — Université

University of Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M Sc

Year this degree conferred — Année d'obtention de ce grade	Name of Supervisor — Nom du directeur de thèse
1981	W.G. Evans

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2 Oct 1981	Eric Maw

THE UNIVERSITY OF ALBERTA

Biology of some *Aphthona* spp. (Col.:Chrysomelidae) feeding on *Euphorbia* spp. (Euphorbiaceae), with special reference to Leafy Spurge (*Euphorbia* sp. near *esula*)

by

© Eric Maw

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science

Entomology

EDMONTON, ALBERTA

Fall 1981

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Eric Maw

TITLE OF THESIS Biology of some *Aphthona* spp. (Col.:Chrysomelidae) feeding on *Euphorbia* spp. (Euphorbiaceae), with special reference to Leafy Spurge (*Euphorbia* sp. near *esula*)

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science

YEAR THIS DEGREE GRANTED Fall 1981

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Biology of some *Aphthona* spp. (Col.:Chrysomelidae) feeding on *Euphorbia* spp. (Euphorbiaceae), with special reference to Leafy Spurge (*Euphorbia* sp. near *esula*) submitted by Eric Maw in partial fulfilment of the requirements for the degree of Master of Science.

W. G. Evans
Supervisor

Ethel Ann Clark

D. A. Craig

Date 30 Sept 1981

A day or two ye shul have digestyves
Of wormes, er ye take youre laxatyves
Of lauriol, centaure, and fumetere,
Or elles of ellebore, that groweth there,
Of katapuce, or of gaitrys beryis,
Of herbe yve, growing in oure yeerd ther,
mery is.

Geoffrey Chaucer, 14th C.

Abstract

Two thirds of the 66 species of the flea beetle genus *Aphthona* Chevrolat for which records are available have been collected from the plant genus *Euphorbia* L., about half exclusively so. Most other confirmed plant associates are limited to a few families.

In the field individual species were taken from several spurges, but were not equally distributed amongst them. *A. flava* Guill. and *A. cyparissiae* Koch occur proportionately more often on *E. cyparissias* L. This apparent preference seems to be real in *A. flava*, and a consequence of the preference for extensive continuous host stands by *A. cyparissiae*. *A. nigriscutis* Foudr. is found in dry habitats and consequently on dry-land-inhabiting spurges. *A. lacertosa* Rosenh. is found on loamy soils and although accepting a wide range of spurge species seems to discriminate against *E. esula*. *A. czwalinae* shows a preference for *E. esula* and an aversion for dry habitats.

A. cyparissiae, *A. flava* and *A. czwalinae* were studied in the laboratory. The host used was North American leafy spurge, commonly referred to as *Euphorbia esula*, but considered here to be a hybrid complex.

Individuals of *A. cyparissiae* and *A. flava* survived as adults for 3 to 4 months, with oviposition taking place throughout this period. Eggs of *A. cyparissiae* and *A. czwalinae* hatch in about 13 days at the optimum temperature of 23°C, and those of *A. flava* in 12 days at the

optimum of 25°; egg hatch rate is reduced and the incubation period protracted at higher temperatures. Early development is arrested below 10°.

There are 3 larval instars. At a given temperature the larval period is quite variable. At 20.5° the first instar of *A. cyparissiae*, *A. flava*, and *A. czwalinae* lasts 8 days, the second instar a minimum of 19 (*A. flava*) to 35 days (*A. czwalinae*), and the third a minimum of 45 days. Post-feeding third instar larvae require a cold treatment to initiate pupation. The pupal stage lasts 20 days at 20°. Post-feeding larvae of *A. flava* are killed by acute exposure to -6.6° temperatures. Some *A. cyparissiae* larvae are killed at about -9°, but others survive to at least -13°.

Larvae feeding on leafy spurge usually mine the roots but may feed externally. First instar larvae initiate feeding and have a greater survival rate on filamentous and young roots than on older perennial roots. Encounters with young roots are more likely to lead to feeding by second and third instar larvae than encounters with perennial roots, but they are found more often on large roots since they spend longer there. All tissues except the phellem and the vascular elements of the xylem are eaten, but there is a hierarchy of acceptability. High laticifer and sclereid density and vigorous latex flow reduce acceptability. The selectivity exhibited by a given larva depends on its size relative to that of the thickness of the tissues concerned and thus to its physical ability to do so. The probability

of initiation of feeding is greatest at points of previous damage, including points of previous attack (resulting in aggregation), and least on unbroken thick phellem. Larvae feeding on otherwise undamaged roots tend to feed towards the root apex.

Of the species studied, *A. cyparissiae* is considered to have the greatest potential as an agent for the control of introduced perennial spurges. Its long developmental period may preclude its use in regions with short growing seasons. The type of damage inflicted may limit its efficacy at sites where other stresses on the plant are minor.

Acknowledgements

This project was suggested by Dr. Peter Harris of the Agriculture Canada Regina Research Station, and I must express my sincere appreciation for many invaluable discussions. Special thanks are also due my thesis supervisor, Dr. W.G. Evans, for his guidance and encouragement, and to Drs. D.A. Craig and J.F. Addicott for their comments and suggestions.

Both the Commonwealth Institute of Biological Control's European Station at Delémont, Switzerland, and Agriculture Canada's Regina Research Station freely provided access to laboratory facilities and materials. At Delémont, Gisela Sommer and Dr. Dieter Schröder were always ready to provide helpful suggestions and discussions. Gisela's willingness to act as part time guide and translator greatly eased and made more profitable my time in Europe. At Regina, Margaret Molloy, M.G. Maw, Margaret Cross and Juliana Soroka unhesitatingly gave their assistance when required and cared for my laboratory cultures during my absences.

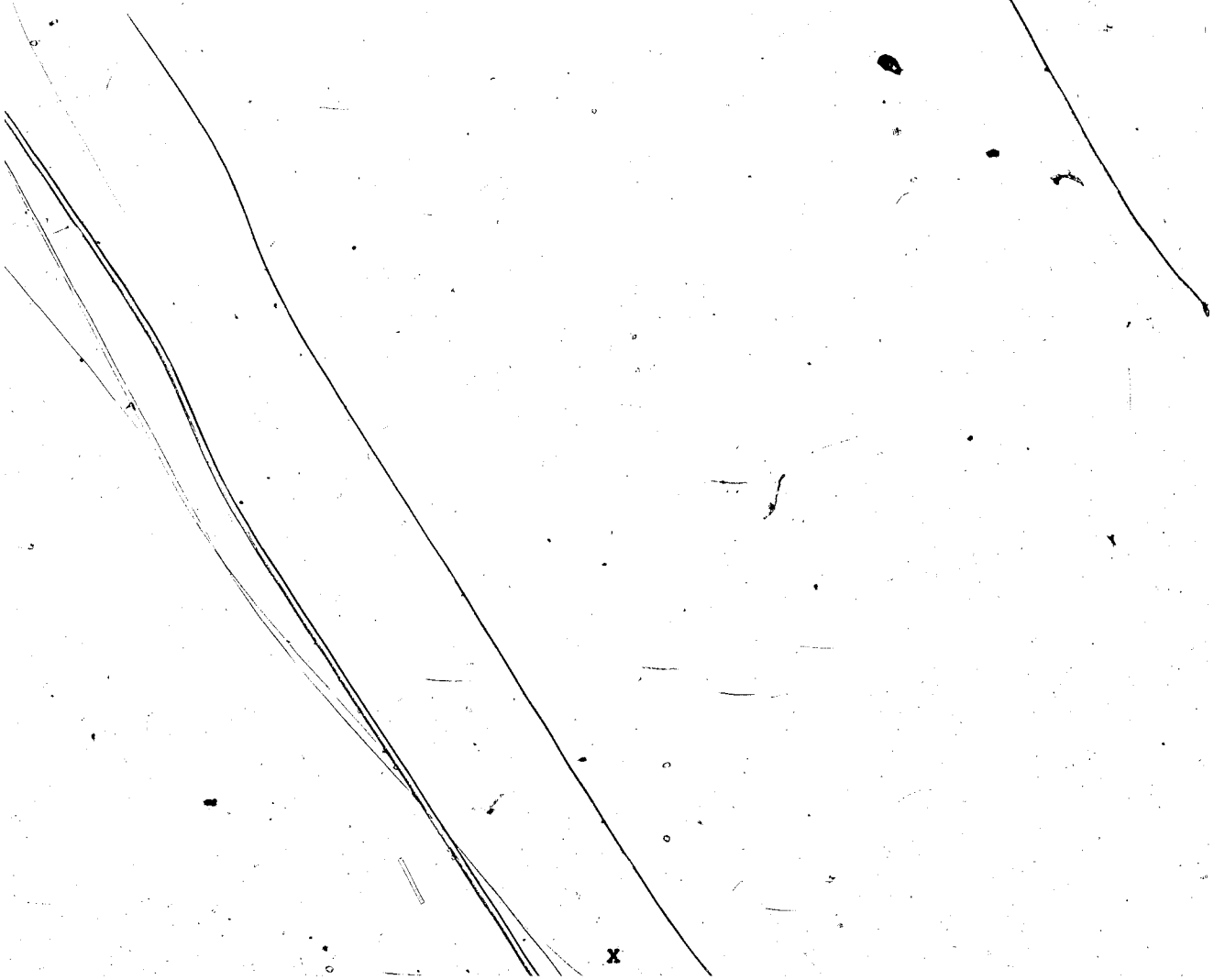
Dr. J.S. Kelleher, Agriculture Canada, Ottawa, kindly provided cypress spurge.

For their comments on this manuscript I thank my examining committee, comprising Drs. W.G. Evans, D.A. Craig and E. Ann Clark. Dr. B.K. Mitchell also read parts of this thesis.

Finacial assistance for work in Europe was derived from CIBC project Aph-468, sponsored by the Province of Alberta,

and a special stipend provided by Agriculture Canada. Subsequent work was supported by Agriculture Canada grant 55-34180 held by Dr. W.G. Evans.

Finally, to all my friends, colleagues and mentors in Delémont, Regina and Edmonton, who each in his own way made this an enjoyable and valuable experience, my gratitude.



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PART I

1. Introduction

1.1 Background

Leafy and cypress spurges are herbaceous perennial plants of palearctic origin, considered to be serious weeds in North America due to their ability to invade native plant communities, their unpalatability and toxicity to livestock, and their resistance to control measures.

Because their control by mechanical or chemical means is, in most locations, both economically and environmentally unsound, and because in North America (unlike the Palearctic) they are not associated with any spurge-specialized herbivore, nor fed on to any extent by polyphagous animals, these plants were felt to be good candidates for a biological control programme. Such a programme was initiated in the early 1960's (Harris and Alex, 1971).

Among the insects feeding on spurges in Europe are species of the chrysomelid genus *Aphthona* Chevrolat. It was decided in the mid-1970's to investigate the potential of this group as control agents, and in 1978 work was begun on the project by the Commonwealth Institute of Biological Control under the sponsorship of the Province of Alberta. A general interest in plant-insect interactions, and a particular interest in spurges, combined to interest me in the *Aphthona* project, and I became involved with it at its inception.

1.2 Objectives

Before this study was begun little was known about *Aphthona* species (except the flax pest *A. euphorbiae* (Schrank)) beyond the following:

1. Host records indicated that most species are restricted to spurge species.
2. The adults are leaf feeders, the larvae root feeders.
3. Those species for which sufficient records were available showed no species-specificity in their host requirements, but tend to be somewhat habitat restricted.
4. Collecting data indicate phenological differences between species.

Even the basic natural history of the group, then, was inadequately known. The first requirement of the study is therefore to gain a more precise knowledge of habitat requirements, host range, and life history through extensive field collecting, in order to provide a firmer base for laboratory work and a suitable context for realistic assessment of lab results.

An extensive root system is the principle character of leafy and cypress spurges contributing to their success as invasive and persistant weeds(Coupland and Alex, 1954). The key to understanding the spurge-*Aphthona* interaction is therefore an analysis of the feeding patterns of the root-feeding larvae.

The latex found in these plants is probably a major contributor to the dearth of feeding by generalized herbivores becaise of its toxicity and the mechanical difficulty it presents to small organisms penetrating the laticiferous tubules. Therefore, the methods used by the larvae in dealing with the latex system are of interest. Biochemical interactions certainly play a very important role. However, I have restricted myself to the mechanical and behavioural components of this problem.

In light of the above, the objectives of this study may be stated thusly:

1. Obtain data on habitat requirements and host range from field collections.
2. Work out life history.
3. Determine the location of feeding on the root system, and the tissues consumed.

At first it was not clear which species of *Aphthona* would be the most suitable for investigation. During the first summer of work, experience with availability, tractability in the lab, host range, and comparability of habitat to areas in North America where spurge is a problem, combined with availability in subsequent years, conspired in the end to limit my laboratory studies to three species: *A. cyparissiae* Koch, *A. flava* Guillebeau, and *A. czwalinae* Weise, with emphasis on the first two.

Of leafy and cypress spurges, leafy spurge was the most readily available to me. All laboratory tests were,

therefore conducted using this plant, although a few were repeated using cypress spurge.

Also included are descriptions of the immature stages of the genus in general, and of those species mentioned above in particular. I also felt that a discussion of the host plant relations of the genus as a whole would prove useful.

In order to accommodate these diverse elements, I have arranged this report in four sections: I. a general introduction, introduction to the spurges, and an introduction to *Aphthona*, with a discussion of the host relationships; II. description of immatures; III. field data; and IV. results of laboratory studies.

2. Overview of the Genus *Euphorbia*

2.1 Introduction to the Genus

Euphorbia L., with anywhere from 700 to 2000 species, is the largest genus of the family Euphorbiaceae. It consists of an extremely diverse assemblage of prostrate annual herbs, herbaceous perennials, shrubs and trees, and succulent-stemmed cactoid forms (Lawrence, 1951). In North America there are about 150 native species (Kartesz and Kartesz, 1980) (of which only three inconspicuous prostrate annuals reach the Canadian prairies (Looman and Best, 1979)). In addition a number of palearctic species are adventive to this continent.

Euphorbia is characterized by the peculiar structure of its inflorescence. A single pedicillate pistillate flower, the perianth of which is reduced to a rudimentary calyx, or absent, is surrounded by several staminate flowers, each consisting of a single naked stamen, usually with minute subtending bracts. The whole is contained within a campanulate or cupulate five-lobed involucre with one to five separate glands, the entire unit being known as a cyathium. The cyathia are usually associated with subtending, more or less modified, often coloured, leaves (often called bracts, but should be differentiated from those subtending the staminate florets). The fruit is a triloculate explosive capsule, and the seeds have a basal

caruncle (Smith and Tutin, 1968; Swift, 1974). As is true of most euphorbiaceous genera, members of this genus possess a system of latex-containing tubules.

Many species are of commercial interest as sources of waxes, rubber and petroleum (Uphof, 1959; Buchanan *et al.*, 1978; Calvin, 1978; Harris *et al.*, MS). Others are of ornamental value (Bailey, 1925). Spurges are common ingredients of folk remedies (see for example Ayensu, 1978, and Choppa *et al.*, 1956). Kupchan *et al.* (1976) found that extracts of *E. esula* L. and another euphorbiaceous plant, *Croton tiglium* L., have antileukemic properties.

Besides the weed problems presented by the perennial leafy and cypress spurges, many annual species are weedy in cultivated field crops.

2.2 Composition and Properties of Latex

The system of laticiferous tubules in spurges permeates all parts of the plant. These laticifers are of the non-articulated type – that is each tubule is a single intrusive cell, rather than a series of interconnected cells (Esau, 1977) – and are apparently derived from a very few (6 to 12) laticifer initials in the embryo, the number being characteristic of the species. Bruni *et al.* (1978) and Mahlberg and Sabharwal (1967, 1968) have studied the morphology of the system in the embryo and seedling of several species, and Gaucher (1898, 1902) in

mature plants.

The latex contained by these tubules is an opaque, white, somewhat viscous fluid. It is apparently under positive – with respect to atmospheric – pressure, and freely wells out from any wound to the plant, forming a gummy semi-solid on drying.

The latex of most, if not all, euphorbias is, to some extent, irritant and/or toxic. In mammals emesis an purgation result if it is taken internally, and temporary blindness often follows application to the eyes (Millspaugh, 1974). Contact with the skin causes anything from a reddening and slight itching to severe blistering, depending on the spurge species and individual sensitivity (Johnston and Smoliak, 1965). The latex of *E. marginata* has been used for branding cattle (McIndoo, 1945). Consumption of several species by man, cattle and sheep has resulted in death (Verdcourt and Trump, 1969; Kingsbury, 1964). It has been demonstrated that certain components of latex are co-carcinogenic – that is, they reduce the dose of some known carcinogens required to induce malignancies (Roe and Price, 1961; and many subsequent authors).

Latex is a complex mixture of dissolved, emulsified and suspended substances. The white colour, and possibly also to a large extent, its viscosity, is imparted by starch granules, of which the shape is often specific to a species or species group. Many authors have assumed that the latex system is therefore a medium for storage and transport of

starch and other primary metabolites. However, Biesboer and Mahlberg (1978) report that starch in the latex of *E. heterophylla* and *E. myrsinites* is removed from the plant's utilizable reserves. If the plants are kept in the dark, starch stored in parenchyma is depleted while latex starch levels are maintained.

Among the other components are sterols, other free alcohols, free fatty acids, triglycerides, di- and triterpenoid esters, and hydrocarbons, the relative proportions varying with species (Buchanan, *et al.*, 1978). The heptane extractable components of *E. lathyrus* constitute 4 to 5% of plant dry weight (Nemethy *et al.*, 1979). The most interesting of the components belong to a particular class of polycyclic diterpene esters, the ingenanes, daphnanes, and tiglianes. It is apparently these compounds which are responsible for the irritant, co-carcinogenic and even the anti-leukemic activity of latex. Since Roe and Price's (1961) report of co-carcinogenic properties for latex of a number of species, there has been an explosion of papers on the isolation and identification of bioactive diterpenes from spurges. Evans and Soper (1978) have provided a review of the structure, distribution, and biological activity of these substances. Daphnanes occur only in plants of the families Euphorbiaceae and Thymelaeaceae. Tiglianes have been isolated only from several euphorbiaceous genera. Ingenanes are restricted to the genus *Euphorbia* and the very closely related genus

Elaeophorbia. One species of *Euphorbia* examined contained at least 30 different diterpene esters. The one species of section *Anisophyllum* and the two species of section *Poinsettia* of the genus *Euphorbia* so far tested are unique in their complete lack of diterpenes of this class.

2.3 *Euphorbia* spp. and Insect Herbivores

There have been repeated allusions in the literature to the resistance of euphorbias to insect attack. For example, Liebmann (1910, quoted by Heikertinger, 1916), writing of the occurrence of the spurge hawk moth on cypress spurge, referred to it as "a plant avoided by all other animals due to its poisonous latex (*einer Pflanze, wegen ihres giftigen Milchsaftes von allen anderen Tieren gemieden wird*)." Bailey (1925), in reference to the use of spurges as ornamentals, states that they are "remarkably free from injurious insects." In North America minor feeding has been noted on leafy and cypress spurges by polyphagous leafhoppers and Lepidoptera only (Harris *et al.*, MS).

However, as Heikertinger (1916) pointed out, the spurges have, at least within their native range, a complement of insect associates comparable in diversity with that of any other plant group. On the other hand, a disproportionately high number (about three quarters) of the insect species recorded from *Euphorbia* have been recorded only from that genus (Harris *et al.*, MS). Furthermore,

local spurge-feeding insects do not often transfer to adventive spurges[1].

Preparations of several species have been used historically as insecticides or insect repellants. *E. tirucalli* L. is planted in Tanzania as a mosquito repellant and extracts used as an insecticide in India (Watt and Breyer-Brandwijk, 1962; Verdcourt and Trump, 1969). *E. neriifolia* L. and *E. antiquorum* L. have been used in concoctions for killing maggots in wounds, and the latex of *neriifolia* has been used as a general insecticide (Watt and Breyer-Brandwijk, 1962; Choppa *et al.*, 1956). The earlier mentioned use of *E. marginata* latex in cattle branding was considered superior to the hot iron since screwworm larvae deposited into the wound were unable to survive (McIndoo, 1945).

Recently there have been several investigations of the insecticidal and repellant properties of spurges. Ether extracts of cypress spurge were found to be fatal to houseflies on contact (Srbova and Paleveyeva, 1962), and an extract of the bracts of poinsettia was found to be more toxic to *Sitophilus oryzae* (L.) than a similar concentration of pyrethrum (Rao, 1957). *E. royleana* Bois. extracts have been assessed as antifeedants for a crucifer-feeding sawfly in India (Pandey *et al.*, 1977, 1979; Sudhakar *et al.*, 1978).

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[1] Hence the above mentioned lack of insects on leafy and cypress spurges in North America, and probably also the source of Bailey's impressions, considering his horticultural point of view.

The larvae of the crucifer-feeding plutellid moth *Plutella maculata* (Curt.) could not be induced to feed on sinigrin-impregnated *E. lathyrus* or *E. milii*, although there was some feeding on *E. poinsettiana* so treated (Gupta and Thorsteinson, 1960).

3. Leafy and Cypress Spurges

3.1 Introduction

The level of concern about leafy spurge is high,and two recent symposia have been devoted to it[2].

This plant occurs as a weed on both cultivated and uncultivated land in all soil types, under most moisture regimes, in woodland and grassland. However, it is most abundant in mesic, open areas on lighter soils (Selleck, 1959). On cultivated land, adequate control may be achieved with a combination of cultural and chemical control measures (Derscheid *et al.*, 1960, 1963).

The serious problems arise on non-arable land. Once established this plant is able to compete successfully with native vegetation (Selleck, 1959). Its presence in pasture land is undesirable since it is unpalatable to livestock and therefore increases on grazed land at the expense of more palatable plants. Carrying capacity reductions of up to 75% have been reported in Montana (Reily and Kaufman, 1979). Control of large infestations on such land is difficult, since the deep root system usually survives treatment of the aerial parts and surface roots. Production of new adventitious shoots from considerable depth and germination

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[2] Leafy spurge Symposium, 5 Nov. 1976, Regina, Saskatchewan; sponsored by Agriculture Canada Regina Research Station. Leafy Spurge Symposium, 26, 27 June, 1979, Bismarck, North Dakota; sponsored by ND State University, USDA, and US Forest Service.

of dormant seed quickly reestablish the patch, so that repeated treatment is necessary until seed reserves in the soil and food reserves in the root are depleted (Bowes and Molberg, 1975; Bowes and Thomas, 1978). The success of the treatment depends on soil type (see Harris *et al.*, MS), nature of competing vegetation and vigilance and persistence of the responsible individuals (Selleck *et al.*, 1962).

On large areas, or in areas which have no intrinsic economic value, but act as reservoirs for infestation, such treatment often becomes uneconomical. Treatment of large areas, especially infestations along waterways, brings with it the deleterious effects of intensive, widespread use of persistent herbicides, and removal of desirable plants from the treated area. For these reasons, biological control is a potentially valuable component of the overall control programme.

Cypress spurge is not looked upon with as much consternation. Most stands are quite small and on economically unimportant land. Since most patches are of a sterile diploid strain, there is a lower probability of spread onto more valuable land. However, a fertile tetraploid occurs at a few localities and poses a potential problem similar to that of leafy spurge (Dunn, 1979).

3.2 Review of the Literature

A reasonably complete survey of the literature relevant to leafy spurge in North America may be obtained by consulting Selleck (1959), Selleck *et al.*(1962), Messersmith (1979), and Best *et al.*(1980) and there is no need to repeat it at length here. The literature dealing with systematic problems and root morphology is considered elsewhere in this chapter. The principle basic investigations are those of Bakke (1936), Hanson and Rudd (1933), and Selleck (1959).

3.3 Taxonomic Status

The term 'leafy spurge' in its narrowest sense refers to the species *E. esula* L., but may be somewhat more loosely applied to a group of closely related, morphologically similar species, of which the most common is *E. virgata* Waldstein and Kitabel, more correctly called upright spurge. Cypress spurge, *E. cyparissias* L., is a very closely related species.

Members of the leafy spurge group present many taxonomic difficulties. Not only are the taxa very similar, but they exhibit considerable ecotypic and ecophenotypic variation (Croizat, 1945). Hybrids apparently occur frequently (Hegi, 1930), and there is probably considerable genetic introgression as well. A hybrid of cypress and leafy spurges has been recorded in Ontario (Moore and Frankton, 1969). Pax and Hoffman (1931) have

broken the genus *Euphorbia* down into 9 sections, and these further into subsections. Leafy and cypress spurges are placed by them in section Tithymalus, subsection Esulae. Prokhanov (1949), using a somewhat different arrangement, places them in subgenus *Paralias* (often called *Esula* in recent works), section Esula, subsection Esulae[3]. Within subsection Esulae, Prokhanov places *E. esula* in series Esulae, along with 10 other Russian species, while *E. cyparissias* is placed in series Virgatae with *E. virgata* and 11 other Russian species. Prokhanov is a splitter and many of his species are considered synonyms or subspecies of established European taxa. Smith and Tutin (1968) go so far as to demote *E. virgata* (under the name *tomasiniana*) to subspecific status within *E. esula*. However, most European botanists maintain both *E. esula* and *E. virgata* as full species.

The exact identity of North American leafy spurge has been the subject of recurrent dispute. According to Groh (1935), the first collections on this continent were referred to *E. esula*. However, by the 1930's the steady range expansion of leafy spurge had become a major concern and was looked at more carefully. Doubts first arose when western material neither fit the descriptions well, nor could be matched with certainty to the available herbarium specimens of eastern '*esula*', and it was the opinion of several

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[3] Pax and Hoffman's section Esulae is much broader than Prokhanov's, including species that the latter author places in two other sections.

botanists that American material was in fact *virgata*. Hanson and Rudd (1933), in the earliest study of its biology, adopted this name. Groh (1935) obtained series of European specimens of both species and concluded that all American specimens could be assigned to *esula* according to the shape of the leaf base. Bakke (1936), comparing his specimens to keys and descriptions, was of the opinion that *esula* and *virgata* are not separable and best considered synonyms under the name *esula*. Morton (1937) believed that all American specimens are properly assigned to *virgata*. Croizat (1945) undertook a detailed review of specimens, both American and European, of what may be loosely called leafy spurge, housed in the Gray Herbarium and the Arnold Arboretum. He encountered no American specimens of *E. esula* in these collections, but found specimens referable to *E. virgata* sensu stricto, *E. virgata orientalis* Boiss. in DC., and *E. virgata montana* Reich. However, he believed that most North American material could be referred to a further taxon, *E. intercedens* Podpera. This name turned out to be a junior homonym of *E. intercedens* Pax and he later (Croizat, 1947) provided *podperae* as a substitute.

In light of the indecision on the part of taxonomists, the weight (and perhaps inertia) of opinion among those who simply wanted a name on which to hang biological and agronomic data favoured *esula*. This practice has continued until today in agricultural circles. The use of *esula* was affirmed with reservations by Moore (1958). He considered

this taxon to be very variable but distinct from *virgata*.

The problem was recently revived when it was found that a clear-winged moth, *Chamaesphecia tenthredinIformis* and an aphid, *Acrythosiphum neerlandicum*, specific to *E. esula* in Europe, could not survive on North American leafy spurge (Harris, 1979). Specimens from throughout the United States compared to European specimens in the Kew herbarium yielded results similar to Croizat's (1945) findings: leafy spurge in North America is not a single entity. The specimens comprised *E. esula* sensu stricto, *E. esula androsaemifolia* Willd., *E. virgata uralensis* (Fisch. ex Link) Boiss., *E. virgata orientalis* Bois. and *E.* ×*pseudovirgata* (Schur) Soó (believed to be an *esula-virgata* hybrid) (Dunn and Radcliffe-Smith, MS). The last named taxon, a synonym of *E. podperae* Croizat, is the most widespread, and western Canadian populations are apparently best assigned to this taxon (Harris *et al.*, MS).

After some field experience with European populations of both *esula* and *virgata*, and Saskatchewan leafy spurge, and after consulting original descriptions of *pseudovirgata* and its synonyms and Croizat's (1945) useful discussion of this taxon, I find this treatment more satisfactory than trying to force our plants into either *esula* or *virgata*, or combining them into a single variable taxon which includes *virgata*. It is especially important to make the distinction in the context of this study, given the discrimination shown by some insects.

However, Dunn and Radcliffe-Smith's report is preliminary only, and I think it premature to assign North American leafy spurge to any particular palearctic taxon with any certainty. As noted by Croizat (1945) "the burden of nomenclature in the 'Esula' group is overwhelming" due to the parochial nature of 19th century floristic works, combined with the inherent variability of the taxa involved.

Furthermore, the extent to which the variation seen in North America is the result of plastic responses to local conditions, as opposed to genetic differences, is unknown. Groh (1944) reported that roots which produced *virgata*-like shoots in Saskatchewan, produced *esula* -like shoots when transplanted to Ottawa. On the other hand, I have seen infestations near Regina, Sask., in which shoots could be assigned to specific adjacent, and often partly overlapping, clones, on the basis of predominant leaf density, shape, and colour, number of axillary florescent shoots, and length of inflorescence rays. Clones also differ in date of first flowering during spring growth, and ratio of sterile to flowering shoots produced in late summer growth.

For the purposes of this study, *E. esula* and *E. virgata* refer to European populations as distinguished by current European flbras typified by Hess *et al.* (1970). North American populations, commonly assigned to one or the other of these taxa, are regarded as part of a complex of an undetermined number of undetermined taxa of the same affinity, probably of hybrid origin.

3.4 Distribution

3.4.1 Origins

The centre of origin of subsection Esulae is apparently the Caucasian region (Croizat, 1945; Kuzmanov, 1964). According to Kuzmanov (1964), Prokhanov's (1949) series Esulae of this subsection now has representatives from the Atlantic across Siberia and Northern China to the Pacific. The greatest diversification in the group has been to the east of the Caucasus – only *E. esula* extends westward, occurring throughout Europe from the Atlantic to the Urals except the extreme north and south. According to Smith and Tutin (1968) it is not native in the northern parts of its present range. This species has also been introduced to northern China (Prokhanov, 1949).

Series Virgatae also reaches its greatest diversity to the west of the Caucasus. *E. virgata* is a southeastern European-Asiatic species, extending from eastern Austria and Czeckoslovakia into central Asia, and locally established in western Europe (Hess *et al.*, 1970; Smith and Tutin, 1968).

E. cyparissias is originally a Mediterranean species but is today widespread in Europe (Smith and Tutin, 1968).

3.4.2 North American Distribution

3.4.2.1 Leafy Spurge

Because North American leafy spurge taxa have been lumped under the single name *esula*, good distributional data are available only for the complex as a whole. Noble *et al.* (1979) estimate about one million hectares are infested in North America. Dunn (1979) has mapped the relative density of leafy spurge on a county by county basis for the United States. It is virtually absent south of 40° north latitude, and almost no infestations of 'economic' or 'potentially economic' density occur east of the Mississippi River. The most widespread infestations occur in Minnesota, but the weed problem is most severe in North Dakota, followed closely by Montana (Noble *et al.*, 1979).

In Canada, leafy spurge has been reported from all provinces except Newfoundland. The main concentration of infestations occurs in southern Manitoba, the southern half of Saskatchewan*, and in Alberta north to the Peace River District (in other words, the prairie provinces south of the Precambrian Shield) (Lindsay, 1951; Selleck *et al.*, 1962).

Simply stated, the North American distribution is primarily the Northern Great Plains. Noble *et al.* (1979) estimate that about 90% of it may be found within 1000 km of Wolf Point in northeastern Montana.

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*Saskatchewan infestations have been mapped over much of the settled area of the province as part of the Saskatchewan Weed Survey, 1952 to 1955 (University of Saskatchewan, Department of Plant Ecology).

3.4.2.2 Cypress Spurge

Dunn (1979) provides a map of cypress spurge infestations in the United States, and Lindsay (1951) and Moore (1958) give the known Canadian distribution.

This plant has been reported from scattered localities in all Canadian provinces and in 25 American states. However, stands are numerous only in southern Ontario, the northeastern States, and Minnesota. Large stands also occur at a few locations in Québec, Nova Scotia, and Virginia. Most stands are of the sterile diploid form, but populations of the fertile tetraploids are known at several sites in Ontario and New York, and one in Massechusetts. The larger patches in Québec and Nova Scotia are also suspected to be tetraploid. A fertile diploid occurs in Europe but has not been reported on this continent.

3.5 Description

3.5.1 Leafy Spurge – General Description

The leafy spurge of the northern Great Plains has been described by Hanson and Rudd (1933), Groh (1935), Bakke (1936), Selleck (1959), Messersmith (1979) and Best *et al.* (1980). The following description is based on Selleck (1959) and Best *et al.* (1980) with supplements as noted.

The plants are perennial hemicryptophytes, the shoots dying back to ground level in winter. The underground part

of the stem produces adventitious shoots the following spring. Stems are erect, glabrous, 0.3 to 1.0 m tall, tough (previous year's dead stems persistent), unbranched at the base, with or without axillary vegetative branches (branching profuse if main axis damaged), above with axillary flowering rays and a terminal compound inflorescence. Stem leaves alternate, entire, glabrous, only the midrib conspicuous, broadly linear to linear-lanceolate or oblanceolate, 20 to 80 mm long, 2 to 10 mm wide, apex acute or obtuse. See Groh (1935) for a description of variation in leaf shape and comparison with typical European *E. virgata* and *E. esula*. In my experience early spring leaves, those of shaded plants, and those of greenhouse-grown plants are often more *esula*-like than those grown in the open later in the season. The stem and leaves of plants growing under drier conditions usually have a heavier waxy bloom (similar to that characteristic of *E. virgata*). The main shoot terminates in a single staminate cyathium subtended by a whorl of seven or more green leaves, shorter and broader than the stem leaves, each with an axillary floral ray. Floral rays with a terminal cyathium subtended by a pair of greenish-yellow to yellowish green broadly ovoid-cordate leaves, these each with an axillary floral ray, the pattern repeated to 3 or 4 levels. The floral rays arising in the stem leaf axils are similar but usually branch only once. The cyathia are as described for the genus in Section 2.2, staminate florets 15 to 20, glands

four in number (abortive cyathium a shoot apex usually with more), yellow to orange-yellow, crescent shaped with 2 horns. Bakke (1936) illustrates the variation observed in gland shape of Iowa specimens (horns short to long, straight or curved, divergent, convergent, or parallel). Saskatchewan material has in addition glands with the horns clavate and sometimes multilobate or denticulate (identical to the shapes seen in European *virgata*).

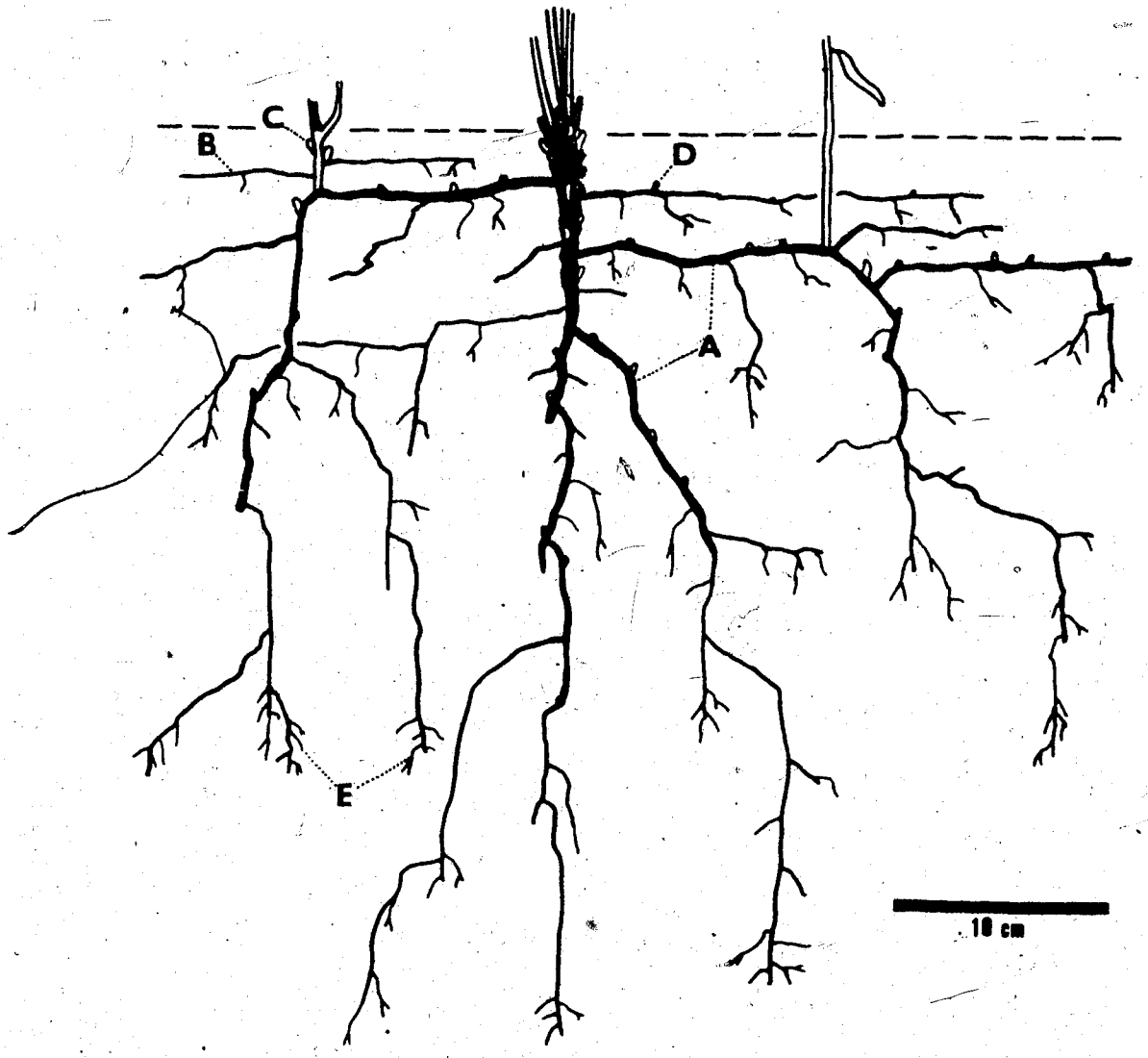
3.5.2 Leafy spurge – gross root morphology

This and the following sections are intended to provide the necessary background for chapters 7 and 8.

The morphology and development of the underground parts of the leafy spurge plant have been described by Hanson and Rudd (1933), Bakke (1936), and in a series of papers by Coupland and his co-workers (Coupland and Alex, 1954, 1955; Coupland *et al.*, 1955; Bakshi and Coupland, 1959; Raju *et al.*, 1963, 1964).

The root system of leafy spurge (Figure 1) has extensive horizontal and vertical components. The major horizontal parts were in the past referred to as rhizomes (underground horizontal stems) but, as shown by Myers *et al.* (1964) (and earlier implied by Raju *et al.*(1963)), they are in fact roots, anatomically indistinguishable from the vertical roots. There are, however, two distinct root types, called by Raju *et al.*(1963) *short* (or filiform) and *long* (or thick) roots. The long roots constitute the

Figure 1. Root system of leafy spurge, simplified from a photograph of a plant excavated near Regina, Sask. A – vertical and horizontal long roots; B – root growing adventitiously from underground part of shoot; C – shoot buds on underground part of shoot; D – shoot buds on long root; E – short roots.


B
C
D
A
E
10 cm

principle horizontal and vertical framework of the mature root system, sometimes reaching depths of several metres (4.8 m reported by Bakke (1936)). These roots are persistent, exhibit secondary tissue development, and are indeterminate in growth. Shoot buds are located at intervals along the roots, the density decreasing with increasing depth (Coupland and Alex, 1955). The short roots are determinate in growth, show no secondary tissue development, and last for only a single season. They may be somewhat branched.

Short roots and those long roots which have not yet begun secondary growth are indistinguishable, and I will refer to them together as *filamentous* roots. Long roots a year or less old with obvious secondary tissues will be called *yearling* roots. Roots over a year old will be referred to as *perennial* roots.

Long roots arise from other long roots or adventitiously from the underground parts of stems. Shoot buds also form at great density on both the roots and shoot bases near the root-shoot junction, so that over the years a large root crown develops, forming the centre of origin of a large number of radial longitudinal roots.

3.5.3 Leafy spurge – root anatomy

A section of mature spurge root may be easily separated with the fingers into a woody central core, and a thick fleshy, outer layer, erroneously referred to in the

literature as the 'cortex'.

The tissues of a typical older root are schematically represented in Figure 2.

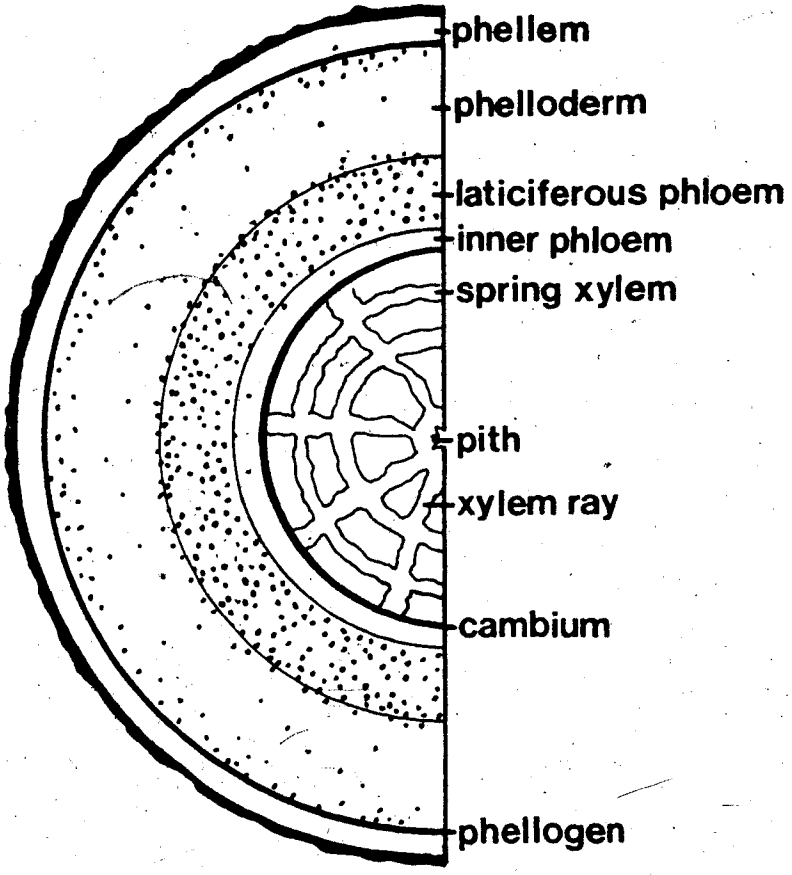
The xylem contains numerous broad parenchymatous rays. In addition, spring xylem does not differentiate into vascular elements, so that a large proportion of the xylem consists of parenchyma.

The phloem is divided into two distinct zones. The inner phloem consists of both sieve elements and parenchyma. As the phloem ages, the parenchyma cells enlarge, the sieve elements are crushed, and the tissue is invaded by laticifers, to form the outer phloem (and will be referred to later as the *laticiferous zone*).

The remaining tissues are derived primarily from the phellogen (cork cambium), which gives rise inwards to the thick parenchymatous phelloderm, and outwards to a dense protective phellem (or cork). Laticifers also invade the phelloderm to some extent, although they are rarely as numerous here as in the phloem. The laticifers adjacent to the phellogen are usually much more active, with those in the older phelloderm tending to degenerate.

Also occurring in the phelloderm are thick-walled brachysclereids. The relative proportion of sclereids to parenchyma is quite variable; I have found plants with almost almost all of the cells of this tissue converted to sclereids, but less than 10% is usual. Sclereids may also be found among the xylem parenchyma, and, rarely, in the phloem.

Figure 2. Distribution of tissues in a mature perennial leafy spurge root (cross section). Location and density if laticifers indicated by stipling.


phellem
phelloderm
laticiferous phloem
inner phloem
spring xylem
pith
xylem ray
cambium
phellogen

The surface of the root is covered by the remains of crushed primary cortex and epidermis, and dead phellem.

The roots I have designated yearlings are essentially similar, except that the phloem is not yet distinctly divided into two zones, and the surface cover still consists largely of living cells.

3.5.4 Cypress Spurge

Cypress spurge is a much lower, more compact plant, with a tendency to branch more than leafy spurge. Shoot 0.1 to 0.5 m tall, erect, glabrous, with many axillary sterile branches, few axillary inflorescence rays. Stem leaves alternate, closely spaced, linear, 15 to 30 mm long, 2 to 3 mm wide. Terminal inflorescence similar to that of leafy spurge, but primary rays more numerous (10 to 20, usually about 15) and the rays shorter. Cyathia as in leafy spurge, the glands crescent shaped. Roots not as thick as those of leafy spurge with less tendency to form massive root crowns. The number of shoots arising from the previous year's stem base is much larger, giving a more tufted appearance.

4. Introduction to *Aphthona* Chevrolat

4.1 Systematic status

Aphthona Chevrolat is closely related to the well known genera *Phyllotreta* Foudras, of economic interest because of its predilection for cruciferous plants, and *Longitarsus* Latreille, which tends to feed on boraginaceous plants. These among others are placed together in tribe Aphthonini of the chrysomelid subfamily Alticinae, commonly known as flea beetles.

The name *Aphthona* (from Greek for 'plentiful') first appeared in Dejean's Catalogue of 1837, where it was attributed to Chevrolat. Under it were listed 4 or 5 species now assigned to this genus, along with several other taxa currently placed elsewhere. A generic diagnosis was not published by Chevrolat until 1842. Maulik (1926) designated *Haltica cyparissiae* Koch, the first species listed by Dejean, as type.

The genus is cosmopolitan in distribution, although the Nearctic is very depauperate. At the time of the most recent review (Heikertinger, 1944), over 200 species were placed here, and more than 100 others have been described since, particularly from the Ethiopian and Neotropical realms.

In North America, there are five species. These are generally southern in distribution, but one, *A. texana*

Crotch, has been reported from as far north as South Dakota (Balsbaugh, 1975).

Adults may be recognized by the external position of the metatibial spur, lack of transverse antebasal and longitudinal laterobasal impressions on the pronotum, impunctate vertex, postantennal tubercles ovoid and more or less oblique, interantennal space subequal to diameter of the antennal socket, antennae quite long, reaching the elytral disc (Samuelson, 1973). Keys to the alticine genera (Heikertinger, 1925; Arnett, 1963; Scherer, 1963; Mohr, 1966; Balsbaugh and Hays, 1972) require that the elytral punctation be irregular. This is true of palearctic species. However, at least two North American species, and many from elsewhere, currently assigned to *Aphthona*, have feebly but distinctly striato-punctate elytra.

In the last three decades,9 a number of species have been transferred to other established genera, or to new genera, especially by Bechyné (1955, 1956, 1958), Bechyné and Springlova de Bechyné (1960, 1965), Scherer (1963, 1969), and Samuelson (1973). A thorough revision of the world aphthonine fauna is required to clarify the situation.

4.2 Review of the Literature

The best known *Aphthona* species is certainly *A. euphorbiae* (Schrank), an important pest of flax crops in Europe. Principi (1941) gave a fairly detailed description

of the ultimate larval instar, and it appears in Ogloblin and Medvedev's (1971) key to the larvae of eastern USSR chrysomelids. The life history and ecology was described by Principi (1941) and Fritzsche (1958). Jourdheuil and Thansigaud (1961) discuss its parasites, and Fritzsche (1958), Jourdheuil (1960), and Manolache and Dobreanu (1959, 1960) discuss methods of control. Jourdheuil (1963) provides a review of the biology and control of this insect.

Only a few other species are discussed in the literature outside of new species descriptions and regional faunal treatments. *A. coerulea* (Paykul) has been reported as a pest of garden iris and methods for its control given (van Poeterin, 1930, 1935; Beneczúr, 1930). Buddeberg (1878) described the larva and its habits. This is the only other *Aphthona* species to appear in Ogloblin and Medvedev's (1971) key. The larva of *A. cyparissiae* (Koch) and its habits were described by Buddeberg (1878), and the larval head by Grandi (1938). Lakhmanov (1970) briefly discussed damage to flax during an outbreak of the 'yellow spurge flea beetle' which he called *Aphtha* (sic) *abdominalis*. Heikertinger discussed the food plant relations of the genus (1916) and reviewed the palearctic species (1944).

4.3 Host Plants of *Aphthona* species

4.3.1 Introduction

My intention here is to bring together the available host data for the genus *Aphthona* as a whole.

Most of the information in the literature is of the form 'insect **A** on plant **B**', presented without further qualification. The significance of such bare statements is difficult to assess. Was **A** feeding on **B**, or just resting? were there only a few or perhaps just one specimen of **A**, or were there many? was the collector selectively searching on plant **B** (a fault of my own collections), or sampling all plant species? was **A** collected by sweeping, or handpicked from **B**? if collecting was by sweeping, was it a pure stand of **B**, or was **B** merely an obvious dominant species? The answers to such questions are essential for proper interpretation, but are rarely provided. Concordance of several independent reports greatly increases the value of such weak records. Europe is sufficiently well collected that such concordance is available. Furthermore, lack of records from other plants is not as likely to be due to a lack of collecting. Unfortunately this is not so in most other parts of the world. The records there are usually solitary and frequently result from attempts to identify an unusual insect found on a crop plant, and therefore having a high probability of being an accidental on that plant.

It is necessary also to be aware that some non-palearctic species now assigned to *Aphthona* may be better placed elsewhere. For example, *A. bimaculata* Jacoby, long known as a sesame pest has been transferred to *Alocypa* by Scherer (1963).

Inferences drawn from the available records must therefore be made with care, keeping the above problems in mind.

4.3.2 Patterns in the *Aphthona* food-plant assemblage

4.3.2.1 Adult food plants

The collection records for the adults of 66 species are summarized in Figure 3. The complete list, with sources, on which this figure is based is provided in Appendix 1 (Tables A-1 and A-2)[5].

The most striking feature of Figure 3 is the special relationship between *Aphthona* and spurges. Although 33 plant families are represented, a full two thirds of the 66 beetle species have been collected from *Euphorbia*, and almost half exclusively so. Only 20% of the species are not known from one or more of five families: Euphorbiaceae, Linaceae (*Linum*), Geraniaceae (*Geranium*, *Erodium*), Cistaceae (*Helianthemum*), and Iridaceae (*Iris*). Of the remaining 23 families, 10 are associated with the single species,

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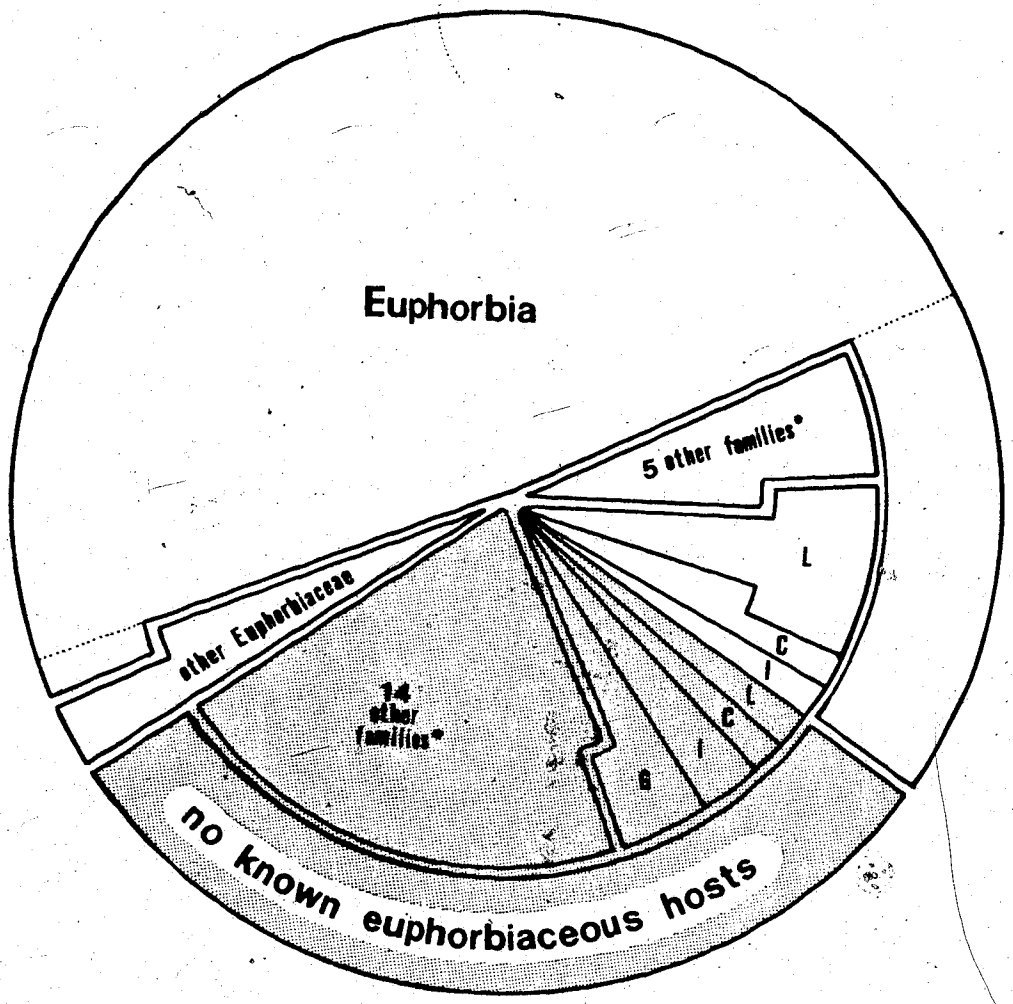
[5] The most doubtfull of the records included in the appendix have been ommitted from figure 3; several others, although suspect, lack any intrinsic basis for their exclusion.

Figure 3. Summary of host records for adults of 66 *Aphthona* species. Number of species in a category is proportional to the angle subtended by the defining arc. Radial overlap of categories indicates species which feed on plants in more than one category.

C – Cistaceae (*Helianthemum*); G – Geraniaceae (*Geranium* and *Erodium*); I – Iridaceae (*Iris*); L – Linaceae (*Linum*); * – [illegible] families in common.


Euphorbia
5 other families*
L
C
I
C
I
C
other Euphorbiaceae
14 other families*
no known euphorbiaceous hosts

A. euphorbiae. Most of the others are isolated reports and must therefore be regarded with some degree of scepticism for the time being. One well supported association is that between *A. lutescens* (Gyll.) and *Lythrum salicaria* L. (Lythraceae), and damage to rosaceous plants has been attributed to this species by two authors (Ritzema-Bos, 1915; Mityaev, 1960).

The pattern seen here is somewhat muddied by additional records, but is otherwise little different from that presented by Heikerting in 1916. He listed the hosts of 27 European and North African species, of which 19 had been collected only from *Euphorbia*, one (*euphorbiae*) from *Euphorbia* and *Linum*, and the other seven distributed among *Iris* (2), *Helianthemum* (1), *Linum* (1), *Lythrum* (1), and *Geranium/Erodium* (2).

4.3.2.2 Larval food plants

Field data on larval hosts is known for only three species: *A. cyparissiae* from *E. cyparissias* (Buddeberg, 1887; Grandi, 1938), *A. coerulea* from *Iris* species (Buddeberg, 1887; Beneczúr, 1930; van Poeterin, 1924), and *A. euphorbiae* from *Linum usitatissimum* (many authors; see Jourdheuil, 1963). Heikertinger (1925) has observed oviposition by *A. cyparissias, delicatula, palida, lutescens, venustula, pygmaea, ovata, and lacertosa*, all on *Euphorbia* species, and *coerulea* and *semicyanea* on *Iris*.

4.3.3 Review of phylogenetic relations between food-plants

The relationships between Euphorbiaceae and other food-plants of *Aphthona* are difficult to define, since the ordinal placement of euphorbiads and the relationships between plant orders are much in dispute. Traditionally, Euphorbiaceae has been included in the order Geraniales or in a separate order, Euphorbiales, closely related[6] to the Geraniales (system of Engler as given in Dalla Torre and Harms, 1907; Bessey, 1915; modified system of Engler of Melchior, 1964). All of these systems include Linaceae in Geraniales. It is interesting to note also Bargagli's (1887) collection of the geranium-feeding *A. nigriceps* from *Citrus* (Rutaceae), and Lopatin's (1960) collection of *A. euphorbiae* from *Peganum* (Zygophyllaceae)[7] given that Rutaceae and Zygophyllaceae are also included in Geraniales (or Rutaceae in Rutales near Geraniales) in all of the above systems.

More recent authors tend to remove Euphorbiaceae from the vicinity of Geraniales entirely. Hutchinson (1959, 1967, 1969) splits the angiosperms into two evolutionary series. Linaceae, Euphorbiaceae, and Rutaceae are placed in different orders[8] in one series, and Geraniaceae in the

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[6] i.e. juxtaposed in a linear sequence, presumably implying some degree of similarity and relationship in the author's mind.

[7] This association is perhaps of limited value in the context of the present discussion, given *euphorbiae*'s apparent broad polyphagy.

[8] His concept of interordinal relationships changes through time, but essentially those of interest are separately derivable from Violales or Tiliales.

other. Takhtajan (1959, 1969) keeps Linaceae and Zygophyllaceae in Geraniales, this order being derived from the Rutales, and places these groups in the class Rosidae. Euphorbiales, however, is placed in the class Dilleniidae. Takhtajan's arrangement is of interest in that the sister group of Euphorbiales is Thymelaeales. Recall from Section 2.2 that the diterpenes known as daphnanes are known only from Euphorbiaceae and Thymelaeaceae. The thymelaead *Edgeworthia papyrifera* is recorded as a host for the far eastern *A. perminuta*. *A. nubila* is recorded from *Elaeagnus glabra*. Although Takhtajan considers Elaeagnaceae only distantly related to any of the other taxa here considered, Melchior (1964) places this family in Thymelaeales.

Cronquist (1968) keeps Geraniaceae, Linaceae, Zygophyllaceae and Rutaceae together, although the ordinal boundaries differ from those in any of the previously mentioned systems (Zygophyllaceae and Rutaceae in Sapindales, Linales and Geraniales derived from Sapindales). Euphorbiales are on a separate lineage within the class Rosidae. Thymelaeaceae are placed in Myrtales on a line independently derived from the basal rosids. Cronquist apparently agrees with Melchior in considering Elaeagnaceae close to Thymelaeaceae, for although he places them in a different order he derives this family from within the Myrtales near Thymelaeaceae.

What of the other plants for which the evidence that they act as food-plants is strong? Lythraceae are generally

(except by Hutchinson) considered to be members of the order Myrtales'. As mentioned, Cronquist (1968) places thymelaeads here, but otherwise no direct relationship is hypothesised between Lythraceae and the other taxa considered above. Despite this lack of phylogenetic closeness to other hosts, and the unique status of the *Lythrum-A. lutescens* association within *Aphthona*, there is almost certainly some form of chemical similarity, since a number of spurge-feeding insects feed on *Lythrum*, or are closely related to species that do so (Schröder, 1976). The Cistaceae are placed somewhere within a group of families generally conceded to be closely related among themselves, although concepts of ordinal limits vary considerably. Both Hutchinson and Takhtajan derive Euphorbiales ultimately from within this group'°, but the relationship to the Cistaceae themselves is not direct. The other systems consider the relationship remote. The Iridaceae, as Monocotyledonae, are obviously unrelated to any other major food plant.

The ordinal distribution of the dicotyledonous families discussed above under the different classification schemes are outlined in Figure 4. We may summarize the relationships as follows: Geraniaceae and Linaceae containing known *Aphthona* food-plants, along with Zygophyllaceae and Rutaceae containing plants from which

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' Note that *Psidium* in Myrtaceae is said to be the host of *A. guavae* (Bryant, 1927, Hargreaves, 1937).

'° Takhtajan from Violales (formerly called Cistales or Cistiflorae); Hutchinson from Tiliales (note Verdcourt's (1950) report of *euphorbiae* from *Tilia* (resting?)).

Figure 4. Ordinal placement and hypothesized relationships between reported host-plant families, according to different schemes of classification.

Engler (In Dalla Torre and Harms, 1907) and Bessey (1915)

GERANIALES
Geraniaceae
Linaceae
Rutaceae
Zygophyllaceae
Euphorbiaceae

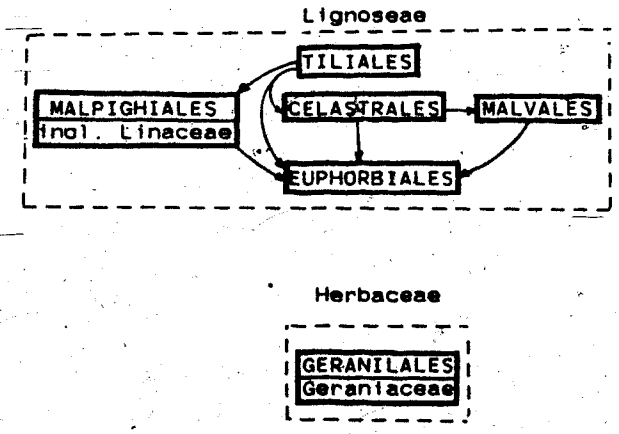
THYMELAEALES
Thymelaeaceae

Melchior (1964)

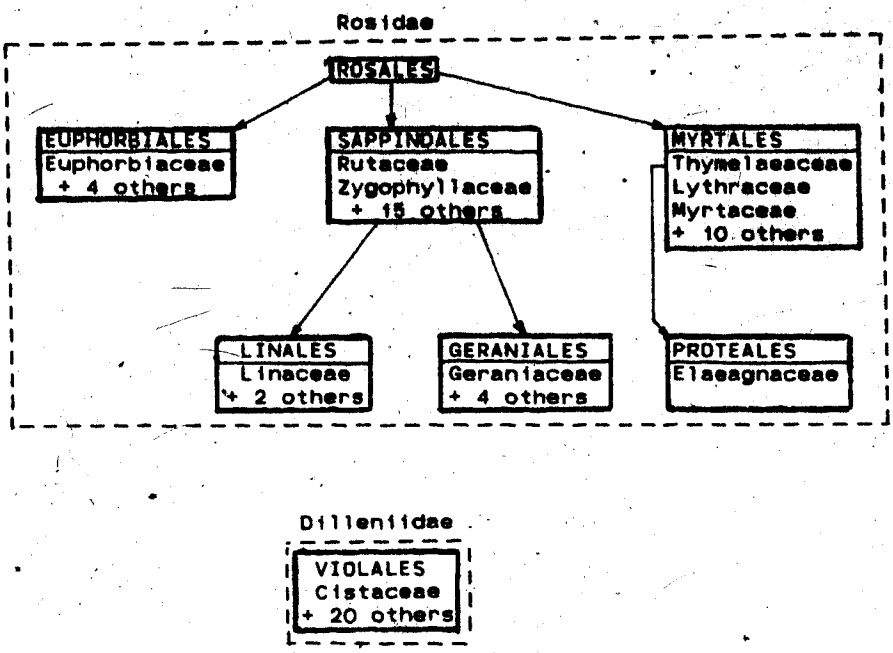
GERANIALES	RUTALES
Geraniaceae	Rutaceae
Linaceae	
Zygophyllaceae	
Euphorbiaceae	
+ others	

THYMELAEALES
Thymelaeaceae

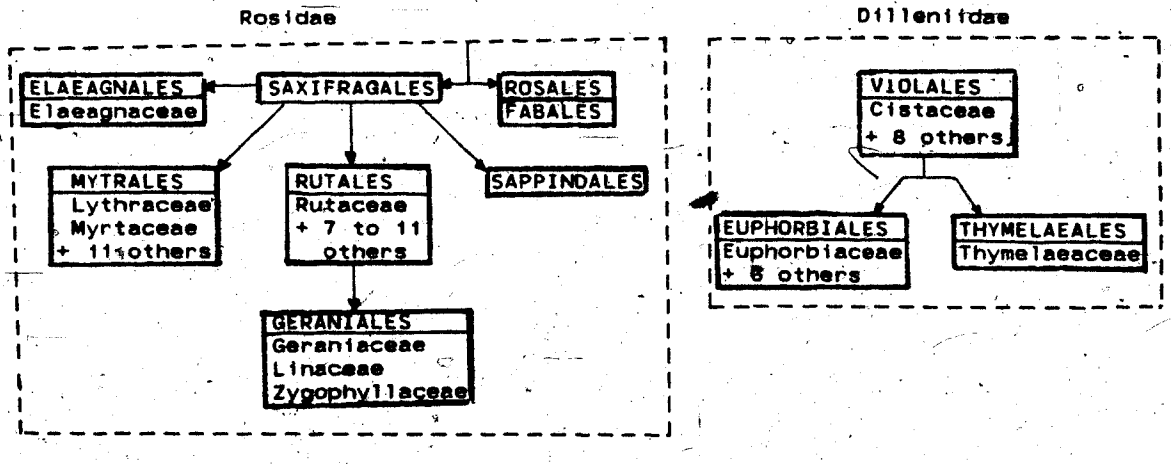
Hutchinson (1967)



Cronquist (1968)



Takhtajan (1969)



Aphthona species have been collected, are generally considered to represent a natural grouping; of the major schemes only Hutchinson's disagrees. The primary host family, Euphorbiaceae, has traditionally been placed within this group, but recent authors tend to consider this family more or less distantly related, perhaps arising from a group of plants related to a confirmed host, *Hellanthemum* spp. (Cistaceae) but not near the latter within this group. Thymelaeaceae, containing a possible *Aphthona* host, and sharing peculiar secondary plant substances with Euphorbiaceae, are placed near Euphorbiaceae by Takhtajan alone. Other known hosts are only remotely related to either Euphorbiaceae or the Geraniales affinity.

4.3.4 Host selection and transfer

The range of plants that an individual of a species of insect herbivore will accept as a food-plant is the result of a complex interaction of several factors, both simultaneous and sequential, as reviewed by Thorsteinson (1960) and Schoonhoven (1968). The plant must be temporally and spatially available; that is, must occur in a habitat that overlaps in full or in part with that of the insect, and must be at a suitable stage in its development in the right season.

The plant must be recognizable; if the insect is a visual searcher it must have the correct conformation and/or colour; for an olfactory searcher it must contain those

chemicals which act as attractants or arrestants for the insect involved in the proper proportions. A perfectly 'good' plant in other respects will be passed up if it cannot be recognized as such.

The plant's physical structure must be suited to the physical and behavioural makeup of the insect. A leaf thickly beset with hairs will foil a small leaf feeder without elongate mouth parts for penetrating between the hairs. A herb is not suitable for a large wood borer.

The plant must not induce behaviour antagonistic to feeding; that is it must lack effective levels of those compounds which act as feeding inhibitors or repellents.

The plant must be palatable, containing the proper combination of chemical constituents to initiate sampling and maintain feeding.

A similar set of criteria applies to induction of oviposition where this behaviour is associated with a range of hosts which may or may not be the same as the adult feeding range.

Within any population of insects, there are likely to be individuals that respond to a range of stimuli wider or somewhat shifted relative to the mode. Such individuals will treat as hosts, plants outside the normal range of the species of which it is a member. If the energetics of the situation are favourable, the trait may increase in frequency in the population, and the plant incorporated into the normal host range of the population. Host range can

similarly be narrowed if individuals that recognize and accept a somehow inferior host are at a reproductive disadvantage. Cycles of broadening and narrowing of range may ultimately result in complete shifts from one host taxon to another. The current host range of a species represents the product of a long history of such shifting and fixation. We may regard closely related species as populations with different such histories.

Both the range of hosts accepted by a single polyphagous population and the overall range of a group of closely related populations or species can give some indication of the factors involved in host selection placing the greatest restrictions on that group. While many insects are heavily dependent on the presence of distinctive secondary compounds as chemical recognition cues, others apparently rely largely on concentration profiles of primary, and therefore generally widespread, plant substances (Thorsteinson, 1960). The latter forms may be expected to move to plants unrelated to the host with a greater degree of probability than the former, resulting in either polyphagous species or greater host plant diversity at higher taxonomic levels. On the other hand, any diversity exhibited by those forms responding to secondary compounds is more likely to be in habitat than host taxon (not to imply greater absolute habitat diversity than may be found among the other).

The prevalence of *Euphorbia* species as hosts of *Aphthona* species, combined with the extreme variety in structure and habitat to be found among those species reported as hosts, suggests that peculiar secondary compounds are a strong component of the relationship between these beetles and their hosts.

Several questions then arise. Do the non-*Euphorbia* hosts represent transfers from *Euphorbia* or do these (or at least some of these) relationships predate the diversification of *Aphthona* on *Euphorbia*? If these do indeed represent transfers from *Euphorbia*, do those species occurring on a given non-euphorb host represent a monophyletic group – that is, did the transfer occur once or several times?

Any attempt to reconstruct the events leading to the current patterns in the host plant assemblage is seriously handicapped by the lack of a phylogenetic analysis of the genus *Aphthona*. In the absence of such an analysis, we must rely on the intuition of those early workers, culminating with Heikertinger, who devised the linear sequence in which the species are now listed, in order to infer relationships between species – a rather hazardous procedure. There is also no indication of the age of *Euphorbia* and the Euphorbiaceae relative to that of *Aphthona* and the Aphthonini.

The *Iris*-feeding species do not seem to be especially closely related to each other. The extreme remoteness of

the relationship between *Iris* and *Euphorbia* suggests that the association is not a historical relict, and that it arose independently by transfer from *Euphorbia*. One species, *A. violacea*, has in fact been reported from both of these genera. The importance of habitat similarity in facilitating host transfer is also illustrated by this species. The spurges fed on are wetland species, as is the common European iris *I. pseudacorus*.

All of the known Geraniaceae-feeding *Aphthona* species, on the other hand, are fairly uniform in appearance, and a fairly small species group may be defined on superficial structural grounds which includes all of these species (as well as some spurge feeders). The transfer to Geraniaceae may well have been a unique event.

The flax-feeding species are superficially similar but real relationships are completely obscure at present. Because several species are reported from both *Linum* and *Euphorbia*, with different species exhibiting different degrees of fidelity to one or the other, I suspect that the adoption of flax has occurred several times in parallel, indicating a definite chemical affinity between these plant groups.

A. euphorbiae is apparently an example of a population with a lowered threshold – common plant components are sufficient to trigger feeding in the absence of specialized cues, giving rise to polyphagy. Oviposition, however, seems to still require that additional signal.

In summary, the genus *Aphthona* is closely tied to the genus *Euphorbia* through the agency of peculiar secondary plant compounds. Exceptions to spurge-feeding are usually not random transfers, but are the result of single events with subsequent diversification, or of independent, but parallel transfers to chemically related plants such as iris or flax.

PART II

5. Description of Immature Stages of some *Aphthona* species

5.1 Subfamilial Characters

The larvae of the chrysomelid subfamilies Galerucinae and Alticinae, as they are currently defined, are not distinguishable, and, indeed, the two have been considered by many authors (for example, Böving and Craighead, 1931) to represent a single taxon coordinate with the other subfamilies of Chrysomelidae. The larvae of the galerucine-alticine complex have been characterized by Böving (1927, 1929), Patterson (1931), and most completely by Ogloblin and Medvedev (1971). In brief, they may be distinguished from other chrysomelids by the following combination of characters: Y-shaped epicranial suture (frontal + coronal sutures) well developed; tormae (swellings at the lateral ends of the epistomal suture) absent; ocelli one pair or absent, if absent then coronal suture short; antennal article 1 lacking, sensory cone of article 2 well developed, article 3 reduced; lacinia present, membranous (sometimes lacinia and galea fused and reduced); maxillary palpus with 3 or 4 articles; labial palpus with 2 articles (absent in leaf miners); eighth abdominal spiracle present, lateral; mandible palmate, with 3 to 5 teeth; legs with a paronychial lobe adjacent to claw.

Ogloblin and Medvedev (1971) recognize three more or less distinct groups based on both structural and habitat

characters. A majority of galerucines and some alticines, notably *Altica* spp., feed openly on leaves both as larvae and as adults. These larvae are rather stout bodied, well pigmented, have well defined, usually large sclerites, usually possess ocelli (a single pair), and tend towards polychaety. Most alticines, including *Aphthona*, and some galerucines are root feeders as larvae, either as edaphobitic root grazers or as partial or complete endophytic feeders, with transition in a few genera to stem mining. These larvae are pale, vermiform, ocelli absent (sometimes present in the first instar), epicranial suture shortened, ninth abdominal tergite expanded to form a sclerotized terminal plate, tenth segment ventral. The third group comprises a few alticine and a very few galerucine genera. These are the leaf-mining forms, prognathous, yellow coloured, and with reduced legs, sclerites and number and size of setae.

5.2 Methods

The descriptions which follow are based on drawings made using a SM-Lux compound binocular microscope with drawing tube attachment. Specimens were cleared in hot 15% KOH, rinsed in 10% aetic acid, taken to 70% ethanol, stained with Eosin (3% w/v in 70% ethanol, for an hour or more), and mounted in glycerine. Detailed observations of mouth parts were made on isolated mouth parts under oil immersion

(x1000). For determination of chaetotaxy and sclerite distribution on the soma, the head was removed, and the integument slit along one side and mounted flat.

The light observations were supplemented by scanning electron micrographs.

5.3 Notes on Terminology

Homologies between the parts of the generalized insect labium and hypopharynx and those of chrysomelid larvae are uncertain. I have adopted the interpretations of Böving (1927), *viz.*: **postmentum** (submentum + mentum) for the region posterior to the semicircular sclerite (submentum of Ogloblin and Medvedev (1971)); **eulabium** (presumably comprising the undifferentiated prementum and palpigers) for the region immediately in front of the semicircular sclerite bearing the palpi (ligula of Patterson (1931), prementum + mentum of Ogloblin and Medvedev (1971), prementum of Anderson (1938)); **ligula** for the anterior region with paired microsetae (hypopharynx of Patterson (1931)); **hypopharynx** for the entire dorsal surface and and anterior margin of the labio-hypopharyngeal complex; **paragnatha** for the lateral lobes of the hypopharynx (superlinguae of Patterson (1931)).

Nomenclature for the 'sclerites' of the abdominal segments follows Böving (1929), but I have interpreted certain thoracic sclerites differently. The setal numbering system is modified from Patterson (1931).

5.4 Characters of the Immatures of Genus *Aphthona*

The larvae of too few species of Alticinae have been adequately described to permit reliable generic characterizations. Ogloblin and Medvedev (1971) provide a diagnosis of larval *Aphthona* based on two species, *A. coerulea* and *A. euphorbiae*, and provide a key to the genera of Galerucinae + Alticinae based on larvae. Unfortunately, *Aphthona* is reached through statement 12 (p. 80) which says, in part, that the terga of the abdominal segments have two transverse rows of sclerites ("*Tergiti bryushnikh segmentov s 2 poperechnimi ryadami skleritov*"). Their Figure 47.4 (p. 98) depicting abdominal segment 2 of *A. coerulea* in dorsal aspect is in agreement with the key. However, all of the specimens I have seen (including specimens of *A. coerulea*) have a third intercalary dorsal sclerite (sc of my Figure 7), as does Principi's (1941) figure of *A. euphorbiae*.

The following detailed description encompasses all nine *Aphthona* species of which the larvae are known to me. These are: *A. euphorbiae* (Schrank) from literature descriptions by Principi (1941), Jourdheuil (1963), and Ogloblin and Medvedev (1971) plus eight species reared by myself comprising: eggs, all larval instars and pupae of *A. cyparissiae* (Koch) (also third instar descriptions by Buddeberg (1878) and Grandi (1938)), *A. flava* Guillebeau and *A. czwalinae* Weise; eggs and all larval instars of *A. coerulea* (Paykul) (also descriptions of third instar by

Buddeberg (1878) and Ogloblin and Medvedev (1971) under the name *nonstriata*); eggs and first instar larvae of *A. venustula* Kutsch., *A. pygmaea* Kutsch., *A. ovata* Foudras, and *A. lacertosa* Rosenh.

Description of immature stages of the genus Aphthona *Chevrolat*

EGG:

Elipsoid, ratio of major axis to minor axis about 1.8; very pale yellow at oviposition, darkening to a slightly brunneous yellow in about 18 hours; microsculpture alveolate, somewhat irregular, some species with secondary radial ridges within the depressions of the primary network.

LARVA:

There are three larval instars. The first instar lacks any specialized egg burster. The following description applies to all instars with exceptions as noted.

Head: (Figure 5)

Well sclerotized, subcompressed, hypognathous; general outline somewhat ovoid-cordate, the posterior dorsal margin being excavate; coronal suture narrowly open behind for a short distance.

Ocelli absent.

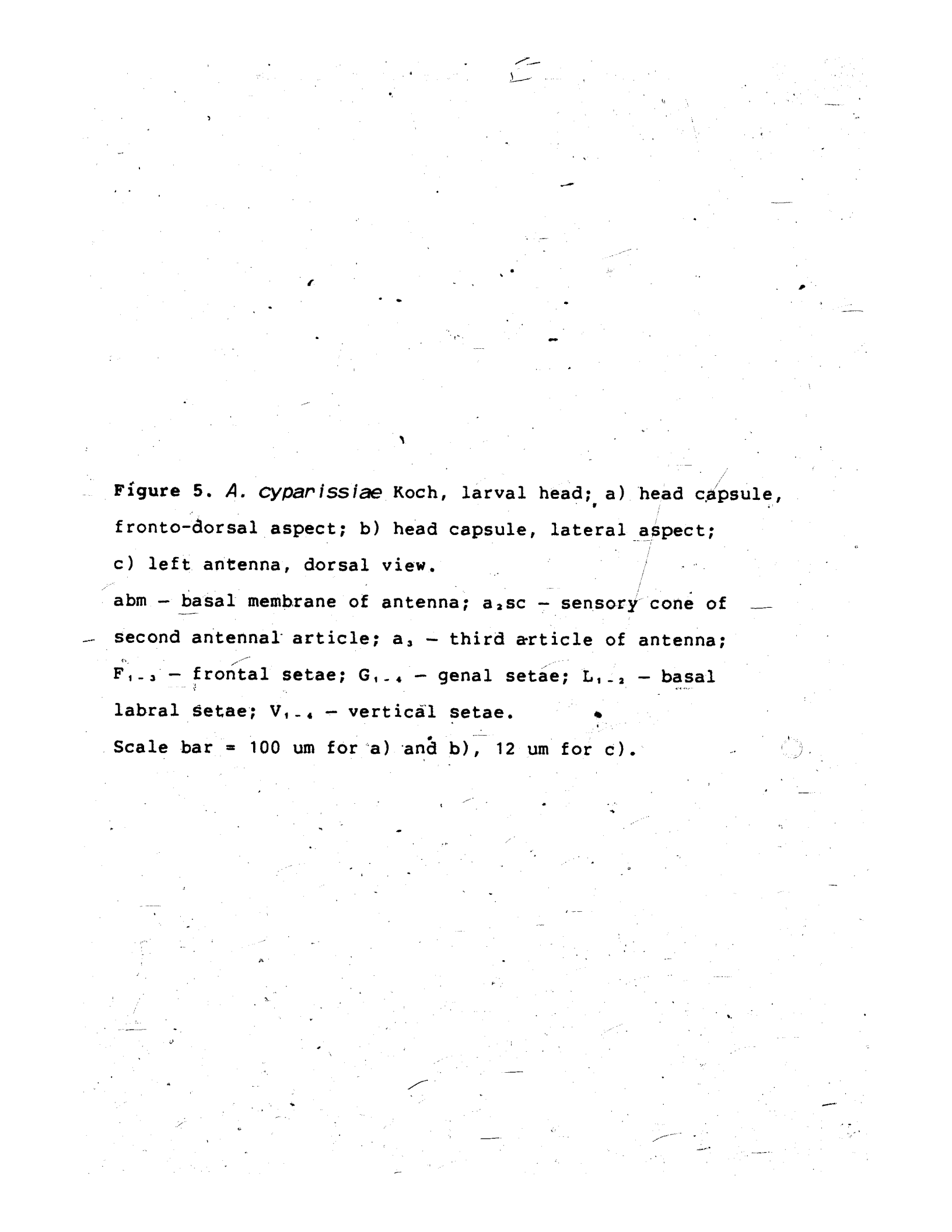
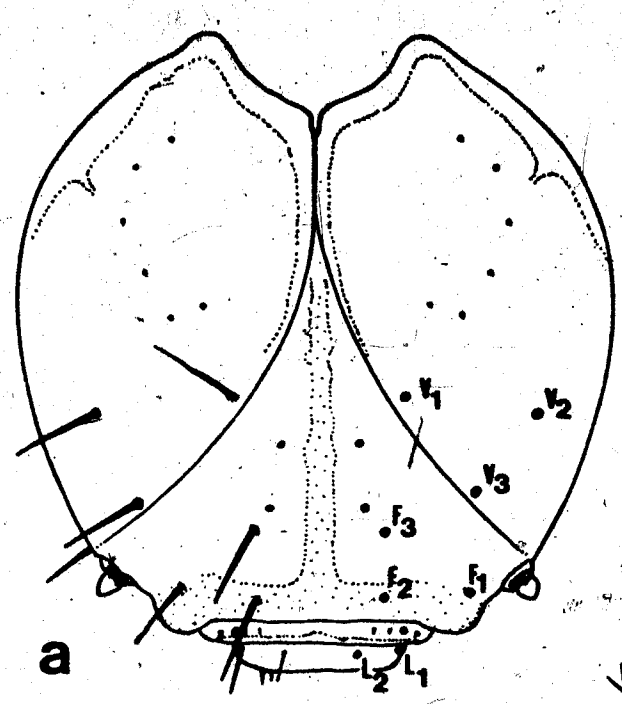


Figure 5. *A. cyparissiae* Koch, larval head; a) head capsule, fronto-dorsal aspect; b) head capsule, lateral aspect; c) left antenna, dorsal view.

abm – basal membrane of antenna; a_2sc – sensory cone of second antennal article; a_3 – third article of antenna; F_{1-3} – frontal setae; G_{1-4} – genal setae; L_{1-2} – basal labral setae; V_{1-4} – vertical setae.

Scale bar = 100 um for a) and b), 12 um for c).



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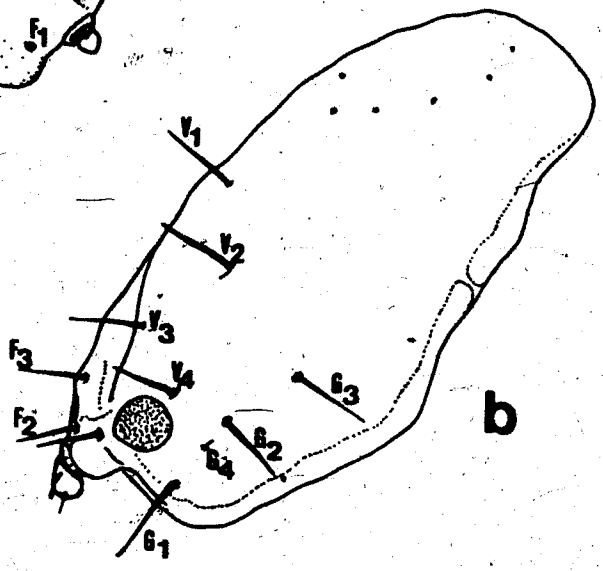

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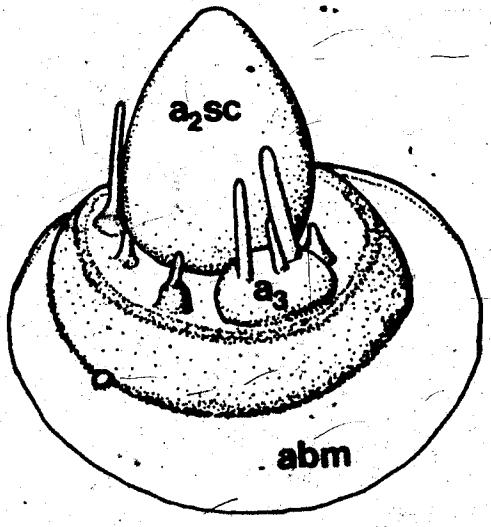


c

Each *parietale* (vertex + gena + occiput) with 6 to 7 setae (3 antero-doral (V_{1-3}), one postantennal (V_4), one hyperstomial (G_1), and two or three genal (G_{2-3})); occipital region with a curved series of sunken peg sensilla; genal region with about 3 such sensilla and a microsetae (G_4).

Frons with 2 pair of epistomial (F_{1-2}) and one pair of submedian setae (F_3); one or two pairs of submedian campaniform sensilla posterior to the submedian setae; length subequal to greatest width.

Clypeus divided into an ante- and postclypeus; postclypeus with 3 pairs of microsetae, and a pair of campaniform sensilla located mediad of the outermost of these.

Labrum with 2 pairs of basal setae (Figure 5a, L_{1-2}), the external pair longer; anterior margin with 2 pairs of short setae (Figure 6a, L_{3-4}).

Epipharynx (Figure 6a) at latero-anterior margin with several pairs of incurved setae (adjacent to marginal setae of labrum); anterior central region densely beset with numerous triangular inwards- and backwards-directed trichae; postero-laterad of this region a pair of sclerotized multilobed structures; postero-mediad of these an unsclerotized similar structures joined by membranous cuticlar bands to a posterior sclerotized pair (possibly homologous with the epipharyngeal organs of Dictyoptera described by Moulin

(1971)).

Head appendages:

Antenna with basal membrane (Figure 5c: abm) extensive; first article obsolete; second bearing a large membranous 'sensory cone' (a$_2$sc), 4 bacilliform to conic appendages (1 anterior and 3 posterior to the insertion of article 3) and 2 campaniform sensilla; third article (a$_3$) reduced, bearing 3 bacilliform appendages.

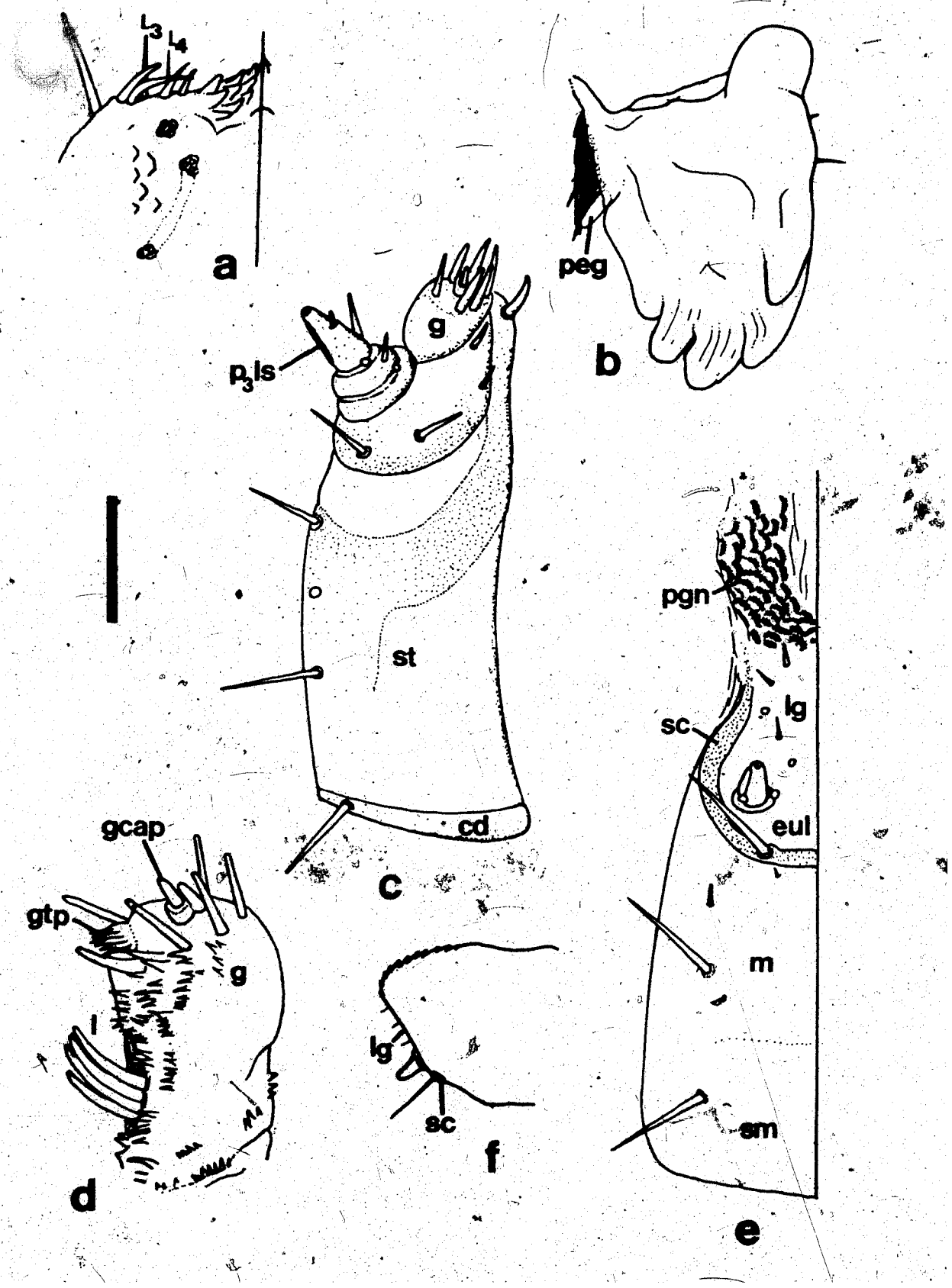
Mandible (Figure 6b) 5-toothed, the posterior tooth small; external surface bisetose; oral margin basally with a thick subconical to cylindrical peglike setal derivative (peg) and a series of long slender setae set in a groove, with a second series of longer setae at the basal angle curving distad.

Maxilla (Figure 6c) separated from labium by a deep groove. Cardo (cd) with a single seta. Stipes (st) externally with 2 setae and a campaniform sensillum; internal margin extending forward, bearing a short seta near apex; internal half of stipital body and area around base of palpifer membranous. Palpifer bisetose. Maxillary palp with three articles, the basal two shorter than broad, the second with a dorso-lateral seta; two campaniform sensilla at junction of basal segment with palpifer and also at junction of articles 1 and 2; terminal article elongate, truncate-conic, with small poorly developed terminal lobes, an elongate lateral plate-like sensillum (p$_3$ls) and one or two

Figure 6. *A. flava* Guilleb., larval mouthparts. a) right half of epipharynx, ventral aspect; b) right mandible, oral surface; c) right maxilla, ventral aspect; d) right galea and lacinia, dorsal aspect; e) labio-pharyngeal complex, right half, laid flat; f) Labio-pharyngeal complex, sagittal section, showing orientation of parts.

cd – cardo; eul – eulabium; g – galea; gcap – central appendix of galea; gtp – trichal plate of galea; l – lacinia; lg – ligula; L_{1-4} – marginal labral setae; m – mentum; p,ls – lateral plate sensillum of third article of maxillary palp; peg – mandibular peg; pgn – paragnath of hypopharynx; sc – semicircular sclerite of labium; sm – submentum; st – stipes.

Scale bar = 50 um for a,b,c,e); 20 um for d).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microsetae. Galea (Figure 6d) short, cylindrical, two short setae ventrally near stipito-galeal junction, apex truncate, membranous, furnished with a circle of marginal setae, the dorsal ones longer, and a complex central appendix (gcap) consisting of a conical structure supported on a larger diameter cylindrical base, and a conic structure ventro-laterad of the first and adnate to its base (probably homologous with the 'lateral' and 'medial sensilla' of Chrysomelinae (Mitchell and Schoonhoven, 1974); dorsal surface of galea with dense fields of flattened trichae''; a group of basally fused trichae forming a dorsal trichal plate at the margin of the truncate galeal apex (gtp).

Labium (Figure 6e,f) merging imperceptibly into the hypopharynx. Submentum (sm) with one pair of setae; mentum (m) with one pair of long proximal setae, a pair of distal microsetae, and a pair of distal peg sensilla. Semicircular sclerite (sc) with a pair of submedial setae. Eulabium (eul) without setae. Labial palpus with two articles, the basal short, the apical truncate-conic, with small poorly developed terminal lobes; with a campaniform sensillum, without setae. Ligula (lg) with six pairs of microsetae and one pair of campaniform sensilla antero-laterad of the proximal setal pair.

'' 'Tricha' is here used to indicate a hair-like cuticular expression merging smoothly with the surrounding integument, probably non-sensory in function.

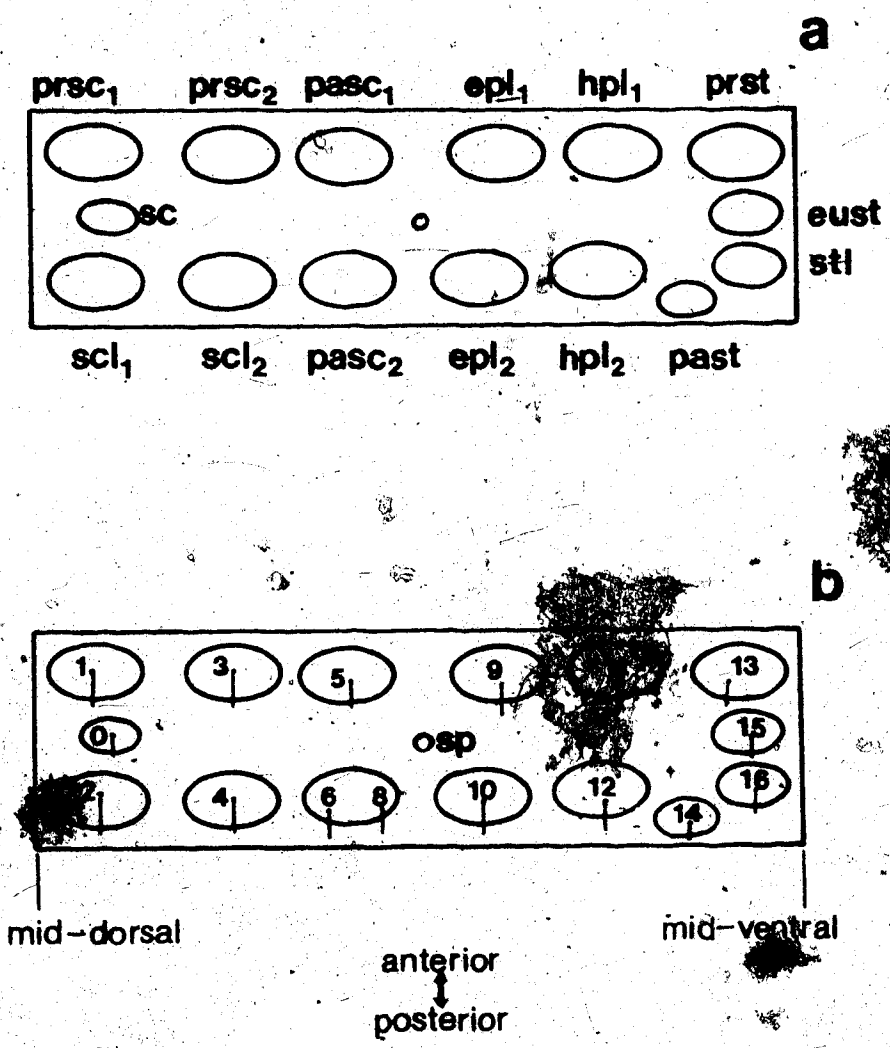
Hypopharynx (Figure 6e,f) with a pair of postero-lateral convex paragnatha (**pgn**); the paragnatha and the anterior median region of the hypopharynx densely covered by minute postero-medially directed trichae, arranged in arcs to form slightly imbricate fimbriate scales; postero-median area between paragnatha glabrous, membranous.

Soma:

Setae set on distinct, smooth, convex sclerites, the intervening cuticle membranous, minutely papillose. Except where noted all postcephalic cuticle is colourless.

A generalized body segment (Figure 7) has two complete annuli of primary setae, with their associated sclerites, and an incomplete intercalary row dorsally and ventrally. The tergal sclerites anteriorly comprise a submedian *interior prescutal* (**prsc**$_1$), a dorsolateral *external prescutal* (**prsc**$_2$), and a sublateral *anterior parascutal sclerite* (**pasc**$_1$); posteriorly, an *internal* and *external scutellar* (**scl**$_1$, **scl**$_2$), and a *posterior parascutal* sclerite (**pasc**$_2$); a submedian *scutal sclerite* (**sc**) between the prescutals and scutellars. The pleural regions bear an *anterior* and *posterior epipleural* (**epl**$_1$, **epl**$_2$) and an *anterior* and *posterior hypopleural* sclerite (**hpl**$_1$, **hpl**$_2$). Sternum with an anterior ventrolateral *presternal* (**prst**), a posterior ventrolateral *parasternal* (**past**), a posterior submedian *sternellar* (**stl**), and an

Figure 7. Generalized larval body segment. a) nomenclature of sclerites; b) setal numbering scheme.
epl_1 – anterior epipleural; epl_2 – posterior epipleural; eust – eusternal; hpl_1 – anterior hypopleural; hpl_2 – posterior hypopleural; $pasc_1$ – anterior parascutal; $pasc_2$ – posterior parascutal; past – parasternal; $prsc_1$ – internal prescutal; $prsc_2$ – external prescutal; prst – presternal; sc – scutal; scl_1 – internal scutellar; scl_2 – external scutellar; stl – sternellar sclerite. sp – spiracle.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2
4
6
8
10
12
14
16
mid-dorsal
mid-ventral
anterior
posterior

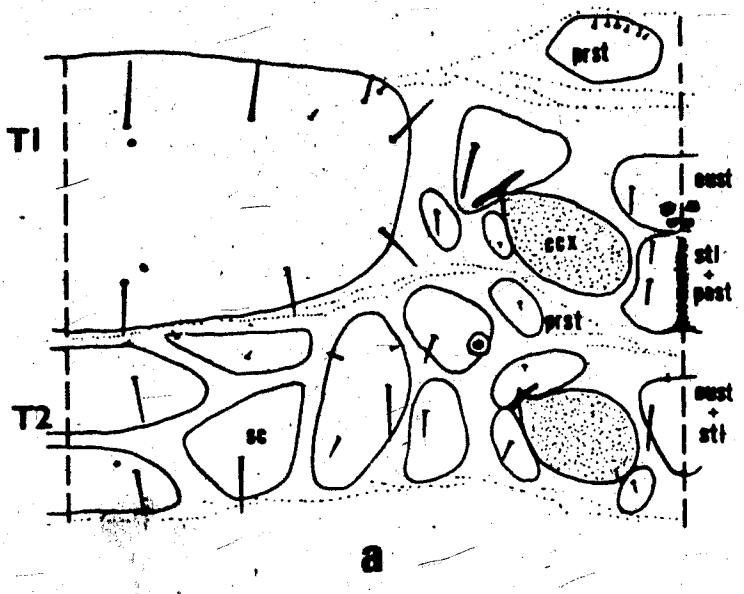
intercalary submedian *eusternal* sclerite (eust). There has been a varying degree of fusion (both longitudinal and transverse) and loss on different body segments, resulting in a reduced number of sclerites and multisetose sclerites. Setal numbering is given in Figure 7b).

Prothorax (Figure 8a; T1) with extensive fusion of tergal sclerites and epl, to form a lightly pigmented tergal shield with midline slightly impressed, colourless; disc with a lightly impressed coarse alutaceous sculpture; anterior margin finely alutaceous to papillose; seven pairs of subperipherally arranged setae (seta 5 shorter), two to four pairs of campaniform sensilla, and one or two pairs of microsetae in the antero-lateral region. epl, free, oval. Hypopleural sclerites forming the antero-dorsal and postero-dorsal margins of the coxal cavity (ccx), hpl, with a sclerotized ridge on which the coxa articulates. eust fused across the midline with its contralateral counterpart to form a broad oval or subtriangular plate. stl and past fused to each other and across the midline to form a trapezoidal or somewhat campanuliform median plate; approaching, contiguous with, or narrowly joined to eust+eust; midline more stronly sclerotized. prst far forward, in cervical region, with several microsetae along its anterior margin, its primary seta (seta 13) missing.

Figure 8. *A. cyparissiae* Koch, larva, sclerite and setal distribution. a) thoracic segments, right half; b) fifth abdominal segment, right half; c) eighth and ninth abdominal segments, dorsal aspect; d) eighth to tenth abdominal segments, ventral aspect.

T1 – prothorax; T2 – mesothorax; A8-10 – eighth to tenth abdominal segements; ccx – coxal cavity; other abbreviations as in Fig. 7.

Scale bar = 50 um.



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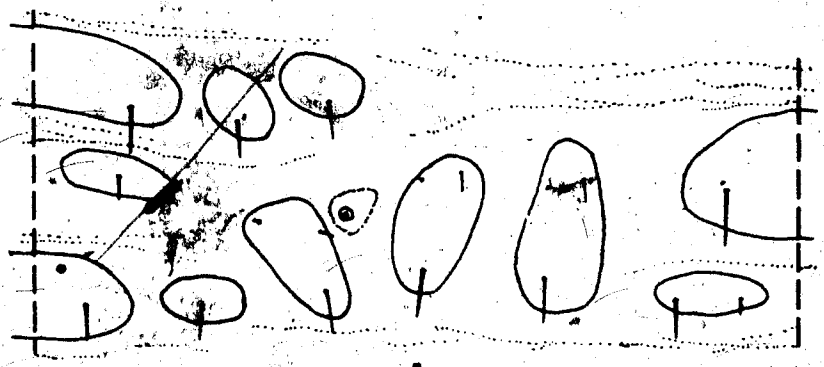

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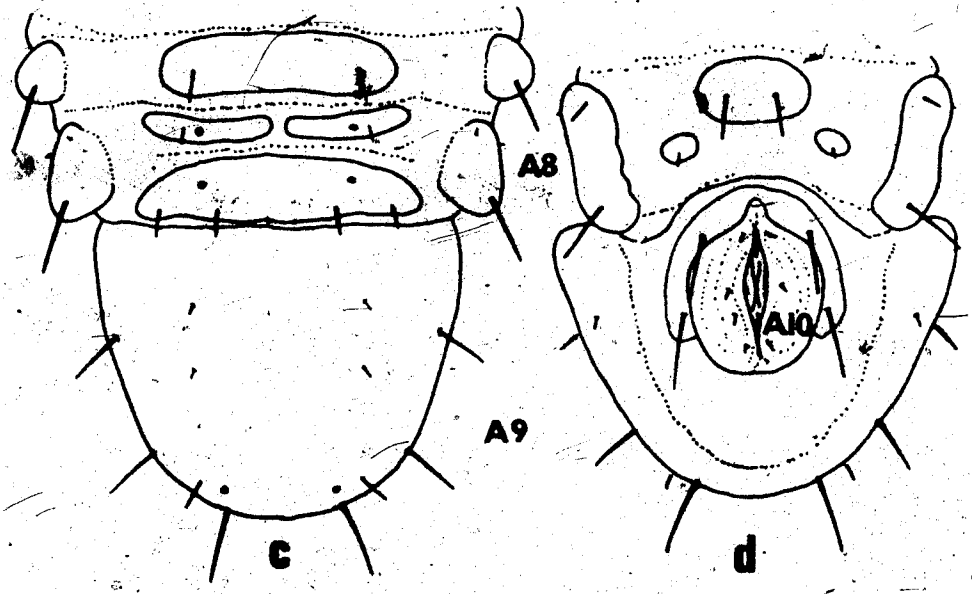


c d

Mesothorax (Figure 8a, T2) with less extensive fusion. prsc$_1$'s fused across midline, each with a forward directed socketed peg sensillum on its anterior margin. scl$_1$'s fused across the midline, each with a campaniform sensillum; anterior margin medially approximate to the prsc$_1$. sc large, triangular, the apex of the triangle intruding between prsc$_1$ and scl$_1$. prsc$_2$ transverse-oblique, the dorsal apex poorly defined, intruding between prsc$_1$ and the preceding segment; its primary seta reduced, very short or represented by a microseta; dorsal apex with a sunken peg sensillum, this sometimes found on the interscleritic membrane. scl$_2$, pasc$_1$ and pasc$_2$ fused into a single unit with one long, two shorter, and one very short seta. epl$_1$ bearing a spiracle on its postero-ventral margin; separate from epl$_2$. hpl$_1$ forming the antero-dorsal margin of the coxal cavity, bearing an articular ridge; its seta very short. hpl$_2$ forming the postero-dorasal margin of coxal cavity. eust and stl fused to each other, and across the midline, to form a triangular plate; seta 15 reduced to a microseta on the anterior margin of this plate. prst anterior to hpl$_1$; seta much reduced. past separate, on the ventral margin of the coxal cavity.

Metathorax similar to mesothorax but without a spiracle.

Abdominal segments 1 to 7 (Figure 8b) identical. **prsc**$_1$ fused across the midline. **scl**$_1$ fused across the midline, with a campaniform sensillum anteriad of the seta. **sc** separate, located between **prsc**$_1$ and **scl**$_1$, its seta shorter. **prsc**$_2$, **scl**$_2$, **pasc**$_1$ and **pasc**$_2$ separate; **pasc**$_2$ with one long seta, one short seta and a microseta. Spiracle (**sp**) located ventrad of **pasc**$_2$ on a separate poorly defined sclerite without setae. **epl**$_1$ and **epl**$_2$ fused, seta 9 shorter than 10; a socketed peg on **epl**$_2$. **hpl**$_1$ and **hpl**$_2$ fused, seta 11 shorter than 12. **eust** fused across the midline, large. **past** lateral to **stl** and fused to it, these not fused across the midline; seta 16 shorter than 14. **prst** absent.

Abdominal segment 8 (Figure 8c,d: **A8**) similar to segments 1 to 7, but with **sc** more transverse, con[redacted] or fused at the midline, and **scl**$_2$ fused to **scl**$_1$.

Abdominal segment 9 (Figure 8c,d: **A9**) with all dorsal sclerites fused into a more or less semicircular, marginally reflexed, sclerotized anal plate; the slightly swollen margin weakly delimited by a broad, shallow submarginal impression; margin evenly rounded, smooth, except second and third instars of *A. coerulea* which have a pair of raised subapical denticulate fields[12]; each half with 2 short setae on the disc, 4

[12] not a single pair of blunt 'spines' as indicated by Buddeberg (1878; *zwei kurze, stumpfe Spitzen über dem After*), and Ogloblin and Medvedev (1971; *c 2 shiroko rasstavlenimi, korotkimi, zagnutimi kverkhu, khitinovimi ostriyami*), at least in the specimens I have seen.

long setae on the periphery, and a very short seta laterally on the underside of the reflexed margin. Ventral sclerites fused into a transverse median plate with 2 pairs of setae

Abdominal segment 10 (Figure 5.4d: A10) small, cylindrical, eversible; sclerites and macrosetae absent; 4 pairs of microsetae around anus.

Thoracic appendages: (Figure 9)

All thoracic legs equally developed.

Coxa (cx) with a transverse anterior basal sclerite with 4 macrosetae along its stronly sclerotezed distal margin, and 4 microsetae near base; posterior face with one macroseta and one microseta; posterior basal margin with a stronly sclerotized band bearing one or two microsetae.

Basal margin of *trochanten* (tr) with a *V*-shaped sclerotized band with a series of campaniform sensilla and a microseta on the anterior arm; ventral surface with 5 macrosetae and a campaniform sensillum.

Femur (fm) with a saddle shaped sclerite on dorsal surface; one dorsal and 6 apical macrosetae.

Tibia (tb) cylindrical, most of surface lightly sclerotized; 3 dorsal and 4 apical macrosetae, and a dorsal-apical campaniform sensillum.

Tarsunguls with a single claw and a membranous, radially ridged paronychial lobe (pon) overlying the claw; a single seta at the base of the claw.

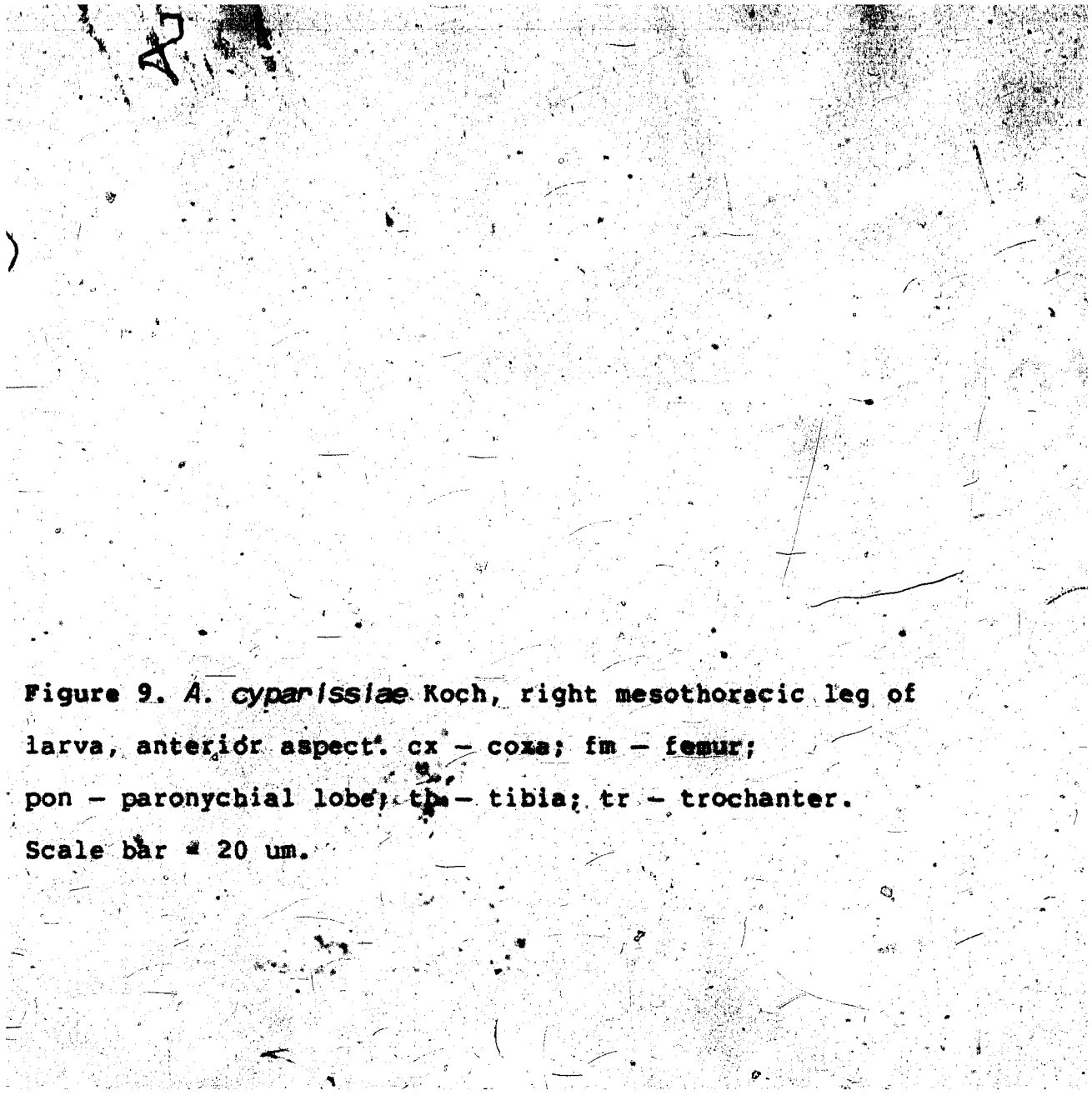
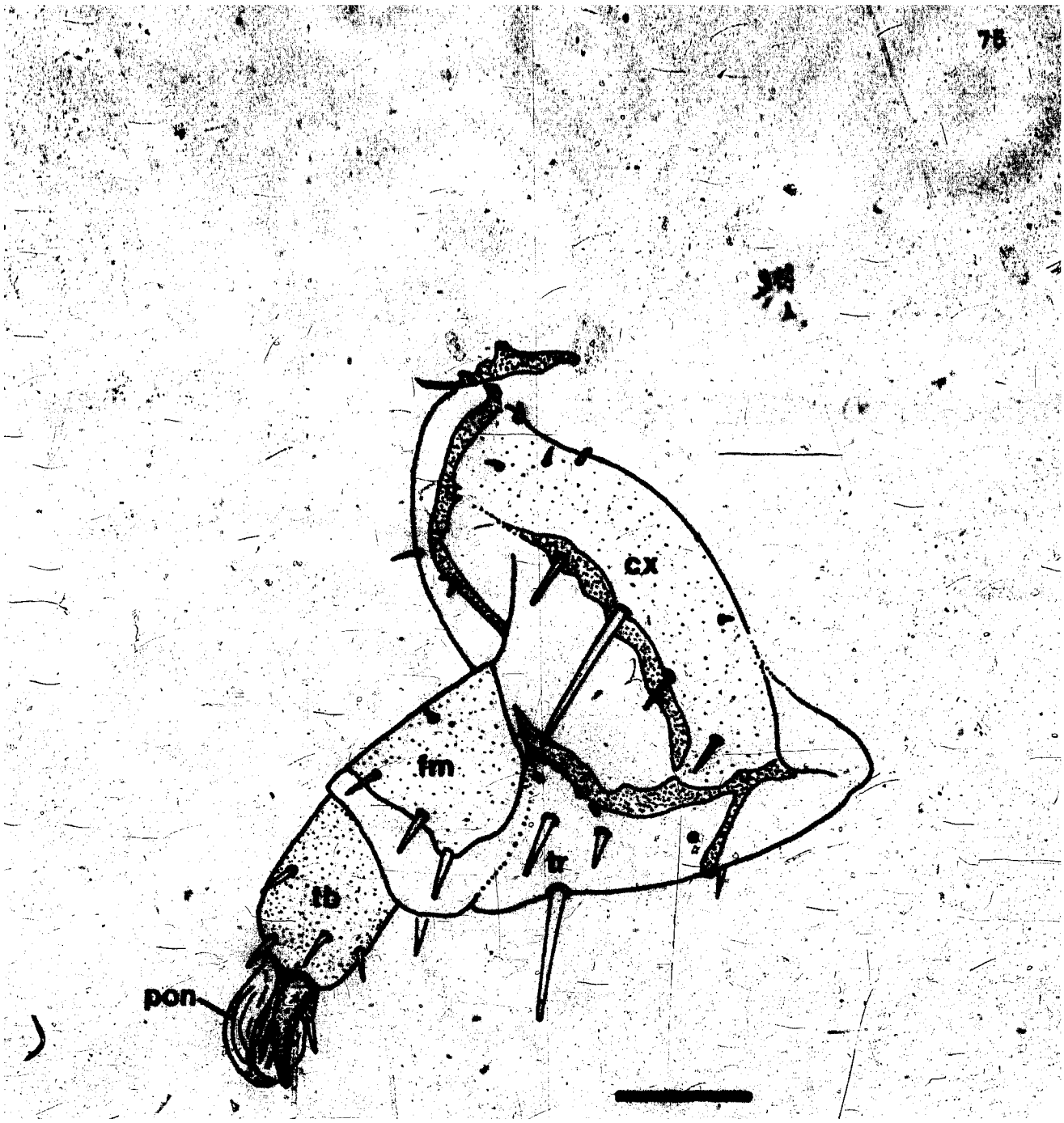


Figure 9. *A. cyparissiae* Koch, right mesothoracic leg of larva, anterior aspect. cx – coxa; fm – femur; pon – paronychial lobe; tb – tibia; tr – trochanter. Scale bar = 20 um.


cx
fm
tr
tb
pon

PUPA: (Figure 10)

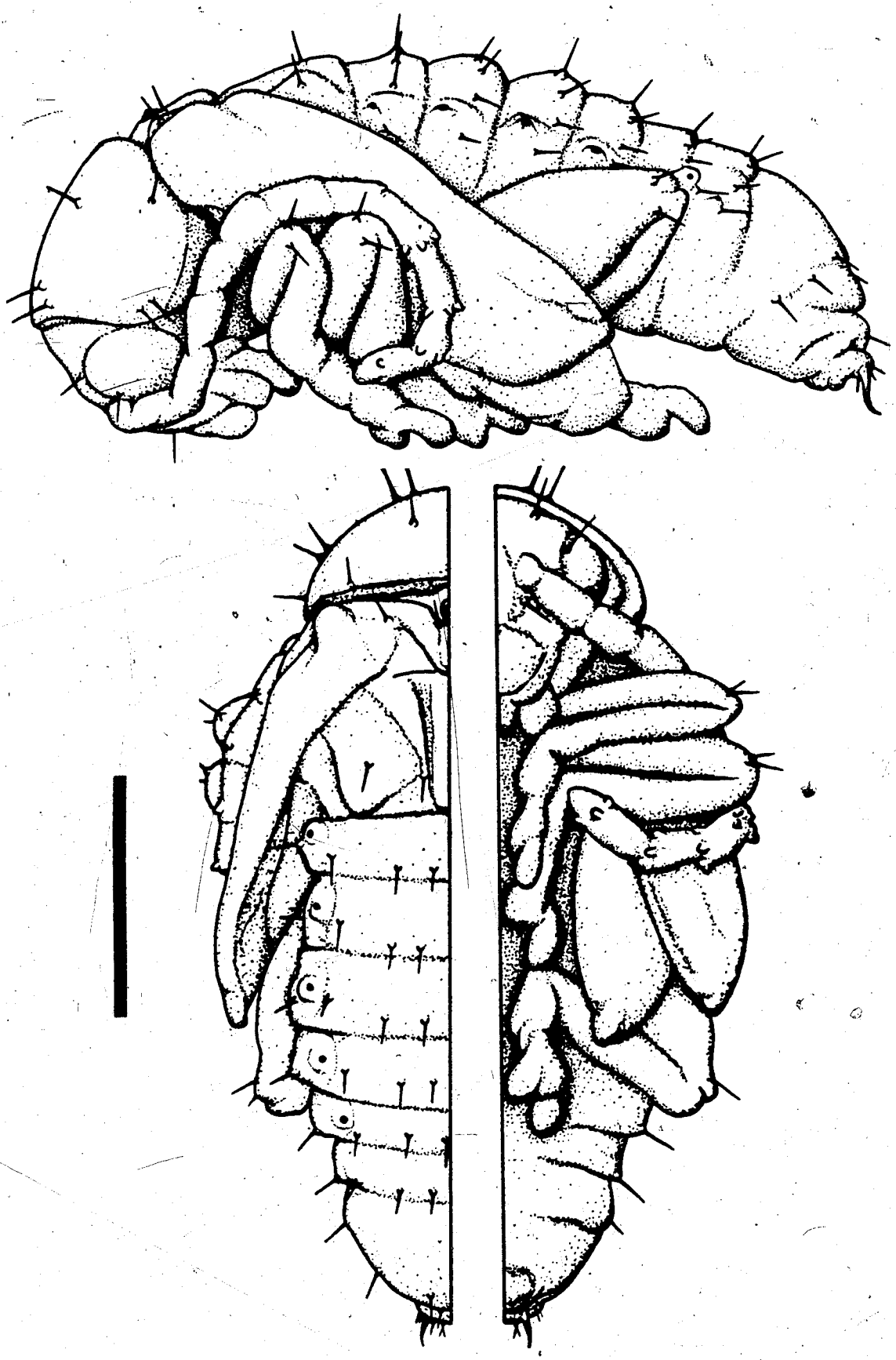
Head with one pair of ocular, one pair of supraorbital, and one pair of subantennal setae. Pronotum with 2 pairs submedian setae on the anterior margin, 2 pairs at the anterior angle, one pair at the posterior angle; one submedian pair on the hind margin, and one or two pairs on the disc. Terga of meso- and metathoraces each with 2 pairs of setae. Abdominal terga 1 to 6 with 2 or 3 pairs of setae, pleura with a supra- and subspiracular seta. Seventh and eighth abdominal segments with 3 pairs of setae; Segment 9 with 3 pairs of setae and provided with a pair of large curved heavily sclerotized spines. All femora with 2 or 3 subapical setae. Segment 10 of female represented by a pair of ventral papillae on segment 9.

5.5 Immatures of Selected Species

Only the three species *A. cyparissiae*, *A. flava*, and *A. czwalinae* for which complete reared material is available and which are treated in the subsequent chapters are dealt with here.

The larvae of the three species are extremely difficult to separate. The following characters are held in common by these three species, but not by all the species examined in the previous sections:

Figure 10. *A. czwalinae* Weise, pupa.



Egg microsculpture compound rather than simple alveolate, similar over the entire surface. Frons with 2 pairs of campaniform sensilla. Posterior pair of ligular setae longer than the others. eust+eust of abdominal segments wider than long. Margin of anal plate smoothly rounded. The second anterior coxal seta is the longest and the fourth the shortest of the four.

Measurements of larvae were made to the nearest 5 um and means have been rounded off in the same way.

5.5.1 *A. cyparissiae*

EGG:

Measurements (n=120)

Length: mean 0.67 mm, standard deviation 0.03 mm, range 0.56 to 0.77 mm.

Width: mean 0.39 mm, s.d. 0.05 mm, range 0.31 to 0.43 mm.

Ratio length to width: mean 1.73, range 1.37 to 2.29.

Sculpture as in Figures 11a and b. Primary alveoli 20 to 24 um in diameter; ridges in cross section flat topped, rounded at edges (Figure 11c). Number of secondary cells per primary alveolus varies with locality: Rhine valley material with 3 to 6, mode 5 (Figure 11a; eastern Hungarian material with 6 to 10, mode 7 (Figure 11b).

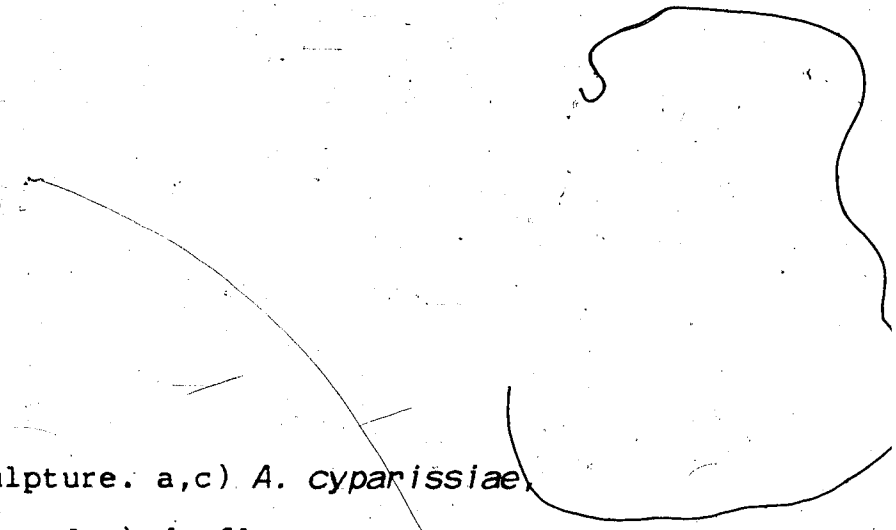
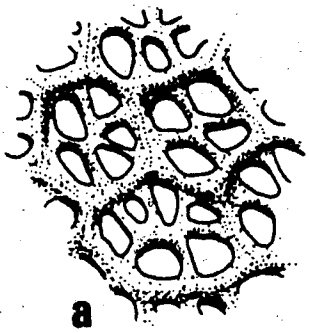


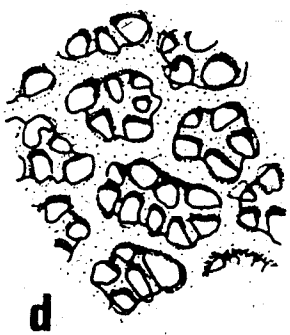
Figure 11. Egg microsculpture. a,c) *A. cyparissiae*, Rhine-Valley, b) Hungary; d,e) *A. flava*; f,g) *A. czwalinae*.
a,b,d,f) superficial aspect, scale bar = 20 um; c,e,g) section through primary alveolus.



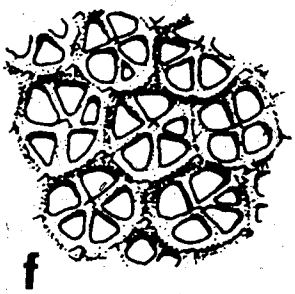
a

b

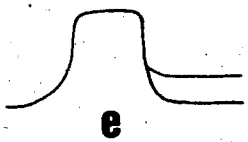
c



d



f



e

g

LARVA:

Measurements:

First instar (n=25)

Head width: 180 um, standard deviation 40 um, range 165 to 190 um.

Anal plate width: 180 um, s.d. 30 um, range 160 to 205 um.

Anal plate length: 175 um, s.d. 35 um, range 165 to 195 um.

Second instar (n=20)

Head width: 355 um, s.d. 45 um, range 340 to 395 um.

Anal plate width: 450 um, s.d. 90 um, range 425 to 470 um.

Anal plate length: 445 um, s.d. 80 um, range 430 to 485 um.

Third instar (n=30)

Head width: 420 um, s.d. 55 um, range 405 to 450 um.

Anal plate width: 525 um, s.d. 70 um, range 540 to 625 um.

Anal plate length: 550 um, s.d. 80 um, range 480 to 510 um.

Diagnosis:

Mandibular **peg** straight, blunt or abruptly narrowed (Figure 6b). Galea with lateral component of **gcap** (Figure 6d) terete in cross section; marginal trichal plate of 5 to 6 trichae (only 4 in first instar larvae). Posterior ligular setae about equidistant between middle ligular setae and labial palpi. Anal plate, on average, longer than its greatest width in third instar; isodiametric in first and second instars. Fat bodies white.

PUPA:

Pronotum with outer submedian anterior seta less than 2/3 length of inner; 2 discal pairs of setae. Abdominal segments 3 to 6 usually with 2 posterior and 1 anterior tergal setae. Femora with 3 setae.

5.5.2 *A. flava*

EGG:

Measurements: (n=60)

Length: mean 0.69 mm, standard deviation 0.03 mm, range 0.66 to 0.77 mm.

Width: mean 0.40 mm, s.d. 0.04 mm, range 0.36 to 0.42 mm.

Ratio length to width: mean 1.72, range 1.49 to 1.97.

Sculpture as in Figure 11d. Primary alveoli 20 to 30 um in diameter. Intervening ridges in cross section flat topped, edges more precipitous, sometimes overhanging the alveoli (Figure 11e). Number of subcells per primary alveolus 4 to 10, mode 8.

LARVA:

Measurements:

First instar (n=25)

Head width: 180 um, standard deviation 35 um, range 160 to 195 um.

Anal plate width: 180 um, s.d. 40 um, range 160 to 190 um.

Anal plate length: 175 um, s.d. 40 um, range 155 to 185 um.

Second instar (n=20)

Head width: 365 um, s.d. 50 um, range 345 to 395 um.

Anal plate width: 420 um, s.d. 55 um, range 395 to 445 um.

Anal plate length: 395 um, s.d. 50 um, range 375 to 420 um.

Third instar (n=30)

Head width: 435 um, s.d. 20 um, range 405 to 450 um.

Anal plate width: 575 um, s.d. 70 um, range 540 to 610 um.

Anal plate length: 530 um, s.d. 55 um, range 485 to 595 um.

Diagnosis:

Indistinguishable from *A. cyparissiae*, except that hatchlings have yellow fat bodies, fading in a few days to white (bleached out in alcoholic preservatives), and most specimens with length of anal plate less than the greatest width.

PUPA:

Similar to that of *A. cyparissiae*.

5.5.3 *A. czwalinae*

EGG:

Measurements (n=30)

Length: mean 0.68 mm, standard deviation 0.03 mm, range 0.59 to 0.79 mm.

Width: mean 0.35 mm, s.d. 0.04 mm, range 0.26 to 0.48 mm.

Ratio length to width: mean 1.94, range 1.61 to 2.54.

Sculpture as in Figure 11f. Primary alveoli 18 to 25 µm in diameter. Primary ridges in cross section narrow at top (Figure 11g), higher at intersection points. Secondary cells 3 to 6 per primary cell, mode 5, arranged radially, hub peaked.

LARVA:

Measurements:

First instar (n=20)

Head width: 180 um, standard deviation 5 um, range 170 to 185 um.

Anal plate width: 155 um, s.d. 10 um, range 140 to 165 um.

Anal plate length: 140 um, s.d. 10 um, range 130 to 155 um.

Second instar (n=20)

Head width: 260 um, s.d. 10 um, range 250 to 270 um.

Anal plate width: 260 um, s.d. 30 um, range 235 to 295 um.

Anal plate length: 260 um, s.d. 35 um, range 220 to 290 um.

Third instar (n=30)

Head width: 435 um, s.d. 15 um, range 420 to 455 um.

Anal plate width: 455 um, s.d. 25 um, range 430 to 510 um.

Anal plate length: 430 um, s.d. 10 um, range 420 to 450 um.

Diagnosis:

Mandibular curved, acute, gradually tapered. Galea with lateral component of **gcap** compressed in cross section, at least in basal half; marginal trichal plate of 4 trichae. Posterior pair of ligular setae nearer labial palpi than middle pair. Length of anal plate less than greatest width.

PUPA:

Outer submedian anterior seta of pronotum only a little shorter than inner; one pair of discal setae. Abdominal terga 1 to 6 with 2 setae. Femora with 2 setae.

PART III

6. Observations on Field Collections of Adults

6.1 Introduction

The results of two centuries of collecting indicate that the more common spurge-feeding *Aphthona* species, for which multiple records are available, may be taken from several, but not all available spurges (Appendix Table A-1), and are generally known from characteristic habitat types. In this chapter, I examine the nature of these apparent associations. Are the observed host 'preferences' and ranges a result of differential acceptability or simply relative abundance of a set of equally acceptable plant species? To what extent are habitat associations a function of host habitat, rather than intrinsic requirements of the beetle?

6.2 Sampling Sites

In the discussions which follow, 'site' should be taken to mean an area more or less homogenous with respect to physical parameters and general vegetational characteristics, containing patches of one or more species of potential host plants; a 'sample' is all beetles yielded by a single plant species within a site; a 'collection' is a series of beetles of a particular species collected from a given host at a given site.

During the summer of 1978, Gisela Sommer of the Commonwealth Institute of Biological Control, and I, sampled

populations of as many spurge species as possible for the occurrence of *Aphthona* species. Samples were taken from other known hosts of European *Aphthona* species, namely, *Linum*, *Geranium*, *Helianthemum* and *Iris*, when encountered. Collections were made in northwest Switzerland in May, June, July and September; the Rhine valley on both sides of the German-French border, in June, July and September; in Lower Austria, in June and July; and in Hungary in July. A total of 380 samples were taken at 203 sites, yielding 16 species of *Aphthona* from *Helianthemum nummilarium* (L.) Dunal, *Iris pseudacorus* L. and 17 taxa of *Euphorbia*. Samples from *Geranium* and *Linum* were barren. The number of sites for each plant taxon, in each of the regions surveyed, is given in Table 1. Eastern and western Hungary show several differences in spurge flora and are listed as separate regions.

Only four species, *A. cyparissiae*, *virgata*, *esula*, and *seguieriana*, were found at more than 20 sites, and three others (*palustris*, *salicifolia*, and *exigua*) at only a single locality. Although the species appearing most often in our sample sites are also the most abundant species, the frequency of occurrence in the table should not be taken as an indicator of actual abundance. Rather, an emphasis on the sampling of mesic to dry, open habitats not under cultivation means that certain groups of quite common species are severely under-represented. *E. palustris* and *salicifolia*, for example, are certainly not uncommon, but are plants of very wet areas. *E. helioscopia* and *exigua*,

Table 1: Number of sites sampled for each plant taxon, by region.

Plant Taxon	Number of Sites					
	Jura Switzerland	Rhine-Alsace	e. Austria	Hungary w. of Danube	Hungary e. of Danube	Total
Euphorbia						
cyparissias L.	4	18	23	47	25	117
virgata Wald.+ Kit.	-	-	27	13	20	60
e.x v.*	-	-	-	-	5	5
esula L.	-	-	29	19	4	52
hebecarpa Boiss.	-	-	-	-	4	4
lucida Wald. + Kit.	-	-	-	4	9	13
salicifolia Host	-	-	-	-	1	1
palustris L.	-	-	-	1	-	1
amygdaloides L.	2	1	-	-	-	3
seguieriana Necker	-	8	3	21	1	33
pannonica Host	-	-	-	6	2	8
verrucosa L.	3	1	-	-	-	4
stricta L.	2	5	2	5	-	14
platyphyllos L.	-	-	-	10	6	16
helioscopia L.	-	-	8	4	1	13
falcata L.	1	-	8	-	-	2
exigua L.	-	-	1	-	-	1
Geranium	1	1	-	1	-	3
Helianthemum	1	4	-	-	-	5
Linum	-	-	1	1	-	2
Iris	-	2	-	-	-	2
Total # of sites	4	21	58	63	56	203

* Unassigned populations with characters intermediate between *E. esula* and *E. virgata*.

among others, are common weeds of cultivated crops. Appendix 3 gives the classification according to Prokhanov (1949) of the *Euphorbia* species encountered and summarizes their characteristics.

Table 2 shows the number of sites and number of samples in which each *Aphthona* species was present.

A complete list of sites, with dates of collection, potential host plants present, and beetle species collected from each host, is provided in Appendix 2 (Table A-3).

6.3 Methods

When practical, spurge population and patch dispersion, and density and frequency of occurrence (explained later) were estimated for each *Aphthona* species, at each site.

The significant differences in architecture between spurge species , and differences in nature of interspersed vegetation density, and in patch size within species made use of a standard technique for all samples counterproductive. Instead, the following procedures were used depending on growth form and patch conformity of the particular spurge population.

The counting unit for the spurges depended on the growth habit of the species. For creeping perennial species (mainly *E. esula, virgata, cyparissias, lucida*), a 'unit' should be taken as one or more shoots arising from the same shoot base or root crown (see descriptions in Chapter 3). For tufted perennials (*E. seguieriana, pannonica, verrucosa*),

Table 2: Number of sites and number of samples for *Aphthona* species, by region.

Aphthona species	Number of sites/number of samples					
	Jura Switzerland	Rhine-Alsace	e. Austria	Hungary w. of Danube	Hungary e. of Danube	Total
cyparissiae (Koch)	1/2	12/17	23/29	18/30	1/1	55/79
flava Guillebeau	-	-	1/1	34/38	4/4	39/43
nigriscutis Foudras	-	-	-	14/20	6/6	20/26
abdominalis (Duftschmidt)	1/1	5/5	1/1	2/2	-	9/9
lutescens (Gyll.)	-	-	-	1/1	-	1/1
czwalinae Weise	-	-	7/10	5/7	-	12/17
violacea (Koch)	-	-	-	2/2	7/8	9/10
pygmaea Kutschera	3/4	7/11	-	8/8	2/2	20/25
cyanella (Redtenbacher)	1/1	-	-	-	-	1/1
delicatula Foudras	1/3	-	-	-	-	1/3
venustula Kutschera	3/7	13/19	5/5	5/5	-	27/36
euphorbiae (Schrank)	-	-	-	-	3/3	3/3
coerulea (Paykull)	-	2/3	-	-	-	2/3
lacertosa Rosenh.	-	-	7/8	12/17	23/26	42/51
herbigrada Curtis	1/2	6/6	-	-	-	7/8
ovata Foudras	-	-	3/7	1/1	1/1	5/9
no Aphthona	0/7	1/13	24/56	19/70	22/43	66/189

a unit is equivalent to the individual plant: that is, a number of rarely branched shoots arising from a common crown. A unit for annual species (*E. stricta, platyphyllos, helioscopa, exigua, falcata*) is the plant, consisting of a single often, branched shoot.

The total population of a patch (number of units) was counted directly when units were not extremely numerous. For larger populations, the number of units per m^2 was counted in 10 (or more in very large patches) one square metre areas, and the mean thus obtained used to estimate the total population for the patch. The particular spots to be counted were selected systematically as every fourth pace along transects through the patch.

To estimate relative beetle populations where units were not numerous, the individual shoots were placed in the mouth of a collecting net and the beetles shaken out and aspirated from the net, or the beetles aspirated directly from small plants. The same technique was used for the large species (*E. lucida, palustris, salicifolia*) and for *E. esula* and *E. virgata* when discontinuously distributed, even when abundant. Continuous stands of *E. cyparissias, esula,* and *virgata* were swept in their entirety in the normal manner with a net flattened on one side to give a wider interception area near the ground. About 50 'units' were sampled in the manner described above to correct for the relative inefficiency of sweeping. This correction factor proved to be about 3.5 for collections from

E. cyparissias and 3 for collections from *E. esula* and *E. virgata* on sunny days. (Beetle abundance data for collections on cool or wet days were coded as missing for analysis).

The values obtained in the manner described above were recorded as follows:

Spurge population was converted to a scale of 1 to 5:

1. <10 units per patch, scarce
2. 11 - 100, few
3. 101-1000, moderate
4. 1001 - 10 000, abundant
5. >10 000, very abundant

Patch dispersion was assessed on a very subjective basis as:

1. isolated units
2. plants in small patches or well intermixed with other vegetation
3. continuous stand

Beetle population was converted to a scale of 1 to 5:

1. 1 - 5 individuals
2. 6 - 20
3. 21 - 100
4. 101 - 400
5. >400

In making adjustments for differences in efficiency between sweeping and beating, it was assumed that all *Aphthona* species are sampled with equal efficiency. This is not

strictly true, since laboratory observations indicated that certain species require somewhat more violent stimulation than others to dislodge them from their host, but the difference is probably not significant under the imprecise sampling methods used here.

Beetle frequency is the number of beetles per spurge unit. This was coded as:

1. <0.001
2. >0.001 to 0.010
3. >0.01 to 0.10
4. >0.1 to 1.0
5. >1

Voucher specimens of all distinguishable spurge phena were collected. Limitations of space permitted the collection of representative spurge specimens only.

Spurge species were determined using *Flora der Schweiz* (Hess *et al.*, 1970), *Flora Europeae* (Smith and Tutin, 1968), and *Flora URSS* (Prokhanov, 1949). Heikertinger's (1944) key was used to identify specimens of *Aphthona*.

Several superficial habitat characteristics were assessed subjectively. *Soil texture* was determined using the 'finger technique' described by Osmond (1967) and assigned to one of the classes indicated in Column 1 of Table 3. My classification is much simplified and does not coincide exactly with any standard system of classifying soil texture. I have essentially substituted a clay-sand distinction of particle size for the usual clay-silt-sand

Table 3: Soil texture classes used in this study and comparable standard classes (see Soil Survey Staff, USDA (1951)).

Classes used here	Standard Classes
1. heavy clay	heavy clay
2. clay	clay, silty clay
3. clay loam	clay loam, silty clay loam
4. loam	loam, silty loam, silt (part)
5. sandy loam	sandy loam
6. loamy sand, fine sand	loamy sand, silt (part)
7. sand	sand
8. sandy gravel	—
9. gravelly clay to gravelly loam	—

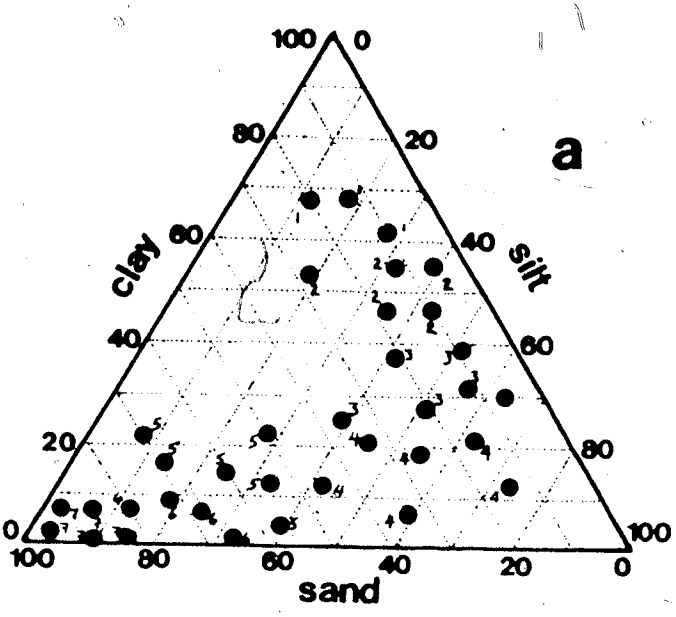
distinction. Certain complex soils did not fit satisfactorily into this linear sequence and an additional class (9) was formed to accommodate these. As a check on constancy of my subjective class assignments through the season, and for comparison to standard classification systems, 20 soil samples before, 12 after, and 5 during the field season, were collected and their composition later determined in terms of proportion of clay, silt and sand sized particles by the hydrometric method (Day, 1965). These results were compared to previous subjective determinations. The results of these analyses are plotted in Figure 12a. Figure 12b. maps my texture classes as a function of percent of clay, silt and sand sized particles based on these results. Note that clay-sand mixtures do not fit into this system. Standard classes corresponding to my classes are shown in column 2 of Table 3.

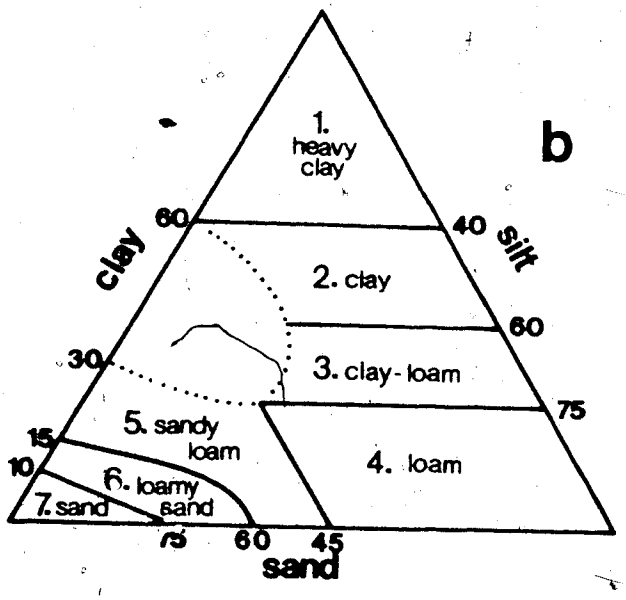
Available moisture at each site was coded on a scale of 1 to 5:

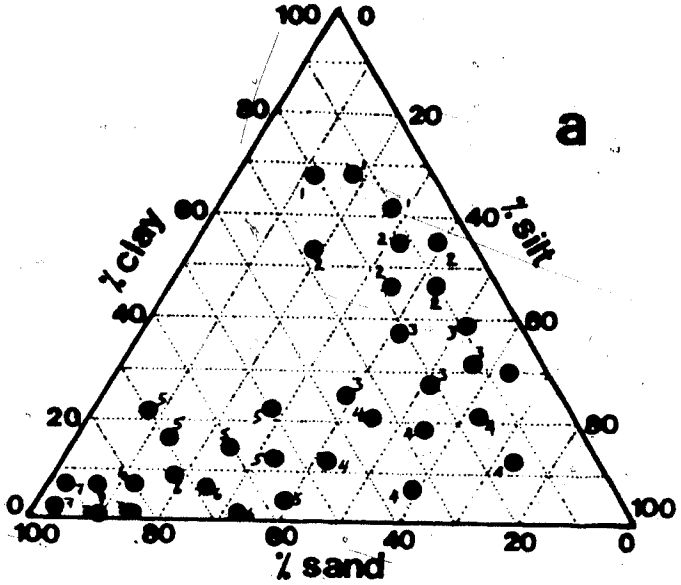
1. Saturated
2. Wet
3. Mesic
4. Dry
5. Very dry

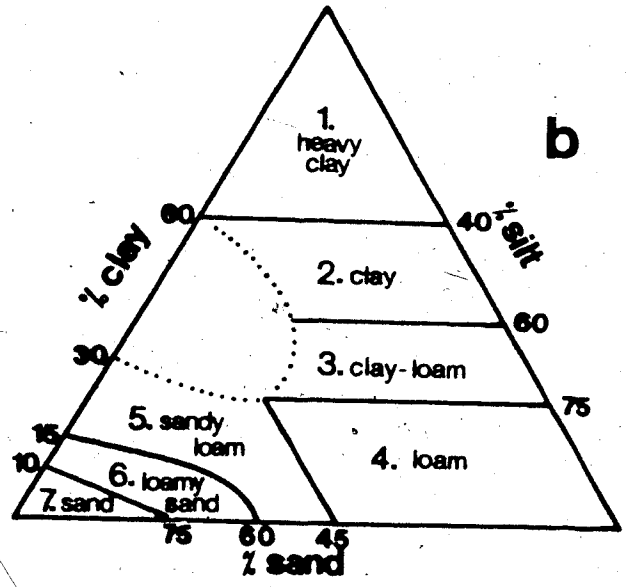
Class assignment was based on a subjective estimate of chronic moisture conditions as implied by the presence of indicator plant species and associations.

Figure 12. Soil texture as a function of per cent sand (> 2 um), silt (0.02 to 2 um), and clay (< 0.02 um) sized particles. a) results of particle size analysis of check samples (numbers correspond to subjective texture classes as given in Table 13);
b) map of texture subjective classes used in this study.


a
clay
silt
sand
100
80
60
40
20
0


b
1. heavy clay
2. clay
3. clay-loam
4. loam
5. sandy loam
6. loamy sand
7. sand
clay
silt
sand
60
40
30
75
15
10
45


a
% clay
% silt
% sand
100
80
60
40
20
0


b
1. heavy clay
2. clay
3. clay-loam
4. loam
5. sandy loam
6. loamy sand
7. sand
% clay
% silt
% sand
60
40
30
75
15
10
45

The microclimatic conditions experienced by a beetle in the immediate vicinity of a host plant are strongly influenced by the moderating effects of evapotranspiration from, and shading by, the surrounding vegetation. The *vegetational character* of the site was therefore recorded and coded as follows:

1. closed canopy – host plants an understory component in a closed canopy woods.
2. open canopy – host plants an understory component in an open canopy woods.
3. transition – host plants among shrubs or at margin of wooded area.
4. tall/dense – surrounding vegetation herbaceous, taller than host plant, shoots in general more or less contiguous (host plant closely invested by other vegetation).
5. tall/sparse – surrounding vegetation herbaceous, taller than host plant, shoots in general not contiguous.
6. short/dense – surrounding vegetation herbaceous, shorter than host plant, shoots in general contiguous (host plant free standing).
7. short/sparse – surrounding vegetation herbaceous, shorter than host plant, shoots in general not contiguous (host plant free standing).
8. bare – no other vegetation, surrounding ground bare (host plant free standing).

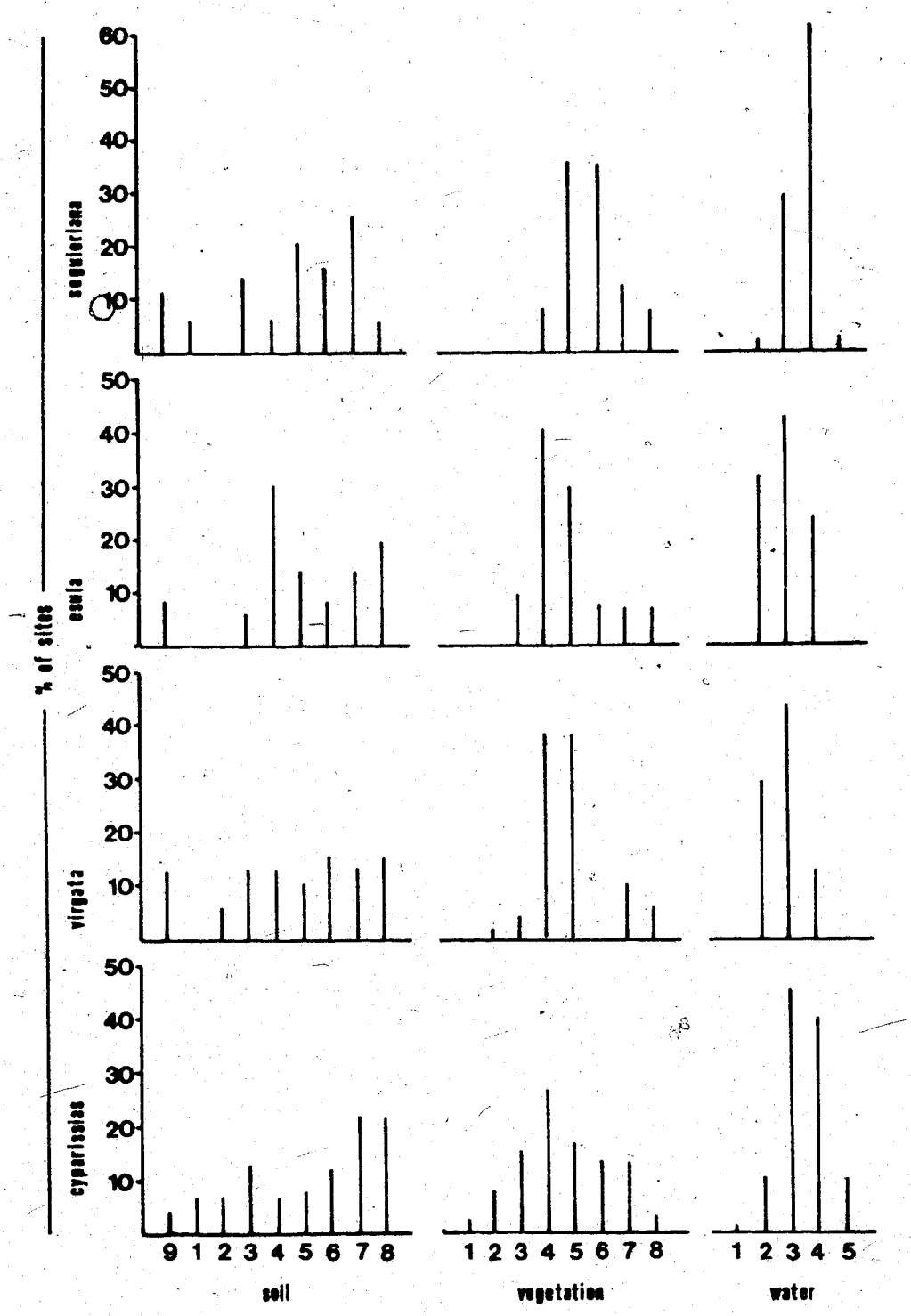
Slope *angle* and *aspect* were noted where applicable.

The estimated habitat parameters are certainly strongly interrelated. The moisture levels of coarse-grained soils, which have a lower water holding capacity, are very sensitive to topographic variations, and therefore dry or very dry habitats are much more likely to occur on sandy soils. Available soil moisture has a strong influence on the general nature of the vegetation. The trends from wooded to open, tall to short, dense to sparse, indicated earlier, are largely correlated with a wet to dry trend. The sites labelled 'bare' are generally elevated sandy or gravelly sites which usually can be invaded only from the periphery by a plant like cypress spurge with a deep, creeping root system. However, wet areas may also be sandy and unpalatable cypress spurge may stand as sentinels on closely cropped sheep pastures which would otherwise support a lush growth of other plants. It was therefore felt that the three parameters taken together would best indicate the overall nature of the habitat given that this was an initial survey, requiring an extensive rather than intensive approach.

6.4 Results

For reference, the distribution on the various habitat parameters of the more common hosts encountered are shown in Figure 13.

Figure 13. Relative frequency of soil texture, vegetation, and hydric classes at sites for the most commonly collected spurge species.


% of sites
saguiriana
esula
virgata
cyparissias
60
50
40
30
20
10
9 1 2 3 4 5 6 7 8
1 2 3 4 5 6 7 8
1 2 3 4 5
soil
vegetation
water

6.4.1 *A. cyparissiae*

6.4.1.1 Hosts

The host data are summarized in Figure 14a. The left half of the figure shows the number of samples from each host in which *A. cyparissiae* was present ('encounter frequency').

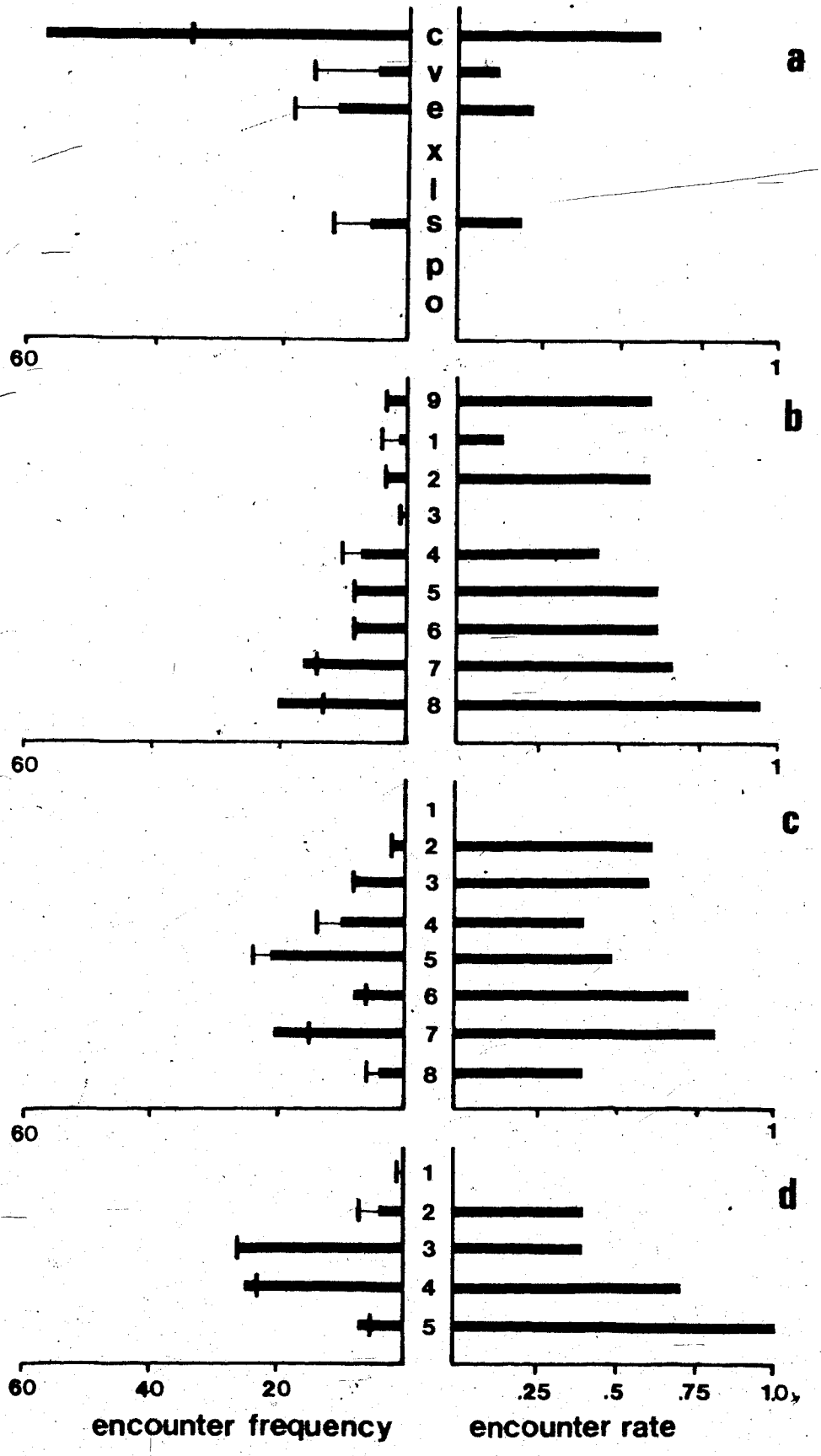
Most collections were from *E. cyparissias*, distantly followed by *esula*, *seguieriana* and *virgata*. The absolute values confound any differences in occurrence with the relative abundances of the spurge species. In order to control for this, we must consider the proportion of sites for each spurge species at which the beetle was present ('encounter rate'). After such correction for relative abundance of the spurges within the range of *A. cyparissiae* (*i.e.* eastern Hungarian sites excluded) (right side of Figure 14a), the same pattern is shown. Of particular interest is the very low incidence on *E. virgata*, and absence from all annuals. Expected encounter frequencies are calculated in Table 4 under the hypotheses that a) this beetle occurs on all spurge species in proportion to their abundance, b) no discrimination is shown between those species on which it does occur, and c) no discrimination is shown between *E. esula*, *E. virgata*, and *E. seguieriana*. Expected values under hypothesis (b) are indicated on the left side of Figure 14a by cross bars. Calculation of the X^2 statistic shows that the departure from the expected

Figure 14. Encounter frequency and encounter rate for *A. cyparissiae* at sites with different a) spurge species, b) soil textures, c) vegetational classes, and d) hydric classes.

'Encounter frequency' (left side of graph) is the total number of sites at which the beetle was present; 'encounter rate' (right side)is the proportion of the total sites of a given character at which beetles were present. Cross bars on the left indicate encounter frequencies expected if beetles show no discrimination among those spurges on which they occur, given the relative number of sites at which those spurge species were sampled.

Euphorbia species: c – *cyparissias*; v – *virgata*; e – *esula*; x – *esula* x *virgata*; l – *lucida*; s – *seguieriana*; p – *pannonica*; o – others.

Soil texture classes as in Table 6.3; vegetational classes as on page 100; hydric classes as on page 97.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5
60
40
20
.25
.5
.75
1.0
encounter frequency
encounter rate

Table 4. Comparison of observed and expected frequency of encounter for *A. cyparissiae* on spurge species. Expected values calculated according to three different hypotheses: a) all spurges equally acceptable, b) no discrimination shown among *E. cyparissias*, *virgata*, *esula*, and *sequieriana*, c) no discrimination among *E. virgata*, *esula* and *sequieriana*.

		Encounter Frequency (# samples with beetles)			
	# of		Expected		
Spurge	Sites	Observed	a)	b)	c)
cyparissias	92	57	28	34	
virgata	40	5	12	15	7
esula	48	11	14	18	9
seguieriana	31	6	9	12	6
others	51	0	15	–	–
X^2			52.4 ***	28.3 ***	1.3 NS

*** - $p<0.005$; NS - not significant ($p>0.10$)

Table 5. Frequency of encounter of *A. cyparissiae* (number of samples with beetles) at sites where two host spurges occur together.
cyp = *E. cyparissias*, vir = *E. virgata*,
esu = *E. esula*, seg = *E. seguieriana*, + = beetles present,
- = beetles absent.

	vir+	vir-	esu+	esu-	seg+	seg-
cyp+	2	7	4	11	5	13
cyp-	1	–	1	1	1	–
vir-	–	–	2	–	0	–
vir+	–	–	0	1	0	0

values is highly significant ($p < 0.005$) under hypotheses (a) and (b). No statistically supportable discrimination can be demonstrated among the three hosts exclusive of *E. cyparissias* ($p > 0.10$).

The matter is not one of a simple preference hierarchy, however. Table 5 shows the encounter frequencies on potential hosts where those plants occur together at a site, often in mixed stands. Beetles were present on each of *E. esula*, *virgata*, and *seguieriana* and absent on *E. cyparissias* at one site. Similarily, beetle were present on *esula* over *seguieriana* at one and over *virgata* at two sites, and *virgata* over *esula* at one.

6.4.1.2 Soil Texture

Encounter frequency and encounter rate for *A. cyparissiae* on different soil texture classes is shown in Figure 14b. Most collections were from areas with sandy to sand-gravel soils, but the deviation from what would be expected given the frequency of occurrence of the soil types is not significant ($p > 0.10$, Table 6).

6.4.1.3 Vegetational character of site.

Encounter frequencies and rates for *A. cyparissiae* in different vegetational character classes is shown in Figure 14c. Most collections were from sites with sparse vegetation. Again, this is a reflection of host-plant habitat since encounter frequencies were as expected (Table 7).

Table 6. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. cyparissiae* at sites with different soil texture classes.

Soil	9	1	2	3	4	5	6	7	8
# of Sites	5	7	5	2	16	13	13	24	21
Observed frequency	3	1	3	0	7	8	8	16	20
Expected frequency	3	4	3	1	10	8	8	14	13

X^2 = 7.2, $p>0.1$ (classes 9, 1, 2, 3, grouped).

Table 7. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. cyparissiae* at sites with different vegetational character classes.

Class	1	2	3	4	5	6	7	8
# of Sites	0	3	15	25	43	11	26	10
Observed frequency	0	2	8	10	21	8	21	4
Expected frequency	-	2	8	14	24	6	15	6

X^2 = 5.4, $p>0.1$ (classes 2 and 3 grouped).

Table 8. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. cyparissiae* at sites with different hydric character.

Class	1	2	3	4	5
# of Sites	2	10	40	35	7
Observed frequency	0	4	26	25	7
Expected frequency	1	7	26	23	5

X^2 = 3.3, $p>0.1$ (classes 1 and 2 grouped).

6.4.1.4 Hydric character of site

Encounter frequencies and rates are shown in Figure 14d, and expected frequencies in Table 8. Mesic to dry sites predominate, but once again the observed frequencies conform to the relative proportion of the different moisture classes in the samples.

6.4.2 *A. flava*

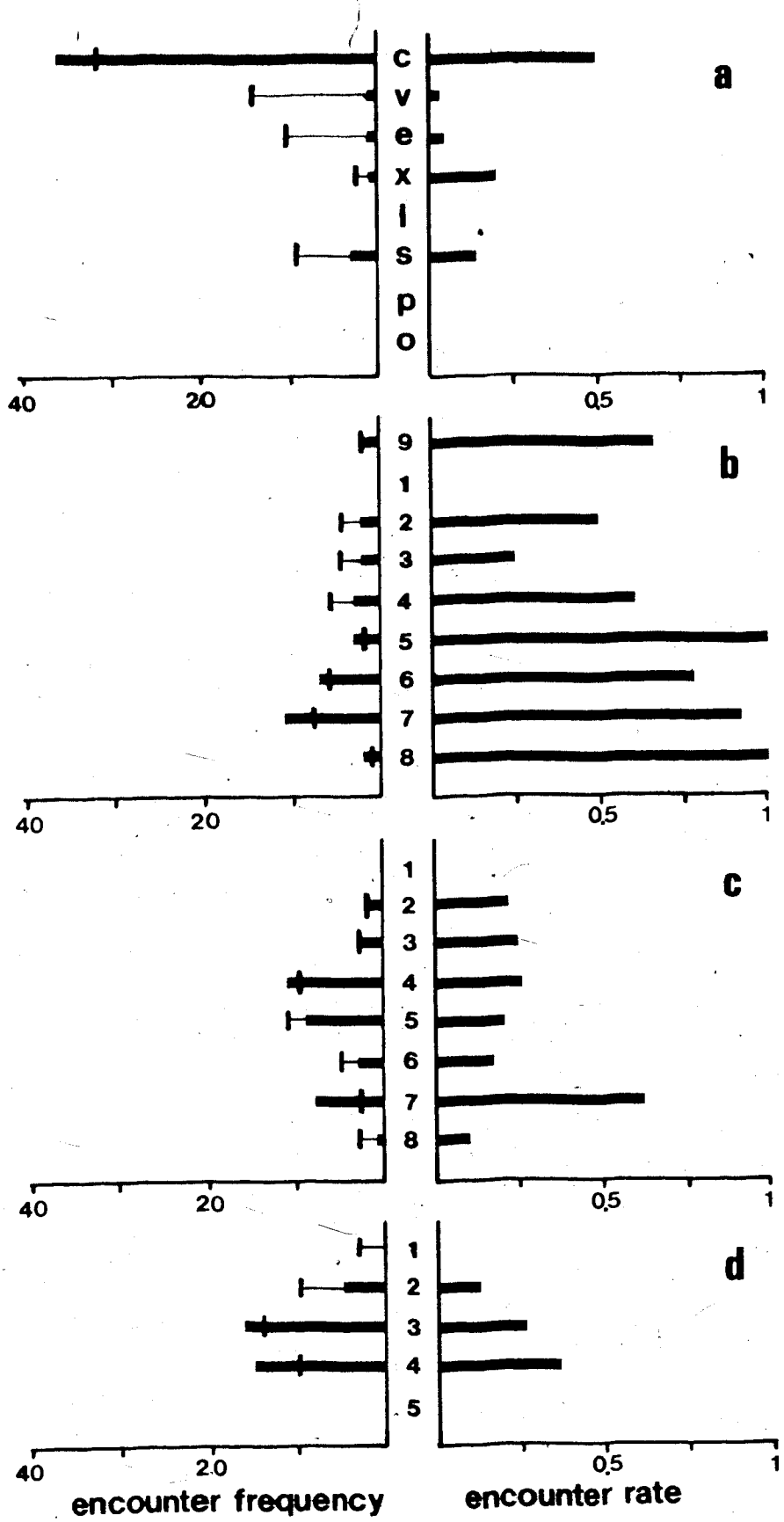
6.4.2.1 Hosts

Like *A. cyparissiae*, *A. flava* shows a marked preference for *E. cyparissias* (Figure 15a, Table 9) and an absence of collections from annuals. In fact, *A. flava* was collected from only three sites where *E. cyparissias* was absent. Beetles were present at 5 sites where *E. cyparissias* occurred with *E. virgata*, 7 with *E. esula*, 18 with *E. seguieriana*, 4 with *E. pannonica*, and 4 with annual spurges. In all cases, except three sites with *E. seguieriana*, *A. flava* was found on *E. cyparissias* only.

6.4.2.2 Soil texture

Because *A. flava* is apparently so strongly tied to *E. cyparissias*, only those sites where this plant was present are taken into consideration. Sites with sandy soils are most prominent in Figure 15b, and lighter soils seem to be over-represented, while heavier soils are under-represented after adjusting for overall soil texture class frequency. Although this deviation is not significant

Figure 15. Encounter frequency and encounter rate for *A. flava* at sites with different a) spurge species, b) soil textures, c) vegetational classes, and d) hydric classes See Table 14 for explanation.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1
2
3
4
5
40
2.0
0.5
1
encounter frequency
encounter rate

Table 9. Comparison of observed and expected encounter frequency (number of samples with beetles present) for *A. flava* on spurge species. Expected values are separately calculated for all spurges sampled, and for those species from which this beetle was actually collected ('Hosts').

Spurge	# of Sites	Encounter Frequency		
		Observed	Expected	
			All spurge	'Hosts'
cyparissias	72	36	15	30
virgata	33	1	8	14
esula	23	1	5	10
virgata × esula	5	1	1	2
seguieriana	22	3	4	9
others	53	0	11	-
X^2			51.7 ***	27.1 ***

*** - $p<0.005$

Table 10. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. flava* at sites with different soil texture classes.

Soil	9	1	2	3	4	5	6	7	8
# of Sites	3	0	4	8	5	3	9	12	3
Observed frequency	2	-	2	2	3	3	7	11	2
Expected frequency	2	-	3	6	4	2	6	8	1

X^2 = 3.5, $p>0.1$ (classes 2+3, 4+5, 7+8+9 grouped)

(Table 10, $p < 0.10$), the regularity of the change in polarity of the deviations suggests that some trend may well be present.

6.4.2.3 Vegetational character of site

Except for areas where associated vegetation is sparse and shorter than the host, *A. flava* was encountered in proportion to the frequency of the various vegetation classes in the samples (Figure 15c). The hypothesis of proportionate representation cannot be rejected despite this apparent excess of collections from class 7 ($p > 0.10$, Table 11).

6.4.2.4 Hydric character of site

Considering all sampled sites within the range of *A. flava*, collections of this beetle are under-represented on wet sites (Figure 15d, Table 12; $p < 0.05$). However, the proportions are about what would be expected ($p > 0.010$) if we control for host encounter rate by taking only *E. cyparissias* sites into consideration.

Table 11. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. flava* at sites with different vegetation character classes.

Class	1	2	3	4	5	6	7	8
# of Sites	0	9	12	43	45	19	13	11
Observed frequency	-	2	3	11	9	3	8	1
Expected frequency	-	2	3	10	11	5	3	3

X^2 = 2.66, $p>0.1$ (classes 2+3 and 7+8 grouped).

Table 12. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. flava* at sites of different hydric character classes. (a) all sites, (b) sites with *E. cyparisslas* only.

Class	1	2	3	4	5
# of Sites (a)	11	43	62	42	0
# of Sites (b)	1	11	32	18	0
Observed frequency	0	5	16	15	?
Expected frequency (a)	3	10	14	10	?
Expected frequency (b)	1	6	19	11	?

X^2 (a) = 7.69, $0.050>p>0.025$ (classes 1+2 grouped)
X^2 (b) = 2.89, $p>0.1$ (classes 1+2 grouped).

6.4.3 *A. nigriscutis*

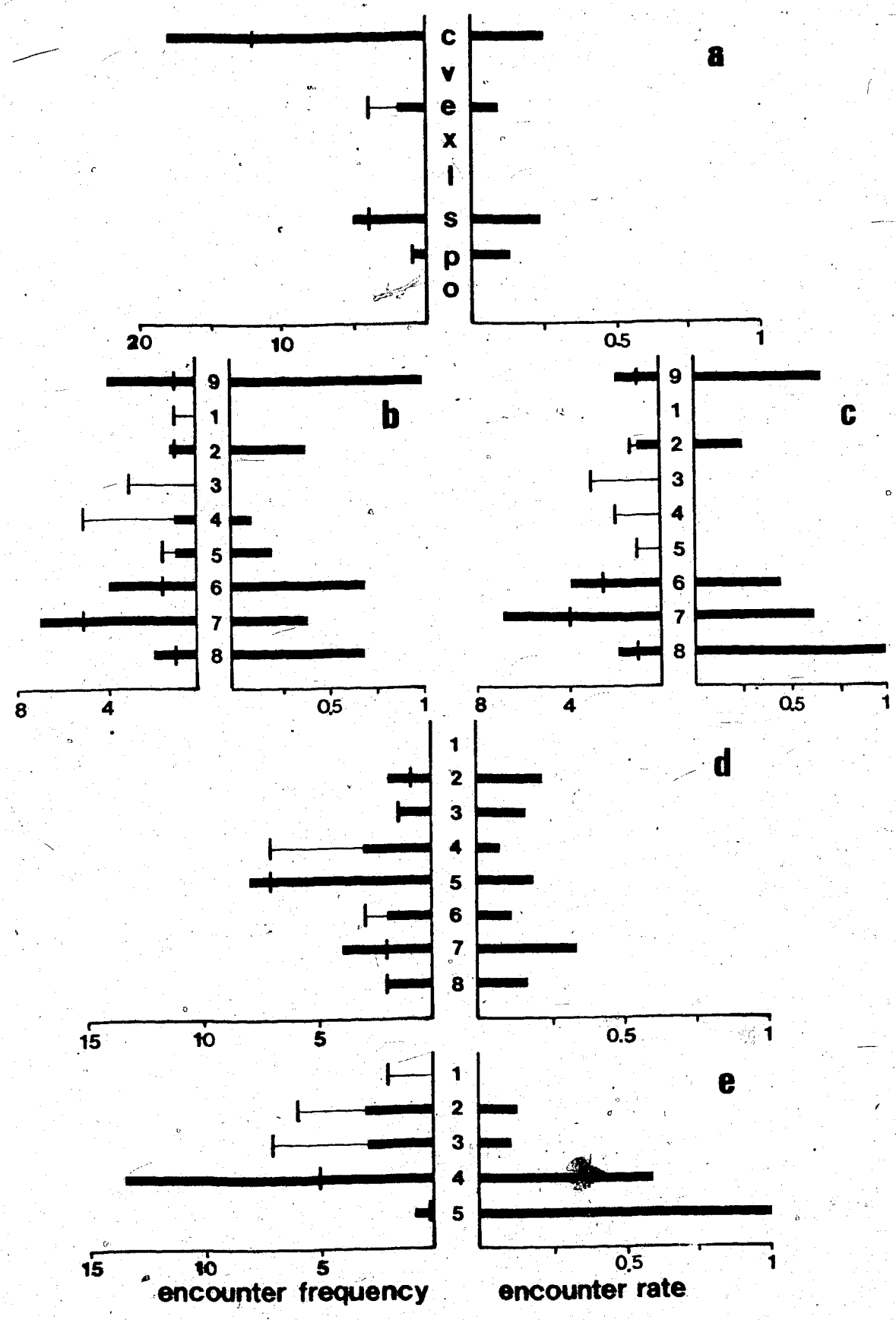
6.4.3.1 Hosts

Like the previous two species, *A. nigriscutis* was collected most frequently from *E. cyparissias* and not at all from annual spurges (Figure 16a, Table 13). It was also absent from *E. virgata*. *E. seguieriana* is well represented in the host spectrum of this species apparently being equally as acceptable as *E. cyparissias*. The evidence from the 14 sites where *E. cyparissias* and *E. seguieriana* occur together confirms that no discrimination is shown between these two plants – in all cases the beetles are distributed in proportion to the abundance of the hosts, or where one greatly outnumbers the other, on the more abundant only.

6.4.3.2 Soil texture

A. nigriscutis collections show a peculiar soil texture spectrum (Figure 16b, Table 14) with a deficiency in loamy soils (classes 3 to 5), while coarse soils, clay and gravelly clay are well represented. A majority (58%) of Hungarian *E. virgata* sites are on loamy soils. Host discrimination is not, however, sufficient to explain the soil texture spectrum since the pattern persists if only a single host (*E. cyparissias*) is considered (Figure 16c), nor do soil 'preferences' explain differential occurrence on host plants if we consider the fact that 42% of Hungarian *E. virgata* sites are on soils well represented in the *A. nigriscutis* collection sites.

Figure 16. Encounter frequency and encounter rate for *A. nigriscutis* at sites with different a) spurge species, b) soil textures, all sites; c) soil texture, *E. cyparissias* sites, d) vegetational classes, and e) hydric classes. See Table 14 for explanation.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encounter frequency
encounter rate

Table 13. Comparison of observed and expected encounter frequency for *A. nigriscutis* on spurge species. See Table 9 for details.

		Encounter Frequency		
			Expected	
Spurge	Sites	Observed	All Spurge	'Hosts'
cyparissias	72	18	9	12
virgata	33	0	4	-
esula	23	2	3	4
virgata × esula	5	0	1	?
seguieriana	22	5	3	4
pannonica	8	1	1	1
others	45	0	6	-
X^2			21.5 ***	4.3 NS

*** - $p<0.005$; NS - not significant ($0.10>p>0.05$)

Table 14. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. nigriscutis* at sites with different soil texture classes.

Soil	9	1	2	3	4	5	6	7	8
# of Sites	4	3	3	12	18	8	6	19	3
Observed Frequency	4	0	1	0	1	1	4	7	2
Expected Frequency	1	1	1	3	5	2	2	5	1

X^2 = 11.91, $p<0.005$ (classes 1+2+3, 5+6, 7+8+9 grouped).

6.4.3.3 Vegetational character of site

No consistent pattern of deviation from expected can be discerned in the distribution of *A. nigriscutis*, in sites of different vegetational character (Figure 16d, Table 15).

6.4.3.4 Hydric character of sites

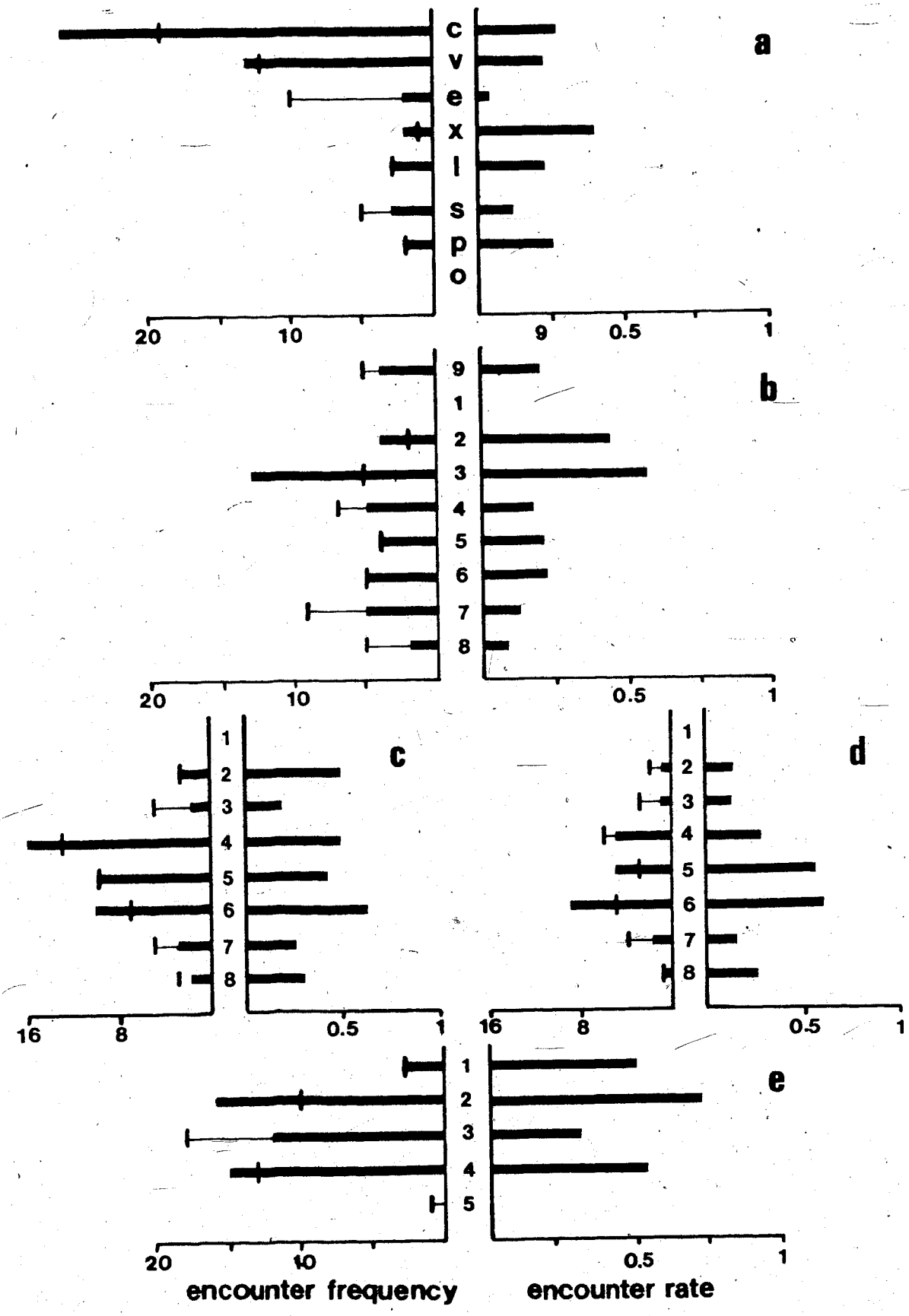
A. nigriscutis shows a very strong association with dry sites (Figure 16e, Table 16). Within Hungary, *E. virgata* was sampled at only one, and *E. esula* at no dry (class 4 or 5) sites (although a number of such sites were sampled in northeast Austria, outside the range of this beetle). This may be postulated as a reason for the deficiency of *A. nigriscutis* collections from these spurges, but the available evidence is not sufficient to distinguish this from a real host discrimination on the part of this beetle.

6.4.4 *A. lacertosa*

6.4.4.1 Hosts

The host relations of *A. lacertosa* are indicated in Figure 17a. Once again, no collections were taken from annual spurges. *E. esula* is markedly under-represented. Comparison of the observed encounter frequencies for all host species with the value expected from the frequency of occurrence of those species shows a significant deviation (Table 17, $p < 0.010$). If the X^2 analysis is partitioned,

Figure 17. Encounter frequency and encounter rate for *A. lacertosa* at sites with different a) spurge species, b) soil textures, c) vegetational classes, all sites, d) vegetational classes, *E. cyparissias* sites, and e) hydric classes.
See Table 14 for explanation.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1
encounter frequency
encounter rate

Table 15. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. nigriscutis* at sites with different vegetational character classes.

Class	1	2	3	4	5	6	7	8
# of Sites	0	9	12	43	45	19	13	11
Observed frequency	0	2	2	3	8	2	4	2
Expected frequency	-	1	2	7	7	3	2	2

X^2 = 2.7, p>0.1 (classes 2+3,6+7+8 grouped).

Table 16. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. nigriscutis* at sites of different hydric character.

Class	1	2	3	4	5
# of Sites	9	26	29	22	1
Observed frequency	0	3	3	13	1
Expected frequency	2	6	7	5	0

X^2 = 14.4 p<0.005 (classes 1+ 2, 4+5, grouped).

Table 17. Comparison of observed and expected encounter frequency for *A. lacertosa* on spurge species. See Table 9 for details.

Spurge	# of Sites	Encounter Frequency		
		Observed	Expected	
			All Spurge	'Hosts'
cyparissias	95	26	16	19
virgata	60	13	10	12
esula	52	2	9	10
virgata × esula	5	2	1	1
lucida	13	3	2	3
seguieriana	25	3	4	5
pannonica	8	2	1	2
others	44	0	7	-
X^2			14.6 **	11.0 *

** - $0.010 > p > 0.005$; * - $0.050 > p > 0.025$
for *E. esula* ommited, $X^2 = 2.19$, $p > 0.10$
for *E. esula* vs. all others, $X^2 = 8.35$, $p < 0.005$

Table 18. Frequency of *A. lacertosa* on co-occurring hosts.cyp = *E. cyparissias*, vir = *E. virgata*, esu = *E. esula*, exv = intermediate forms, seg = *E. seguieriana*, pan = *E. pannonica*, + = beetles present, - = beetles absent.

.	cyp+	vir+	esu+	exv+	luc+	seg+	pan+
cyp-	–	2	1	1	0	1	1
vir-	3	–	1	0	1	0	0
esu-	2	1	–	0	0	0	0
exv-	0	1	0	–	0	0	0
luc-	0	0	0	0	–	0	0
seg-	7	1	0	0	0	–	0
pan-	0	2	0	0	0	0	–
cyp+	–	1	1	0	0	1	2
esu+	–	–	1	1	0	0	0

the other spurges conform well to their expected frequencies ($p > 0.10$), while a test of the frequency of *esula* against the combined frequencies for the other hosts remains highly significant ($p < 0.005$). Interestingly, at both sites where *A. lacertosa* was taken from *E. esula*, the beetle was taken only from this plant, even though *E. cyparissias* was present at one of the sites, and *E. virgata* at the other (Table 18). At three sites the converse applies. At another site, *A. lacertosa* was collected from a patch consisting of plants intermediate between *E. virgata* and *E. esula* in appearance, but not found on *E. virgata* or *E. cyparissias* at the same site. There were too few larger beetle populations (class 3 or more) to analyse, but a relative excess was taken from *E. virgata*. The single large population on *E. lucida* was at a site where *E. virgata* was present, but without beetles of this species. Three of the barren *E. sequieriana* samples were from sites where large numbers of *A. lacertosa* occurred on *E. cyparissias* or *E. virgata*.

6.4.4.2 Soil texture

Soil texture class encounter frequency and rate for sites with host spurges present are shown for *A. lacertosa* in Figure 17b.

The nonconformity with expected is significant (Table 19, $0.025 > p > 0.010$), with the greatest deviation being contributed by class 3. Partitioning the analysis, other frequencies conform to expectation, while comparison of

Table 19. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. lacertosa* on sites with different soil texture classes.

Soil	9	1	2	3	4	5	6	7	8
# of Sites	20	1	9	23	30	19	23	39	24
Observed frequency	4	0	4	13	5	4	5	5	2
Expected frequency	5	0	2	5	7	4	5	9	5

X^2 = 16.33 0.025>p>0.010 (classes 9+1+2 grouped).
X^2 = 4.45, p>0.10 (9+1+1 grouped, class 3 ommitted).
X^2 = 13.55, p<0.005, comparing class 3 to others.

Table 20. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. lacertosa* at sites with different vegetational character classes. a) all sites; b) sites with *E. cyparissias*.

Class	1	2	3	4	5	6	7	8
# of Sites (a)	1	6	11	32	24	16	12	8
# of Sites (b)	1	7	8	18	9	15	13	4
Observed frequency (a)	0	3	2	16	10	10	3	2
Observed frequency (b)	1	7	8	18	9	15	13	4
Expected frequency (a)	0	3	5	13	10	7	5	3
Expected frequency (b)	0	1	1	5	5	9	2	1

X^2(a) = 4.35, p>0.1 (classes 1+2+3, 7+8 grouped).
X^2(b) = 6.88, 0.10>p>0.05 (classes 1+2+3, 4+5, 7+8 grouped).

Table 21. Comparison of observed and expected encounter frequency (number of sites with beetles present) for *A. lacertosa* at sites of different hydric character.

Class	1	2	3	4	5
# of Sites	6	22	39	28	3
Observed frequency	3	16	12	15	0
Expected frequency	3	10	18	13	1

X^2 = 4.80, 0.10>p>.0.05 (classes 1+2, 4+5 grouped).

class 3 with the combined frequencies of the other classes is highly significant ($p < 0.005$). There seems, therefore, to be a distinct association between this species and loamy sites.

6.4.4.3 Vegetational character of sites

If all sites where hosts of *A. lacertosa* are present are considered, no significant departure from expected is detectable (Table 20a, $p>0.10$) although there is an apparent peak in classes 4 to 6 (Figure 17c)

The two most important hosts, *E. cyparissias* and *E. virgata*, have somewhat different habitat spectra. If we consider only those sites with *E. cyparissias*, present the trends mentioned above are even more pronounced, peaking in classes 5 and 6 (Figure 17d) (but still not significant at the 95% level, Table 20b, $0.10>p>0.05$).

6.4.4.4 Hydric character of site

A. lacertosa was not collected from very dry habitats, and mesic sites are under-represented relative to both wet and dry sites (Figure 17e). The departure from expected values is not significant (Table 21, $0.10>p>0.05$).

6.4.5 *A. czwalinae*

6.4.5.1 Hosts

Despite the small number of *A. czwalinae* collections, its 'preference' for *E. esula* is quite evident, occurring on

this plant twice as often as would be expected (Figure 18a). Large numbers (number class 3 and 4, one site each) were taken from *E. esula* only.

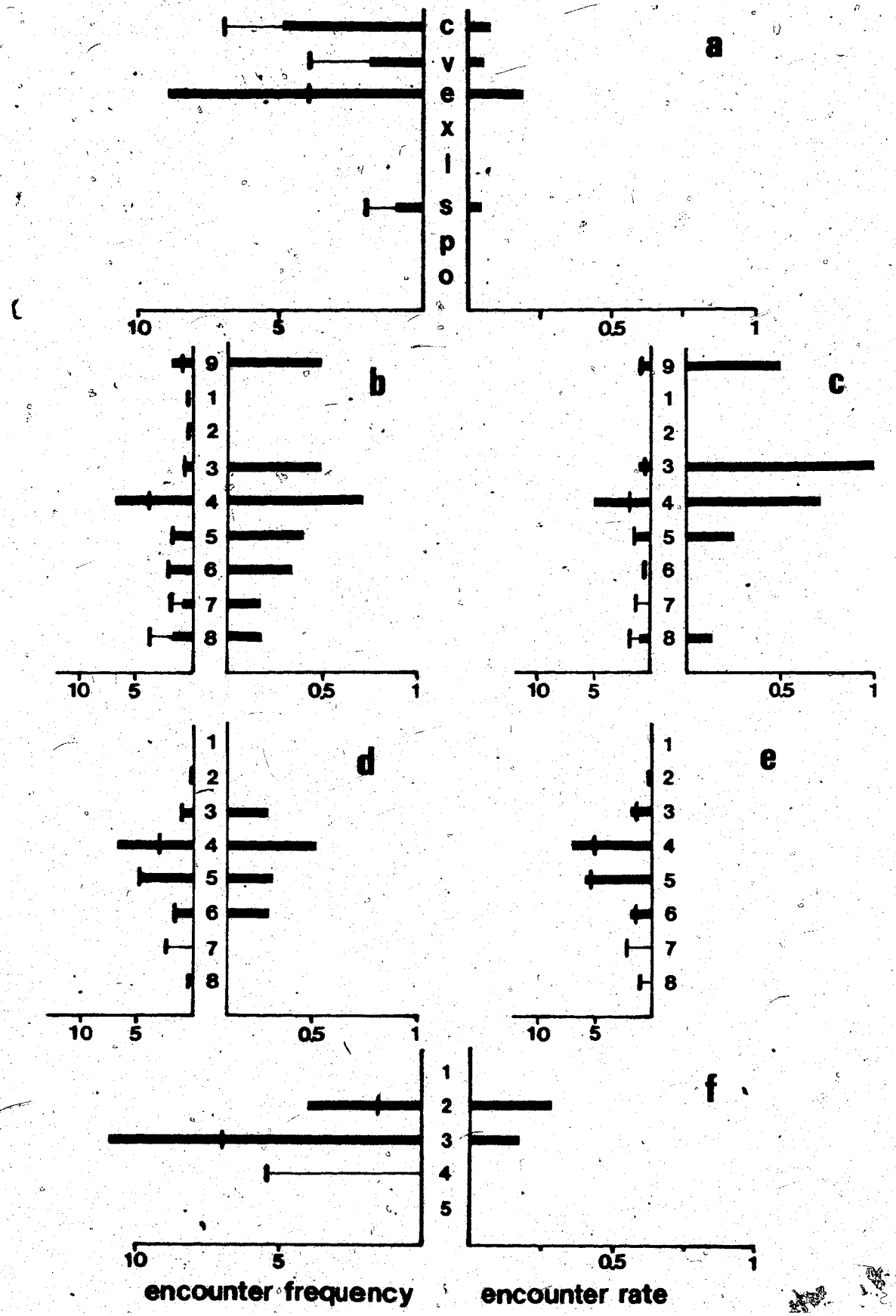
Sites with co-occurring hosts provide ambiguous data. At two localities, *E. cyparissias*, *E. esula* and *E. virgata* were found together, with *A. czwalinae* on the more abundant *E. cyparissias* only. At one site with *E. cyparissias* and *E. esula*, the beetle was collected from both, but at another, from the less abundant *E. esula* only. *E. esula* and *E. virgata* were growing together (without *A. cyparissiae*) at three *A. czwalinae* sites. The beetles were found on both plants at two of these sites, the number of beetles being approximately proportional to the number of shoots of each host. At the third, however, beetles were found only on *E. esula*, although the two were growing intermixed, with *E. virgata* shoots considerably outnumbering those of *E. esula*. There were no collections from annual spurges.

6.4.5.2 Soil texture

Our collections of *A. czwalinae* tended to be found at loamy sites (Figure 18b), peaking in class 4 (loam). *E. esula* also peaks in this soil type (Figure 13). If *E. esula* sites only are considered, the same trend holds (Figure 18c), although the small numbers exaggerate differences in encounter rate values.

Figure 18. Encounter frequency and encounter rate for *A. czwalinae* at sites with different a) spurge species, b) soil textures, all sites, c) soil textures, *E. esula* sites, d) vegetational classes, all sites, e) vegetational classes weighted for host encounter frequency, and f) hydric classes.

See Table 14 for explanation.


a
c
v
e
x
l
s
p
o
10
5
0.5
1
b
9
1
2
3
4
5
6
7
8
c
d
e
f
encounter frequency
encounter rate

6.4.5.3 Vegetational character of site

Frequency and rate of encounter of *A. czwalinae* for different vegetational classes are shown in Figure 18d. Class 4 is over-represented, and no beetles were collected from the most open sites (classes 7 and 8). As would be expected from the similarity of the vegetation class spectra of the host spurges (Figure 2), a similar pattern is apparent, even after weighting for host plant (Figure 18e).

6.4.5.4 Hydric character of site

A. czwalinae was absent from dry sites (Figure 18f). No saturated sites were sampled within the geographic range of this species. All spurges from which this beetle was collected have fairly strong representation on dry (class 4) sites. The observed distribution is thus not likely to be a function of differential occurrence on the various host plants.

6.4.6 *A. venustula*

6.4.6.1 Hosts

With the exception of the greatly over-represented *E. amydaloides*, the spurges from which this beetle species were collected are represented in approximate proportion to their occurrence in the samples (Figure 19a, Table 22). At the three sites where *E. amygdaloides* and *E. cyparissias* were both present, *A. venustula* was found on both in proportion to the abundance of these spurges. Unlike the

Figure 19. Encounter frequency and encounter rate for *A. venustula* at sites with different a) spurge species, b) soil textures, c) vegetational classes, and d) hydric classes.

See Table 14 for explanation.

a – *E. amygdaloides*; other abbreviations as in Table 14.

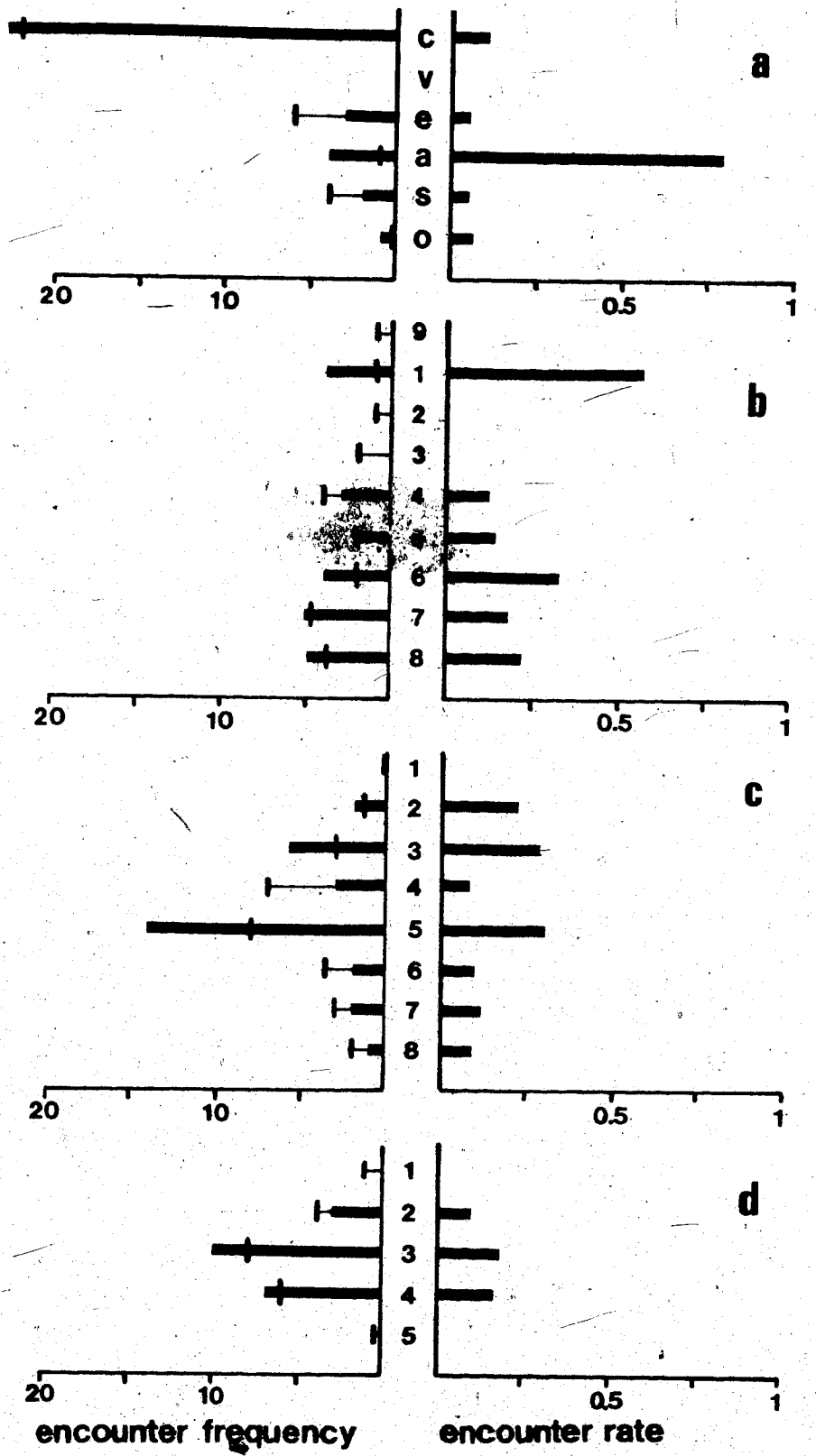

c
v
e
a
s
o
a
20
10
0.5
1
9
1
2
3
4
5
6
7
8
b
20
10
0.5
1
1
2
3
4
5
6
7
8
c
20
10
0.5
1
1
2
3
4
5
d
20
10
0.5
1
encounter frequency
encounter rate

Table 22. Comparison of observed and expected encounter frequency (number of samples with beetles present) for *A. venustula* on spurge species.

Spurge	# of Sites	Encounter Frequency Observed	Expected
cyparissias	236	23	22
esula	63	3	6
amygdaloides	5	4	1
seguieriana	39	2	4
stricta	14	1	1

previous species, *A. venustula* was collected at one site from an annual spurge, *E. stricta*. At this site the beetle was abundant on both *E. amydaloides* and *E. cyparissias*, but only a few specimens were found on the numerous *E. stricta* plants. At other sites no beetles were found on *E. stricta* even when quite numerous on *E. cyparissias*.

6.4.6.2 Soil texture

The principle feature of the soil texture spectrum of *A. venustula* is the high encounter rate on heavy clay soils. Otherwise deviations from expected are minimal (Figure 19b).

6.4.6.3 Vegetational character of site

A. venustula was collected on a large proportion of those sites with taller vegetation than in the more open sites and was the most abundant *Aphthona* species wooded to transitional areas in Western Europe (Figure 19c).

6.4.6.4 Hydric character of site

This species was not collected at very dry or very wet sites. Actual and expected encounter frequencies were quite close (Figure 19d).

6.4.7 Other species

In general, other species were collected at too few sites to exhibit any patterns. However, a few trends are noteworthy. *A. violacea* was found on both annual and perennial species, but at wet sites only. Both *A. ovata* and

abdominalis were collected mainly from *E. cyparissias*, but also occasionally from annual spurges as well as other perennials. *A. ovata*, *pygmaea*, and *deliculata* were collected primarily from mesic sites with vegetational classes 3 or 4 (*i.e.* with fairly closed vegetation). *A. abdominalis*, on average, was collected from drier more open sites than the above species.

Both *A. lutescens* and *herbigrada* were collected from *E. cyparissias*. These species have not been previously recorded from spurges, although well known from *Lythrum* and *Helianthemum* respectively.

6.5 Summary

Certainly no one feature of a site acts in isolation, but the evidence from these species is that certain parameters act a primary cues. It is also apparent that for different *Aphthona* species, quite different aspects of the habitat are the best predictors of presence.

Perhaps two generalizations may be made. First, the large species, *A. cyparissiae*, *flava*, *nigriscutis*, *lacertosa*, and *czwalinae* were not collected from annual spurges, and there is only a single literature record of such an association (*A. cyparissiae* from *E. peplus*, by Heikertinger (1916); also a specimen in the British Museum). The smaller species, on the other hand have been collected from annuals. This is probably a reflection of life history

requirements – the larvae of the larger species feed well into the autumn, after annual spurges have died (see Chapter 7). Second, yellow species (*A. cyparissiae*, *flava*, *nigriscutis*, and *abdominalis*) tend to occur in drier, more open habitats than the black species.

A. cyparissiae is very broad in its occurrence with respect to all habitat parameters. It also accepts a wide range of perennial spurges but tends to be found most often on *E. cyparissias*. It is perhaps significant that this species was rarely found where the host was scattered, no matter what the host. Since the proportion of *E. cyparissias* stands which were large and continuous was greater than that of any other spurge, this may be the source of the observed host 'preference'. The slight trend towards drier, sandier habitats may also be attributed to this phenomenon, since it is under these conditions that continuous spurge stands develop.

A. flava seems to show a real preference for *E. cyparissias*, since it rarely occurs on other species even when they do form continuous stands. Furthermore, populations of this species are larger in patches of *E. cyparissias* than in patches of other spurge species of equal density and size. Among *E. cyparissias* sites, *A. flava*, like *A. cyparissiae*, is more likely to be present if the patch is continuous, and like that species, the trends towards lighter soils and more open conditions probably are a shadow of this fact.

A. nigriscutis , however, shows a distinct association with dry sites and the observed host spectrum is apparently a reflection of this, as is its soil texture spectrum.

The primary determinant for *A. lacertosa* is soil texture. The trends in vegetational association are perhaps a function of this. Host selectivity also seems to be important in this species. It is interesting to note that the two perennial spurges most common on loamy soils, *E. esula* and *E. virgata*, are sharply distinguished, while less common more distantly related species are accepted. There seems also to be in this species a tendency for local populations to form special preferences.

A. czwalinae shows particular associations in all the parameters looked at, although this may be a function of the small number of collections. The most notable features are its strong ties to *E. esula* in contrast to rejection of this species by *A. lacertosa* and its absence in dry habitats. That this species requires somewhat higher humidity is supported by experience with rearing this species in the laboratory – unless the cage was covered in plastic and sprayed with water daily, adult mortality was high.

A. venustula is mainly a creature of shaded and transition areas and other trends are likely reflections of this.

The habitat associations expressed by a population may be a consequence of active searching for suitable sites, or of survival and persistance in such sites. The first

implies relative mobility, the second relative immobility. Certainly both approaches are used by *Aphthona* species. The discrimination of *E. virgata* and *E. esula* at the same site shown by *A. lacertosa*, for example, is undoubtedly a result of behavioural bias. However, the soil preferences shown by this species are more likely a product of differential larval survival under different soil conditions. It is perhaps no coincidence that this, the only species examined which clearly shows a soil preference, is apterous, and therefore rather limited in its dispersal ability.

PART IV

7. Life History Studies

7.1 Introduction

Collections of adults indicate that there are three distinct seasonal patterns among European species of *Aphthona*. Some species, such as *A. euphorbiae* overwinter as adults. Others appear as adults in late summer and fall, overwintering as eggs, or perhaps as early instar larvae. A third group overwinters as pupae or ultimate instar larvae, the adults appearing in spring or early summer. The three species treated here belong to this last group.

No detailed field studies have been done. The following pages describe observations made under laboratory conditions.

7.2 General Methods and Materials

Eggs were collected by confining up to 150 adults to cages (30 cm × 45 cm × 30 cm high or 60 cm × 60 cm × 60 cm) provided with cypress or leafy spurge shoots loosely wrapped at the base in blotting paper or filter paper and inserted into a piece of 10 mm diameter tubing, which was in turn pushed through a hole in the cap of a water filled 5 cm × 10 cm vial. Eggs were laid between the layers of the wet filter paper. These were collected daily, placed in petri dishes with moist filter paper, and reared in darkness (except for a brief daily visual check) at a constant

temperature in an incubation chamber. The temperatures used are indicated in the appropriate context later.

Upon hatching the larvae were transferred to sections of field-collected spurge root in plastic dishes 10 cm in diameter. At first, moist filter paper was placed on the bottom of these dishes to maintain humidity, but it was found that the larvae tended to crawl under the paper and become trapped, resulting in an unacceptably high mortality rate. This problem was later solved by substituting damp fine sand. At approximately weekly intervals, the roots were dissected and the larvae weighed and instar determined by head capsule measurement. For finer resolution, other hatchlings were placed on filamentous roots so that dissection disturbance was not necessary, and checked daily to determine the instar for the first two weeks then transferred to larger roots.

Sources of parental material are as follows:

A. cyparissiae

- Various localities in western Hungary, collected from *E. cyparissias* in early July, 1978.
- Rhine valley, from *E. cyparissias*, 15 August, 1979.
- Swiss Valais, from *E. cyparissias*, 11-12 June 1980.

A. flava

- Various Hungarian localities, from *E. cyparissias*, early July, 1978.
- Various Hungarian localities, from *E. cyparissias*, early July, 1979.

A. czwalinae

- Atzenbrugg, Austria, from *E. esula*, 14 July, 1978.
- Various Hungarian localities, from *E. esula*, early July, 1979.
- Atzenbrugg, Austria, from *E. esula*, 25 June, 1980.

Adults and larvae were reared in 1978 on *E. cyparissias* at Delémont, Switzerland, and in 1979 and 1980 on North American leafy spurge from Township 17 Range 17 West of the Second Meridian, east of Regina, Saskatchewan.

Special methods for specific experiments are provided in the following sections where appropriate.

7.3 Oviposition and Egg Development

7.3.1 Adult longevity and Egg Production

In the Rhine Valley, adults of *A. cyparissiae* were found from the end of May until mid-September (see Appendix 2). Teneral adults were collected in Hungary as late as July 8. Sommer (1979) reports that specimens of this species collected in mid-August, 1979, survived in the laboratory until November and oviposition continued until the beginning of October. Beetles she sent me from the same collection survived until the end of September with eggs being laid until this time. The last individuals of a June 12 collection sent to me did not die until October 10, producing eggs up to this time. Some of these beetles therefore lived at least of 4 months as imagines. The

period of major mortality, however, was mid-September (see Figure 20a) or about 3 months after collection. Oviposition in the few laboratory-produced adults began 6 days after emergence. *A. flava* collected in the first 2 weeks of July 1979 survived until October 5 (see Figure 20b). Their laboratory reared progeny lived as adults for 3 to 4 months (Figure 20c) producing eggs for up to 3.5 months. Oviposition in this species also began 6 days after emergence. The oviposition period is thus very extended. However, as shown in Figure 21 the proportion of viable eggs produced after about 2 months decreases and is more variable, lower.

Each female has 16 ovarioles (although only 15 were active in almost all females dissected), maturing a batch of eggs every 3 to 5 days during the first 2.5 months, and less complete batches at less frequent intervals in later life. In order to determine total egg production per female, 20 male-female pairs of each of *A. cyparissiae* and *A. flava* were separately caged in 10 mm × 15 mm vials with the bottom replaced by 1 mm screening. Over a three month period, the 15 *A. cyparissiae* pairs which survived that long produced an average of 285 eggs (with a range of 256 to 308 (s.d.=22)). Two females caged without males produced 305 and 296 eggs (none viable). *A. flava* pairs produced 120 to 330 eggs with a mean of 224 (s.d.=36, n=16). Sommer (1980) reports a mean of 100 with a maximum of 216 for 12 *A. cyparissiae* pairs.

Figure 20. Survivorship of adult *Aphthona* in the laboratory. a) *A. cyparissiae*, collected June 12, age structure unknown; b) *A. flava*, collected early July, age structure unknown; c) *A. flava*, laboratory reared, reconstructed single-age cohort.

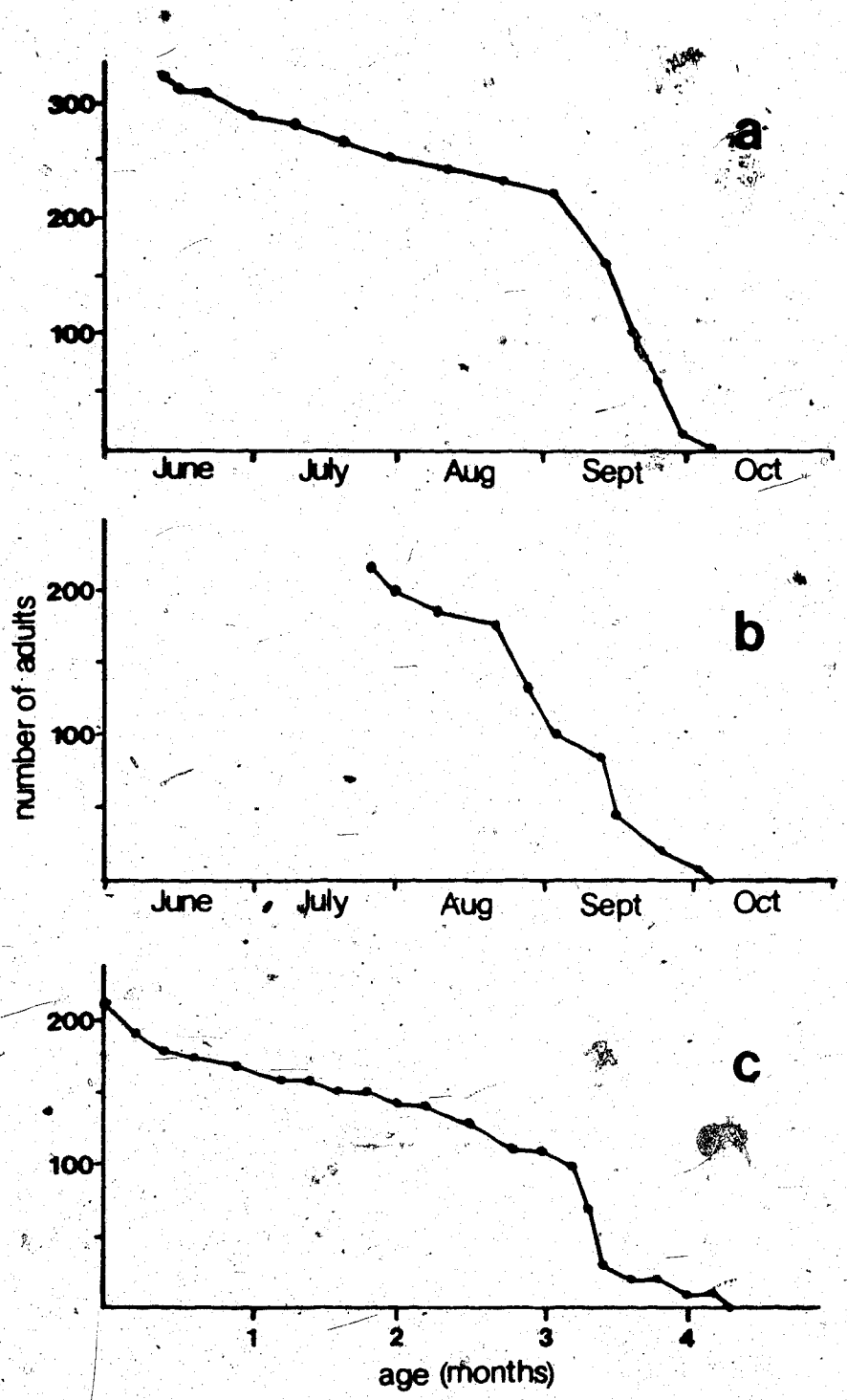
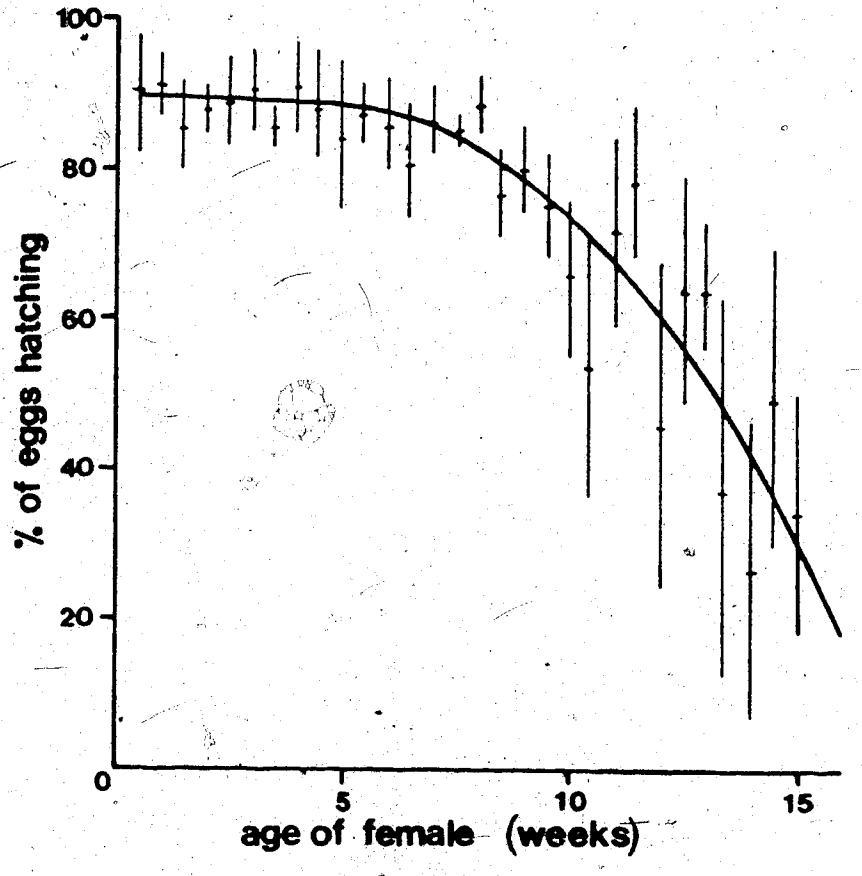

300
200
100
a
June
July
Aug
Sept
Oct
number of adults
200
100
b
June
July
Aug
Sept
Oct
200
100
c
1
2
3
4
age (months)

Figure 21. Effect of female immaginal age on egg hatch in *A. cyparissiae*. Bars represent one standard deviation based on arcsine-transformed data. Each sample point is0 derived from 60 groups of 10 to 15 eggs. Curve hand-fitted.


100
80
60
40
20
0
% of eggs hatching
5
10
15
age of female (weeks)

7.3.2 Oviposition Sites

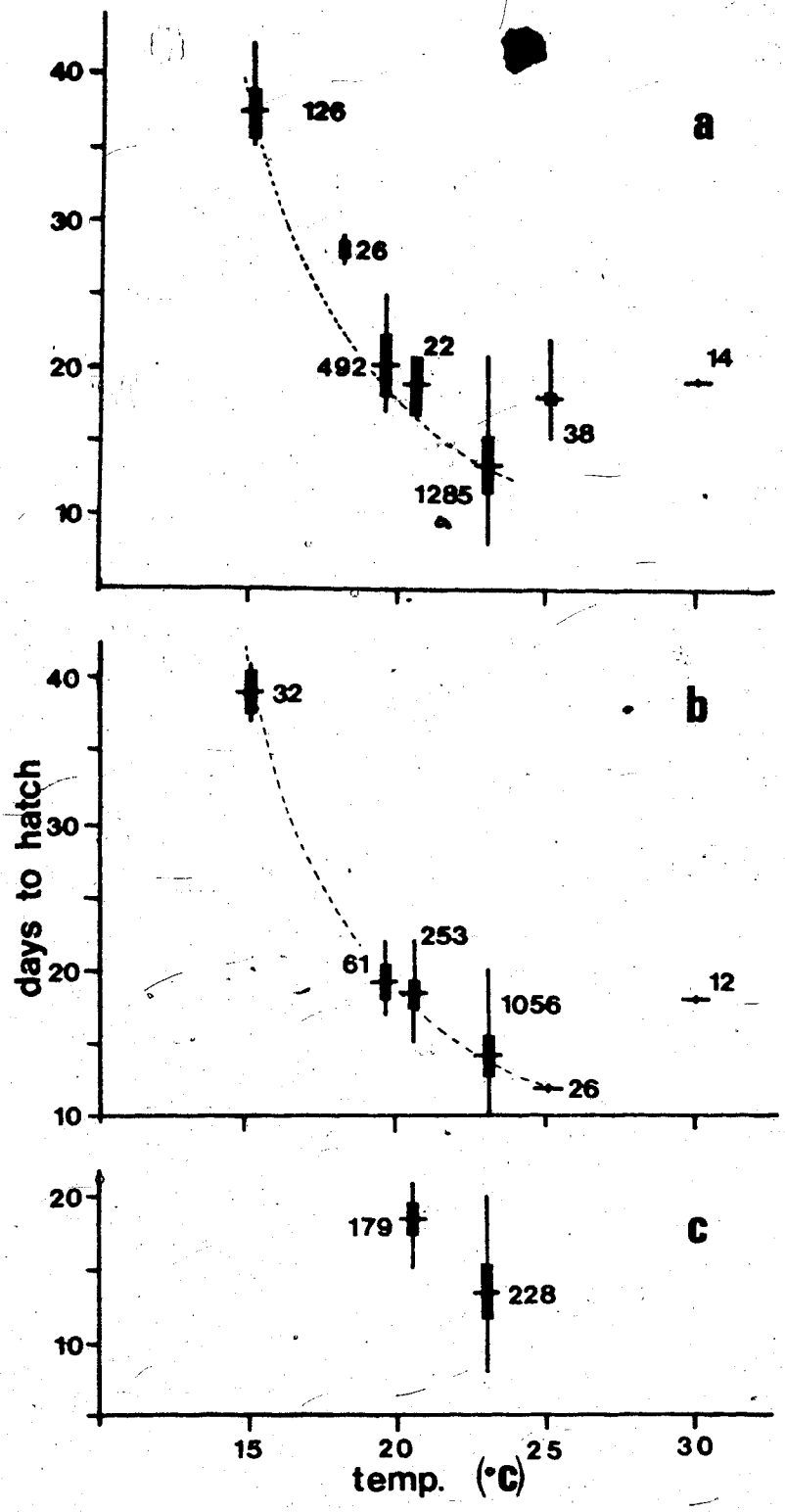
When caged with potted plants females crawl down the shoot into the soil (if possible), then turn around and probe with the ovipositor for crevices in which to deposit the eggs.

High humidity seems to be preferred but not essential. If shoots wrapped with both dry and wet filter paper are provided, the wet is used in preference to the dry by a ratio of about 3:1. Also, high humidity condition seem to relax the requirement for crevices in which to place the eggs. Females confined to unventilated vials with a spurge shoot preferentially lay into the paper at the shoot base, but also leave one in five eggs on flat surfaces.

7.3.3 Egg Development and Temperature

The effect of temperature on the incubation period of each of the species are shown in Figure 22. The optimum temperature for *A. cyparissiae* appears to be about 23°C, with a developmental period of 13 days, the period increasing on either side of this temperature. For the most part, the distribution of values about the mean is quite tight, but a few individuals show rather remarkable deviations, requiring as little as 5 days less than the mean and as much as 7 days more. Development period for *A. flava* shows a similar pattern, and at most temperatures it was within a day of *A. cyparissiae*, but it continues to decrease to a higher temperature (25°). The development rate for *A. czwalinae* is

Figure 22. Egg development time at different temperatures. Means, standard deviations and ranges are shown. Curves are regression curves based on a degree day accumulation model. Numbers give number of eggs in sample.
a) *A. cyparissiae*, b) *A. flava*, c) *A. czwalinae*.


a
126
126
492
22
14
38
1285
b
32
253
61
12
1056
26
c
179
228
40
30
20
10
days to hatch
15
20
25
30
temp. (°C)

essentially identical to that for *A. cyparissiae* at 20.5° and 23°. This species was not tested at temperatures between 15 and 20° or at 30°.

At 25° eggs of this species failed to hatch – a change in colour indicated that they died between 5 and 8 days after being laid. The other two species experienced increased egg mortality at higher temperatures. Figure 23 shows the relationship between temperature and per cent hatch for *A. cyparissiae* and *A. flava*.

A model predicting incubation period as a function of simple degree day accumultion takes the form

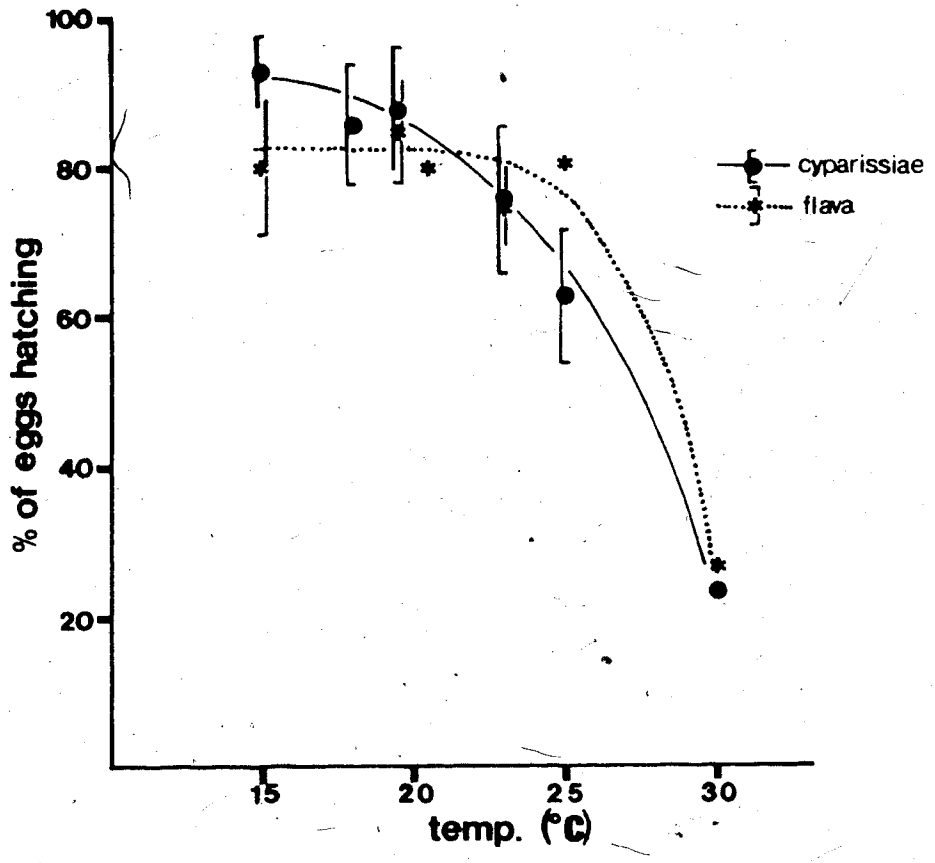
$$t=D(T-T_0)^{-1}$$

where t is incubation period, T the temperature, T_0 the minimum threshod temperature at which development takes place, and D the total required accumlated degree days above T_0. The reciprocal of t is a simple linear function of T of the form

$$t^{-1}=D^{-1}T-T_0D^{-1}.$$

A least squares regression of reciprocal hatch time on temperature (ommitting values above the optimum) for *A. cyparissiae* and *A. flava* indicates that the simple model provides a fairly good fit to the observed data ($r^2=0.869$ for *A. cyparissiae* and 0.898 for *A. flava*). The estimated required degree days accumulation for *A. cyparissiae* is 165 with a threshold of 10.6°. For *A. flava*, the value is 168 days, with a threshold of 11.0°. The prediction lines based on these values are indicated on Figure 22. The two points for *A. czwalinae* predict a base

Figure 23. Effect of incubation temperature on egg viability. Bars represent one standard deviation based on arcsine-transformed hatch rate of daily egg collections.


100
80
60
40
20
% of eggs hatching
15
20
25
30
temp. (°C)
cyparissiae
flava

temperature of 13.7° and 127 degree days.

A base temperature between 10 and 15° agrees with the observation that, when kept at 10°, no eggs of any species had hatched after 4 months. *A. cyparissiae* eggs kept at 10° for 32 to 35 days, then transferred to 20.5°, hatched after an average of a further 17.6 days (s.d.=3.7, range 10 to 21, n=27), a period not significantly less than appropriate for eggs kept at 20.5° from the time of oviposition ($p>0.05$, Student's t-test for equal means), but the representation of shorter periods was relatively much greater. Eggs kept at 10° for 2 months, 4° for 4 months, a second period of 10° for 5 days, then to 20.5°, hatched 20.2 days after return to 20.5°, a period slightly but not significantly greater than that for those reared at a constant 20.5° ($p>0.05$).

A. czwalinae eggs held at 10° for 31 to 35 days, then transferred to 20.5° hatched 20.9 days after the transfer, a period significantly longer (by about 2 days; n=25, $p<0.005$) than the values for constant 20.5° conditions.

The same experiment, using *A. flava*, gave quite suprising results. The eggs did not hatch until 27 to 39 days (mean 32.8, s.d. 4.6, n=22) after the transfer to the higher temperature, compared to the 18.4 days needed at a constant 20.5°. An even longer delay was obtained for this species under the 10°:2 month / 4°:4 month / 10°:5 day / 20.5° regime (29 to 40 days, mean=38.2, s.d.=4.1, n=44). These results suggest that in this species, and possibly also in *A. czwalinae*, there is not merely a slow down in development

at 10°, but a major physiological shift – in other words a facultative diapause – and requires a readjustment period after return to higher temperatures before normal development can proceed. A facultative diapause mechanism of this type, operating with this relatively high threshold, temperature can be envisioned to have two possible functions – to delay the hatch of eggs laid early in the season by prematurely emerging adults, or to prevent the hatch of eggs laid late in the fall until the following year.

Oviposition sites are close to the surface and, given their geographic range, both *A. cyparissiae* and *A. flava* would be expected to encounter freezing temperatures if the eggs were to overwinter, as suggested by the latter alternative. However, eggs of both species treated with 2 months at 10°, 2 months at 4°, 3 days at -1°, 2 months at 4°, and 5 days at 10°, showed the colour changes associated with egg death after subsequent exposure to 20.5°. Even a short period of light freezing was not tolerated under laboratory conditions.

It would be instructive to determine whether diel alternation of temperatures above and below the threshold, are effective in inducing this delay. Unfortunately, this experiment was attempted with late season eggs and none hatched.

There is at least one further complication. The effects of 10° temperatures on egg development are not equally felt at all stages in this development. *A. flava*

incubated at 20.5° for 12 days, then transferred to 10° hatched after an additional 24.4 days (s.d.=1.6, range 21 to 27, n=35). Had the eggs been kept at 20.5°, only 6.4 additional days would have been expected. We can then calculate that about 70 days would have been required at 10° for hatch if development had progressed at this rate throughout. This has serious implications for prediction of hatch times based on degree day data. An extensive series of experiments investigating the interaction of temperature, especially at the lower end, and stage of development, is needed to sort out this problem.

7.3.4 Humidity and Egg Mortality

The relatively dry habitats frequented by *A. cyparissiae* and *A. flava*, and the proximity of the eggs to the soil surface suggest that the eggs may be exposed to desiccation, and some drying tolerance would therefore be expected. It would not be suprising if eggs of *A. czwalinae*, usually found in more moist areas, were less tolerant to drying. In order to test this, eight groups of 10 eggs each, of *A. cyparissiae* and *A. czwalinae* were reared at 19.5° in desiccators at saturation deficits of 0, 0.12, 0.24, 0.35, 0.45, 0.70, and 1.12 kPa (equivalent to 100, 95, 90, 85, 80, 70, and 50% relative humidity respectively at the temperature used), maintained by appropriate concentrations of H_2SO_4. The results are indicated in Figure 24. Both species failed to hatch after 1 month at a deficit of 0.45 kPa

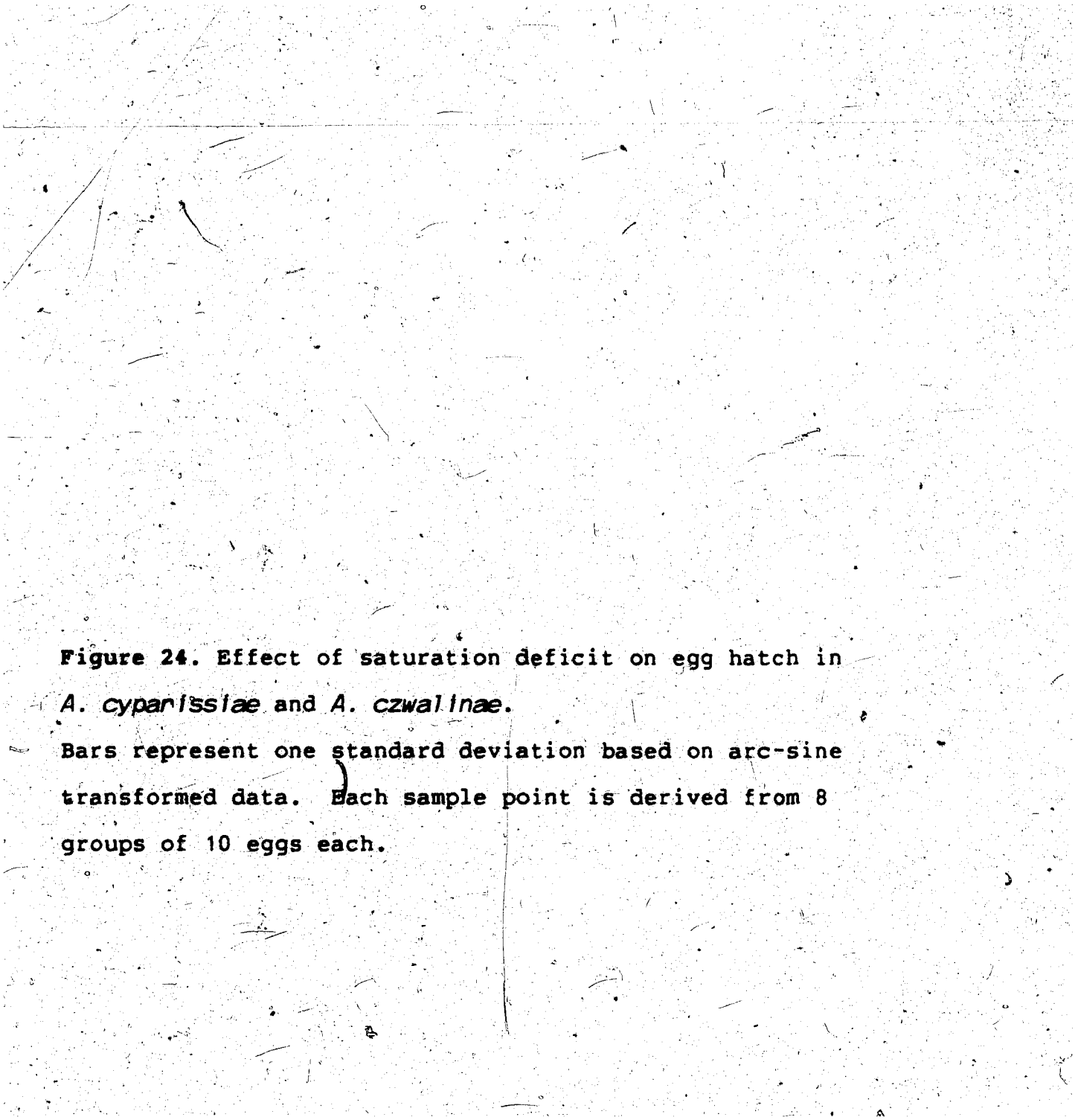
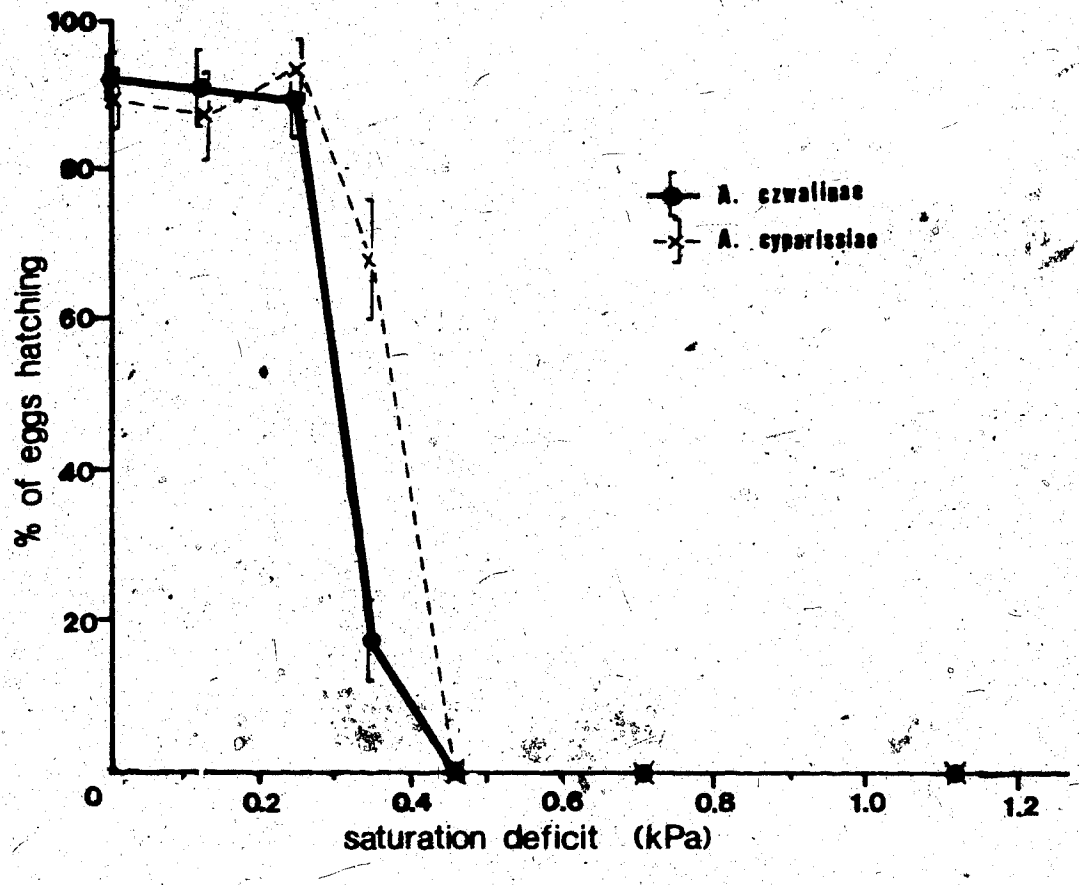


Figure 24. Effect of saturation deficit on egg hatch in *A. cyparissiae* and *A. czwalinae*.
Bars represent one standard deviation based on arc-sine transformed data. Each sample point is derived from 8 groups of 10 eggs each.


100
80
60
40
20
0
% of eggs hatching
0.2
0.4
0.6
0.8
1.0
1.2
saturation deficit (kPa)
A. czwalinae
A. cyperissiae

or greater while hatch at all levels over 0.24 kPa was normal. *A. cyparissiae* had greater hatch success at 0.37 kPa than *A. czwalinae* ($p<0.05$), although I am not convinced that this is a real difference. Those *A.cyparissiae* eggs at the lower humidity levels which did not collapsed were transferred to saturated air after 1 month. None hatched. Eggs of both species, then, cannot withstand conditions which may be expected in very dry soil.

7.4 Larval Growth

7.4.1 Instar Duration

There are three larval instars. The duration of each varies considerably within a species but is very similar between species. Figure 25 illustrates the proportion of the larvae of each instar at a given age (reared at 20.5°). The minimum duration of the first instar for all species is about 8 days at this temperature. The minimum observed second instar duration was 24 days for *A. flava*, 19 days for *A. cyparissiae*, and 35 days for *A. czwalinae*. The active feeding period of the third instar lasts a minimum of 45 days. The total active feeding period therefore lasts at least 75 days. However, as can be seen if Figure 25, some larvae are still in the second instar at this time. Many were still actively feeding at 4 months of age.

At the end of the feeding period the larva enters the soil and forms a cell in which it will eventually pupate. In forming this cell the larva arches its body to compact the soil particles and applies a

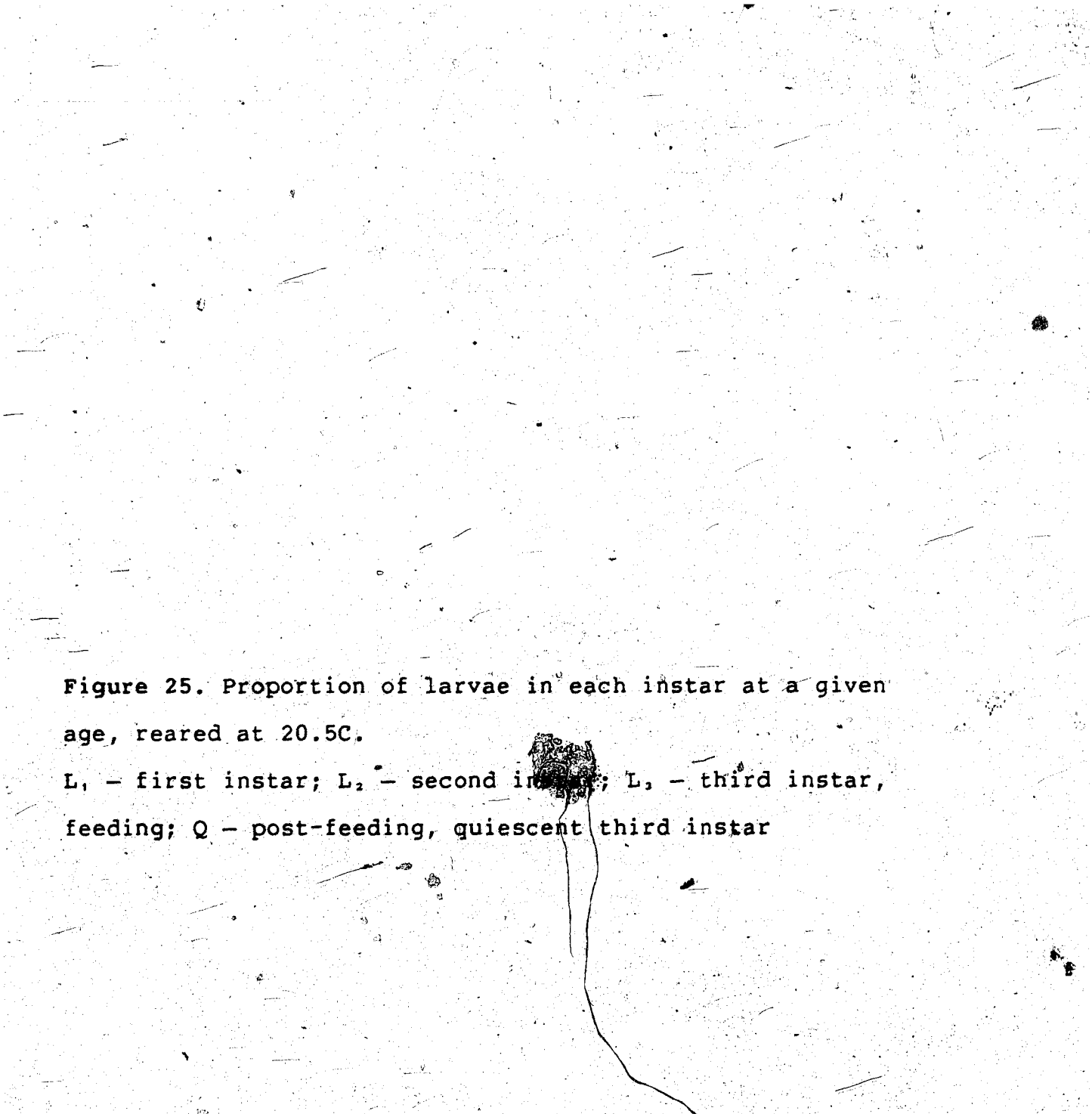
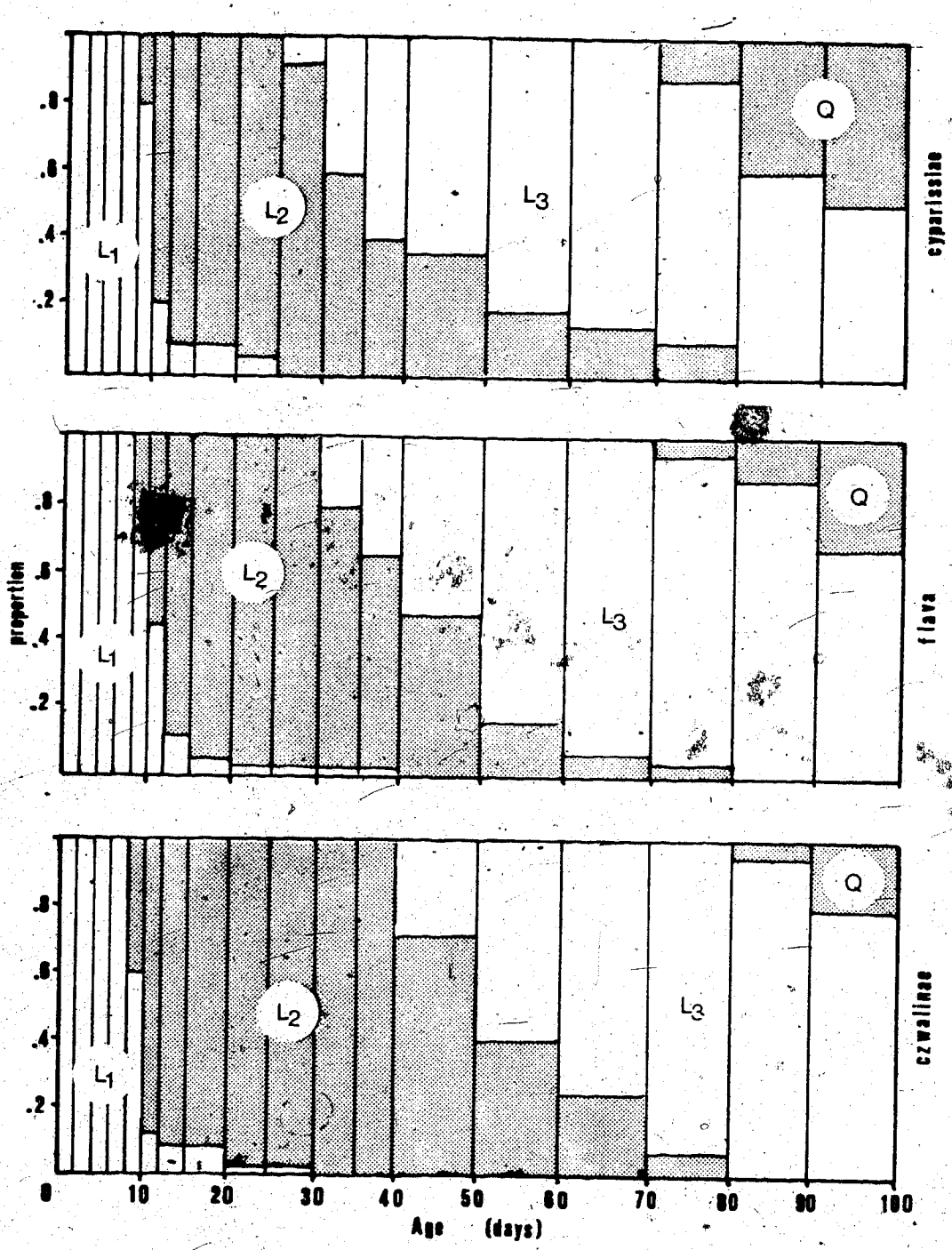


Figure 25. Proportion of larvae in each instar at a given age, reared at 20.5C.
L_1 – first instar; L_2 – second instar; L_3 – third instar, feeding; Q – post-feeding, quiescent third instar


.8
.6
.4
.2
L1
L2
L3
Q
cyparissias
proportion
flava
czwalinae
0
10
20
30
40
50
60
70
80
90
100
Age (days)

cementing fluid which penetrates to a depth of about 1 mm in the fine sandy soil used. The origin of this secretion is not known. Larvae moving across a smooth surface may be seen to secrete a small amount of fluid from the anus as an adhesive aid for the anal proleg, and this may be the same fluid used in forming the pupal cell.

Similar cells are formed by some second instar larvae for the change to third instar. Many larvae, however, excavate a chamber within the root in which they were feeding if it is sufficiently large. Anywhere from 2 to 7 days are spent in this cell.

The extreme heterogeneity of development rate at a given temperature, apparently due to differences in the quality of individual roots from which as food souces, confounded the effects of temperature on growth rate. Minimum first instar duration was 6 to 7 days at 25° and 9 to 10 days at 15° for *A. cyparissiae*, and the first appearance of post-feeding third instar larvae was at 95 days at 15°.

7.4.2 Larval Weights

Table 23 gives the live weight of larvae at identifiable points in their development — *i.e.* at eclosion, ecdyses, and feeding cessation. *A. flava* is, in general, heaviest, and *A. czwalinae* lightest, at any given stage (in accord with relative adult sizes). In all species, the total weight gain in the last instar is 4 or 5 times that of the previous two instars combined.

Table 23. Live weights of larvae at specific points in development. L_1/L_2 - first to second instar ecdysis; L_2/L_3 - second to third instar ecdysis.

Larval stage	Mean Weight ± s.d. (mg) (range)		
	cyparissiae	*flava*	*czwalinae*
Hatchling*	0.05 (n=150)	0.05 (n=130)	0.05 (n=50)
L_1/L_2	0.16±0.01 (0.14–0.18) (n=18)	0.22±0.03 (0.18–0.38) (n=14)	0.12±0.00 (0.11–0.14) (n=12)
L_2/L_3	0.91±0.09 (0.66–1.46) (n=34)	1.23±0.22 (0.83–2.37) (n=36)	0.74±0.04 (0.70–0.80) (n=4)
Cessation of feeding	5.82±0.98 (3.45+7.10) (n=150)	6.27±1.03 (3.83+9.05) (n=185)	—

* Hatchlings were weighed in bulk rather than individually. The total number of larvae indicated represent 6 batches of each species.

7.5 Overwintering

7.5.1 Temperature Requirements

7.5.1.1 Introduction

Many insects have obligatory diapause periods, which must be broken bt specific stimuli. Among these stimuli are freezing or near-freezing temperatures. The three *Aphthona* species being considered spontaneously enter a quiescent period at the end of the third instar, suggesting the possibility of diapause in this group. The following experiment was performed to determine whether the quiescent period would cease spontaneously, and, if this is not true, to determine whether a period of low temperature is necessary and sufficient to break diapause.

7.5.1.2 Methods

Because 10° seems to be a critical temperature in egg development, I felt that this was a suitable intermediate temperature. 4° conditions were readily available as a representative 'cold' temperature, and has been shown to be sufficient to break diapause in other insects.

Three to four and a half month old larvae, reared at 20.5° were subjected to five different temperature regimes, over a 12 week period. Both feeding and post-feeding larvae of all three species were used. All larvae were provided with food. The number of larvae used depended on the number available when the treatment was begun.

In initial trials, it was found that a direct drop from 20.5° to 4° resulted in increased mortality. A three week acclimation period at 10° was therefore included in all 4° treatments.

The treatments were:

1. Continuation of 20.5° conditions (*A. cyparissiae*: 40 feeding larvae, 148 post-feeding; *A. flava*: 20 feeding, 30 post-feeding; *A. czwalinae*: 9 feeding, 12 post-feeding).
2. 12 weeks at 10°, followed by return to 20.5° (*A. cyparissiae*: 40 feeding, 100 post-feeding; *A. flava*: 20 feeding, 30 post-feeding; *A. czwalinae*: none).
3. 3 weeks at 10°, 8 weeks at 4°, 5 days at 10°, return to 20.5° (*A. cyparissiae*: 46 feeding, 154 post-feeding; *A. flava*: 26 feeding, 94 post-feeding; *A. czwalinae*: 9 feeding, 18 post-feeding).
4. As in Treatment 3, but with only 3 weeks at 4° (*A. cyparissiae*: 40 post-feeding).
5. 3 weeks at 10°, 8 weeks at 4°, then to 10° (*A. cyparissiae*: 125 post-feeding).

7.5.1.3 Results

Under Treatment 1, two *A. cyparissiae* adults appeared. All other larvae of all species gradually lost weight. All but a single *A. cyparissiae* larva were dead three months later.

Under Treatment 2, feeding larvae continued to feed and eventually reached the post-feeding stage. However, all were dead within 1.5 months of return to 20.5°. All original post-feeding larva lost weight and died within one month of return to 20.5°.

Under Treatment 3, those larvae which had ceased feeding before the low temperature treatment fared much better – 69% of the *A. cyparissiae*, 60% of the *A. flava*, and 5 of the 18 *A. czwalinae* had become at least pharate pupae by 1.5 months after the return to 20.5°. The remainder had died or become severely underweight. Feeding larvae continued to feed at 4° (albeit very slowly). Some reached the post-feeding stage during this period and formed pupal cells, and, after being returned to high temperatures, developed in a manne identical to that of those larvae which had reached the post-feeding stage before the cold treatment. The remaining feeders eventually reached the post-feeding stage after return to 20.5°, but then lost weight. All were dead after 3 months.

Under Treatment 4, only 20% of the larvae became pharate pupae.

Under Treatment 5, 64% became obvious pharate pupae after return to 10°, comparable to the results for Treatment 3.

It is evident from the above that a period of cold temperature after the larvae have ceased feeding and entered the soil to form a pupal cell is required to initiate

pupation (with the exception of 2 individuals). Cold treatment before this time has no effect. Individuals derived from late hatching eggs are likely to survive the winter, but they will not contribute to the following generation if they do not complete feeding before the cold period is over.

Three weeks of treatment is not a sufficient period for most individuals (compare Treatments 3 and 4). The upper limit for the temperature required to break diapause (between 4° and 10°) remains undetermined.

7.5.2 Low Temperature Tolerance

7.5.2.1 Introduction

Although well protected from temperature extremes by their edaphobitic habits, overwintering larvae are c[redacted] enough to the surface that they are likely to experience freezing temperatures. An organism may survive such temperatures either by having the ability to withstand freezing of its tissues, or by avoiding freezing of its tissues. This freezing-point depression may be brought about by 1) a high solute concentration in the body fluids, 2) increased concentrations of compounds, such as glycerol, which have anti-freeze capabilities beyond simple solute depression, or, 3) cooling below the normal freezing point without freezing by avoiding formation of freezing nuclei (supercooling). The following experiment was

designed to determine the freezing point of post-feeding third instar larvae of *A. cyparissiae* and *A. flava*.

7.5.2.2 Methods

The larvae used had experienced 2 weeks of 10° and to 6 weeks at 4° before being used in this experiment. A total of 5 individuals of *A. flava* and 6 of *A. cyparissiae* were tested.

A light coating of silicon grease was used to fasten each larva to a small (3 mm diameter) thermistor probe. The probe was attached via a telethermometer to a chart recorder, and inserted into a small controlled-temperature chamber. The temperature was lowered from +4° at a rate of 1° per hour in approximately 0.1° decrements. At the point of freezing the heat of crystallization results in a momentary rise in temperature. The temperature was then increased to 4° (also at 1°/h), held at this temperature for a day, then taken up to 10° to determine if the larva was still alive (dead larvae exhibit a loss of turgor).

Once a freezing point was determined, the procedure was repeated using 5 additional larvae, but with the minimum temperature just above the maximum observed freezing point, as a control treatment. The minimum temperature that can be achieved with the apparatus used is -13°, operating at room temperature.

7.5.2.3 Results

A representative tracing of temperature versus time is shown in Figure 26.

All *A. flava* specimens froze. The individual freezing points were -6.2°, -6.5°, -6.8°, and -7.0°, for a mean of -6.6°. All were killed by the treatment, while the control group taken down to -5.5° survived with no apparent ill effects.

Two of the six *A. cyparissiae* larvae had not frozen after an hour at the minimum attainable temperature of -13°, and were still alive after the experiment. The others froze at -8.0°, -9.0°, -9.0°, and -9.7° (mean 8.9°). The treatment was fatal. The five controls taken down to -7.2° showed no ill effects.

The ion concentrations to be found in any organism will depress the freezing point below that of water. The freezing points obtained are somewhat lower than would be expected from this cause alone, suggesting that these species possess a specialized mechanism for freezing resistance. The fact that two *A. cyparissiae* individuals were cooled to well below what was otherwise a fairly well defined freezing point, indicates that supercooling is possible.

The importance of supercooling as a freezing avoidance mechanism in these animals remains unknown. These larvae are well hydrated in their quiescent stage, a condition which increases the probability of internal formation of

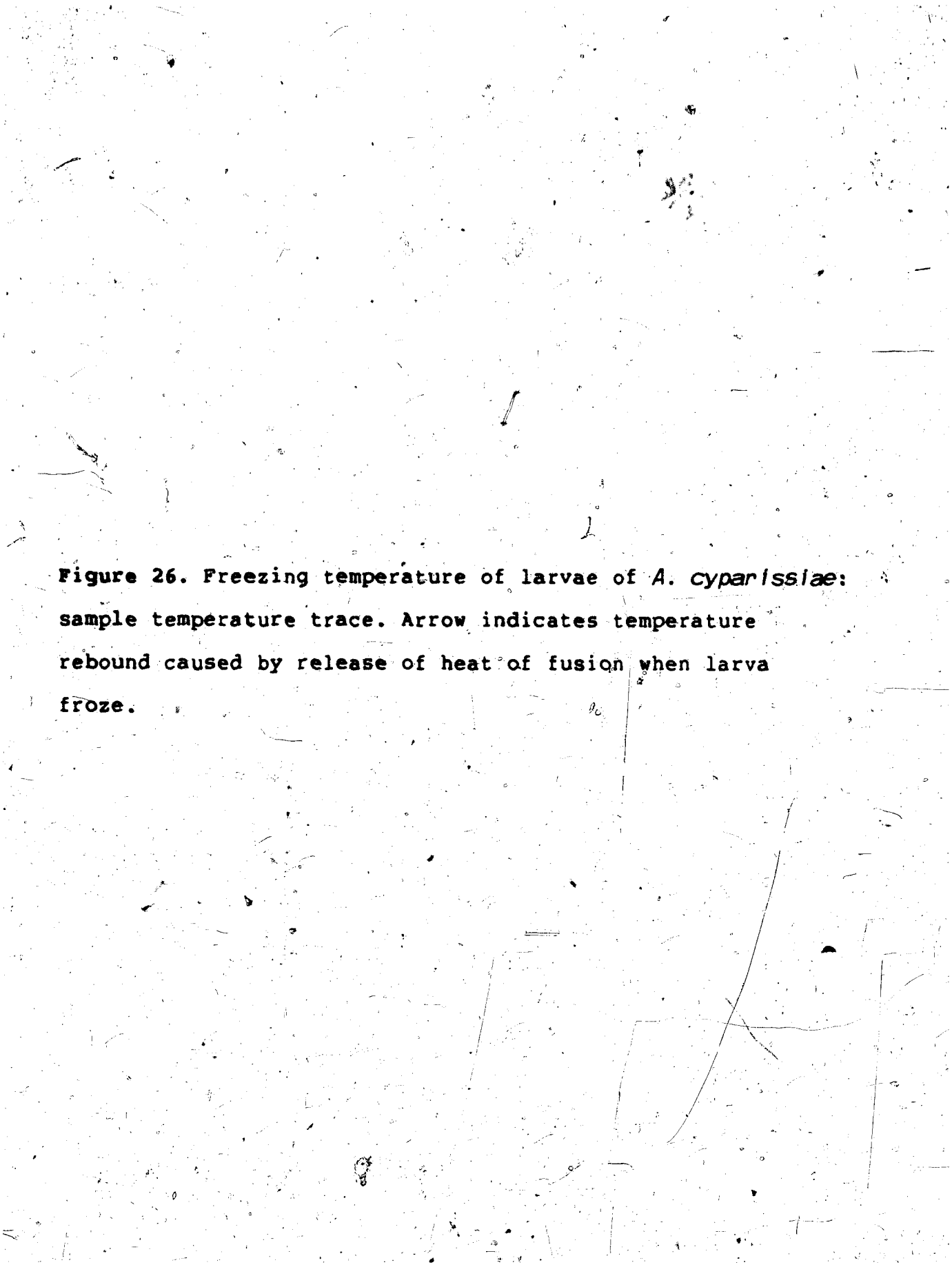
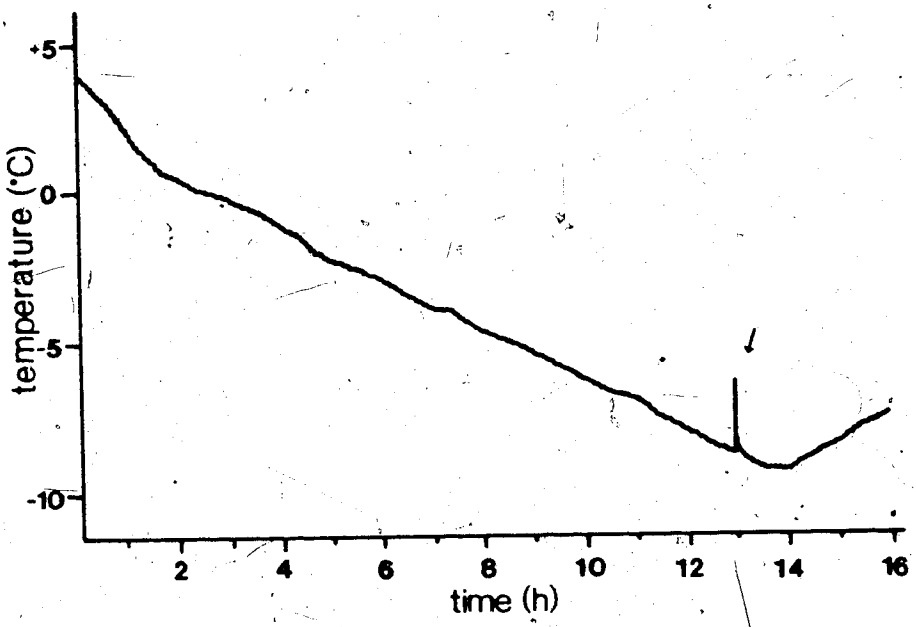


Figure 26. Freezing temperature of larvae of *A. cyparissiae*: sample temperature trace. Arrow indicates temperature rebound caused by release of heat of fusion when larva froze.


+5
0
-5
-10
temperature (°C)
2
4
6
8
10
12
14
16
time (h)

freezing nuclei. In addition, larvae in their pupal cell are in close contact with the soil, allowing ample opportunity for invasive nucleation from ice forming in the soil. I therefore suspect that supercooling is not a reliable mechanism in these organisms, but may be of benefit during acute exposure to temperatures below their freezing point.

Some indication of the temperatures experienced in spurge-growing areas of the Canadian Prairies, may be obtained by considering the soil temperature records at Regina (Agriculture Canada Research Station). The mean mid-January temperature (for the period 1965 to 1977) at 20 cm depth is about -7°, and the mean mid-January minimum about -13°. The temperatures were recorded at a site with little snow-trapping vegetation. A typical spurge habitat would be expected to have a deeper snow cover, and consequently, higher temperatures. Temperatures at 20 cm depth may be expected to be about 4° higher under a constant 20 cm cover of loose snow, than under bare ground (Shul'gin, 1965). This, however, can be no more than a very gross estimate for a given site, since the history of snow accumulation is as important as the immediate snow depth. Given a deep enough snow cover *A. cyparissiae* may be expected to survive at this depth in the soil, in this region. Long term survival of *A. flava* is somewhat less likely unless larva migrate downwards fairly deeply into the soil.

7.6 Pupae

7.6.1 Pupal Weights

Only the heavier of those third instar larvae that quit feeding became pupae. The mean pupal weight for *A. cyparissiae* was 6.12 mg (s.d.=0.86, n=33) with the minimum at 5.95 mg. For *A. flava*, the mean was 6.67 mg (s.d.=1.04, n=34) and the minimum, 4.94 mg (the next smallest, 5.65 mg) (compare weights for post-feeding larvae, last row of Table 23).

7.6.2 Pupal Development

The following description applies to both *A. flava* and *A. cyparissiae*.

Larvae overwintered in cold storage and transferred to 19.5° temperatures began to show evidence of pharate pupal development (shortening and thickening of the body and development of a hump-backed appearance) from 28 to 57 days later. Three quarters (52 of 68) had shown this change by the 33d day. Those overwintered larvae taken up to 10° became pharate pupae after the same length of time, indicating that this may be a relatively temperature-independent physiological shift from a diapause condition, rather than a temperature-dependent developmental period.

Pupal ecdysis took place 9 days later. Total pupal duration was 20 days with a few stragglers taking up to 25 days (mean 21.1±1.5 days, n=32). Development of body

pigmentation followed a fairly rigid schedule: eyes on day 11, appendages on days 14 to 16, wings (both elytra and hind wings) on days 17 to 18. After imaginal eclosion, the beetle remained in its pupal cell for up to 8 days while it developed full pigmentation and sclerotization. This sequence was described by Buddeberg (1878) with similar results.

Unfortunately, the culture of pharate pupae at 10° developed a fungal infestation and all were killed.

7.7 Discussion

The development of the 3 species considered here is very protracted. At a constant 20°, a minimum of 21 weeks is required from end of diapause until cessation of feeding. Such extensive periods at this temperature do not occur within the geographic range of these beetles, so the developmental period in the field is certainly longer. The initial diapause-breaking stage would not be much extended by the lower spring temperatures, so that allowing for an extended pupal stage, 10 to 12 weeks from diapause break to appearance of adults should be sufficient. Soil temperatures in the vicinity of Regina do not reach the 4 to 10° range until late April. Imagines may be expected in early July, a month later than in the warmer Rhine valley. Oviposition would then begin during the summer temperature maximum, a desirable state of affairs, given the

sensitivity of egg development rate to temperature, and hatching in late July and August. Since larvae continue to develop normally down to 4°, feeding can continue until mid-November, provided larvae near the surface migrate downwards as the soil cools, so that early hatching larvae may be expected to complete development. On the other hand, if the larvae must go down too far into the soil, either to permit late feeding, or to avoid very low temperatures, spring emergence may be delayed.

The life cycle, then, may be completed under a temperature regime such as that found at Regina but it may be a tight fit, representing the northern limits of its potential range in North America. *A. flava* will have to go deeper into the soil to survive the winter at a given site, than will *A. cyparissiae*, and may, therefore, have greater difficulty in completing full development the following season. Site aspect and snow cover will play important roles in determining whether or not any of these species can become established at a particular location.

8. Feeding by Larvae on the Root System of Leafy Spurge

8.1 Definition of the Problem

The effects that the larvae will have on their food plant depends to a large extent on the exact location of feeding, since not all components of the root system are equally important in the propagation and perennation of the plant.

Where larvae feed is a complex question, and may be broken down into a number of components. The following are considered in this chapter.

1. Do different instars have different feeding patterns?
2. How vagile are the larvae? If the larvae are relatively mobile, they at least have the capacity to search for particular preferred sites, but if they cannot move much selectivity may be disadvantageous.
3. What organs are attacked? Do the larvae preferentially feed on shoot bases, shoot buds, short roots or long roots?
4. Are there any particular conformational conditions required? For example, does feeding begin under a leaf scale, or perhaps at root junctions?
5. Within a given organ, what tissues are eaten?
6. What effect does the physiological state of a particular part of the root system have on the probability that feeding will be initiated or sustained?

8.2 General Methods

Three separate procedures were followed.

1. *Isolated Roots*: Hatchlings or second or third instar larvae were placed on sections of filamentous, yearling or perennial roots freshly dug up in the field. The rearing containers were closed plastic dishes 10 cm wide × 10 cm deep with a layer of moist sand on the bottom.

   After 1 week for hatchlings and second instars, and after 2 weeks for third instars, the root was placed in FAA (formalin-alcohol-acetic acid[13]) for later dissection.

   Upon dissection the following were noted;

   a. Root type and diameter.
   b. Location of initiation of non-sustained feeding with respect to location of shoot buds, junctions between principle and lateral roots, and presence or absence of previous damage, and phellem thickness.
   c. Location of initiation of sustained feeding with respect to the above characters.
   d. Tissues consumed.
   e. Laticifer density in cross section in phloem and phelloderm on a scale of low, moderate, high, very high (low – ratio of non-laticifers to laticifers = 3:1; moderate – 3:1 to 1:1; high – 1:1 to 1:5; very high – less than 1:5).

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[13] formalin:glacial acetic acid:absolute EtOH:water = 6:2:46:46

f. Density of sclereids in the phelloderm on a scale of low, moderate, high, very high (low – parenchyma:sclereids = 10:1; moderate – 10:1 to 5:1; high – 5:1 to 1:1; very high – sclereids more abundant than parenchyma cells)

The rearing temperature was a constant 19.5° or 20.5°C, in darkness.

2. *Potted plants*: Leafy spurge plants grown from root cuttings in the green-house in 3 for0 cm clay pots 4 to 6 months were placed in a cage with adults for 5 days then removed and grown at room temperature under a regime of 16 hours light, 8 hours darkness. Eight pots were so treated for each of *A. flava* and *A. cyparissiae*. Two pots for each species were washed free of soil 4, 6, 8, and 14 weeks after removal from the cage, and the roots examined and dissected. The characters listed above under *isolated roots* were noted, as well as the polarity of the feeding track – that is whether the larvae went towards or away from an active shoot or root crown after initiation of feeding.

3. *Root boxes*: Plants grown in clay pots for 4 months were washed free of soil and replanted in narrow plexiglass boxes 150 mm × 150 mm × 6 mm, such that all the roots were lying against one face of the box. The roots were trimmed as required to allow them to lie flat without overlapping of roots. The boxes were stored at a 30° angle from vertical at all times with the roots on the

lower face so that the geotropic responses of the root tips would cause new growth to stay in contact with the front face of the box, thus remaining visible. After allowing 3 weeks for the plant to adjust to transplanting procedure, 5 to 10 eggs or hatchlings were placed in positions at the shoot base comparable to those in which naturally laid eggs would be expected.

The movements of individual larvae both through the soil and within the thinner roots were able to be traced from twice daily observations (continuous observation at first, until the larva began sustained feeding) and recorded on photographs of the root system.

The locations of initiation of sustained and non-sustained feeding were noted as before. Also noted was the location of any new growth relative to feeding sites; the number and total length of new roots per unit length of original main root; and the relative probability of encountering roots of a given type. The latter was estimated by laying an acetate sheet divided into 5 × 5 mm squares over the root box and counting the number of squares in which each type occurred.

The observations were continued until the larvae ceased feeding or until most of the available root had been eaten.

Ten such boxes were prepared for both *A. flava* and *A. cyparissiae* using leafy spurge as well as 5 without larvae, and 2 with *A. cyparissiae* on cypress spurge.

The rearing temperature was 19.5° or 20.5°.

All three of *A. flava*, *A. cyparissiae*, and *A. czwalinae* were used in procedures 1 and 2; *A. czwalinae* was not used in procedure 3.

In order to determine the limits of the various tissues in preserved material (laticifers are especially difficult to distinguish from parenchyma), thick sections were soaked for 15 minutes in a warm Clorox-10% KOH solution, rinsed in 10% acetic acid-30% EtOH, stained with a mixture of equal parts of 10% light green, 5% alcoholic oil red, and 5% aniline blue for 30 minutes, rinsed in water for an hour, and finally placed in 1% acetic acid for observation. Sclereids showed dark, parenchyma and sieve cells blue-green, and xylem elements red. The latex swelled and extruded from the tubules, appearing on the surface of the section as short lustrous white hairs. This treatment is not suitable for production of permanent preparations.

In the following discussions the term *sample encounter* will be used. This is meant to describe an encounter with a root in which the larva takes one or more bites, forming a hole in the root up to head capsule-size, but does not continue feeding. If feeding continues it is a *feeding encounter*.

8.3 Type of Root

8.3.1 First Instar

Upon hatching the larva is adjacent or very close to the underground part of a shoot, or, if the female was able to get down far enough, near its junction with the root. It then has 3 possible courses of action. It can remain where it is, feeding on the shoot; follow the shoot down and feed there; or strike off through the soil until it finds a suitable feeding site. All of the hatchlings under continuous observation in the root boxes followed the third course, wandering through the soil for several hours sampling roots, before engaging in sustained feeding. Only 8 of 85 *A. cyparissiae* and 12 of 65 *A. flava* larvae followed in detail had ceased their wanderings after 6 hours, and 5 *A. cyparissiae* and two *A. flava* did not begin to feed in earnest until 35 hours after hatching. Thirty-nine *A. cyparissiae* and 36 *A. flava* never did begin to feed, and died after 3 days.

The frequency of sample encounters with roots of each type and the frequency of sustained feeding on each type are compared in Tables 24a and 24b (*A. cyparissiae* and *A. flava* respectively) to the proportions in which those types occur in the root boxes. Both species sampled roots in the same proportion in which they occur. However, sustained feeding occurred less often on perennial and more often on yearling roots than would be expected.

Table 24a. Frequency of sample and feeding encounters by first instar *A. cyparissiae* larvae on organs of different types compared to expected distribution. F = filamentous roots, Y = yearling roots, P = perennial roots, Sh = shoots. Freqencies are relative, with absolute frequencies in parentheses..

	F	Y	P	Sh	X^2
Relative frequency of root type	0.41	0.31	0.25	0.03	
Observed sample encounters	0.37 (85)	0.34 (79)	0.26 (60)	0.03 (8)	2.41
Expected sample encounters	0.41 (92)	0.31 (69)	0.25 (56)	0.03 (7)	
Observed feeding frequency	0.43 (20)	0.52 (24)	0.04 (2)	0 (0)	16.50
Expected feeding frequency	0.41 (19)	0.30 (14)	0.26 (12)	0.02 (1)	

Table 24b. Frequency of sample and feeding encounters by first instar *A. flava* larvae on organs of different types compared to expected distribution. Abbreviations as in Table 24a.

	F	Y	P	Sh	X^2
Relative frequency of root type	0.46	0.32	0.20	0.02	
Observed sample encounters	0.49 (58)	0.24 (29)	0.26 (31)	0.08 (1)	4.16
Expected sample encounters	0.46 (53)	0.32 (37)	0.20 (23)	0.02 (2)	
Observed feeding frequency	0.45 (13)	0.48 (14)	0.07 (2)	0 (0)	6.35
Expected feeding frequency	0.45 (13)	0.31 (9)	0.20 (6)	0.03 (1)	

Data from isolated root sections show that about 80% of first instar larvae which begin feeding successfully on filamentous and yearling roots survive to the second instar (*A. cyparisslae*: 100 of 124 on filamentous, and 116 of 140 on yearling roots; *A. flava*: 82 of 110 on filamentous, and 116 of 140 on yearling roots) while only about 50% survive to this age on perennial roots (*A. cyparisslae*: 25 of 52; *A. flava*: 64 of 125). These results indicate that large roots present greater obstacles to first instar larvae than do younger roots. Those larvae which sampled perennial roots, and then abandoned the attempt, never penetrated the phellem. This tough tissue may well have made the difference to such small organisms.

Dead larvae within perennial roots were often coated with latex. Whether this was a cause of death or occurred subsequently is unknown.

8.3.2 Second and Third Instars

Results for the root boxes and potted plants indicate that at a given time third and late second instar larvae are almost always found feeding on perennial roots, and early second instars on both yearling and main roots. Observations on the root boxes show, on the other hand, that a higher proportion of the total encounters with filamentous and yearling roots result in feeding than do those with perennial roots (Table 25). The observed instantaneous distribution of larvae has its basis not on 'preferences' of

Table 25. Encounters by second and third instar larvae of *A. cyparissiae* and *A. flava* with leafy spurge roots of different types, resulting in sustained feeding. (Roots grown in root boxes).

	Root Type		
	Filamentous	Yearling	Perennial
A. cyparissiae total encounters	85	93	38
feeding encounters	33	52	8
feeding/total	0.39	0.56	0.21
A. flava total encounters	85	112	49
feeding encounters	41	56	12
feeding/total	0.48	0.50	0.24

the larvae but on the different amount of time spent on the different root types. Any larva, although not as mobile as a hatchling, will move to a new location if it exhausts the food supply at the old site. A large larva which begins feeding on a filamentous root will soon destroy it, but if it starts to feed on a large root it can complete development on the single root segment.

It should be kept in mind that the soil moisture levels in all rearing procedures was fairly high. It is possible that under drier soil conditions larvae may show a preference for roots large enough for them to mine, rather than risk desiccation by feeding externally on smaller roots.

Similar patterns were observed of *A. cyparissiae* on cypress spurge. Of the total of 22 encounters with filamentous, 11 with yearling, and 8 with perennial roots, 50, 18 and 0% respectively resulted in feeding.

8.4 Tissue type

8.4.1 First Instar

First instar larvae mine longitudinally in filamentous roots, consuming all tissues except the epidermis.

Yearling roots have a much more strongly lignified xylem. First instar larvae always avoid this tissue in these roots. Consumption of other tissues depends on the

state of the latex system. In isolated root fragments with apparently low latex pressure, all tissues except the xylem and phellem are eaten. Roots still attached to actively growing plants (as in the root boxes), but with a low or moderate laticifer density, are treated similarily. However, in attached roots with a high laticifer density only the phelloderm is eaten. No exceptions to this pattern were found among the feeding traces examined (Table 26 gives the number of feeding traces examined on roots of different types and conditions for first instar larvae).

All first instar larvae were restricted to the phelloderm of perennial roots.

8.4.2 Second Instar

Filamentous roots are eaten in their entirety, or the epidermis left intact, depending on whether the larvae is larger in diameter than the root or not. All tissues except the xylem and phellem were eaten in yearling roots, regardless of the state of the latex system.

The tissues consumed in perennial roots depends on the state of the latex system, sclereid density, and size of the root relative to the size of the larva. All tissues except phellem and xylem are eaten in roots with low laticifer density and low to moderate sclereid density. Isolated root fragments with high laticifer density are treated similarily. If the laticifer density is high to very high and sclereid density low to moderate, feeding is primarily

Table 26. Number of larval feeding traces examined on leafy spurge roots of different types and conditions, for three species of *Aphthona*.

Instar/Root type	*cyparissiae*	*flava*	*czwalinae*
First instar			
Filamentous roots	30	20	5
Yearling roots			
isolated sections	20	20	3
high laticifer density	14	8	2
low laticifer density	11	21	0
Perennial roots	30	30	5
Second instar			
Filamentous roots	15	15	5
Yearling roots	15	15	4
Perennial roots			
high sclereid density	4	0	0
latex flow strong*	12	2	0
others	28	18	16
Third instar			
Filamentous roots	20	30	15
Yearling roots	40	40	15
Perennial roots			
high sclereid density	6	8	0
latex flow strong*	16	18	4
others	38	42	22

* i.e. laticifer density high and root attached to actively growing plant.

restricted to the phelloderm, although if a feeding track is followed along the root it can be seen to dip into the outer phloem fairly frequently, especially as the larvae becomes larger. Occasional specimens may be found feeding on the inner functional phloem between the xylem and laticiferous outer phloem. In roots with high or very high density of sclereids in the phelloderm, feeding was restricted to to phloem, both outer and inner zones.

The number of feeding traces examined is tabulated in Table 26.

8.4.3 Third Instar

Third instar larvae entirely obliterate filamentous roots. All tissues of yearling roots, including the xylem, but excluding the phellem, are eaten.

Most feeding traces in main roots involve all tissues between the xylem and phellem. However, high sclereid density will restrict feeding to the phloem, and high laticifer density in intact plants will restrict it to the phelloderm. Feeding in the phelloderm often takes the form of surface grooving of the root, since the body size is normally greater than the thickness of the phelloderm.

Two very stunted larvae (0.38 mg) were found feeding in the xylem parenchyma. Following the excavations back to their origins it became apparent that they had been originally feeding in a yearly lateral root and followed the xylem fibres into the xylem of the main root. This is

clearly an aberrant (not to mention counter-productive) situation.

The number of feeding traces examined on roots of different types are shown in Table 26.

8.4.4 Summary of Tissues Eaten

Consolidation of the foregoing patterns shows that all tissues except the very toughest (old xylem and outer phellem) are eaten, but a hierarchy of acceptability is apparent.

1. Periderm with low to moderate densities of sclereids, the inner phloem, and the laticiferous zone in roots where laticifers are at low to moderate densities and the latex system has been disrupted by damage or previous feeding, are accepted without restriction.
2. Periderm with high sclereid density, and the laticiferous zone in roots with an intact latex system but only moderate laticifer density are acceptable but avoided if the size of the larva relative to the widths of the various tissues permits it to feed selectively in a particular zone of the root.
3. Xylem parenchyma and pith, very stoney periderm, and recently produced phellem are generally shunned but may be eaten when no alternative is available.
4. The outer phloem with a high to very high density of laticifers and a vigorous latex flow, the vessel elements and tracheids, and mature phellem are avoided.

8.5 Orientation of Feeding Traces

8.5.1 Polarity

The polarity of feeding traces was not random (Table 27). Larvae which initiated feeding in undamaged roots attached to an actively growing plant mined towards the root tip more often than in the other direction. Feeding on root fragments, or attached roots which had been damaged by prior feeding at a point above the point of feeding initiation, exhibited no distinct differences in polarity. Results are the same for both vertical and horizonal roots.

There are several possible explanations of these observations. The latex pressure will be maintained above a damage point at a greater level than below, since the resources of the entire plant body are still available to the root section above this point – this may be observed directly by comparing the diameter of laticifers above and below a damage point in sections of fixed specimens. It may therefore simply be mechanically easier to mine towards the root tip. It is also possible that the metabolic drain of detoxifying the more noxious latex components is sufficient to make this course of action energetically advantageous. Thirdly, separation of a root section from the plant body causes a number of changes, among them the release of shoot

Table 27. Polarity of feeding by third instar larvae in yearling and perennial leafy spurge roots.

Root type and condition	Polarity of feeding*			
	A. flava		*A. cyparissiae*	
	+	-	+	-
Yearling				
undamaged	25	9	22	11
damaged-attached	27	29	31	28
isolated	25	30	33	31
Perennial				
undamaged	45	19	42	26
damaged-attached	42	38	58	63
isolated	84	96	74	61

* + = towards root tip, - = away from root tip.

buds from inhibition. Presumably associated with this acceleration of growth is a mobilization of nutrients. Such changes might increase the concentration of sapid chemicals in that part of the root making it more attractive.

8.5.2 Trace Conformation

Feeding traces are, in general, more or less longitudinal. However, the larvae are easily deflected by the vascular traces of shoot buds and lateral roots. A deflected larva frequently then continues to move obliquely. As a result, most mines tend to form a more or less loose spiral track along the root. Regions with a high density of vascular traces, as in an old root crown, cause many direction changes, and usually broad 'blotch' mines are formed at these locations.

8.6 Factors Influencing Initiation of Feeding

The characteristics of feeding initiation sites on perennial roots are shown in Table 28. Encounters with the general surface rarely lead to feeding. This was especially true when the phellem and the dead tissue overlying it (together called the dermis in the table) were thick. Over half the feeding on isolated roots began at the cut ends. Ignoring this for comparison to attached roots, encounters with sites of previous feeding by other larvae resulted in the highest incidence of feeding, followed by shoot buds,

Table 28. Proportion of total encounters with perennial leafy spurge roots resulting in feeding, according to the nature of the encounter point (combined data for *A. cyparissiae* and *A. flava*).

	Feeding Encounters	Total Encounters	% Feeding
Cut ends	138	186	74%
General surface			
dermis > 0.2 mm thick	3	74	4%
dermis < 0.2 mm thick	8	64	13%
Prior feeding	55	84	65%
Other damage	2	3	67%
Shoot bud	21	65	33%
Root junction	17	58	29%
Total	244	543	

and intersections of yearling and perennial roots. The suitability of sites of previous feeding resulted in aggregations of larvae. Roots were often found with four to five larvae feeding in parallel, virtually obliterating all tissues between the phellem and xylem around the entire circumference of the root.

Encounters with intact yearling roots showed no specific patterns, encounters with unmodified root surface leading to feeding as often as root or shoot bud junctions.

The over-riding factor for intact roots seems to be ability to penetrate the dermis and the superficial laticiferous zone associated with it. The developing phellem of yearling roots apparently presents no obstacle to penetration. The build up of dead tissues as the root ages frustrates many feeding attempts. This layer is absent on filamentous roots and shoot buds, and once feeding has begun on these they provide easy access to the interior of the main root.

The situation on roots with feeding damage may be more complex. The same argument of accessability still applies, but also coming into the picture are the changes in latex flow and nutrient mobilization mentioned in Section 8.5.1 with respect to polarity of feeding.

8.7 Effect of Feeding on Plant Growth

The total length of new roots produced per unit main root was greater in the infested root boxes than in the controls (mean±s.d. – control: 4.8±0.4; infested: 8.7±2.6). Total number of new shoots was also greater in the infested boxes (none in controls, none or one in infested). However, total length of shoot produced per unit length of main root was greater in the controls (2.8±0.6 in controls; 0.9±0.5 in infested). Larval feeding evidently stimulates root production and shoot disinhibition, but slows production of new shoot material.

8.8 Summary and Discussion

Ultimately, no matter what the local effects, larval feeding is of consequence only through its contribution to changes in growth and reproductive potential. The secondary effects of feeding which have a bearing on these aspects are as follows.

1. Feeding on the storage parenchyma of the phelloderm reduces stored reserves.
2. Removal of feeder roots reduces water and nutrient uptake ability of the root system.
3. Destruction of phloem sieve elements and laticifers disrupts translocation.
4. Damage to the phellem increases water loss (even though rarely eaten the phellem above a mine soon dies).

5. Penetration of the phellem provides sites for the initiation secondary damage and infection. The amount of tissue killed by feeding is greater than that actually consumed due to die back from the edges of the feeding zone.
6. Feeding isolates root fragments. Depending on the location of breaks relative to shoot location, this essentially removes photosynthetic input to the root section. If the size of the root section and its depth are such that it does not have sufficient reserves to send a new shoot to the surface, it will die.

The buffering capacity provided by the extensive lateral interconnections within a clone is considerable, so that any given unit of damage is much less disruptive to the plant as a whole, than would be experienced by a tap-rooted plant, for example.

Larvae are small relative to the primary elements of the root system. A single larva feeding on a given root segment generally affects only a narrow strip and probably has minimal effects on the host. It is here that the tendency to feed at previously attacked sites is of importance. Several larvae feeding in parallel virtually destroy a section of root. A large number of blotch mines in a root crown effectively girdles it causing die-back of the associated shoots.

It is evident that relatively high densities of larvae are required to place a significant load on a well

established clone – high enough that feeding is fairly well distributed laterally in the clone, while still allowing for multiple feeding at each point of invasion.

9. General Discussion – Suitability of *Aphthona* spp. as Biological Control Agents

The assessment of the suitability of an agent has three more or less independent components: determination of host range to establish the safety of introduction; determination of the ability of the agent to survive in the region of interest; and an investigation of the ability of the potential agent to have a noticeable negative effect on the target population.

The first of these is in the final phases of investigation by G. Sommer of the Commonwealth Institute of Biological Control, at Delémont, Switzerland. Certain elements of the other two aspects of the problem have been touched upon in the preceeding pages, although no final resolution is offered.

9.1 Potential for Survival

All three species considered here did well on Saskatchewan leafy spurge and there should be no concerns in this direction. Similarily, cypress spurge is the major natural host of two of these species (*A. flava*, *A. cyparissiae*) and acceptable as an alternate host to the third (*A. czwalinae*).

Habitat considerations present more serious difficulties. Overwintering *A. flava* larvae are at least potentially at risk from freezing over the northern and probably greater part of the leafy spurge range, particularly where snowfall accumulation is low. In this respect,

A. flava is probably of more limited value.

The relatively high humidity requirements of *A. czwalinae* may restrict its usefulness to riparian spurge sites. Such infestations are a major concern in many areas and this beetle should be kept in mind for future consideration if a more generally adaptable agent does not provide adequate control.

Leafy and cypress spurges tend to form extensive stands on this continent larger than those of any spurge species found in Europe, and commonly occur on lighter soils in somewhat dry-mesic habitats. This is in concord with the preferred habitat associations of *A. cyparissiae* reported in Chapter 6, and this is therefore the beetle of choice in this respect.

The protracted life histories of all three species also poses a potential obstacle. As mentioned in Chapter 7, early hatched individuals are likely to complete development under southern Saskatchewan temperature regimes. In order to maximize the probability of establishment, careful consideration of local temperature regimes should be undertaken before making initial releases. It is possible, given the variable developmental response in the lab, that nutritional quality of the roots may be greater in field plants, resulting in a greater growth rate. Perhaps, also, a more quickly developing strain will appear through genetic shift in the population. The magnitude of the increase in developmental rate need not be great.

9.2 Potential Effects on Host Plant

Successful biological control of a plant involves shifting the equilibrium in a complex interplay amongst the plant, competing vegetation, abiotic factors, other heterotrophs associated with the plant, and phenological considerations, by providing added stress. The ultimate effects of a given degree of damage inflicted by an agent will depend on the total stress due to other factors.

The mechanisms by which *Aphthona* larvae can affect the host plant were listed at the end of the last chapter. Certainly the easiest of these to relate to stresses from other sources is the disruption of water supply. Even single larvae can sever the feeder roots, and these are the most susceptible to attack by wandering larvae. Larger roots subject to multiple feeding can also be segregated from the main root network. If chronic low soil moisture levels and/or competition from other vegetation have shifted the available water towards the limit of the optimal range, then larval feeding, by reducing the plant's ability to fully use actual available water supply, reduces the effective available supply to a point below this limit. The plant then has two possible responses. It can cut back on

growth, and possibly suffer some die-back, or it can compensate for the lost roots by expending energy to produce new feeder roots. Both of these processes were observed in the root boxes. Root fragmentation also disinhibits shoot buds, causing a further drain of stored reserves. Reserves lost due to damage incurred early in the feeding season may be recouped once the lost organs are replaced. The deeper the root, however, the greater the drain on resources to push a shoot to the surface. The late but prolonged feeding season ensures that at least some of the loss will not be recovered before winter sets in.

In contrast to the above, plants growing in sites with higher soil moisture probably have considerably greater uptake capacity than necessary to maintain the internal water balances at optimal levels. Larval feeding in this situation would have little real effect.

Assessment of the real effects on the host will, however, require field testing. The extensive root system of these plants provides a buffering system impossible to duplicate in under laboratory conditions, and any effects of feeding observed in the laboratory are certain to be considerably damped under field conditions. The same principles hould, however, apply.

9.3 Recommendations

Of the three species studied, *A. cyparissiae* shows the greatest potential. There are, however, certain limitations. First, its prolonged life cycle, although advantageous in that it prolongs the stress on the plant, necessitates careful choice of initial release areas. Second this agent may not be effective in wetter sites. Combination of this agent with another, such as the recently introduced shoot- and stem-boring cerambycid beetle *Oberea erythrocephala*, may provide the additional stress required at such sites.

In order to maximize survival potential, the initial release sites should have the following features: large and continuous spurge stand; southern aspect to prolong the length of the feeding season; and a good winter snow cover for protection of overwintering larvae. A moisture gradient across the site is also recommended, as partial protection against unexpectedly dry conditions during the egg incubation period, and at the time of hatch.

In summary, I feel that as long as its limitations are recognized, *A. cyparissiae* is a potentially useful tool in reducing the reproductive capacity of introduced perennial spurges.

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Appendix 1

Recorded host plants for *Aphthona* spp.

A list of plants from which *Aphthona* spp. have been collected has been compiled from the following sources:

1. Records reported in the literature.
2. Observations by Gisela Sommer and myself in the summer of 1978, supplemented by collections by Sommer in 1979 (e Austria, Hungary, nw Switzerland, sw BRD, ne France).
3. Collections by the USDA, 1978. (Romania, Hungary, Italy)(A. Rizza and P. Pecora[1]).
4. Data from specimens in the British Museum (Natural History) (Compiled by D. Schröder[2]).
5. Data contained in a letter from O.V. Kovalev[3] to P. Harris[4].

An attempt has been made to avoid published accounts which are simply repetitions of earlier records, but duplication has certainly occurred. Certain of the British Museum records are probably specimens on which some of the literature reports are based. In particular, there is a suspiciously close correspondence between these records and those of Heikertinger (1912a, b, 1916, 1925).

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[1] A. Rizza and P. Pecora. 1978. *Euphorbia* project. Unpublished annual report of USDA-ARS, Biological Control of Weeds European Lab, Rome, Italy

[2] Commonwealth Institute of Biological Control, European Station, Delémont, Switzerland.

[3] Zoological Institute, Academy of Sciences of the USSR, Leningrad.

[4] Agriculture Canada Research Station, Regina, Sask.

All but a very few records (see Section 4.3.2.2 for references to larval hosts) are based on adults only. Many of these are undoubtedly resting records: very few actually specify that feeding has occurred, and neither the number of specimens nor number of sites is indicated. Records reported by a single source must therefore be interpreted with care, particularily for non-euphorbiaceous, non-linaceous or non-geraniaceous plants. Those records which internal evidence indicates are resting records, or which I feel are resting records, or seem to be due to beetle misidentification, I have placed in parentheses. See the notes following Table A-1 for further details. There remain many suspicious records about which I am less certain and which I have therefore let stand.

A further complication is the lack of a world revision or review of the species. Many non-palearctic species have in recent years been assigned to other genera. Until the relationships between the palearctic *Aphthona* species and the world Aphthonine fauna have been elucidated, inferences about the host range of the genus as a whole are somewhat weak.

Fortunately, most of these records are from the relatively well known west palearctic fauna (Europe, North Africa, the Middle East, and the Caspian region) where the generic concepts are more stable. The remaining species may be broken down geographically as follows:

1. Eastern Palearctic region
   a. Central Asia: *jacuta, sarjanica, samartica, tolli*
   b. Far east: *formosana, foudrasi, nubila, perminuta*
2. Oriental region – India: *hugeli*
3. Oceania: *bicolorata, nanyoensis, samoana, yeitchi*
4. Ethiopean region: *guavae, marshalli, sierraeleonis, whitfieldi* (also *bimaculata*, but see note 6.)
5. Macaronesia: *crassipes, laevissima, paivana*
6. New World: *argentinae, crucifera, insolita, texana*

I have followed Heikertinger's (1944) treatment of the palearctic species in assigning names used in the literature to their synonyms, and to sort out the misapplication of the name '*euphorbiae*' to several other species by mid-nineteenth century authors.

Table A-1 lists records alphabetically by beetle, with their source reference, and is followed by explanitory notes referenced in the table by number. **Table A-2** lists records by plant family.

Table A-1.
Recorded host plants for *Aphthona* spp. Alphabetic list by beetle. Entries in parentheses indicate indefinite or doubtful records. See notes following table for details.

Aphthona	Plant family	Plant species	Source (1,2)
abdominalis (Duftsch.)	Euphorbiaceae	Euphorbia cyparissias	!,BM, Heik. 1912b, Kuntze 1931, Weise 1892
		E. paralias	de Peyerimoff 1915
		E. seguieriana	!
		E. stricta	!
		E. sp.	Doguet & Tempere 1975, Lopatin 1980
	Linaceae	Linum (3)	Lakhmanov 1970
aenomicans Allard	Euphorbiaceae	Euphorbia esula	BM, Weise 1889b
	Linaceae	Linum	Weise 1889b
alexander Berti & Rap.	Euphorbiaceae	Euphorbia sp.	Berti & Rapilly 1973
argentinae Bryant	Euphorbiaceae	Euphorbia portulacoides	BM
atrovirens Forster	(Cistaceae)	(Helianthemum) (4)	Heik. 1944
	Euphorbiaceae	Euphorbia cyparissias	BM, Weise 1892
	(Linaceae)	(Linum) (4)	Heik. 1944
beauprei Pic	Cistaceae	Helianthemum victitans	Pic 1915
		H. nummilarium	de Peyerimoff 1915
bicolorata Jacoby	(Cucurbitaceae)	(Citrullus) (5)	Gressitt 1955
	Euphorbiaceae	Euphorbia	Gressitt 1955 , Samuelson 1973
	Gramineae	Oryza	Froggatt 1939
		(Zea mays) (5)	Gressitt 1955
(bimaculata Jacoby)(6)	Pedaliaceae	Sesamum indicum	Harris 1937, Ritchie 1937, Smee 1937, 1945
bonvouloiri Allard	Euphorbiaceae	Euphorbia pilosa	USDA
		E. sp.	Heik. 1916, Sahlberg 1913
coerulea (Geoffroy)	(Pinaceae)	(Pinus) (7)	Nordlinger 1848
	Iridaceae	Iris pseudacorus	!, Bach 1859, Bedel 1891, Beneczur 1930, Buddeberg 1888, Heik. 1916, Kutschera 1861
		I. sibirica	Poeterin 1924, 1935
crassipes (Wollaston)	Crassulaceae	Sempervivum	Wollaston 1865
		Sedum	Wollaston 1865

Aphthona	Plant family	Plant species	Source
crucifera Blake	Myricaceae	Myrica	Blake 1964
cyanella (Redtenbacher)	Euphorbiaceae	Euphorbia cyparissias	Hefk. 1912b
		E. esula	Bedel 1888
		E. verrucosa	!
cyparissiae (Koch)	Euphorbiaceae	Euphorbia cyparissias	!, BM, Bedel 1888, Buddeberg 1887, Heik. 1912a, Kaltenbach 1874, Kuntze 1931, Kutschera 1861
		E. esula	!, BM, Heik. 1916
		E. peplus	BM, Heik. 1916
		E. seguieriana (8)	!, BM, Heik. 1916
		E. virgata	!
czwalinae Weise	Euphorbiaceae	Euphorbia cyparissias	!
		E. esula	!, BM, Weise 1888
		E. seguieriana	!
		E. virgata	!, BM, Heik. 1925
delicatula Foudras	Euphorbiaceae	Euphorbia cyparissias	!
		E. dulcis	BM, Heik. 1912b
		E. verrucosa	!
depressa Allard	Euphorbiaceae	Euphorbia dulcis	Heik. 1944
		E. helioscopia	de Peyerimoff 1915, 1919
		E. victitans	de Peyerimoff 1919
		E. medicaginea	de Peyerimoff 1911
erichsoni (Zetterst.) (9)	Marchantiaceae (Bryophyta)	Marchantia	Heik. 1944
	Cyperaceae	Carex irrigua	Ogloblin & Medvedev 1971
euphorbiae (Schrank)	Caryophyllaceae	Lychnis sp.	Principi 1941
	Chenopodiaceae	Beta maritima	Allard 1860
		B. vulgaris	Kurdyumov 1917, Massee 1944, Weise 1891
		Chenopodium	Principi 1941
	Ulmaceae	Ulmus	Principi 1941
	Moraceae	Morus	Principi 1941
	(Salicaceae)	(Populus) (21)	Allen 1950
	Cruciferae	mustard	Sacharov 1915
		Sysimbrium	Kurdyumov 1917
	Rosaceae	Malus	Massee 1944
		Prunus (plum)	van Poeteren 1930
		Prunus persica	Principi 1941
	Leguminosae	beans	Manolache & Dobreanu 1960
	(Celastraceae)	(Euonymus japanicus) (10)	Principi 1941

Aphthona	Plant family	Plant species	Source
euphorbiae (cont.)	Euphorbiaceae	Euphorbia amygdaloides	Marsham 1802
		E. cyparissias	!, BM, Heik. 1912b, Weise 1888
		E. esula	!, BM, Heik. 1916
		E. platyphyllos	!
		E. sylvatica	BM
		E. sp.	Fabricius 1801, Kurdyumov 1917, Lopatin 1960
	(Tiliaceae)	(Tilia europaea) (21)	Verdcourt 1950
	Zygophyllaceae	Peganum harmala	Lopatin 1960
	Linaceae	Linum corymbiferum	de Peyerimoff 1915
		L. usitatissimum	many authors (11)
		L. sp.	Kaltenbach 1874
	(Oleaceae)	(Fraxinus) (21)	Allen 1950, Verdcourt 1950
	Convolvulaceae	Convolvulus	Principi 1941
	Plantaginaceae	Plantago media	Fritzsche 1958
	Caprifoliaceae	Viburnum tinus	Principi 1941
	Compositae	Bellis perennis	Fritzsche 1958
		Cirsium arvense (12)	Kurdyumov 1917
		Taraxacum officinale	Fritzsche 1958
	Gramineae	Poa annua	Fritzsche 1958
		"cereals"	Kurdyumov 1917
flava Guillebeau	Euphorbiaceae	Euphorbia cyparissias	!, USDA, Heik. 1944, Kuntze 1931
		E. esula	USDA
		E. virgata	!!
		E. pannonica	!!
flaviceps Allard	Euphorbiaceae	Euphorbia paralias	de Peyerimoff 1915
	Linaceae	Linum usitatissum	Kurdyumov 1917
formosana Chen	Euphorbiaceae	Mallotus sp.	Takizawa 1979
foudrasi Jacoby	Euphorbiaceae	Euphorbia pseudochamaesyce	Chujo & Kimoto 1961
gracilis Falderman	Euphorbiaceae	Euphorbia sp.	Kovalev (*in lit.*)
		E. supina	Chujo & Kimoto 1961
		Phyllanthus urinaria	Chujo & Kimoto 1961
guavae Bryant	Myrtaceae	Psidium	Bryant 1927, Hargreaves 1937
herbigrada Curtis	Cistaceae	Helianthemum canum	Heik. 1912b
		H. nummilarium	!, Bedel 1888, Everts 1922, Heik. 1912b, de Peyerimoff 1911, Weise 1888
	Euphorbiaceae	Euphorbia cyparissias	!, BM
	(Campanulaceae)	(Campanula rotundifolia)	Redtenbacher 1874
hugeli Jacoby	(Cactaceae)	(Pereskia aculeata) (22)	Maulik 1926

Aphthona	Plant family	Plant species	Source
illigeri Bedel	Euphorbiaceae	Euphorbia luteola	de Peyerimoff 1911, 1926
		E. megalatlantica	de Peyerimoff 1926
		E. nicaeensis	de Peyerimoff 1926
		E. segueriana (8)	BM, Allard 1860, Bedel 1888, Deville 1914
		E. squamigera	de Peyerimoff 1926
insolita (Melsheimer)	Caprifoliaceae	Symphoricarpos vulgaris	Blatchely 1910
jacuta Ogloblin	Euphorbiaceae	Euphorbia sp.	Kovalev (*in lit.*)
janthina Allard	Euphorbiaceae	Euphorbia helioscopia	de Peyerimoff 1915
lacertosa Rosenh.	Euphorbiaceae	Euphorbia cyparissias	!, BM, Heik. 1912a, Kuntze 1931
		E. esula	!
		E. lucida	!
		E. pannonica	!
		E. seguieriana	!
		E. virgata	!, BM, Heik. 1916, Heik. 1925
laevissima Wollaston	Euphorbiaceae	Euphorbia tuckeyana	Wollaston 1867
lutescens (Gyllenhal)	Rosaceae	Fragaria	Mityaev 1960
		Rosa	Ritzema-Bos 1915
		Rubus	Mityaev 1960
		(Filipendula ulmaria) (13)	Bedel 1888
	Lythraceae	Lythrum salicaria	Berti & Rapilly 1973, Heik. 1912a, Kutschera 1861, Ritzema-Bos 1915, (Tolg 1938 (14))
	Euphorbiaceae	Euphorbia cyparissias	! (15)
	(Labiatae)	(Mentha aquatica) (14)	Tolg 1938
marshalli Jacoby	Polygonaceae	Polygonum senegalense	Bryant 1957
mohri Warchalowski	Euphorbiaceae	Euphorbia szovitsii	Warchalowski 1973
nanyoensis Chujo (23)	(Cucurbitaceae)	(Citrullus) (5)	Gressitt 1955
	Leguminosae	Pithecellobium dulce	Gressitt 1955
	Euphorbiaceae	Euphorbia atato	Swezey 1942 , Samuelson 1973 (16)
		E. hirta	Swezey 1942
	(Gramineae)	(Zea mays) (5)	Gressitt 1955
nigriceps (W.Redt.)	Rutaceae	Citrus aurantium	Bargagli 1878
	Geraniaceae	Erodium malacoides	Deville 1898
		E. moschatum	de Peyerimoff 1915
		Geranium pratense	Fowler 1890
		G. robertianum	Heik. 1916
		G. rotundifolium	Heik. 1916

Aphthona	Plant family	Plant species	Source
nigrilabris Duvivier	Euphorbiaceae	Euphorbia hirta (16)	Scherer 1969
		E. "dudhi" (17)	Maulik 1926
nigriscutis Foudras	Euphorbiaceae	Euphorbia cyparissias	!
		E. esula	!
		E. pannonica	!
		E. seguieriana	!
		E. spp.	USDA, Lopatin 1960
nigrita Motschulsky	Rubiaceae	Paedera scandens	Kimoto 1966
nubila Weise	Elaeagnaceae	Elaeagnus glabra	Chujo & Kimoto 1961
ovata Foudras	Euphorbiaceae	Euphorbia amygdaloides	BM, Heik. 1916
		E. angulata	BM
		E. cyparissias	!, Heik. 1912a, Kutschera 1861
		E. esula	!, BM, Heik. 1916
		E. helioscopia	Heik. 1916
		E. lucida	!, BM
		E. palustris	BM, Heik. 1916
		E. polychroma	BM, (USDA(18)), Heik. 1916
		E. salicifolia	BM, Heik. 1925
		E. stricta	!
		E. virgata	Heik. 1916
paivana (Wollaston)	Euphorbiaceae	Euphorbia piscatoria	BM, Kutschera 1861
		E. regisjubae	BM, Scott 1959 (19)
		E. spp.	Wollaston 1862
pallida (Bach)	Geraniaceae	Erodium cicutarium	Heik. 1916
		Geranium aconitinium	Kaminski 1935
		G. albanum	Barkowska 1976
		G. collinum	Kaminski 1935
		G. dissectum	Kaminski 1935
		G. macrorrhizum	Kaminski 1935
		G. pratense	Heik. 1916, Weise 1891
		G. pusillum	Heik. 1916
		G. sibiricum	Kaminski 1935
perminuta Baly	Fagaceae	Fagus crenata	Chujo & Kimoto 1961
	Leguminosae	Albizzia julibrissin	Chujo & Kimoto 1961
	Thymelaeaceae	Edgeworthia papyrifera	Chujo & Kimoto 1961

Aphthona	Plant family	Plant species	Source
perrisi Allard	Euphorbiaceae	Euphorbia amygdaloides	de Peyerimoff 1915
		E. characias	Deville 1914
		E. victitens	de Peyerimoff 1915
placida Kutschera	Linaceae	Linum flavum	Heik. 1912b
poupillieri Allard	Euphorbiaceae	Euphorbia pilosa	de Peyerimoff 1911
		E. pubescens	Allard 1860, de Peyerimoff 1911
punctiventris Rey	Euphorbiaceae	Euphorbia characias	de Peyerimoff 1915
pygmaea Kutschera	Euphorbiaciae	Euphorbia amygdaloides	!
		E. cyparissias	!, BM, Heik. 1916, Weise 1892
		E. esula	!
		E. helioscopia	BM, Heik. 1916
		E. pannonica	!
		E. peplus	BM, Heik. 1916
		E. seguieriana	!
sajanica Ogloblin	Euphorbiaceae	Euphorbia sp.	Kovalev (*in lit.*)
sarmatica Ogloblin	Euphorbiaceae	Euphorbia sp.	Kovalev (*in lit.*)
semicyanea Allard	Iridaceae	Iris germanica	Heik. 1916
sierraeleonis Bryant	Leguminosae	Arachis	Hargreaves 1937
signatifrons Wollaston	Compositae	Artemesia gorgonum	Heik. 1944
strigosa Baly	Euphorbiaceae	Mallotus japanicus	Chujo & Kimoto 1961
stussineri Weise	Euphorbiaceae	Euphorbia	Heik. 1944
subovata Allard	Geraniaceae	Erodium malacoides	de Peyerimoff 1919
texana Crotch	Euphorbiaceae	Euphorbia marginata	Popenoe 1877
	Labiatae	Salvia	
	Compositae	Aster	Douglass 1929
		Grindelia	Douglass 1929
		Helianthus	Douglass 1929
		Veronia interior	Schwitzgebel & Wilbur 1942 (15)

Aphthona	Plant family	Plant species	Source
tolli Ogloblin	Euphorbiaceae	Euphorbia sp.	Kovalev (*in lit.*)
variolosa Foudras	Euphorbiaceae	Euphorbia dulcis	Deville ????
vaulogeri Pic	Euphorbiaceae	Euphorbia pubescens	de Peyerimoff 1926
veitchi Bryant (23)	Euphorbiaceae Gramineae	Euphorbia chamissonis bermuda grass (24)	BM, Greenwood 1940 Gressitt 1957
venustula Kutschera	(Boletaceae) (fungus)	(Boletus edulis) (20)	Scheerpeltz & Hofler 1942
	(Fagaceae)	(Quercus)	Verdcourt 1950
	Euphorbiaceae	Euphorbia amygdaloides	!, BM, Heik. 1925
		E. cyparissias	!, BM, USDA, Heik. 1912b
		E. esula	!, BM, Heik. 1912b
		E. helioscopia	Kaminski 1935
		E. salicifolia	BM, Heik. 1925
		E. seguieriana	!
		E. stricta	!, BM, Heik. 1916
		E. sylvatica	Allard 1860, Bedel 1888
		E. virgata	BM, Heik. 1925
violacea (Koch)	(Betulaceae)	(Betula)	Nordlinger 1848
	Euphorbiaceae	Euphorbia lucida	!, BM
		E. palustris	BM, Allard 1860, Bedel 1888, Heik. 1925, Weise 1889a
		E. platyphyllos	!
		E. salicifolia	!, USDA
		E. virgata	!
		E. sp.	Lopatin 1960
	Iridaceae	Iris pseudacorus	Kutschera 1861, Redtenbacher 1874
		I. germanica	Bargagli 1878
whitfieldi Bryant	Leguminosae	Vicia sinensis	Bryant 1933
undetermined spp.	Malvaceae	Gossypium	Zacher 1913
	Cucurbitaceae	Curcubita pepo	Shembel 1922

Explanatory Notes for Table A-1

1. ! indicates collections by G. Sommer and E. Maw, summer 1978; !! by Sommer, summer 1979. BM indicates data taken from specimens in the British Museum (Natural History) by D. Schroeder. USDA indicates collections by USDA personel, 1978 (A. Rizza & P. Pecora, unpulished annual report, 1978).
2. "Heikertinger" has been abbreviated "Heik."
3. ?This record is perhaps referable to *A. flaviceps*.
4. Listed by Heikertinger as possible hosts only.
5. Due to confusion of *A. bicolorata* and *nanyoensis* these records are indefinite.
6. Scherer(1963) has transferred *A. bimaculata* to the genus *Alocypa* and probably should properly not be in this list. However, since it has appeared in the economic literature as *Aphthona* it has been included.
7. "...ihr schrieb ich die Biβstellen zu,..." ("I ascribe the bite marks to it"). As this is very uncharacteristic of *A. coerulea* I doubt that his conclusion was correct. Bargagli (1878) also found this record questionable.
8. All literature records as *E. Gerardiana*.
9. Palm (1943) collected large numbers by treading the vegetation at the edge of *Spagnum*-margined ponds. Although he could not establish the host plant, he suggests *Comarum, Menyanthes, Andromeda, or Oxycoccus*, which he reports as the only plants present ("...vilka

vora de enda örterna, där insekterna anträffades."). Perhaps *Carex* was also present? Cf. record of Ogloblin and Medvedev (1971).

10. Several specimens in May and August but no damage seen ("...pero non ho mai notato erosioni.").
11. *A. euphorbiae* is a pest of cultivated flax, particularily in the USSR.
12. Skeletonized.
13. Teneral aggregations. Heikertinger (1912a) questions the validity of this record.
14. Swept from ditch vegetation which included *Lythrum salicaria* and *Mentha aquatica*.
15. Single specimen.
16. As *E. pilulifera*.
17. According to Maheshwari (1963) the colloquial name "dudhi" refers to both *Euphorbia hirta* and *E. clarkeana*.
18. Single female, "probably *ovata*".
19. Feeding on sap.
20. "Wohl sicher nur zufällig auf den Pilz gelangt." (certainly an accidental occurrence).
21. These beetles were apparently undergoing a population boom and according to Allen (1950) was one of the most common flea beetle species in Britain at this time. *Longitarsus parvulus*, another flax pest, was also abundant.
22. Note that *Pereskia* (or any other cactus for that matter) is not native to India, the source of this record, and

so cannot be the natural host of *A. hugelii*.

23. Samuelson(1973) demoted *A. nanyoensis* to subspecific status in *A. veitchi*. The two are maintained as separate entities for the purposes of this list.

24. By sweeping. This record as *A. samoana* Gressitt; synonymy according to Samuelson (1973).

Table A-2
Recorded 'hosts' of *Aphthona* spp. listed by plant. Sequence of plant families follows Stebbins (1974) .

Plant family	Plant species	Aphthona species
Euphorbiaceae	Euphorbia amygdaloides	euphorbiae, ovata,perrisi, pygmaea, venustula
	E. angulata	ovata
	E. atato	nanyoensis
	E. chamissonis	veitchi
	E. characias	euphorbiae, perrisi, punctiventris
	E. cyparissias	abdominalis, atrovirens, cyanella, cyparissiae, czwalinae, delicatula, euphorbiae, flava, herbigrada, lacertosa, lutescens, nigriscutis, ovata, pygmaea, venustula
	E. dulcis	delicatula, depressa, variolosa
	E. esula	aenomicans, cyanella, cyparissiae, czwalinae, euphorbiae, flava, lacertosa, nigriscutis, ovata, pygmaea, venustula
	E. helioscopia	depressa, janthina, ovata, pygmaea, venustula
	E. hirta	nanyoensis, nigrilabris
	E. lucida	lacertosa, ovata, violacea
	E. luteola	illigeri
	E. marginata	texana
	E. marginata	depressa
	E. megalatlantica	illigeri
	E. nicaeensis	illigeri
	E. palustris	ovata, violacea
	E. pannonica	flava, lacertosa, nigriscutis, pygmaea
	E. paralias	abdominalis, flaviceps
	E. peplus	cyparissiae, pygmaea
	E. pilosa	bonvouloiri, poupillieri
	E. piscatoria	paivana
	E. platyphyllos	euphorbiae, violacea
	E. polychroma	ovata
	E. portulacoides	argentinae
	E. pubescens	poupillieri, vaulogeri
	E. pseudochamaesyce	foudrasi
	E. regisjubae	paivana
	E. salicifolia	ovata, venustula, violacea
	E. seguieriana	abdominalis, cyparissiae, czwalinae, illigeri, lacertosa, nigriscutis, pygmaea, venustula
	E. squamigera	illigeri
	E. stricta	abdominalis, ovata, venustula
	E. supina	foudrasi
	E. sylvatica	euphorbiae, venustula
	E. szovitsii	mohri

Plant family	Plant species	Aphthona species
Euphorbiaceae	E. tuckeyana	laevissima
	E. verrucosa	cyanella, delicatula
	E. victitans	depressa, perrisi
	E. virgata	cyparissiae, czwalinae, flava, lacertosa, ovata, venustula, violacea
	E. 'dudhi'	nigrilabris
	E. sp.	abdominalis, alexander, bicolorata, bonvouloiri, euphorbiae, gracilis, jacuta, nigriscutis, paivana, sajanica, sarmatica, tolli, violacea
	Mallotus sp.	formosana
	Mallotus japanicus	strigosa
	Phyllanthus urinaria	foudrasi
Other families		
Boletaceae	Boletus edulis	(venustula)
Marchantiaceae	Marchantia	erichsoni
Pinaceae	Pinus	(coerulea)
Myricaceae	Myrica	crucifera
Fagaceae	Fagus crenata	perminuta
Betulaceae	Betula	(violacea)
Cactaceae	Pereskia aculeata	(hugeli)
Caryophyllaceae	Lychnis sp.	euphorbiae
Chenopodiaceae	Beta maritima	euphorbiae
	B. vulgaris	euphorbiae
	Chenopodium	euphorbiae
Polygonaceae	Polygonum senegalense	marshalli
Malvaceae	Gossypium	undet. sp.
Ulmaceae	Ulmus	euphorbiae
Moraceae	Morus	euphorbiae

Plant family	Plant species	Aphthona species
Cistaceae	Helianthemum canum	herbigrada
	H. nummilarium	beauprei, herbigrada
	H. victitans	beauprei
	Helianthemum	(atrovirens)
Cucurbitaceae	Citrullus	(bicolorata, nanyoensis)
	Cucurbita pepo	undet. sp.
Cruciferae	mustard	euphorbiae
	Sysimbrium	euphorbiae
Crassulaceae	Sempervivum	crassipes
	Sedum	crassipes
Rosaceae	Fragaria	lutescens.
	Filipendula ulmaria	(lutescens)
	Malus	euphorbiae
	Prunus persica	euphorbiae
	Prunus (plum)	euphorbiae
	Rosa	lutescens
	Rubus	lutescens
Leguminosae	beans	euphorbiae
	Albizzia julibrissin	perminuta
	Arachis	sierraeleonis
	Pithecellobium dulce	nanyoesis
	Vicia sativa	whitfieldi
Lythraceae	Lythrum salicaria	lutescens
Thymelaeaceae	Edgeworthia papyrifera	perminuta
Myrtaceae	Psidium	guavae
Elaeagnaceae	Elaeagnus glabra	nubila
Celastraceae	Euonymus japonicus	(euphorbiae)
Rutaceae	Citrus aurantium	nigiceps
Tiliaceae	Tilia europaea	(euphorbiae)
Zygophyllaceae	Peganum harmala	euphorbiae

Plant family	Plant species	Aphthona species
-aceae	Linum	abdominalis, aenomicans, (atrovirens), euphorbiae
	Linum corymbiferum	euphorbiae
	Linum flavum	placida
	L. usitatissimum	euphorbiae, flaviceps
Geraniaceae	Erodium cicutarium	pallida
	E. malacoides	nigriceps, subovata
	E. moschatum	nigriceps
	Geranium aconitinium	pallida
	G. albanum	pallida
	G. collinum	pallida
	G. dissectum	pallida
	G. macrorrhizum	pallida
	G. pratense	nigriceps, pallida
	G. pusillum	pallida
	G. robertianum	nigriceps
	G. rotundifolium	nigriceps
	G. sibiricum	pallida
Oleaceae	Fraxinus	euphorbiae
Convolvulaceae	Convolvulus	(euphorbiae)
Labiatae	Mentha aquatica	(lutescens)
	Salvia	texana
Plantaginaceae	Plantago media	euphorbiae
Campanulaceae	Campanula rotundifolia	(herbigrada)
Rubiaceae	Paedera scandens	nigrita
Caprifoliaceae	Symphoricarpos vulgaris	insolita
	Viburnum tinus	euphorbiae
Compositae	Artemesia gorgonum	signatifrons
	Aster	texana
	Bellis perennis	euphorbiae
	Chrysanthemum	coerulea
	Cirsium arvense	euphorbiae
	Grindelia	texana
	Helianthus	texana
	Taraxacum officinale	euphorbiae
	Veronia interior	texana

Plant family	Plant species	Aphthona species
Gramineae	Oryza	bicolorata
	Poa annua	euphorbiae
	Zea mays	(bicolorata, nanyoensis)
	bermuda grass	samoana
	"cereals"	euphorbiae
Cyperaceae	Carex irrigua	erichsoni
Iridaceae	Iris germanica	semicyanea, violacea
	I. pseudacorus	coerulea, violacea
	I. sibirica	coerulea

Appendix 2

List of Sampling Localities

Table A-3 lists the beetles found on each host at each sampling locality, for collections made by Gisela Sommer and myself in the summer of 1978.

Entries are grouped by country and by major political subdivision within country (departments of France, cantons of Switzerland, states of West Germany, provinces of Austria, counties of Hungary).

Unless preceded by abbreviated generic names (G.= *Geranium*, H.= *Helianthemum*, I.= *Iris*) the host entries in the third column are *Euphorbia* species.
A dash in the fourth column (*Aphthona* species) indicates no beetles were found. Note that all collections were of imagines only.

Five spurge populations in eastern Hungary exhibited characters intermediate between those appropriate to 'good' *E. esula* and *E. virgata*, or were mosaics of these characters, and could not be assigned to species with which we were familiar. In the list I have designated all of these '*esu.* × *virg.*?' for convenience. Four additional non-flowering populations from the same region were tentatively designated 'hairy esula' in the field. I have here hesitantly assigned these populations to *E. hebecarpa* Boissier (a species of Asia Minor to which Croizat (1945)

assigned the Central European and Balkan *E. Esula pubescens* Griseb., *E. salicifolia angustata* Roch. and *E. paradoxa* Borb.). I am reasonably confident that the remaining determinations are correct within the confines of current European floristic paractices.

Table A-3
List of sampling localities, Sommer and Maw, 1978.

Locality	Date	Host	Aphthona sp.
SWITZERLAND			
Jura			
Delémont	19.V	cyparissias	venustula
	27.V	amygdaloides	pygmaea
			venustula
	25.VII	falcata	—
	7,8.VI	G.robertinianum	—
Soyhières I	6.VI	cyparissias	pygmaea
			venustula
		verrucosa	cyparissiae
			delicatula
			cyanella
	27.VI	cyparissias	cyparissiae
			delicatula
		H. nummilarium	herbigrada
	19.IX	cyparissias	cyparissiae
			delicatula
			pygmaea
			venustula
		H. nummilarium	herbigrada
Soyhières II	6.VI	amygdaloides	venustula
		cyparissias	pygmaea
			venustula
		stricta	—
		verrucosa	—
	27.VII	cyparissias	—
Liesberg	6.VI	cyparissias	—
		stricta	abdominalis
		verrucosa	—
	21.VI	G.robertinianum	—
FRANCE			
Bas Rhin			
Marckolsheim I	10.VI	cyparissias	abdominalis
			cyparissiae
		stricta	—
Marckolsheim II	10.VI	cyparissias	cyparissiae
			cyparissiae
			venustula
		seguieriana	—
Haut Rhin			
Roggenhouse	10.VI	cyparissias	cyparissiae
			venustula
	4.IX	cyparissias	cyparissiae
			venustula
			herbigrada

Locality	Date	Host	Aphthona sp.
Rosenau	22.VII	cyparissias	cyparissiae herbigrada
		seguieriana	——
		H. nummilarium	——
Kembs	22.VII	cyparissias	cyparissiae herbigrada
		stricta	——
GERMAN FEDERAL REPUBLIC			
Baden-Württemberg			
Vogelsang	17.V	cyparissias	venustula
Istein I	29.V	amygdaloides	venustula
		cyparissias	venustula
	4.IX	amygdaloides	venustula
		cyparissias	cyparissiae venustula
Istein II	29.V	stricta	venustula
Istein III	29.V	cyparissias	abdominalis cyparissiae pygmaea venustula
	4.IX	cyparissias	cyparissiae pygmaea
		H. nummilarium	herbigrada
Istein IV	2.VI	cyparissias	pygmaea venustula
	4.IX	cyparissias	cyparissiae herbigrada pygmaea venustula
Rheinweiler	2.VI	cyparissias	abdominalis pygmaea venustula
Bellingen	2.VI	cyparissias	abdominalis venustula
Steinenstadt I	2.VI	cyparissias	cyparissiae pygmaea
		seguieriana	pygmaea
Steinenstadt II	2.VI	cyparissias	cyparissiae pygmaea venustula
		seguieriana	abdominalis cyparissiae pygmaea
		stricta	——

Locality	Date	Host	Aphthona sp.
Neuenburg I	2.VI	cyparissias	pygmaea
			venustula
		H. nummilarium	herbigrada
		seguieriana	—
		stricta	—
		verrucosa	—
Neuenburg II	4.IX	cyparissias	cyparissiae
			pygmaea
			venustula
		H. nummilarium	herbigrada
Huggstetten	17.V	I. pseudacorus	coerulea
	9.VI	I. pseudacorus	coerulea
Vogtsburg I	9.VI	cyparissias	venustula
		seguieriana	venustula
		G. pratense	—
Vogtsburg II	9.VI	cyparissias	—
		seguieriana	—
Jechtingen	9.VI	I. pseudacorus	coerulea
Sasbach	10.VI	cyparissias	cyparissiae
		seguieriana	—
AUSTRIA			
Niederösterreich			
St. Pölten I	21.VI	cyparissias	ovata
		stricta	ovata
		Linum sp.	—
	22.VI	cyparissias	cyparissiae
			ovata
		esula	ovata
St. Pölten II	22.VI	esula	cyparissiae
			venustula
Tausendblum	22.VI	cyparissias	cyparissiae
			ovata
		esula	—
		helioscopia	—
	14.VII	cyparissias	ovata
Kirchstetten I	22.VI	esula	czwalinae
	14.VII	esula	—
Kirchstetten II	22.VI	stricta	—
		virgata	—
Sichelbach	22.VI	cyparissias	—
		esula	cyparissiae
			lacertosa
		exigua	—
		falcata	—
		helioscopia	—
	14.VII	esula	cyparissiae
			czwalinae

Locality	Date	Host	Aphthona sp.
Boheimkirchen I	22.VI	cyparissias	cyparissiae
		esula	cyparissiae
Boheimkirchen II	22.VI	esula	venustula
Kogel	23.VI	cyparissias	cyparissiae
			venustula
Streifhofen I	23.VI	cyparissias	cyparissiae
Streifhofen II	23.VI	cyparissias	cyparissiae
Atzenbrugg	23.VI	esula	cyparissiae
			czwalinae
	14.VII	esula	cyparissiae
			czwalinae
			venustula
Saladorf	23.VI	helioscopia	—
Judenau	23.VI	cyparissias	cyparissiae
		esula	cyparissiae
			czwalinae
Tulln	24.VI	cyparissias	cyparissiae
			venustula
		esula	—
		virgata	—
Trübensee I	24.VI	cyparissias	cyparissiae
		esula	—
		virgata	—
Trübensee II	25.VI	cyparissias	ovata
Starnwörth	25.VI	cyparissias	cyparissiae
Stetteldorf am Wagram	25.VI	virgata	—
Absdorf I	25.VI	esula	—
Absdorf II	25.VI	esula	—
Kleinwiesendorf	25.VI	virgata	lacertosa
Großweikersdorf	25.VI	seguieriana	lacertosa
Unterthern	25.VI	virgata	lacertosa
		seguieriana	—
Oberthern I	25.VI	virgata	—
Oberthern II	25.VI	virgata	lacertosa
Aspersdorf	25.VI	virgata	—
Raffelhof	25.VI	esula	—
Maria-Roggendorf	25.VI	esula	—
		virgata	czwalinae
	26.VI	esula	czwalinae
		virgata	—
		helioscopia	—
Haslach	26.VI	virgata	—
Enzersdorf	26.VI	esula	czwalinae
		virgata	—
Stronsdorf	26.VI	esula	—
		virgata	—
Unterschotterlee	26.VI	virgata	—
Wultendorf	26.VI	cyparissias	cyparissiae
			lacertosa
		virgata	cyparissiae

Locality	Date	Host	Aphthona sp.
Staatz	26.VI	cyparissias	cyparissiae
		esula	—
Falkenstein	26.VI	cyparissias	abdominalis
			cyparissiae
		esula	—
		virgata	—
Poysbrunn	26.VI	virgata	—
Ernsdorf bei Staatz	26.VI	esula	czwalinae
			venustula
		helioscopia	—
		virgata	—
Schletz	26.VI	virgata	—
Pfaffstätten I	27.VI	virgata	—
Pfaffstätten II	27.VI	virgata	—
Gumpoldskirchen	27.VI	cyparissias	—
Mödling I	27.VI	cyparissias	—
		virgata	—
Mödling II	27.VI	esula	cyparissiae
Neu-Guntersdorf	27.VI	virgata	—
Laxenburg	27.VI	esula	—
Munchendorf	27.VI	esula	—
		virgata	—
Mitterndf.a.d.Fischa	27.VI	esula	cyparissiae
			czwalinae
			flava
			lacertosa
Gramatneusiedl	27.VI	cyparissias	cyparissiae
		virgata	—
Fischamend Markt	28.VI	cyparissias	—
Maria Ellend	28.VI	helioscopia	—
Haslau an der Donau	28.VI	cyparissias	cyparissiae
		esula	cyparissiae
Regelsbrunn	28.VI	esula	czwalinae
Hundsheimer Berge	28.VI	cyparissias	cyparissiae
		segetieriana	—
Deutsch Haslau	29.VI	cyparissias	cyparissiae
		helioscopia	—
Neulengbach	14.VII	cyparissias	—
		esula	cyparissiae
Burgenland			
Gattendorf	29.VI	helioscopia	—
		virgata	—
Zurndorf	29.VI	esula	—
		virgata	—

Locality	Date	Host	Aphthona sp.
HUNGARY			
Győr-Sopron			
Hegyeshalom I	29.VI	virgata	—
Hegyeshalom II	13.VII	cyparissias	cyparissiae
		esula	cyparissiae
Hegyeshalom III	13.VII	virgata	—
Mosonmagyaróvár	29.VI	cyparissias	cyparissiae
Öttevény	29.VI	cyparissias	cyparissiae
			czwalinae
			flava
			lacertosa
			venustula
		esula	czwalinae
		platyphyllos	—
	13.VII	cyparissias	cyparissiae
			flava
			nigriscutis
Abda	29.VI	cyparissias	—
		helioscopia	—
		platyphyllos	—
Győr I	29.VI	cyparissias	cyparissiae
			czwalinae
			flava
		seguieriana	cyparissiae
	13.VII	cyparissias	cyparissiae
			czwalinae
			flava
		seguieriana	cyparissiae
			flava
Győr II	30.VI	virgata	—
		stricta	—
Győrújbarát	30.VI	cyparissias	cyparissiae
			czwalinae
			flava
			lacertosa
		esula	—
		virgata	—
Győrszemere	30.VI	cyparissias	cyparissiae
Győrszemere – Tét	30.VI	cyparissias	—
		esula	—
Vámosszabadi I	13.VII	cyparissias	czwalinae
			flava
		esula	—
		virgata	—
Vámosszabadi II	13.VII	virgata	cyparissiae
			czwalinae
			flava
Arak	13.VII	virgata	—

Locality	Date	Host	Aphthona sp.
Veszprém			
Takácsi	30.VI	cyparissias	flava
		helioscopa	—
		stricta	—
Járifőld	30.VI	cyparissias	abdominalis
			flava
			lacertosa
			lutescens
			nigriscutis
		seguieriana	—
Bakonyjákó	30.VI	cyparissias	flava
			venustula
Farkasgyepü	30.VI	cyparissias	flava
			nigriscutis
			venustula
Vörösberény	30.VI	cyparissias	—
		pannonica	—
		seguieriana	—
Szentkirályszabodja	30.VI	cyparissias	cyparissiae
			flava
			lacertosa
			pygmaea
		seguieriana	nigriscutis
		virgata	—
Aszófö	1.VII	cyparissias	—
		seguieriana	nigriscutis
		G. pratense	—
		Linum sp.	—
Péscely I	1.VII	cyparissias	flava
			lacertosa
			nigriscutis
		seguieriana	cyparissiae
			flava
			lacertosa
		pannonica	—
Péscely II	1.VII	cyparissias	lacertosa
		pannonica	lacertosa
			pygmaea
Tótvázsony	1.VII	cyparissias	—
		seguieriana	lacertosa
			nigriscutis
Somogy			
Kőröshegy	1.VII	cyparissias	flava
			lacertosa
			nigriscutis
		seguieriana	nigriscutis
Jct. #61 & #66 Hwy.	2.VII	cyparissias	—
Sántos	2.VII	cyparissias	flava
			nigriscutis
		platyphyllos	—

Locality	Date	Host	Aphthona sp.
Cserénfa	2.VII	esula	—
		platyphyllos	—
Kaposgyarmat	2.VII	cyparissias	flava
		esula	—
		seguieriana	—
		platyphyllos	—
Gálosfa	2.VII	esula	pygmaea
		platyphyllos	—
		stricta	—
Böszénfa	2.VII	cyparissias	flava
		esula	—
Pécs			
Szentdénes	2.VII	esula	—
Szentdénes – Sumony	2.VII	esula	—
		stricta	—
Sumony	2.VII	cyparissias	—
		stricta	—
Nagycsány	2.VII	cyparissias	flava
			nigriscutis
			venustula
		esula	nigriscutis
Siklő	2.VII	virgata	lacertosa
Villány	2.VII	cyparissias	abdominalis
			flava
			lacertosa
			pygmaea
Komló	3.VII	cyparissias	flava
			ovata
			pygmaea
		virgata	—
Zobakpuszta	3.VII	cyparissias	—
		esula	—
Pécs – Vasas	3.VII	esula	—
		helioscopia	—
		platyphyllos	—
Bogád	3.VII	cyparissias	flava
Rumony	3.VII	cyparissias	flava
Pereked I	3.VII	cyparissias	—
		virgata	—
Pereked II	3.VII	cyparissias	cyparissiae
		esula	—
		seguieriana	—
		virgata	flava
Berkesd	3.VII	cyparissias	flava
			lacertosa
		pannonica	lacertosa
		seguieriana	—
Pécsvárad I	3.VII	cyparissias	flava
			nigriscutis
		pannonica	flava
		seguieriana	—

Locality	Date	Host	Aphthona sp.
Pécsvárad II	3.VII	cyparissias	flava
			lacertosa
		seguieriana	—
	4.VII	cyparissias	cyparissiae
			flava
			lacertosa
		seguieriana	czwalinae
Erzsébet	3.VII	cyparissias	cyparissiae
			flava
			lacertosa
		helioscopia	—
		seguieriana	—
Kátoly	3.VII	cyparissias	cyparissiae
			flava
		seguieriana	pygmaea
Himesháza I	3.VII	cyparissias	cyparissiae
			flava
			nigriscutis
		esula	—
		seguieriana	cyparissiae
		virgata	—
Himesháza II	4.VII	cyparissias	cyparissiae
			flava
	-		lacertosa
		seguieriana	cyparissiae
			flava
Fazekasboda	4.VII	seguieriana	pygmaea
			venustula
Dunaszekcső	4.VII	cyparissias	flava
		platyphyllos	—
Tolna			
Báta	4.VII	lucida	violacea
Tolna	4.VII	cyparissias	flava
			nigriscutis
Dombori	4.VII	lucida	—
		platyphyllos	—
		seguieriana	cyparissiae
Pörböly I	5.VII	lucida	—
Pörböly II	5.VII	lucida	violacea
		palustris	—
Kiskun			
Baja	5.VII	cyparissias	flava
			nigriscutis
		esula	—
		pannonica	—
Bácsbokod	5.VII	cyparissias	—
		pannonica	—
Csikéria	5.VII	esula	—

Locality	Date	Host	Aphthona sp.
Csongrád			
Algyő	6.VII	cyparissias	nigriscutis
		seguieriana	—
		virgata	—
AlgyőII	6.VII	lucida	—
		virgata	violacea
Nagyfa	6.VII	virgata	—
Seged – Maroslele I	6.VII	esu. × virg.?	—
Seged – Maroslele II	6.VII	lucida	—
Maroslele – Makó	6.VII	virgata	—
Békés			
Tótkomlós	6.VII	cyparissias	flava
			lacertosa
Kamut I	6.VII	virgata	—
		esu. × virg.?	—
Kamut II	6.VII	virgata	—
Murony	6.VII	cyparissias	—
		helioscopia	—
		virgata	lacertosa
Megyesbodzás	7.VII	virgata	lacertosa
Lökösháza	7.VII	cyparissias	lacertosa
Gerla I	8.VII	esula	—
Gerla II	8.VII	lucida	ovata
Doboz	8.VII	lucida	lacertosa
			violacea
		platyphyllos	euphorbiae
Sarkadkeresztúr	8.VII	cyparissias	—
		platyphyllos	violacea
Nagygyanté	8.VII	lucida	lacertosa
			violacea
		virgata	—
Zsadány	8.VII	virgata	cyparissiae
			lacertosa
Zsadány – Biharuga	8.VII	platyphyllos	—
Biharuga	8.VII	cyparissias	lacertosa
		hebecarpa?	—
Tarkós	8.VII	lucida	—
Békéscsaba	8.VII	virgata	—
Kondoros	9.VII	cyparissias	lacertosa
		virgata	—
Kardos	9.VII	cyparissias	—
		virgata	—
		esu. × virg.?	lacertosa
Orménykút	9.VII	cyparissias	lacertosa
Endrőd	9.VII	virgata	lacertosa
		esu. × virg.?	—
Gyoma	9.VII	virgata	lacertosa
		platyphyllos	—
Körösladány	9.VII	cyparissias	—
		virgata	lacertosa

Locality	Date	Host	Aphthona sp.
Hajdú-Bihar			
Körösnagyharsány	8.VII	hebecarpa?	—
Mezősas	8.VII	esu. × virg.?	flava
			lacertosa
Berettyóújfalu I	8.VII	cyparissias	euphorbiae
Berettyóújfalu II	9.VII	esula	—
		virgata	—
Berettyóújfalu III	10.VII	cyparissias	lacertosa
Furta	8.VII	cyparissias	lacertosa
Bélmegyer	8.VII	lucida	lacertosa
			violacea
Biharnagybajom	9.VII	cyparissias	—
Nagyrábé	9.VII	cyparissias	—
Bakonszeg	9.VII	hebecarpa?	—
		virgata	lacertosa
Hosszúpályi	9.VII	platyphyllos	—
Monostorpályi	9.VII	lucida	violacea
		salicifolia	violacea
Kismarja	9.VII	cyparissias	lacertosa
Bedő	9.VII	hebecarpa?	—
		platyphyllos	—
Náduvar	10.VII	virgata	—
Hajdúszovát I	10.VII	cyparissias	lacertosa
Hajdúszovát II	10.VII	cyparissias	lacertosa
		virgata	—
Hajdúszoboszló	10.VII	cyparissias	lacertosa
Lévértes	10.VII	lucida	—
Vámospércs	10.VII	platyphyllos	violacea
Hajdúsámson	11.VII	esula	euphorbiae
			nigriscutis
Nyíradony	11.VII	cyparissias	nigriscutis
Szabolcs-Szatmar			
Nyírbéltelek	11.VII	cyparissias	nigriscutis
			pygmaea
Terem	11.VII	cyparissias	—
Nyírgyulaj	11.VII	cyparissias	flava
			nigriscutis
Pest			
Aszód	12.VII	cyparissias	—
		pannonica	—
Pilisvörösvár	12.VII	cyparissias	flava
			nigriscutis
			pygmaea
		esula	—
		seguieriana	nigriscutis

Locality	Date	Host	Aphthona sp.
Komárom			
Tát	12.VII	cyparissias	—
Lábatlan I	12.VII	cyparissias	—
		esula	—
		platyphyllos	—
Lábatlan II	12.VII	cyparissias	cyparissiae
		seguieriana	cyparissiae

Appendix 3

Euphorbia species encountered during field work

(see chapter 6)

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1. **Classification** (according to Prokhanov (1949))

subgenus *Esula*	
section **Tulocarpa**	
subsection **Lutescentes**	*stricta, platyphyllos, palustris*
subsection **Purpuratae**	*verrucosa*
subsection **Helioscopiae**	*helioscopia*
section **Murtekias**	
subsection **Coniocarpae**	
series **Sequierianae**	*seguieriana*
series **Nicaeensis**	*pannonica*
section **Esula**	
subsection **Esulae**	
series **Esulae**	*esula*
series **Lucidae**	*lucida, salicifolia*
series **Virgatae**	*virgata, cyparissias*
subsection **Patellares**	*amygdaloides*
section **Cymatospermum**	
subsection **Oleraceae**	*exigua, falcata*

2. The spurges

E. stricta, *platyphyllos*, *helioscopia*, *exigua*, and *falcata* are annual, often weedy species.

E. seguieriana, *pannonica*, and *verrucosa* are tufted perennials. *E. verrucosa* occurs on mesic sites in western Europe. *E. sequieriana* is a plant of mesic to dry sites across Europe, and *E. pannonica* in south-eastern Europe.

E. palustris is a tall perennial of wet habitats.

E. lucida and *salicifolia* are creeping perennials of mesic habitats.

E. esula, *virgata*, and *cyparissias* are creeping perennials as discussed elsewhere.

E. amygdaloides is a creeping woodland perennial of Europe with bienniel shoots.

All of the above species are herbaceous.

Biographical Note

I was born in April, 1955 in Oxford, England, but grew up in Belleville, Ontario, completing my primary, and beginning my secondary schooling there. My family later moved to Regina, Sask., where I completed my secondary education.

In 1973, I entered the University of Regina, and obtained a Bachelor of Science Degree in Biology in 1977. In the same year, I enrolled in a Master of Science programme in this Department, the results of which are presented herewith.