Comparative morphology of terminal-instar larvae of Cynipoidea: phylogenetic implications

JOSÉ LUIS NIEVES-ALDREY, HEGE VÅRDAL & FREDRIK RONQUIST

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We describe the external morphology of the terminal-instar larvae of 30 species of Cynipoidea (Hymenoptera), with special reference to the head capsule and mouthparts. Twenty-five of the species belong to the Cynipidae and are gall inducers or phytophagous inquilines (guests) in galls, while five represent different insect-parasitic lineages of the Cynipoidea. Although we find only limited variation in body shape, the head sclerites and mandibles offer many characters of potential phylogenetic value. For instance, the mandibles of the parasitoids have one large pointed tooth, with several smaller dents along the inner margin in core figitids, whereas the phytophagous gall inducers and inquilines have mandibles with two or three blunt teeth of subequal size. The mandibles of inquiline larvae are unique in being covered by vertical striations and in having a dominating, broad second tooth. We summarize the qualitative variation among the studied terminal-instar larvae in terms of 33 morphological characters and one life-history trait and examine the phylogenetic implications of these data by running parsimony analyses under uniform character weights and under implied weights (Goloboff weights). The analysis under uniform weights is poorly resolved but the relationships suggested by the implied-weights analysis are largely congruent with previous analyses of adult morphology and molecular data. The larval data support inclusion of the genus *Liposthenes* in the *Neaylax–Isocolus* clade, in agreement with the molecular data but in weak conflict with adult morphology. However, the larval data agree with adult morphology and conflict with the molecular data in supporting monophyly of the inquilines.

José Luis Nieves-Aldrey, Departamento de Biodiversidad, Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006 Madrid, Spain. E-mail: aldrey@mncn.csic.es

Hege Vårdal & Fredrik Ronquist, Department of Systematic Zoology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, SE-752 36 Uppsala, Sweden. E-mail: hege.vardal@ebc.uu.se, fredrik.ronquist@ebc.uu.se

Fredrik Ronquist, Florida State University, Department of Biological Science, Tallahassee, FL 32306, USA. E-mail: ronquist@csit.fsu.edu

Introduction

The third largest superfamily of parasitic Hymenoptera, Cynipoidea, includes species exhibiting a wide range of life modes, from parasitoids living inside larvae of various insect orders to phytophagous gall inducers (Ronquist 1999). The larvae of the parasitoid families Austrocynipidae, Ibaliidae, Liopteridae, and Figitidae develop inside embryos or larvae of other endopterygote insects, initially without disturbing the normal growth of the host. Most of the phytophagous Cynipidae, on the other hand, induce galls on plants, particularly on *Quercus* spp. (Fagaceae).

The European species are currently classified into five tribes, four of which include gall-inducing forms: the Cynipini and Pediaspidini galling oaks and maples, respectively; the Diplolepidini galling roses; and the 'Aylacini', a paraphyletic ensemble of basal cynipid lineages, typically galling herbs of plant families such as the Asteraceae, Lamiaceae, and Rosaceae. The fifth group, the inquilines (tribe Synergini), cannot induce galls on their own but instead develop inside the galls of cynipid gall inducers, where they primarily feed on the gall tissue. Despite being dependent on other species for gall initiation, the inquilines often modify the structure of the host gall, sometimes conspicuously so (Shorthouse 1980). The world fauna of Cynipidae includes only one additional tribe that is not found in Europe. This tribe is Eschatocerini, recognized for a few species of South-American gall-inducers attacking *Acacia* and related woody plants in the family Fabaceae.

The Cynipidae induce a great variety of galls, among them some of the most complex of all insect galls. It is not clear how the cynipid larva manipulates the host plant development to its own benefit. The plant tissue is in some cases modified late in the egg stage of the gall inducer (Beyerinck 1883; Magnus 1914; H. Vårdal, unpublished data), but the development of the gall is not accelerated before the larva hatches from the egg. Thus it is commonly believed that the larva plays a major role in the development of the gall, perhaps by means of chemical signals transferred from the young larva to the host plant tissue (Rohfritsch 1992). Alternative hypotheses suggest that symbiotic viruses injected by the ovipositing female could facilitate gall induction (Cornell 1983). Virus-like particles suppressing the cellular immunity of the host larva have been reported in the parasitoid cynipoid *Leptopilina heterotoma* (Figitidae) (Rizki & Rizki 1990).

Our understanding of the external morphology of adult cynipoids and of the phylogenetic relationships among major cynipoid lineages has improved greatly during the last decade (Ronquist 1994, 1995, 1999; Liljeblad & Ronquist 1998; Nieves-Aldrey 2001). However, few immature stages of Cynipoidea have been described and the variability of larval morphology within the superfamily remains poorly defined. Thus, it is not currently possible to use larval characters for phylogenetic inference or to make any detailed reconstructions of the evolutionary changes in larval morphology during the radiation of the Cynipoidea.

Despite the lack of detail, some basic facts are known about cynipoid larvae. For instance, all described terminal-instar cynipoid larvae are similar in general appearance. They are hymenopteriform: that is, they have a ventrally curved, cylindrical body without legs. The cuticle is normally smooth and white or yellowish. The number of segments has been reported to be 12 (Rössig 1904; Roth 1949; Ionescu 1957) or 13 (Cameron 1889; Evans 1965; Nieves-Aldrey 2001). Unlike many other parasitic wasp larvae, the integument carries no setae except for a few small ones around the mouth.

The known larvae of the insect-parasitic cynipoids go through hypermetamorphosis, typically starting their development with a tail and a series of paired body appendages that are subsequently lost. Two types of early instar larvae with appendages are commonly recognized. One is the eucoiliform larva, which carries three pairs of rather long appendages in the thoracic region and a long cauda or tail posteriorly (Keilin & Baume-Pluvinel 1913). The other is the polypod or polypodeiform larva, which has short, paired appendages on most of the body segments. The developmental pattern is apparently different among the major insect-parasitic lineages, but it is difficult to draw robust conclusions based on the scanty information currently available.

The insect-parasitic cynipoids fall into two groups (Ronquist 1999): (1) the parasitoids of wood- or cone-boring Hymenoptera, Coleoptera, and Lepidoptera larvae (Austrocynipidae, Liopteridae, Ibaliidae); (2) the generally smaller parasitoids of Diptera, Hymenoptera, and Neuroptera larvae, typically developing inside decomposing organic matter, in the aphid community or in galls (Figitidae). Among group 1, only the larvae of Ibaliidae have been described. A particularly detailed study of *Ibalia leucospoides* was published by Chrystal (1930). This species develops as a parasitoid in the wood-boring larvae of horntails (Siricidae) and has some of the largest larvae in the Cynipoidea. The *Ibalia* larva goes through four instars. The first instar, which develops inside the siricid larva, is polypodeiform, like that of many other parasitic wasps (Clausen 1940). The second instar is similar, while the third and fourth instars are hymenopteriform. The development of another species of the same genus, *Ibalia drewseni*, corresponds well with the description given for *I. leucospoides* (Spradbery 1970).

Several descriptions of the external morphology and development of the larvae of the diverse family Figitidae have been published. Most of these concern the core clade of Diptera-parasitic Figitidae (including the subfamilies Eucoilinae, Figitinae, Aspicerinae, Emargininae, and Pycnostigminae; Ronquist 1999), in particular the species-rich Eucoilinae. Eucoiline species with published descriptions of larvae include *Trybliographa* (formerly *Eucoila*) *keilini* (Keilin & Baume-Pluvinel 1913), *Trybliographa* (formerly *Cothonaspis*) *rapae* (James 1928; Wishart & Monteith 1954), *Kleidotoma marshalli* and an unidentified species of *Kleidotoma* (James 1928), *Kleidotoma japonica* (Huzimatu 1940), *Leptopilina heterotoma* (Jenni 1951), *Hexacola* sp. (Simmonds 1952) and *Aganaspis pelleranoi* (Ovruski 1994). Eucoiline larvae apparently go through five larval instars. The first and often also the second instar larvae are eucoiliform with a long cauda and three pairs of thoracic appendages of varying length (Keilin & Baume-Pluvinel 1913; Clausen 1940). A polypodeiform larval stage has been found to follow the eucoiliform stage in some eucoilines (e.g. James 1928) but not in others, among them *Kleidotoma japonica* (Huzimatu 1940). There is only one published description of the larvae of a Diptera-parasitic figitid that is not an eucoiline; this is the study of the larval development of *Figites anthomyiarum* (Figitidae: Figitinae) published by James (1928). The larval stages of this species are essentially similar to that of the eucoilines with an intermediate polypodeiform stage (James 1928).

Among the figitid subfamilies that do not attack Diptera, larvae have been described for the Charipinae (secondary parasitoids of Homoptera through other parasitic wasps) and Anacharitinae (parasitoids of Neuroptera larvae). The larvae of the three studied species of the genus *Alloxysta* (Charipinae) lack the thoracic appendages in the primary instar. However, the second instar carries both the terminal cauda and the thoracic appendages, albeit not as long and prominent as in the eucoilines (Haviland 1921). The larva of *Anacharis melanoneura* (Anacharitinae) is apparently polypodeiform throughout its development (Miller & Lambdin 1985; Fergusson 1986). This larval type is similar to the first- and second-instar larva of *Ibalia* (Chrystal 1930) and the second-instar larvae of the eucoiline *Kleidotoma marshalli* and the figitine *Figites anthomyiarum* (James, 1928).

In many respects, larvae of the gall-inducing and inquilinous Cynipidae are better known than those of the parasitoids. A few comparative studies of gall-inducing larvae, mostly focusing on internal anatomy, were undertaken in the late nineteenth century and first half of the twentieth (Adler 1877; Beyerinck 1883; Rössig 1904; Roth 1949). In contrast to the insect-parasitic forms, the phytophagous cynipid larva remains hymenopteriform throughout its development. However, there are some changes in body shape; both Rössig (1904) and Roth (1949) report that 2nd and 3rd body segments generally make up one-third of the total body length of young larvae, but that later the body segments become more equal in size. The terminal-instar larva is generally characterized by having equal-sized segments and no appendages, although ventral protuberances in the thoracic region have been observed in larvae of the oak galler *Plagiotrochus suberi* (Cynipini) (Díaz 1973). A few morphological studies have been published on the inquiline (Synergini) larvae, namely on those of *Synergus pacificus* (Evans 1965) and *Periclistus brandtii* (Nordlander 1973). Nordlander (1973) also illustrated the larva of the European rose galler *Diplolepis rosae* (Diplolepidini). More recently, Shorthouse & Leggo (2002) examined external and internal features of immature stages of the North American (Nearctic) rose galler *Diplolepis triforma* (Diplolepidini). Descriptions of the terminal-instar larvae of two Aylacini species, *Neaylax salviae* (Mayr) and *Isocolus leuzeae* appear in two recent papers (Nieves-Aldrey 2002; Nieves-Aldrey & Parra 2003). Despite these studies of cynipid larvae, however, we still lack detailed comparative analyses of their external morphology.

Here we present the first attempt at a comparative analysis of the external morphology of terminal-instar cynipoid larvae. The analysis is based on a sample of 30 species, representing all the main European cynipid tribes and most of the genera, as well as five different taxa of insect-parasitic cynipoids. We primarily used scanning electron microscopy to study characters and we focused in particular on the head capsule and mouthparts. The variation is summarized in terms of a number of qualitative characters and the phylogenetic information in this dataset is compared with results from previous analyses based on adult morphology and molecular data.

Materials and methods

Selected taxa

Twenty-one species of gall inducers, four species of inquilines and five species of insect-parasitic cynipoids were selected. The selected taxa and their life modes are listed in Table 1.

Preparation and imaging

For general study, larvae were transferred directly from absolute alcohol onto an SEM-stub and into the microscope at low vacuum without prior fixation or coating. This technique gave a much better result than the traditional method of fixation involving dehydration in alcohol followed by critical-point drying and gold-sputter coating. However, as the larvae degrade rapidly, they should not be removed from the alcohol until immediately before study under the microscope. They can be retrieved and stored again in alcohol after being studied. In order to study the mandibles, which are normally covered by the clypeus and labrum, we removed them from the larvae by dissection in alcohol, then air-dried and mounted them on stubs, and finally coated them with gold before examination under SEM.

In the SEM microscope, we photographed the ventral view of the whole larvae, the anterior view of the head, and close-ups of the anterior view of the mouthparts. Right and left mandibles were photographed in anterior and posterior view. The images are deposited in MorphBank (http://morphbank.net), accession numbers 3702–3838.

Terminology

We follow the terminology illustrated in Fig. 1 and based on earlier papers on hymenopteran larvae (Vance & Smith 1933; Short 1952). We interpret this terminology in the cynipid context as follows (all letter abbreviations refer to Fig. 1): The *vertex* (a) extends from the top of the head anteriorly on either side of the incision or *metopic suture* (Vance & Smith 1933) that most often separates the front of the head into two halves. The *antennal areas* are paired rounded structures of varying size ventrad of the vertex, each normally consisting of a flat disc surrounded by a socket. The disc sometimes carries an *antennal seta* (c). A *lateral seta* (b) is sometimes present on each side laterad of the antennal area. More ventrally, a *genal seta* (d) can be found on each gena. The mouth region is protected anterodorsally by the *clypeus* (f), sometimes carrying a pair of *clypeal setae* (e). The upper limit (*epistoma*) of the clypeus towards the *frons* is most often concealed. The *labrum* (h) forms the upper border of the preoral cavity. The bases of the well sclerotized and pigmented *mandibles* (g) can be seen on each side of the mouth, the apices often concealed by the labrum. The paired *maxillae* (i) are present on either side ventro-laterad of the mouth. A rudimentary *maxillary palpus* (j) is usually seen in the area lateral of the terminal lobe and one or two *maxillary setae* are sometimes found lateral to the palpus. The apical part of the *labium* (k) bears the orifice of

Table 1 Classification, life mode and collection data for the cynipoid species included in the study. Scanning electron micrographs of the larva, head and mandible were prepared for most species. For species marked *, only mandibles were prepared, and for species marked $^{\#}$, only larva and head were examined. Of the Cynipini, the agamic generation is marked A, and the sexual generation S. Depository: JLNA — J. L. Nieves-Aldrey collection, Museo Nacional de Ciencias Naturales, Madrid.

Species	Classification	Life mode	Host	Collection data
1 *Ibalia leucospoides*	Ibaliidae	Parasitoid	larva of *Sirex* (Siricidae)	Australia (South)
2 *Ibalia anceps**	Ibaliidae	Parasitoid	larva of *Tremex* (Siricidae)	USA, Texas
3 *Alloxysta victrix**	Figitidae, Charipinae	Hyperparasitoid	aphids through *Aphidius* (Braconidae)	UK, Newport
4 *Leptopilina boulardi*	Figitidae, Eucoilinae	Parasitoid	larva of *Drosophila* (Dipt: Drosophilidae)	France, Gif sur Yvette
5 *Parnips nigripes*	Figitidae, Parnipinae	Parasitoid	larva of *Barbotinia* and *Aylax* n. sp. (Cynipidae)	Spain, Marçà (JLNA)
6 *Periclistus brandtii*	Cynipidae, Synergini	Inquiline	gall of *Diplolepis rosae* (Cynipidae)	Spain, Cotos de Monterrey (JLNA)
7 *Synophrus politus*	Cynipidae, Synergini	Inquiline	galls of *Andricus burgundus complex* on *Quercus suber* (Cynipidae)	Spain, Algatocín (JLNA)
8 *Synergus clandestinus*	Cynipidae, Synergini	Inquiline	Stunted acorns on *Q. pyrenaica*	Spain, El Escorial (JLNA)
9 *Synergus incrassatus*	Cynipidae, Synergini	Inquiline	Galls of *Andricus quercusradicis* agam. on *Q. faginea* (Cynipidae)	Spain, El Bosque (JLNA)
10 *Neaylax salviae*	Cynipidae, Aylacini	Gall inducer	*Salvia lavandulifolia* (Lamiaceae)	Spain, Arganda (JLNA)
11 *Liposthenes kerneri*	Cynipidae, Aylacini	Gall inducer	*Nepeta beltranii* (Lamiaceae)	Spain, Rivas (JLNA)
12 *Isocolus lichtensteini*	Cynipidae, Aylacini	Gall inducer	*Centaurea aspera* (Asteraceae)	Spain, Arganda (JLNA)
13 *Aulacidea hieracii*$^{\#}$	Cynipidae, Aylacini	Gall inducer	*Hieracium sabaudum* (Asteraceae)	Spain, El Escorial (JLNA)
14 *Aulacidea pilosellae**	Cynipidae, Aylacini	Gall inducer	*Hieracium pilosellae* (Asteracae)	Spain, El Ventorrillo (JLNA)
15 *Xestophanes potentillae*	Cynipidae, Aylacini	Gall inducer	*Potentilla reptans* (Rosaceae)	Spain, Cotos de Monterrey (JLNA)
16 *Diastrophus rubi*	Cynipidae, Aylacini	Gall inducer	*Rubus* sp. (Rosaceae)	Spain, Aguasmestas (JLNA)
17 *Barbotinia oraniensis*	Cynipidae, Aylacini	Gall inducer	*Papaver rhoeas* (Papaveraceae)	Spain, Rivas (JLNA)
18 *Aylax papaveris*	Cynipidae, Aylacini	Gall inducer	*Papaver rhoeas* (Papaveraceae)	Spain, El Cardoso (JLNA)
19 *Phanacis centaureae*	Cynipidae, Aylacini	Gall inducer	*Centaurea* sp. (Asteraceae)	Spain, Arganda (JLNA)
20 *Timaspis lampsanae*	Cynipidae, Aylacini	Gall inducer	*Lampsana communisi* (Asteraceae)	Spain, El Escorial (JLNA)
21 *Diplolepis rosae*	Cynipidae, Diplolepidini	Gall inducer	*Rosa* sp. (Rosaceae)	Spain, El Escorial (JLNA)
22 *Pediaspis aceris* (A)	Cynipidae, Pediaspidini	Gall inducer	*Acer opalus* (Sapindaceae)	Spain, Colldejou (JLNA)
23 *Andricus foecundatrix* (A)	Cynipidae, Cynipini	Gall inducer	*Quercus faginea* (Fagaceae)	Spain, Chiloeches (JLNA)
24 *Andricus panteli* (A)	Cynipidae, Cynipini	Gall inducer	*Quercus faginea* (Fagaceae)	Spain, Boadilla (JLNA)
25 *Andricus quercusradicis* (A + S*)	Cynipidae, Cynipini	Gall inducer	*Quercus faginea* (Fagaceae)	Spain, El Bosque (JLNA)
26 *Callirhytis glandium* (A)	Cynipidae, Cynipini	Gall inducer	*Quercus suber* (Fagaceae)	Spain, Saucelle (JLNA)
27 *Cynipis divisa* (A)	Cynipidae, Cynipini	Gall inducer	*Quercus robur* (Fagaceae)	Spain, Arins (JLNA)
28 *Neuroterus quercusbaccarum* (S)	Cynipidae, Cynipini	Gall inducer	*Quercus faginea* (Fagaceae)	Spain, Arganda (JLNA)
29 *Plagiotrochus quercusilicis* (S)	Cynipidae, Cynipini	Gall inducer	*Quercus coccifera* (Fagaceae)	Spain, Arganda (JLNA)
30 *Biorhiza pallida* (A + S*)	Cynipidae, Cynipini	Gall inducer	*Quercus pyrenaica* (Fagaceae)	Spain, Miraflores (JLNA)
31 *Trigonaspis mendesi* (A$^{\#}$)	Cynipidae, Cynipini	Gall inducer	*Quercus faginea* (Fagaceae)	Spain, El Bosque (JLNA)

the silk press (*salivary orifice*) and a marginal sclerotization, the *labial sclerite*. The labium normally also carries a pair of *labial palps* (l) and one or two pairs of *labial setae*.

Phylogenetic analyses

Thirty-three qualitative morphological characters were coded based on the larval images and one larval life-history character was added to this dataset (Table 2, Appendix). Two multistate characters (14 and 26) were treated as ordered, since the states appeared to fall in a natural transformation series; all other characters were treated as unordered. Phylogenetic analyses were performed in Paup* 4.0b (Swofford 1998) using 5000 random addition sequences followed by TBR-swapping, with branches of maximum length zero collapsed; bootstrap analyses used the same settings but only five random addition sequence replicates.

The following parsimony searches were run: (1) with equal weights on all characters and no constraints; (2) with equal weights on all characters and the Cynipidae, Cynipini, Synergini, and Figitidae constrained to be monophyletic according to previous phylogenetic estimates (Ronquist 1994, 1995, 1999; Liljeblad & Ronquist 1998; Ronquist & Nieves-Aldrey 2001); (3) using the implied weighting option (Goloboff 1993) and no constraints; and (4) using the implied weighting option (Goloboff 1993) and the Cynipidae, Cynipini, Synergini, and Figitidae constrained to be monophyletic. Character evolution was explored using MacClade 4.02 (Maddison & Maddison 2001).

Results

The qualitative variation in larval morphology is summarized in 33 characters (Table 2, Appendix). The taxon-specific

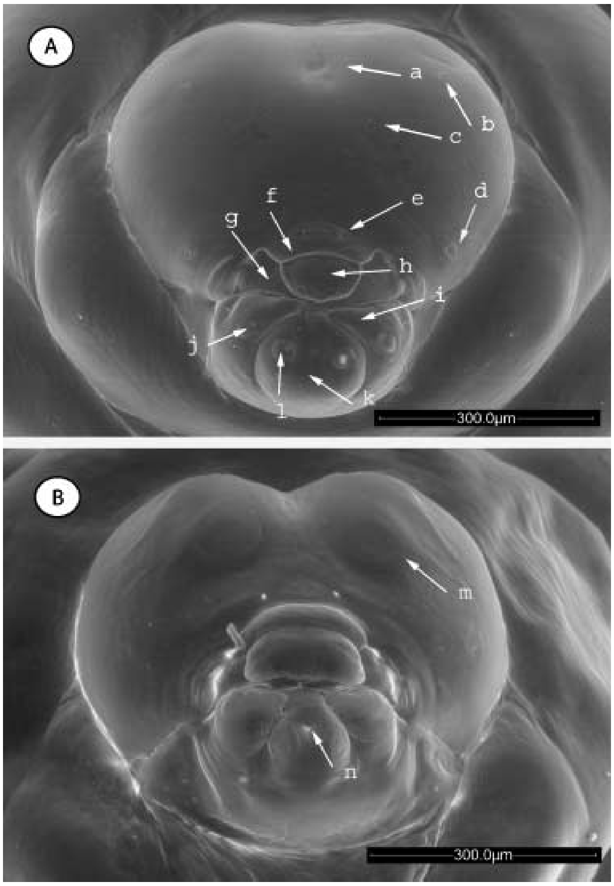

Fig. 1 A, B. The head of the larva of *Periclistus brandtii* in anterior view, illustrating the terminology used in this paper (see text). Letters refer to the following structures: a, vertex; b, setae lateral to antennal areas; c, antennal setae; d, genal setae; e, clypeal setae; f, clypeus; g, mandible; h, labrum; i, maxillae; j, maxillary palp; k, labium; l, labial palp.

descriptions below provide some additional information but do not repeat the data coded in the appendix and Table 2.

Ibaliidae

The larvae of the two studied species, *Ibalia anceps* and *I. leucospoides*, are by far the largest studied here (Fig. 2A). They are elongate and the body is fusiform, gradually tapering from the middle towards both ends. The body segments of *I. leucospoides* appear to be broader at the posterior end, but this is not the case in *I. anceps*.

The head of the larva is retracted into the body and the vertex is not incised (Fig. 3A). The antennal area is large and inconspicuous. The labrum is high and broad, with the apical margin slightly concave. The maxillae are triangular, and the labium is rounded apically. Some setae can be seen in the genal region and on the maxillae and labium. Maxillary and labial palps are inconspicuous.

The mandibles of the two species are similar with three pointed teeth, of which the apical is the dominating. However, the outer margin of the *I. anceps* (Fig. 5B) mandible is quite curved, whereas it is almost straight in *I. leucospoides* (Fig. 5A).

Figitidae

We studied three different species representing three different subfamilies: *Parnips nigripes* (Parnipinae) *Alloxysta victrix* (Charipinae), and *Leptopilina boulardi* (Eucoilinae) (Table 1). The larva of *A. victrix* is described in less detail because we were not able to obtain adequate SEM micrographs of the larval body and head of this species. The three figitid larvae are quite different. In *Alloxysta*, the first half of the larval body is broader than the rest. In *Leptopilina*, only the first three body segments are broad while the 4th is distinctly narrower, constricting the larva just anterior to the middle (Fig. 2B). The body segments of the *Parnips* larva are more or less of equal width (Fig. 2C).

The head is generally prominent, the vertex of *Parnips* being rounded (Fig. 3C) whereas that of *Leptopilina* is strongly incised (Fig. 3B). The antennal area is small and inconspicuous in *Parnips* and large in *Leptopilina*. The labrum is narrow with a slight incision in the apical margin in *Parnips*, but has a more triangular shape and straight apical margin in *Leptopilina*. The maxillae are narrow and triangular in *Parnips*, and slightly more rounded in *Leptopilina*. The labium is strongly triangular in *Parnips* and square in *Leptopilina*. Setae can be seen in the antennal area and on the clypeus, genae and maxillae of *Parnips*, but are inconspicuous in *Leptopilina*. Maxillary and labial palps are only conspicuous in *Leptopilina*.

The mandibles of *Alloxysta* and *Leptopilina* are very similar to each other. They are more or less symmetrical and have a single dominant tooth, the inner edge of which is serrated, being equipped with 4–8 very sharp teeth (Fig. 5C,D). The *Parnips* mandibles (Fig. 5E) are slightly asymmetrical, having two acute teeth on the right mandible and three on the left. The apical tooth is by far the largest in both the left and right mandibles.

Cynipidae

Synergini. The studied genera include *Synergus*, *Synophrus*, and *Periclistus* (Table 1). The inquiline larvae are quite similar to each other, with a ventrally curved body (Fig. 2D) that is broadest around the middle and typically tapers gradually towards the posterior end. Especially in the *Synergus* species, the head is quite large relative to the body. In general, the vertex is slightly incised, and the antennal area is small and inconspicuous (Fig. 3D). The labrum is rectangular, not covering the apices of the mandibles in the *Synergus* species (Fig. 4A). The maxillae are triangular, and the labium varies from almost triangular (*Synophrus politus*; Fig. 3E) to round

Table 2 Data matrix based on the characters listed in the Appendix. '?' indicates missing data due to inability to observe the character state in the specimens examined; '-' is used if the character is inapplicable for homology assessment for a particular species.

	Characters			
Species	1	11	21	31
Ibalia leucospoides	0000000000	0002000011	0010020110	0000
Ibalia anceps	000000000?	0002000011	0110020110	0000
Alloxysta victrix	000???????	??????????	???0001---	--00
Leptopilina boulardi	0010010001	0002000010	0?00001---	--00
Parnips nigripes	0000001111	0002000011	0010020110	1000
Periclistus brandtii	0000011110	0010110010	0001120103	2011
Synophrus politus	1001001110	0011110010	0001120103	2011
Synergus clandestinus	0000011110	0011111000	0010120002	2111
Synergus incrassatus	0000011110	0011111000	100012000?	3111
Xestophanes potentillae	0000011110	0011110010	0000120002	1001
Diastrophus rubi	1010011110	0011110010	0001120102	1001
Neaylax salviae	0000001110	0011110000	100?120?0?	1001
Liposthenes kerneri	0001001110	0011110000	1000110101	1001
Isocolus lichtensteini	0000001110	0011110000	1000110101	1-01
Aulacidea hier/pilos	0010011??0	0011111000	1000120101	1001
Barbotinia oraniensis	0001011110	0011110000	0000110001	1001
Aylax papaveris	0001011110	0011110000	0000110101	1001
Phanacis centaureae	0201101000	0011110?00	???0120001	1001
Timaspis lampsanae	0201101000	0010110000	0000120001	1001
Diplolepis rosae	1011001101	0101111011	0?10120100	0001
Pediaspis aceris	0000001100	0012100111	1110110111	1001
Plagiotrochus quercusilicis	0100010001	0013110111	0100110001	1001
Callirhytis glandium	0101010011	0002010001	0100120001	1001
Andricus foecundatrix	0100010001	0002010011	0110120001	1001
Andricus panteli	0000010001	0002010111	0110110001	1-01
Andricus quercusradicis	0000010001	0002000111	0000120001	1001
Neuroterus quercusbaccarum	01000?0001	0003000111	0100100---	-001
Cynips divisa	00010100?1	0003000101	0100110111	1001
Trigonaspis mendesi	0000010001	0003000111	0110110111	1001
Biorhiza pallida	0000000001	1002000111	0110100---	--01

(*Periclistus brandtii*, *Synergus clandestinus*; Fig. 3D) or more or less hexagonal (*Synergus incrassatus*). There is one seta in each antennal area, another on each side lateral to the antennal area, one pair on the clypeus, two pairs on the labrum, one seta on each gena, two setae on each maxilla, and two setae on each side of the labium. The setae are particularly long in *S. politus*. The palps are large and conspicuous, slightly more protruding in *S. politus* than in the other species. The salivary orifice is small and rounded, surrounded by a conspicuous tuberculate area in *Synergus incrassatus* (Fig. 4A) and having the shape of a vertical crevice in *S. politus* (Fig. 3E).

The mandibles each have three teeth, with the second tooth being broader than the other two. In *Synergus incrassatus*, the large second tooth is divided into two equal-sized lobes (Fig. 5I). The mandibles have a pattern of vertical and sometimes horizontal striations on the base. The striations are particularly abundant in *Synergus clandestinus* (Fig. 5H), where they can be seen both on the anterior and posterior face of the mandibles. In the other inquilines, the striations are primarily visible on the anterior face of the mandible. *Periclistus brandtii* (Fig. 5F,G) and *Synophrus politus* (Fig. 5J,K) have strongly asymmetrical mandibles with the second tooth being prominent in the left mandible but reduced in the right mandible.

Aylacini. The studied species include representatives of the gallers of Asteraceae (*Aulacidea*, *Isocolus*, *Phanacis*, *Timaspis*), Lamiaceae (*Liposthenes*, *Neaylax*), Papaveraceae (*Aylax*, *Barbotinia*) and Rosaceae (*Diastrophus*, *Xestophanes*) (Table 1). *Aulacidea hieracii* and *A. pilosellae* are regarded as closely related (Nieves-Aldrey 2001); we examined the larva and head of the former and the mandibles of the latter and combined the observations into a single composite taxon when coding character states (Table 2). Most of the terminal-instar Aylacini larvae have the common fusiform shape (Fig. 2G) but the larvae of *Phanacis centaureae* and *Timaspis lampsanae* (both developing inside stems of herbs) are more elongate and have segments of even thickness along the whole body, giving them a rectangular appearance (Fig. 2E). The shape of the larva of *Diastrophus rubi* also deviates from the other Aylacini in that the 4th body segment is narrower than the others, making the larva constricted anterior to the middle.

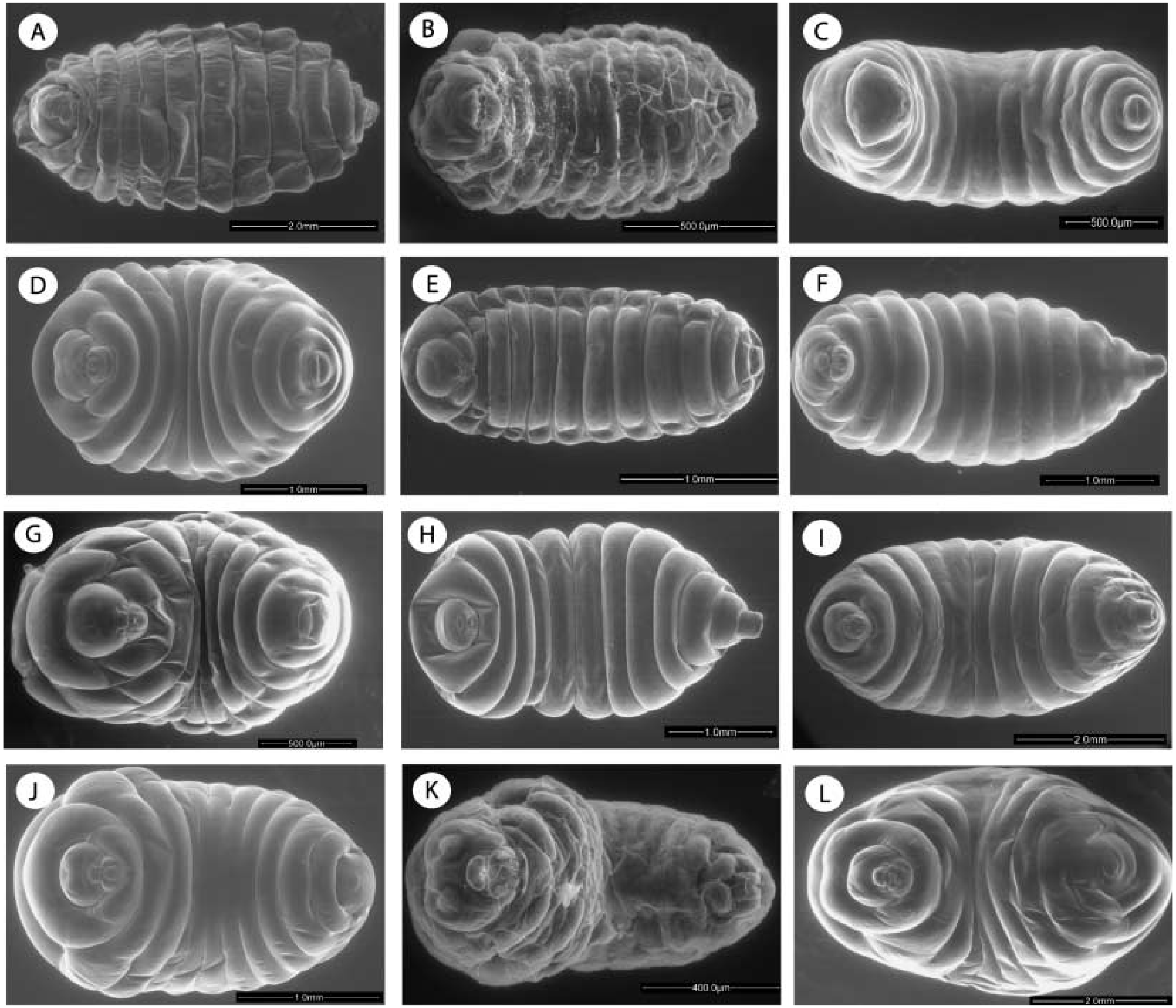

Fig. 2 A–L. Ventral view of the body of terminal-instar larvae of Cynipoidea. —A. *Ibalia leucospoides* (Ibaliidae). —B. *Leptopilina boulardi* (Figitidae, Eucoilinae). —C. *Parnips nigripes* (Figitidae, Parnipinae). —D. *Synergus clandestinus* (Cynipidae, Synergini). —E. *Timaspis lampsanae* (Cynipidae, Aylacini). —F. *Diastrophus rubi* (Cynipidae, Aylacini). —G. *Isocolus lichtensteini* (Cynipidae, Aylacini). —H. *Diplolepis rosae* (Cynipidae, Diplolepidini). —I. *Pediaspis aceris* (agamic gen.) (Cynipidae, Pediaspidini). —J. *Callirhytis glandium* (agamic gen.) (Cynipidae, Cynipini). —K. *Plagiotrochus quercusilicis* (sexual gen.) (Cynipidae, Cynipini). —L. *Biorhiza pallida* (agamic gen.) (Cynipidae, Cynipini).

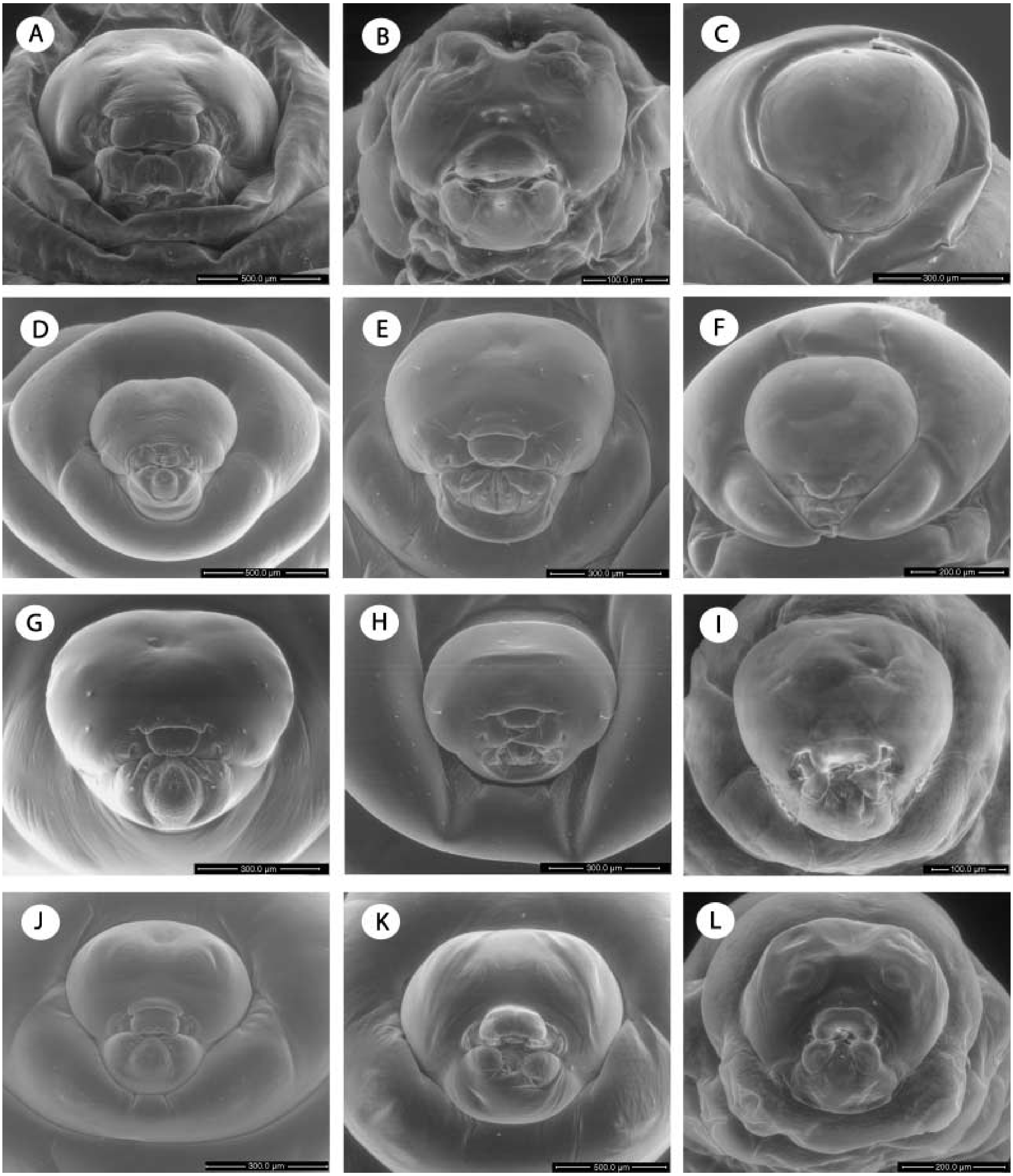

Fig. 3 A–L. Anterior view of the head of terminal-instar larvae of Cynipoidea. —A. *Ibalia leucospoides* (Ibaliidae). —B. *Leptopilina boulardi* (Figitidae, Eucoilinae). —C. *Parnips nigripes* (Figitidae, Parnipinae). —D. *Synergus clandestinus* (Cynipidae, Synergini). —E. *Synophrus politus* (Cynipidae, Synergini). —F. *Timaspis lampsanae* (Cynipidae, Aylacini). —G. *Neaylax salviae* (Cynipidae, Aylacini). —H. *Diplolepis rosae* (Cynipidae, Diplolepidini). —I. *Pediaspis aceris* (agamic gen.) (Cynipidae, Pediaspidini). —J. *Callirhytis glandium* (agamic gen.) (Cynipidae, Cynipini). —K. *Biorhiza pallida* (agamic gen.) (Cynipidae, Cynipini). —L. *Trigonaspis mendesi* (agamic gen.) (Cynipidae, Cynipini).

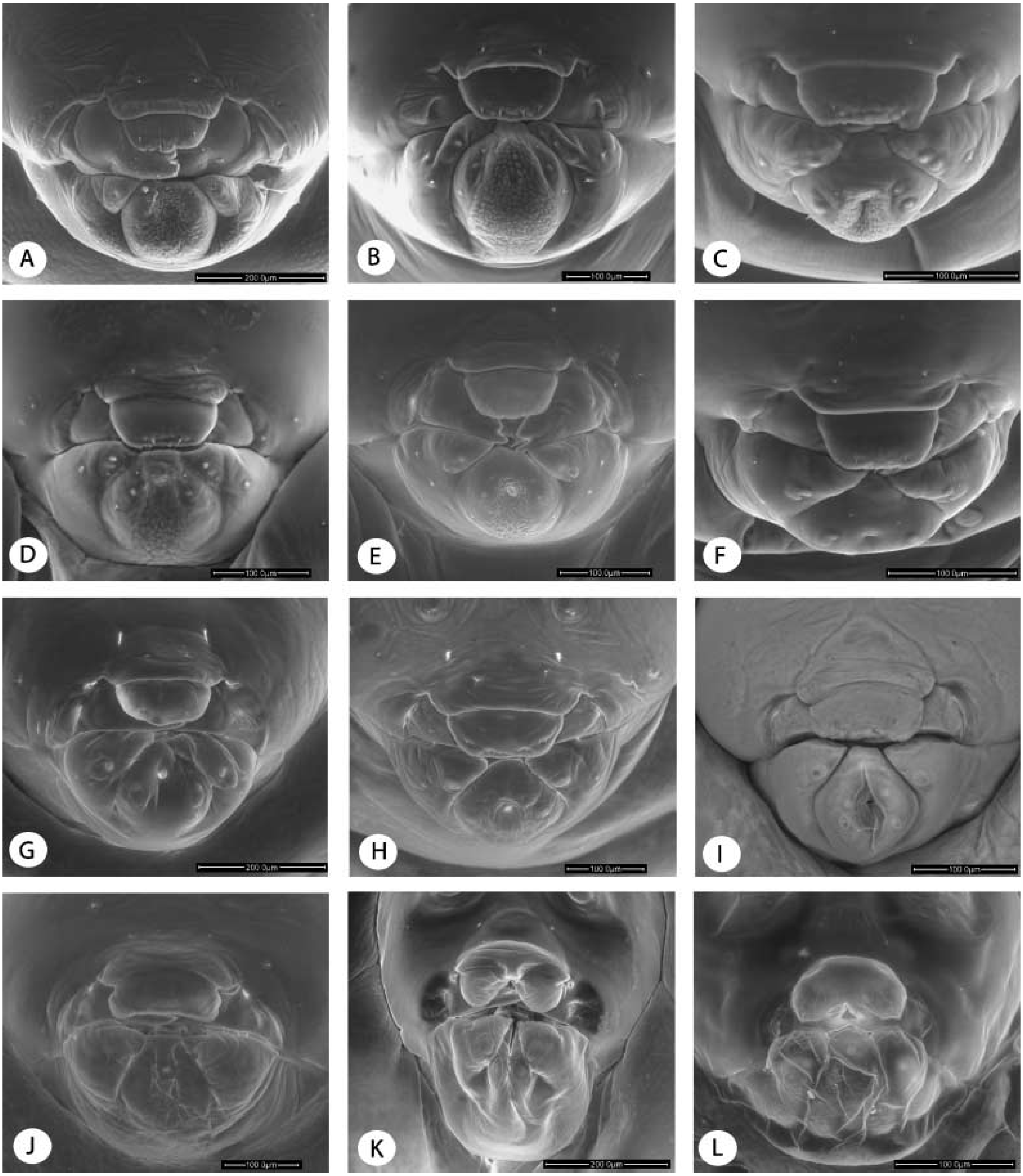

Fig. 4 A–L. Anterior view of mouthparts of terminal-instar larvae of Cynipidae. A. *Synergus incrassatus* (Synergini). —B. *Neaylax salviae* (Aylacini). —C. *Liposthenes kerneri* (Aylacini). —D. *Isocolus lichtensteini* (Aylacini). —E. *Aulacidea hieracii* (Aylacini). —F. *Xestophanes potentillae* (Aylacini). —G. *Diastrophus rubi* (Aylacini). —H. *Barbotinia oraniensis* (Aylacini). —I. *Aylax papaveris* (Aylacini). —J. *Andricus foecundatrix* (agamic gen.) (Cynipini). —K. *Cynips divisa* (agamic gen.) (Cynipini). —L. *Plagiotrochus quercusilicis* (sexual gen.) (Cynipini).

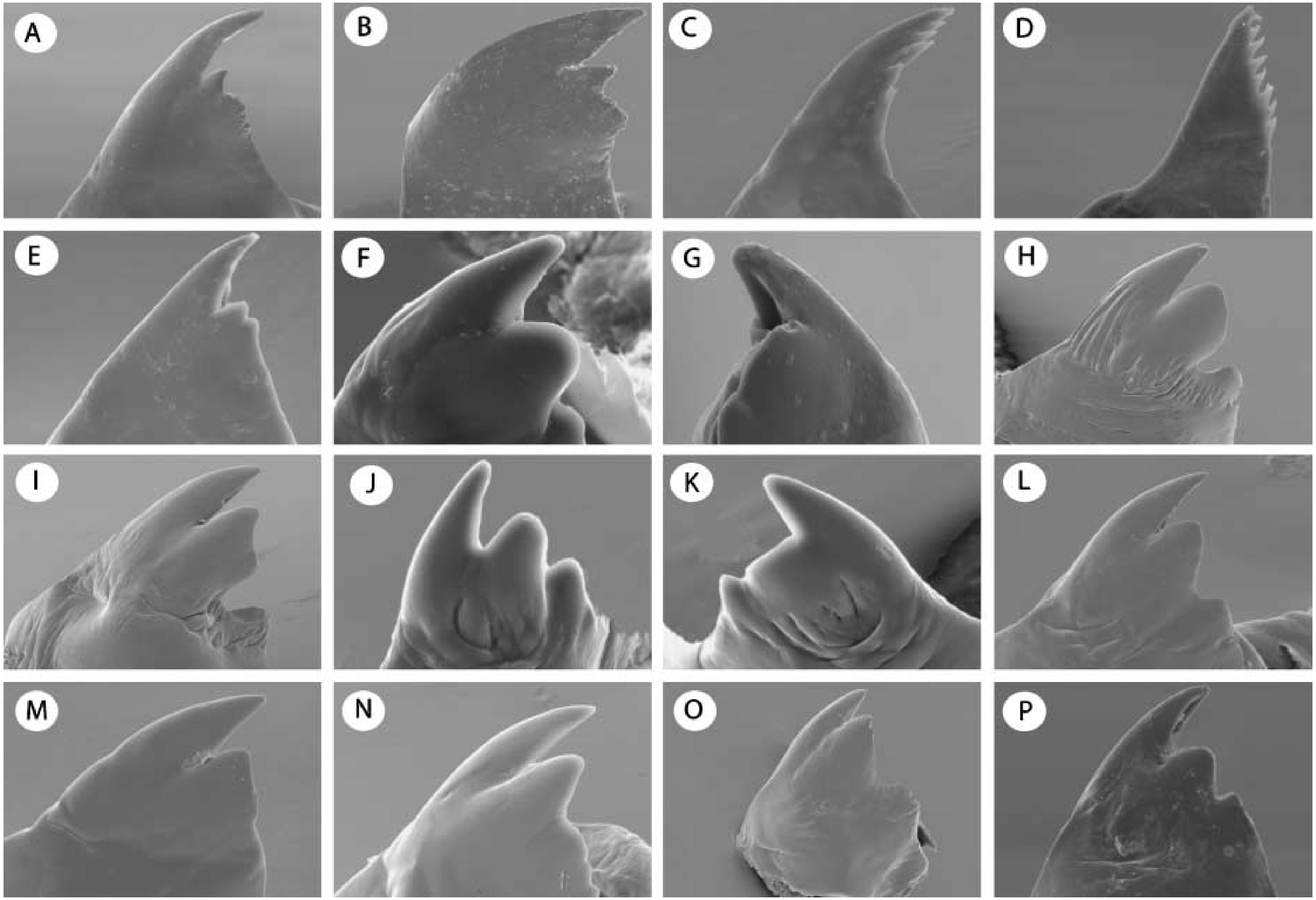

Fig. 5 A–P. Anterior view of mandibles of terminal-instar larvae of Cynipoidea (left mandible except as indicated). —A. *Ibalia leucospoides* (Ibaliidae). —B. *Ibalia anceps* (Ibaliidae). —C. *Alloxysta victrix* (Figitidae, Charipinae). —D. *Leptopilina boulardi* (Figitidae, Eucoilinae). —E. *Parnips nigripes* (Figitidae, Parnipinae). —F. *Periclistus brandtii* (Cynipidae, Synergini). —G. *ibidem* (right mandible). —H. *Synergus clandestinus* (Cynipidae, Synergini). —I. *Synergus incrassatus* (Cynipidae, Synergini). —J. *Synophrus politus* (Cynipidae, Synergini). —K. *ibidem* (right mandible). —L. *Neaylax salviae* (Cynipidae, Aylacini). —M. *Liposthenes kerneri* (Cynipidae, Aylacini). —N. *Isocolus lichtensteini* (Cynipidae, Aylacini). —O. *Aulacidea pilosellae* (Cynipidae, Aylacini). —P. *Xestophanes potentillae* (Cynipidae, Aylacini).

Furthermore, the last two body segments are cylinder-shaped and form a separate, narrow posterior extension of the larval body (Fig. 2F).

The head of the Aylacini larva typically has a rounded to slightly incised vertex, except for *Aulacidea hieracii*, in which it is strongly incised. The antennal area is almost completely invisible in *Isocolus*, *Aulacidea*, *Neaylax* and the *Phanacis/Timaspis* complex but visible although small in *Aylax*, *Barbotinia* and *Xestophanes*. The labrum is always rectangular with a more or less straight apical margin. In all species, except *A. hieracii* (Fig. 4E), the labrum covers the apices of the mandibles (Fig. 4B–D,F–I). The maxillae are triangular, whereas the labium can be rounded, triangular or diamond-shaped. An area along the mid-region of the labium, surrounding the salivary orifice, has a tuberculate pattern in *A. hieracii* (Fig. 4E), *Isocolus lichtensteini* (Fig. 4D), *Liposthenes kerneri* (Fig. 4C) and *Neaylax salviae* (Fig. 4B). The pattern is especially conspicuous in *L. kerneri* and *N. salviae*, both galling plants in the family Lamiaceae. The salivary orifice is situated in a vertical crevice in *Aylax papaveris* (Fig. 4I) while the genus *Barbotinia* has the salivary opening situated in a funnel-shaped depression (Fig. 4H). In the other species, the region around the salivary orifice is not distinctly depressed. There is typically one seta lateral to the antennal area, one pair on the clypeus, two pairs on the labrum, one seta on each gena, a pair on each maxilla and another pair on each side of the labium. Maxillary and labial palps are visible in all species, but inconspicuous in some.

The mandibles are symmetrical except in *Diastrophus rubi*, in which the second tooth of the right mandible is reduced in size compared to that of the left mandible (Fig. 6A). The second mandibular tooth of this species, and to a certain degree also that of *Xestophanes potentillae* (Fig. 5P), is broadly rounded apically on both left and right mandibles. The number of mandibular teeth is two or three in the Aylacini. Small dents are present on the inner edge of the mandibles of *Aulacidea pilosellae* (Fig. 5O), *Aylax papaveris* (Fig. 6D) and *Isocolus lichtensteini* (Fig. 5N).

Diplolepidini. The 4th body segment of the larva of the single studied species (*Diplolepis rosae*) is narrow, giving the larva a constriction just anterior to the middle. The two last body segments are narrow and cylindrical (Fig. 2H). In both respects, it resembles the larva of *Diastrophus* (Aylacini) (see above).

The head is small relative to the larval body. It is almost square dorsally and a transverse crest can be seen on the upper frons (Fig. 3H). The antennal areas are small and inconspicuous. The labrum is rectangular with a straight apical margin, and it does not cover the apices of the mandibles completely. The maxillae are triangular and the labium may be somewhat rounded. The head is equipped with a short seta in each antennal area, a long genal seta on each side, two pairs of long labral setae, one long labial seta on each side, and one shorter maxillary seta on each maxilla. The maxillary palps are slightly protruding and the labial palps are relatively inconspicuous. The mandibles are symmetrical and carry three teeth (Fig. 6F). The apices of the mandibular teeth are relatively pointed.

Pediaspidini. In the single studied species, *Pediaspis aceris* (agamic generation) the larva is typically fusiform and the last body segment is cylindrical as in *Diplolepis* (Fig. 2I). The head has a rounded vertex (Fig. 3I). The antennal areas are visible. The labrum is rectangular with a slight incision on the apical margin but it still conceals the apices of the mandibles. The maxillae are rounded and the labium is somewhat square. Setae are present in the antennal area, on the clypeus, two pairs on the labrum, one pair on each maxilla, and one seta on each side of the labium. The maxillary and labial palps are inconspicuous. The mandibles are symmetrical; mandibles of larvae of the sexual generation carry one single acute long tooth as well as a minute second tooth basally. The second tooth is much more conspicuous in larvae of the agamic generation (Fig. 6G).

Cynipini. We studied larvae of all major European genera (*Andricus*, *Neuroterus*, *Plagiotrochus*, *Callirhytis*, *Biorhiza*, *Trigonaspis*, and *Cynips*; Table 1). The larvae are of two types. The first is the common fusiform type; in this group we find the larvae of *Andricus panteli* (agamic), *A. quercusradicis* (sexual and agamic), *Biorhiza pallida* (sexual and agamic) (Fig. 2L), *Trigonaspis mendesi* (agamic) and *Cynips divisa* (agamic). The second type has an enlarged thoracic region and can be further subdivided into two types. In the larvae of *A. foecundatrix* (agamic) and *Callirhytis glandium* (agamic) (Fig. 2J) body segments 1–3 have dorsolateral protuberances, whereas in the larvae of *Neuroterus quercusbaccarum* (sexual) and *Plagiotrochus quercusilicis* (sexual) (Fig. 2K), these segments are broadened.

The head can be rounded or slightly incised dorsally. The antennal areas are always large and conspicuous. The labrum is often slightly narrower at the base than at the apex. The apical margin can be straight, as in *A. panteli* (agamic) (Fig. 1B), *A. quercusradicis* (agamic) (Fig. 4J) and *Ca. glandium* (agamic) (Fig. 3J); slightly concave, as in *A. foecundatrix* (agamic) and *B. pallida* (agamic) (Fig. 3K), or strongly incised, as in *Cy. divisa* (agamic) (Fig. 4K), *N. quercusbaccarum* (sexual), *P. quercusilicis* (sexual) (Fig. 4L) and *T. mendesi* (agamic) (Fig. 3L). The mandibles of *B. pallida* (sexual and agamic) are very slender and completely exposed (Fig. 3K). In the other species, the apices of the mandibles are either concealed by the labrum or partly exposed if the labrum is strongly incised. The maxillae are rounded in all the species except in *A. foecundatrix* (agamic), *Ca. glandium* (agamic) (Fig. 3J) and

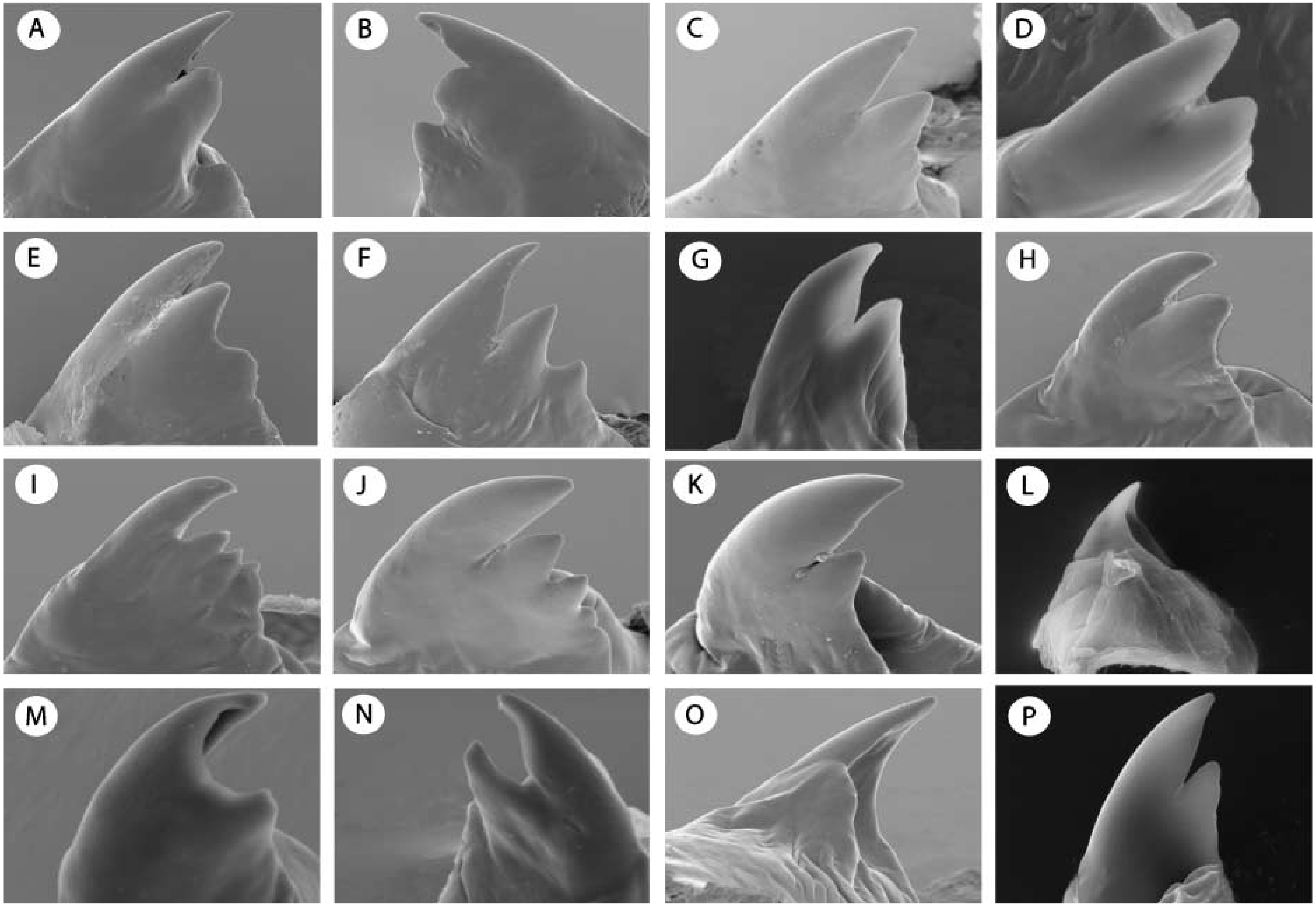

Fig. 6 A–P. Anterior view of mandibles of terminal-instar larvae of Cynipoidea (left mandible except as indicated). —A. *Diastrophus rubi* (Cynipidae, Aylacini). —B. *ibidem* (right mandible). —C. *Barbotinia oraniensis* (Cynipidae, Aylacini). —D. *Aylax papaveris* (Cynipidae, Aylacini). —E. *Timaspis lampsanae* (Cynipidae, Aylacini). —F. *Diplolepis rosae* (Cynipidae, Diplolepidini). —G. *Pediaspis aceris* (agamic gen.) (Cynipidae, Pediaspidini). —H. *Andricus panteli* (agamic gen.) (Cynipidae, Cynipini). —I. *Andricus quercusradicis* (sexual gen.). (Cynipidae, Cynipini). —J. *Callirhytis glandium* (agamic gen.) (Cynipidae, Cynipini). —K. *Cynips divisa* (agamic gen.) (Cynipidae, Cynipini). —L. *Neuroterus quercusbaccarum* (sexual gen.) (Cynipidae, Cynipini). —M. *Plagiotrochus quercusilicis* (sexual gen.) (Cynipidae, Cynipini). —N. *ibidem* (right mandible). —O. *Biorhiza pallida* (agamic gen.) (Cynipidae, Cynipini). —P. *Trigonaspis mendesi* (agamic gen.) (Cynipidae, Cynipini).

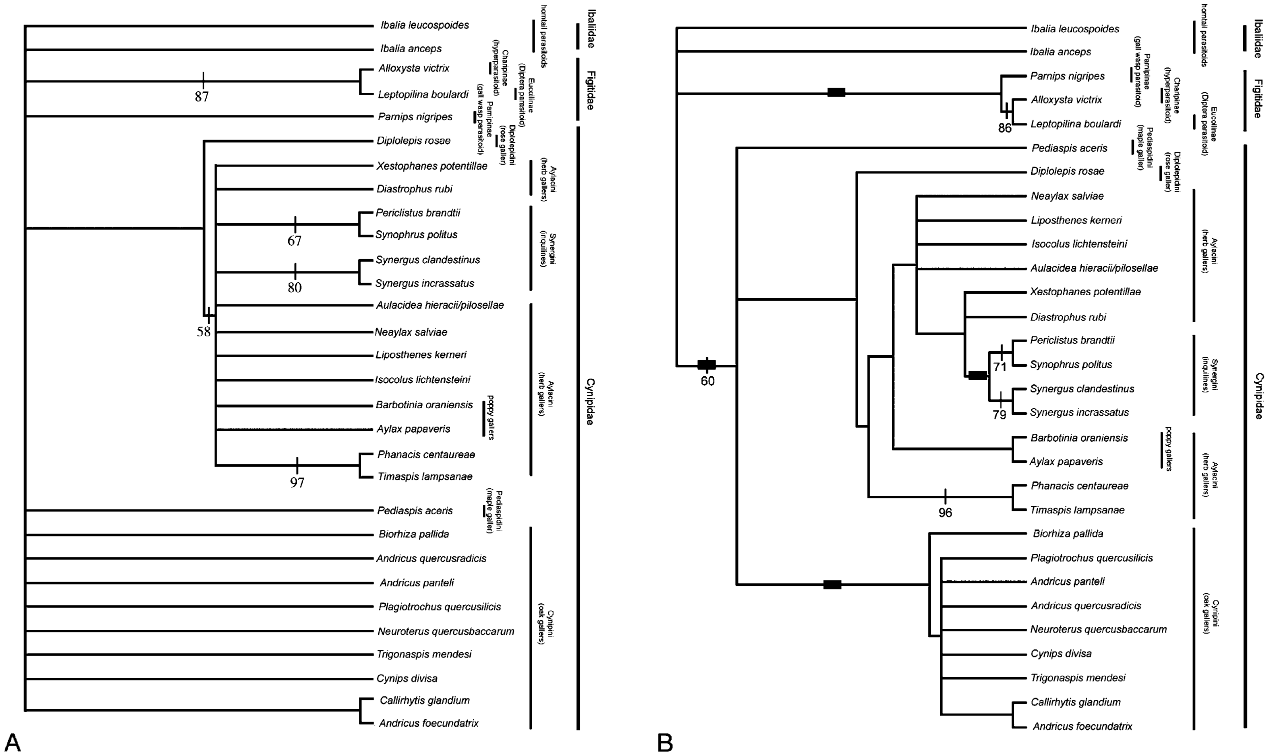

Fig. 7 A, B. Strict consensus trees from phylogenetic analyses of larval data. Numbers below branches indicate bootstrap support values above 50%; clades marked with rectangular boxes were constrained to be monophyletic. —A. Uniform weights, no constraints. —B. Uniform weights; Cynipidae, Cynipini, Figitidae, Synergini constrained to be monophyletic.

Cy. divisa (agamic) (Fig. 4K), where they are triangular. The labium is rounded or square in most cases. Setae can be seen in the lateral antennal area, on the genae, on the clypeus, and often one seta on each side of the labium. Only a few species have setae on the labrum. Labial and maxillary palps are only conspicuous in a few species, but probably present in all.

The number of mandibular teeth varies between one and five: the mandibles of *B. pallida* (both generations) (Fig. 6O) and *N. quercusbaccarum* (sexual generation) (Fig. 6L) have one tooth; those of *A. panteli* (agamic) (Fig. 6H), *Cy. divisa* (agamic) (Fig. 6K), *P. quercusilicis* (sexual) and *T. mendesi* (agamic) have two (Fig. 6P); and those of *A. quercusradicis* (both generations) carry four. In *Ca. glandium* (agamic) the right mandible has three teeth and the left four. Asymmetry also occurs in *A. quercusradicis* (agamic) (Fig. 6I), where the teeth appear smaller and closer together on the right mandible than on the left, and in *P. quercusilicis* (sexual) (Fig. 6M), where the second tooth is much longer on the right mandible than on the left.

Phylogenetic analyses

The 33 morphological characters coded for the studied larvae were combined with one ecological character, namely whether larvae are phytophagous or insect-parasitic (Table 2, Appendix). Heuristic searches of the uniformly weighted combined dataset produced one island with 2318 equally parsimonious trees, which was hit 4818 times in 5000 random addition replicates (Fig. 7A). The trees had a length of 104 steps, an ensemble consistency index (CI) of 0.404, and an ensemble retention index (RI) of 0.738.

The strict consensus tree was largely unresolved. For instance, none of the four 'well established' higher groupings — Figitidae, Cynipidae, Synergini and Cynipini — appeared as monophyletic. Only five groupings were supported in more than 50% of the bootstrap replicates: *Alloxysta* + *Leptopilina*, *Phanacis* + *Timaspis*, *Synergus clandestinus* + *S. incrassatus*, *Periclistus* + *Synophrus*, and Aylacini + Synergini (Fig. 7A). The first three groupings are expected based on traditional taxonomy and previous phylogenetic results of adult morphology (Fig. 10A) and molecular data (Fig. 10B). The two latter are in conflict with previous results, but they are also the two least supported groups among the five.

Enforcing the monophyly of Cynipidae, Cynipini, Synergini, and Figitidae, we found one island with 361 trees, which was hit 4775 times in 5000 random addition replicates (Fig. 7B). The lengths of these trees were 106 steps (CI = 0.396, RI =

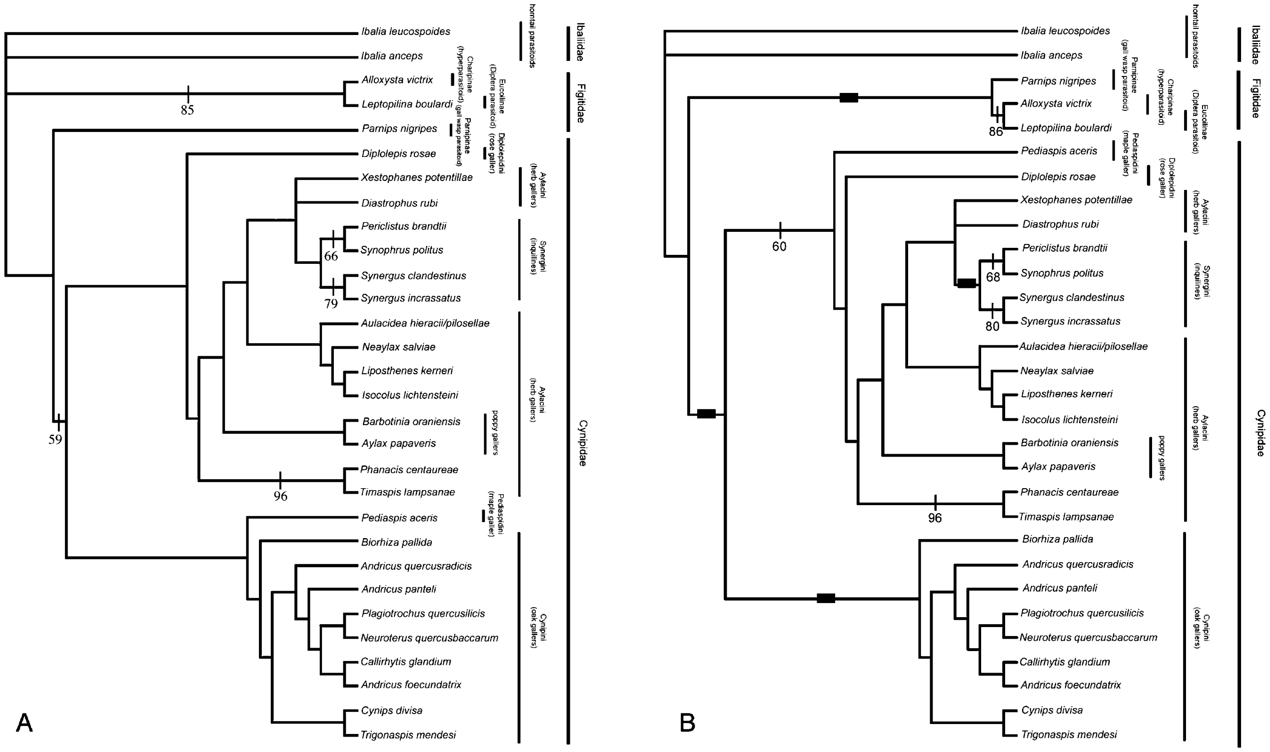

Fig. 8 A, B. Strict consensus trees from phylogenetic analyses of larval data. Numbers below branches indicate bootstrap support values above 50%; clades marked with rectangular boxes were constrained to be monophyletic —A. Implied weights (constant of concavity, *k* = 2), no constraints. —B. Implied weights, constraints as in Fig. 7B.

0.730); that is, two steps longer than the shortest trees. The constrained analysis added some resolution to the unconstrained parts of the phylogeny. For instance, the Aylacini Rosaceae gallers (*Xestophanes* and *Diastrophus* in this analysis) grouped with the inquilines (Synergini: *Periclistus*, *Synophrus*, *Synergus*), and the two poppy gallers (*Aylax*, *Barbotinia*) appeared as a monophyletic group. None of these groups were supported in more than 50% of the bootstrap replicates, however.

When we analysed the same data matrix using implied weights (Goloboff 1993) (*k* = 2, no Pee-Wee emulation), we found one island containing nine trees with a score of (–) 21.64405, which was found in 841 of 5000 random addition sequence replicates (Fig. 8A). The length of these trees with uniformly weighted characters was 104 steps (CI = 0.404; RI = 0.738); that is, they were among the most parsimonious trees obtained in the unconstrained analysis with uniformly weighted characters. The implied weights added quite a bit of resolution to the tree.

In addition to the clades that were supported in the uniform-weights analysis, the tree supported a clade of Lamiaceae + Asteraceae gallers, including *Liposthenes* + *Neaylax* + *Aulacidea* + *Isocolus*, as well as the previously mentioned clades of poppy gallers (*Aylax*, *Barbotinia*) and Aylacini Rosaceae gallers, plus inquilines (*Xestophanes*, *Diastrophus*, *Periclistus*, *Synophrus*, *Synergus*). For the oak gall wasps (Cynipini), the tree was completely resolved, indicating close relationship between *Plagiotrochus* and *Neuroterus* as well as between *Cynips* and *Trigonaspis*. Among the higher-level clades, the Cynipidae, Cynipini, and Synergini all appeared as monophyletic and Pediaspidini (*Pediaspis*) grouped with the Cynipini (the oak gall wasps). However, the Figitidae were paraphyletic, since *Parnips* appeared as the sister group to the Cynipidae rather than to the core figitids (*Alloxysta* and *Leptopilina*). Furthermore, *Diplolepis* + Aylacini + Synergini appeared as monophyletic, just like in the constrained analysis under uniform weights.

Enforcing the monophyly of the Figitidae (and Cynipidae, Cynipini, and Synergini), we found three equally parsimonious trees with the score (–) 21.51677 in one island, which was hit 2067 times in 5000 random addition sequence replicates (Fig. 8B). With uniformly weighted characters, these trees had a length of 106 (CI = 0.396; RI = 0.730); that is, these trees were among those found in the constrained search under uniform character weights. They were identical to the unconstrained implied-weights tree, except that *Pediaspis*

Table 3 Character fit values for the unconstrained phylogenetic estimates obtained in the present study (Fig. 6A,C). The Goloboff fit (GF), consistency index (CI) and retention index (RI) are given as worst/best fit unless these values are identical. For uninformative characters, where the maximum number of steps is the same as the minimum number of steps, '—' replaces RI values.

	Uniform weights			Implied weights		
Characters	GF	CI	RI	GF	CI	RI
1. Body shape	0.60	0.33	0.00	0.6	0.33	0.00
2. Segment width	0.60/1.00	0.50/1.00	0.50/1.00	1.00	1.00	1.00
3. 4th segment	0.50	0.25	0.00	0.50	0.25	0.00
4. Head width	0.38/0.43	0.17/0.20	0.38/0.50	0.38	0.17	0.38
5. 1st segment ventrally	1.00	1.00	1.00	1.00	1.00	1.00
6. Vertex	0.33/0.50	0.14/0.25	0.46/0.73	0.43	0.20	0.64
7. Antennal area	0.75	0.5	0.91	0.75	0.50	0.91
8. Antennal seta	0.6	0.33	0.85	0.60	0.33	0.85
9. Lateral antennal seta	0.50/0.60	0.25/0.33	0.75/0.83	0.60	0.33	0.83
10. Clypeal seta	0.60	0.33	0.82	0.60	0.33	0.82
11. Vertical ocular line	1.00	1.00	—	1.00	1.00	—
12. Transversal crest	1.00	1.00	—	1.00	1.00	—
13. Labral lateral margin	0.60	0.33	0.83	0.60	0.33	0.83
14. Labral apical margin	0.43/0.60	0.43/0.60	0.77/0.88	0.60	0.60	0.88
15. Labral ventrolateral seta	0.60	0.33	0.82	0.60	0.33	0.82
16. Labral medioapical seta	0.50/0.75	0.25/0.50	0.67/0.89	0.60	0.33	0.78
17. Mandible apex shape	0.60/0.75	0.33/0.50	0.33/0.67	0.60	0.33	0.33
18. Maxilla apex shape	0.6/0.75	0.33/0.50	0.71/0.86	0.75	0.50	0.86
19. Maxilla form	0.43/0.60	0.20/0.33	0.64/0.82	0.43	0.20	0.64
20. Maxillary palp	0.75	0.50	0.92	0.75	0.50	0.92
21. Salivary orifice area	0.50/0.60	0.25/0.33	0.40/0.60	0.60	0.33	0.60
22. Labial sclerite	0.6	0.33	0.78	0.60	0.33	0.78
23. Labial palp	0.33/0.43	0.14/0.20	0.33/0.56	0.33	0.14	0.33
24. Mandible symmetry	0.75/1.00	0.50/1.00	0.50/1.00	0.75	0.50	0.50
25. Incisor shape	0.75/1.00	0.50/1.00	0.75/1.00	1.00	1.00	1.00
26. Number of mand. teeth	0.27/0.43	0.20/0.33	0.47/0.73	0.30	0.22	0.53
27. First tooth structure	1.00	1.00	1.00	1.00	1.00	1.00
28. 2nd left tooth length	0.43/0.60	0.20/0.33	0.60/0.80	0.43	0.20	0.60
29. 2nd right tooth length	0.75	0.50	0.80	0.75	0.50	0.80
30. 2nd left tooth apex	0.60/0.75	0.60/0.75	0.67/0.83	0.75	0.75	0.83
31. 2nd right tooth apex	0.60/0.75	0.60/0.75	0.50/0.75	0.75	0.75	0.75
32. Gap 2nd–3rd teeth	1.00	1.00	1.00	1.00	1.00	1.00
33. Mandible striations	0.75/1.00	0.50/1.00	0.67/1.00	1.00	1.00	1.00
34. Larval feeding	0.75/1.00	0.50/1.00	0.75/1.00	1.00	1.00	1.00

now appeared as the sister group to *Diplolepis* + Aylacini + Synergini rather than to the Cynipini.

The character consistency indices and Goloboff fits (Goloboff 1993) on the unconstrained phylogenetic estimates obtained under uniform and implied weights are presented in Table 3. Table 4 lists some putative synapomorphies of clades in the unconstrained implied-weights tree.

Discussion

Larval shape

The cynipid larva has previously been described as a ventrally curved, fusiform grub with little variation among species. A few exceptions have been noted, such as the unusually elongate larvae of *Pediaspis aceris* (sexual generation) and some other species with spacious larval chambers, such as *Diplolepis eglanteriae* and *Andricus inflator* (as *A. globuli*) (agamic generation) (Roth 1949). Although our results confirm that most cynipid larvae indeed have the ventrally curved, fusiform shape, we also discovered several distinct body shape variants. The most striking modification was seen in the larvae of *Phanacis centaureae* and *Timaspis lampsanae* (Fig. 2E), both of which are elongate, straight, dorso-ventrally depressed and almost rectangular in shape (Synapomorphy 1, Table 4; Character 2, Table 2, Appendix; Fig. 9). The same type of larva is also found in several other members of the *Phanacis/Timaspis* complex and also in *Iraella luteipes* (Nieves-Aldrey, unpublished data). Common to all these larvae is that they induce galls in herb stems. Some of these galls are cryptic and do not involve any visible external modification of the host plant; others cause a distinct swelling of the attacked portion of the stem.

Table 4 Putative synapomorphies of the unconstrained implied-weights tree (Figs 8A, 9). All synapomorphies are unique (no homoplasy among the examined taxa on the implied-weights tree) except synapomorphy 3, which displays secondary reversal in *Callirhytis glandium* and *Andricus foecundatrix*. Synapomorphy 5 shows one independent gain in *Synergus incrassatus*.

Putative synapomorphy	Group
1. Elongate, subrectangular shape of larvae in cryptic elongate gall chambers	*Phanacis–Timaspis*
2. Enlarged 1st–3rd larval body segments	*Plagiotrochus–Neuroterus–Callirhytis–Andricus foecundatrix*
3. Conspicuously rounded maxillae	Cynipini
4. Large antennal areas	Cynipini
5. Tuberculate area around salivary orifice	*Aulacidea–Neaylax–Liposthenes–Isocolus*
6. Large, blunt mandibular teeth	Cynipidae
7. Serrated inner margin of mandibles	*Alloxysta–Leptopilina*
8. Second mandibular tooth broader and blunter than incisor	Synergini
9. Sculpture on the base of the mandible	Synergini

Because of the association with a particular gall type, it is possible that the elongate larval form is a convergent adaptation; however, other evidence suggests that it may be a phylogenetically conserved, homologous trait. For instance, elongate larvae neither occur in gallers of woody stems or twigs (such as *Diastrophus*) nor in the gallers of elongate herb stolons (*Xestophanes*). This is contrary to what one would have expected if there were a strong convergent trend towards elongate larvae in these types of galls. Furthermore, in a couple of species inducing almost indistinguishable cryptic galls on stems of *Silybum marianum* (Asteraceae) belonging to two different cynipid phylogenetic lineages (*Aulacidea freesei* Nieves-Aldrey and *Phanacis zwolferi* Nieves-Aldrey), only the latter has the long elongate and depressed form whereas the larva of the former has the typical fusiform ventrally curved form (Nieves-Aldrey, unpublished data).

Further evidence for the homology of this trait is provided by the congruence with characters from adult morphology. In the most comprehensive analysis of adult morphology to date, the genera *Phanacis* and *Timaspis* form a monophyletic clade (with *Asiocynips*), and they also share affinities with *Iraella*, which forms the closest outgroup to *Phanacis* + *Timaspis* and their sister clade (Fig. 10A; Liljeblad & Ronquist, 1998).

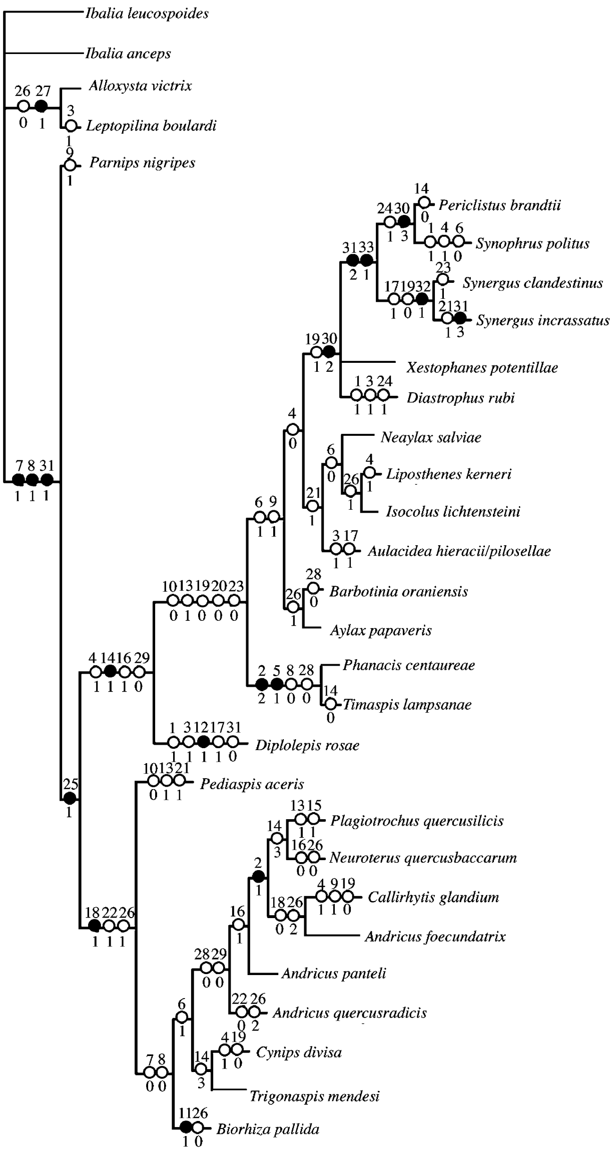

Fig. 9 Morphological larval characters optimized on a strict consensus tree based on larval data under implied weights (see also Fig. 8A). Filled circles indicate changes in characters with no homoplasy on the given tree and open circles indicate changes in homoplastic characters. Numbers above the circles indicate character number (see Appendix) and the numbers below indicate the character state change.

In several of the Cynipini species, we found that body segments 1–3 are enlarged (Synapomorphy 2, Table 4; Character 2, Fig. 9). The enlargement can be a broadening of the whole segment, as in *Neuroterus quercusbaccarum* (sexual gen.) and *Plagiotrochus quercusilicis* (sexual gen.) (Fig. 2K) or dorsolateral protuberances as in *Callirhytis glandium* (agamic gen.) (Fig. 2J) and *Andricus foecundatrix* (agamic gen.). Protuberances in the thoracic region have been illustrated before in the oak-galling *Plagiotrochus suberi* (agamic gen.) (Díaz 1973). The functional significance of the enlargement of the thoracic region is not clear, but in some species this condition appears to become more pronounced the closer the larvae gets to the prepupal and pupal stage (unpublished data). It is

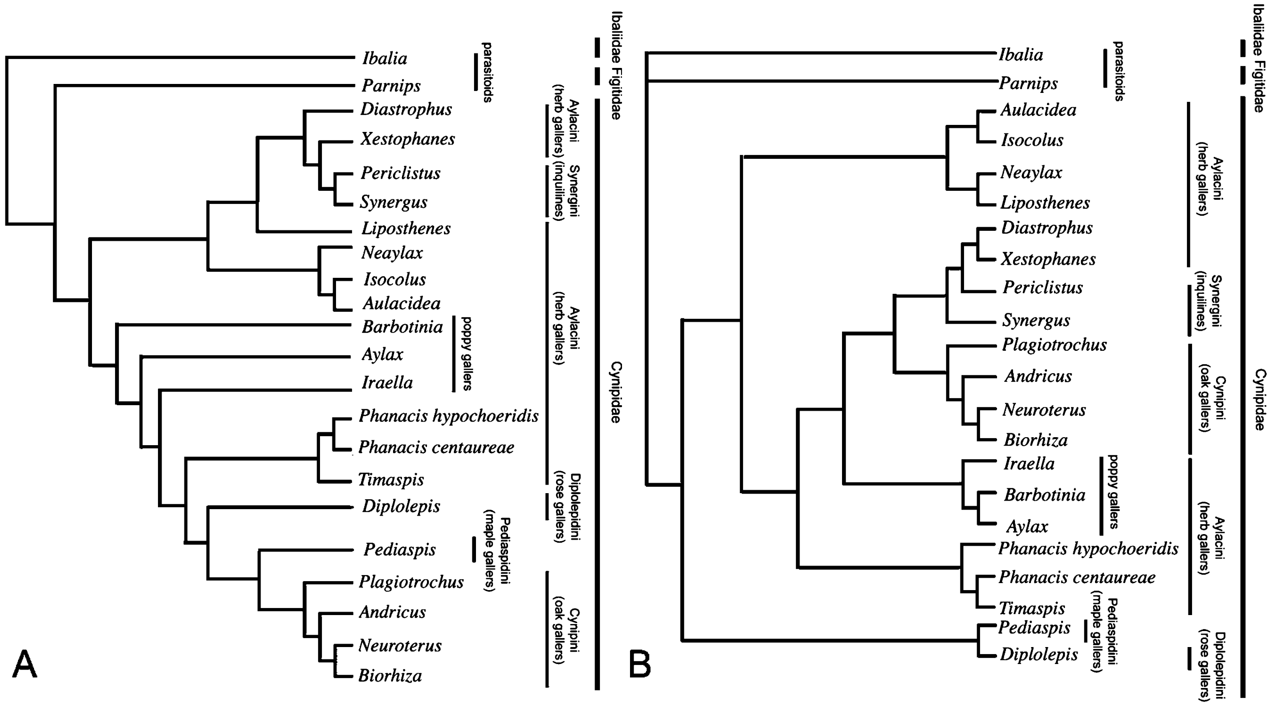

Fig. 10 A, B. Phylogenetic relationships among the studied taxa, and some additional taxa mentioned in the discussion (*Iraella luteipes* and *Phanacis hypochoeridis*), according to previous analyses. —A. Parsimony analyses of adult morphology (Ronquist 1994, 1995, 1999; Liljeblad & Ronquist 1998). The results of adult morphology analyses indicated that *Aulacidea* is poly- or paraphyletic, but the core group, which are gall inducers on Asteraceae, forms the sister group of *Isocolus*. —B. Bayesian analysis of molecular data from four genes (Nylander *et al*. 2004).

possible that the feature has some phylogenetic value; for instance, certain adult morphological features suggest that *Neuroterus* and *Plagiotrochus* may be closely related (unpublished data). The fact that the trait only occurs within the Cynipini is also notable.

We also found that two cynipid species that are apparently not closely related (Fig. 10; Ronquist 1994, 1999; Liljeblad & Ronquist 1998; Nylander *et al*. 2004), namely the *Rosa* galler *Diplolepis rosae* (Fig. 2H) and the *Rubus* galler *Diastrophus rubi* (Fig. 2F), have similar types of terminal-instar larvae. The posteriormost body segment is prolonged into a narrow cylinder-shaped extension and the 4th body segment is narrower than the rest of the segments, so that the larva is constricted anterior to the middle. Although the two species induce galls in similar types of bushes, *D. rosae* induces galls in young leaf buds whereas *D. rubi* induces stem galls, making it difficult to explain the similarity as convergent adaptation to a particular gall type. Although the median constriction in the larval body is only seen in *D. rosae* and *D. rubi*, the terminal segment is cylinder-shaped in the final-instar larva of *Pediaspis aceris* (agamic gen.) as well.

Among the insect-parasitic cynipoids, we found that the larvae of the ibaliid species are elongate while those of the figitids are more rounded. Again, there is a correlation with the larval habitat: the ibaliids develop inside the tunnels of wood-boring siricid larvae while the figitids develop inside more sphaerical structures (galls, aphid mummies, puparia). The distribution of larval shape also fits presumed phylogenetic relationships well (Ronquist 1995, 1999), possibly a by-product of the conservative nature of life-history evolution in the Cynipoidea (Ronquist 1999).

Mandibles

One of the major differences we found in the mandibles was that between the insectivorous parasitoids and the phytophagous forms. Whereas the former have mandibles with one major tooth with an acute point, the latter normally have mandibles with two or more large and blunt teeth (Synapomorphy 6, Table 4; Character 25, Table 2, Appendix; Fig. 9). The distribution of this character does fit the phylogeny, in that the phytophagous cynipids form a monophyletic lineage within the Cynipoidea (Ronquist 1995). Nevertheless, it seems likely that the structure of the mandible is largely determined by its usage.

The parasitoid larvae initially develop inside endopterygote insect larvae. Later, they use their mandibles to chew their way through the integument of the host larva, after which the latter is consumed by external feeding. The larva apparently never uses the mandibles for boring exit tunnels or for other hard work. As a consequence, the mandibles mainly need to function as scissors and therefore are relatively delicate with pointed apices. The phytophagous larvae, on the other hand, feed on plant tissue. Although this tissue (the nutritive layer of the gall) is void of tough sclerenchyma cells, the cells are still surrounded by normal cellulose walls and presumably require heavy mandibles with large, blunt teeth to be used in crushing and piercing.

Another highly interesting feature is the serrated inner margin of the larval mandible of *Alloxysta* (Figitidae: Charipinae; an aphid hyperparasitoid through other parasitic wasp larvae) and *Leptopilina* (Figitidae: Eucoilinae; a parasitoid of *Drosophila* larvae) (Synapomorphy 7, Table 4; Character 27, Table 2, Appendix; Fig. 9). The same kind of mandible is reported from another eucoiline figitid, *Kleidotoma japonica* (Huzimatu, 1940). It is possible that the serrated mandible is a synapomorphy of some core group of figitids, including eucoilines, charipines and probably a number of other figitid subfamilies as well. An apparently more primitive kind of mandible, with a few teeth along the inner margin, is present in ibaliids as well as in *Parnips nigripes* (Figitidae: Parnipinae), the sister group of all other figitids (Ronquist 1999; Ronquist & Nieves-Aldrey 2001). A mandible with a serrated inner margin has also been described from some endoparasitic ichneumonoid larvae, where it is believed to help the mature parasitoid larva escape from the host larva (Short 1952; Hagen 1964).

The mandibles of the Synergini species are highly characteristic. In all the examined species, including both rose inquilines (*Periclistus*) and oak inquilines (*Synergus*, *Synophrus*), the second tooth is very broad and there is a pattern of vertical and sometimes horizontal striations on the base of the mandibles (Synapomorphies 8 and 9, Table 4; Characters 30, 31 and 33, Table 2, Appendix; Fig. 9). Both of these traits are unique to inquilines among the larvae examined here. In addition, the mandibles of *Synophrus politus* and *Periclistus brandtii* are both strongly asymmetrical (Character 24, Fig. 7C), in that the second tooth is well developed on the left mandible but almost totally reduced on the right mandible; this asymmetry does not exist in the examined *Synergus* species. The mandibles of the Rosaceae-galling Aylacini species *Diastrophus rubi* and *Xestophanes potentillae* are similar to those of the Synergini in being slightly more asymmetrical and having a larger second tooth than usual for cynipid larvae.

Inquiline larvae develop in gall chambers that are essentially identical to those of gall-inducing species; therefore, it is difficult to explain the shared inquiline traits as convergences. Instead, these mandibular characters provide evidence for monophyly of the inquilines. This agrees well with previous analyses of adult morphology, solidly supporting inquiline monophyly (Fig. 10A; Ronquist 1994; Liljeblad & Ronquist 1998). Adult morphology also suggests that the Aylacini Rosaceae gallers (*Diastrophus*, *Gonaspis*, *Xestophanes*) are the closest relatives of the inquilines (Liljeblad & Ronquist 1998), consistent with the finding that they share some similarities with the inquilines in their larval mandibles. Interestingly, recently published molecular data suggest that the rose inquilines may be more closely related to the Aylacini Rosaceae gallers than to the oak inquilines (Fig. 10B; Nylander *et al.* 2004). Clearly, this is difficult to reconcile with the larval characters, particularly the similarities between *Periclistus* (a rose inquiline) and *Synophrus* (an oak inquiline, the latter closely related to *Synergus* according to both adult morphological (Ronquist 1994, 1999; Liljeblad & Ronquist 1998) and molecular data (unpublished data).

Labium

A structure of potential phylogenetic importance is the tuberculate pattern in the labial area surrounding the salivary orifice in the larvae of some Aylacini species, namely *Neaylax salviae* (Fig. 4B), *Liposthenes kerneri* (Fig. 4C), *Aulacidea hieracii* (Fig. 4E), and *Isocolus lichtensteini* (Fig. 4D; Synapomorphy 5, Table 4; Character 21, Table 2, Appendix; Fig. 7C). A similar structure also occurs in one of the Synergini species, *Synergus incrassatus* (Fig. 4A). Although the character is obviously independently derived in the latter species, it may be a good synapomorphy for the Aylacini species in which it is present.

In their analysis of adult morphology, Liljeblad & Ronquist (1998) identified a weakly supported clade of Aylacini species, the *Isocolus–Neaylax* group. It consisted of *Cecconia* (a galler of *Valerianella*), two lineages of Asteraceae gallers (*Antistrophus* and *Isocolus* + *Aulacidea*), and all Lamiaceae-galling cynipids except *Liposthenes* (among them *Neaylax*; Fig. 10A). Recently published molecular data (Nylander *et al.* 2004) suggest that *Liposthenes* should also be included in the *Isocolus–Neaylax* group (Fig. 10B). The tuberculate labial area in terminal-instar larvae supports a more widely circumscribed group, since this unusual feature is also present in *Liposthenes*. In fact, the turberculate larval labium is the best putative morphological synapomorphy yet for the group in the broad sense (including *Liposthenes*).

Another unusual labial feature is found in *Papaver*-galling Aylacini. In both *Aylax papaveris* (Fig. 4I) (this paper) and *Iraella luteipes* (unpublished data), the salivary opening is shaped like a vertical crevice, while in *Barbotinia* it is situated in a funnel-shaped depression. If these two states were homologous, they would provide support for the monophyly of the *Papaver*-galling Aylacini. Again, this would be congruent with molecular data (Fig. 10B; Nylander *et al.* 2004) but in weak conflict with adult morphology, which suggests that the *Papaver*-galling Aylacini form a paraphyletic basal grade of cynipid lineages (Fig. 10A; Liljeblad & Ronquist, 1998).

However, the labial crevice/funnel character appears to conflict with the shape of the larva, suggesting affinities between *Iraella* on one hand and *Phanacis* and *Timaspis* (Asteraceae gallers) on the other (see above). The occurrence of a vertical crevice around the salivary opening in the larva of *Synophrus politus*, a member of the Synergini, shows that convergence has occurred in this character and casts some doubt on the homology of the states present in the *Papaver* gallers.

Phylogenetic implications

Although the uniformly weighted analysis of larval characters supported only a few groups (Fig. 7A), the close correspondence between the implied-weights analysis (Fig. 8A) and previous phylogenetic results (Fig. 10) indicated that there was nevertheless a considerable amount of phylogenetic information in the larval data. The only major difference between the unconstrained implied-weights tree (Fig. 8A) from the larval data and previous analyses of adult morphology (Fig. 10A) was in the rooting of the Cynipidae tree. Adult morphology suggests that the insect-parasitic cynipoids should attach to the branch between the Aylacini Rosaceae gallers + Synergini and the rest of the cynipid tree, whereas the larval data attach them to the branch between *Diplolepis* (+ Aylacini + Synergini) and *Pediaspis* (+ Cynipini). The unexpected larval result could simply be an artifact of the small number of studied parasitoid larvae, causing difficulties in rooting the Cynipidae tree correctly. Further study of the insect-parasitic cynipoid larvae might be able to clarify whether this is the case.

When analysed in more detail, four additional conflicts between the larval tree (Fig. 8A) and previously obtained adult-morphology trees (Fig. 10A) emerge. First, larval data did not group the recently described genus *Parnips* with the core figitids, as might have been expected based on adult morphology (Ronquist 1999; Ronquist & Nieves-Aldrey 2001), but with the Cynipidae. Again, this could be an erroneous result obtained because of the small number of parasitoid larvae, particularly figitid larvae, studied here. In adult morphology, *Parnips* is known to share a number of unusual plesiomorphies with *Barbotinia*, a basal lineage of gall wasps (Fig. 10A); similar plesiomorphies could easily be mistaken for apomorphies within the context of a small outgroup taxon sample, such as the larval sample studied here.

Two of the minor conflicts concern the poppy gallers (*Aylax* and *Barbotinia*) and the *Isocolus–Neaylax* clade, both of which have been discussed above. The last conflict occurs within the inquilines. The larval data suggest that the oak inquiline *Synophrus politus* is more closely related to the rose inquiline *Periclistus* than to the other studied oak inquilines, the two *Synergus* species (Figs 7, 8). This is highly unlikely to reflect true relationships. Traditional taxonomy, *post hoc* analysis of adult morphology (Ronquist 1994, 1999), and analysis of molecular sequences (unpublished data) all support monophyly of a clade consisting of the genera *Synophrus*, *Saphonecrus*, and *Synergus*, all of which are inquilines in Cynipini galls on oaks. Actually, there has been some doubt in the literature whether *Synophrus* is an inquiline or a true gall inducer, since galls containing *Synophrus* are very different from all potential host galls. However, recent observations (unpublished data) suggest that the *Synophrus* 'gall' is the result of conspicuous modification of a small host gall, namely that of the *Andricus burgundus* complex of species (Cynipidae: Cynipini).

A possible reason for the anomalous larval result concerning inquiline relationships is that the apparent synapomorphies of *Periclistus* and *Synophrus* are really inquiline synapomorphies that have been secondarily modified into an apparently primitive state in the studied *Synergus* species. For instance, in *Periclistus* and *Synophrus* the second tooth of the right mandible is reduced, whereas it is conspicuously large in the *Synergus* species. While it may be more parsimonious to interpret the large *Synergus* tooth as homologous to the primitive, nonreduced tooth of most other cynipid larvae, it is remarkable that it should be so much larger in the two *Synergus* species than in all other cynipids. Possibly, this could indicate that the large tooth in *Synergus* was independently derived from the broad and reduced tooth present in *Periclistus* and *Synophrus*. Further study of *Synergus*-complex larvae might be able to shed additional light on this issue.

Perhaps the most important difference between the larval (Figs 7, 8) and molecular trees (Fig. 10B) is the support for inquiline monophyly in the former but not in the latter. Larval support for inquiline monophyly is primarily due to the mandibular characters discussed above, and agrees well with results from previous analyses of adult morphology (Ronquist 1994; Liljeblad & Ronquist 1998). However, Bayesian combined analysis of molecular data and adult morphology fails to retrieve monophyletic inquilines (Nylander *et al.* 2004), and addition of the larval data is unlikely to change this result. Many systematists would probably dismiss the morphological result as being caused by convergent similarities among inquilines due to their life mode. Ronquist (1994) investigated this possibility for adult morphology using special techniques to screen out the effect of hypothesized convergent trends and concluded that the support for inquiline monophyly was not due to convergent similarities in conflict with true relationships.

Another way of exploring the plausibility of strong convergent trends causing inquiline similarities is to examine each of the putative morphological synapomorphies of inquilines individually. If a feature is convergent, it should be possible to find some link between it and the inquiline life mode. Surprisingly often, this is difficult. For instance, the terminal-instar larvae of inquilines live in the same environment as gall-inducing larvae and feed on the same type of plant tissue, making it difficult to explain why the inquiline mandibles should show unique similarities. Indeed, larval support for inquiline monophyly suggests that we need to take the alternative hypothesis seriously, namely that the morphological similarities among inquilines are true synapomorphies and that the molecular result is incorrect, perhaps caused by imperfections in current models of molecular evolution (Nylander *et al*. 2004).

Although there are several points of conflict, as discussed above, the larval data mostly support previous phylogenetic results and simply add new characters in support of established groupings. For instance, although the oak gall wasps (Cynipini) have always been considered a natural group, and have been supported as monophyletic in both adult morphology and molecular analyses (Fig. 10), there have previously been relatively few known morphological synapomorphies for this clade. The larval data add several new putative synapomorphies, including the round maxillae and the large antennal areas (Synapomorphies 3 and 4, Table 4; Characters 7 and 18, Table 2, Appendix; Figs 3J–L, 4K,L and 9).

Concluding remarks

Hopefully, our study demonstrates that cynipoid larvae offer a surprisingly rich source of external morphological characters. Comparisons of the larval phylogenetic signal with the results based on other types of data indicate that the larval characters can potentially be reliable indicators of relationships. However, larval characters are not only interesting from a phylogenetic point of view. Study of the morphological variation in larvae will also help us more reliably separate cynipoid larvae of different taxa. The latter is particularly interesting for the gall-associated species, since very similar gall-inducing, inquilinous and insect-parasitic cynipoid larvae may inhabit the same plant galls, and the risk of misidentification is considerable. This study has elucidated several consistent differences between these three types of larvae, although others probably remain to be discovered.

Undoubtedly, further study of final-instar larvae will be rewarding from the perspectives of both phylogeny and larval identification. In particular, there is an urgent need to study a better sample of terminal-instar larvae of the insect-parasitic cynipoids. Even for the phytophagous gall-inducers and inquilines, larvae of many important taxa remain to be described in detail.

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Appendix

Morphological characters of cynipoid larvae used for phylogenetic analysis.

Larval body

1. Larval body: (0) gradually tapering towards the posterior end (Fig. 2D,J,I); (1) abruptly tapering towards posterior end (Fig. 2F,H).
2. Segments of the larval body: (0) are widest approximately around the middle, giving larva a fusiform appearance (Fig. 2G); (1) are widest at body segments 1–3 (Fig. 2J); (2) have approximately equal width, giving larva a subrectangular appearance (Fig. 2E) (unordered).
3. Fourth body segment (ventral view) is: (0) not narrower than the 5th segment (Fig. 2E,I); (1) clearly narrower than the 5th segment (Fig. 2F,H).
4. Head width (ventral view): (0) clearly more than half the width of the first body segment (Fig. 2C,K); (1) less than half the width of the first body segment (Fig. 2H,J).
5. Anterior and posterior margins of ventral part of first body segment: (0) are more or less parallel-sided, forming an even edge posterior to the head or converge slightly to a thinner ventralmost area (Fig. 2D) (1) are almost touching at the ventralmost point (Fig. 2E).

Head region

6. Vertex of head: (0) rounded (Fig. 3E); (1) slightly to deeply incised medially (Fig. 3B,D).
7. Antennal area: (0) large and conspicuous (Fig. 3J); (1) small and inconspicuous (Fig. 3F).
8. Antennal seta: (0) absent (Fig. 3F,J); (1) present (Fig. 3E,H).
9. Lateral seta (laterad of antennal area): (0) absent (Fig. 3F,H); (1) present (Fig. 3E).
10. Clypeal seta: (0) present (Fig. 3G); (1) absent (Fig. 3J).
11. Vertical ocular line: (0) absent (Fig. 3G); (1) present (Fig. 3K).
12. Transversal crest on upper frons: (0) absent (Fig. 3E); (1) present (Fig. 3H).

Mouthparts

Labrum

13. Lateral margins: (0) parallel or subparallel (Fig. 4J); (1) converging towards the basal end (Fig. 4E).
14. Apical margin: (0) convex (Fig. 4G); (1) straight (Fig. 4C); (2) slightly concave (Fig. 4J); (3) strongly incised (Fig. 4K,L) (ordered).
15. Ventrolateral seta: (0) absent (Fig. 4J); (1) present (Fig. 4B).
16. Medioapical seta: (0) absent (Fig. 4J) (1) present (Fig. 4D).
17. Mandible: (0) More or less covered by labrum (Fig. 4C,F); (1) exposed (Fig. 4A,E).

Maxillae

18. Apex of maxilla: (0) pointed (Fig. 4E); (1) rounded (Fig. 4L).
19. Apical half of maxilla: (0) not marked, evenly sloping inwards (Fig. 4C); (1) markedly bulging outwards before curving inwards (Fig. 4L).
20. Maxillary palp: (0) conspicuous (Fig. 4B); (1) absent or inconspicuous (Fig. 4J).

Labium

21. Area surrounding salivary opening: (0) smooth (Fig. 4I,H,J); (1) with tuberculate sculpture (Fig. 4B,D).
22. Labial sclerite: (0) well defined (Fig. 4E); (1) not marked (Fig. 4K).
23. Labial palp: (0) clearly present (Fig. 4G); (1) absent or inconspicuous (Fig. 4J).

Mandibles

24. Left and right mandibles: (0) more or less symmetrical (Fig. 6M,N); (1) strongly asymmetrical (Fig. 5J,K).
25. Structure of mandibular incisor: (0) sharp, thin and slender (Fig. 5A,C,E); (1) strong and blunt (Fig. 5F,H,N).
26. Number of teeth on left mandible: (0) one (Fig. 6L,O); (1) two (Figs 5M, 6G); (2) three or more (Fig. 6F,J) (ordered 0, 1, 2).
27. Structure of first tooth: (0) straight, even inner margin (Fig. 5A,N); (1) serrated inner margin (Fig. 5C).
28. Second tooth of right mandible: (0) reaching at least to the middle of the apical tooth (Fig. 6N); (1) clearly shorter than half the length of the apical tooth (Fig. 6B).
29. Second tooth of left mandible: (0) reaching at least to the middle of the apical tooth (Figs 5O, 6C); (1) clearly shorter than half the length of the apical tooth (Figs 5A, 6K).
30. Shape of apex of second tooth of the right mandible: (0) sharply acute (Fig. 6N); (1) slightly blunt (not illustrated); (2) strongly rounded (Fig. 6B); (3) truncate (Fig. 5K) (unordered).
31. Shape of apex of second tooth of the left mandible: (0) sharply acute (Fig. 5A,C); (1) slightly blunt (Figs 5M, 6H); (2) strongly rounded (Fig. 5F,J); (3) truncate (Fig. 5I) (unordered).
32. Deep and wide gap separating the second and the third tooth: (0) absent (Figs 5J, 6A,E); (1) present (Fig. 5I).
33. Surface of mandible: (0) more or less smooth (Figs 5B, 6J); (1) sculptured at the base of the teeth with strong longitudinal and/or transversal striations (Fig. 5H,J).

Ecology

34. Larval feeding: (0) parasitoid of insect larva (1) plant feeder (phytophagous).