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Comparative morphology and biology of terminal-instar larvae of some *Eurytoma* (Hymenoptera, Eurytomidae) species parasitoids of gall wasps (Hymenoptera, Cynipidae) in western Europe

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ABSTRACT
We present a taxonomic and biological study of the genus *Eurytoma* Illiger, 1807 (Hymenoptera, Eurytomidae), based on the morphology and biology of the terminal-instar larvae of 13 species living as parasitoids in the galls of European species of cynipid gall wasps. We provide the first detailed descriptions of the terminal-instar larvae of the studied species, illustrating diagnostic characters for the family and the studied genera with SEM pictures. We also provide a species key for the identification of *Eurytoma* larvae associated with cynipid galls, based on particular characters associated with the head, mouthparts and mandibles. Although we find only limited informative variation in body shape, the head and mandibles provide many characters of potential taxonomic and phylogenetic value. We summarise the larval biology of the 13 *Eurytoma* species inhabiting cynipid galls. *Eurytoma* larvae are usually solitary idiobiont ectoparasitoids of the host larva or of larvae of cynipid inquilines that also often feed on gall tissue.

KEY WORDS
Insecta,
Hymenoptera,
Chalcidoidea,
Eurytomidae,
Eurytoma,
larva,
parasitoids,
cynipid galls,
identification keys.

RÉSUMÉ

*Morphologie comparée et biologie des larves de dernier stade de certaines espèces d'*Eurytoma *(Hymenoptera, Eurytomidae) parasitoïdes associés aux Cynipidae galligènes (Hymenoptera, Cynipidae) en Europe occidentale.*

Nous présentons une étude taxonomique et biologique du genre *Eurytoma* Illiger, 1807 (Hymenoptera, Eurytomidae), basée sur la morphologie et la biologie des larves de dernier stade de 13 espèces vivant comme parasitoïdes dans les espèces européennes de Cynipidae galligènes. Nous fournissons les premières descriptions détaillées des larves de dernier stade des espèces étudiées, illustrant des caractères diagnostiques pour la famille et les genres étudiés avec des images MEB. Nous présentons également une clé d'identification des larves d'*Eurytoma*, fondée en particulier sur les caractères associés à la tête, les pièces buccales et les mandibules. Bien que l'information apportée par la variation de la forme du corps soit limitée, la tête et les mâchoires fournissent de nombreux caractères potentiellement informatifs d'un point de vue taxonomique et phylogénétique. Nous résumons la biologie des larves des 13 espèces d'*Eurytoma* associées aux galles des Cynipidae. Les larves d'*Eurytoma* sont généralement des ectoparasites solitaires et idiobiontes de la larve hôte ou des larves des cynipides inquilins qui se nourrissent également souvent des tissus de galle.

MOTS CLÉS
Insecta,
Hymenoptera,
Chalcidoidea,
Eurytomidae,
Eurytoma,
larve,
parasitoïdes,
galles de cynipides,
clé d'identification.

INTRODUCTION

The superfamily Chalcidoidea Latreille, 1817 is recognized as the second largest superfamily of parasitic Hymenoptera (Sharkey & Fernandez 2006), being presently divided into 19 families. Within the Chalcidoidea, the large and cosmopolitan family Eurytomidae Walker, 1832 comprises approximately 1500 species in around 88 genera. It is usually divided into three subfamilies, Eurytominae Walker, 1832 (73 genera and 1366 species), Heimbrinae Burks, 1971 (2 genera and 7 species) and Rileyinae Ashmead, 1904 (6 genera and 69 species), with one unplaced species – *Eurytomidia dubia* Masi, 1917 (Noyes 2003; Gates & Hanson 2006; Gates 2008; Lotfalizadeh *et al.* 2007b). The eurytomids display a wide range of biologies, but all are either endophytophagous herbivores, parasitoids of other insects, or have lifecycles involving both feeding modes (Bouček 1988). Phytophagous eurytomids develop as seed-feeders on Apiaceae, Fabaceae and Rosaceae (including pests of many economically important apiaceous and fabaceous species, including almonds and pistachios); as stem-feeders on cereal crops and wild grasses, or in relatively few cases as gall inducers (Crosby 1909; Bugbee 1941; Zerova 1981, 1993; Bouček 1988; Henneicke *et al.* 1992; Askew & Blasco-Zumeta 1998; La Salle 2005). Most *Eurytoma* Illiger, 1807 species are entomophagous for at least part of their larval development, with host ranges including Coleoptera, Diptera, Hymenoptera and Lepidoptera (Claridge & Askew 1960; Bouček 1988; Narendran *et al*. 1995; Yang 1996; Georgviev & Stojanova 2003; Zerova *et al*. 2004; Csóka *et al*. 2005; van Noort *et al*. 2007). Not all hosts of eurytomids are phytophagous, and some *Eurytoma* species are parasitoids of predatory insects including sphecid wasps (Danks 1971). Eurytomids resemble torymids in that both groups frequently attack gall-inducing hosts, particularly cynipid wasps and tephritid flies (Claridge & Askew 1960; Askew & Shaw 1986; Csóka *et al*. 2005), and some *Eurytoma* species augment a parasitoid life history by feeding on plant tissues in their host's gall (Phillips 1927; Varley 1937; Askew 1961, 1984). *Eurytoma* species can develop on an entirely phytophagous diet in cynipid galls (Askew 1999), although this probably happens rarely in these communities.

Approximately 370 eurytomid species are recorded for the Palaearctic (Zerova 1995; Noyes 2003), of

which 31 are members of the rich, chalcid-dominated, parasitoid communities centred on cynipid galls (Askew 1961, 1984; Ko 1971; Schönrogge *et al.* 1995, 1996a, b; Nieves-Aldrey 2001; Stone *et al.* 2002; Ito & Hijii 2002, 2004; Askew *et al.* 2006; Csóka *et al.* 2005; Aebi *et al.* 2006; Gómez *et al.* 2006; Abe *et al.* 2007). Twenty-six eurytomid species have been recorded from host cynipid galls on herbs, bushes and sycamore trees (induced by gallers in the Cynipinae tribes Aylacini, Diplolepidini and Pediaspidini), while 7 species (some of them polyphagous parasitoids of the other cynipid tribes) have been reared from cynipid galls on oaks (induced by gallers in the tribe Cynipini) throughout the Holarctic (Askew 1961, 1984; Schönrogge *et al.* 1995, 1996a, b; Schönrogge & Crawley 2000; Nieves-Aldrey & Askew 2002; Melika *et al.* 2002a, b; Gordinier 2003; Askew *et al.* 2006, unpubl. data; Gómez *et al.* 2006; Leggo & Shorthouse 2006; Rizzo & Massa 2006; Abe *et al.* 2007). There are about 1400 described cynipid species, of which 340 are known from Europa (Nieves-Aldrey 2001; Stone *et al.* 2002; Csóka *et al.* 2005). More than 200 chalcidoid species are associated with gall wasp communities in the western Palaearctic (Askew *et al.* 2006) and the Eurytomidae is one of the dominant chalcidoid families in these communities. Gall wasps are an important model system in work on trophic interactions in insects (e.g., Schönrogge & Crawley 2000; Price *et al.* 2004; Hayward & Stone 2005), and deep analysis of gall wasp food webs requires species level identification of community members. To date, species level identification is restricted almost entirely to emerging adults, limiting the incorporation of data for larval forms although molecular information have been recently tested as an important source of information for trophic relationship within parasitoid communities (Kaartinen *et al.* 2010). In a previous paper, we analysed the larval morphology of chalcid parasitoids in the family Torymidae Walker, 1833 associated with Cynipidae Newman, 1834 galls (Gómez *et al.* 2008) in Europe. Here we provide a parallel analysis for key species of the genus *Eurytoma*.

Immature stages, particularly final instars larvae, have been the subject of analyses in other groups of parasitic Hymenoptera (Vance & Smith 1933), including Ichneumonidae Latreille, 1802 (Short 1952, 1959) and Braconidae Wharton, 1998 (Čapek 1969, 1970, 1973). Despite their global significance in insect food webs, surprisingly little has been published on the larval morphology of Chalcidoidea since the pioneering work of Parker (1924) on general chalcid larval morphology, and the first accurate description of a final instar chalcid larval head by Cutler (1955), for *Nasonia vitripennis* Walker, 1836 (Pteromalidae). Several papers have been published on the taxonomy of Eurytomidae since Walker (1832) defined the family (Ferrière 1950; Claridge 1959a, b, 1961a-c; Bugbee 1967, 1975; Szelényi 1976a, b; Bouček 1988; Zerova 1967, 1971, 1978, 1979; Narendran 1994), a highlight in the context of the current paper being Claridge & Askew's (1960) work on the *Eurytoma rosae* group, some of which attack hosts in cynipid galls. In particular, few larval eurytomids have been described and morphological variation within the family remains poorly defined. Parker (1924) described the basic morphology of some Eurytomid larvae, and papers since have described aspects of the biology and larval morphology of *Eurytoma* and *Tetramesa* Walker, 1848 (Claridge 1959a, 1961b), *Eurytoma tumoris* Bugbee, 1962 (Stark & Koehler 1964), *E. pissodis* Girault, 1917 (Stevenson 1967), *E. amygdali* Enderlein, 1907 (Plaut 1972), *E. nesiotes* Crawford, 1911 (Tiwari 1974), *E. bouceki* (= *E. boucekia* Zerova, 2007) (Skrzypczynska 1975), *Bephratelloides pomorum* (Fabricius, 1804) (Barbosa *et al.* 1998), of a new species of phytophagous eurytomids (Gates & Cascante-Marín 2004), *Aximopsis nodularis* (Boheman, 1836), *E. heriadi* Zerova, 1984 (Tormos *et al.* 2004) and *E. sivinskii* Gates & Grissell, 2004 (Gates *et al.* 2008). More wide-ranging studies on the larval morphology of Eurytomidae were published by Roskam (1982), Zerova *et al.* (1983) and Zerova (1993). Henneicke *et al.* (1992) and Dawah & Rothfritz (1996) published detailed work on the taxonomy, morphology and biology of eurytomids associated with grasses.

Here we aim to contribute to the knowledge of the immature stages of eurytomid wasps in two ways. First, we identify and describe larval and biological characters that are potentially useful in taxonomic and morphological phylogenetic work on Eurytomidae. We have primarily used scanning

TABLE 1. — Host gall, host plant and sample site data for the eurytomid species included in the present study. Abbreviations: see Material and methods.

Species	n	Cynipid host	Plant host	Collection data
1. *Eurytoma aspila*	3	*Aulacidea follioti*	*Sonchus asper* (Asteraceae)	France, Vallée d'Aspe (Pyrénées-Atlantiques) (JLNA)
	24	*Aulacidea tragopogonis*	*Tragopogon* spp. (Asteraceae)	Spain, Arganda, Dehesa de Arganda (Madrid) (JLNA)
	12	*Phanacis caulicola*	*Picris echioides* (Asteraceae)	Spain, Rubiá (Orense) (JLNA)
2. *Eurytoma brunniventris*	1	*Andricus coriarius* (A)	*Quercus faginea* (Fagaceae)	Spain, La Suara (Cádiz) (JLNA)
	1	*Andricus hispanicus* (A)	*Quercus pyrenaica* (Fagaceae)	Spain, El Escorial (Madrid) (JLNA)
	1	*Cynips quercus* (A)	*Quercus faginea* (Fagaceae)	Spain, Dehesa de Arganda (Madrid) (JLNA)
	4	*Cynips quercus* (A)	*Quercus pyrenaica* (Fagaceae)	Spain, El Escorial (Madrid) (JLNA)
	2	*Plagiotrochus australis* (S)	*Quercus ilex* (Fagaceae)	Spain, El Pardo (Madrid) (JLNA)
	4	*Plagiotrochus australis* (A)	*Quercus ilex* (Fagaceae)	Spain, Dehesa de Navacerrada (Madrid) (JLNA)
	4	*Plagiotrochus panteli* (S)	*Quercus coccifera* (Fagaceae)	Spain, Dehesa de Arganda (Madrid) (JLNA)
	1	*Trigonaspis synaspis* (A)	*Quercus pyrenaica* (Fagaceae)	Spain, Miraflores de la Sierra (Madrid) (JLNA)
3. *Eurytoma cynipsea*	11	*Aulacidea freesei/Phanacis zwolferi*	*Silybum marianum* (Asteraceae)	Spain, Arganda, Monte Pajares (Madrid) (JLNA)
	3	*Aulacidea pilosellae*	*Hieracium pilosella* (Asteraceae)	Spain, Valgallego (Madrid) (JLNA)
	1	*Isocolus lichtensteini*	*Centaurea aspera* (Asteraceae)	Spain, Arganda (Madrid) (JLNA)
	1	*Timaspis cichorii*	*Cichorium intybus* (Asteraceae)	Spain, Arganda (Madrid) (JLNA)
	2	*Timaspis urospermi*	*Urospermun picroides* (Asteraceae)	Spain, Casares (Málaga) (JLNA)
	1	*Phanacis hypochoeridis*	*Hypochoeris* spp. (Asteraceae)	Spain, Islas Cíes (Pontevedra) (JLNA)
4. *Eurytoma infracta*	2	*Aylax minor*	*Papaver* spp. (Papaveraceae)	Spain, Rivas-Vaciamadrid (Madrid) (JLNA, JFG)
	12	*Neaylax verbenacus*	*Salvia verbenaca* (Lamiaceae)	Spain, Dehesa de Arganda (Madrid) (JLNA)
5. *Eurytoma mayri*	116	*Diastrophus rubi*	*Rubus* spp. (Rosaceae)	Spain, Ajuyán-Oviedo (Asturias) (LP)
6. *Eurytoma pediaspisi*	2	*Pediaspis aceris* (S)	*Acer opalus* (Sapindaceae)	Spain, Colldejou (Tarragona) (JLNA)
7. *Eurytoma robusta*	1	*Isocolus scabiosae* form *rogenhoferi*?	*Centaurea* spp. (Asteraceae)	Spain, Pozo de Guadalajara (Guadalajara) (JLNA)
8. *Eurytoma rosae*	65	*Diplolepis mayri*	*Rosa* spp. (Rosaceae)	Spain, Hayedo Tejera Negra, Retiendas (Guadalajara); San Esteban (León); Cotos de Monterrey, El Escorial (Madrid); Cabrejas del Pinar, Embalse de la Cuerda del Pozo (Soria) (JLNA, JFG)
	7	*Diplolepis rosae*		
	6	*Diplolepis nervosa/ D. eglanteriae*		
9. *Eurytoma rufipes*	2	*Xestophanes brevitarsis*	*Potentilla erecta* (Rosaceae)	Spain, Arins (La Coruña) (JLNA)
	22	*Xestophanes potentillae*	*Potentilla reptans* (Rosaceae)	Spain, Cotos de Monterrey (Madrid); Colldejou (Tarragona) (JLNA, JFG)
10. *Eurytoma* sp. cf. *aspila*	17	*Aulacidea subterminalis*	*Hieracium pilosella* (Asteraceae)	Spain, Miraflores de la Sierra (Madrid); Villasrubias (Salamanca) (JLNA, MHN)
11. *Eurytoma* sp. cf. *jaceae*	3	*Iraella luteipes*	*Papaver somniferum* (Papaveraceae)	Spain, Soto de Oreja, Valdemorillo (Madrid) (JLNA)
12. *Eurytoma strigifrons*	6	*Isocolus lichtensteini*	*Centaurea melitensis* (Asteraceae)	Spain, Pozo de Guadalajara (Guadalajara); Arganda, La Marañosa, Valgallego (Madrid) (JLNA)
13. *Eurytoma timaspidis*	24	*Timaspis phoenixopodos*	*Lactuca viminea* (Asteraceae)	Spain, Dehesa de Arganda (Madrid) (JLNA)

electron microscopy and have focused primarily on the head capsule, mouthparts and mandibles. Second, we provide a key enabling the identification of the *Eurytoma* larvae associated with cynipid galls.

MATERIALS AND METHODS

Selected taxa and specimens

We examined a total of 325 larval specimens belonging to 13 species of *Eurytoma*. Host cynipid galls were collected in the autumn and winter of 2002-2005 from a range of plants (including Asteraceae, Fagaceae, Lamiaceae, Papaveraceae, Rosaceae and Sapindaceae) at sites in Spain and France. Host cynipid species were identified using keys for the Iberian Cynipidae in Nieves-Aldrey (2001) and the identification of host plant species was based on the *Flora Europaea* (Tutin *et al*. 1980).

Sampling and rearing

Collected galls were divided into two parts; one set was kept in rearing cages, while the remaining galls were dissected under a light microscope. Pictures of larvae *in situ* were taken with a digital camera attached to the light microscope. At least 50% of the larvae dissected from galls were transferred immediately to absolute alcohol; the remainder were allowed to develop to maturity in small gelatine capsules, as described by Dawah (1987) for phytophagous eurytomid larvae.

Larvae were identified to species using known cynipid gall and host plant associations jointly with existing references on larval morphology. We verified our larval identifications by comparison with corresponding adults reared from gelatine capsules, and by comparison with adults obtained from the outdoor rearing cages. Adults were identified to species using keys by Zerova (1995) and Thuróczy & Askew (unpubl. data). In addition, most identifications were checked by Dr R. R. Askew as part of a joint on-going project to catalogue the parasitoids of Palaearctic gall wasps (Askew *et al*. 2006, unpubl. data). Our work includes 13 species of *Eurytoma*, the main eurytomid genera associated with cynipid galls. Information on the host cynipid galls, galler food plants and collection sites for all eurytomid species in this study are listed in Table 1. Voucher specimens of all species are deposited in the entomology collections of the Museo Nacional de Ciencias Naturales, Madrid (Spain) and the Muséum national d'Histoire naturelle, Paris (France).

Preparation and imaging for morphological study

Larvae were transferred directly from absolute alcohol onto a SEM stub and into a microscope (FEI Quanta 2000™) at low vacuum without prior fixation or coating, following the method described by Nieves-Aldrey *et al.* (2005) for cynipoid larvae. Four different images of each species were taken as follows: ventral view of the whole larva, lateral view of the whole larva, anterior view of the head, and close-ups of the anterior view of the mouth parts. In addition, both mandibles were photographed in anterior and posterior views. Except for *Eurytoma strigifrons* Thomson, 1876 whose mandibles are asymmetrical, we present only right mandible images for studied species. Analysis of the mandibles required prior dissection from the larval head, separate mounting and coating with gold, for normal high vacuum observation under SEM. The images are available in Morphbank (http://morphbank.net) with acession numbers: 470788-470800; 470807-470819; 470826-470838; 470845-470857 and 470864-470876.

Terminology

General terminology used in larval descriptions follows Vance & Smith (1933), Short (1952) and Roskam (1982), and specific terminology follows Henneicke *et al.* (1992) for eurytomid larvae. Our terminology is also consistent with Cutler's (1955) work on Pteromalidae larval head morphology and Gómez *et al*. (2008) work on torymid larvae. The measurements given in larval descriptions were taken from samples preserved in absolute alcohol. Body length was measured as in Henneicke *et al.* (1992), as head length plus the combined length of all the remaining segments. The antero-dorsal protuberances described further below were included in the maximum body width measurement. Measurements are given as means with their range in parentheses.

The ratio length/width of the body (henceforth L/W) was measured at the 3rd abdominal segment in ventral view. We also measured the ratio of the distance between antennae (SA) to the length of the antero-medial setae of the antennal area (LAA) (henceforth SA/LAA) and also to the distance between the antero-medial setae of vertex (DAV) (henceforth SA/DAV). The ratio length/width of the first tooth of the mandible (henceforth L/W 1T) was calculated with the length of the tooth measured from the base to apex and the width measured at its base. The relative position of antennae on the head was estimated measuring the distance between the antennae to the anterior margin of clypeus related to the one between them to the upper margin of vertex (henceforth AC/AV).

Cluster analysis

A cluster analysis was performed. Morphological variation between all of the studied larvae of *Eurytoma* species was coded in an observation matrix of character states, which included coding of 21 characters related to external morphology based on SEM images (Appendices 1; 2). Cluster analyses, UPGMA (unweighted pair group method analysis), was performed in PAUP* 4.0b10b (Swofford 2002) to obtain an overall similarity phenogram.

Abbreviations

Anatomy

adp	antero-dorsal protuberances;
af	antennal foramina;
am	antero-medial setae on the antennal region;
an	antennae;
anr	antennal region;
cl	clypeus;
cs	clypeal setae;
dls	dorso-labral setae;
epc	externally opening lateral spiracles;
fr	frons;
gn	genal setae;
gr	genal region;
hr	hypostomal region;
hs	hypostomal setae;
lb	labrum;
lbi	labium;
lbs	labral setae;
md	mandible;
mp	maxillary palps;
mpu	underlip complex;
ms	maxillary setae;
mx	maxillae;
ul	antero-medial labial setae;
vam	antero-medial setae of the vertex;
vlr	ventro-lateral region;
vmr	ventro-medial region;
vr	vertex region.

Reproductive status

A	agamic (parthenogenetic) generation;
S	sexual generation.

Collectors and repositories

JFG	J. F. Gómez;
JLNA	J. L. Nieves-Aldrey;
LP	Luis Parra;
MHN	M. Hernández Nieves;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris.

RESULTS

General larval morphology of *Eurytoma*

Qualitative variation in larval morphology is summarized in 21 characters (see Appendices 1 and 2). The terminal-instar larvae of all studied species are generally very similar morphologically (and share many features in common with other chalcidoid larvae) and although they show a range of characteristic morphological features, *Eurytoma* species often share character states. The larvae are characterised by a pair of strong mandibles, which are visible externally and have more than one tooth. The body setae are short or almost absent on the abdominal segments, but range from short to moderately long on the thorax and head. Six pairs of setae are present on the head capsule (Roskam 1982; Henneicke *et al.* 1992).

The larvae of Ormyridae Förster, 1856 and Eurytomidae Walker, 1832 are superficially similar, and share the same pattern of setae over the head and body. The mandibles clearly distinguish these two families: they are simple, one-toothed and not visible externally in Ormyridae, rather than bidentate and partially visible externally in Eurytomidae. The labrum of Ormyridae and Eurytomidae is also similar in being divided into a medial and two lateral lobes; however, while the medial lobe

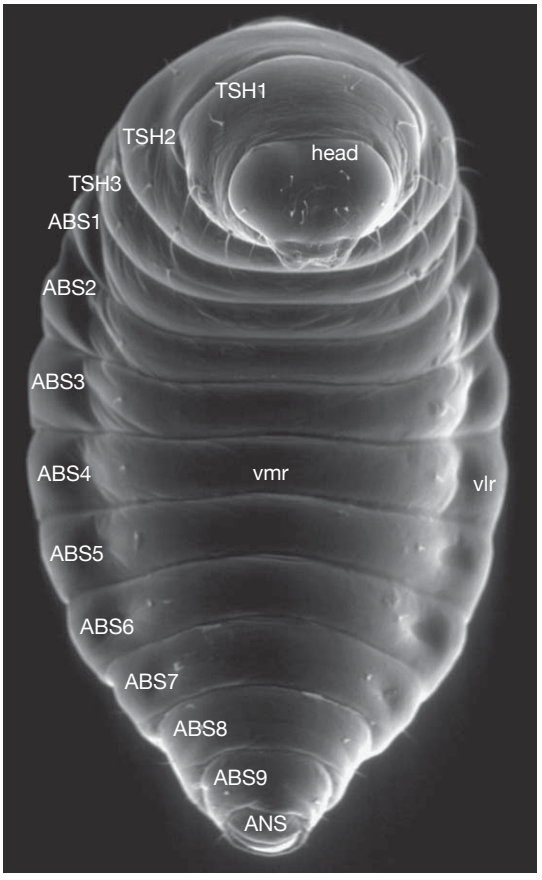

FIG. 1. — Body in ventral view of *Eurytoma brunniventris* Ratzeburg, 1852, illustrating the terminology used for general description. Abbreviations: **ABS1-ABS9**, abdominal segments; **ANS**, anal segment; **THS1-THS3**, thoracic segments; other abbreviations, see Material and methods.

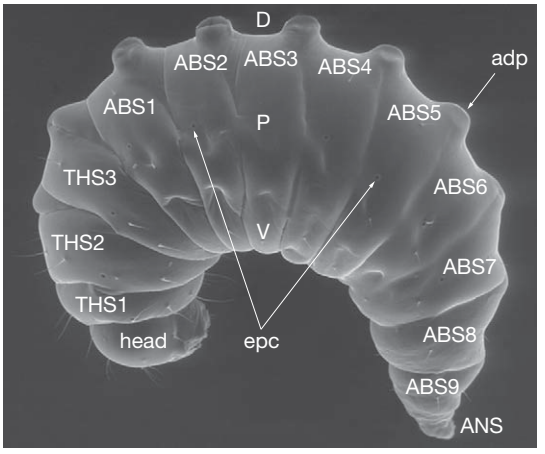

FIG. 2. — Body in lateral view of *Eurytoma cynipsea* Boheman, 1836. Abbreviations: **ABS1-ABS9**, abdominal segments; **ANS**, anal segment; **THS1-THS3**, thoracic segments; other abbreviations, see Material and methods; distributions of setae are referred to as: **D**, dorsal area; **P**, pleural area; **V**, ventral area.

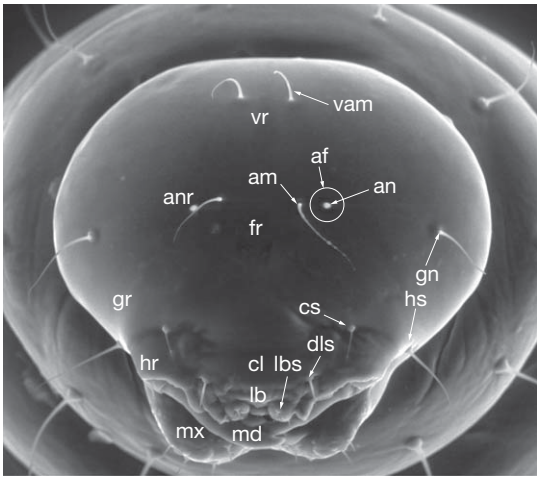

FIG. 3. — Anterior view of head of *Eurytoma cynipsea* Boheman, 1836, illustrating the terminology used for general description. Abbreviations: see Material and methods.

in *Ormyrus* Westwood, 1832 is usually undivided or superficially divided into three lobes, the medial part of the labrum of *Eurytoma* is usually divided into five lobes.

Head (Fig. 3)

The head is usually trapezoid, more or less broadened in anterior view (Fig. 3). It is always narrower than the first body segment (Figs 3; 5; 6) and without visible sculpture. Antennae always visible on the frons below the vertex area, usually short and button-like. The basal region or antennal foramina remains indistinct, resulting in a diffuse antennal region. The head bears 6 pairs of setae: 1) a pair of antero-medial setae on the vertex; 2) a pair of antero-medial setae on the antennal area; 3) a pair of genal setae on the genae; 4) a pair of hypostomal setae on the hypostomal area; 5) a pair of clypeal setae situated above the clypeus; and 6) a pair of dorso-labral

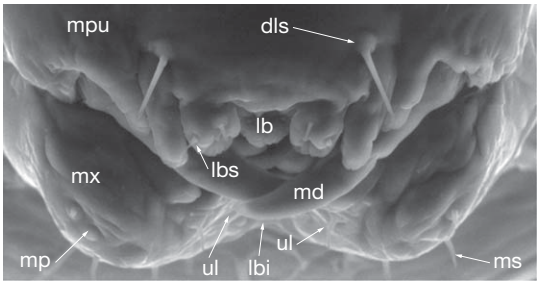

Fig. 4. — Anterior view of mouthparts of *Eurytoma timaspidis* Mayr, 1904. Abbreviations: see Material and methods.

setae situated on the ventral margin of the clypeus above the labrum. There is also a pair of weakly visible labral setae.

Anterodorsal to the mouth region is the clypeus, a more or less triangular region with a variably shaped ventral margin. The labrum, a single structure above the underlip complex, is usually divided into two pairs of lateral flaps and one medial part, the latter subdivided into three more or less differentiated lobes, depending on the species.

Mouth parts (Figs 4; 11; 12)

Mouthparts comprise the mandibles and the underlip complex, formed by the hypopharynx (hardly discernible), the maxillae and labium. The mandibles are considered in more detail below. In contrast to other chalcid families, in *Eurytoma* the maxillae and labium are clearly separated. The maxillae comprise a pair of triangular structures on both upper sides of the underlip complex. The maxillary palps are generally visible and conspicuous. Lateral to and below the maxillae is the labium, which is usually concave medially. The maxillae and labium bear two pairs of short setae, often hardly visible, named as follows: a pair of antero-medial labial setae and a pair of maxillary setae on one of the two maxillary palps.

Mandibles (Fig. 13)

Eurytoma larval mandibles are well-sclerotized and quite visible, especially at their blades. There are often relatively conspicuous differences between species, making mandible structure an important character in systematics and taxonomy. As far as is known, all eurytomid larvae have mandibles with at least two teeth, rarely more than two, the second tooth being clearly shorter and smaller than the first one.

Body (Figs 1; 2; 5-8)

Segmentation (Figs 1; 2). As in most Chalcidoidea larvae, the body consists of 13 post-cephalic segments plus the head. Three segments form the thorax (THS1-THS3) and the remaining ten segments form the abdomen including the anal segment (ABS1-ABS9, ANS). Anterodorsal protuberances are always present on at least one segment and sometimes protrude clearly outside the dorsal margin of the body. They can be present on abdominal and thoracic segments.

Spiracles (Fig. 2). The tracheal system is peripneustic, with nine pairs of externally opening lateral spiracles situated on segments THS2 to ABS7 (Roskam 1982; Henneicke *et al.* 1992).

Chaetotaxy in lateral view (Fig. 2). Following Roskam (1982), we divided the body segments into three areas in lateral view: the pleural area, which includes the spiracles, and the two areas situated ventrally and dorsally, which are denoted the ventral and dorsal areas respectively. Accordingly, the setae are referred to as dorsal, pleural or ventral (D, P and V respectively).

In general, *Eurytoma* larvae have few body setae in comparison with torymid and eupelmid larvae, but they are hairier than other chalcids such as pteromalids or eulophids. There are three rows of setae at least in the thoracic segments (dorsal, lateral and ventral rows), which are much shorter than the length of the body segment except in the thoracic segments. These have relatively longer setae but even these are not much longer than the length of their body segment. Setae are generally longest on the thoracic segments and shortest on the abdominal segments.

Chaetotaxy in ventral view (Fig. 1). In ventral view, we divided the body into a ventro-medial region (*vmr*) and a ventro-lateral region (*vlr*). Both

regions are hairy in thoracic segments although the density of setation is not high.

Taxonomy

Descriptions of the taxa studied are based mainly upon preserved material but with additional observations from living larvae. The diagnosis of the genus *Eurytoma* is partly based on previous work by Roskam (1982), Henneicke *et al.* (1992) and Dawah & Rothfritz (1996). The remaining descriptions of larval species and the key to genera are new. Eurytomid nomenclature follows Noyes (2003). Resulting tree of the cluster analysis carried out for taxonomic purposes is showed in Figure 16.

This key identifies the larvae of the 13 species studied in this paper, which represent the core or commonest eurytomid species associated with oak galls in Europe. The following species also listed in the catalogues of Eurytomidae parasitoids of gall wasp from the West Palaearctic, which are rare, of dubious status, or distributed in eastern Europe were not included (Askew *et al.* 2006, unpubl. data): *Eurytoma adleriae* Zerova, 1995; *E. aemula* Szelenyi, 1974; *E. jaceae* Mayr, 1878; *E. pistacina* Rondani, 1877; *E. pseudocynipsea* Zerova, 2003; *E. punctatella* Zerova, 1978; *E. querceticola* Zerova, 1995; *E. salvicola* Zerova, 2003 and *E. spinipes* Kalina, 1970.

Key to the terminal-instar larvae of the *Eurytoma* Illiger, 1807 commonest species associated with European cynipid-galls

1. Outer margin of first tooth of mandible almost straight; tip not recurved (Fig. 13L, M); inner margin of mandible from the base of second tooth (anterior view) forming a small projection close to the base of the second tooth (Fig. 13M) ..... *E. strigifrons*
— Outer margin of first tooth of mandible strongly convex; tip moderately or strongly recurved (Fig. 13A-K, N); inner margin of mandible from the base of second tooth (anterior view) without a small projection; if a small projection is present, then it is situated relatively far from the base of the second tooth 2

2. Antero-medial setae of the antennal area clearly below the antennae (Figs 9D, E; 10A); dorsal-labral setae longer than clypeal setae (Figs 11E, F; 12B); ventral margin of clypeus distinct (Figs 11E, F; 12B) 3
— Antero-medial setae of the antennal area at the same level or slightly either above or below the antennae (Figs 9A-C, F; 10B-D, F); dorsal-labral setae usually as long as clypeal setae (Figs 11A-D; 12A, C, D, G); ventral margin of clypeus indistinct, except in *E.* sp. cf. *jaceae* (Figs 11A-D; 12A, C, D, G) 5

3. First tooth of mandible relatively short and wide; second tooth with the apex moderately recurved inwards; mandible exposed with apical tooth almost completely visible (Fig. 13H); antero-medial setae of vertex situated relatively high on the upper face; much closer to the anterior margin of vertex than to the antennae (Fig. 10A); divisions of medial part of the labrum deep, almost reaching the level of labral setae; five lobes and two shorter lateral flaps clearly differentiated (Fig. 12B); maxillary palps inconspicuous (Fig. 12B) ..... *E. rosae*
— First tooth of mandible relatively longer and narrower; second tooth with the apex straight (Fig. 13E) or strongly recurved inwards (Fig. 13F); mandible exposed only in part, the tip being visible (Fig. 13E, F); antero-medial setae of vertex situated more or less half way between anterior margin of vertex and the antennae (Fig. 11D, E); divisions of medial part of the labrum slight and usually limited to apical part; five lobes not as well differentiated (Fig. 11E, F); maxillary palps conspicuous (Fig. 11E, F) 4

4. Apex of the second tooth of the mandible straight, directed upwards in the same direction as the first tooth; inner margin of mandible from the base of second tooth (anterior view) forming two small projections close to the base of the second tooth; the mandible appearing to have four teeth (Fig. 13E); anterodorsal protuberances (lateral view) clearly protruding beyond the dorsal margin of body (Fig. 7E) ..... *E. mayri*
— Apex of the second tooth of the mandible strongly recurved inwards; inner margin of mandible from the base of second tooth (anterior view) straight and not interrupted (Fig. 13F); anterodorsal protuberances (lateral view) not protruding beyond the dorsal margin of body (Fig. 7F) ..... *E. pediaspisi*

5. Inner margin of mandible from the base of second tooth (anterior view) forming a small projection relatively far from the base of the second tooth (Fig. 13I); distance between the antero-medial setae of vertex 1.4 as far as the distance between antennae (Fig. 10B); antero-medial setae of vertex situated approximately half way between anterior margin of vertex and the antennae (Fig. 10B) ..... *E. rufipes*
— Inner margin of mandible from the base of second tooth (anterior view) not forming a small projection (Fig. 13A-D, G, J, K, N); distance between the antero-medial setae of vertex <1.2 as far as distance between antennae (Figs 3; 9A, B, F; 10C, D, F); antero-medial setae of vertex situated relatively high on the upper face; much closer to the anterior margin of vertex than to the antennae (Figs 3; 9A, B, F; 10C, D, F) 6

6. Dorsal-labral setae longer than clypeal setae (Fig. 13E); ventral margin of clypeus distinct (Fig. 12E); maxillary palps inconspicuous (Fig. 12A) .... *Eurytoma* sp. cf. *jaceae* (ex *Iraella luteipes*)
— Dorsal-labral setae usually as long as clypeal setae (except in *E. timaspidis*) (Figs 4; 11A, B; 12A, D); ventral margin of clypeus indistinct (Figs 4; 11A, B; 12A, D); maxillary palps conspicuous (Figs 4; 11A, B; 12A, D) 7

7. Divisions of medial lobe of the labrum slight, usually limited to apical part of labrum; five lobes not well differentiated (Figs 11B, D; 12A, D); right and left mandibles always with two teeth (Fig. 13B, D, G, J); mandible partially exposed, with only the tip visible (except in *E.* sp. cf. *aspila*) (Figs 11B, D; 12A); maxillae inconspicuous, not well differentiated from labium (Figs 11B, D; 12A, D); distance between the antero-medial setae of vertex about as long as distance between antennae (except in *E.* sp. cf. *aspila*) (Fig. 9B, C, F) 8
— Divisions of medial lobe of the labrum deep, almost reaching the level of labral setae; five irregular lobes differentiated (Figs 4; 11A, C); right mandible with three teeth; left mandible with two or three (Fig. 13A, C, N); mandible clearly exposed; apical tooth almost completely visible (Figs 4; 11A, C); maxillae conspicuous, well differentiated from labium (Figs 4; 11A, C); distance between the antero-medial setae of vertex less than distance between antennae (Figs 3; 9A; 10F) 11

8. Inner margin of mandible from the base of second tooth (anterior view) strongly convex (Fig.13D); upper margin of vertex straight (Fig. 9C) ..... *E. infracta*
— Inner margin of mandible from the base of second tooth (anterior view) straight or with other shape (Fig. 13B, G, J); upper margin of vertex concave (Figs 9B, F; 10C) 9

9. Second tooth of mandible relatively longer; 0.42 as long as first tooth (Fig. 13J); antero-medial setae of vertex situated relatively high on the upper face, much closer to the anterior margin of vertex than to the antennae; distance between the antero-medial setae of vertex greater than distance between antennae (Fig. 10C)..... ..... *Eurytoma* sp. cf. *aspila* (ex *Aulacidea subterminalis*)

— Second tooth of mandible relatively short; 0.14-0.22 as long as first tooth (Fig. 13B, G); antero-medial setae of vertex located more or less half way between anterior margin of vertex and the antennae; distance between the antero-medial setae of vertex about as long as distance between antennae (Fig. 9B, F) 10

10. Body relatively short and wide, 1.4 times as long as wide (Fig. 5G); second tooth of mandible 0.22 as long as the first tooth (Fig. 13G) ..... *E. robusta*
— Body relatively longer and narrow, 1.9 times as long as wide (Fig. 5B); second tooth of mandible 0.14 as long as the first tooth (Fig. 13B) ..... *E. brunniventris*

11. Right mandible with three teeth (Fig. 13A) ..... *E. aspila*
— Right mandible with only two teeth (Fig. 13C, N).....12

12. Second tooth of mandible 0.28 as long as the first tooth (Fig. 13N); clypeal setae shorter than lobes of labrum; labral setae longer than clypeal setae (Fig. 12G) ..... *E. timaspidis*
— Second tooth of mandible 0.43 as long as the first tooth (Fig. 13C); clypeal setae as long as lobes of labrum; labral setae as long as clypeal setae (Fig. 11C) ..... *E. cynipsea*

Descriptions of terminal-instar larvae of species of *Eurytoma* associated with cynipid galls

Our descriptions combine earlier accounts on the larvae of *Eurytoma* (Roskam 1982; Henneicke *et al*. 1992; Dawah & Rothfritz 1996) with our own new data. However the descriptions of the species are entirely new excepting when mentioned in the text.

Family Eurytomidae Walker, 1832

Genus *Eurytoma* Illiger, 1807

Description

Body in ventral view (Figs 5; 6) fusiform or barrel-shaped in most species, slightly broadest around the middle (segments ABS3-ABS5) and tapering gradually towards anal segment, which is normally broader than long; the ratio L/W is usually 1.3-2.2; in lateral view (Figs 7; 8) body ventrally curved; ventral margin of abdominal body segments usually clearly convex in profile. Anterodorsal protuberances always visible at least in one thoracic and abdominal segment, being clearly protruding outwards in most species. Colour whitish. Integument generally smooth or slightly rugose in body and cephalic capsule. Body moderately setose displaying a pattern composed by only three rows of setae at least in the thoracic segments (a dorsal, lateral and ventral rows); setae much shorter than length of body segment except in the thoracic area that could have relatively longer setae but not more than the length of a body segment.

Head in anterior view (Figs 9; 10) more or less hemispherical or trapezoid, with mouth parts protruding; head approximately 1.1-1.3 times as broad as high, with anterior margin of vertex slightly concave in most species and the medial area of vertex not incised. Head with basic chaetotaxy, comprising no more than 5-7 pairs of clearly visible setae.

Vertex with one pair of relatively short erect setae with the separation between this pair varying between species; antero-medial setae of antennal area situated mostly at the same level or slightly either above or below the antennae, their length in most species intermediate but varying between them; the antero-medial setae of vertex usually situated relatively high on the upper face, much closer to the anterior margin of the vertex than to the antennae, as their precise position constitutes a variable character between species. Antennal area indistinct; antennae variable in size and situated more or less at the middle of the head; one pair of clypeal setae present, situated laterally above the level of ventral margin of clypeus; a pair of dorsal-labral setae present, situated above the labrum just at the level of ventral margin of clypeus, and generally as long as clypeal setae. Ventral margin of clypeus straight and more or less visible in each species.

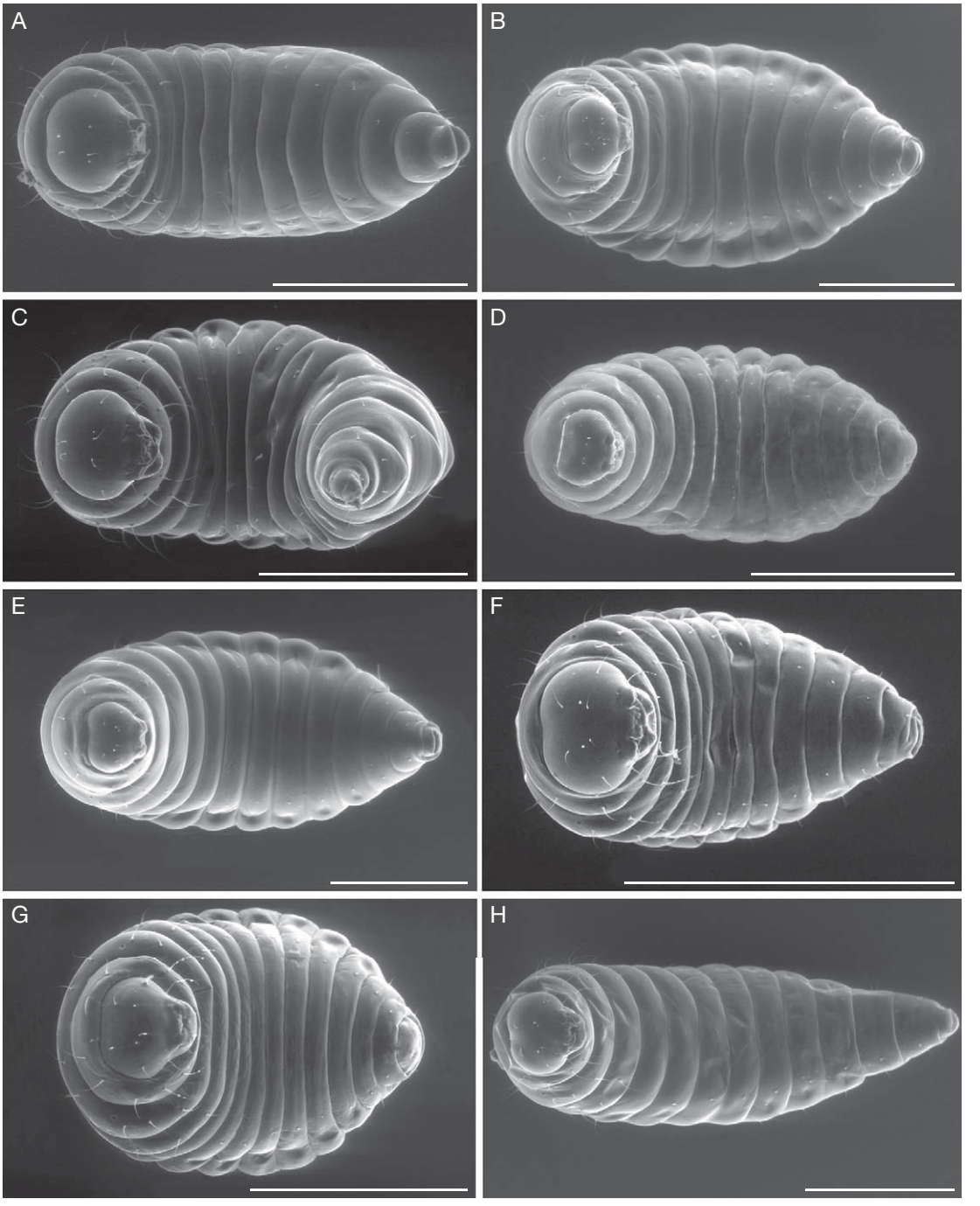

Fig. 5. — Ventral views of terminal-instar eurytomid larvae: **A**, *Eurytoma aspila* (Walker, 1836) ex *Phanacis caulicola*; **B**, *E. brunniventris* Ratzeburg, 1852 ex *Cynips quercus* (A); **C**, *E. cynipsea* Boheman, 1836 ex *Phanacis hypochoeridis*; **D**, *E. infracta* Mayr, 1904; **E**, *E. mayri* Ashmead, 1887; **F**, *E. pediaspisi* Pujade i Villar, 1994; **G**, *E. robusta* Mayr, 1878; **H**, *E. rosae* Nees, 1834 ex *Diplolepis rosae*. Scale bars: 1 mm.

Mouth parts (Figs 11; 12) with labrum subrectangular and divided into two lateral flaps and one medial part, which is in turn subdivided into five more or less differentiated lobes; subdivision of medial part of the labrum can be slight, and ranges from limited to the apical part of labrum (e.g., *Eurytoma brunniventris*) to deep and almost reaching the level of labral setae (e.g., *Eurytoma rosae*), according to species. Maxillae differentiated or not from labium but only slightly protruding from it; maxillary palps sometimes easily visible; labial palps visible or not, sometimes conspicuous.

Mandibles (Fig. 13) usually symetrical (except for *Eurytoma strigifrons* within studied species), with the apical tooth generally visible or exposed in part, at least the tip being visible; always more than one tooth in each mandible with the shape of the first tooth variable according to species, ranging from relatively short and wide (e.g., *Eurytoma rosae*) to long and slender (e.g., *Eurytoma infracta*) (ratio L/W 1T variable); secondary tooth smaller and shorter than first, its tip either straight or recurved or slightly blunt.

Monophyly and recognition

With around 699 described species, *Eurytoma* is the largest genus of the Eurytomidae (Noyes, 2003). The genus is complex and still presents many taxonomic and phylogenetic problems (Zerova 1988; Lotfalizadeh *et al.* 2007a). The lack of a useful and valid phylogenetic classification for *Eurytoma* species is associated with uncertainty over the generic limits of *Eurytoma*, *Bruchophagus* and allied genera. Identification keys have long used artificial arrangements, as in the key proposed by Burks (1971). A recent review based on morphological characters of adults indicates *Eurytoma* is polyphyletic (Lotfalizadeh *et al*. 2007a).

The species whose larvae we have studied belong to three different *Eurytoma* species groups – the *cynipsea* group, the *robusta* group and the *rosae* group. A general pattern in some *Eurytoma* groups is the presence of sibling species that are very similar as adults but which show some differences in their immature stages (Claridge & Askew 1960). Differences among *Eurytoma* species will be discussed later.

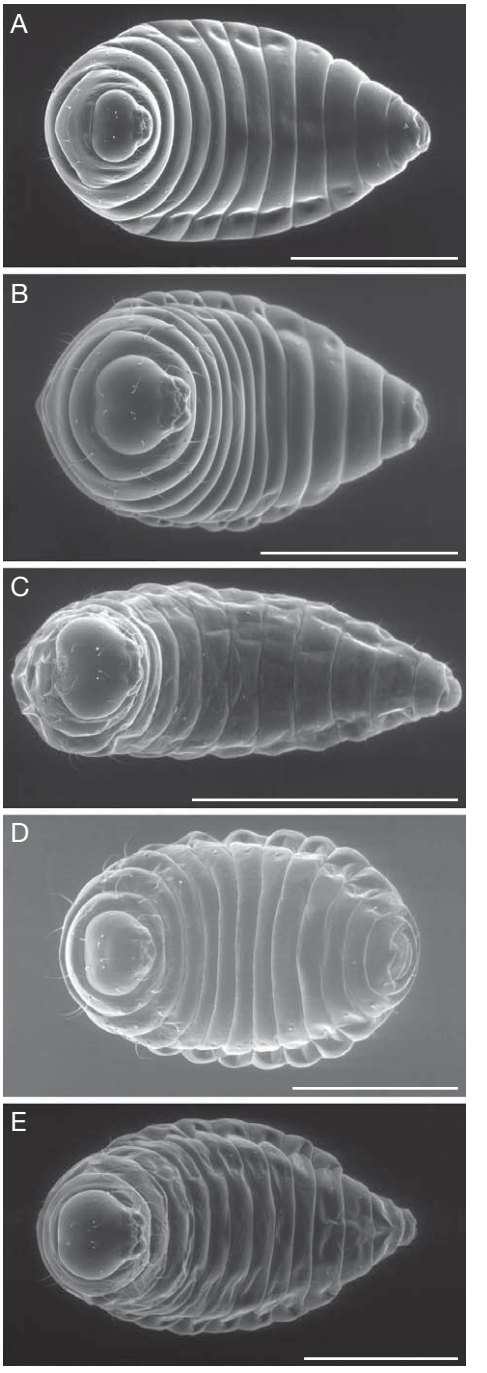

Fig. 6. — Ventral views of terminal-instar eurytomid larvae: **A**, *Eurytoma rufipes* Walker, 1832; **B**, *E.* sp. nr. *aspila*; **C**, *E.* sp. nr. *jaceae*; **D**, *E. strigifrons* Thomson, 1876; **E**, *E. timaspidis* (Mayr, 1904). Scale bars: 1 mm.

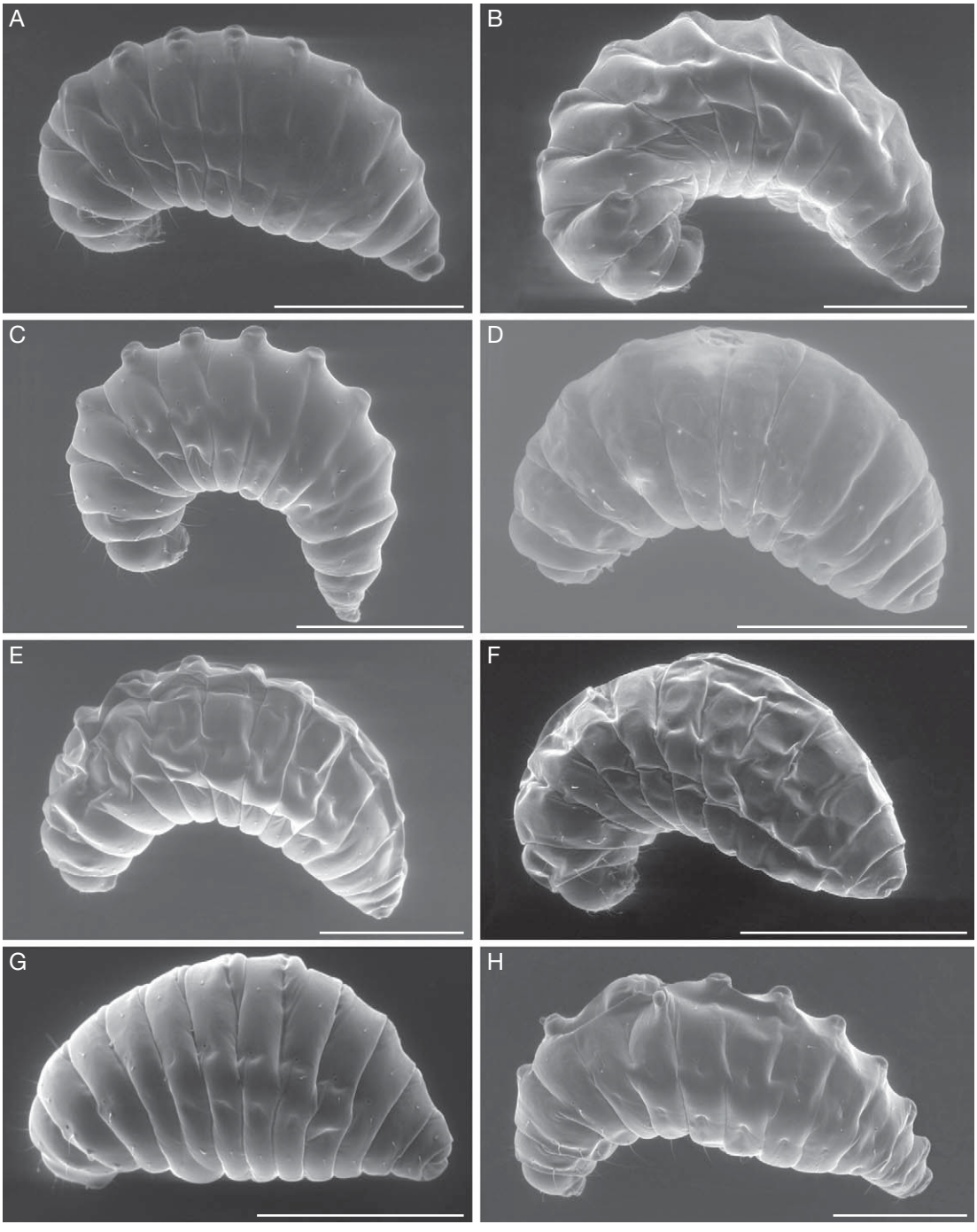

FIG. 7. — Lateral views of terminal-instar eurytomid larvae: **A**, *Eurytoma aspila* (Walker, 1836) ex *Phanacis caulicola*; **B**, *E. brunniventris* Ratzeburg, 1852 ex *Cynips quercus* (A); **C**, *E. cynipsea* Boheman, 1836 ex *Phanacis hypochoeridis*; **D**, *E. infracta* Mayr, 1904; **E**, *E. mayri* Ashmead, 1887; **F**, *E. pediaspisi* Pujade i Villar, 1994; **G**, *E. robusta* Mayr, 1878; **H**, *E. rosae* Nees, 1834 ex *Diplolepis rosae*. Scale bars: 1 mm.

BIOLOGY

Species of *Eurytoma* are predominantly endophytic, either as phytophagous or as parasitoids of phytophagous insects. The species included in this study are all ectoparasitoids in galls of Cynipidae on herbs, shrubs and trees in the families Lamiaceae, Asteraceae, Rosaceae, Sapindaceae and Fagaceae. Almost all of the species also feed on gall plant tissue at the end of their final larvae stage.

Eurytoma aspila (Walker, 1836)

MATERIAL EXAMINED. — Ex *Aulacidea follioti*: **France**. Pyrénées-Atlantiques, vallée d'Aspe, 7.VIII.2003, J. L. Nieves leg (n = 3).
Ex *A. tragopogonis*: **Spain**. Madrid, Arganda, 18.X.2003, J. L. Nieves leg (n = 2). — Dehesa de Arganda, 6.XI.2002, J. L. Nieves leg (n = 22).
Ex *P. caulicola*: **Spain**. Orense, Rubiá, 18.VII.2003, J. L. Nieves leg (n = 12, of which 2 specimens MNHN-EY6411).

DESCRIPTION

n = 39; body length 1.5 mm (range 1-2.2); body width 0.8 mm (0.47-1.0) (Figs 5A; 7A; 14A); body elongate, fusiform, tapering slightly anteriorly and posteriorly; ratio L/W = 2.02; ventral margin of body segments 4-8, in lateral view, clearly convex; anterodorsal protuberances present from the second thoracic to fifth abdominal segment, clearly protruding beyond the dorsal margin of body (Fig. 7A).

Antero-medial setae of vertex relatively high on the upper face, close to this margin; ratios SA/DAV = 0.47 and SA/LAA = 0.41 (Fig. 9A); dorsal-labral setae as long as clypeal setae; ventral margin of clypeus indistinct, without any discernible suture; divisions on the medial part of labrum deep and almost reaching the level of labral setae, two short lateral flaps and five lobes being visible; maxillary palps conspicuous (Fig. 11A).

A pair of symmetrical mandibles present and well developed, their apical teeth completely exposed (Figs 11A; 13A); both mandibles with three teeth, one larger and two shorter with the ratio L/W = 1.61; first tooth short and wide; outer margin of first tooth strongly convex; tip moderately recurved; the shape of apex of the second tooth varies ac-

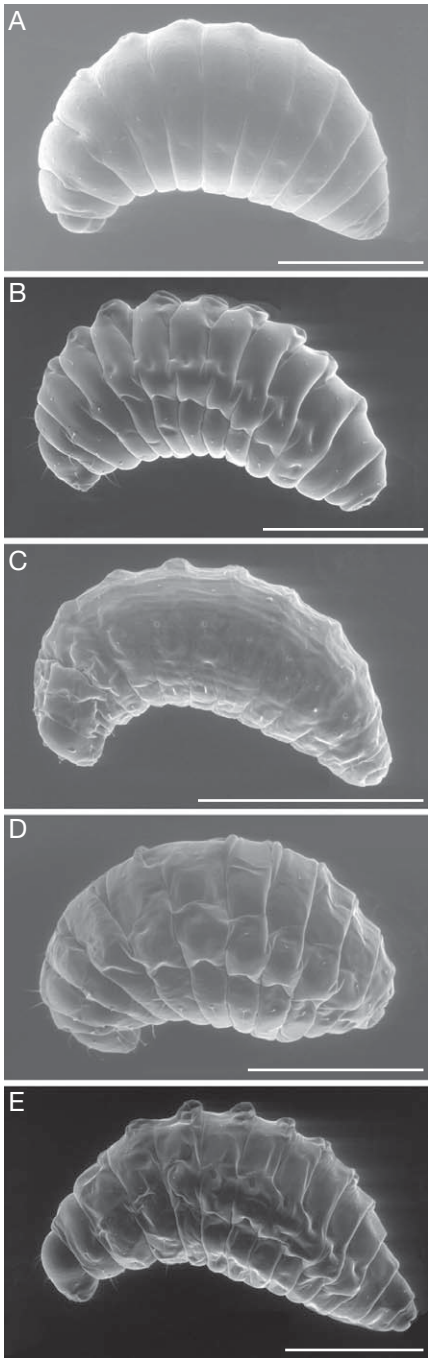

FIG. 8. — Lateral views of terminal-instar eurytomid larvae: **A**, *Eurytoma rufipes* Walker, 1832; **B**, *E.* sp. cf. *aspila*; **C**, *E.* sp. cf. *jaceae*; **D**, *E. strigifrons* Thomson, 1876; **E**, *E. timaspidis* (Mayr, 1904). Scale bars: 1 mm.

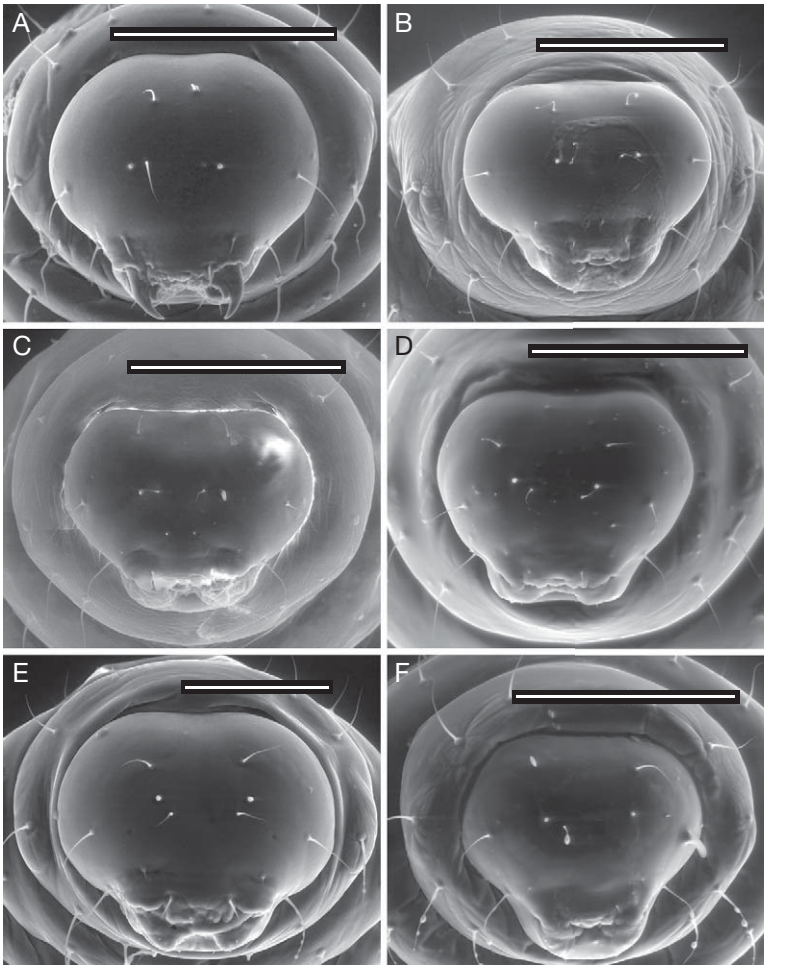

FIG. 9. — Anterior views of the head of terminal-instar eurytomid larvae: **A**, *Eurytoma aspila* (Walker, 1836) ex *Phanacis caulicola*; **B**, *E. brunniventris* Ratzeburg, 1852 ex *Cynips quercus* (A); **C**, *Eurytoma infracta* Mayr, 1904; **D**, *Eurytoma mayri* Ashmead, 1887; **E**, *Eurytoma pediaspisi* Pujade i Villar, 1994; **F**, *Eurytoma robusta* Mayr, 1878. Scale bars: A, B, D, F, 400 µm; C, 300 µm; E, 200 µm.

cording to the host from pointed to straight, and is directed upwards in the same direction of the first tooth (Fig. 13A).

BIOLOGY

Eurytoma aspila is a polyphagous ectoparasitoid associated with Aylacini gall wasps on herbs. It is usually reared from galls of *Aulacidea* and *Phanacis* on different species of Asteraceae. Fully-grown larvae overwinter inside gall cells (Fig. 14B), and adults emerge in the spring, in synchrony with cynipid oviposition on the stems and the development of new gall chambers.

REMARKS

The larva of *E. aspila* is readily separated from the other *Eurytoma* larvae discussed here by their three-toothed mandibles (Fig. 13A).

Eurytoma sp. cf. *aspila*

MATERIAL EXAMINED. — Ex *Aulacidea subterminalis*: **Spain**. Madrid, Miraflores de la Sierra, 2-4.VIII.2002, J. L. Nieves leg (n = 6, of which 1 specimen MNHN-EY6417). — Salamanca, Villasrubias, 23.XI.2004, M. Hernández leg (n = 11).

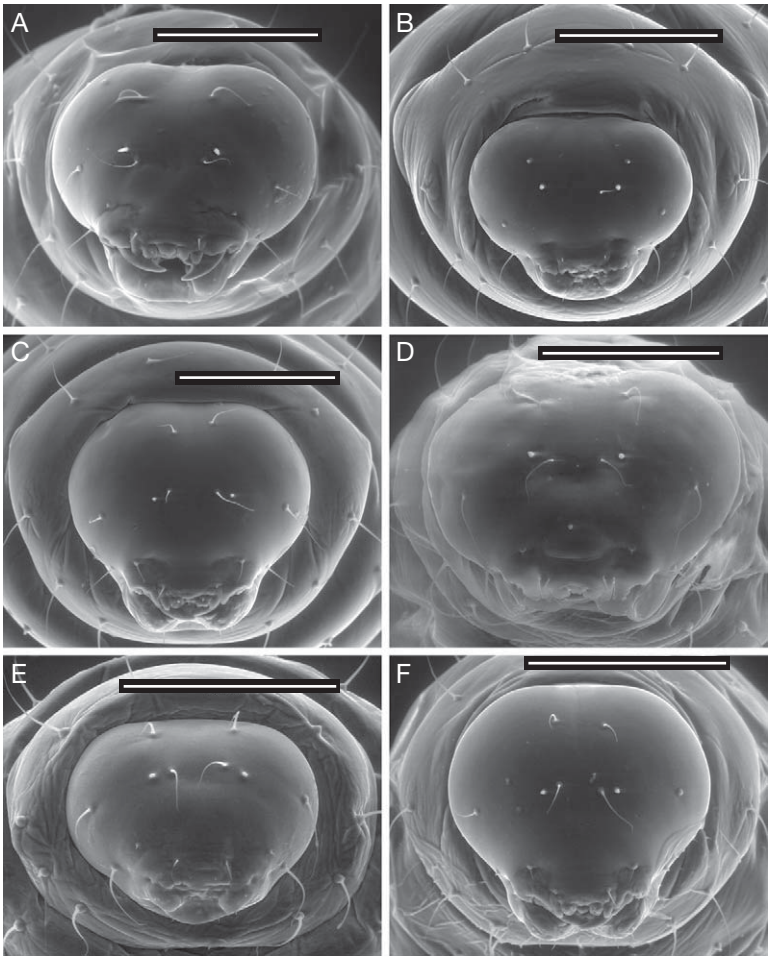

FIG. 10. — Anterior views of the head of terminal-instar eurytomid larvae: **A**, *Eurytoma rosae* Nees, 1834 ex *Diplolepis rosae*; **B**, *E. rufipes* Walker, 1832; **C**, *E.* sp. cf. *aspila*; **D**, *E.* sp. cf. *jaceae*; **E**, *E. strigifrons* Thomson, 1876; **F**, *E. timaspidis* (Mayr, 1904). Scale bars: A-C, 300 µm; D, 200 µm; E, F, 400 µm.

DESCRIPTION

n = 17; body length 1.74 mm (range 1-2.3); body width 0.8 mm (0.5-1.2) (Figs 6B; 8B); body widest at segments 1-3, relatively short and wide; ratio L/W = 1.63; shape of ventral margin of body segments clearly convex; anterodorsal protuberances present from the second thoracic to eighth abdominal segment clearly protruding beyond dorsal margin of body (Fig. 8B).

Antero-medial setae of antennal area situated slightly above the antennae and relatively high on the upper face (Fig. 10C); ratios SA/LAA = 0.59 and SA/DAV = 0.51; dorsal-labral setae as long as clypeal setae; ventral margin of clypeus indistinct; labrum with slight divisions limited to apical part of labrum and five poorly differentiated lobes; maxillary palps conspicuous (Fig. 12D).

Mandibles with two teeth (Fig. 15D); right mandible appears to have a third tooth, but not as developed as in *E. aspila*; exposed in part, with at least the tip visible (Fig. 12D; 13J); ratio L/W = 1.96; outer margin of first tooth strongly convex with the tip moderately recurved; shape of apex of the second tooth straight, directed upwards in the

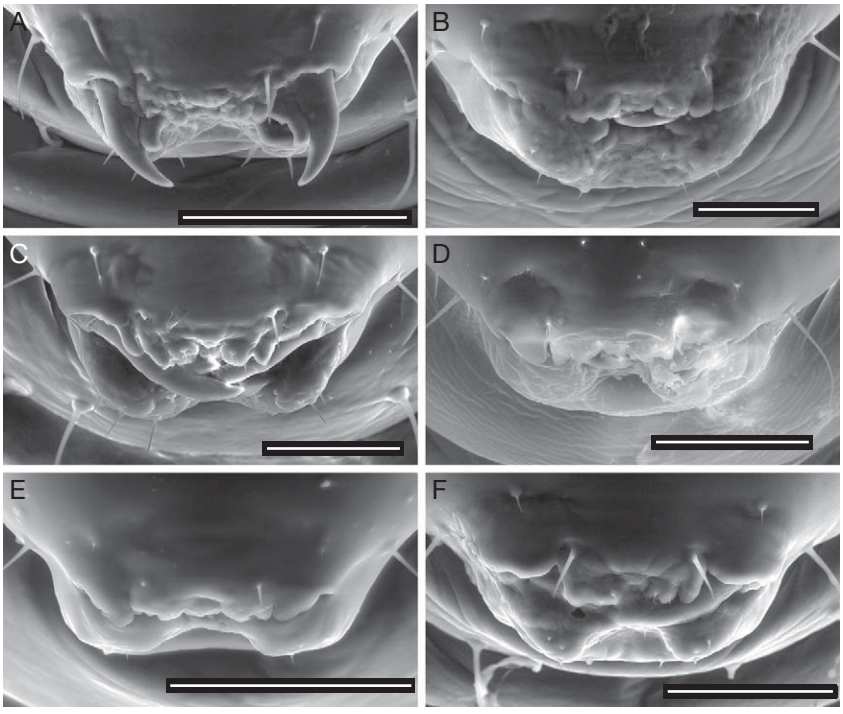

Fig. 11. — Anterior views of mouthparts of terminal-instar eurytomidae larvae: **A**, *Eurytoma aspila* (Walker, 1836) ex *Phanacis caulicola*; **B**, *E. brunniventris* Ratzeburg, 1852 ex *Cynips quercus* (A); **C**, *E. cynipsea* Boheman, 1836 ex *Phanacis hypochoeridis*; **D**, *E. infracta* Mayr, 1904; **E**, *E. mayri* Ashmead, 1887; **F**, *E. pediaspisi* Pujade i Villar, 1994. Scale bars: A, E, 200 µm; B-D, F, 100 µm.

same direction as the first tooth and more or less pointed; inner margin of mandible from the base of second tooth more or less straight, with the margin not interrupted (Fig. 13J).

Biology

This species has only been reared from galls of *Aulacidea subterminalis* Niblett, 1946 on runners of *Hieracium pilosella* L. (Asteraceae), living as a primary ectoparasitoid. It appears to be a monophagous species. The fully-grown larvae of this species of *Eurytoma* usually overwinter in old galls of *A. subterminallis* (Fig. 15C); adults emerge in the spring in synchrony with the development of new host galls.

Remarks

The adult of this species is closely allied to that of *E. aspila* but it cannot be assigned to this species. According to Askew (pers. comm.), it could represent a new undescribed species, and was recorded as such in a published catalogue (Askew *et al.* 2006). However the larvae of the two species are rather different. They can be distinguished by the two-toothed mandibles.

Eurytoma brunniventris Ratzeburg, 1852

Material examined. — Ex *Andricus coriarius*: **Spain**. Cádiz, La Suara-Jérez, 16.X.2004, J. L. Nieves leg (n = 1)
Ex *Cynips quercus*: **Spain**. Madrid, Dehesa de Arganda, 24.X.2004, J. L. Nieves leg (n = 1).
Ex *Plagiotrochus panteli*: **Spain**. Madrid, Dehesa de Arganda, 6.VI.2004, J. L. Nieves leg (n = 4).
Ex *Plagiotrochus australis*: **Spain**. Madrid, Dehesa de Navacerrada, 27.VI.2002, J. L. Nieves leg (n = 1).
Ex *Andricus hispanicus*: **Spain**. Madrid, El Escorial, 2.VIII.2003, J. L. Nieves leg (n = 1).
Ex *Andricus kollari*: **Spain**. Madrid, El Escorial, 2.VII.2003,

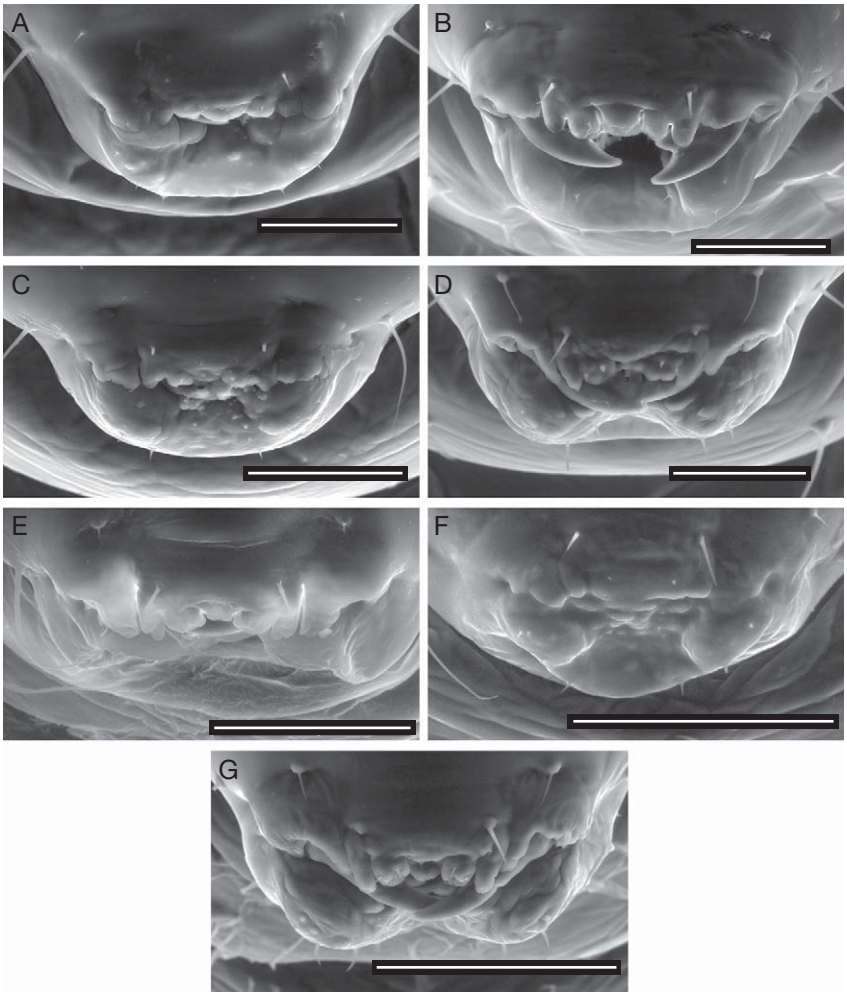

FIG. 12. — Anterior views of mouthparts of terminal-instar eurytomidae larvae: **A**, *Eurytoma robusta* Mayr, 1878; **B**, *E. rosae* Nees, 1834 ex *Diplolepis rosae*; **C**, *E. rufipes* Walker, 1832; **D**, *E.* sp. cf. *aspila*; **E**, *E.* sp. cf. *jaceae*; **F**, *E. strigifrons* Thomson, 1876; **G**, *E. timaspidis* (Mayr, 1904). Scale bars: A-E, 100 µm; F, G: 200 µm.

J. L. Nieves leg (n =1, MNHN-EY6410).
Ex *Cynips quercus*: **Spain**. Madrid, El Escorial, 2.VIII.2003, J. L. Nieves leg (n = 4).
Ex *Plagiotrochus australis*: **Spain**. Madrid, El Pardo, 13.III.2004, J. L. Nieves leg (n = 2).
Ex *Trigonaspis synaspis*: **Spain**. Madrid, Miraflores de la Sierra, 3.IX.2005, J. L. Nieves leg, (n = 1).

DESCRIPTION

n = 15; body length 1.87 mm (range 1.3-2.7); body width 1.04 mm (0.5-1.6) (Figs 5B; 7B; 14D); body barrel-shaped or fusiform, tapering anteriorly and posteriorly: ratio L/W = 1.9; body segments widest in the mid-region; anterodorsal protuberances clearly protruding from second thoracic segment to the eighth abdominal (Fig. 7B). Ratio SA/LAA = 0.45; antero-medial setae of the antennal area situated at the same level as the antennae; ratio SA/DAV = 1.13; antero-medial setae of the vertex relatively high on the upper face much closer to the anterior margin of vertex than to antennae (Fig. 9B); dorsal-labral setae as long as clypeal setae; ventral margin of clypeus indistinct and without any discernible suture;

labrum with slight divisions limited to apical part; maxillary palps conspicuous (Fig. 11B).

Mandibles invisible, covered by labrum (Fig. 11B); two teeth in both mandibles (Figs. 13B; 14G); ratio L/W 1T = 2; outer margin of the first tooth of mandible strongly convex; tip moderately recurved. Apex of second tooth more or less pointed and straight, directed upwards in the same direction as the first tooth. Inner margin of mandible from the base of second tooth more or less straight and not interrupted (Fig. 13B).

Biology

An ectoparasitoid species associated with more than 75 different oak cynipid galls across the Palaearctic. Published data (Ács *et al*. 2002) and our own unpublished molecular data show this species to represent a complex of several sibling species. The life cycle is multivoltine and larvae attack the gall-inducing cynipid larva and inquiline cynipids (Askew 1961, 1975, 1984; Schönrogge *et al*. 1995, 1996a, b) (Fig. 14C). Fully-grown larvae overwinter inside the gall and the adults emerge in synchrony with the development of new host galls (Schönrogge *et al*. 1996a, b; Fig. 14E). As this species frequently supplements its diet by also feeding on gall tissue, plant debris are usually found in larval cells containing *E. brunniventris* (Fig. 14F); this species is the only polyphagous chalcid in cynipid galls known to eat gall tissue.

Remarks

The larva of *E. brunniventris* is quite similar to that of *E. robusta*. The body shape and relative size of the second mandible tooth separates the two species. *Eurytoma brunniventris* is the commonest eurytomid species associated with cynipid galls on oaks.

Eurytoma cynipsea Boheman, 1836

Material examined. — Ex *Aulacidea freesei*/*Phanacis zwolferi*: **Spain**.Madrid, Arganda, 7.XI.2002, J. L. Nieves leg (n = 1). — Madrid, Monte Pajares, 7.XI.2002, J. L. Nieves leg (n = 10, of which 2 specimens MNHN-EY6412).
Ex *Aulacidea pilosellae*: **Spain**. Madrid, Valgallego, 19.VI.2004, J. L. Nieves leg, (n = 3).
Ex *Isocolus lichtensteini*: **Spain**. Madrid, Arganda, 24.III.2002, J. L. Nieves leg (n = 1).
Ex *Timaspis cichorii*: **Spain**. Madrid, Arganda, 8.XI.2003, J. L. Nieves leg (n = 1).
Ex *Timaspis ursopermi*: **Spain**. Málaga, Casares, VIII.2002 and II.2003, J. L. Nieves leg (n = 2).
Ex *Phanacis hypochoeridis*: **Spain**. Pontevedra, Islas Cíes, 16.VII.03, J. L. Nieves leg, (n = 1).

Description

n = 19; body length 1.6 mm (range 1.0-2.3); body width 0.9 mm (0.4-1.5) (Figs 5C; 7C); body fusiform, ratio L/W = 1.7; ventral margin of body segments clearly convex; anterodorsal protuberances protruding from second thoracic segment to the seventh abdominal segment (Fig. 2). Antero-medial setae of antennal area at the same level as the antennae; ratio SA/LAA = 0.55; ratio SA/DAV between 0.38-0.53; antero-medial setae of vertex situated relatively high on the upper face (Fig. 3); dorsal-labral setae as long as clypeal setae; ventral margin of clypeus indistinct; labrum with deep divisions forming a pair of flaps and five well differentiated lobes; maxillary palps conspicuous (Fig. 11C). Both mandibles with two teeth and apical tooth clearly visible (Fig. 11C); ratio L/W 1T between 0.6-2.0, varying according to each specific host; outer margin of first tooth strongly convex, with the tip moderately recurved; the shape of apex of the second tooth varies from pointed to blunt depending on the specific host, but is always straight and directed upwards in the same direction as the first tooth (Fig. 13C).

Biology

The species *Eurytoma cynipsea* is also a polyphagous ectoparasitoid reared from galls of different Aylacini species (Cynipidae) on various species of Asteraceae. Fully-grown larvae consume gall tissue, and slightly enlarge the host gall cell (Fig. 14H, I). Larvae overwinter and adults emerge in the following year when new galls are available on the host plants.

Remarks

As with *E. aspila*, *E. cynipsea* belongs to the *cynipsea* species-group (Zerova 1993); their larvae have a similar appearance, with very large sclerotized and exposed mandibles. However, the mandible of *E. cynipsea* has only two teeth.

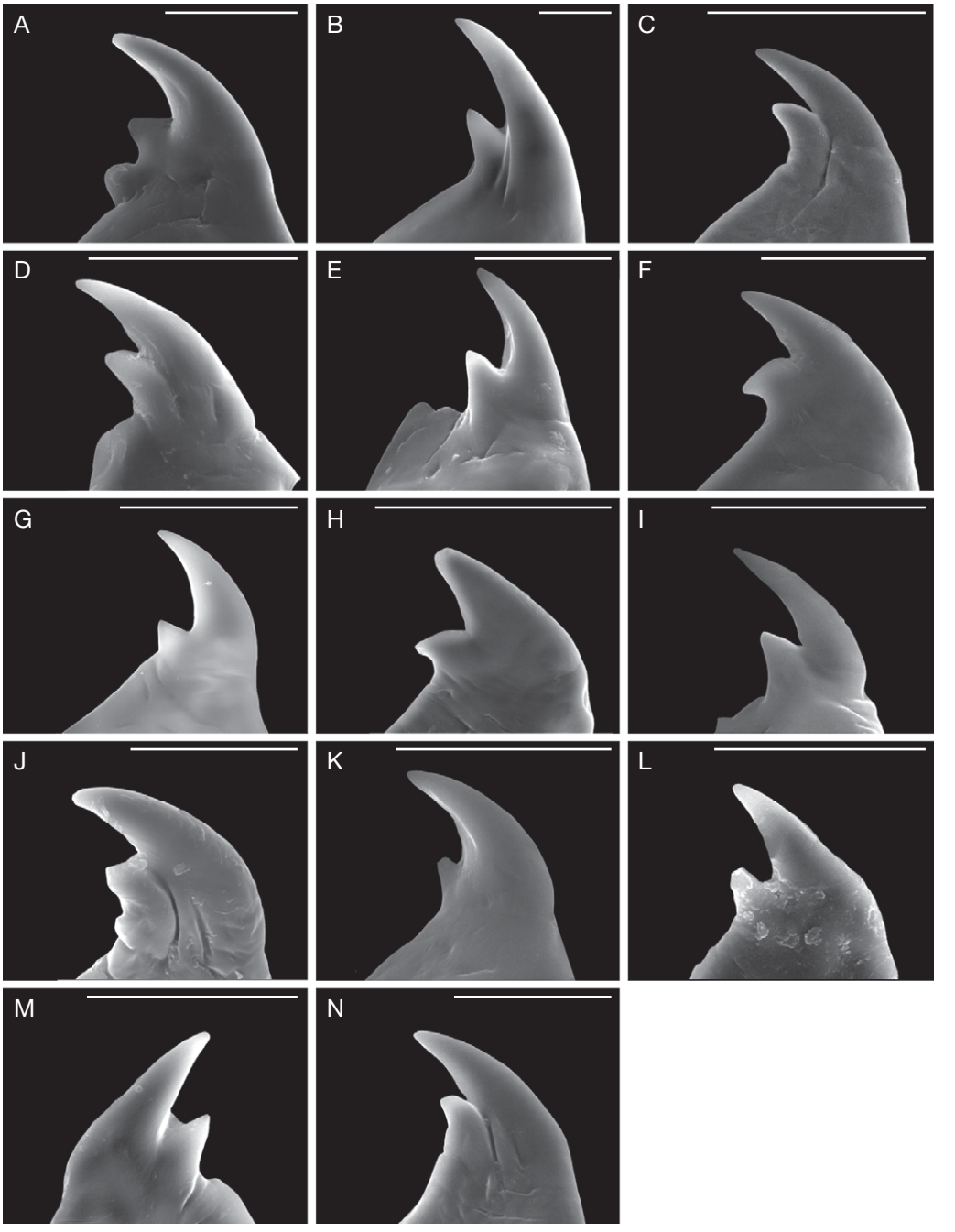

FIG. 13. — Anterior views of the right mandible of terminal-instar eurytomid larvae: **A**, *Eurytoma aspila* (Walker, 1836) ex *Phanacis caulicola*; **B**, *E. brunniventris* Ratzeburg, 1852 ex *Cynips quercus* (A); **C**, *E. cynipsea* Boheman, 1836 ex *Phanacis hypochoeridis*; **D**, *E. infracta* Mayr, 1904; **E**, *E. mayri* Ashmead, 1887; **F**, *E. pediaspisi* Pujade i Villar, 1994; **G**, *E. robusta* Mayr, 1878; **H**, *E. rosae* Nees, 1834 ex *Diplolepis rosae*; **I**, *E. rufipes* Walker, 1832; **J**, *E.* sp. cf. *aspila*; **K**, *E.* sp. cf. *jaceae*; **L**, *E. strigifrons* Thomson, 1876 (right mandible); **M**, *E. strigifrons* (left mandible); **N**, *E. timaspidis* (Mayr, 1904). Scales bars: A, D-G, I-N, 50 µm; B, 20 µm; C, H, 100 µm.

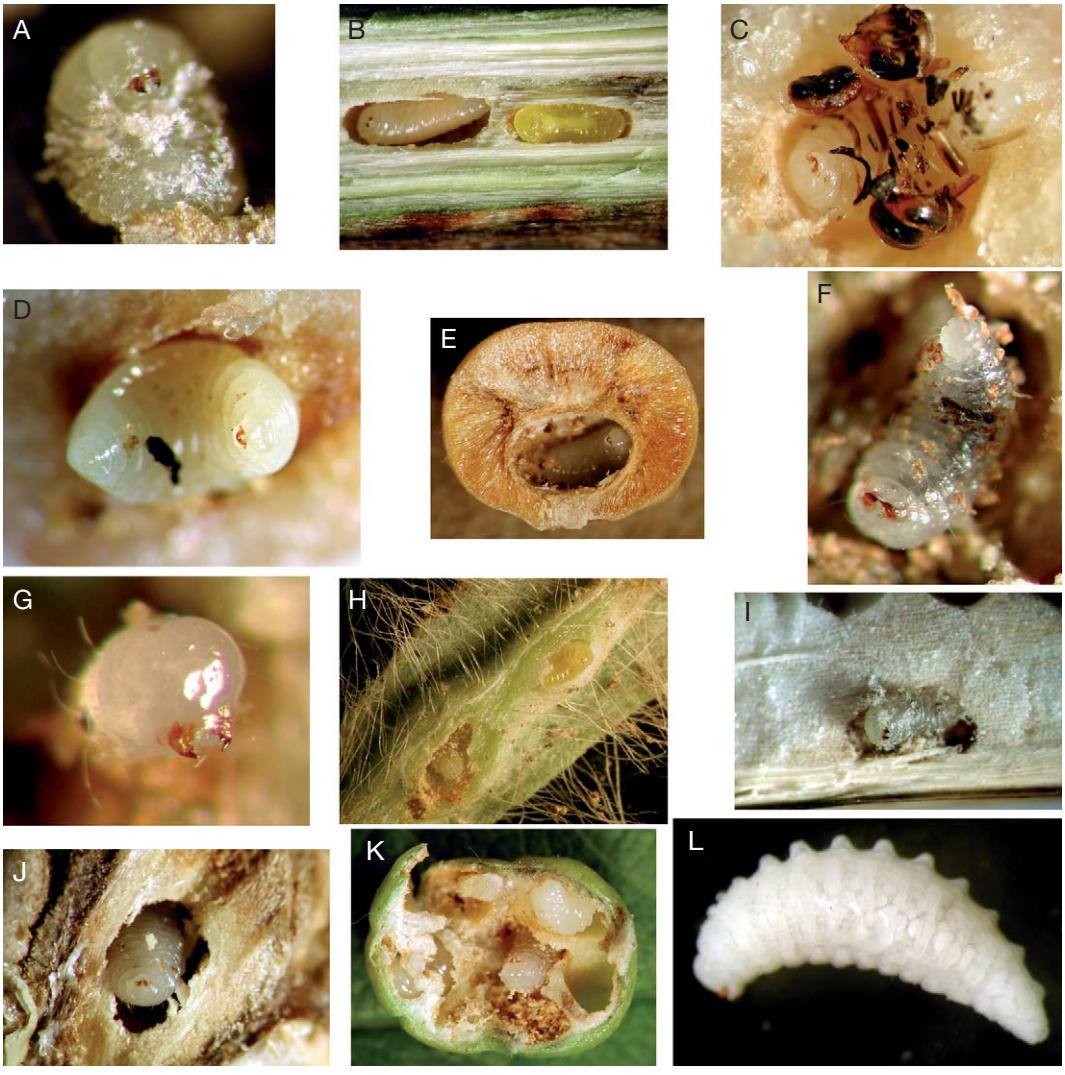

Fig. 14. — **A**, terminal-instar larva of *Eurytoma aspila* (Walker, 1836) ex gall of *Aulacidea tragopogonis*; **B**, larval cells of *Phanacis centaureae* with terminal-instar larvae of *E. aspila*; **C**, cross-section of *Cynips quercus* (A) leaf gall showing terminal-instar larva of *E. brunniventris* Ratzeburg, 1852, with debris of adult host; **D**, ventral view of terminal-instar larva of *E. brunniventris* ex gall *of C. quercus* (A); **E**, cross-section of a gall of *Cynips divisa* (A) showing fully-grown larva of *E. brunniventris*; **F**, terminal-instar larva of *E. brunniventris* ex gall of *Plagiotrochus australis* (S); **G**, anterior view of head of fully-grown larva of *E. brunniventris* ex gall of *P. australis* (S); **H**, larval cells of *Aulacidea pilosellae* with terminal-instar larva of *E. cynipsea* Boheman, 1836; **I**, larval cell on *Silybum marianum* with terminal-instar larva of *E. cynipsea* feeding on gall tissue; **J**, terminal-instar larva of *E. robusta* Mayr, 1878 in cell of *Isocolus leuzeae* gall; **K**, cross-section of *Diplolepis centifoliae* leaf gall showing terminal-instar larva of *E. rosae* Nees, 1834; **L**, lateral view of fully-grown larva of *E. rosae* ex gall of *D. centifoliae*.

Eurytoma infracta Mayr, 1904

Material examined. — Ex *Aylax minor*: **Spain**. Madrid, Rivas Vaciamadrid, 14.V.2003, J. L. Nieves leg (n = 2). Ex *Neaylax verbenacus*: **Spain**. Madrid, Dehesa de Arganda, 1.VI.2003, J. L. Nieves leg (n = 4). — Same locality, 6.VI.2004, J. L. Nieves leg (n = 8, of which 2 specimens MNHN-EY6408).

FIG. 15. — **A**, section of a gall of *Diplolepis mayri* showing a fully-grown larva of *Eurytoma rosae* Nees, 1834; **B**, cross-section of *Xestophanes brevitarsis* (Thomson, 1877) gall showing fully-grown larva of *E. rufipes* Walker, 1832 with host larva; **C**, cross-section of old gall of *Aulacidea subterminalis* Niblett, 1946 showing fully-grown larva of *E.* sp. cf. *aspila*; **D**, detail of mandibles of *E.* sp. cf. *aspila* ex gall of *A. subterminalis*; **E**, lateral view of terminal-instar larva of *E. strigifrons* Thomson, 1876 ex gall of *Isocolus lichtensteini* (Mayr, 1882); **F**, cross-section of fresh gall of *Timaspis phoenixopodos* Mayr, 1882 showing fully-grown larvae of *E. timaspidis* (Mayr, 1904); **G**, larval cell of *T. phoenixopodos* with terminal-instar larvae of *E. timaspidis*.

DESCRIPTION

n = 14; body length 1.67 mm (range 1.3-2.0); body width 0.73 mm (0.7-0.8) (Figs 5D; 7D); body more or less fusiform, ratio L/W = 2; ventral margin of body segments clearly convex; anterodorsal protuberances present from second thoracic segment to the third abdominal and not protruding beyond the dorsal margin of body segments (Fig. 7D).

Head with upper margin of vertex straight; antero-medial setae of the antennal area situated at the same level as the antennae; ratios SA/LAA = 0.38 and SA/DAV = 1.1; antero-medial setae of vertex situated relatively high on the upper face (Fig. 9C); dorsal-labral setae as long as clypeal setae; ventral margin of clypeus indistinct; labrum with slight divisions restricted to its apical part; flaps or lobes not well differentiated; maxillary palps conspicuous (Fig. 11D).

Mandibles with two teeth and exposed in part, with the tip of the first tooth visible (Fig. 11D); first tooth relatively long and slender; ratio between the length at its base and the width 2.38; outer margin of first tooth strongly convex, tip moderately recurved; apex of the second tooth straight, directed upwards in the same direction as the first tooth and more or less acute; inner margin of mandible from the base of second tooth strongly convex (Fig. 13D).

BIOLOGY

This species is a primary oligophagous ectoparasitoid, reared from galls of Aylacini cynipids in

fruits of species of *Salvia* (Lamiaceae) and *Papaver* (Papaveraceae) (Askew *et al*. 2006). It is univoltine; fully-grown larvae usually overwinter and adults emerge in summer when the new host galls are developing.

Remarks

The straight upper margin of the vertex and the strongly convex inner margin of the base of the second mandible tooth allow separation of the larva of this species from the others in this study.

Eurytoma sp. cf. ***jaceae***

Material examined. — Ex *Iraella luteipes*: **Spain**. Madrid, Soto de Oreja, 3.VI.2006, J. L. Nieves leg (n = 2). — Madrid, Valdemorillo, 13.VI.2003, J. L. Nieves (n = 1).

Description

n = 3; Body length 1.5 mm; body width 0.65 mm (range 0.6-0.7) (Figs 6C; 8C); ratio L/W = 2.57; ventral margin of body segments straight; anterodorsal protuberances present from second thoracic segment to the seventh abdominal, protruding beyond the dorsal margin of body segments (Fig. 8C).

Antero-medial setae of the antennal area situated slightly below the antennae; antero-medial setae of vertex situated relatively high on the upper face, much closer to the anterior margin of vertex than to the antennae (Fig. 10D); ratios SA/LAA = 0.66 and SA/DAV = 1.02; dorsal-labral setae longer than clypeal setae; ventral margin of clypeus with a distinct suture; labrum with deep divisions reaching the level of labral setae; lobes clearly differentiated; maxillary palps inconspicuous (Fig. 12E).

Mandibles with two teeth and exposed in part, with the tip of the first tooth visible (Fig. 12E); ratio L/W 1T = 1.67; outer margin of first tooth strongly convex, with the tip moderately recurved; apex of the second tooth straight, directed upwards in the same direction as the first tooth and more or less acute; inner margin of mandible from the base of second tooth more or less straight with the margin not interrupted (Fig. 13K).

Biology

This species is only known as a monophagous primary ectoparasitoid in the stem galls of *Iraella luteipes* (Thomson, 1877) on opium poppy (*Papaver somniferum* L. [Papaveraceae]). It is univoltine and the fully-grown larvae overwinter inside the old galls, with adults emerging in the spring in synchrony with the development of new host galls.

Remarks

The identification of material for this species as *E. jaceae* is doubtful, and it may represent an undescribed species. The adults of this material and typical *E. jaceae* differ in several morphological traits (Askew, pers.comm.).

Eurytoma mayri Ashmead, 1887

Material examined. — Ex *Diastrophus rubi*: **Spain**. Asturias, Ajuyán-Oviedo, 7.IX.2005, L. Parra leg (n = 116, of which 2 specimens MNHN-EY6414).

Description

n = 116; body length 2.03 mm (range 1.0-2.7); body width 0.73 mm (0.5-1.5) (Figs 5E; 7E); body fusiform, slightly broadest in mid-region, tapering slightly anteriorly and posteriorly; ratio L/W = 2; ventral margin of body segments clearly convex; anterodorsal protuberances present from second thoracic segment to the eighth abdominal and clearly protruding beyond the dorsal margin of body segments (Fig. 7E).

Antero-medial setae of the antennal area situated below the antennae; antero-medial setae of vertex situated midway between anterior margin of vertex and the antennae (Fig. 9D); ratios SA/LAA = 0.22 and SA/DAV = 1.33; dorsal-labral setae longer than clypeal setae; ventral margin of clypeus indistinct; labrum with slight divisions restricted to its apical part; two lateral flaps and five poorly differentiated lobes; maxillary palps conspicuous (Fig. 11E).

Mandibles with tip of the first tooth clearly visible (Fig. 11E) with two main teeth, but with the inner margin forming two small projections close to the base of the second tooth, giving an appearance of four teeth; ratio L/W 1T = 2; outer margin of first

tooth strongly convex, tip moderately recurved; apex of the second tooth straight, directed upwards in the same direction as the first tooth and more or less acute (Fig. 13E).

BIOLOGY

The species *Eurytoma mayri* is a primary monophagous ectoparasitoid of *Diastrophus rubi* (Bouché, 1834) on different species of *Rubus* (Rosaceae). Fully-grown larvae usually overwinter and adults emerge in the spring when the new *Diastrophus* galls are developing on the running twigs of *Rubus*.

REMARKS

The larvae of this species are readily separated from larvae of other species associated with cynipid galls by the peculiar shape of their mandibles, with the two small projections near the base of second tooth giving an appearance of four teeth.

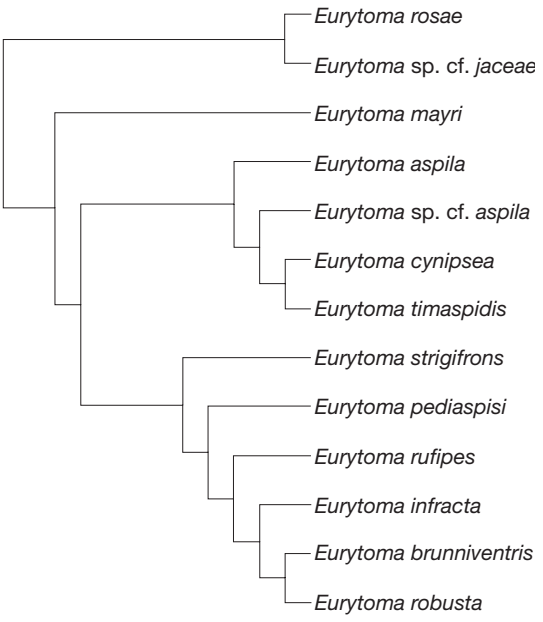

FIG. 16. — Overall similarity phenogram of a UPGMA tree (cluster analysis, unweighted pair group method analysis) of the studied *Eurytoma* larvae.

Eurytoma pediaspisi Pujade i Villar, 1994

MATERIAL EXAMINED. — Ex *Pediaspis aceris* (S): **Spain**. Tarragona, Colldejou, 14.VIII.2003, J. L. Nieves leg (n = 2).

DESCRIPTION

n = 2; body length 1.37 mm (range 1.1-1.7); body width 0.63 mm (0.6-0.67) (Figs 5F; 7F); body relatively short and wide; ratio L/W = 1.75; ventral margin of body segments convex; anterodorsal protuberances present from second thoracic segment to the third abdominal, not protruding beyond the dorsal margin of body segments (Fig. 7F). Antero-medial setae of the antennal area situated below the antennae, antero-medial setae of vertex situated more or less midway between anterior margin of vertex and the antennae (Fig. 9E); ratios SA/LAA = 0.33 and SA/DAV = 1.07; dorsal-labral setae longer than clypeal setae; ventral margin of clypeus with a distinct suture; labrum with slight divisions limited to apical part of labrum; flaps or lobes poorly differentiated; maxillary palps conspicuous (Fig. 11F).

Mandibles with two teeth; exposed in part, the tip of the first tooth visible (Fig. 11F); ratio L/W 1T = 1.82; outer margin of first tooth strongly convex, with the tip moderately recurved; apex of the second tooth strongly recurved inwards and more or less acute; inner margin of mandible from the base of second tooth more or less straight, with the margin not interrupted (Fig. 13F).

BIOLOGY

A primary monophagous ectoparasitoid in sexual generation galls of *Pediaspis aceris* (Gmelin, 1790) on different species of *Acer* (Sapindaceae).

REMARKS

Larvae of *E. pediaspisi* are similar to those of *E. mayri* in head setation patterns. However the shape of second mandibular tooth of *E. pediaspisi* allows an easy separation of the two species. In this latter feature the larva of *E. pediaspisi* resembles the larva of *E. rosae*, but in the latter, the second tooth is not as strongly curved inwards as in the *E. pediaspisi* larva (Fig. 13F, H).

Eurytoma robusta Mayr, 1878

MATERIAL EXAMINED. — Ex *Isocolus scabiosae* form *rogenhoferi*: **Spain**. Guadalajara, Pozo de Guadalajara, 3.X.2004, J. L. Nieves leg (n = 1).

DESCRIPTION

n = 1; body length 2 mm; body width 1.2 mm (Figs 5G; 7G); body short and wide; ratio L/W = 1.38; ventral margin of body segments convex; anterodorsal protuberances present from second thoracic segment to the seventh abdominal and not protruding beyond the dorsal margin of body segments (Fig. 7G).

Antero-medial setae of the antennal area situated slightly below the antennae; antero-medial setae of vertex relatively high on the upper face, closer to the anterior margin of vertex than to the antennae (Fig. 9F); ratios SA/LAA = 0.29 and SA/DAV = 1.18; dorsal-labral setae as long as clypeal setae; ventral margin of clypeus indistinct; labrum with slight divisions limited to apical part of labrum; the five medial lobes are not well differentiated; maxillary palps conspicuous (Fig. 12A).

Mandibles with two teeth, exposed in part, with the tip of the first tooth visible (Fig. 12A); ratio L/W 1T = 2.08; outer margin of first tooth strongly convex; its tip moderately recurved; apex of the second tooth straight, directed upwards in the same direction as the first tooth, and more or less acute; inner margin of mandible, from the base of second tooth, more or less straight and not interrupted (Fig. 13G).

BIOLOGY

This species has been recorded as a common ectoparasitoid of some galling tephritid fly species in heads of *Centaurea* and stems of *Cirsium* (Asteraceae). It is not clear whether it is a parasitoid of the cynipid gall species *Isocolus scabiosae* (Giraud, 1859) form *rogenhoferi* Wachtl, 1880 as well, which occupies similar habitats. We have reared this species from heads of *Centaurea scabiosa* L. (Fig. 14J) containing both cynipid and tephritid galls. Varley (1937) describes *E. robusta* as being partially phytophagous after consuming the host larva. Johannesen & Seitz (2003) also studied larval distributions of *Eurytoma robusta* in galls of the tephritid gall fly *Urophora cardui* Linnaeus, 1758.

REMARKS

Eurytoma robusta is one of the few eurytomid species associated with cynipid communities whose larva has already been thoroughly described, by Varley (1937). Our diagnosis provides additional data.

Eurytoma rosae Nees, 1834

MATERIAL EXAMINED. — Ex *Diplolepis nervosa/D. eglanteriae*: **Spain**. Guadalajara, Hayedo de Tejera Negra, 24.VII.2005, J. L. Nieves leg (n = 3). — Madrid, El Escorial, 13.XI.2002, J. L. Nieves leg (n = 3).
Ex *D. mayri*: **Spain**. Guadalajara, Retiendas, 24.I.2004, J. L. Nieves leg (n = 22, of which 2 specimens MNHN-EY6416). — Madrid, Cotos de Monterrey, 24.VI.2003, J. F. Gómez leg (n = 31). — Same locality, 9.VIII.2002, J. L. Nieves leg (n = 3). — Soria, Cabrejas del Pinar, 14-15.II.04, J. F. Gómez leg (n = 5). — Soria, Embalse de la Cuerda del Pozo, 15.II.2004, J. F. Gómez leg (n = 4).
Ex *D. rosae*: **Spain**. Guadalajara, Retiendas, 24.I.2004, J. L. Nieves leg (n = 1). — Madrid, El Escorial-La Herrería, 4.II.2004, J. F. Gómez leg (n = 2). — Soria, Cabrejas del Pinar, 14-15.II.2004, J. F. Gómez leg (n = 1). — León, San Esteban, 16.VII.2005, J. F. Gómez leg (n = 3).

DESCRIPTION

n = 78; body length 2 mm (range 1.3-3.5); body width 0.81 mm (0.5-1.33) (Figs 5H; 7H; 14L); body fusiform, elongated, slightly tapering anteriorly and a little more posteriorly; ratio L/W = 2.92; ventral margin of body segments convex; anterodorsal protuberances present from second thoracic segment to the tenth abdominal, protruding beyond the dorsal margin of body segments (Fig. 7H).

Antero-medial setae of the antennal area situated clearly below the antennae; ratio SA/LAA = 0.67; separation of antero-medial setae of vertex equal to the distance between antennae and with these setae situated relatively high on the upper face, closer to the anterior margin of vertex than to the antennae (Fig. 10A); dorsal-labral setae longer than clypeal setae; ventral margin of clypeus with a distinct suture; labrum with a pair of short lateral flaps and a medial part with deep divisions defining five ir-

regular but clearly differentiated lobes; maxillary palps inconspicuous (Fig. 12B).

Mandibles with two teeth; apical tooth completely visible (Fig. 12B); ratio L/W 1T = 1.36; outer margin of first tooth strongly convex, with the tip moderately recurved; apex of the second tooth moderately recurved inwards and more or less acute; inner margin of mandible from the base of second tooth more or less straight, with the margin not interrupted (Fig. 13H).

Biology

The larva of this species preferentially attacks the cells of the inquiline species *Periclistus brandtii* (Ratzeburg, 1831) and *P. caninae* (Hartig, 1840), and our unpublished molecular data confirm that the same species also attacks inquilines in oak cynipid galls. According to Nordlander (1973) and Redfern & Askew (1992) the larva of *E. rosae* feeds on more than one *Periclistus* larva by biting its way from one chamber to another, and thus in a strict sense, the larva should be referred as a predator rather than a parasitoid. In Spain, we found larvae of *E. rosae* to be predominantly associated with *D. mayri* galls containing cells of *P. brandtii* and with *D. nervosa* galls occupied by *P. caninae* (Fig. 14K). In both cases the mature parasitoid larva fed on the lining of the host larval chamber, as shown by the presence of chips of plant tissue adhering to the larval body of *E. rosae* and the deformation of the original inquiline larval cell (Figs 14K; 15A). Lotfalizadeh *et al.* (2007b) have recently carried out a review of the species based on adult morphology and molecular data describing a new species, *E. caninae* Lotfalizadeh, Delvare & Rasplus, 2007 previously overlooked with *E. rosae*. Both species are reared from galls of *Diplolepis* in Palaearctic area although in our study *E. caninae* have not been considered.

Remarks

The moderately inwards recurved shape of the second mandible tooth readily separates the larva of *E. rosae* from the larva of *E. brunniventris*, two species that, according to Claridge & Askew (1960), are otherwise undistinguishable on the basis of adult morphology.

Eurytoma rufipes Walker, 1832

Material examined. — Ex *Xestophanes brevitarsis*: **Spain**. La Coruña, Arins, 17.VII.2003, J. L. Nieves leg (n = 2). Ex *X. potentillae*: **Spain**. Madrid, Cotos de Monterrey, 24.VI.2004, J. F. Gómez leg (n = 16, of which 1 specimen MNHN-EY6413). — Tarragona, Colldejou, 14.VIII.2003, J. L. Nieves leg (n = 6).

Description

n = 24, body length 1.7 mm (range 1.2-2.4;); body width 0.9 mm (0.3-1.3) (Figs 6A; 8A); body barrel-shaped, tapering posteriorly, widest at segments 1-3; ratio L/W = 1.74; ventral margin of body segments slightly convex; anterodorsal protuberances present from second thoracic segment to the eighth abdominal and not protruding beyond the dorsal margin of body segments (Fig. 8A).

Antero-medial setae of the antennal area situated slightly below the antennae; antero-medial setae of vertex situated more or less midway between anterior margin of vertex and the antennae (Fig. 10B); ratios SA/LAA = 0.2 and SA/DAV = 1.4; dorsal-labral setae as long as clypeal setae; ventral margin of clypeus with a distinct suture; labrum with slight divisions limited to apical part of labrum, showing a pair of lateral flaps and five poorly differentiated lobes; maxillary palps conspicuous (Fig. 12C).

Mandibles with two teeth, exposed in part, with the tip of the first tooth visible (Fig. 12C); ratio L/W 1T = 1.93; outer margin of first tooth strongly convex, tip moderately recurved; apex of the second tooth straight, directed upwards in the same direction as the first tooth, and more or less acute; inner margin of mandible, from the base of second tooth, forming a small projection relatively separated from the base of the second tooth (Fig. 13I).

Biology

This is an ectoparasitoid associated with galls of *Xestophanes brevitarsis* (Thomson, 1877) and *X. potentillae* (Retzius, 1783), both developing in runners on different species of *Potentilla* (Rosaceae). Univoltine and oligophagous, attacking the gall-inducing cynipid larva (Fig. 15B). Fully-grown larvae overwinter inside the gall and the adults emerge in synchrony with the development of new *Xestophanes* galls.

Remarks

The larvae of *E. rufipes* is similar to the larvae of *E. mayri* and *E. pediaspisi* in terms of the position on the head of the antero-medial setae of vertex, and by the presence of only slight apical divisions on the medial part of the labrum. They differ from other larvae in having mandibles with a small projection on the inner margin at the base of the second tooth.

Eurytoma strigifrons Thomson, 1876

Material examined. — Ex *Isocolus lichtensteini*: **Spain**. Madrid, Arganda, 6.XI.2002, J. L. Nieves leg (n = 2). — Madrid, La Marañosa, 3.XI.2004, J. L. Nieves leg (n = 3, of which 1 specimen MNHN-EY).
Ex *Isocolus leuzeae*: **Spain**. Madrid, Valgallego, 4.VIII.2002, J. L. Nieves leg (n = 1).

Description

n = 6; body length 1.8 mm (range 1.7-2.0); body width 1.1 mm (1.0-1.3) (Figs 6D; 8D); body barrel-shaped, short and wide, slightly tapering anteriorly and posteriorly; ratio L/W = 1.47; ventral margin of body segments slightly convex; anterodorsal protuberances present from second thoracic segment to the eighth abdominal and not protruding beyond the dorsal margin of body segments (Fig. 8D).

Antero-medial setae of antennal area slightly above the antennae; antero-medial setae of vertex situated relatively high on the upper face (Fig. 10E); ratios SA/LAA = 0.5 and SA/DAV = 0.9; dorsal-labral setae longer than clypeal setae; ventral margin of clypeus with a distinct suture; labrum with slight divisions limited to apical part, with undifferentiated lobes; labium and maxillary palps usually not differentiated (Fig. 12F).

Mandibles asymmetric, exposed in part, tip of the first tooth visible (Fig. 12F); right mandible with two teeth (Fig. 13L); left mandible with three teeth (Fig. 13M); first tooth of both mandibles long and slender; ratio L/W 1T = 2.25; outer margin of first tooth almost straight; tip slightly recurved; apex of the second tooth straight, directed upwards in the same direction as the first tooth, and more or less acute; inner margin of mandible, from the base of second tooth, forming a small projection close to the base of the second tooth (Fig. 13L, M).

Biology

Eurytoma strigifrons is an oligophagous ectoparasitoid commonly reared only from galls induced by several species of the tribe Aylacini on herbs, more commonly from galls of *Isocolus* species on Asteraceae (Askew *et al*. 2006) (Fig. 15E). Claridge (1961a) recorded the species as a specific parasitoid of *I. rogenhoferi*, a species that induces galls in achenes of *Centaurea*. However we have reared it in Spain more frequently from conspicuous stem galls of *I. lichtensteini* on *Centaurea aspera* and *C. melitensis* (Fig. 15E).

Remarks

Similar in shape to the larvae of *E. robusta*, larvae of *E. strigifrons* are readily separated from other eurytomid larvae in this study by having an almost straight, or only slightly recurved first mandible tooth.

Eurytoma timaspidis (Mayr, 1904)

Material examined. — Ex *Timaspis phoenixopodos*: **Spain**. Madrid, Dehesa de Arganda, 29.VI.2005, J. L. Nieves leg (n = 24, of which 1 specimen MNHN-EY6409).

Description

n = 24; body length 2 mm (range 1.8-2.7); body width 1.05 mm (0.9-1.2) (Figs 6E; 8E; 15G); body more or less fusiform anteriorly and posteriorly; ratio L/W = 1.84; ventral margin of body segments clearly convex; anterodorsal protuberances present from second thoracic segment to the seventh abdominal, and protruding beyond the dorsal margin of body segments (Fig. 8E).

Antero-medial setae of antennal area situated at the same level as antennae; antero-medial setae of vertex situated relatively high on the upper face (Fig. 10F); ratios SA/LAA = 0.57 and SA/DAV = 0.65; dorsal-labral setae longer than clypeal setae; ventral margin of clypeus indistinct; labrum with deep divisions almost reaching the level of labral setae; a pair of lateral flaps and five relatively well-differentiated irregular lobes; maxillary palps conspicuous (Fig. 12G).

Mandibles with two teeth; tip of the first tooth completely visible (Fig. 12G); ratio L/W 1T =

1.77; outer margin of first tooth strongly convex, tip moderately recurved; apex of the second tooth straight, directed upwards in the same direction as the first tooth and rounded; inner margin of mandible, from the base of second tooth, more or less straight with margin not interrupted (Fig. 13N).

BIOLOGY

The species *Eurytoma timaspidis* is a polyphagous primary ectoparasitoid associated with several cynipid galls on herbs. It has been recorded from galls of *Isocolus*, *Phanacis* and *Timaspidis* species (Askew *et al*. 2006). The specimens in this study were reared from galls of *Timaspis phoenixopodos* Mayr, 1882 on stems of *Lactuca viminea* (L.) J. Presl & C. Presl (Asteraceae). Fully-grown larvae of *E. timaspidis* feed actively on gall tissue and enlarge the original host larval cell (Fig. 15F). Fully-grown larvae overwinter inside the gall and the adults emerge in synchrony with the appearance of new *Timaspis* galls.

REMARKS

Larvae of *E. timaspidis* are similar to those of *E. aspila* and *E. cynipsea* in having left mandibles with three teeth. *Eurytoma timaspidis* is easily separated from the others by its clearly two-toothed right mandibles; *Eurytoma timaspidis* differs from *E. cynipsea* mainly by having a relatively shorter second mandible tooth.

DISCUSSION

TERMINAL-INSTAR LARVA MORPHOLOGY AND *EURYTOMA* TAXONOMY

Despite prior work about eurytomid larval morphology (Roskam 1982; Henneicke *et al.* 1992; Dawah & Rothfritz 1996), the phylogenetic value of final-instar larval characters has yet to be examined in depth, although Roskam (1982) has suggested their value, especially where there are no good adult diagnostic characters. We now discuss the main morphological traits of *Eurytoma* larvae and their potential value in the taxonomy of this group.

Larval shape and chaetotaxy

Previous works (Roskam 1982; Henneicke *et al.* 1992) have not considered larval shape as a potentially diagnostic character. *Eurytoma* larvae are generally ventrally curved, fusiform or barrel-shaped, and show some systematic variation. For example, *Eurytoma rufipes* and *E.* sp. cf. *aspila* are widest in the thoracic segments (1-3), while others *Eurytoma* have a more elongate, cylindrical body with parallel lateral margins. However, we found larval shape to vary intraspecifically according to host and regard larval shape to be of limited taxonomic value.

Nevertheless, as in other Chalcidoid families, chaetotactic patterns have clear taxonomic value. More generally among the ectoparasitoid outgroups, *Eupelmus* and *Torymus* have abundant external setae, while *Ormyrus* shows reduced setae, but still has conspicuous setae on head and thorax. This latter pattern is similar to that seen in *Eurytoma* larvae, which characteristically show three rows of setae (dorsal, lateral and ventral) on at least the thoracic segments, sometimes extending to the rest of the body although with relatively shorter setae.

Head, mouthparts and mandibles

Previous studies have emphasised the fact that most larval characters useful in the taxonomy and phylogeny reconstruction of parasitic Hymenoptera are associated with the mouthparts (Vance & Smith 1933; Short 1952; Cutler 1955; Roskam 1982; Nieves-Aldrey *et al.* 2005). The eurytomid head has been reported as usually slightly sclerotized, hemispherical and narrower than the first thoracic segment (Henneicke *et al.* 1992), although we found in the studied species that the head is usually slightly trapezoid (between 1.1 and 1.3 times as broad as high).

We recognize the basic setal pattern described by Henneicke *et al.* (1992) for *Eurytoma*, but have renamed some of them based on our own wider analysis of the larval morphology of chalcidoidea parasitoids of gall wasps, to better reflect their positions in these taxa. Specifically, we have renamed Henneicke's superior and inferior frontal setae as the antero-medial setae of vertex and antennal areas respectively; labral setae have been renamed as dorso-labral setae. Variation in the position and

relative length of setae is taxonomically informative. In most of the studied species, the antero-medial setae of vertex are clearly situated on the upper face closer to the vertex margin. However, a group of species (*Eurytoma mayri*, *E. pediaspisi* and *E. rufipes*) show an alternate pattern, with these setae located midway between the anterior margin of the vertex and antennae. Most species have the antero-medial setae of the antennal area situated at more or less the same level as the antennae, while a group of species (*E. mayri*, *E. pediaspisi* and *E. rosae*) have these setae clearly below the antennae. These latter three species are all associated exclusively with galls on Rosaceae or Sapindaceae, and share further morphological features, described below.

Other considered characters are the relative length of antero-medial setae of vertex and dorsal-labral setae. *Eurytoma* study species have relatively long antero-medial setae of vertex. Dorsal labral setae divide the studied species into two groups. In almost half the group of species (*E. mayri*, *E. pediaspisi* and *E. rosae* associated with Rosaceae and Sapindaceae, together with *E.* sp. cf. *jaceae*, *E. strigifrons* and *E. timaspidis*), the labral setae are longer than the clypeal setae, while in the remainder the opposite is true.

The mouthparts of *Eurytoma* larvae are usually well-developed and provide most of the characters of potential taxonomic or phylogenetic value. The clypeus and labrum are quite variable across species. *Eurytoma pediaspisi*, *E. rosae* and *E. rufipes* have a distinct ventral margin of clypeus, bearing a suture which, although visible, is not an easy discernible character. The subdivision of the medial part of the labrum is a taxonomically very important character. However *Eurytoma* larvae usually lack such deep divisions of the labrum, limited to the apical part of the central part, giving a general impression of five less well-differentiated lobes. The maxillary palps are conspicuous in *Eurytoma* studied species, excepting again the case of *E. rosae* and *Eurytoma* sp. cf. *jaceae*.

The mandibles of eurytomid larvae have important taxonomic and phylogenetic characters. They vary in their exposure, but are always visible externally at least in part. All species except *E. aspila* and *E. mayri* have mandibles with two teeth, one being bigger than the other. The mandibles are symmetrical in all species except *Eurytoma strigifrons*, in which the left mandible has three teeth and the right has two. Such asymmetry is less marked in these eurytomids than it is in other parasitic Hymenoptera (Nieves-Aldrey *et al.* 2005). The remaining differences in mandible traits between species were found in the shape, relative size and direction of both teeth, outer margin of first tooth and the shape of inner margin of mandible from the base of second tooth. The mandibular morphology of eurytomid larvae may be related to their biology. Most eurytomid species are in part phytophagous, and bidentate mandibles could be an adaptation to such a diet. Mandibles with two or more large teeth are found in gall-inducing cynipoids (Nieves-Aldrey *et al.* 2005) and are used to crush and pierce the plant cells that make up the nutritive tissues lining the larval chamber (Stone *et al.* 2002).

Relationships between *Eurytoma* and other Chalcidoidea parasitoids of gall wasps

Monophyly of Eurytomidae

Recently, Lotfalizadeh *et al.* (2007a) proposed monophyly of the subfamily Eurytominae based on morphological characters of the adults, and proposing the Rileyinae (= Buresiinae) as a sister group. Although the dataset is very limited, *Eurytoma* studied species represent the core diversity of the subfamily, and we identified the following putative synapomorphies for *Eurytoma* species parasitoids of cynipid wasps in Europe: larvae with one pair of clypeal setae situated above the level of ventral margin of clypeus; labrum divided into two lateral lobes and one medial lobe, the latter subdivided into five more or less differentiated lobes, and mandibles usually exposed at least in part with two (rarely three) teeth.

The genus *Eurytoma*. With about 700 described species, *Eurytoma* is by far the largest eurytomid genus. Unsurprisingly given its size, previous taxonomic studies have failed to find clear distinguishing morphological features for the entire genus. *Eurytoma* is one of the more taxonomically difficult genera of Chalcidoidea, and most species have very

similar adult morphology. For that reason, *Eurytoma* groups many species that cannot be assigned to other genera (Bouček 1988). Recent molecular and morphological phylogenetic analyses with different limited samples of species have produced contradictory results, supporting either monophyly (Ghajarieh *et al.* 2006) or para/polyphyly (Chen *et al.* 2004; Lotfalizadeh *et al.* 2007a) for *Eurytoma*. Zerova (1995) used morphological and biological traits to divide Palaearctic *Eurytoma* species into 14 species groups. Our study included representatives of three groups, the *robusta*, *rosae* and *cynipsea*. We could not detect clear synapomorphies shared by the larvae of all *Eurytoma* species studied. However, they still share some common diagnostic features, including head chaetotaxy, shape of labrum and relative size and shape of the mandibles. Our results furthermore suggest that the larvae possess traits that are useful in distinguishing species.

The "*robusta*" species-group. This species group includes *E. infracta*, *E. strigifrons* and *E. robusta* (Zerova & Seryogina 2006). The phylogenetic relationships between these species and their placement within *Eurytoma* are unresolved.

The "*rosae*" species-group. This species group includes *E. rosae* and *E. brunniventris*, two of the commonest parasitoids associated with gall wasps, together with more than 30 other Palaearctic species (Zerova 1995). Claridge & Askew (1960) regard this group as a complex of sibling species that are indistinguishable by adult morphology but separable on the basis of egg morphology. A recent preliminary molecular analysis (Ács *et al.* 2002) supported differentiation between *E. brunniventris* and *E. rosae*. We have found that the larvae of *E. rosae* and *E. brunniventris* show additional clear morphological differences, especially in the mandibular structure.

Biological traits

The Eurytomidae comprise one of the richest elements of the parasitoids associated with cynipid galls, rivalled only by the Pteromalidae and Torymidae (Askew 1984; Askew *et al.* 2006). The Eurytomidae are most diverse in galls of the cynipid tribe Aylacini, which develop on herbaceous plants of the families Asteraceae, Lamiaceae, Papaveraceae and Rosaceae. 28 species have been recorded until now (Askew *et al.* 2006), accounting for life histories ranging from monophagous to oligophagous and polyphagous. In contrast, the Eurytomidae are less species-rich in oak gall wasp parasitoid communities, with not more than 10 species recognised in Europe. However at least one *Eurytoma* species (*E. brunniventris*) is relatively common and widespread in oak gall parasitoid communities (Askew 1961, 1984; Zerova 1995; Schönrogge *et al.* 1995, 1996a, b; Aebi *et al.* 2006). Our preliminary DNA sequence data strongly suggest that specimens currently attributed to *Eurytoma brunniventris* in Europe represent a complex of at least five morphologically very similar species.

The *Eurytoma* species associated with Aylacini herb galls are predominantly found on plants in the family Asteraceae, resulting from the abundance of gall wasps belonging the genera *Isocolus*, *Phanacis* and *Timaspis*, on these host plants. Our data suggest a close relationship between a group of *Eurytoma* species of the *cynipsea* species-group that are associated with cynipid galls on Asteraceae, suggesting the possibility of host-plant shifts by sibling *Eurytoma* species. The remaining *Eurytoma* species included in our analysis attack cynipid galls on Lamiaceae, Asteraceae, Rosaceae, Sapindaceae and Fagaceae, but it is premature to speculate on patterns in their radiation across host cynipids and host plants.

Concluding remarks

Our results show that, as reported previously (Roskam 1982; Henneicke *et al.* 1992), eurytomid larvae offer a surprisingly rich source of external morphological characters. These characters can be used in the future to discriminate among species that are hardly discernible on the basis of adult morphology, and should be of value in food-web studies of cynipid gall communities.

A wide-ranging revision of eurytomid taxonomy and phylogeny is required, and larval characters are of considerable potential value in this work. More generally, analysis of larval morphology may be of significant value in the taxonomy and phylogeny of the Chalcidoidea.

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APPENDIX 1

Characters of *Eurytoma* larvae used for systematic study.

Characters are listed by body region, for the body, head and under lip complex, which for the latter is subdivided between labrum, maxillae and mandibles.

Larval body

1) Segments of the larval body: (0) widest approximately around the middle giving the larva a fusiform appearance (Fig. 5A); (1) widest at body segments 1-3 (Fig. 6B).
2) Relation between body length and body width in ventral view (measured at the 3rd abdominal segment): (0) body relatively long and narrow; 2.3-2.9 times as long as wide (Fig. 5A); (1) body relatively short and wide; 1.3-2.2 times as long as wide (Fig. 5F).
3) Shape of ventral margin of body segments 4-8 (lateral view): (0) straight or slightly convex (Fig. 8A); (1) clearly convex (Fig. 8B).
4) Anterodorsal protuberances (lateral view): (0) present on at least one segment, not protruding beyond the dorsal margin of body (Fig. 7D); (1) present on at least one segment, clearly protruding beyond the dorsal margin of body (Fig. 7H).

Head

5) Upper margin of vertex: (0) slightly concave (Fig. 10A) (1) straight (Fig. 9C).
6) Position of antero-medial setae of the antennal area: (0) at the same level or slightly either above or below the antennae (Fig. 3); (1) clearly below the antennae (Fig. 9E).
7) Ratio between length of antero-medial setae of the antennal area and separation of antennae: (0) intermediate length, 0.2-0.5 distance between antennae (Fig. 9A); (1) long, 0.5 < the distance between antennae (Fig. 10A).
8) Relative distance between the antero-medial setae of vertex: (0) shorter than distance between antennae; ratio 0.33-0.65 (Fig. 9A); (1) about as long as distance between antennae; ratio 0.89-1.18 (Fig. 9B); (2) longer than distance between antennae; ratio 1.33-1.46 (Fig. 9D).
9) Relative position of antero-medial setae of vertex: (0) situated relatively high on the upper face; much closer to the anterior margin of vertex than to the antennae (Fig. 3); (1) situated more or less midway between anterior margin of vertex and the antennae (Fig. 9E).
10) Length of the dorsal-labral setae: (0) as long as clypeal setae (Fig. 11A); (1) longer than clypeal setae (Fig. 11F).
11) Ventral margin of clypeus: (0) distinct (with a distinct suture) (Fig. 11F); (1) indistinct, the suture is not discernible (Fig. 11A).

Under lip complex

Labrum

12) Divisions of medial part of the labrum: (0) slight, divisions usually limited to apical part of labrum; five poorly differentiated lobes (Fig. 12A); (1) deep, almost reaching the level of labral setae; five clearly differentiated lobes (Fig. 12B).

Maxillae

13) Maxillary palps: (0) absent or inconspicuous (Fig. 12B); (1) conspicuous (Fig. 11C).

Mandibles

14) Mandible: (0) exposed in part, at least the tip being visible (Fig. 11B); (1) apical tooth almost completely visible (Fig. 11A).
15) Number of teeth on right mandible: (0) two (Fig. 13B); (1) three or four (Fig. 13A).
16) Number of teeth on left mandible: (0) two (1) three or four (Fig. 13M).
17) Shape of the first or only tooth: (0) relatively short and wide, ratio between the length at its base and the width = 1.36 (Fig. 13H); (1) intermediate shape, ratio between the length at its base and the width = 1.59-2.08 (Fig. 13E); (2) long and slender, ratio between the length at its base and the width = 2.19-2.59 (Fig. 13D).
18) Shape of tip of first tooth: (0) outer margin of first tooth strongly convex; tip moderately or strongly recurved (Fig. 13G); (1) outer margin of first tooth almost straight or slightly convex; tip slightly or not recurved (Fig. 13L).
19) Shape of apex of the second tooth: (0) more or less acute (Fig. 13B); (1) blunt or rounded (Fig. 13N).

20) Direction of the apex of the second tooth: (0) straight, directed upwards in the same direction as the first tooth (Fig. 13C); (1) moderately recurved inwards (Fig. 13H); (2) strongly recurved, inwards (Fig. 13F).

21) Inner margin of mandible from the base of second tooth (anterior view): (0) more or less straight, inner margin not interrupted (Fig. 13B); (1) second tooth broader at its base such that the inner margin first slopes abruptly downwards and then continues straight (Fig. 13C); (2) inner margin forming a small projection close to the base of the second tooth; (3) inner margin forming a small projection relatively distant from the base of the second tooth (Fig. 13M); (4) inner margin forming two small projections close to the base of the second tooth; the mandible appearing to have four teeth (Fig. 13E); (5) inner margin strongly convex (Fig. 13D).

APPENDIX 2

Character states of *Eurytoma* larvae used for systematic study.

Species	Characters		
	1	8	15
Eurytoma aspila (Walker, 1836)	0011000	0001111	1110-0-
Eurytoma brunniventris Ratzeburg, 1852	0111000	1001010	0010000
Eurytoma cynipsea Boheman, 1836	011100-	0001111	00-0-0-1
Eurytoma infracta Mayr, 1904	0110100	1001010	0020005
Eurytoma mayri Ashmead, 1887	0111010	2111010	1110004
Eurytoma pediaspisi Pujade i Villar, 1994	0110010	1110010	0010020
Eurytoma robusta Mayr, 1878	0110000	1001010	0010000
Eurytoma rosae Nees, 1834	0011011	1010102	0000010
Eurytoma rufipes Walker, 1832	1100000	2100010	0010003
Eurytoma sp. cf. *aspila*	1111001	0001010	0010000
Eurytoma sp. cf. *jaceae*	0001001	1010100	0010000
Eurytoma strigifrons Thomson, 1876	0110000	10100-0	0121002
Eurytoma timaspidis (Mayr, 1904)	0111001	0011111	0010100