A revision of the genus *Chaetorellia* Hendel (Diptera: Tephritidae) including a new species associated with spotted knapweed, *Centaurea maculosa* Lam. (Asteraceae)

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Abstract

Chaetorellia acrolophi sp. n. is associated with some European species of the subgenus *Acrolophus* of *Centaurea*. It is a potential biocontrol agent of some *Acrolophus* species that are adventive noxious weeds in North America. *Ch. acrolophi* sp. n. is described, and a key is provided to all nine species. The confirmed host-plants, knapweed, starthistles and related plants, belong to the genera *Centaurea*, *Carthamus* and *Chartolepis* (Asteraceae), and these are listed. Available biological data are reviewed, and some details of egg, larval and pupal morphology are described. Host-plant choice tests and canonical variates analysis were used to justify the separation of some species and to help identify some populations. The following nomenclatural changes are made (junior synonyms in brackets): *Chaetorellia conjuncta* (Becker) is removed from synonymy with *Ch. succinea* (Costa); *Ch. hexachaeta australis* Hering is raised to specific status; *Ch. hestia* Hering (= *Ch. nigropicta* Hering); *Ch. loricata* (Rondani) (= *Ch. mara* Hering and *Ch. loricata septentrionalis* Hering). Questionable synonyms include: *Ch. australis* Hering (?= *Trypeta hexachaeta* Loew); *Ch. hestia* (?= *T. vittata* Rondani); *Chaetostomella cylindrica* (Robineau-Desvoidy) (?= *Tephritis algira* Macquart, which is removed from *Chaetorellia*).

Introduction

Chaetorellia, a western and central Palaearctic genus, belongs to the tribe Terelliini (Tephritidae, Tephritinae). The nine known species attack the capitula of *Centaurea*, *Carthamus* and *Chartolepis* species, which are knapweeds and starthistles belonging to the subtribe Centaureinae (Asteraceae, Cardueae). Twenty-seven species of Palaearctic Centaureinae are adventive in North America (Moore, 1972), and safflower *Carthamus tinctorius*, is a crop plant there. Within their native range, safflower and eleven of the species adventive in North America are attacked by *Chaetorellia*. Some *Chaetorellia* species are potential biological control agents of noxious weeds in North America, namely *Ch. acrolophi* sp. n. for spotted knapweed, *Centaurea* sp. nr *maculosa*, and possibly diffuse knapweed, *Ce. diffusa*, and *Ch. australis* Hering for yellow starthistle, *Ce. solstitialis*. The importance of these three weeds is exemplified by yellow starthistle, which covers over 3

million hectares of the western USA, most of which would be rangeland were it not for this plant (Maddox, 1981; Maddox & Mayfield, 1985; Maddox *et al.*, 1985). Diffuse knapweed is mostly found to the north of the yellow starthistle area, particularly in an area of low rainfall centred on the Okanagan Valley of British Columbia and the Okanogan Valley of Washington State; spotted knapweed infests areas of higher rainfall to the east of the Okanagan Valley (Harris & Myers, 1984; Piper, 1985; Story, 1985). A general review of the possible origins, taxonomy, control and distribution of these knapweeds is given by Roché *et al.* (1986).

The aim of the present study was to group *Chaetorellia* populations into species so that a host-plant list and a key to the species could be produced. Particular emphasis was placed on the study of populations associated with spotted knapweed and its relatives within the subgenus *Acrolophus* of *Centaurea*. It was concluded that these populations represented an undescribed species, *Ch. acrolophi* sp. n., and much of the following paper concerns its separation from four morphologically similar species; preliminary results were reported by White (1989*b*). Studies of other groups of European Tephritidae of value to weed biocontrol have also been produced (White, 1989*a*; White & Clement, 1987; White & Korneyev, 1989).

The genus *Chaetorellia* was described by Hendel (1927) to include ten nominal species, and of these only the type-species, *Tephrytis jaceae* Robineau-Desvoidy, has a type host, namely *Ce. jacea*. Subsequently, Stackelberg (1929) described *Ch. carthami* from *Ca. tinctorius* and Hering (1937*a*; *b*; 1940) described nominal species associated with *Ce. apiculata*, *Ce. scabiosa* and *Ce. solstitialis*. The first key to the genus was produced by Hendel (1927), and Hering (1937*b*) expanded it to include new species; the key by Dirlbek & Dirlbekova (1974) is simply a copy of Hering's key. Recently, Foote (1984) catalogued the 19 nominal species, and Korneyev (1983; 1985) listed some further synonyms.

Attempting to identify a reared series of specimens with any previously published key usually results in different answers for different specimens in a reared series that almost certainly represents a single species. Most of the characters used in previous keys are good generalizations, but they cannot be used as a basis for reliable identification. The lack of a reliable key has also caused large numbers of misidentifications, e.g. the name *Ch. hexachaeta* (Loew) has been applied to four different species. In the present study, evidence is presented to justify the grouping of several host-defined populations into nine species and two species-groups.

Materials

Most specimens were collected during field surveys of Cardueae-associated insects, carried out by weed biocontrol specialists. The sampling was carried out in western Europe (CIBC, CIE, CSIRO), Greece (USDA, CIBC, CIE), Hungary (CIBC, CIE), Israel (TAU, CIE), Poland (CIBC), Romania (CIBC), Turkey (CIBC, USDA) and the Caucasus (ACR). Where possible, reared samples were used for the morphometric analysis. However, the population density of some *Chaetorellia* populations is very low, often only one female per 100 capitula, and sweeping single species stands of *Centaurea* was sometimes the only method by which adequate samples could be obtained. The materials examined sections that accompany the notes on each species only give full data for material included in the morphometric analyses and for type specimens; full data for all dissected specimens is available from the senior author.

Institutions who lent specimens for this study, or who carried out surveys, were as follows: Agriculture Canada, Weed Biocontrol Research Station, Regina, Canada (ACR); British Museum (Natural History), London, England (BMNH); Canadian National Collection, Agriculture Canada, Ottawa, Canada (CNC); CAB International Institute of Biological Control, Delémont, Switzerland (CIBC); CAB International Institute of Entomology, London, England (CIE); Commonwealth Scientific and Industrial Research Organization, Montpellier, France (CSIRO); Lehrstuhl für Tierokologie, Universität Bayreuth, West Germany (LTUB); Muséum d'Histoire Naturelle, Lille, France (MHNL); Muséum National d'Histoire Naturelle, Paris, France (MNHNP); Museo Zoologico dell'Università

degli Studi di Firenze, Florence, Italy (MZF); Naturhistorisches Museum, Basel, Switzerland (NHMB); Naturhistorisches Museum, Vienna, Austria (NHMV); All-Union Institute of Biocontrol for Plant Protection, Kishinev, USSR (IBPPK); Staatliches Museum für Naturkunde, Stuttgart, BRD (SMNS); Tel Aviv University, Israel (TAU); Termeszettudomanyi Muzeum, Budapest, Hungary (TMB); United States Department of Agriculture, Weed Biological Control Laboratory, Rome, Italy (USDA); National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); Zoological Institute, Soviet Academy of Sciences, Leningrad, USSR (ZIL); Zoologisches Museum, Humboldt Universität, Berlin, DDR (ZMHB); Zoological Museum, Ukrainian Academy of Sciences, Kiev, USSR (ZMK); Zoological Museum, University of Bergen, Norway (ZMUB); Zoologisk Museum, Universitets Copenhagen, Denmark (ZMUC).

## Species-group characters and biology

The genus *Chaetorellia* was divided into the *Ch. loricata* (Rondani) and *Ch. jaceae* species-groups by Korneyev (1985) on the basis of adult characters. These groups also differ in egg morphology and oviposition behaviour. *Ch. succinea* (Costa) and *Ch. carthami* deposit groups of eggs under the middle involucral bracts of *Ce. solstitialis* (H. Zwölfer, unpublished CIBC data, 1972) and *Carthamus* species (Al-Ali *et al.*, 1979), respectively. These species both belong to the *Ch. loricata* species-group, all of which have a uniform egg structure (Fig. 2) typical of many Terelliini. Unfortunately, the oviposition habits of the other two members of this species-group are unknown. Eggs were dissected from gravid females of all species, and the structure of these *Ch. loricata* group eggs was found to be similar to that of *Dacus oleae* (Gmelin), which has an anterior cup-shaped structure through which the micropylar canal passes (Margaritis, 1985).

Ch. australis, a member of the *Ch. jaceae* species-group, usually deposits a single egg per flower bud of its host (H. Zwölfer, unpublished CIBC data, 1972; I. Pittara, unpublished USDA data, 1985), but up to seven eggs have been found together (Sobhian & Zwölfer, 1985). The eggs of *Ch. acrolophi*, *Ch. conjuncta* (Becker) and *Ch. jaceae* have also been observed *in situ* and they were usually found singly beneath a middle involucral bract (very few observations were made of *Ch. conjuncta* and *Ch. jaceae*). Species belonging to the *Ch. jaceae* species-group also have a uniform egg structure (Fig. 1), but it differs from that of other known species of Terelliini, except for *Craspedoxantha* species (Friedberg, 1985). Eggs of the former are remarkable for the long tube which separates the anterior cup-shaped structure from the main body of the egg. Eggs were dissected from gravid females of all species, and they were each found to have an egg body about 1·0 mm long. The egg tube of *Ch. conjuncta* is exceptionally long, varying in length from about 2·6 to 3·0 mm, but the other four species of the *Ch. jaceae* group have shorter egg tubes (1·1–2·6 mm). After oviposition, these egg tubes are orientated vertically up the bract from the main body of the egg (Figs 22–24), but their function is not understood. According to Varley (1937), the first-instar larva of *Ch. jaceae* develops with its head directed away from the micropyle, which is contrary to the norm. However, *Ch. acrolophi* develops with its head directed towards the micropyle, but it turns within the chorion before eclosion; it is likely that Varley (1937) examined *Ch. jaceae* at this stage.

The only published larval description of a species of *Chaetorellia* is by Varley (1937), who described *Ch. jaceae*; Efflatoun (1927) described a mixed sample of *Ch. conjuncta* and *Acanthiophilus helianthi* (Rossi), and called it *Ch. jaceae*, in error. In the present study, the larvae and/or pupae of *Ch. acrolophi*, *Ch. australis*, *Ch. conjuncta*, *Ch. hestia* Hering, *Ch. jaceae*, *Ch. loricata* and *Ch. succinea* were examined. No distinct differences were found in the form of the cephalopharyngeal skeleton or the posterior spiracles. The openings of each anterior spiracle varied in number from five to seven in *Ch. jaceae*; other species fitted within this range, but too few specimens were examined to know if they also varied as much as *Ch. jaceae*. In all species of *Chaetorellia* examined, the posterior spiracle openings were placed at about 45° to each other (Figs 3, 4) (they are almost parallel in *A. helianthi*). The only distinct interspecific difference observed was in the branching of the spiracular hairs of the posterior spiracles; *Ch. acrolophi*, *Ch. australis*, *Ch. conjuncta*, *Ch. hestia*, *Ch.*

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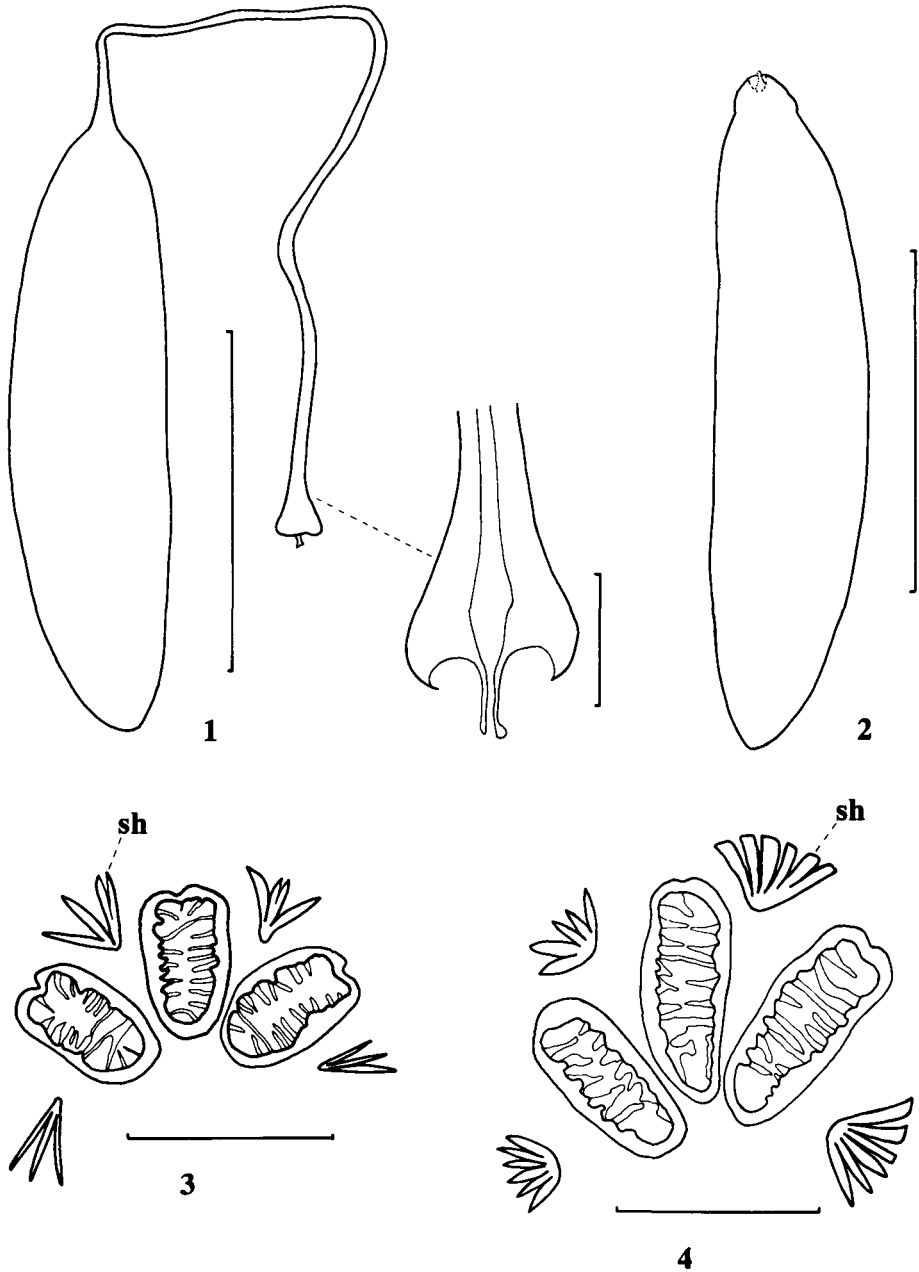
Figs 1–2.—Eggs; 1, *Chaetorellia jaceae* (Robineau-Desvoidy), with detail of presumed micropyle; 2, *Ch. carthami* Stackelberg (scale lines for eggs = 0·5 mm; scale line for egg detail = 0·05 mm). Figs 3–4.—Posterior spiracles of final instar larvae; 3, *Ch. acrolophi* sp. n.; 4, *Ch. succinea* (Costa) (scale lines for spiracles = 0·05 mm; sh, spiracular hair).
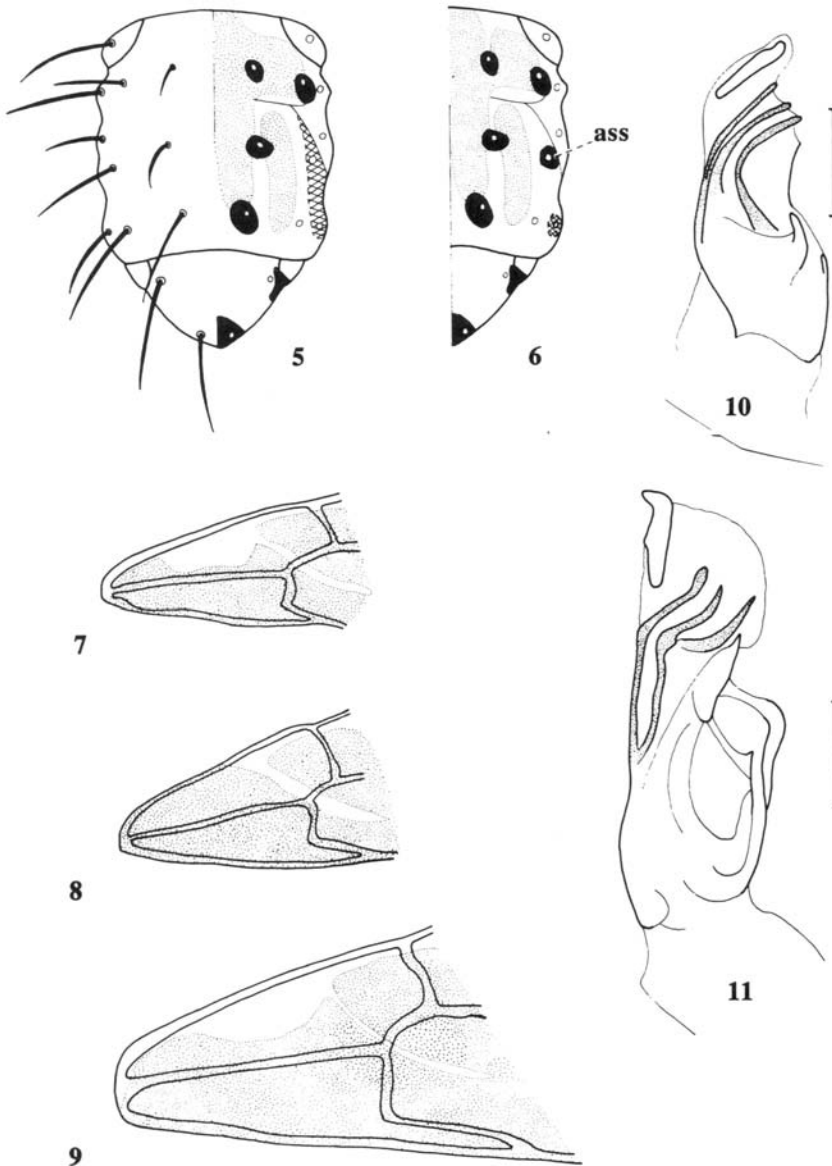
Figs 5–6.—Scutal patterning; 5, *Chaetorellia jaceae* (Robineau-Desvoidy) species-group, with cross-hatching to mark area that is black in some populations of *Ch. hestia* Hering and a few overwintered individuals of *Ch. australis* Hering; 6, *Ch. loricata* (Rondani) species-group, with cross-hatching to mark additional spot found on some individuals (ass, position of anterior supra-alar seta). Figs 7–9.—Wing cells *bm* and *cup* with yellow patterned areas stippled; 7, usual form of *Ch. acrolophi* sp. n., *Ch. australis*, *Ch. conjuncta* (Becker) and *Ch. jaceae*; 8, usual form of *Ch. hestia*; 9, usual form of *Ch. loricata* group species. Figs 10–11.—Aedeagal glans with taxonomically important areas stippled; 10, *Ch. jaceae* (other members of the group are similar); 11, *Ch. loricata* (other members of the group are similar); (scale lines = 0·1 mm).

jaceae and *Ch. loricata* have three branched hairs (Fig. 3), with each branch sometimes secondarily divided, but *Ch. succinea* has five or six broad branches (Fig. 4). Sobhian & Zwölfer (1985) reported a behavioural difference in the larvae of the two generations of *Ch. australis* that develop in *Ce. solstitialis*; the summer generation larvae spin a loosely woven cocoon from 'pappus hairs' (error for receptacle scales ?) and pupate in a vertical position, but the overwintering larvae spin a more tightly woven cocoon and usually pupate in a horizontal position. Similarly, *Ch. acrolophi* in *Ce. vallesiaca* spins a cocoon from receptacle scales which is loosely woven in the summer generation but tightly woven in the overwintering generation.

Adult males of all species were dissected, and two types of aedeagal glans were found. Species assigned to the *Ch. loricata* group all have a sinuate duct through the aedeagal glans (Fig. 11); conversely, species of the *Ch. jaceae* group lack the sinuation in this duct (Fig. 10). Other species-group characters are the spot pattern on the scutum (Figs 5, 6), the length of the extension to cell *cup* (Figs 7–9) and the shape of the female's aculeus (Figs 13–21). Unfortunately, no differences were found in the male terminalia that could help in the recognition of individual species.

Analysis of the *Chaetorellia jaceae* species-group

Four different approaches were taken to the problem of testing which hosts-associated populations appeared to represent distinct species. Gel electrophoresis and hybridization tests were attempted but had to be abandoned due to difficulty in obtaining suitable samples. The remaining two approaches to the problem were the multivariate morphometric analysis of adults associated with different host-plants and the analysis of host-choice behaviour.

In the morphometric analyses, the assumption was made that any specimens associated with a single species of *Centaurea* at a single locality represented a single species of *Chaetorellia*; however, prior to analysis, it was not assumed that flies from the same host in different areas were the same species, nor that flies from different hosts were different species. Where possible, measurements were taken from wings and dissected abdomens that had been slide-mounted. Characters that are measured from microscope slides can be measured more accurately than the curved surfaces of head and thorax characters; additionally, the wing characters gave an index of body size and the ovipositor characters appear to be adaptive to the host-plants.

The following ten characters were measured initially: 1, length of cell *dm* along vein *M*; 2, length of *dm* along *M* to *r-m* crossvein; 3, length of *C* between R_1 and R_{2+3}; 4, length of *C* between R_{2+3} and R_{4+5}; 5, length of *C* between R_{4+5} and *M*; 6, length of R_{4+5} beyond *r-m*; 7, length of *M* beyond *dm-cu*; 8, length of aculeus; 9, length of ventral lobes of aculeus; 10, angle of aculeus apex. Wing length was not used for analysis because the wing base was often damaged during slide preparation. Character 10, the *aculeus apex angle*, is the angle between imaginary lines placed tangentially across each side of the tapering aculeus apex (Fig. 17); it was measured using a protractor viewed through the drawing tube of a compound microscope. Terminology follows McAlpine (1981), with modifications proposed by Foote & Steyskal (1987), Norrbom & Kim (1988) and White (1988).

Eighty-two specimens from nine species of host-plant were measured for a preliminary analysis of the ten characters. These data were studied by principal component analysis, which indicated that the chosen characters tended to group specimens according to host-plant. A one-way analysis of variance was carried out for each of the ten characters and nine host-associated groups. It was found that all characters had significantly more (mostly $P<0.001$) between-group than within-group variance, but some *F* values were far greater than others. The wing characters had *F* ratios of between 6 and 26, but the aculeus characters had *F* ratios of between 118 and 222. The low within-group variance of the aculeus characters indicated that they should be very good discriminatory characters. It was decided that aculeus length and aculeus apex angle should be used for further study, together with the two wing characters that received the highest *F* ratios. The validity of the character selection was confirmed by comparing the results of canonical variates (CV)

analyses based on all ten characters and the four selected characters; the two analyses gave very similar results, indicating that the six rejected characters were redundant.

A canonical variate (CV) analysis is an extension of principal component analysis, which facilitates study of the relationship of group means rather than individuals. CV analysis takes into account within-group and between-group variance, and produces a set of character weights that are then applied to the measured characters. This results in a set of values that express the position of the group means with respect to transformed axes; for a technical account see Campbell & Atchley (1981). Following CV analysis, the character weights can be used to calculate the position of a new individual or sample mean on each axis, so a likely identification can be made of this new individual or sample by calculating which of the original group means it falls closest to. The CV analyses were carried out using a BASIC computer program, based on a FORTRAN program by Blackith & Reyment (1971).

The following abbreviations were used for measurements in the key and elsewhere in this paper:

$$AA = \text{Aculeus apex angle;}$$
$$AL = \text{Aculeus length;}$$
$$AVL = \text{Aculeus ventral lobe length;}$$
$$C2L = \text{Length of second costal section, between end } R_1 \text{ and } R_{2+3};$$
$$RL = \text{Length of } R_{4+5} \text{ beyond } r\text{-}m \text{ crossvein;}$$
$$WL = \text{Length of wing;}$$
$$C2L/AL = \text{Ratio formed by dividing C2L by AL;}$$
$$RL/AL = \text{Ratio formed by dividing RL by AL;}$$
$$AVL/AL = \text{Ratio formed by dividing AVL by AL.}$$

Each description includes the minimum and maximum observed values of the relevant measurements. In the descriptions of *Ch. jaceae* group species, values of the mean and 95% confidence interval of the mean are given in brackets, and all values derive from the samples ($n \geqslant 10$) used for the CV analysis.

Twenty-five samples of between 10 and 77 specimens were measured with respect to the four selected characters (C2L, RL, AL, AA). Aberrant individuals were removed from small samples by using Grubb's t test for outliers carried out by a BASIC computer program by Wainwright & Gilbert (1987). Eight specimens were found to be outliers with respect to at least one character, and they were removed from the data set; two samples were reduced to nine specimens, and they were also rejected, leaving 23 samples totalling 499 specimens. In theory, CV analysis requires the assumption that all data are normally distributed and that variances are homogeneous. Each of the 92 separate data sets (23 samples of 4 characters) were tested for normality (Filliben's r test using the program by Wainwright & Gilbert, 1987), and only 11 data sets (12%) were found to be improbable samples ($P<0·05$) of normally distributed populations; this small departure from normality was ignored.

Two CV analyses were carried out, one using the four separate characters (C2L, RL, AL, AA) and the other using ratios of wing and aculeus characters (C2L/AL, RL/AL, AA). Both analyses gave very similar results, differing only in the placement of the sample taken from *Ce. leucophaea*. In the first analysis, this sample was placed close to samples off *Ce. solstitialis* and *Ce. cyanus* (see White, 1989b); however, in the analysis of ratio characters, it was placed closer to samples from related plants, namely *Ce. maculosa* and *Ce. vallesiaca*. Both analyses were almost identical in other respects, but ratio characters produced results more closely fitting the available biological evidence provided by the oviposition behaviour experiments, and only that analysis is described in this paper. The canonical variate scores and other parameters are presented in Tables I and II, and a plot of the CV means with respect to CV axes I and II are presented in Fig. 12. It can be seen that duplicated samples from a single host all grouped closely, with the exception of the spring and summer samples from *Ce. solstitialis*. When a further 36 smaller samples

($n = 4 - 9$, totalling 207 individuals), were compared to these CV results, it was found that the extra samples also closely matched other samples from the same hosts.

TABLE I.   *Canonical variate scores on CV axes I and II*

	CVI	CVII	EVI	EVII
C2L/AL	−1·01	19·05	−0·04	0·70
RL/AL	10·57	−4·68	0·40	−0·17
AA	0·43	−0·33	0·92	−0·69
Variance	91·66%	7·32%		

Multivariate analysis of variance, $P<0·001$:
  Wilk's $\lambda = 0·0255$; converted to χ^2 approx. of 1771 & 66 degrees of
  freedom.
EVI and EVII are the normalized eigenvector values which indicate
  the relative contribution of each character to the results.

TABLE II.   *Summary of canonical variate (CV) analysis results*

Species and host	CVI	CVII	Symbol	Locality, n
Chaetorellia acrolophi				
Ce. leucophaea	21·8	0·8	l	France, St. Paul area, 21
Ce. maculosa	19·2	1·5	m	Austria, Dürnstein, 26
Ce. maculosa	19·5	1·2	m	Austria, Hornstein, 23
Ce. maculosa	19·5	1·7	m	Hungary, Velence, 13
Ce. vallesiaca	20·5	1·8	v	Switzerland, Brig (swept), 20
Ce. vallesiaca	20·3	1·5	v	Switzerland, Brig (spring), 11
Ce. vallesiaca	20·4	1·4	v	Switzerland, Lalden (summer), 12
Chaetorellia australis				
Ce. cyanus	22·6	2·2	c	Greece, Agios Prodromus, 30
Ce. cyanus	22·7	2·0	c	Greece, Thermi, 21
Ce. solstitialis	23·0	2·4	s	Greece, Kilkis area (summer), 18
Ce. solstitialis	24·8	3·9	S	Greece, Thermi (spring), 13
Chaetorellia conjuncta				
Ce. aegyptiaca	26·9	1·5	A	Israel, Ramat Boqer, 77
Ce. aegyptiaca	26·9	1·0	A	Israel, Sede Boqer, 14
Ce. lanulata	26·7	1·7	L	Israel, En Gedi, 15
Ce. pallescens	26·8	0·8	P	Israel, En Mor, 12
Ce. pallescens	27·4	1·0	P	Israel, Nahal Paran, 20
Ce. pallescens	27·5	0·5	P	Israel, Sede Boqer, 23
Ce. iberica	24·5	1·1	I	Israel, Mount Hermon, 48
Chaetorellia hestia				
Ce. aspera	28·4	4·7	a	Spain, Lobres, 24
Ce. aspera	28·3	4·2	a	Spain, St Christina, 15
Chaetorellia jaceae				
Ce. jacea	14·6	2·0	j	Hungary, Lake Velence, 13
Ce. nigra	16·8	3·0	n	England, Riddlesdown (early), 18
Ce. nigra	17·0	3·4	n	England, Riddlesdown (late), 13

The CV group means for each of the 23 samples on CV axes I and II are listed above, together with the symbol
  used for each point in Fig. 12, host, locality and number of specimens (n).

The possibility that different generations of a single population may differ was investigated by calculating Hotelling's T^2 statistic between pairs of samples ($n \geqslant 10$) of different generations from a single host-plant and locality. This statistic was calculated using a BASIC program for linear discriminant analysis, based on a FORTRAN program by Davies (1971); it was also used to make a comparison of samples ($n \geqslant 10$) taken from different hosts at a single locality (Table III).

The distribution of *Chaetorellia* populations between adjacent (parapatric) natural stands of two *Centaurea* species were studied at two sites, one comprising *Ce. maculosa* and *Ce. jacea* in Hungary, with the aim of finding field evidence for the separation of *Ch. acrolophi* from *Ch. jaceae* (Table IVA); the other *Ce. leucophaea* and *Ce. solstitialis* in France (Table IVB). Flies swept from two plant stands separated by a few metres of grassland were identified using the CV analysis and the following key, and these free-flying populations were found to have a strong preference for alighting only on their own hosts
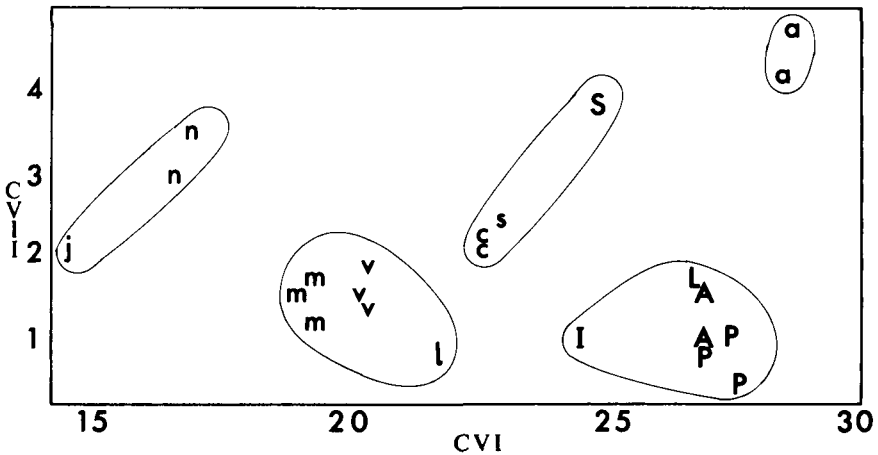
Fig. 12.—Plot of canonical variates I and II of 23 samples of the *Chaetorellia jaceae* (Robineau-Desvoidy) species-group; sample means are marked by the initial letter of the host-plant (listed in Table II); lines encircle samples which are believed to be conspecific; *Ch. acrolophi* sp. n. (l, m, v); *Ch. australis* Hering, summer form (c, s) and overwintering spring form (S); *Ch. conjuncta* (Becker) (A, I, L, P); *Ch. hestia* Hering (a); *Ch. jaceae* (j, n).

Table III. *Comparison of samples of* Chaetorellia *populations from different generations or hosts*

Between-generation comparisons
Ce. vallesiaca (Valais) spring v. summer	ns
Ce. nigra (Riddlesdown) spring v. summer	ns
Ce. solstitialis (N.E. Greece) spring v. summer	$P<0.001$

Between-host comparisons
Ce. aegyptiaca v. *Ce. pallescens* (Sede Boqer)	ns
Ce. cyanus v. *Ce. solstitialis* (N.E. Greece—summer)	ns
Ce. cyanus v. *Ce. solstitialis* (N.E. Greece—spring)	$P<0.001$
Ce. jacea v. *Ce. maculosa* (Velence)	$P<0.001$

Significance was determined from Hotelling's T^2, derived from linear discriminant analyses.

(Table IV*A*, *B*). The lack of flies on *Ce. maculosa* during the second visit to the Hungarian site (Table IV*A*) reflects a difference in the phenology of the two plants, as *Ce. maculosa* was no longer flowering in late August.

Unfortunately, most combinations of host-plants either do not occur at single sites or only occur in inaccessible areas. Some combinations were therefore simulated by laboratory, field and caged-plant host-choice tests and by larval transfer tests. Particular attention was paid to testing the separation of *Ch. acrolophi* from *Ch. jaceae* and *Ch. australis*. In addition, results of field (Table IV*C*) and laboratory (I. Pittara, unpublished USDA data, 1985) tests using *Ch. australis* were made available to us. The experimental methods used for *Ch. acrolophi* were as follows:

1. A laboratory oviposition choice test was carried out using small cages, each of which consisted of a flower pot filled with sand and covered with a ventilated Perspex cylinder. Two males and two females were placed in each cage, together with two buds from each of four randomly selected test plant species and the control plant. Each pair of excised buds was kept fresh in a small vial containing water, and the flies were fed with a honey and yeast hydrolysate solution offered on filter-paper strips. After two days, the buds were dissected, and the number of eggs in each bud

Table IV.   *Host-choice of* Chaetorellia *when two or more host species occurred in the same area*

A.   *Ch. acrolophi* and *Ch. jaceae* on two *Centaurea* species at Lake Velence, Hungary; nearest plants of differing species about 10 m apart. Figures indicate numbers of females swept on visit one + visit two (18.vii & 23.viii.1986) (males could not be reliably determined).

	Ch. acrolophi	*Ch. jaceae*
Ce. (Acrolophus) maculosa	10 + 0	0 + 0
Ce. (Jacea) jacea	0 + 0	5 + 5

B.   *Ch. acrolophi* on two *Centaurea* species at St Paul, Herault, France; nearest plants of differing species about 1 m apart. Figures indicate number of females + males swept off similar sized plant stands (males determined by association with females).

Ce. (Acrolophus) leucophaea	19 + 37
Ce. (Solstitiaria) solstitialis	0 + 1

C.   *Ch. australis* attack on a randomized block of three *Centaurea* species, *Carthamus tinctorius* and three other Asteraceae, planted in an area of *Ce. solstitialis* at Thessaloniki, Greece. Figures indicate number of females + males reared (males determined by association with females).[1]

Ca. tinctorius	0 + 0
Ce. (Acrolophus) diffusa	0 + 0
Ce. (Acrolophus) maculosa	0 + 0
Ce. (Solstitiaria) solstitialis	71 + 52
Other species[2]	0 + 0

[1] Data from CIE coll. A20013, leg. K. Groppe (CIBC) & R. Sobhian (USDA).
[2] *Cirsium creticum* (Lam.) D'Urv., *Cynara scolymus* L. & *Helianthus annuus* L.

was recorded. If possible, 20 replicates of each combination of test plant species were made, giving a total of 40 replicates of each test plant species.

2. A field test with a restricted number of test plants was carried out at Lalden, Switzerland, where *Ch. acrolophi* occurs naturally on *Ce. vallesiaca*. Seven *Centaurea* (*Acrolophus*) species were planted in a Latin square design, surrounded by a natural population of *Ce. (A.) vallesiaca* which provided the source of test flies. Samples of capitula were taken from the test plants at two-week intervals and examined for larvae or pupae.

3. Another kind of multiple choice oviposition test was carried out in large outdoor field cages (1·5 × 1·3 × 1·3 m high) containing potted test plants; the cages were located in the garden of the CIBC Station at Delémont, Switzerland. A random selection of 5–10 test plant species, plus the control, were placed in each cage together with several dozen pairs of flies. These cages were set up in June, and the test plants were examined for larvae or pupae during September.

4. Larval transfer tests were carried out by transferring newly emerged larvae, or eggs containing fully developed embryos, from the control plant to a position under a bract of a test bud of a potted plant. Each bud was covered with a small gauze bag, and the plant was kept for about four weeks in an unheated greenhouse, after which the amount of successful development in each test bud was assessed by counting final-instar larvae. The number of larvae or eggs transferred to each test plant species was usually about 40 in the tests using specimens taken from field-collected *Ce. vallesiaca*. However, *Ce. leucophaea* does not grow near Delémont and *Ce. jacea* is not known to be attacked by *Chaetorellia* in that area. Consequently, larvae and eggs were taken from the controls in the laboratory oviposition tests and only ten individuals were available for each transfer from these plants. It was hoped that these tests would show that *Ch. acrolophi* and *Ch. jaceae* were unable to develop in the hosts of some other *Chaetorellia* species, as H. Zwölfer (unpublished CIBC data, 1972) found for *Ch. carthami* and *Ch. succinea*.

A subset of these tests was carried out for *Chaetorellia* flies from three different populations, namely *Ch. acrolophi* from *Ce. vallesiaca* (Table V) and *Ce. leucophaea* (Table VI), and *Ch. jaceae* from *Ce. nigra* (Table VII); some test combinations could not be carried out, usually due to inadequate numbers of available flies. Only a summary of the results is presented here; full data are available from the second author.

TABLE V. *Host-choice test results for* Chaetorellia acrolophi *reared from* Centaurea vallesiaca

Plant	1 Lab. test	2 Field-plot test	3 Cage test	4 Larval transfer
Control				
Ce. (Acrolophus) vallesiaca	+	+	+	+
Natural hosts of *Chaetorellia acrolophi*				
Ce. (Acrolophus) arenaria	+	+	+	+
Ce. (Acrolophus) diffusa	+	−	+	+
Ce. (Acrolophus) leucophaea	+	.	(+)	+
Ce. (Acrolophus) maculosa	+	+	+	+
Ce. (Acrolophus) virgata	.	.	−	.
Natural hosts of *Chaetorellia jaceae*				
Ce. (Jacea) jacea	+	.	+	+
Ce. (Jacea) nigra	+	.	.	+
Ce. (Jacea) pannonica	+	.	.	.
Ce. (Phalolepis) alba	+	.	.	.
Natural hosts of *Chaetorellia australis*				
Ce. (Cyanus) cyanus	−	.	−	−
Ce. (Solstitiaria) solstitialis	−	.	(+)	+
Natural hosts of *Chaetorellia conjuncta*				
Ce. (Calcitrapa) calcitrapa	+	.	−	(+)
Ce. (Calcitrapa) iberica	.	.	−	.
Ce. (Calcitrapa) procurrens	.	.	−	.
Natural hosts of *Chaetorellia hestia*				
Ce. (Calcitrapa) aspera	−	.	.	.
Plants which are not known to be hosts of *Chaetorellia jaceae* species-group				
Ce. (Acrolophus) biebersteinii DC.	+	+	+	+
Ce. (Acrolophus) friderici Vis.	+	+	.	+
Ce. (Centaurea) ruthenica Lam.	.	.	−	.
Ce. (Cyanus) montana L.	−	.	.	.
Ce. (Jacea) nigrescens Willd.	.	.	−	+
Ce. (Lopholoma) scabiosa	+	.	−	−
Ce. (Phalolepis) troitzkyi	.	.	−	.
Ce. (Psephellus) dealbata Willd.	.	.	−	.
Ce. (Solstitiaria) nicaeensis All.	.	.	−	.

Origin of test flies: Lalden, Switzerland.
+ = Positive result in at least 5% of replicates.
(+) = Positive result in less than 5% of replicates.
− = Negative result in all replicates.
. = Test not carried out.

In test 1, positive means eggs laid; in tests, 2–4 positive means larvae developed.

TABLE VI. *Host-choice test results for* Chaetorellia acrolophi *reared from* Centaurea leucophaea

Plant	1 Lab. test	3 Cage test	4 Larval transfer
Control			
Ce. (Acrolophus) leucophaea	+	+	+
Natural hosts of *Chaetorellia acrolophi*			
Ce. (Acrolophus) diffusa	+	−	.
Ce. (Acrolophus) maculosa	+	+	+
Ce. (Acrolophus) vallesiaca	+	−	.
Natural host of *Chaetorellia jaceae*			
Ce. (Jacea) jacea	−	−	.
Natural hosts of *Chaetorellia australis*			
Ce. (Cyanus) cyanus	−	.	.
Ce. (Solstitiaria) solstitialis	−	−	+

Origin of test flies: St Paul, France.
+ = Positive result in at least 5% of replicates.
− = Negative result in all replicates.
. = Test not carried out.

In test 1, positive means eggs laid; in tests 3 & 4, positive means larvae developed.

TABLE VII.   *Host choice test results for* Chaetorellia jaceae *reared from* Centaurea nigra

Plant	3 Cage test	4 Larval transfer
Control		
Ce. (Jacea) jacea [Ce. nigra not available at time of test]	+	+
Natural hosts of Chaetorellia acrolophi		
Ce. (Acrolophus) diffusa	+	+
Ce. (Acrolophus) leucophaea	−	.
Ce. (Acrolophus) maculosa	+	+
Ce. (Acrolophus) vallesiaca	+	.
Natural host of Chaetorellia australis		
Ce. (Solstitiaria) solstitialis	−	.

Origin of test flies: Riddlesdown, England.
+ = Positive result (development of larvae occurred) in at least 5% of replicates.
− = Negative result in all replicates.
. = Test not carried out.

Variation in *Chaetorellia jaceae* group populations

For the morphometric analyses to be of value in assigning populations to biologically recognized species, it was necessary to eliminate the possibility that the observed between-population variation was largely caused by factors other than genotypic differences. Mayr (1969) lists the major causes of variation that may occur within a population or species, and those which may apply to a phytophagous holometabolous insect are: variation between generations, habitat variation, variation induced by temporary climatic conditions, host-determinated variation, density-dependent variation, allometric variation and geographic variation.

Allometric variation may occur in the *Ch. jaceae* group, but its effect is clearly very small as the characters measured show a near linear relationship to each other, and geographic differences were not detected in flies attacking a single host. If variation between habitat, climate and population density were significant, the samples would have grouped randomly rather than into groups determined by host-plant.

Variation between generations was specifically tested for in populations associated with *Ce. nigra* and *Ce. vallesiaca*, but no differences were found between these samples (Table III). Conversely, in north-eastern Greece *Ce. solstitialis* is attacked by two morphometrically distinct forms of *Ch. australis*, which may be explained by the unusual life-cycle of this fly. In that area, *Ch. australis* attacks two distantly-related hosts, namely *Ce. (Cyanus) cyanus* and *Ce. (Solstitiara) solstitialis*. Both of the Greek samples from *Ce. cyanus* are similar to one sample from *Ce. solstitialis* (Fig. 12, points c & s) that was included in the CV analysis, and to all other small (*n* < 10) samples that were not included in that analysis. Adults from all of these similar samples emerged during the summer (mostly in July). The single sample from *Ce. solstitialis* which is distinct from the other samples (Fig. 12, point S; *P* < 0·001 in Table III) was unique, as these flies had overwintered as larvae and emerged in the spring. USDA staff in Greece made a field observation that the overwintered flies which emerge from *Ce. solstitialis* in late April or early May are the flies which attack *Ce. cyanus* (S. L. Clement, pers. comm.). These observations led them to conclude that the flies which subsequently emerged from *Ce. cyanus* attacked *Ce. solstitialis* and that this third generation attacked that same plant species again to produce overwintering larvae. Laboratory two-choice host tests (I. Pittara, unpublished report, USDA, 1986), based on flies previously ovipositing in either host, indicated that the flies would oviposit into either of these plants but not into any of the other plants tested (*Ce. (Acrolophus) diffusa*, *Ce. (Calcitrapa) calcitrapa*, *Ce. (Lopholoma) macedonica* Boiss. and *Ce. (L.) salonitana*). These results support the suggestion that a single species attacks both hosts; however, Pittara does not say which generations her test flies belonged to, and

positive results in artificial host-choice tests have to be interpreted cautiously, because unnatural hosts may be accepted (see Harris, 1988). Assuming the field observations were correctly interpreted, then the two morphometrically distinct forms attack different hosts. The spring flies which emerge from *Ce. solstitialis* have a short ovipositor and attack *Ce. cyanus*; conversely, the summer flies from either host have a slightly longer ovipositor and attack *Ce. solstitialis* regardless of which host they emerged from. The flies that emerge in the spring are darker in colour than those which emerge in the summer, and the possibility that *Ch. australis* is phenotypically changed by winter diapause cannot be ruled out. However, its two hosts differ markedly in the structure of the bracts behind which the flies lay their eggs, and the size changes may be advantageous for oviposition on different substrates.

This only leaves host-plant-related variation, which obviously occurs but could be either ecophenotypic or due to genetic adaptation to different hosts. Many insects, such as aphids, vary ecophenotypically according to the host-plant on which they have developed. Adult females that emerged from unnatural test hosts and control hosts in the larval-transfer tests were examined morphometrically to determine if development in an unnatural host-plant had resulted in atypical morphology. Unfortunately, the progeny from these tests suffered high final-instar and pupal mortality, largely due to mite attack, and the remaining samples were very small. The generalized distance (D^2) from the sample to each reference group of wild flies included in the CV analysis was calculated; all samples were found to be more similar to wild flies reared from the control plant than to wild flies reared from the test plant (Table VIII, CV). Flies reared from larval host transfers to non-control plants, were also identified with respect to linear discriminant analyses of wild flies reared from the control and the test plant species; in these tests, the experimentally-reared flies were found to be most similar to wild flies reared from the control host (Table VIII, LDc). Similarly, some specimens of *Ch. australis* whose first-instar larvae had been removed from their host and reared on an artificial diet (olive fly medium, Tzanakakis & Economopoulos, 1967) were made available to us by I. Pittara; these were found to be within the normal range of variation of *Ch. australis* populations associated with *Ce. cyanus* and *Ce. solstitialis*, although their sample mean best matched flies from *Ce. leucophaea* (Table VIII, CV). It is concluded that development in an unnatural host, or even on an artificial medium, does not markedly alter the morphometrics of the flies, and ecophenotypic variation is therefore insignificant in determining interpopulation differences.

TABLE VIII. *Morphometric form of adults of* Chaetorellia *spp. after larval transfer*

Host	D^2(CV)		D^2(LDc)	D^2(LDt)	n
Parental stock reared from *Ce. vallesiaca*					
Control (*Ce. vallesiaca*)	0·22	(*Ce. vallesiaca*)	.	.	6
Ce. nigra	0·14	(*Ce. vallesiaca*)	2·0	21.0	2
Ce. solstitialis	1·55	(*Ce. leucophaea*)	1·8	7·9	1
Parental stock reared from *Ce. leucophaea*					
Control (*Ce. leucophaea*)	0·64	(*Ce. leucophaea*)	.	.	4
Ce. solstitialis	0·02	(*Ce. leucophaea*)	0·1	6·1	3
Parental stock reared from *Ce. nigra*					
Ce. maculosa	2·92	(*Ce. jacea*)	0·4	12·2	1
Parental stock reared from *Ce. solstitialis* and *Ce. cyanus*					
Artificial diet	0·77	(*Ce. leucophaea*)			5
	1·11	(*Ce. cyanus*)			

D^2 = Generalized distance.
D^2(CV) = D^2 estimated from CV analysis with nearest sample in brackets (second nearest also shown for artificial diet material).
D^2(LDc) and D^2(LDt) = D^2 estimated from linear discriminant analysis of wild-type flies ex control plant (LDc) and ex test plant (LDt).
n = Number of experimental females measured.

Separation of *Chaetorellia jaceae* group species

Ch. conjuncta is the only member of the *Ch. jaceae* species-group which is distinct on purely morphological characters. The egg tube is remarkably long compared to the other

four species, and it is the only member of the group which usually has its discal and preapical wing crossbands joined. However, many specimens, particularly from the western part of the species' range, lack this simple character, so its identification is not always any easier than that of the remaining four species.

Ch. hestia also has a wing-pattern character by which it usually differs from the other four species, namely that cell *bm* lacks a hyaline area (Fig. 8). Unfortunately, some individuals of *Ch. hestia* do not lack this hyaline area, and it is lacking in a few individuals of the remaining species; consequently, identification of *Ch. hestia* is not as simple as previously published keys would suggest. The combination of the fact that the populations associated with subgenus *Seridia* of *Centaurea* are morphometrically very distinct from populations found on other hosts (Fig. 12, points a), and the common occurrence of a wing pattern difference, indicates that *Ch. hestia* is probably a distinct species.

Ch. jaceae on *Ce. jacea*, has an aculeus length of at least 2·0 mm, whereas *Ch. acrolophi*, found on *Ce. maculosa* and *Ce. vallesiaca*, has an aculeus less than 1·9 mm long. Its separation from *Ch. acrolophi* was confirmed by a natural field test in Hungary, where free-flying populations of the two species were found to have segregated onto their own hosts and to have different phenologies (Table IVA). In a cage test, it was found that *Ch. jaceae* would not attack a host of the very much smaller *Ch. australis* but would attack some hosts of *Ch. acrolophi* (Table VII, test 3). Similarly, *Ch. acrolophi* would oviposit on hosts of *Ch. jaceae* under artificial conditions (Table V, tests 1, 3); however, the eggs of *Ch. acrolophi* that were laid on 'incorrect' plants, were usually placed behind a bract appendage rather than in the normal position behind the main body of the bract. Under natural conditions, such badly-positioned eggs would be more exposed to adverse climatic conditions, and possibly to predators and parasites, than eggs buried deep between bracts, and it is unlikely that they would survive. Furthermore, it is known that artificial host-specificity tests exaggerate an insect's host range (Harris, 1988), presumably because some parts of the mechanism for differentiating between host and non-host plants in the field are somehow lost or masked under artificial conditions. This means that only negative results from artificial tests are of any value in this kind of taxonomic study, so the test results do not disprove the separation of *Ch. acrolophi* from *Ch. jaceae*.

Ch. acrolophi is described as a distinct species to include a biologically- and morphometrically-distinct group of populations which attack *Ce. vallesiaca* in Switzerland and the closely-related *Ce. maculosa* in eastern Austria, Hungary and north-eastern Greece. Morphometrically, *Ch. acrolophi* falls between *Ch. jaceae* and *Ch. australis* (Fig. 12, points m, v). Its separation from *Ch. australis* is supported by a field test (Table IVC) in which *Ch. australis* would not oviposit on a host of *Ch. acrolophi* (*Ce. maculosa*); artificial host tests (Table V, tests 1, 3) showed that *Ch. acrolophi* would not attack hosts of *Ch. australis* (*Ce. cyanus*, *Ce. solstitialis*), although transferred larvae could develop on one of these (Table V, test 4); artificial host tests also showed that *Ch. australis* reared from *Ce. solstitialis* would only attack *Ce. solstitialis* in two choice tests with *Ce. maculosa* (I. Pittara, unpublished USDA data, 1986). Unfortunately, no large sympatric samples were available for the combination of *Ch. acrolophi* and *Ch. australis*. However, samples too small for detailed analysis ($n<10$) were available off *Ce. maculosa* and *Ce. cyanus* from a single area (Thermi, Greece), and the flies in both of these samples were morphometrically typical of flies from these hosts elsewhere, indicating that the two plants almost certainly support separate species of *Chaetorellia* in areas of sympatry. The cage test (Table V, test 3) also supports the separation of *Ch. acrolophi* from *Ch. conjuncta*, and the laboratory host test (Table V, test 1) supports its separation from *Ch. hestia*.

The above evidence serves to separate the five recognized species in the *Ch. jaceae* species-group. However, several other monophagous populations still needed to be identified. In general, these populations were assigned to the five species by morphometric and biological similarity, because evidence to separate them was lacking. For example, *Ce. nigra* is a western European member of the subgenus *Jacea* of *Centaurea* which often forms hybrids with *Ce. jacea*; the flies from these two host-plant species are morphometrically similar (Fig. 12, points j, n) and they are assumed to be a single species.

Individuals of *Ch. acrolophi* associated with *Ce. (Acrolophus) maculosa* are not only larger than *Ch. australis*, but they have a ratio difference from *Ch. australis* (see Key below, couplet 5). This ratio character also applies to populations associated with other species of the subgenus *Acrolophus*, such as *Ce. diffusa* and *Ce. leucophaea*, even though these flies are very small and closely resemble *Ch. australis* in size. Field (Table IV*C*) and laboratory (I. Pittara, unpublished USDA data, 1986) evidence showed that *Ch. australis* would not attack *Ce. diffusa*. Similarly, both field (Table IV*B*) and experimental (Table VI, tests 1, 3) data show that flies associated with *Ce. leucophaea* do not attack *Ce. solstitialis* although they are capable of developing on it (Table VI, test 4, plants from the Thermi area, Greece). These observations indicate that flies found on *Ce. diffusa* and *Ce. leucophaea* are unlikely to be *Ch. australis*, although they resemble that species in size. The similarity of ratio characters between *Ch. acrolophi* on *Ce. maculosa* and *Ce. vallesiaca* with flies found on other species of the subgenus *Acrolophus* suggests that all of these *Acrolophus*-associated populations may be conspecific. However, the host-choice experiments suggest otherwise.

Flies originating on *Ce. leucophaea* attacked *Ce. maculosa* in the cage test but not the very closely related *Ce. vallesiaca* or *Ce. diffusa* (Table V, test 3); these negative results suggest that the population associated with *Ce. leucophaea* is not conspecific with populations found on any of these plants. Similarly, the more realistic field-plot test, using flies originating from *Ce. vallesiaca*, showed that these flies would not oviposit on *Ce. diffusa* (Table V, test 2); this negative result suggests that flies found on *Ce. diffusa* may not be conspecific with flies found on *Ce. vallesiaca*. The available small samples ($n<10$) of flies found on species of the subgenus *Acrolophus* other than *Ce. maculosa* and *Ce. vallesiaca* were identified using CV analysis (Table IX); from these results, it can be seen

TABLE IX. *Morphometric form of flies similar to* Chaetorellia acrolophi *and* Ch. australis

Sample	D²(CEL)	D²(CEM)	D²(CEV)	D²(CHA)	n
Samples from hosts not in CV analysis					
Ca. tinctorius	9·43	8·2–11·23	3·85–7·53	3·97–5·29	4
Ce. arenaria	2·8	0·9–1·8	**0·0–0·2**	5·3–7·2	7
Ce. depressa	4·5	6·2–8·8	2·1–4·5	3·5–3·7	5 (2 pooled)
Ce. diffusa	1·3	2·6–3·9	**0·6–0·7**	2·8–4·4	14 (3 pooled)
Ce. pectinata	2·2	2·7–3·9	**0·9–1·1**	2·6–4·1	1
Ce. spinabadia	1·7	1·7–2·7	**0·2–0·5**	3·9–5·8	5
Ce. virgata	**0·6**	7·6–9·4	3·3–3·9	**0·5–1·9**	1
Controls (samples of *Chaetorellia acrolophi* from 3 *Centaurea* spp. and summer form of *Ch. australis*)					
Ce. leucophaea	**0·5**	8·6–10·9	4·2–4·7	1·6–3·1	12 (5 pooled)
Ce. maculosa	7·5	**0·2–0·5**	1·5–2·4	11·6–14·5	9
Ce. vallesiaca	3·8	0·6–1·4	**0·1–0·4**	6·1–7·9	8
Ch. australis	7·1	17·7–21·4	10·0–12·2	**0·5–1·7**	9

D² values were calculated between samples ($n<10$) not included in the CV analysis, and the reference samples included in the analysis. Reference samples from *Ce. leucophaea* (CEL), *Ce. maculosa* (CEM) and *Ce. vallesiaca* (CEV), plus the summer generation of *Ch. australis* (CHA).
Ranges indicate D² values between the closest and most distant reference sample. Controls were representative samples ($n<10$) not included in the CV analysis; numbers of samples pooled are noted. The *Ch. australis* control was from the type locality.
Likely identifications are shown in bold type.

that flies associated with other species of the subgenus *Acrolophus* are morphometrically inseparable from flies associated with *Ce. vallesiaca*. Without field host-choice test results for all combinations of species of this subgenus that are hosts to *Chaetorellia* populations, it is not possible to delimit further biological species. Consequently, all populations associated with the subgenus *Acrolophus* are here tentatively identified as host races of *Ch. acrolophi*.

Separation of *Chaetorellia loricata* group species

Ch. loricata is easily separated from the remaining three species of this group by the

distinctive shape of its aculeus (Fig. 21). The remaining three species have in common a caudata aculeus apex (Figs 18–20). On the basis of the eight females of *Ch. isais* Hering that were examined, this species would appear to be easy to separate from *Ch. carthami* and *Ch. succinea* by the extraordinary length of its aculeus apex (Fig. 18).

The remaining two species are *Ch. carthami* and *Ch. succinea*. These are very closely related, and Sobhian & Zwölfer (1985) called the latter *Chaetorellia* sp. near *carthami* and referred to them as semispecies of a *Ch. carthami* complex. Experiments with individuals of *Ch. succinea* and *Ch. carthami* (H. Zwölfer, unpublished CIBC data, 1972) showed that these two taxa differ biologically; this work is reviewed by Zwölfer (1970) and Sobhian & Zwölfer (1985). Zwölfer transferred eggs of *Ch. carthami* from *Ca. tinctorius* to other *Ca. tinctorius* plants (control host) and to *Ce. solstitialis* (test host); a similar set of host transfers was performed using eggs of *Ch. succinea* from *Ce. solstitialis*. He found that larval development could only be completed on the control host. However, adults of these *Chaetorellia* species could be crossed to produce fertile offspring and when hybrid eggs were transferred, larval development was equally successful in control and test hosts. Zwölfer (Unpublished CIBC data, 1972) also carried out univariate analyses on nine morphometric and four colour characters of 'wild-type' populations and showed that these two *Chaetorellia* species are morphometrically distinct. Zwölfer (1970) also noted a behavioural difference between them; *Ch. succinea* required its host-plant to possess spinose bracts, otherwise oviposition behaviour did not occur; conversely, *Ch. carthami* would oviposit on *Ca. tinctorius* even if the bract spines had been removed. Unfortunately, no populations of *Ch. succinea* on *Ce. solstitialis* are known from areas where *Ch. carthami* attacks *Ca. tinctorius*, so the experiments had to be carried out with allopatric populations. However, the behavioural difference suggests that these two populations would probably be reproductively isolated even if they did occur sympatrically, and they should be regarded as separate species.

Very few specimens of *Ch. carthami* were available for the present study, so detailed analyses could not be used to help in the separation of these two very similar species. However, univariate analyses (*t* tests) were carried out on two characters (C2L, AL) and five samples (Table X). These results show that the three samples of *Ch. succinea* off *Ce. solstitialis* all differ in their aculeus length from *Ch. carthami* off *Ca. tinctorius*. The sample off *Ce. pallescens* matches the Turkish and Italian samples off *Ce. solstitialis* in both aculeus length and colour characters, but not in the wing-length characters, and it is assumed to represent *Ch. succinea*. The small (*n*=3) sample of *Chaetorellia* off *Ca. tenuis* from Israel matches the coloration of *Ch. carthami*, rather than the darker patterning of *Ch. succinea*, but the flies are intermediate in size between those found on *Ca. tinctorius* or

TABLE X.   t *Tests of a wing and an aculeus measurement, between samples of* Chaetorellia carthami *and* Ch. succinea

		TIN	PAL	SOLF	SOLI	SOLT
TIN	C2L	–	*	–	–	–
	AL	–	**	**	***	***
PAL	C2L		–	–	*	**
	AL		–	**	–	*
SOLF	C2L			–	–	–
	AL			–	*	*
SOLI	C2L				–	–
	AL				–	⁔
SOLT	C2L					–
	AL					–

* *P*<0·05,   ** *P*<0·01,   *** *P*<0·001.
Samples (*n*⩾5) abbreviated as follows:
  TIN = *Ch. carthami* off *Carthamus tinctorius* in Israel;
  PAL = *Ch. succinea* off *Centaurea pallescens* in Israel;
  SOLF, SOLI and SOLT, are *Ch. succinea* off *Ce. solstitialis* from France, Italy
    and Turkey, respectively.
The characters tested were C2L and AL.

Centaurea species. In the absence of better data, it is assumed that the flies associated with *Ca. tenuis* are also *Ch. carthami*.
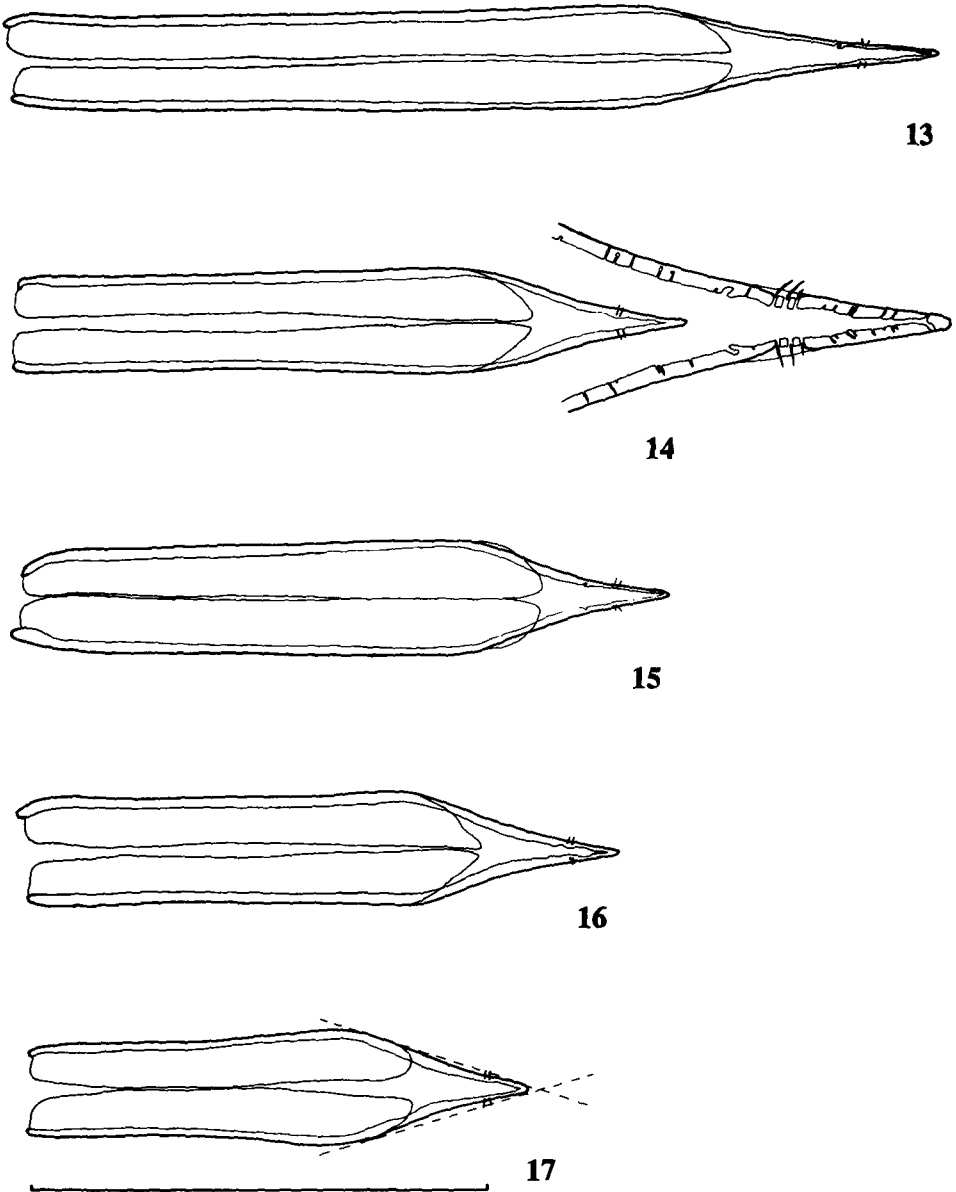
Key to species of *Chaetorellia*

Only *Ch. loricata* and *Ch. isais* can be reliably determined using a conventional key. The key which follows should allow correct identification of at least 70% of specimens. The accuracy of the key approaches 100% if sample means are used to answer measurement questions, and in most cases the host-plant and distribution data should highlight errors. The accuracy of each character is indicated in the key by the inclusion of the percentage of specimens that may be expected to have a given character state (values derived from the matrix of 499 individuals).

Identifications may also be made by consulting the host list (Table XI) and comparing measurements to those given in the species description, or by calculating the position of the new sample with respect to CV axes I and II, and comparing the values with those of reference samples from the same or related hosts (Table II). If the calculated CV values fall within 2 units of the reference sample for a single specimen and well within 1 unit for values calculated from the means of a large sample, then it may be assumed that the new sample came from the same population as the reference sample. Unfortunately, identifications based on the results of the CV analysis require measurement of the aculeus apex angle, which can only be measured if a drawing tube is available, so its use was kept to a minimum in the key. The CV values should be calculated as follows (formulae derived from Table I):

$$\text{CVI} = (10\cdot6 \times \text{RL/AL}) + (0\cdot4 \times \text{AA}) - \text{C2L/AL}$$
$$\text{CVII} = (19\cdot1 \times \text{C2L/AL}) - (4\cdot7 \times \text{RL/AL}) - (0\cdot3 \times \text{AA})$$

1 Anterior supra-alar seta based on a yellow ground (Fig. 5) or in a black stripe (Fig. 5, cross-hatched area). Aedeagal glans with an evenly curved main duct (Fig. 10). Aculeus apex evenly narrowed (acuminate) (Figs 13–17). Wing cell *cup* not extending well beyond end of cell *bm* (Figs 7, 8). .... *Ch. jaceae* species-group ...2
— Anterior supra-alar seta based in a black spot (Fig. 6). Aedeagal glans with main duct sinuate (Fig. 11). Aculeus apex either narrowed in two steps (Fig. 21) or sharply narrowed well before apex (caudate) (Figs 18–20). Wing cell *cup* usually extending well beyond end of cell *bm* (Fig. 9). .... *Ch. loricata* species-group 6
2 Aculeus usually (98%) longer than 1·8 mm. [Anterior supra-alar seta based on a yellow ground. Cell *bm* usually (98%) with a hyaline area in its basal two-thirds (Fig. 7), except in a high proportion of Italian specimens. Discal and preapical crossbands usually (98%) well separated. Aculeus ending in a very acute point (Fig. 13). Associated with some species of *Centaurea (Jacea)* and *Centaurea (Phalolepis)*. Widely distributed in Europe.] .... *jaceae* (Robineau-Desvoidy)
— Aculeus shorter then 1·8 mm, except for some (2%) specimens of *Ch. acrolophi* which are associated with *Ce. maculosa* and *Ce. vallesiaca* 3
3 Aculeus usually (97%) shorter than costal section 2 (R_1-R_{2+3}). Wing cell *bm* usually (91%) without a hyaline area in its basal two-thirds (Fig. 8). Scutal spots very large; each presutural dorsocentral spot usually about equal in breadth to distance between the prescutellar acrostichal spots. Anterior supra-alar seta sometimes placed on a black vitta (a form known from Algeria and Italy). [Discal and preapical crossbands well separated. Aculeus very short, less than 1·2 mm long, with apex angle at least 31°; and often very much broader before tapering section than at base (Fig. 17). Normally associated with some species of *Centaurea (Seridia)* in France, Italy and Spain; also known from Algeria.] ...... *hestia* Hering
— Aculeus longer than costal section 2 (R_1-R_{2+3}) (except for 70% of the spring form of *Ch. australis*, which is not known west of Greece, and 32% of *Ch. conjuncta* associated with *Ce. pallescens*, *Ce. aegyptiaca* and *Ce. lanulata* in the Middle-East). Wing cell *bm* usually (90%) with a hyaline area in its basal two-thirds (Fig. 7).

Figs 13–17.—Aculei of *Chaetorellia jaceae* (Robineau-Desvoidy) group species, in dorsal view; 13, *Ch. jaceae*; 14, *Ch. acrolophi* sp. n., with apex detail; 15, *Ch. conjuncta* (Becker); 16, *Ch. australis* Hering; 17, *Ch. hestia* Hering, with dashed lines defining the aculeus apex angle (scale line = 1·0 mm).

Scutal spots small; each presutural dorsocentral spot usually about equal in breadth to half the distance between the prescutellar acrostichal spots. Anterior supra-alar seta almost always based on a yellow ground (except in very rare examples of *Ch. australis*). 4

4 Discal and preapical crossbands usually (88%) joined, or nearly joined, close to the costal margin (most non-joined specimens were from Turkey). Aculeus apex blunt
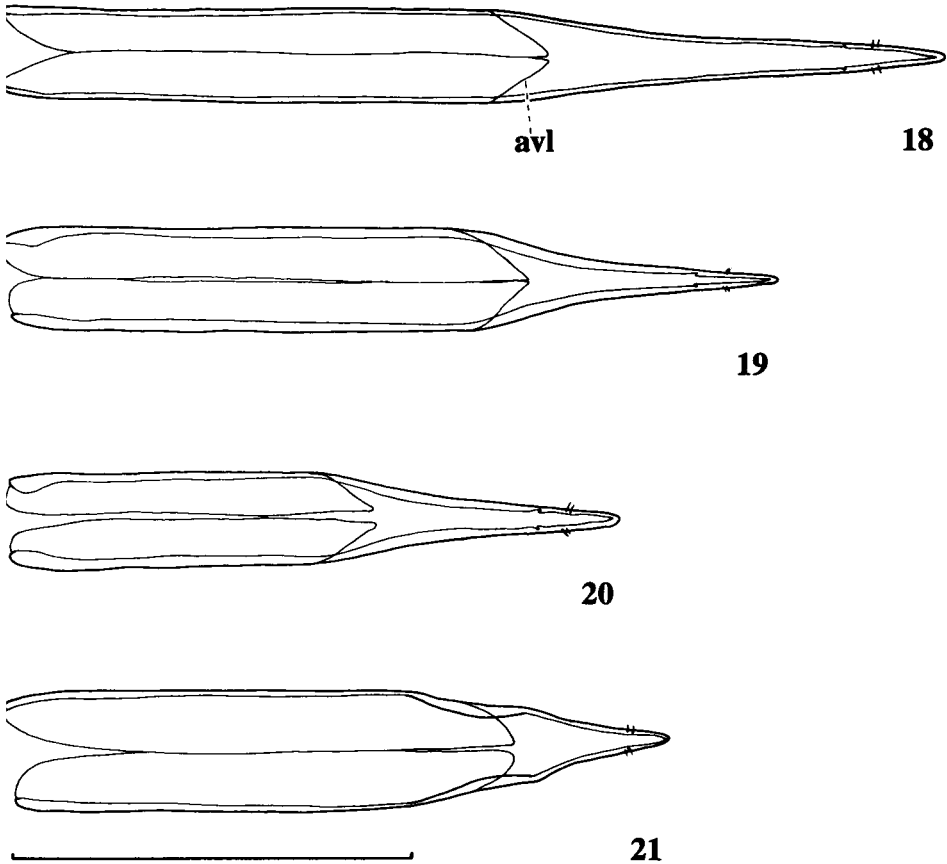
Figs 18–21.—Aculei of *Chaetorellia loricata* (Rondani) group species, in dorsal view; 18, *Ch. isais* Hering; 19, *Ch. carthami* Stackelberg; 20, *Ch. succinea* (Costa); 21, *Ch. loricata* (scale line = 1·0 mm; avl, aculeus ventral lobe).

(Fig. 15) (apex angle exceeding 29°, except for 19% of the form on *Ce. iberica*). [Associated with some species of *Centaurea (Calcitrapa)* and *Centaurea (Solstitiaria)* in Egypt, Israel and Jordan; *Ce. calcitrapa* in Turkey; also known from Albania, Cyprus, Iran, Iraq, Kazakh SSR, Lebanon, Pakistan and Syria.] .... *conjuncta* (Becker)

— Discal and preapical crossbands clearly separate. Aculeus apex sharp (Figs 14, 16) (apex angle at most 29° in *Ch. acrolophi* on *Ce. maculosa* and *Ce. vallesiaca*, but more than 29° in 20% of *Ch. acrolophi* on other hosts, and in 16% of *Ch. australis*). 5

5 Aculeus usually (90%) less than 1·3 times as long as costal section 2. [Aculeus usually (99%) shorter than apical section of vein R_{4+5} and usually (93%) less than 1·4 mm long. Associated with both *Ce. solstitialis* and *Centaurea (Cyanus)* in N.E. Greece, Hungary and Turkey; associated with *Ce. solstitialis* in Bulgaria and Moldavian SSR. Also known from Ukrainian SSR.] .... *australis* Hering

— Aculeus usually (91%) at least 1·3 times as long as costal section 2. [Normally associated with *Centaurea (Acrolophus)*. Aculeus of specimens associated with *Ce. maculosa* and *Ce. vallesiaca* usually (84%) longer than apical section of R_{4+5} and usually (90%) at least 1·5 mm long; shorter in presumed conspecific populations on

other hosts. Associated with *Ce. maculosa* in Austria, Byelorussian SSR, Hungary and Switzerland, and *Ce. vallesiaca* in Switzerland. Populations presumed to be conspecific, on *Ce. arenaria* in Romania; *Ce. diffusa* in Romania and the Caucasus; *Ce. leucophaea* and *Ce. spinabadia* in southern France; *Ce. virgata* in Turkey. Also known from Spain and Ukrainian SSR.] .... *acrolophi* sp. n.

[Specimens from the Balkans and neighbouring areas associated with *Ce. arenaria* and *Ce. diffusa* are very similar to *Ch. australis* (summer form); the following linear discriminant function helps in their separation: df = $(18 \cdot 1 \times \text{RL}) + (75 \cdot 6 \times \text{AA})$; based on material ex *Ce. arenaria* ($n=7$) plus *Ce. diffusa* ($n=14$, 3 samples pooled), and *Ch. australis* ($n=69$, 3 samples pooled); 43% ex *Ce. arenaria* plus *Ce. diffusa* have df<58; 76% of *Ch. australis* have df>62; individuals with df between 58 and 62 cannot be determined; samples can be compared to the means for *Ce. arenaria* plus *Ce. diffusa* ($57 \cdot 6$) and *Ch. australis* ($62 \cdot 8$).]

6   Aculeus apex narrowed in two steps (Fig. 21). Frons sometimes black (a form known from southern USSR and from a single French specimen). [Normally associated with some species of *Centaurea (Lopholoma)*. Widespread in most of Europe, except the north.] .... *loricata* (Rondani)

— Aculeus apex evenly narrowed (Figs 18–20). Frons always yellow or orange. 7

7 Aculeus more than $2 \cdot 0$ mm long (Fig. 18); aculeus ventral lobe less than $0 \cdot 6$ times as long as aculeus. [Associated with *Chartolepis intermedia* in Kazakh SSR (northern); also known from Russian SFSR (near Volgograd) and an unconfirmed record from China.] .... *isais* Hering

— Aculeus less than $2 \cdot 0$ mm long (Figs 19, 20); aculeus ventral lobe usually (95%) more than $0 \cdot 6$ times as long as aculeus. 8

8 Aculeus usually (70%) less than $1 \cdot 6$ mm long (Fig. 20). General body colour dull orange-yellow. Scutal pattern (other than spots) usually dark, especially in posterior half. [Associated with some *Centaurea (Solstitiaria)* species in France, Greece (Crete), Italy and Turkey; *Centaurea (Calcitrapa)* in Israel; also known from Cyprus and N.E. Greece.] .... *succinea* (Costa)

— Aculeus usually (70%) more than $1 \cdot 6$ mm long (Fig. 19). General body colour bright yellow. Scutal pattern (other than spots) pale, rarely with any darkening posteriorly. [Associated with some *Carthamus* species in Israel, Iraq and Kirghizian SSR; also known from Cyprus.] .... *carthami* Stackelberg

Chaetorellia Hendel

Chaetorellia Hendel, 1927: 121. Type-species: *Tephritis jaceae* Robineau-Desvoidy, 1830; 766, by original designation.

Generic diagnosis. *Chaetorellia* species are distinguished from most other species of Terelliini by the presence of presutural dorsocentral setae (White, 1988), the exception being *Terellia blanda* (Rikhter), which differs from *Chaetorellia* in several respects (male and female paratypes examined, TMB). For example, the apical wing crossband of *T. blanda* is divided into two large apical spots and its male terminalia differ from those of *Chaetorellia* species. The head profile shape and wing pattern of the type-species, *Ch. jaceae*, has been illustrated by White (1988).

Chaetorellia jaceae species-group

Species-group description. Egg: presumed micropyle separated from main body of egg by a tube (Fig. 1). Larva and puparium: spiracular hairs each with three branches (Fig. 3). Adult: thorax: scutum with eight black spots, one at the base of each presutural and postsutural dorsocentral seta, each presutural supra-alar seta and each prescutellar acrostichal seta; anterior and posterior (postsutural) supra-alar setae based on a yellow ground or in a black stripe. Wing: cell *cup* not extending well beyond end of cell *bm* (Figs 7, 8). Abdomen: aedeagal glans with an evenly curved main duct (Fig. 10); aculeus apex acuminate (Figs 13–17).

Remarks. The content of this group differs from that listed by Korneyev (1985) in the following respects: *Ch. algira* (Macquart) and *Ch. succinea* are removed from the group, and *Ch. nigropicta* Hering and *Ch. vittata* (Rondani) are added as synonyms of *Ch. hestia*.

Chaetorellia acrolophi sp. n.

Orellia hexachaeta (Loew, 1862); Séguy, 1934: 135 (in part) [misidentification].
Chaetorellia hexachaeta (Loew, 1862); Hering 1937*b*: 252 (in part); Dirlbek & Dirlbekova,

1974; 84 (in part); Zwölfer, 1974*b*: 149; Sobhian & Zwölfer, 1985: 311 (in part); White, 1989*b* (in part) [misidentifications].

Chaetorellia hexachaeta hexachaeta (Loew, 1862); Hering, 1940: 13 [misidentification].

Chaetorellia hexachaeta (Loew, 1862); Mihályi, 1960: 35 (in part); Rikhter, 1970; 151 (in part); Zwölfer, 1974*a*: 13 [misidentifications].

Chaetorellia jaceae (Robineau-Desvoidy, 1830); Zwölfer, 1965: 138; Leclercq, 1967: 96 (in part) [misidentifications].

Chaetorellia sp. nr *jaceae* (Robineau-Desvoidy, 1830); Zwölfer, 1965: 140.

Description. Egg: tube short (1·1–1·9 mm). Larva-puparium: similar to *Ch. jaceae*, described by Varley (1937), but cephalopharangeal skeleton shorter, 0·54–0·65 mm long. Adult: general body colour orange-yellow. Head: frons yellow to orange. Thorax: anterior and posterior (postsutural) supra-alar setae based on a yellow ground; scutal spots small, each presutural dorsocentral spot usually about equal in breadth to half the distance between the prescutellar acrostichal spots; scutal pattern (other than spots) pale brown, usually not much darker than ground colour of scutum, at most darkened posteriorly; subscutellum pale brown to black; katepisternum usually pale brown. Wing: cell *bm* usually (87%) with a hyaline area in its basal two-thirds (Fig. 7); discal and preapical crossbands usually (98%) well separated, at most narrowly joined (Fig. 14). Abdomen: each tergite usually with a lateral and a medial pair of dark spots; aculeus apex acuminate (Fig. 14). Measurements: WL♀=2·4–3·9 mm; form on *Ce. maculosa* and *Ce. vallesiaca*, C2L=0·9–1·4 mm (mean 1·17±0·02), RL=1·2–1·8 mm (1·50±0·03), AL=1·3–1·8 mm (1·59±0·02), AA=21–29° (24·7±0·3), C2L/AL=0·6–0·9 (0·74±0·01), RL/AL=0·8–1·1 (0·95±0·01); presumed conspecific form on *Ce. leucophaea*, C2L=0·8–1·1 mm (0·93±0·03), RL=1·1–1·3 mm (1·20±0·03), AL=1·1–1·3 mm (1·19±0·03), AA=26–31° (28·2±0·6), C2L/AL=0·7–0·9 (0·78±0·03), RL/AL=0·9–1·1 (1·0±0·02); individuals found on *Ce. arenaria, Ce. diffusa* and *Ce. spinabadia* are similar in size characters (C2L, RL, AL) to the form on *Ce. leucophaea*, and the ratio characters (C2L/AL, RL/AL, AA) to the form on *Ce. maculosa* and *Ce. vallesiaca*.

Diagnosis. Normally associated with species of the subgenus *Acrolophus* of *Centaurea*; no other *Chaetorellia* species is known to attack this group of plants. This species also differs morphometrically from the closely related *Ch. jaceae* and *Ch. australis*, and the critical diagnostic characters are explained in the key (couplets 2 & 5).

Hosts. The normal hosts of *Ch. acrolophi* are closely related plants belonging to the subgenus *Acrolophus* of *Centaurea*, which includes the North American weed species *Ce. diffusa* and *Centaurea* sp. nr *maculosa*. Unfortunately, no good samples were available from *Ce. diffusa*, and populations associated with plants other than *Ce. maculosa* and *Ce. vallesiaca* are not confirmed as belonging to this species. The known geographic range of *Ch. acrolophi* extends from Spain, through the European Alps to Greece and the south-western areas of the USSR. There are some morphometric differences between some of these populations, as indicated by the separation along CV axis I of samples associated with *Ce. leucophaea, Ce. maculosa* and *Ce. vallesiaca* (Fig. 12, points l, m & v).

Material examined. Holotype ♀ (not dissected, but aculeus exposed), **Ce. vallesiaca**: SWITZERLAND, Valais, Lalden, 9.vii.1985 (swept) (*I. M. White, C. S. A. Stinson*) (BMNH). Paratypes, **Ce. maculosa**: 1 ♀, AUSTRIA, Dürnstein, 8.viii.1985 (emerged 21.viii.1985) (*C. S. A. Stinson*) (BMNH); 25 ♀, 1 ♂, Dürnstein, 19.viii–14.ix.1985 (some reared, emerged 1986) (*C. S. A. Stinson*) (BMNH, CNC); 8 ♀, Hornstein, swept 16.viii.1985 (*C. S. A. Stinson*) (BMNH, CNC); 17 ♀, 4 ♂, Hornstein, 16.viii.1985 (emerged by 30.vi.1986) & swept 20.vii.1986 (*I. M. White, C. S. A. Stinson*) (BMNH, CNC); 9 ♀, Sollenau, swept 20.vii.1986 (*I. M. White, C. S. A. Stinson*) (BMNH, CNC); 6 ♀, GREECE, Thermi, vi.1986 (emerged vii.1987) (*Sobhian*) (BMNH). 7 ♀, HUNGARY, Budapest, Julia Major, 2.viii.1985 (some reared, emerged 15.v.1986) (*C.S.A. Stinson*) (BMNH, CNC); 10 ♀, Lake Balaton, Tihany, swept 19.vii.1986 (*I. M. White, C. S. A. Stinson*) (BMNH, CNC); 4 ♀, Lake Velence, 3.viii.1985 (reared) (*C. S. A. Stinson*) (BMNH, CNC); 9 ♀, Lake Velence, swept 18.vii.1986 (*I. M. White, C. S. A. Stinson*) (BMNH, CNC). 3 ♀, ROMANIA, Iasi-Socola, 14.x.1985 (emerged 5–9.v.1986) (*C. S. A. Stinson*) (BMNH, CNC). 6 ♀, SWITZERLAND, Valais, Ausserberg, by railway siding, swept 7.vii.1987 (*I. M. & F. J. White, K. Marquardt*) (BMNH, CNC) [these plants are probably alien to the region]. 1 ♀, USSR, Byelorussian SSR, Brest Prov., Peplovka Dist., 9.viii.1976 (emerged 1–5.ix.1976, ex "*Ce. pseudomaculosa*") (*M. D. Zerova*) (ZIL); 3 ♀, Ukrainian SSR, Kiev, 2.iv–7.iv.1985 (?reared, ex "*Ce. pseudomaculosa*") (*V. Korneyev*) (IBPPK). **Ce. vallesiaca**: 21 ♀, SWITZERLAND, Valais; Brig, swept 9.vii.1985 (*I. M. White, C. S. A. Stinson*) (BMNH, CNC), 11 ♀, Brig, autumn 1985 (emerged spring 1987) (*K. Marquardt*) (BMNH); 2 ♀, Brigerbad, swept 9.vii.1985 & 7.vii.1987 (*I. M. & F. J. White, C. S. A. Stinson*) (BMNH); 10 third-instar larvae, Lalden, 29.viii.1988 (*K. Marquardt*) (CIBC); 13 ♀, Lalden, early summer 1987 (emerged late summer 1987) (*K. Marquardt*) (BMNH); 8 ♀, 2 ♂, Lalden, swept 9.vii.1985 & 6.vii.1987 (*I. M. & F. J. White, K. Marquardt, C. S. A. Stinson*) (BMNH, CNC); 2 ♀, 3 ♀, Pfynwald, swept 24.vi.1987 (*K. Marquardt*) (BMNH). Non-type material. **Ce. arenaria**: 1 ♀, ROMANIA, Hanu Conachi (reared) (BMNH). 7 ♀, USSR, Ukrainian SSR, Rubezhnoe (reared) (ZMK). **Ce. cariensis longipapposa**: 1 ♀ (aculeus tip broken), TURKEY, Gelendorf-Akçehir Rd. (reared) (BMNH) [plant determined by G. Wagenitz]. **Ce. diffusa**: 6 ♀, ROMANIA, Somova & Tulcea (not reared) (BMNH, CNC). 4 ♀, USSR, Moldavian SSR, Kishinev & Korzhevo (not reared) (BMNH, IBPPK); 6 ♀, Ukrainian SSR, Voevodovka (reared) (ZMK). **Ce. leucophaea**: 3 ♀, FRANCE, Herault, Cournonterral, swept 13.vi.1987 (*I. M. & F. J. White*) (BMNH) [plant determined by G. Wagenitz]; 19 ♀, 5 ♂, Herault, St. Paul, swept 11–13.vi.1987 (*I. M. & F. J. White*) (BMNH, CNC); 14 ♀, Rhone Valley area near Avignon (Alpilles, Avignon, St. Martin, Montellimar, Roquemaure, St. Remy) (reared) (BMNH, LTUB) [labelled as ex *Ce. paniculata*, but this is not separated from the almost indistinguishable *Ce. leucophaea* in this work]. **Ce. pectinata**: 1 ♀, SPAIN, Gerona Prov., Pals (reared) (BMNH). **Ce. spinabadia**: 5 ♀, 5 ♂, FRANCE, Pyrenees Oriental, Collioure, Tour Madeloc (not reared) (BMNH) [plant determination checked by G. Wagenitz]. **Ce. virgata**: 1 ♀, TURKEY, S.W. of Bor, Nigde (reared) (USNM). **No host data**: 4 ♀, YUGOSLAVIA, Macedonia, Prespa Geul, Otesovo (BMNH).

Chaetorellia australis Hering stat. n.

? *Trypeta hexachaeta* Loew, 1862; 53. Probable holotype ♀, POLAND (ZMHB) [examined].

Chaetorellia hexachaeta (Loew, 1862); Hering, 1937*b*: 252 (in part); Mihályi, 1960: 35 (in part); Rikhter, 1970: 151 (in part); Dirlbek & Dirlbekova, 1974; Sobhian & Zwölfer, 1985: 311 (in part); Clement & Mimmocchi, 1988: 47; White, 1989*b* (in part) [possible misidentifications].

Chaetorellia hexachaeta australis Hering, 1940: 12. Syntypes, USSR (BMNH) [examined].

Chaetorellia jaceae (Robineau-Desvoidy, 1830); Leclercq, 1967: 95 [misidentification].

Redescription. Egg: tube short (1·1–2·0 mm). Adult (summer form): general body colour orange-yellow. Head: frons yellow to orange. Thorax: anterior (postsutural) supra-alar setae always based on a yellow ground; scutal spots small, each presutural dorsocentral spot usually about equal in breadth to half the distance between the prescutellar acrostichal spots; scutal pattern (other than spots) pale brown to black (specimens from Turkey and Greece usually pale, Moldavian specimens dark); subscutellum and katepisternum pale brown to black. Wing: cell *bm* usually (98%) with a hyaline area in its basal two-thirds (Fig. 7); discal and preapical crossbands well separated. Abdomen: each tergite usually with a lateral and a medial pair of spots; aculeus apex acuminate (Fig. 16). Measurements: WL♀=2·9–3·9 mm, C2L=1·0–1·3 mm (mean 1·13±0·02), RL=1·2–1·7 mm (1·45±0·03), AL=1·2–1·5 mm (1·30±0·02), AA=25–31° (27·8±0·03), C2L/AL=0·7–1·0 (0·87±0·01), RL/AL=1·0–1·3 (1·11±0·01). Adult (form overwintering as larva), as summer form except for the following: anterior and posterior (postsutural) supra-alar setae usually based on a yellow ground, rarely on a black stripe; scutal pattern (other than spots) black; subscutellum and katepisternum black. Measurements: C2L=1·1–1·3 mm (1·19±0·05), RL=1·2–1·7 mm (1·51±0·07), AL=1·1–1·3 mm (1·17±0·04), AA=27–31° (28·7±0·8), C2L/AL=1·0–1·1 (1·02±0·02), RL/AL=1·2–1·4 (1·29±0·03).

Nomenclature. The oldest name which might apply to this species is *Trypeta hexachaeta* Loew, which was described from Poland. The Loew collection (ZMHB) contains two males and two females standing against this name. As Loew (1862) only mentions a female (WL=3·4 mm, as 1·6 lines) in the original description, the two males cannot be syntypes. One female was dissected and found to be a typical specimen of *Ch. hestia*, which is very unlikely to have been found in Poland. The other female may be the holotype, but it has lost its abdomen (WL=3·4 mm; C2L=1·16 mm; RL=1·48 mm) and is of a size that could fit any member of the *Ch. jaceae* species-group except *Ch. jaceae*; correspondingly, the name *hexachaeta* has been applied to all members of the group other than *Ch. jaceae*. Mature seed heads of likely hosts for *Chaetorellia* species were collected in Poland, namely *Ce. cyanus* and *Ce. maculosa*, but no *Chaetorellia* emerged. To avoid further confusion, *T. hexachaeta* is here treated as a probable synonym of *Ch. australis*. Hering (1940) described *Ch. australis* as a subspecies of *Ch. hexachaeta* on the basis that they differed in size and in the relative lengths of wing cells *c* and *sc*. As Hering refers to '*hexachaeta*' as being a large insect (WL♀=3·6–3·9 mm) compared to *Ch. australis* (WL♀=2·8–3·4 mm), it is likely that he was in fact separating *Ch. australis* from *Ch. acrolophi*; examination of long series of each of these species indicated that the *c:sc* ratio does not separate them.

Hosts. *Ch. australis* attacks both *Ce. cyanus* and *Ce. solstitialis* in north-eastern Greece, and its unusual life-cycle has been described above. The samples off *Ce. depressa*, a very close relative of *Ce. cyanus*, do not exactly match any reference sample included in the CV analysis (Table IX), but it is within the observed range of variation of *Ch. australis* and their host association indicates that they are most likely to be this species.

Material examined. *Ce. cyanus*: 32 ♀, 5 ♂, GREECE, Macedonia, Agios Prodromus, 23.vi.1985 (emerged 1–3.vii.1985) (*S. L. Clement, R. Sobhian*) (BMNH, USNM); 22 ♀, Macedonia, Thermi, emerged vii.1987 (*R. Sobhian*) (BMNH); 12 ♀, Macedonia, Doirani, Kilkis & Thessaloniki areas (reared) (BMNH, USNM). 4 ♀, HUNGARY, Csenger & Nagyteteny (reared) (TMB). *Ce. depressa*: 5 ♀, TURKEY, Güldarpi-Çubuk Rd. & Mürted-Yenimahalle Rd. (reared) (BMNH). *Ce. solstitialis*: 5 ♀, BULGARIA, Nesebar & Obrasov (some reared) (LTUB, NHMV). 4 ♀, GREECE, Macedonia, Doirani, 5.vii.1985 (emerged by 31.vii.1985) (*C. E. Turner*) (USNM); 11 ♀, Macedonia, near Kilkis, Kambani, 1986 (reared) (*I. Pittara*) (BMNH); 4 ♀ Macedonia, between Thessaloniki & Kilkis, 11.vii.1985 (emerged by 31.vii.1985) (*C. E Turner*) (USNM); 13 ♀, Macedonia, Thermi, autumn 1984 (emerged early v.1985) (*R. Sobhian*) (BMNH, USNM); 10 ♀, 1 puparium, Macedonia, Thermi & Tessaloniki areas (reared) (BMNH, LTUB, USNM). 2 ♀, HUNGARY, Budapest (reared) (TMB). 31 ♀, TURKEY, Aydin, Burdur, Bursa, Erzurum, Sansum, Sivas & Tire areas (reared) (BMNH, USNM). 14 ♂ (10 dissected), 2♂ (not dissected), USSR, Moldavian SSR, Bendery (as "Tighina"), vii.1938 (reared) (*M. Hering*) (includes ♂, ♀ syntypes, labelled as type ♂ & ♀ in BMNH, and other specimens erroneously labelled as paratypes) (BMNH, NHMB, SMNS, ZMHB)). **No host data:** 1 ♀, POLAND, southern area and Poznan (as "Schlesien und bei Posen" in description), labelled "2/8 44" (possible holotype *T. hexachaeta*) (ZMHB). 2 ♀, USSR, Ukrainian SSR, Wolczkowce (as "Wolczkow, Podol.") (BMNH) [found about 100 miles from the type-locality area of *T. hexachaeta*].

Chaetorellia sp. near *australis* Hering

Chaetorellia hexachaeta (Loew, 1862); White, 1989*b* (in part) [misidentification].

Diagnosis. Resembles *Ch. australis* but differs morphometrically (placed at CVI=21·5, CVII=3·1). Measurements: WL♀=2·6–3·0 mm, C2L=0·86–1·02 mm; RL=1·2–1·3 mm; AL=1·1 mm; AA=23–26°; C2L/AL=0·8–1·0; RL/AL=1·0–1·2.

Hosts. These specimens were said to be reared from safflower, *Ca. tinctorius*, and they fail to match any population of *Chaetorellia* included in the CV analysis (Table II), although the sample runs to *Ch. australis* in the key. However, they are unlikely to represent that species because field (Table IVC) and laboratory host tests (Sobhian & Zwölfer, 1985) indicated that *Ch. australis* does not attack *Ca. tinctorius*. The possibility that the plant was incorrectly identified cannot be ruled out; however, this sample may represent another undescribed *Chaetorellia* species.

Material examined. **Ca. tinctorius**: 4 puparia, 4 ♀, 1 ♂, labelled "em. 17.v–3.vi.1968, safflower, Brauerman & Tashiro" (USNM) [P. Dunn, USDA Rome, traced the collectors, but no further data could be obtained].

Chaetorellia conjuncta (Becker)

Terellia conjuncta Becker, 1912: 642.
Terellia jaceae (Robineau-Desvoidy, 1830); Efflatoun, 1924: 82, 1927: 33 (in part); Phillips, 1946: 124 [misidentifications].
Chaetorellia conjuncta (Becker, 1912); Hendel, 1927: 122.
Chaetorellia succinea (Costa, 1844); Hendel, 1927: 123; Stackelberg, 1929: 225; Hering, 1937b: 250; Phillips, 1946: 111; Mihályi, 1960: 34; Rikhter, 1965: 143, 1970: 151; Leclercq, 1967: 95, 96; Foote, 1967: 51, 1984: 79; Dirlbek & Dirlbekova, 1974: 84; Korneyev, 1985: 632 [misidentifications].
Chaetorellia jaceae (Robineau-Desvoidy, 1830); Friedberg, 1974: 136; Kugler & Friedberg, 1975: 61 [misidentifications].
Chaetorellia sp. ? *hexachaeta* (Loew, 1862); Petney & Zwölfer, 1985: 150 [misidentification].

Redescription. Egg: tube long (2·6–3·0 mm). Adult: general body colour orange-yellow. Head: frons yellow to orange. Thorax: anterior and posterior (postsutural) supra-alar setae based on a yellow ground; scutal spots small, each presutural dorsocentral spot usually about equal in breadth to half the distance between the prescutellar acrostichal spots; scutal pattern (other than spots) pale brown, sometimes darkened posteriorly, rarely black; subscutellum and katepisternum pale brown. Wing: cell *bm* usually (98%) with a hyaline area in its basal two-thirds (Fig. 7); discal and preapical crossbands usually (88%) joined in cell r_1. Abdomen: each tergite often with a lateral and a medial pair of spots; aculeus apex acuminate (Fig. 15). Measurements: WL♀=3·3–4·8 mm; form associated with *Ce. aegyptiaca*, *Ce. lanulata* and *Ce. pallescens*, C2L=0·9–1·7 mm (mean 1·33±0·03), RL=1·2–2·1 mm (1·78±0·03), AL=1·0–1·7 mm (1·38±0·02), AA=30–39° (33·7±0·3), C2L/AL=0·8–1·1 (0·96±0·01), RL/AL=1·1–1·5 (1·29±0·01); form associated with *Ce. iberica* (populations on *Ce. calcitrapa* and *Ce. hyalolepis* are similar), C2L=1·0–1·6 mm (1·30±0·04), RL=1·3–2·1 mm (1·72±0·05), AL=1·2–1·7 mm (1·5±0·04), AA=27–34° (30·9±0·5 C2L/AL=0·7–1·0 (0·87±0·02), RL/AL=1·0–1·3 (1·16±0·02).

Nomenclature. Unfortunately, the holotype of *Terellia conjuncta* could not be located. However, the reference in the original description to the four wing crossbands being connected, combined with the type locality and the thoracic spot pattern, leave little doubt that this is the species that occurs throughout the Middle East on starthistles belonging to the subgenera *Calcitrapa* and *Solstitiaria* of *Centaurea*. *T. conjuncta* was previously placed in synonymy with *Ch. succinea*, due to a misinterpretation of these species.

Hosts. In Israel, *Ch. conjuncta* attacks several species of the subgenera *Solstitiaria* and *Calcitrapa* of *Centaurea*; Petney & Zwölfer (1985) record it from *Ce. iberica* and *Ce. pallescens* in Jordan; in Turkey, it attacks *Ce. calcitrapa*, and Efflatoun (1927) records it from *Ce. pallescens* and *Ce. calcitrapa* in Egypt. Although *Ch. conjuncta* was described from south-eastern Iran, its hosts to the east of Jordan are unknown.

Forms. *Ch. conjuncta* includes two morphometrically distinct groups (note separation on CV axis I in Fig. 12). One of these attacks *Ce. calcitrapa* in Turkey and the closely related *Ce. hyalolepis* and *Ce. iberica* in Israel; all these hosts belong to the subgenus *Calcitrapa*. The second form, which tends to have a shorter aculeus than the first, attacks *Ce. (Calcitrapa) pallescens*, and two species of the subgenus *Solstitiaria*, namely *Ce. aegyptiaca* and *Ce. lanulata*, in Israel.

Material examined. **Ce. aegyptiaca**: 5 ♀, ISRAEL, Mizpe Ramon (not reared) (BMNH); 2 larvae, 1 puparium, 80 ♀, 5 ♂, Israel, Ramat Boqer, 28.iv.1987 (most reared, emerged by 1.vi.1987) (*I. M. White, A. Freidberg*) (BMNH);

16 ♀, 10 ♂, Sede Boqer, 29.iv.1987 (emerged by 1.vi.1987) (*I. M. White, A. Freidberg*) (BMNH). *Ce. calcitrapa*: 9 ♀, GREECE, Macedonia, 10 km E Alexandroupoli (reared) (BMNH); 23 ♀, TURKEY, Bursa, Erzincan, Erzurum, Icel & Pirnakapan areas (reared) (BMNH, USDA). *Ce. hyalolepis*: 8 ♀, 3 ♂, ISRAEL, Banyas, Beer Sheva, Bet Qama & Devira (some reared) (BMNH, TAU). *Ce. iberica*: 48 ♀, 5 ♂, ISRAEL, Mount Hermon, 700–2000 m, v–vii, 1979–87 (most reared) (*A. Freidberg, J. Kugler, W. N. Mathis, I. M. White*) (BMNH, TAU, USNM); 2 ♀, 4 ♂, Mount Meiron (not reared) (BMNH). 1 ♀, TURKEY, Edime (reared) (LTUB). 1 ♀, USSR, Kirghizian SSR, near Prunze, Lebedinovka (reared) (IBPPK). *Ce. lanulata*: 4 ♀, 3 ♂, ISRAEL, 15–20 km E. Arad (not reared) (BMNH); 16 ♀, En Gedi Spa, iv–v.1970–87 (some reared) (*A. Freidberg, J. Kugler, I. M. White*) (BMNH, TAU). *Ce. pallescens*: 9 ♀, ISRAEL, En Hazeva & Jericho (most reared) (BMNH, TAU); 15 ♀, 4 ♂, En Mor Gorge, 29.iv.1987 (emerged by 1.vi.1987) (*I. M. White, A. Freidberg*) (BMNH); 20 ♀ 3 ♂, Nahal Paran, 29.iv.1987 (most reared, emerged by 1.vi.1987) (*I. M. White, A. Freidberg*); 27 ♀, Sede Boqer, 29.iv.1987 (emerged by 1.vi.1987) (*I. M. White, A. Freidberg*) (BMNH). 1 ♀, JORDAN, Deir Alla (reared) (LTUB). *Ce. procurrens*: 1 ♀, ISRAEL, Tel Aviv (reared) (TAU). **No host data**: 1 ♀, ALBANIA, Tirana (BMNH). 1 ♀, CYPRUS, Zakaki (BMNH). 1 ♀, EGYPT, Wadi-Hoff (NHMV) [Efflatoun (1927) implies that *Ce. pallescens* is the host at this locality]. 1 ♀, IRAN, 19 miles NW Zanjan (BMNH). 1 ♀, IRAQ, Al Amarah, R. Tigris (BMNH). 1 ♀, LEBANON, Becharre, Cedern (BMNH). 1 ♂, PAKISTAN, Quetta (BMNH). 1 ♀, SYRIA, Duma (MNHNP). 5 ♀, USSR, Kazakh SSR, Alma-Ata Province, Semireche'e region, Almatinka River (ZIL).

Type data. Holotype. ♂, IRAN: Makran Coast, Chah Bahar (as "Tschachbar"), 16.iii.1901 (*N. Zarudny*), not located.

Chaetorellia hestia Hering

? *Tripeta vittata* Rondani, 1870: 111. Syntype ♀, ITALY (MZF) [examined].
Tripeta exachaeta (Loew, 1862); Rondani, 1870: 111 [misidentification].
Chaetorellia hexachaeta (Loew, 1862); Hendel, 1927: 122; Zwölfer, 1965: 141 [misidentifications].
Orellia hexachaeta (Loew, 1862); Séguy, 1934: 135 (in part) [misidentification].
Chaetorellia hestia Hering, 1937b: 252. Syntype ♀♂, SPAIN (BMNH) [examined].
Chaetorellia nigropicta Hering, 1937b: 251. Syntype ♀♂, ALGERIA (ZMHB) [examined].
   Syn. n.

Redescription. Egg: tube short (1·3 mm). Adult: general body colour orange-yellow. Head: frons yellow to orange. Thorax: anterior and posterior (postsutural) supra-alar setae usually based on a yellow ground, sometimes in a black stripe; scutal spots large, each presutural dorsocentral spot usually about equal in breadth to the distance between the prescutellar acrostichal spots; scutal pattern (other than spots) usually black; subscutellum black; katepisternum black. Wing; cell *bm* usually (91%) without a hyaline area (Fig. 8); discal and preapical crossbands well separated. Abdomen: each tergite with a lateral and a medial pair of spots; aculeus often very much broader before tapering section than at base (Fig. 17). Measurements: WL♀=2·9–4·2 mm, C2L=0·9–1·4 mm (mean 1·22±0·04), RL=1·2–1·8 mm (1·52±0·05), AL=0·9–1·2 mm (1·04±0·02), AA=31–36° (33·4±0·05), C2L/AL=1·0–1·3 (1·17±0·03), RL/AL=1·3–1·7 (1·45±0·03).

Nomenclature. The only specimen standing against the name *Trypeta vittata* in the Rondani collection (MZF) has its aculeus broken near the apex (estimates: AL=1·01 mm, AA=38°) and, as it is not possible to be certain about the identity of this specimen, *Ch. vittata* is here regarded as a probable synonym of *Ch. hestia*.

Hosts. *Ch. hestia* has usually been found in association with species of the subgenus *Seridia* of *Centaurea*, in particular, on *Ce. aspera*. It is known from both the Atlantic and Mediterranean coastal areas of France, Spain, Italy and Algeria.

Forms. Specimens of *Chaetorellia* with dark lateral vittae along the line of the supra-alar setae were previously called *Ch. nigropicta*. However, these flies are morphometrically similar to *Ch. hestia*, and in one large sample of *Ch. hestia* (Lobres, Spain), eight out of 64 specimens had a darkening of the supra-alar area. It is likely that the darkening occurred with age in this population, but the completely black supra-alar vittae may be the normal coloration in some areas of Italy and Algeria (this form is known from Rome, ex *Ce. sphaerocephala*, and Algeria). Some specimens of the spring form of *Ch. australis* also have this dark vitta. It is concluded that *Ch. nigropicta* is a synonym of *Ch. hestia*.

Material examined. *Ce. aspera*: 27 ♀, 5 ♂, FRANCE, Avignon, Bordeaux, Montpellier & eastern Pyrenees areas (some reared) (BMNH). 15 ♀, SPAIN, Gerona Province, Santa Christina d'Aro, 28.viii.1987 (emerged ix.1987) (*M. Carles-Tolra*) (BMNH); 1 puparium, 24 ♀, Granada Province, Lobres, adults swept 15–18.iv.1986 (*I. M. & F. J. White*) (BMNH); [all material off *Ce. aspera* lacks black supra-alar vittae]. *Ce. collina*: 2 ♀, FRANCE, Herault, La Triadou (reared) (BMNH) [these lack black supra-alar vittae]. *Ce. sphaerocephala*: 5 ♀, ITALY, Anzio & Rome (reared) (BMNH, USNM) [these specimens have black supra-alar vittae]. **No host data**: 2 ♀, ALGERIA, Phillipeville (MNHNP); 1 ♀, 1 ♂, iv, #52243 (syntypes of *Ch. nigropicta*) (ZMHB); 1 ♀. 2 ♂ (erroneously labelled as paratypes of *Ch. nigropicta*) (BMNH, ZMHB). 1 ♀, 1 ♂ (neither dissected), SPAIN, Montserrat, vi.1933 (syntypes of *Ch. hestia*) (*M. Hering*) (BMNH); 2 ♀, 7 ♂, (1 ♀ dissected), Albarracin, vi.1933 (erroneously labelled as paratypes of *Ch. hestia*) (BMNH). 1 ♀, ITALY, Parma (as "agri parmensis") (no label data) (syntype of *T. vittata*) (*MZF*).

Chaetorellia jaceae (Robineau-Desvoidy)

Tephrytis jaceae Robineau-Desvoidy, 1830: 766.
? *Tephrytis dorsalis* Robineau-Desvoidy, 1830: 766.
? *Tephrytis pusilla* Robineau-Desvoidy, 1830: 766.
Trypeta punctata (Schrank, 1781); Loew, 1844: 328 [misidentification].
Chaetorellia jaceae (Robineau-Desvoidy, 1830); Hendel, 1927: 122.
Orellia jaceae (Robineau-Desvoidy); Séguy, 1934: 135; Phillips, 1946: 116.
Trypeta (Chaetorellia) jaceae (Robineau-Desvoidy); Varley, 1937: 117; Kabos, 1959: 15.

Redescription. Egg: tube short (1·6–2·6 mm) (Fig. 1). Larva: described by Varley (1937). Adult: general body colour orange-yellow. Head: frons yellow to orange. Thorax: anterior and posterior (postsutural) supra-alar setae always based on a yellow ground; scutal spots small, each presutural dorsocentral spot usually about equal in breadth to half the distance between the prescutellar acrostichal spots; scutal pattern (other than spots) pale brown to black; subscutellum pale brown to black; katepisternum pale brown. Wing: cell *bm* usually (98%) with a hyaline area in its basal two-thirds (Fig. 7); discal and preapical crossbands usually (98%) well separated, at most narrowly joined in cell r_1. Abdomen: each tergite usually with a lateral and a medial pair of spots; aculeus apex acuminate (Fig. 13). Measurements: WL♀=3·7–4·6 mm; form associated with *Ce. jacea*, C2L=1·2–1·6 mm (mean 1·38±0·09), RL=1·5–2·0 mm (1·71±0·11), AL=2·0–2·7 mm (2·35±0·12), AA=16–19° (17·7±0·6), C2L/AL=0·5–0·6 (0·59±0·02), RL/AL=0·7–0·8 mm (0·73±0·03); form associated with *Ce. nigra*, C2L=1·3–1·8 mm (1·52±0·04), RL=1·6–2·1 mm (1·88±0·04), AL=1·8–2·3 mm (2·11±0·04), AA=17–22° (19·2±0·4), C2L/AL=0·6–0·8 (0·72±0·02), RL/AL=0·8–1·0 (0·89±0·02).

Nomenclature. Unfortunately, no Tephritidae remain in the Robineau-Desvoidy collection, but as Robineau-Desvoidy (1830) associated *Tephrytis jaceae* with *Ce. jacea* there is little doubt that he was describing the species of *Chaetorellia* that attacks that plant. Robineau-Desvoidy (1830) also described *T. dorsalis* and *T. pusilla* as being similar species, and they are here regarded as probable synonyms of *Ch. jaceae*.

Hosts. *Ch. jaceae* normally attacks species of the subgenus *Jacea* of *Centaurea*, but in Italy is also attacks *Ce. (Phalolepis) alba*. The published record of *Ch. jaceae* attacking *Cirsium vulgare* (Savi) Ten. (= *C. lanceolatum* (L.) Scop.), which derives from Kieffer (1891), is probably a misidentification of *Chaetostomella cylindrica* (Robineau-Desvoidy), which is a superficially similar species that does attack *Cirsium vulgare*. This erroneous record has subsequently been repeated by several other authors (Hendel, 1927; Séguy, 1934; Phillips, 1946; Leclercq, 1967; Rikhter, 1970). *Ch. jaceae* is known from most areas of Europe, including Scandinavia and some Mediterranean areas, and it has been found as far east as the Caucasus.

Material examined. *Ce. alba*: 6 ♀, ITALY, Ferriere & Rome (reared) (BMNH, CSIRO). *Ce. jacea*: 1 ♀, DENMARK, Maribo (probably reared) (BMNH); 10 ♀, FRANCE, Avignon, eastern Pyrenees, Poiton & Sologne areas (most reared) (BMNH, SMNS, TAU, USNM); 10 ♀, GERMAN FEDERAL REPUBLIC, Black Forest, Budenheim, Freiberg, N. Wurttemberg & Klein Kemps (most reared) (BMNH, SMNS, USNM). 4 ♀, HUNGARY, Budapest area (not reared) (BMNH); 5 ♀, Lake Velence, 18.vii.1986 (*I. M. White, C. S. A. Stinson*) (BMNH); 8 ♀, 3 ♂, Lake Velence, 23.viii.1986 (3 ♀ reared, emerged 1987) (*I. M. White, K. M. Harris, A. L. Norrbom*) (BMNH). 9 ♀, ITALY, Arsoli & Rome (reared) (BMNH, USNM). 4 ♀, SWEDEN, Dalarna, Taktbo (ZMUC). 3 ♀, USSR, Moldavian SSR, Kishinev & Korzhevo (reared) (BMNH); 1 ♀, Estonian SSR, Isborsk (possibly reared) (BMNH); 2 ♀, Ukrainian SSR, Krimea & Novo-Aidar areas (IBPPK, ZMK). *Ce. nigra*: 6 ♀, ENGLAND, Kent, Gillingham (not reared) (BMNH); 2 puparia, 18 ♀, 5 ♂, Surrey, Purley, Riddlesdown, 29.vi–6.vii.1986 (not reared) (*I. M. & F. J. White, R. A. I. Drew*) (BMNH); 14 ♀, Riddlesdown, 10–31.viii.1986 (apparently a second generation) (not reared) (*I. M. & F. J. White, P. Harris, A. L. Norrbom*) (BMNH). 25 ♀, 4 ♂, FRANCE, Autun-Mer, Brittany, Caen, eastern & western Pyrenees (many reared) (BMNH, NHMB, USNM). 2 ♀, GERMAN FEDERAL REPUBLIC, Black Forest (reared) (LTUB). *Ce. pannonica*: 1 ♀, AUSTRIA, Eisenstadt (reared) (SMNS). **No host data:** 2 ♀, GREECE, Macedonia, 9·5 km W. Veria (USNM). 9 ♀, NORWAY, Vestfold (ZMUB), 1 ♀. YUGOSLAVIA, Slovenia, Lipica (BMNH).
Type data. Syntypes of *T. jaceae*, *T. dorsalis* and *T. pusilla* are all presumed destroyed; they were probably from France.

Chaetorellia loricata species-group

Species-group description. Egg: presumed micropyle not separated from main body of egg by a long tube (Fig. 2). Adult: thorax; scutum with ten black spots, one at the base of each presutural and postsutural dorsocentral seta, each presutural and anterior (postsutural) supra-alar seta, and each prescutellar acrostichal seta; scutum sometimes with two extra black spots, which are placed at the base of each posterior (postsutural) supra-alar seta; scutal spots small, each presutural dorsocentral spot usually about equal in breadth to half the distance between the prescutellar acrostichal spots. Wing: cell *cup* extending well beyond end of cell *bm* (Fig. 9). Abdomen: aedeagal glans with a sinuate curved main duct (Fig. 11); aculeus apex not acuminate.

Remarks. The content of this species-group differs from that listed by Korneyev

(1985) in the following respects: *Ch. nigropicta* and *Ch. vittata* have been removed from the group, and *Ch. succinea* has been added.

Chaetorellia carthami Stackelberg

Chaetorellia carthami Stackelberg, 1929: 225.
Chaetorellia jaceae (Robineau-Desvoidy, 1830); Selim, 1977: 75 [misidentification].

Redescription. Adult: general body colour bright yellow. Head: frons yellow. Thorax: scutal pattern (other than spots) pale brown or absent; subscutellum and katepisternum pale brown. Wing: cell *bm* usually (98%) with a hyaline area in its basal two-thirds; discal and preapical crossbands sometimes (14%) joined in cell r_1. Abdomen: each tergite sometimes with a lateral and a medial pair of spots; aculeus apex caudate (Fig. 19). Measurements: WL♀=3·4–4·5 mm, C2L=1·1–1·5 mm, AL=1·5–1·9 mm, AVL/AL=0·64–0·69.

Hosts. This species attacks commercially-grown safflower, *Ca. tinctorius*, in the Middle East, and it was called the yellow safflower-fly by Al-Ali *et al.* (1979), who described its biology in Iraq. It has also been recorded from *Ca. tinctorius* in many areas of southern USSR, and in Israel it additionally attacks *Ca. tenuis*.

Material examined. *Ca. tenuis*: 36 ♀, ISRAEL, Arad (reared) (BMNH). *Ca. tinctorius*: 2 ♀, 1 ♂, IRAQ, Abughraib (? reared) (BMNH). 5 ♀, ISRAEL, Beth-Govrin (reared) (BMNH, USNM). **No host data**: 1 ♀, 1 ♂, CYPRUS, Asomatos (BMNH).

Type data. Holotype, ♀, *Ca. tinctorius*: USSR, Kirghizian SSR, near Tashkent, Jaroslavskoe, 30.vii.1926 (reared) (ZIL) [examined by V. Korneyev, who made his unpublished redescription available to us].

Chaetorellia isais Hering

Chaetorellia isais Hering, 1937b: 253. Holotype ♀, USSR (SMNS) [examined].
Chaetorellia loricata (Rondani, 1870); Rikhter, 1965: 143; Ivannikov. 1977: 31 [misidentifications].

Redescription. Adult: general body colour orange-yellow. Head: frons yellow to orange. Thorax: scutal pattern (other than spots) usually black, at least in posterior half; subscutellum black; katepisternum pale brown to black. Wing: cell *bm* usually with a hyaline area in its basal two-thirds; discal and preapical crossbands sometimes narrowly joined in cell r_1. Abdomen: each tergite often with a lateral and a medial pair of spots; aculeus apex caudate (Fig. 18). Measurements: WL♀=3·5–4·9 mm, C2L=1·18–1·54 mm, RL=1·64–2·10 mm, AL=1·92–2·68 mm, AVL=1·12–1·40, AVL/AL=0·52–0·59.

Hosts. The only reared specimens examined were associated with *Chartolepis intermedia (Centaurea intermedia* in Klokov *et al.*, 1963; Wagenitz, 1980). Foote (1984) records *Ch. isais* from China, but the origin of that record could not be traced.

Material examined. **Chartolepis intermedia**: 2 ♂ (1 not dissected), 4 ♀ (2 not dissected), USSR, Kazakh SSR, Akmolinskaya Oblast Province, Kokchetav, near Tersakkan River (reared) (ZIL). **Chartolepis sp.**: 2 ♀ (1 not dissected), USSR, Kazakh SSR, Tselinograd Prov., Kokshetau Mts (reared) (ZIL). **No host data**: 1 ♀, USSR, Kazakh SSR, Tselinograd Prov., Kokshetau Mts (ZIL); 1 ♀, Russian SFSR, near Volgograd, Sarepta, No. 42084 in coll. Becker (holotype) (SMNS).

Chaetorellia loricata (Rondani)

Tephritis jaceae Robineau-Desvoidy, 1830; von Frauenfeld, 1863: 215 [misidentification].
Tripeta loricata Rondani, 1870: 111. Probable syntype ♂, ITALY (MZF) [examined].
Chaetorellia holosericea Hendel, 1927: 122. Holotype ♀, USSR (NHMV) [examined].
Chaetorellia jaceae (Robineau-Desvoidy, 1830); Hendel, 1927: 122 (in part); Phillips, 1946: 110 (in part); Mihályi, 1960: 35 (in part); Leclercq, 1967: 97; Rikhter, 1970: 151 (in part); Zwölfer, 1974a: 13 (in part) [misidentifications].
Chaetorellia loricata (Rondani, 1870); Hendel, 1927: 123.
Orellia jaceae (Robineau-Desvoidy, 1830); Séguy, 1934: 135 (in part); Phillips, 1946: 124 (in part) [misidentifications].
Chaetorellia caradjai Hering, 1937a: 3. Syntypes, USSR (BMNH, SMNS, ZMHB) [examined].
Chaetorellia mara Hering, 1937b: 252. Holotype ♂, USSR (BMNH) [examined]. **Syn. n.**
Chaetorellia loricata septentrionalis Hering, 1937b: 253 Syntype ♀♂, GERMAN DEMOCRATIC REPUBLIC (ZMHB) [examined]. **Syn. n.**
Terellia jaceae (Robineau-Desvoidy, 1830); Phillips, 1946: 124 (in part) [misidentification].
Trypeta jaceae (Robineau-Desvoidy, 1830); Phillips, 1946: 127 [misidentification].

Redescription. Larva and puparium: spiracular hairs each with three branches (similar to Fig. 3). Adult:

general body colour orange-yellow. Head: frons yellow to orange, rarely black. Thorax: scutal pattern (other than spots) usually black, at least in posterior half; subscutellum and katepisternum pale brown to black. Wing: cell *bm* usually (95%) with a hyaline area in its basal two-thirds; discal and preapical crossbands sometimes (14%) joined in cell r_1. Abdomen: each tergite usually with a lateral and a medial pair of spots; aculeus apex (Fig. 21). Measurements: WL♀=3·4–5·2 mm, C2L=1·22–1·90 mm, RL=1·52–2·40 mm, AL=1·24–2·04 mm.

Nomenclature. Unfortunately, the only syntype of *Tripeta loricata* is a male, described from Parma, northern Italy. Although it is not possible to identify male specimens, it has the typical dark coloration of the species that attacks *Ce. scabiosa*, which is known from Italy and fits the established use of the name *Ch. loricata*. Four other species-group names have been applied to *Ch. loricata*. *Ch. holosericea* has been regarded as a separate species from *Ch. loricata* by most previous authors because of its black frons. However, Korneyev (1983) placed these nominal species in synonymy because he found some specimens with a black frons and others with a pale-coloured frons in a single reared series; this form appears to occur commonly in south-western USSR and is also known from France (MNHNP) and Kazakh SSR (Rikhter, 1965). Korneyev (1985) placed *Ch. caradjai* in synonymy with *Ch. loricata*, and subspecies *septentrionalis* is here placed in synonymy with it. All these nominal species were recorded from *Ce. scabiosa* or a closely-related plant, and they all have the same characteristic aculeus shape.

Hosts. In most of Europe, *Ch. loricata* attacks *Ce. scabiosa*, but it has also been recorued from some other closely related species of the subgenus *Lopholoma* of *Centaurea*. In the Caucasus, a single female has been reared from *Ce. (Psephellus) troitzkyi*. Previous authors have separated *Ch. loricata* from other members of the *Ch. loricata* species-group using colour characters, but these are not reliable.

Material examined. *Ce. apiculata*: 1 ♀, HUNGARY, Miskloc (reared) (LTUB). 5 ♀ (2 dissected), 3 ♂, USSR, Moldavian SSR, Bendery (as "Tighina"), vi.1936 (not reared) (*M. Hering*) (*Ch. caradjai* syntypes) (BMNH, SMNS, ZMHB). *Ce. orientalis*: 1 ♀, USSR, Ukrainian SSR, Novoaidar (reared) (ZMK). *Ce. salonitana*: 4 ♀, GREECE, Macedonia, Langadas & Theotokos areas (reared) (USNM). *Ce. scabiosa*: 2 ♀, AUSTRIA, Hornstein (not reared) (BMNH). 8 ♀, ENGLAND, Surrey & Wiltshire (reared) (BMNH); 5 ♀, 4 ♂, FRANCE, Pyrenees-Oriental, Font-Romeu (reared) (BMNH); 2 ♀, 1 ♂, GERMAN DEMOCRATIC REPUBLIC, Saale, Naumberg, 3.viii.1935 (reared) (*R. Elkner, L. Lange*) (includes *Ch. loricata septentrionalis* ♀, ♂ syntypes) (ZMHB). 3 ♀, HUNGARY, Budapest (some reared) (BMNH, TMB). 8 ♀, ITALY, Pieve di Teco (reared) (BMNH). 1 ♀, SWITZERLAND, Tessin (reared) (TAU). 1 ♂, USSR, Moldavian SSR, Bendery (as "Tighina"), vii.1936 (reared) (*Ch. mara* holotype) (BMNH). *Ce. troitzkyi*: 1 ♀, USSR, Russian SFSR, Caucasus area, near Teberda (reared) (BMNH). **No host data:** 1 puparium, 1 ♀, FRANCE, Marne, Aulnay (MNHNP). 1 ♂, ITALY, Parma area (as "agri parmensis"), no label data (probable syntype of *T. loricata*) (MZF). 1 ♀, TURKEY, Ankara (BMNH). 1 ♀, USSR, Russian SFSR, near Volgograd, Sarepta, from coll. Becker (*Ch. holosericea* holotype) (NHMV); 1 ♀, Ukrainian SSR, Crimea, Almi Valley (ZIL).

Chaetorellia succinea (Costa)

Trypeta succinea Costa, 1844: 93.

Trypeta mellea Costa, 1844: 118. **Nom. nud.**

Chaetorellia sp. nr *carthami* Stackelberg, 1929; Zwölfer, 1970: 36; Petney & Zwölfer, 1985: 151; Sobhian & Zwölfer, 1985: 310 [misidentifications].

Chaetorellia sp.; Zwölfer, 1974a: 18; Neuenschwander & Freidberg, 1983: 86.

Chaetorellia loricata (Rondani, 1870); Kugler & Freidberg, 1975: 62 [misidentification].

Redescription. Larva and puparium: spiracular hairs each with 5–6 branches (Fig. 4); previously described by Zwölfer (unpublished CIBC data, 1972). Adult: general body colour orange-yellow. Head: frons yellow to orange. Thorax: scutal pattern (other than spots) usually black, at least in posterior half; subscutellum and katepisternum pale brown to black. Wing: cell *bm* usually (95%) with a hyaline area in its basal two-thirds; discal and preapical crossbands often (33%) joined in cell r_1. Abdomen: each tergite often with a lateral and a medial pair of spots; aculeus apex caudate (Fig. 20). Measurements: WL♀=3·4–4·2 mm, C2L=0·8–1·5, AL=1·1–1·8, AVL/AL=0·58–0·70.

Nomenclature The name *Ch. succinea* was used by previous authors to refer to *Ch. conjuncta*. However, it is clear from the original illustration given by Costa (1844: Pl. II, Fig. 5) that this Italian species has spots at the base of its supra-alar setae, unlike *Ch. conjuncta*, and has all four wing crossbands joined anteriorly. The only known southern Italian *Chaetorellia* species fitting this description is the species which attacks *Ce. solstitialis*, and *Ch. succinea* is assumed to be that species; it is therefore removed from synonymy with *Ch. conjuncta*.

Hosts. This species is very closely related to *Ch. carthami*, and the biological evidence supporting their separation was discussed earlier (see Separation of *Ch. loricata* group

species). In southern France and Italy, it attacks *Ce. solstitialis*, and what appears to be the same species has been reared from *Ce. hyalolepis* and *Ce. pallescens* in Israel and has been swept from *Ce. idaea* in Crete. Because of its association with *Ce. solstitialis*, this species was once considered as a potential biocontrol agent of that plant in North America (Zwölfer, 1970; Sobhian & Zwölfer, 1985). However, a doubt about *Ch. succinea* being distinct from *Ch. carthami*, which is associated with the cultivated *Ca. tinctorius*, led to its rejection as a potential biocontrol agent for fear that it might adapt to attacking *Ca. tinctorius* (safflower) crops (Sobhian & Zwölfer, 1985).

Material examined. *Ce. hyalolepis*: 2 ♀, ISRAEL, Beer-Sheva (reared) (TAU). *Ce. idaea*: 1 ♀, GREECE, Crete, Melaxa (not reared) (BMNH). *Ce. pallescens*: 11 ♀, ISRAEL, Jericho (reared) (TAU). 1 ♀, JORDAN, Deir Alla (reared) (LTUB). *Ce. solstitialis*: 5 ♀, 4 ♂, FRANCE, Avignon & Montpellier areas (most reared) (BMNH, TAU). 1 puparium, 34 ♀, ITALY, Apulia, Calabria, Lazio & Puglia areas (reared) (BMNH, USNM). 19 ♀, TURKEY, Amasya, Erzurum, Sansun & Sivas areas (reared) (USNM). **No host data**: 2 ♀, CYPRUS, Limassol (BMNH). 1 ♀, GREECE, Macedonia, Struma Vall. (USNM).

Type data.   Syntypes, ITALY: ♀ illustrated by Costa (1844), Puglia, Foggia (as "Trovata in Foggia"), not located.

Species removed from the genus

Tephritis algira Macquart, 1843: 380.
Chaetorellia algira (Macquart, 1843); Hering, 1937b: 251; Foote, 1984: 78.

Syntypes: two specimens in the Macquart collection (MHNL) are mould-covered and unfit for study. The original illustration of this Algerian species (Macquart, 1843: Pl. 30, Fig. 5) shows all four crossbands separated, a feature unknown in the genus *Chaetorellia*; it is therefore unlikely that this is a species of *Chaetorellia*, and it is here placed as a probable synonym of *Chaetostomella cylindrica* (Robineau-Desvoidy, 1830: 767).

Discussion

It is normal practice to group specimens into presumed species by looking for distinct characters, such as terminalia form. Two species of *Chaetorellia* are easily recognized by distinct aculeus shape characters, namely *Ch. loricata* and *Ch. isais* (Figs 21, 18). Similarly, most specimens of *Ch. hestia* and *Ch. conjuncta* can be recognized by simple wing pattern characters, although previous keys using these features (Hendel, 1927; Hering, 1937b) made no reference to the fact that they apply to only about nine specimens in ten. When distinct characters cannot be found, specimens can sometimes be grouped by discontinuities in variable characters. Canonical variate (CV) analysis facilitated the study of discontinuities in the *Ch. jaceae* species-group. Differences between sympatric samples from different host-plants (Table III), the results of host-plant choice tests (Tables IV–VII) and other fragmentary biological data were then used in combination to determine which populations probably represented a species.

Although there are probably several causes of variation in *Chaetorellia* species, most of the intraspecific variation appears to be related to the choice of different host-plants. There is some evidence that much of the observed variation is related to the structure of the host's capitulum. For example, the spring form of *Ch. australis*, which emerges from *Ce. solstitialis* but attacks *Ce. cyanus*, differs from the summer form, which attacks *Ce. solstitialis*, regardless of which host the summer flies emerged from. This suggests a mechanism designed to match the form of the fly to the intended host. Similarly, populations of *Ch. acrolophi* differ in size in proportion to the capitulum size of their hosts. The smallest hosts of *Ch. acrolophi* are *Ce. leucophaea* and *Ce. diffusa*, and the associated flies are correspondingly very small; the largest hosts are *Ce. vallesiaca* and *Ce. maculosa*, and the associated flies are correspondingly the largest.

The analysis of variance carried out for seven wing characters and three aculeus characters showed that the aculeus characters had F values an order of magnitude greater than those for the wing characters. This suggests that any phenotypic effects related to the nutritional quality of an individual host capitulum cause greater variation in wing size than in ovipositor dimensions, suggesting the presence of a growth control mechanism to ensure that small-winged flies have an ovipositor almost as long as the medium-sized members of the population and that long-winged individuals have ovipositors almost as short as medium-sized flies. For such a mechanism to have evolved there must be a great need for

precise ovipositor dimensions. A similar result was found in an analysis of *Urophora quadrifasciata* (Meigen) from different host-plant species (R. Wild, unpublished CIE data, 1987), and similarly, there is a correlation between *Urophora* ovipositor lengths and host capitulum size (Zwölfer, 1983).

Although the aculeus length of *Ch. acrolophi* appears to vary in proportion to the size of its host's capitulum, no such relationship exists across the whole genus in the manner of *Urophora*. Instead, there appears to be a relationship between ovipositor length and the bract structure of the host-plants. The total length of the ovipositor is not known, because it is made up of syntergosternite 7 (= oviscape), plus the portion of the aculeus which is extended at the time of oviposition, and possibly part of the preabdomen; aculeus length is therefore only an index of true ovipositor length. Both *Ch. isais* and *Ch. jaceae* have aculeus lengths that are usually in excess of 2·0 mm, but the other seven species each have a shorter aculeus. Correspondingly, *Ch. isais* and *Ch. jaceae* are the only species which are known to attack host-plants which have bract appendages (or phyllaries) that are so large that they each cover the bract above. *Chaetorellia* species lay their eggs under the bracts, so large bract appendages that lie flat against the side of the capitulum must be a hindrance to oviposition. The long ovipositors of *Ch. jaceae* and *Ch. isais* may therefore be adaptations to allow their ovipositors to be pushed beyond the bract appendages of their hosts, allowing their eggs to be correctly positioned below the actual bracts (Fig. 22). In the host-choice tests using *Ch. acrolophi* (Table V, tests 1, 3), eggs laid on plants that were natural hosts of *Ch. jaceae*, were usually laid behind the bract appendage, suggesting that the ovipositor of *Ch. acrolophi* was too short to allow placement of the egg behind the bract.

With the exception of *Ch. acrolophi*, all *Chaetorellia* species attack host-plants that have a reflexed bract appendage (Fig. 24). The narrow decurrent appendage of *Ce. cyanus*, the broad spinose bract of *Carthamus*, and the narrow spinose bract appendages of the subgenera *Calcitrapa*, *Seridia* and *Solstitiaria* of *Centaurea* all protrude from the side of the capitulum in such a way that they would not obviously hinder oviposition by *Chaetorellia*; correspondingly, the flies that attack these plants all have short ovipositors. *Ch. acrolophi* attacks plants belonging to the subgenus *Acrolophus* where each bract has a decurrent bract appendange which about half covers the next bract above (Fig. 23), thus providing an intermediate form of bract between the reflexed type and the complete coverage type found in the hosts of *Ch. jaceae*. The aculeus length of *Ch. acrolophi* varies considerably in size between populations that attack hosts with different-sized capitula, but it corresponds to this intermediate type of bract; the largest individuals have an ovipositor which is second in size to that of *Ch. jaceae*, and the smallest are similiar to the flies that attack plants with a reflexed appendage.

Most host-plants of any one *Chaetorellia* species are closely related, typically belonging to a single subgenus; however, some *Chaetorellia* species have been recorded from two subgenera of *Centaurea*. *Ch. jaceae* usually only attacks those members of the subgenus *Jacea* which have large flat bract appendages, but it has been recorded from *Ce. (Phalolepis) alba*, which also has large flat bract appendages. *Ch. acrolophi* normally only attacks members of the subgenus *Acrolophus*, but a small sample was reared from *Ce. (Jacea) pectinata* in north-eastern Spain; this plant belongs to a section of the subgenus *Jacea* which have recurved feather-like bract appendages, rather than the large appendages found in the hosts of *Ch. jaceae*, and it might provide an oviposition substrate very similar to that of a species of the subgenus *Acrolophus*. *Ch. hestia* normally attacks *Ce. (Seridia) aspera*, but it has also been reared from *Ce. (Lopholoma) collina*; the subgenus *Seridia* is characterized by bract appendages comprising at least three short subequal spines, and some species of the subgenus *Lopholoma*, including *Ce. collina*, have a bract appendage with very stout fimbriae which are almost spinose and therefore similar to those of species of the subgenus *Seridia*.

Bract structure might be an important visual or tactile cue in host choice, and the reason for most *Chaetorellia* species normally attacking only one subgenus may be an artifact of the subgeneric classification of *Centaurea*, which is largely based on bract
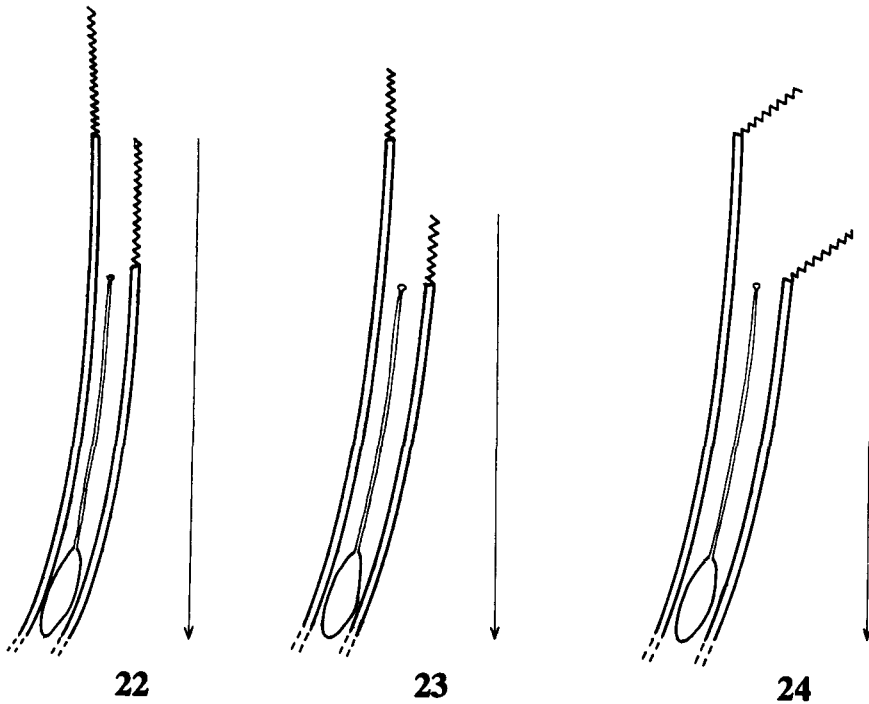
Figs 22–24.—Diagramatic cross section of intermediate involucral bracts in two adjacent whorls, with bract appendage marked by a zig-zag line, showing position of a *Chaetorellia jaceae* (Robineau-Desvoidy) species group egg, and with required functional depth of ovipositor marked by an arrowed line; 22, appendage completely covering next bract, as in a host of *Ch. jaceae*; 23, appendage partly covering next bract, as in a host of *Ch. acrolophi* sp. n.; 24, appendage reflexed away from next bract, as in the hosts of *Ch. australis* Hering, *Ch. conjuncta* (Becker) and *Ch. hestia* Hering.

structure. Zwölfer (1970) noted that *Ch. succinea* required bract spines as a release stimulus for oviposition behaviour. Similarly, host chemistry must also be important to some species, as larval host-transfer tests of *Ch. succinea* onto *Ca. tinctorius* and *Ch. carthami* onto *Ce. solstitialis* resulted in larval death (Zwölfer, unpublished CIBC data, 1972); however, host chemistry appears to be of little importance to *Ch. acrolophi* and *Ch. jaceae*, both of which survived almost any larval transfer (Tables V–VII, test 4).

One of the aims of this study was to resolve some of the confusion that past misidentifications introduced into the host list for *Chaetorellia* species; this confusion had to be resolved before any *Chaetorellia* species could be considered for introduction into North America as a weed biocontrol agent. The second aim of this study was the production of an identification system for *Chaetorellia* species. Most *Chaetorellia* species are very variable in form and it is impossible to produce an accurate key for their identification. The key presented in this paper works for all the population means of the samples studies and for over 70% of individual specimens.

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TABLE XI. *Host-plants of* Chaetorellia

Host-plant	Chaetorellia sp.
Centaurea L. [knapweeds, starthistles, cornflowers]	
Subgenus *Lopholoma* (Cass.) Dobrocz [some knapweeds]	
Ce. apiculata Ledeb.	*Ch. loricata*
Ce. collina L.	*Ch. hestia**
Ce. orientalis L.	*Ch. loricata*
Ce. salonitana Vis.	*Ch. loricata*
Ce. scabiosa L. [greater knapweed]	*Ch. loricata*
including *Ce. sadleriana* Janka	
Subgenus *Acrolophus* (Cass.) Dobrocz [some knapweeds]	
Ce. arenaria Bieb. ex Willd.	*Ch. acrolophi* ?
Ce. cariensis longipapposa Wagenitz	*Ch. acrolophi* ?
Ce. diffusa Lam. [diffuse knapweed]	*Ch. acrolophi* ?
Ce. maculosa Lam. [spotted knapweed]	*Ch. acrolophi*
including *Ce. rhenana* Boreau	
Ce. leucophaea Jordan	*Ch. acrolophi* ?
including *Ce. paniculata* L.	
Ce. spinabadia Bubani ex Timb.-Lagr.	*Ch. acrolophi* ?
Ce. vallesiaca (DC.) Jordan	*Ch. acrolophi*
Ce. virgata Lam.	*Ch. acrolophi* ?
Subgenus *Calcitrapa* (Heister ex Fabr.) Hayek [some starthistles]	
Ce. calcitrapa L. [red starthistle]	*Ch. conjuncta*
Ce. hyalolepis Boiss.	*Ch. conjuncta*
	Ch. succinea
Ce. iberica Trev. ex Spreng.	*Ch. conjuncta*
Ce. pallescens Del.	*Ch. conjuncta*
	Ch. succinea
Ce. procurrens Sieb. ex Spreng.	*Ch. conjuncta*
Subgenus *Seridia* (Juss.) Czerep. [some starthistles]	
Ce. aspera L. [rough starthistle]	*Ch. hestia*
Ce. sphaerocephala L.	*Ch. hestia*
Subgenus *Solstitiaria* (Hill) Dobrocz [some starthistles]	
Ce. aegyptiaca L.	*Ch. conjuncta*
Ce. idaea Boiss. & Heldr.	*Ch. succinea*
Ce. lanulata Eig	*Ch. conjuncta*
Ce. solstitialis L. [yellow starthistle]	*Ch. australis*
	Ch. succinea
Subgenus *Phalolepis* (Cass.) Dobrocz. [some knapweeds]	
Ce. alba L.	*Ch. jaceae*
Subgenus *Jacea* (Miller) Hayek [some knapweeds]	
Ce. jacea L. [brown knapweed]	*Ch. jaceae*
Ce. nigra L. [black knapweed]	*Ch. jaceae*
including *Ce. debeauxii* Gren. & Godron	
including *Ce. microptilon* Gren. & Godron	
Ce. pannonica (Heuffel) Simonkai	*Ch. jaceae*
Ce. pectinata L.	*Ch. acrolophi* ?*
Subgenus *Psephellus* (Cass.) Schmalh. [some knapweeds]	
Ce. troitzkyi (Sosn.) Sosn.	*Ch. loricata**
Subgenus *Cyanus* (Miller) Hayek [cornflowers]	
Ce. cyanus L. [the cornflower]	*Ch. australis*
Ce. depressa Bieb.	*Ch. australis*
Chartolepis Cass. [some knapweeds]	
Chart. intermedia Boiss.	*Ch. isais*
Carthamus L. [safflower, some thistles]	
Ca. tenuis (Boiss. & Bl.) Bornm. [a thistle]	*Ch. carthami*
Ca. tinctorius L. [safflower]	*Ch. carthami*
	Ch. sp. near *australis*

Some specimens from the Ukraine (ZMK) were apparently reared from *Ce. scabiosa* and they appear to represent *Ch. acrolophi* and *Ch. jaceae*; these may represent unusual host associations or misidentifications of the host-plant.

* Atypical host association known from a single rearing record (possibly an aberrant host association).
? Populations which are morphometrically inseparable from, or similar to, *Ch. acrolophi*; negative results in host tests suggest that some of these populations may represent additional undescribed species.

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APPENDIX. HOST-PLANT LIST AND NOTES ON HOST TAXONOMY

Known hosts of *Chaetorellia* are listed in Table XI. Most species attack members of the genus *Centaurea*, which includes about 600 species (Feinbrun-Dothan, 1978). The generic and subgeneric classification used in the present paper is that of Dostál (1973, 1975, 1976), who divides European *Centaurea* into subgenera and further sections; this system was chosen because it was possible to fit all *Chaetorellia* hosts into its subgenera and because it was descriptive of the host relationships of the genus. The alternative classification used for Middle-Eastern *Centaurea* species (Wagenitz, 1975; 1980; Feinbrun-Dothan, 1978) divides the genus into a large number of sections into which some species could not be placed with certainty. Many species of *Centaurea* are very difficult to identify, and some closely-related species often hybridize. It is therefore likely that many of the host-plant names associated with museum specimens of *Chaetorellia* refer to species-complexes of *Centaurea* rather than single species. Consequently, some species-groups of *Centaurea* which are very similar and difficult to separate were treated as single species, and these are indicated in the following list as 'included' species. The nomenclature of *Centaurea* species follows Dostál (1976) for European species, Klokov *et al.* (1963) for non-European USSR, Wagenitz (1975) for Turkey, Feinbrun-Dothan (1978) for Israel and Wagenitz (1980) for the rest of the Middle East. It should, however, be noted that some workers now regard *Ce. maculosa* and *Ce. vallesiaca* as subspecies of *Ce. stoebe* L., and *Ce. rhenana* as a synonym of *Ce. stoebe* (Fuchs-Eckert, 1980; G. Wagenitz, pers. comm.). European *Ce. maculosa* is a diploid ($2n=18$), but North American *Centaurea* sp. nr *maculosa* is a tetraploid ($2n=36$), which may be *Ce. biebersteinii* DC (Harris & Myers, 1984; Harris, 1985).