COMPARATIVE MORPHOLOGY OF THE OVIPOSITOR OF SOME PARASITIC HYMENOPTERA IN RELATION TO CHARACTERISTICS OF THEIR HOSTS

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Abstract

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Although the structure of the ovipositor of parasitic Hymenoptera is largely uniform, interspecific variation in its morphology can be observed. Such variability may be related to the diversity of hosts attacked. To verify such an hypothesis, we compared, using correspondence analysis, the morphological characteristics of the ovipositors of 20 species in three categories: (*i*) species belonging to the same taxonomic unit and attacking the same type of host, (*ii*) species belonging to the same taxonomic unit but attacking different types of host, and (*iii*) species belonging to different taxonomic units but attacking the same type of host. Results show that variability in some morphological traits of the ovipositor can be related to host characteristics. Adaptive convergence in morphological variations observed between species is discussed.

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Résumé

L'ovipositeur des Hyménoptères parasites présente une structure très constante mais il existe de grandes variations morphologiques entre les espèces. Ces variations pourraient être reliées à la diversité des hôtes attaqués. Pour vérifier cette hypothèse, nous avons comparé, en utilisant une analyse des correspondances, les caractères morphologiques de l'ovipositeur de 20 espèces dans les trois cas suivants: (*i*) des espèces appartenant à la même unité taxonomique et attaquant le même type d'hôtes, (*ii*) des espèces appartenant à la même unité taxonomique mais attaquant des hôtes de types différents et (*iii*) des espèces appartenant à des unités taxonomiques différentes mais attaquant le même type d'hôtes. Les résultats montrent que les variations morphologiques de certains caractères de l'ovipositeur peuvent être mises en relation avec des caractéristiques de l'hôte importantes pour la réussite du processus d'infestation. L'éventuelle signification adaptative de la diversité morphologique observée entre les espèces est discutée.

Introduction

The ovipositor of parasitic Hymenoptera is a specialized organ with which the female probes and drills the substrate where the host lives, pierces the integument of the host, injects substances from the accessory glands, perceives stimuli involved in the host selection process, and guides and lays eggs.

Hosts attacked by these parasitoids are diverse. Members of most pterygote orders, of all developmental stages, fixed or mobile and exposed or concealed in different substrates, can be parasitized. This wide range of situations produces a diversity of constraints to which the ovipositor must adapt. Morphological and functional features of the ovipositor should, therefore, vary with host diversity.

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It has been shown that studies of the ovipositor can clarify phylogenetic relationships in some taxa of Hymenoptera (Fergusson 1988; Austin 1990; Quicke, Ficken, and Fitton 1992; Quicke, Fitton, and Ingram 1992; Quicke et al. 1994), but there are few studies on the morphology of the ovipositor from an adaptive and functional point of view. Usually, only a few morphological traits are considered. For example, Heatwole and Davis (1965) and Gibbons (1979) showed that in three species of the genus *Megarhyssa*, the length of the ovipositor is the principal factor involved in host sharing and in their derivation from a common ancestor. The importance of ovipositor length in host utilization has also been studied in oophagous parasitoids (Livingstone and Yacoob 1986; Vu Quang Con and Nguyen Van San 1987).

Here, we identify morphological traits of the ovipositor that are associated with host characteristics. The structure, sensory equipment, and functioning of the ovipositor from 20 species are analysed mainly by means of electron microscopy (Le Ralec 1991). Results are synthesized using a multiple correspondence analysis to group the species according to ovipositor structure. These groups are compared with the known systematic position of the parasitoids and with different features of their hosts.

Material and Methods

Parasitoid Species. Twenty species belonging to four superfamilies and eight families were chosen (Table 1). This choice allowed the following comparisons to be made:

Species belonging to the same taxonomic unit (family) and attacking the same type of host. Aphidiinae (Braconidae, Ichneumonoidea): *Aphidius uzbekistanicus* Luzhetzki, *Ephedrus cerasicola* Stáry, *Ephedrus plagiator* (Nees), *Lysiphlebus fabarum* (Marshall), *Lysiphlebus testaceipes* (Cresson), *Praon volucre* (Haliday), and *Trioxys angelicae* (Haliday): parasitoids of aphids.

Eucoilidae (Cynipoidea): *Ganaspis xanthopoda* (Ashmead), *Leptopilina boulardi* (Barbotin, Carton et Kelner-Pillault), and *Leptopilina heterotoma* (Thompson): parasitoids of larvae of *Drosophila*.

Species belonging to the same taxonomic unit (superfamily or family) but attacking different types of host. Cynipoidea: Eucoilidae, *G. xanthopoda*, *Leptopilina boulardi*, and *Leptopilina heterotoma*, attacking larvae of *Drosophila* vs. Charipidae, *Alloxysta victrix* (Westwood) and *Phaenoglyphis* sp., endophagous hyperparasitoids of aphids.

Encyrtidae (Chalcidoidea): *Ageniaspis fuscicollis praysincola* (Silvestri), a parasitoid of lepidopteran eggs vs. *Epidinocarsis lopezi* (De Santis) and *Leptomastix dactylopii* (Howard), parasitoids of mealybugs.

Aphelinidae (Chalcidoidea): *Aphelinus abdominalis* Dalman, a parasitoid of aphids vs. *Encarsia formosa* Gahan, a parasitoid of whiteflies.

Species belonging to different taxonomic units (superfamily or family) but attacking the same type of host. Aphidiinae (Ichneumonoidea) (*Aphidius uzbekistanicus*, *Ephedrus cerasicola*, *Ephedrus plagiator*, *Lysiphlebus fabarum*, *Lysiphlebus testaceipes*, *Praon volucre*, and *Trioxys angelicae*) and Aphelinidae (Chalcidoidea) (*Aphelinus abdominalis*), primary parasitoids of aphids.

Megaspilidae (Ceraphronoidea), *Dendrocerus carpenteri* (Curtis), and Pteromalidae (Chalcidoidea), *Asaphes vulgaris* Walker, ectophagous hyperparasitoids of aphids.

Encyrtidae (Chalcidoidea), *Ageniaspis fuscicollis*, and Trichogrammatidae (Chalcidoidea), *Trichogramma brassicae* Bezdenko, parasitoids of lepidopteran eggs.

Electron Microscopy. Scanning electron microscopy. Most specimens were fixed in 2.5% glutaraldehyde buffered to pH 7.4 for 1 h, washed in 0.1 *M* sodium cacodylate buffer, gradually dehydrated in alcohol or in acetone, and critical-point-dried. When fixation was not necessary, samples were simply progressively dehydrated and air-dried.

TABLE 1. Parasitoid species and their hosts

Parasitoid			Host		
Species	Classification	Type of parasitism	Species	Classification	Attacked stage
*Aphidius uzbekistanicus**	Aphidiinae	End. I	*Sitobion avenae*	Aphididae (Hemiptera)	Larvae – Adults
Ephedrus cerasicola	Aphidiinae	End. I	*Myzus persicae*	Aphididae (Hemiptera)	Larvae – Adults
*Ephedrus plagiator**	Aphidiinae	End. I	*Sitobion avenae*	Aphididae (Hemiptera)	Larvae – Adults
Lysiphlebus fabarum	Aphidiinae	End. I	*Aphis* sp.	Aphididae (Hemiptera)	Larvae – Adults
Lysiphlebus testaceipes	Aphidiinae	End. I	*Aphis gossypii*	Aphididae (Hemiptera)	Larvae – Adults
*Praon volucre**	Aphidiinae	End. I	*Sitobion avenae*	Aphididae (Hemiptera)	Larvae – Adults
Trioxys angelicae	Aphidiinae	End. I	*Aphis gossypii*	Aphididae (Hemiptera)	Larvae – Adults
Ageniaspis fuscicollis praysincola	Encyrtidae	End. I	*Prays oleae*	Hyponomeutidae (Lepidoptera)	Eggs
*Epidinocarsis lopezi**	Encyrtidae	End. I	*Phenacoccus manihoti*	Pseudococcidae (Hemiptera)	Larvae
*Leptomastix dactylopii**	Encyrtidae	End. I	*Planococcus citri*	Pseudococcidae (Hemiptera)	Larvae
Aphelinus abdominalis	Aphelinidae	End. I	*Macrosiphum euphorbiae*	Aphididae (Hemiptera)	Larvae – Adults
Encarsia formosa	Aphelinidae	End. I	*Trialeurodes vaporariorum*	Aleyrodidae (Hemiptera)	Larvae
Trichogramma brassicae	Trichogrammatidae	End. I	*Ostrinia nubilalis*	Pyralidae (Lepidoptera)	Eggs
*Asaphes vulgaris**	Pteromalidae	Ect. II	*Ephedrus plagiator*	Aphidiidae (Hymenoptera)	Larvae 4 – Pronymphs
Ganaspis xanthopoda	Eucoilidae	End. I	*Drosophila melanogaster*	Drosophilidae (Diptera)	Larvae
*Leptopilina boulardi**	Eucoilidae	End. I	*Drosophila melanogaster*	Drosophilidae (Diptera)	Larvae
Leptopilina heterotoma	Eucoilidae	End. I	*Drosophila melanogaster*	Drosophilidae (Diptera)	Larvae
*Alloxysta victrix**	Charipidae	End. II	*Aphidius uzbekistanicus*	Aphidiidae (Hymenoptera)	Larvae 1-2-3
Phaenoglyphis sp.	Charipidae	End. II	*Aphidius uzbekistanicus*	Aphidiidae (Hymenoptera)	Larvae 1-2-3
*Dendrocerus carpenteri**	Megaspilidae	Ect. II	*Aphidius uzbekistanicus*	Aphidiidae (Hymenoptera)	Larvae 4 – Pronymphs

End. I = primary endoparasite; End. II = secondary endoparasite; Ect. II = secondary ectoparasite; * species reared in the laboratory.

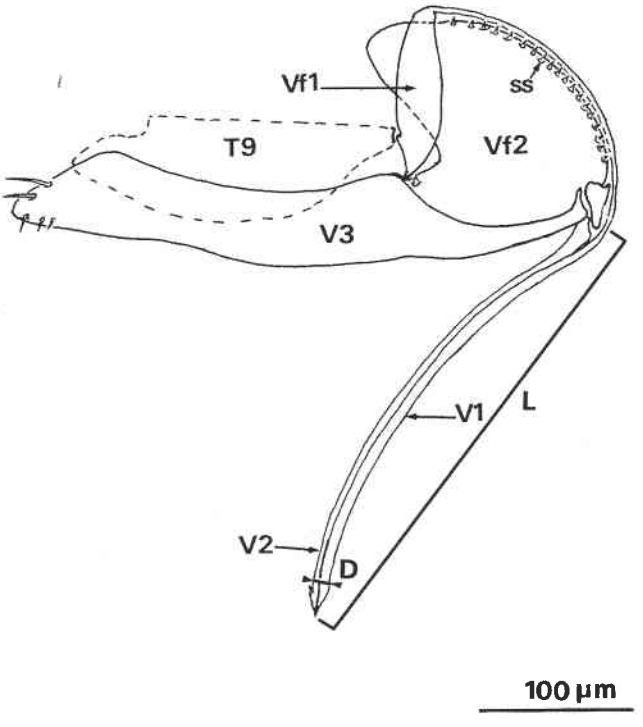

FIG. 1. Diagram of the ovipositor of a hymenopterous parasitoid, *Epidinocarsis lopezi* (Encyrtidae) (lateral aspect). [*D* = ovipositor diameter; L = ovipositor length; ss = styloconic sensilla; T9 = tergite 9; V1, V2, and V3 = first, second, and third valvulae; Vf1, Vf2 = first and second valvifers.]

In some instances, complementary cleaning methods were used to obtain samples with clearly observable surfaces; such specimens were either sonicated at the end of the dehydration period or enzymatically scoured in 5% trypsin for 1 h before fixation.

Once dry, samples were sputter-coated with fine gold and observed in a JEOL J.S.M.35 microscope.

Transmission electron microscopy. After dissection in Ringer's solution, samples were fixed in 1% osmic acid buffered to pH 7.4, for 2 h, washed in 0.1 *M* sodium cacodylate buffer, gradually dehydrated in acetone, and included in an Epon-araldite resin. Thin sections (<0.5 µm) were collected on colloid grids, contrasted with uranyl acetate and lead citrate, and finally observed in a JEOL 100 CX microscope.

Traits Studied. Snodgrass (1933) recognized the uniformity in basic organization of female genitalia among Hymenoptera. In spite of disagreement concerning homology of certain structures, further studies (Smith 1968, 1969, 1970*a*, 1970*b*; Copland and King 1971, 1972*a*, 1972*b*, 1972*c*; Copland et al. 1973; Copland 1976; Matsuda 1976) have confirmed this structural uniformity. Despite the fact that many authors used the terminology of Scudder (1971), we prefer that of Snodgrass (1933) and Matsuda (1976), which has been used widely to describe hymenopterous ovipositors and has no implications concerning the still unproved sternal or appendicular origin of the valves.

The ovipositor of parasitic Hymenoptera consists of three pairs of valvulae borne by two pairs of valvifers (Fig. 1). The second valvifers (Vf2) bear ventrally the second valvulae (V2) and posteriorly the third valvulae (V3). The internal concave faces of the third valvulae

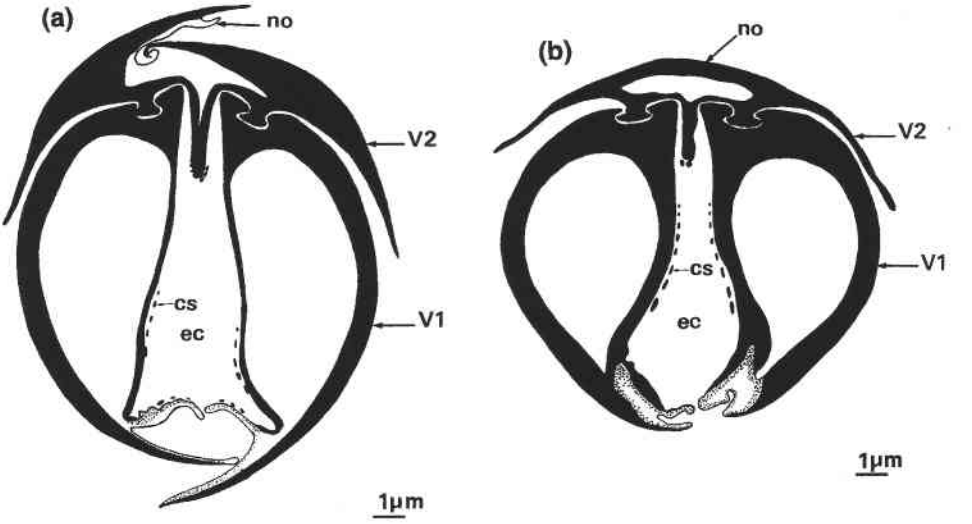

FIG. 2. Tranverse sections through (*a*) proximal and (*b*) distal regions of the ovipositor of *Epidinocarsis lopezi*. [cs = cuticular scale; ec = egg-canal; no = notum; V1 = first valvula; V2 = second valvula.] The notum is membranous (*a*) except at the tip of the second valvulae (*b*).

surround the first and second valvulae when they are not in use. The first valvulae (V1), borne by the first valvifers (Vf1), are positioned ventrally. The second valvulae are fused to each other along their lengths, their fused dorsal edges forming the notum (no) (Smith 1969) (Figs. 2*a*, *b*, 3). The interlocked first and second valvulae form the shaft of the ovipositor and enclose the egg-canal (ec). The surface of the latter is covered with cuticular scales (= spines, ctenidia, or pectines) that help the eggs to advance posteriorly within the shaft of the ovipositor when the valvulae are sliding longitudinally upon each other (Austin and Browning 1981). The shaft is the only part penetrating the substrate where the egg is laid. One of its functions is to bore a hole. Either the first or second valvulae bear, at their tips, serrations forming a saw-shaped structure used to perforate plant tissues or host integument.

To describe variations observed in basic organization among ovipositors of different species, a set of morphological and functional traits was selected (Table 2). All sense organs found on the different parts of the ovipositor were inventoried. Using transmission electron microscopy, the nature of these sensilla was determined for females of five species (*Praon volucre*, *Ephedrus plagiator*, *Epidinocarsis lopezi*, *Leptopilina boulardi*, *Dendrocerus carpenteri*). From these observations and the literature (Altner 1977; Altner and Prillinger 1980; Zacharuk 1980, 1985; Keil and Steinbrecht 1984; Städler 1984; McIver 1975, 1985), a function for the sense organs of 15 other species was proposed. Possible mechanoreceptors, proprioreceptors, and contact chemoreceptors (associated or not with mechanoreceptors) were found. Their number, structure, function, and distribution were compared among the 20 species.

Thirty-four variables (Table 2) were selected to compare the ovipositors of 19 parasitoid species (*Phaenoglyphis* sp. was not considered in the analysis because of missing data). To complete the analysis, seven additional variables, describing host characteristics, were used. Quantitative traits were allocated to distinct classes to transform them into qualitative variables. Scores were assigned to each species for 41 variables (Tables 2, 3). Table 3 was then transformed in a 19 by 112 matrix so that scores for each species could be represented by 0 or 1. This binary table was analysed using PROC CORRESP of the SAS/STAT package

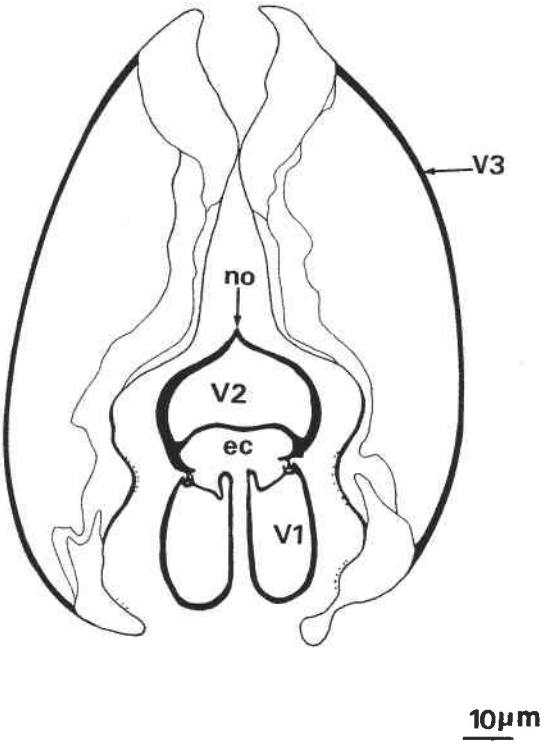

FIG. 3. Tranverse section through the ovipositor of *Aphidius uzbekistanicus*. [ec = egg-canal; no = notum; V1 = first valvula; V2 = second valvula; V3 = third valvula.] The notum is sclerotized along the length of the second valvula.

(SAS Institute Inc. 1990). This procedure was used to perform a multiple correspondence analysis of Table 3 (Lebart et al. 1977), which, in fact, corresponds to a weighted principal component analysis of a multi-way contingency table. The analysis projects the 19 species onto successive axes with decreasing importance (i.e. inertia), according to scores of the different descriptive variables. Only the first 34 variables (Table 3) were used to compute the coordinates of the species (i.e. "active" variables), the others being declared supplementary. Therefore, species with coordinates close to each other had ovipositors with similar morphological traits. Distances between species were graphically described in a dendrogram (hierarchical ascending clustering) produced by PROC CLUSTER (option: CENTROID) of the SAS/STAT package (SAS Institute Inc. 1990). Coordinates of species on the first 10 axes only were taken into account in this computation.

Results

Along the first axis of the multiple correspondence analysis, the seven members of Aphidiinae appear lumped together (Fig. 6*a*) and are set well apart from other species. The second axis mainly separates the eucoilids (parasitoids of *Drosophila*) from the ectophagous hyperparasitoids of aphids and from the encyrtid parasitoids of mealybugs (Fig. 6*a*). *Ageniaspis fuscicollis*, an oophagous encyrtid, is isolated from the other Encyrtidae; this separation is much more clear on the fourth axis (Fig. 6*b*). Both third and fourth axes clearly separate the ectophagous hyperparasitoids of aphids from the two primary mealybugs parasites. The fourth axis separates the two aphelinids, and the *Ephedrus* spp. from other aphidiines.

TABLE 2. Variables and scores used to describe interspecific differences among ovipositors of selected parasitic Hymenoptera

Variables	Scores			
	1	2	3	4
1: Female body length (μm)[1]	<1450	1450–1650	1650–2045	>2045
2: Ovipositor length (μm)[2]	<170	170–250	250–400	>400
3: Ovipositor diameter (μm)[3]	<7	7–9.5	9.5–19.5	>19.5
4: Ovipositor rigidity	Rigid	Flexible		
5: Ovipositor tip morphology	Very sharp, with strongly marked denticulations	Very sharp, with weakly marked denticulations or none	Pointed with strongly marked denticulations	Pointed with weakly marked denticulations
6: Serrations	None	On first valvulae	On second valvulae	
7: Number of serrations	<6	6	>6	
8: Notum of second valvula [4]	Cuticular	Membranous pre-apically		
9: Form of cuticular scales in egg-canal[5] (Fig. 4)	Ctenidia	Spines	Ctenidia + spines	
10: Arrangement of cuticular scales in egg-canal (Fig. 4)	Overlapping	In rows, non-overlapping		
11: Number of sensillar types on third valvulae (Fig. 5*f*, *g*)	0	1	2	3
12: Number of trichoid sensilla on third valvulae	<4	4–11	>11	
13: Number of styloconic sensilla on third valvulae	0	1–5	>5	
14: Number of other sensilla on third valvulae (basiconic, campaniform)	None	1 or more		
15: Sensillar area at tip of third valvulae [6] (Fig. 5)	No	Yes		
16: Sensillar distribution on ovipositor shaft	Only on the first valvulae	On both the first and second valvulae		
17: Total number of sensilla on ovipositor shaft	<20	20–30	>30	
18: Number of sensillar types on ovipositor shaft	1 or 2	3	4 or 5	
19: Number of trichoid sensilla on ovipositor shaft	None	1 or more		
20: Number of type 1 (small-size) campaniform sensilla	0	1–8	>8	
21: Number of type 2 campaniform sensilla (large-size)	0	1 or more		
22: Number of basiconic or styloconic sensilla	0	1–8	>8	
23: Number of mechanoreceptor 'pores'	0	1 or more		
24: Number of type A[7] chemoreceptors	0	1 or more		
25: Number of type B [7] chemoreceptors	0	1 or more		

TABLE 2 (*Concluded*)

Variables	Scores				
	1	2	3	4	
26: Arrangement of mechanoreceptors	Distal regrouping	Distal regrouping + partial alignment	Alignment		
27: Arrangement of chemoreceptors	Isolated sensillum or alignment	3 sensilla in triangle at the tip of each first valvula			
28: Existence of sensilla in egg-canal	No	Yes			
29: Number of sensilla on edge of the second valvifers (Fig. 1, ss)	0	1–10	>10		
30: Attack position of female	Face to host	Back to host	On host		
31: Duration of oviposition (seconds)	<10	10–60	>60		
32: Existence of host-feeding	No	Yes			
33: Type of parasitism	Endoparasitism	Ectoparasitism			
34: Level of parasitism	Primary	Secondary or tertiary			
35: Superfamily of parasitoid	Ichneumonoidea	Chalcidoidea	Cynipoidea	Ceraphronoidea	
36: Attacked stages	Egg	Larvae (Holometabola)	All homopterous stages except eggs		
37: Thickness of holes envelopes (μm)[8]	1–2	3–9	>10		
38: Hardness of envelopes	Flexible, not sclerotized	Hard, sclerotized			
39: Host mobility	Mobile	Immobile or fixed			
40: Host accessibility	Directly accessible, exposed	Hidden			
41: Host systematic position	Hemiptera Aphididae	Other Hemiptera	Lepidoptera	Diptera	Hymenoptera

[1] This trait enables a relative comparison of ovipositor length.
[2] Length of the interlocking first and second valvulae, from junction between second valvula and second valvifers to distal tip (Fig. 1).
[3] Largest diameter of the interlocked first and second valvulae, in the part penetrating the host, just before the distal narrowing of the ovipositor shaft (Fig. 1).
[4] For score 2, the notum is never membranous at the tip of the ovipositor (Fig. 2*a*, *b*).
[5] For some species, structure of scales can vary along the egg-canal. Here, only the most frequent type of structure is considered. This type is usually found in the mid part of the canal. For score 3, ctenidia and spines can be found either on the same valvulae (Fig. 4*a*, *b*) or separately on valvulae 1 and 2 (Fig. 4*f*).
[6] Sensilla can either be evenly distributed on the third valvulae (score 1) (Fig. 5*c*) or concentrated at the tip, forming a sensillar area (score 2). In the latter case, some sensilla can also be found (Fig. 5*e*) or not (Fig. 5*d*) on the remaining part of the valvulae.
[7] Type A chemoreceptors: no cuticular process, sensilla reduced to a pore; type B chemoreceptors: cuticular process in a cupule with a basal or terminal pore.
[8] Data obtained from ultra-fine sections (transmission electron microscopy) when not available in literature.

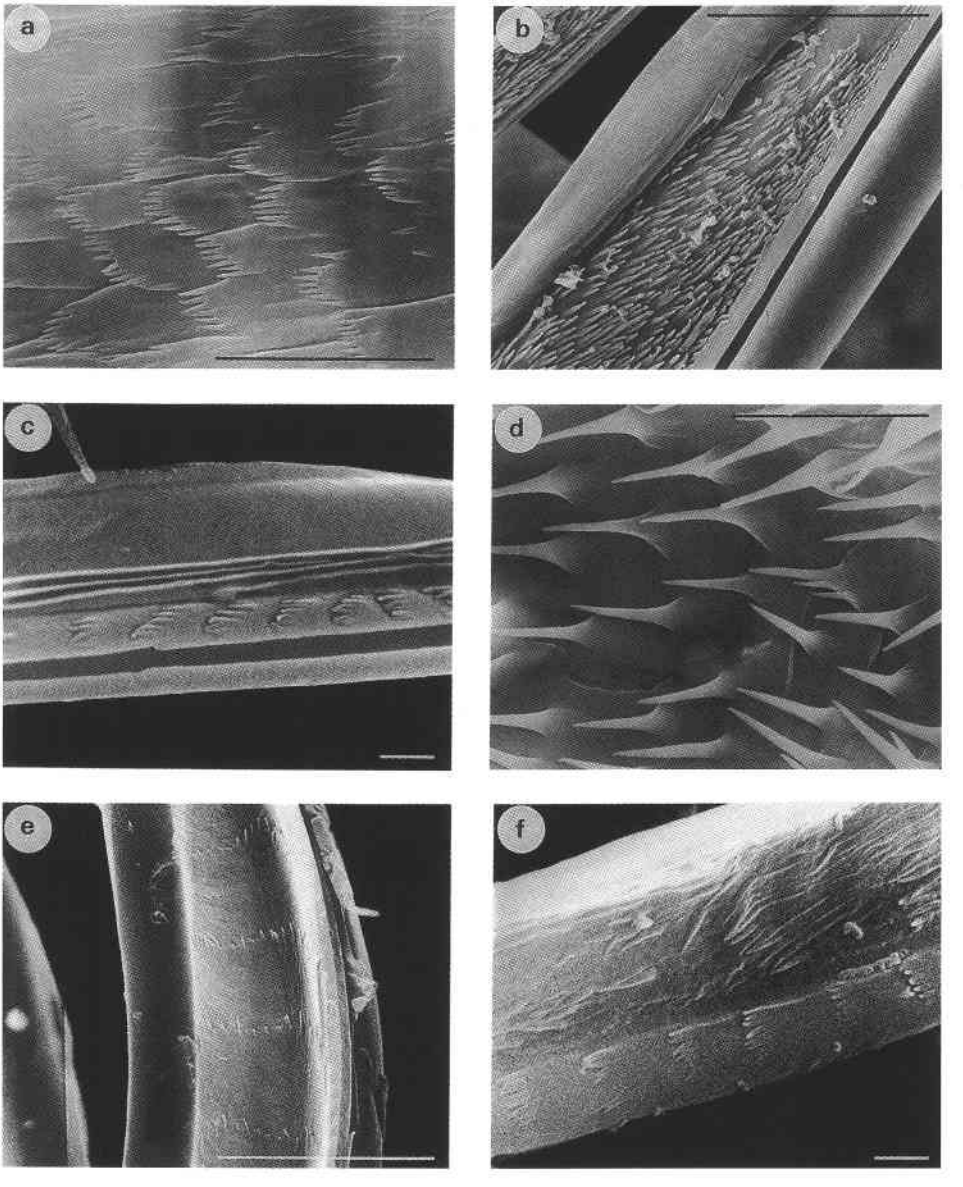

FIG. 4. Cuticular scales within the egg-canal (variables 9 and 10 of the analysis, Table 2): (*a*) overlapping ctenidia on the second valvulae in *Ephedrus plagiator*; (*b*) overlapping spines on a first valvula in *E. plagiator*; (*c*) non-overlapping ctenidia on a first valvula in *Trioxys angelicae*; (*d*) overlapping spines on the second valvulae in *Praon volucre*; (*e*) non-overlapping spines, in row, on a first valvula in *Leptopilina boulardi*; (*f*) non-overlapping ctenidia and overlapping spines on a first valvula in *Encarsia formosa*. [Scale bars = 10 μm for *a*, *b*, *d*, and *e*, and 1 μm for *c* and *f*.]

Using the relative contribution of active variables to the construction of axes, the position of Aphidiinae on the first axis can be explained by the fact that this group of species shares characteristics in contrast with those found in all other species: no sensilla on the anterior margin of valvifers 2; egg-laying behaviour (the female bends the abdomen under

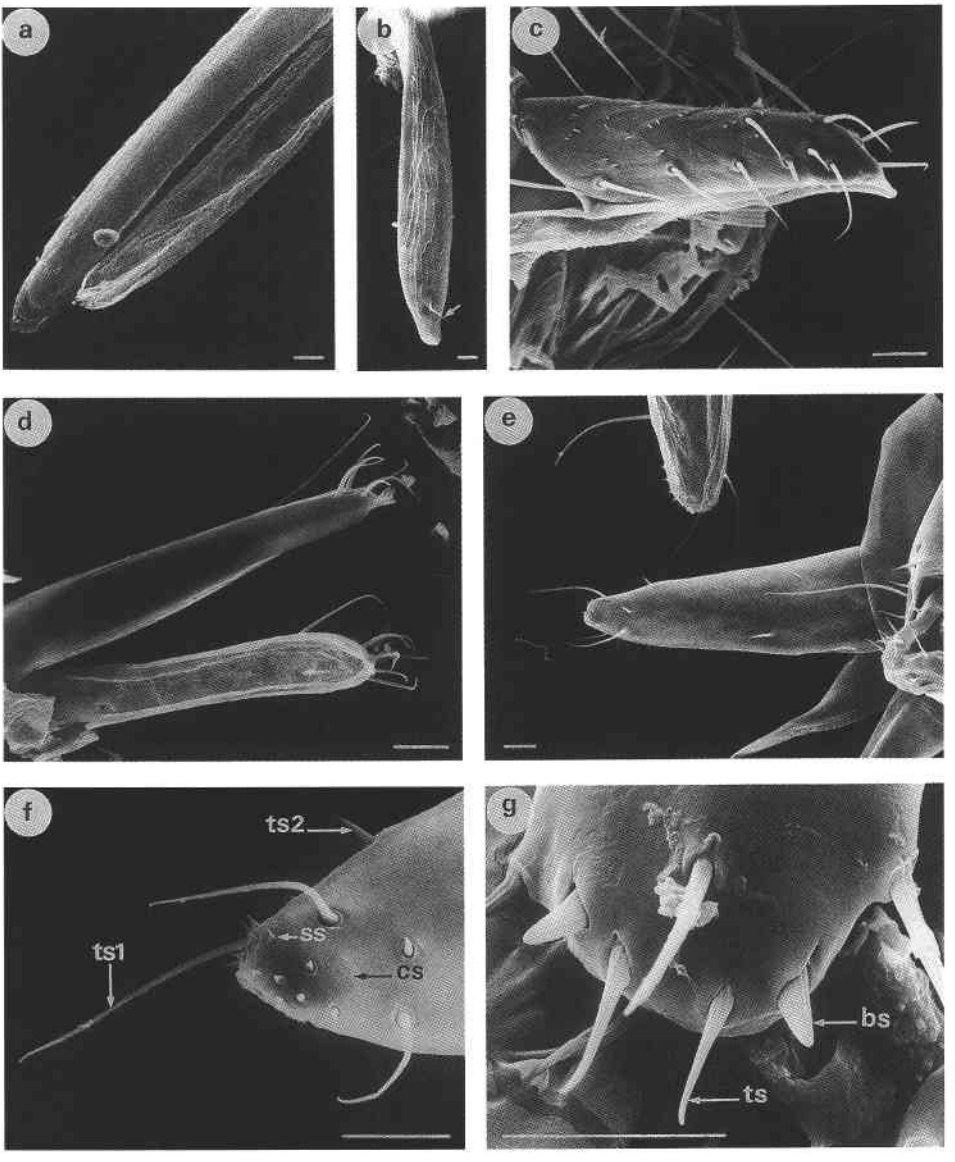

FIG. 5. Types and distribution of sensilla on the third valvulae (variables 11–15 of the analysis, Table 2): (*a*) *Alloxysta victrix*; no sensilla; (*b*) *Aphelinus abdominalis*, two sensilla of two types, trichoid (arrow) and styloconic; (*c*) *Ageniaspis fuscicollis*, 10 trichoid sensilla, evenly distributed on the valvula; (*d*) *Encarsia formosa*, trichoid sensilla gathered at the tip of the valvula (sensillar area); (*e*) *Lysiphlebus fabarum*, sensillar area with four types of sensilla (long trichoid, short trichoid, styloconic, campaniform) and some trichoid sensilla on the rest of the valvula; (*f*) *L. fabarum*, sensillar area at tip of valvula; (*g*) *Praon volucre*, sensillar area at tip of valvula with two types of sensilla, trichoid and basiconic. [bs = basiconic sensillum; cs = campaniform sensillum; ss = styloconic sensillum; ts = trichoid sensillum; ts1 = long trichoid sensillum; ts2 = short trichoid sensillum; scale bars = 10 μm.]

her body); no type B chemoreceptor (see Table 2); type A chemoreceptors; spines in egg-canal overlapping; mechanoreceptors gathered at tip of ovipositor; ovipositor very sharp; two or three types of sensilla on third valvulae; basiconic or campaniform sensilla on third valvulae; usually, styloconic sensilla on third valvulae.

TABLE 3. Scores of 41 variables observed for 19 parasitic Hymenoptera (see Table 2)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
Aphidius uzbekistanicus	3	2	2	1	1	2	2	1	1	1	3	2	3	1	2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1
Praon volucre	4	3	3	1	1	2	2	1	2	1	3	3	1	2	2	2	2	1	1	3	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1
Ephedrus plagiator	4	2	1	1	1	2	3	1	3	1	4	3	2	2	2	2	1	1	1	2	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	3	1	1	1	1	1
Ephedrus cerasicola	2	1	1	1	1	2	3	1	2	1	4	3	2	2	2	2	1	1	1	2	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	3	1	1	1	1	1
Lysiphlebus fabarum	3	1	1	1	1	2	2	1	1	1	4	2	3	2	2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	3	1	1	1	1	3	1	1	1	1	1
Lysiphlebus testaceipes	3	1	2	1	1	2	2	1	1	1	4	2	3	2	2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1
Tryoxis angelicae	3	2	2	1	2	1	1	1	1	2	3	3	3	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1
Aphelinus abdominalis	1	4	2	1	1	3	1	2	2	2	3	1	2	1	1	1	2	1	1	3	1	1	1	1	2	2	1	1	2	2	3	1	1	1	2	3	1	1	1	1	1
Encarsia formosa	1	2	2	1	3	3	3	2	3	2	2	2	1	1	2	1	1	2	1	3	2	1	1	1	2	3	2	1	2	3	2	2	1	1	2	3	2	1	2	1	2
Epidinocarsis lopezi	2	3	4	1	3	3	2	2	2	2	3	1	2	1	2	1	3	2	1	1	2	1	2	1	2	2	2	1	3	2	3	2	1	1	2	3	3	1	1	1	2
Leptomastix dactylopii	4	3	4	1	3	3	2	2	2	2	3	1	2	1	2	1	3	2	1	1	1	2	2	1	2	2	2	1	3	2	2	2	1	1	2	3	3	1	1	1	2
Ageniaspis fuscicollis	1	2	1	1	2	3	1	2	2	2	2	2	1	1	1	1	2	1	1	3	1	1	1	1	2	3	1	1	2	2	2	2	1	1	2	1	2	1	2	1	3
Trichogramma brassicae	1	1	1	1	3	3	3	2	2	2	3	2	1	1	2	1	2	3	1	1	2	2	2	1	2	3	1	1	2	3	2	1	1	1	2	1	2	1	2	1	3
Leptopilina boulardi	2	4	3	2	2	2	2	1	2	2	2	1	1	1	1	2	3	1	1	1	1	3	1	1	2	3	2	1	2	3	2	2	1	1	3	2	2	1	1	2	4
Leptopilina heterotoma	3	4	3	2	2	2	2	1	2	2	2	1	1	1	1	2	3	1	1	1	1	3	1	1	2	3	2	1	2	3	2	1	1	1	3	2	2	1	1	2	4
Ganaspis xanthopoda	3	4	3	2	2	2	2	1	2	2	2	1	1	1	1	2	3	2	1	2	1	3	1	1	2	3	2	1	2	3	2	1	1	1	3	2	2	1	1	2	4
Alloxysta victrix	1	3	3	1	3	3	3	1	2	2	1	1	1	1	1	1	1	2	1	2	1	2	1	1	2	1	2	1	2	3	2	1	1	2	3	2	1	1	1	2	5
Dendrocerus carpenteri	2	3	4	2	4	3	1	1	2	2	2	3	1	1	2	1	2	2	2	1	1	1	1	1	2	2	1	2	2	2	3	1	2	2	4	2	3	2	2	2	5
Asaphes vulgaris	4	4	4	2	4	3	3	2	2	2	2	3	1	1	2	2	3	3	2	3	1	2	1	1	2	3	2	2	3	3	3	2	2	2	2	2	3	2	2	2	5

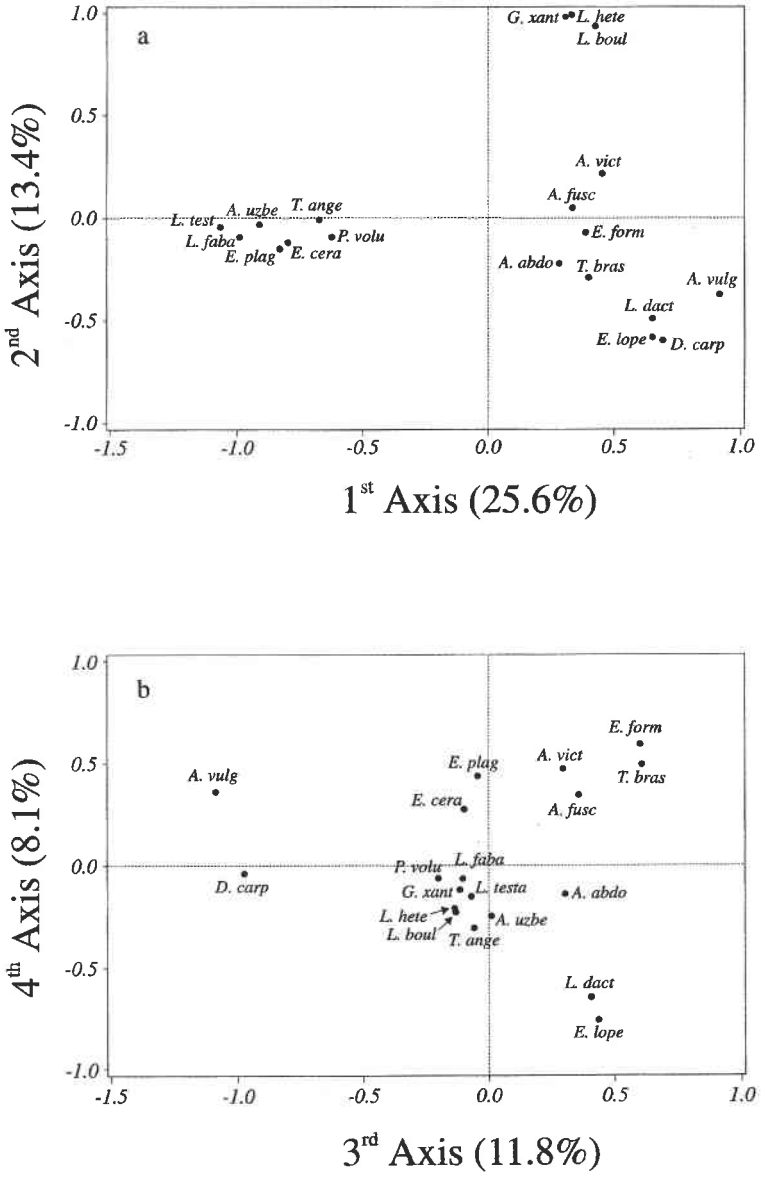

FIG. 6. Graphical results of a multiple correspondence analysis done on the data presented in Table 3. Only points corresponding to the species are represented. (*a*) first and second axis; (*b*) third and fourth axis. [*A. abdo* = *Aphelinus abdominalis*; *A. fusc* = *Ageniaspis fuscicollis*; *A. uzbe* = *Aphidius uzbekistanicus*; *A. vict Alloxysta victrix*; *A. vulg* = *Asaphes vulgaris*; *D. carp* = *Dendrocerus carpenteri*; *E. cera* = *Ephedrus cerasicola*; *E. form* = *Encarsia formosa*; *E. lope* = *Epidinocarsis lopezi*; *E. plag* = *Ephedrus plagiator*; *G. xant* = *Ganaspis xanthopoda*; *L. boul* = *Leptopilina boulardi*; *L. dact* = *Leptomastix dactylopii*; *L. faba* = *Lysiphlebus fabarum*; *L. hete* = *Leptopilina heterotoma*; *L. test* = *Lysiphlebus testaceipes*; *P. volu* = *Praon volucre*; *T. ange* = *Trioxys angelicae*; *T. bras* = *Trichogramma brassicae*.]

The Aphidiinae and Eucoilidae are in the centre of Figure 6*b*. However, according to the fourth axis, the two species of *Ephedrus* are apart from this group because the ovipositors of these species have more serrations.

The three eucoilids, parasitoids of larval *Drosophila*, are all at the top of the second axis and are clearly separated from the other species by the great number of basiconic mechanoreceptors on the shaft of the ovipositor, no sensilla area at the tip of the third valvulae, and a long ovipositor.

At the bottom end of the second axis, *Dendrocerus carpenteri* and *Asaphes vulgaris*, ectophagous hyperparasitoids of aphids, can be found. These two species also remain close to each other in Figure 6*b*. Their distinctive characteristics are a thick ovipositor, a dull ovipositor tip with weakly marked denticulations, the existence of trichoid sensilla on valvulae 1 and/or 2, the presence of sensilla on the inner face of the egg-canal, and both are ectophagous parasitoids.

On the first and second axes (Fig. 6*a*), *Epidinocarsis lopezi* and *Leptomastix dactylopii*, parasites of mealybugs, are close to *Dendrocerus carpenteri* and *Asaphes vulgaris*. They all have a thick, pointed ovipositor. However, on the third and fourth axes (Fig. 6*b*), *Epidinocarsis lopezi* and *Leptomastix dactylopii* are separated from the other species. They are far from the ectophagous hyperparasitoids on the third axis because they differ in the morphology of the denticulations and do not have trichoid sensilla. They are apart from *Ageniaspis fuscicollis*, the third encyrtid studied, on the fourth axis because of differences in number of serrations, the lack of small-size campaniform sensilla (type 1), the relatively large size of females, and the presence of mechanoreceptors at the tip of the first valvulae. Globally, this analysis shows that, among the encyrtids studied, parasites of mealybugs and oophagous species have ovipositors with very different characteristics.

The four remaining species (*Alloxysta victrix*, *Aphelinus abdominalis*, *Encarsia formosa*, and *Trichogramma brassicae*), and also *Ageniaspis fuscicollis*, are found in the centre of Figure 6*a*. However, in Figure 6*b*, they occupy a distal position relative to other species. *Aphelinus abdominalis* is located close to the aphidiines which are also parasitoids of aphids, but remains far from *Encarsia formosa*, the second aphelinid. *Aphelinus abdominalis* and *Encarsia formosa* differ in number of serrations, arrangement of mechanoreceptors on the first valvulae, and number of sensillar types on the third valvulae. Moreover, *Ageniaspis fuscicollis* appears relatively close to the other oophagous species, *Trichogramma brassicae*, which is, surprisingly, located next to *Encarsia formosa* (Fig. 6*b*). In fact, the ovipositors of these last two species are rather similar. *Alloxysta victrix* is always located far away from the eucoilids, despite the fact that they are systematically related.

A dendrogram (Fig. 7) synthesizes relationships based on ovipositor similarity.

Discussion and Conclusions

Distances between species, computed from the morphology of their ovipositors (Fig. 7), do not correspond to phylogenetic relationships. To understand such discordance, host characteristics must be taken into account.

Parasitoid Species Belonging to the Same Family and Attacking the Same Type of Host. Aphidiine (aphid parasitoids) and eucoilid species (parasitoids of *Drosophila*) are each clearly grouped by the analysis, isolated from all other species, and share morphological and functional characteristics of their ovipositors. This homogeneity is interesting because these species present, in other respects, important differences in morphology and biology. Such differences have enabled some authors to describe phylogenetic relationships among genera of Aphidiinae (Mackauer 1961). In eucoilids, interspecific variations observed in the host location process (Vet and Van Alphen 1985) do not appear to relate to morphological features of the ovipositor.

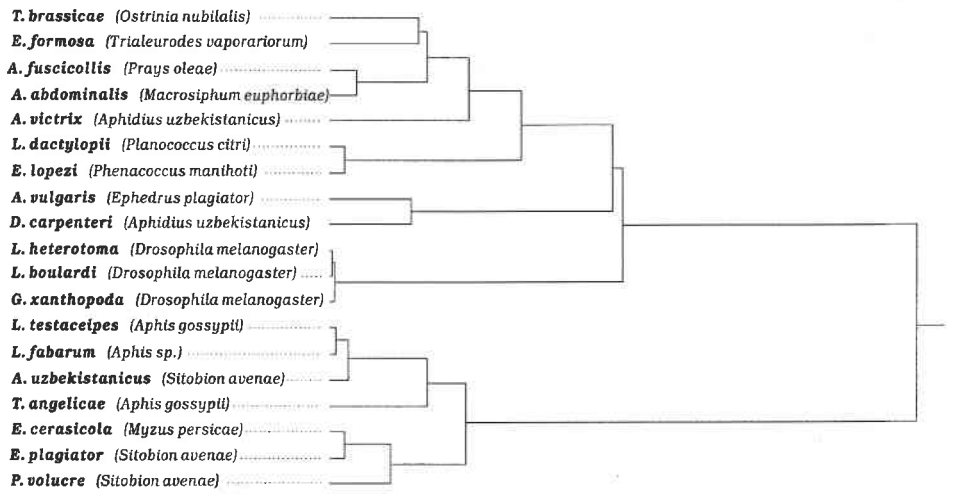

FIG. 7. Dendrogram, constructed from the multiple correspondence analysis, showing the distance between 19 parasitoid species, according to morphology of their ovipositors (hosts in parentheses).

Parasitoid Species Belonging to the Same Family and Attacking Different Types of Host. Among the encyrtid species, *Ageniaspis fuscicollis*, a parasitoid of lepidopteran eggs, is clearly apart from the two mealybug parasitoids (Fig. 6*a*, *b*), and its ovipositor shows morphological characteristics differing substantially from those of the other two (Fig. 8*a*, *d*). *Epidinocarsis lopezi* and *Leptomastix dactylopii* have very similar characteristics (Fig. 8*b–f*). In this case, there is no relationship between ovipositor structure and systematic relationship, but rather convergence in morphology resulting from host attacked.

A similar distinction can be observed between the two aphelinids, *Aphelinus abdominalis* (aphid parasitoid) and *Encarsia formosa* (whitefly parasitoid), but this is less obvious, and appears only on the fourth axis (Fig. 6*b*). Hosts of these two parasitoids are both juvenile Homoptera Sternorrhyncha, but belong to two distinct superfamilies: Aphidoidea and Aleyrodoidea. Differences between these hosts are probably less pronounced than between hosts of Encyrtidae.

Parasitoid Species Belonging to the Same Superfamily and Attacking Different Types of Host. Fergusson (1988) considered there to be three types of ovipositors in Cynipoidea. Those of Charipidae belong to type A ("curved genitalia") and those of Eucoilidae to type B ("elbowed genitalia"). He considered type A to be plesiomorphic and types B and C ("looped ovipositor") to be derived from the curved type. Our analysis, based on consideration of a large number of different morphological traits, supports this conclusion.

Alloxysta victrix, an endophagous hyperparasitoid of aphids, is far from the three parasitoids of larval *Drosophila* (Fig. 6*a*, *b*). The ovipositor of *Phaenoglyphis* sp. is very similar to that of *Alloxysta victrix*. No species showing a Fergusson's type C ovipositor was studied. The traits involved in distinguishing these two groups in our analysis can be linked functionally to characteristics of their hosts.

For Fergusson (1988, p. 22), the three types "reflect the habits of the adult: type A is used to penetrate shallow plant tissue or animal tissue; type B, less accessible animal tissue; and type C, wood or deep plant tissue." The relationship between type of substrate and characteristics of the ovipositor is probably even more prominent in Cynipoidea. Indeed, in each of the three types, based on characters of the second valvifers and on the way the first and second valvulae are accommodated within the gaster, there is great diversity. For

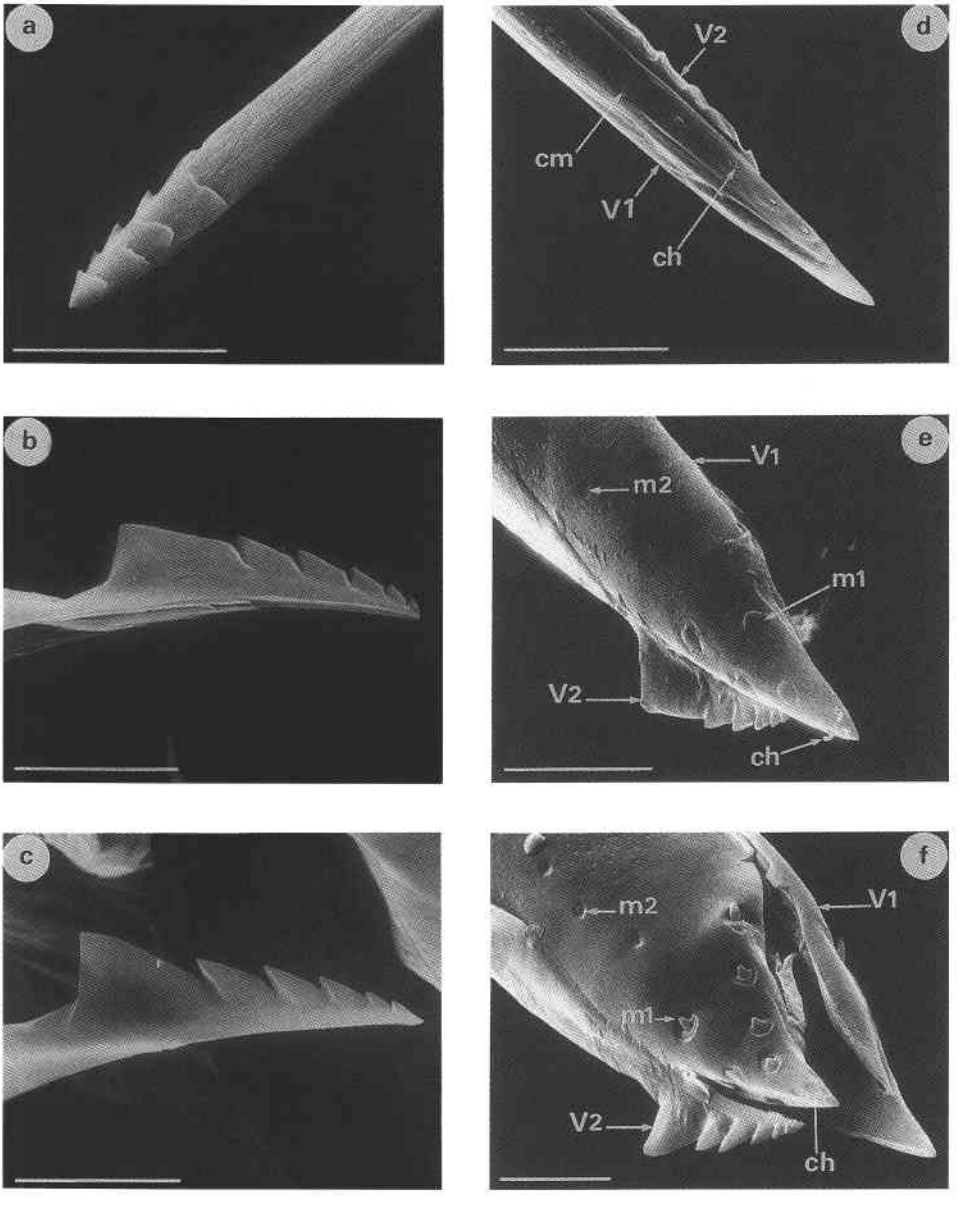

FIG. 8. Ovipositors of Encyrtidae: (*a*) tips of second valvulae in *Ageniapsis fuscicollis*; (*b*) tips of second valvulae in *Epidinocarsis lopezi*; (*c*) tips of second valvulae in *Leptomastix dactylopii*; (*d*) tips of the interlocked first and second valvulae in *A. fuscicollis*; (*e*) tips of the interlocked first and second valvulae in *E. lopezi*; (*f*) tips of the interlocked first and second valvulae in *L. dactylopii*. [ch = chemoreceptor; cm = small campaniform mechanoreceptor; ml = large campaniform mechanoreceptor; m2 = "pore-like" mechanoreceptor; V1 = first valvula; V2 = second valvula; scale bars = 10 μm.] The serrations of *E. lopezi* (*b*) and *L. dactylopii* (*c*) are very similar, with six marked, sclerotized denticulations and are very different from those of *A. fuscicollis* (*a*) which has only four thin, double denticulations. Tips of the first valvulae are also quite different in oophagous species and in mealybug parasitoids: more slender for *A. fuscicollis* with two types of sense organs on each, four aligned chemoreceptors distally and seven aligned small campaniform mechanoreceptors; in *E. lopezi* and *L. dactylopii*, three chemoreceptors at the tip of the valvula, then respectively five and six large campaniform mechanoreceptors on the edges, and, finally, 14 and 15 aligned, pore-like mechanoreceptors.

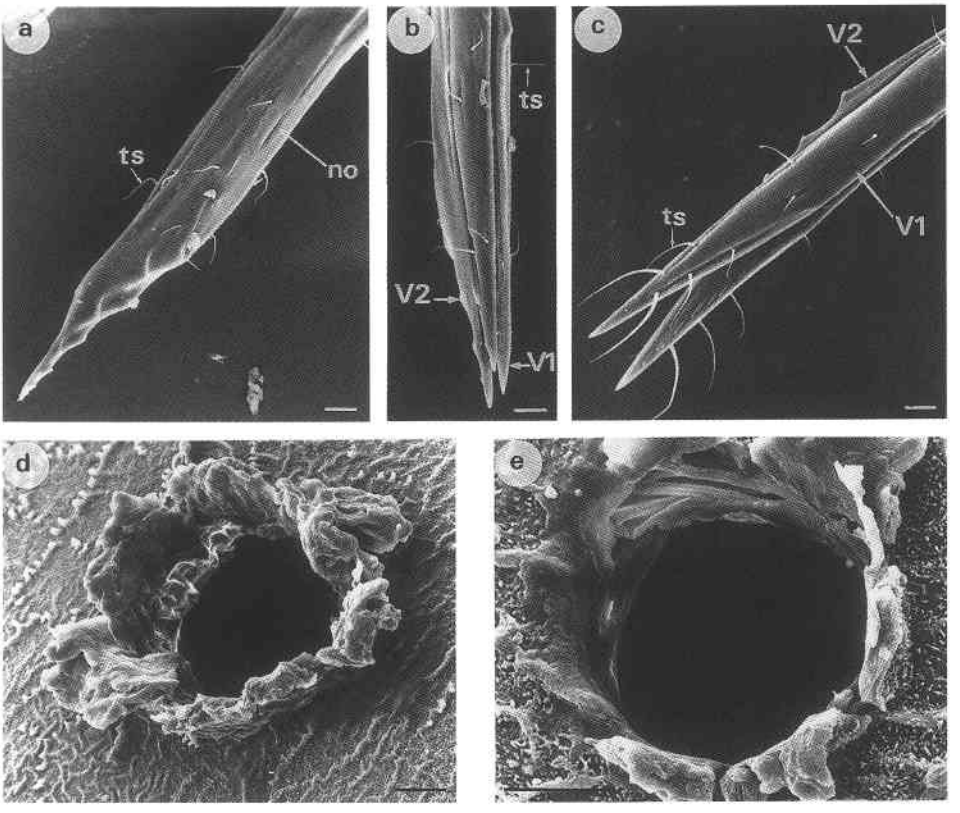

FIG. 9. Ovipositors of ectophagous hyperparasitoids of aphids: (*a*) tips of second valvulae in *Asaphes vulgaris*; (*b*) tips of the interlocked first and second valvulae in *A. vulgaris*; (*c*) tips of the interlocked first and second valvulae in *Dendrocerus carpenteri*; (*d*) oviposition hole in integument of a mummified aphid made by a female of *A. vulgaris*; (*e*) same by a female of *D. carpenteri*. [no = notum; ts = trichoid sensillum; V1 = first valvula; V2 = second valvula; scale bars = 10 μm.] The ovipositors of *A. vulgaris* and *D. carpenteri* show similar features: the tip of the interlocked valvulae is heavily sclerotized while the rest is flexible; denticulations of the second valvulae are strong but weakly marked; there are trichoid mechanoreceptive sensilla on the valvulae. The hole resulting from oviposition in an aphid mummy is similar for the two species.

instance, the type A ovipositor of *Diplolepis rosae*, a gall-forming Cynipidae (Bronner 1985), differs considerably from that of *Alloxysta victrix* and *Phaenoglyphis* sp. It has very long and flexible first and second valvulae, fewer serrations at the tip of the second valvulae, and no sense organs on the outer faces of these valves. A detailed analysis of such differences, according to substrate used for oviposition, could provide information concerning phylogeny of the group.

Parasitoid Species Belonging to Different Superfamilies and Attacking the Same Type of Host. Two ectophagous hyperparasitoids, *Dendrocerus carpenteri* and *Asaphes vulgaris*, attacking last-instar Aphidiinae just after aphid mummification, have ovipositors with very similar characteristics in the perforating part of the ovipositor, not found in the other species (Fig. 9*a*–*c*): distal cuticular thickening of first and second valvulae; thick but weakly marked denticulations; proximal flexibility of valvulae; and trichoid sensilla. Thus, there is substantial convergence in female genitalia of non-related parasitoid species attacking the same type of host. There is also great similarity in the way females of both species drill the integument of mummies and in the mark left after oviposition (Fig. 9*d*, *e*).

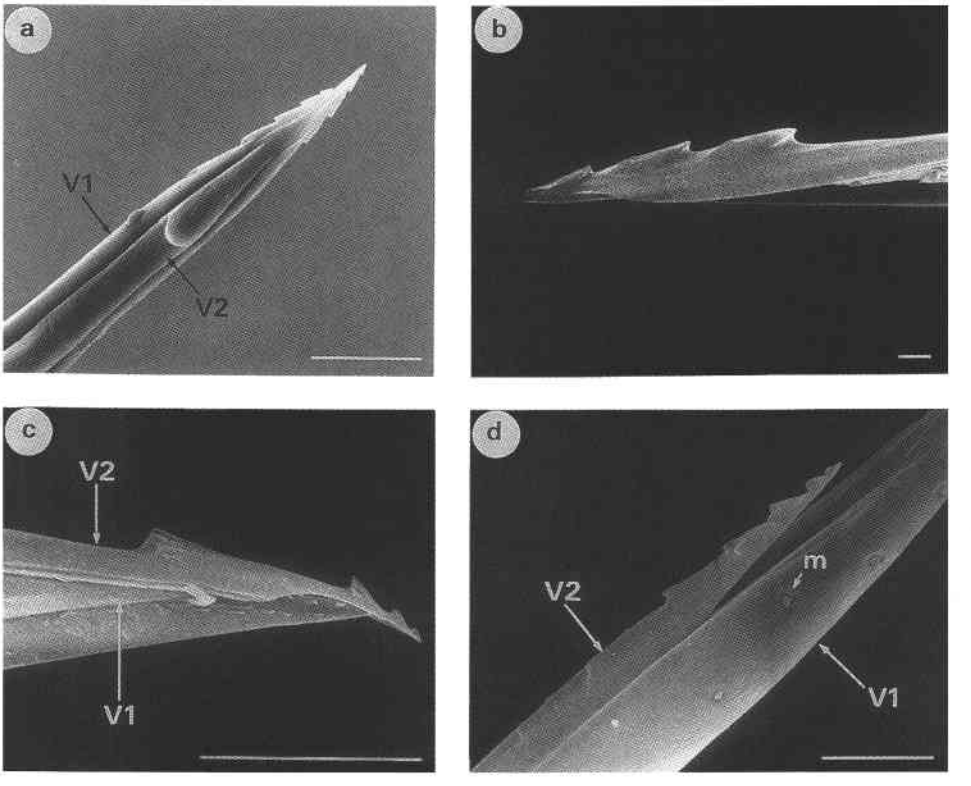

FIG. 10. Ovipositors of parasitoids that pierce the integument of a living aphid: (*a*) tip of the interlocked first and second valvulae in *Ephedrus plagiator*, dorsal aspect; (*b*) tip of first valvula in *Lysiphlebus fabarum*, lateral aspect; (*c*) tips of the interlocked first and second valvulae in *Aphelinus abdominalis*, lateral aspect; (*d*) tips of the first and second valvulae in *Alloxystra victrix*, lateral aspect. [m = mechanoreceptor; V1 = first valvula; V2 = second valvula; scale bar = 10 μm for *a*, *c*, and *d*, and 1 μm for *b*.]

Such morphological convergence is not so clear in some other examples. *Ageniaspis fuscicollis* and *Trichogramma brassicae*, both parasitoids of lepidopteran eggs, do not have similar ovipositors. In fact, *Trichogramma brassicae* appears to share more traits with *Encarsia formosa* (attacks whitefly larvae) than with *Ageniaspis fuscicollis*. Similarly, aphidiines and aphelinids are not grouped by the analysis, despite the fact all are aphid parasitoids.

The ovipositors of neither *Trichogramma brassicae* and *Ageniaspis fuscicollis* nor of aphidiines and *Aphelinus abdominalis* converge, or such a convergence is masked because the analysis attributes the same weight to all variables. Indeed, some variables must be more functionally important than others. For example, in those parasitoids that bore through the thin and fragile integument of aphids (i.e. aphidiines, *Aphelinus abdominalis*, and charipides), the most important part of the ovipositor, functionally, is the tip. These species all share a very sharp and slender ovipositor with numerous, small, sharp serrations (Fig. 10*a*–*d*). Moreover, for primary parasitoids of the Aphidiinae and Aphelinidae, no matter what the length of the ovipositor, only a very short, distal part of the valvulae actually penetrates the host. Thus, females of these species share functionally important characteristics that adapt the ovipositor to pierce the thin integument of a living host without causing haemolymph outflow or large wounds.

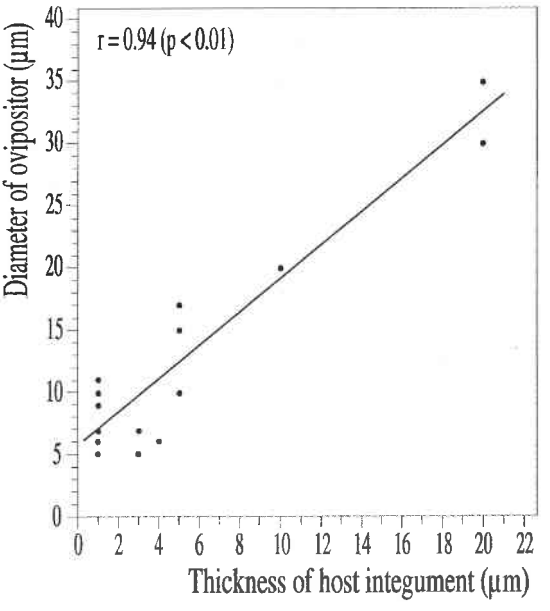

FIG. 11. Correlation between thickness of host integument drilled and ovipositor diameter of parasitic Hymenoptera.

The two oophagous parasitoids, *Ageniaspis fuscicollis* and *Trichogramma brassicae*, share only a few characteristics: small female size; a slender ovipositor; and the same arrangement of mechanoreceptors and chemoreceptors on the first valvulae. Therefore, for these parasitoids, the analysis correctly shows the absence of convergence.

This discussion leads to the hypothesis that morphological convergence between parasitoid species not taxonomically related but attacking the same type of host will be marked if hosts have specific traits strongly constraining ovipositor structure.

Functional Relationships between Parasitoid Ovipositors and Host Characteristics. Comparison among the ovipositors of 20 species shows the existence of traits specific to each superfamily but not connected with type of host parasitized. For instance, in certain Ichneumonoidea (Aphidiinae), the second valvulae are completely fused dorsally (cuticular notum) and serrations are borne by the first valvulae. These features are also found in ovipositors of the ichneumonid *Dolichomitus agnoscendus* (Roman) (Le Ralec 1991). In cynipoid females, the second valvulae are also completely fused. Conversely, in Chalcidoidea, the second valvulae still exhibit their paired origin (membranous notum; Fig. 2*b*) (Quicke et al. 1994) and bear serrations. However, there are few such traits and they usually concern features not directly involved in host parasitization, such as those of the valvifers. Those characters not discriminant in our analysis could be of phylogenetic importance at lower taxonomic levels.

Some ovipositor differences and convergences cannot be explained by systematic position of the parasitoids, but are related instead to type of host attacked. Therefore, in parasitic Hymenoptera, some traits of the genitalia seem to result from adaptive convergence and to be related to the host's characteristics. For example, there is a significant relationship between the ovipositor diameter and thickness of the host integument (Fig. 11). Those parasitoid females having to perforate the thickest and hardest integuments have ovipositors

with the largest diameter and a particular kind of tip, as in ectophagous hyperparasitoids of aphids. In the ichneumonoid *Dolichomitus agnoscendus*, an ectoparasitoid of xylophagous cerambycid larvae, the ovipositor has a diameter of 240 μm and the tip has a thick cuticle with numerous but weakly marked denticulations (Le Ralec 1991). These features could be related to the need for drilling through wood to reach the host. On the other hand, aphid parasitoids have thin ovipositors, to perforate thin, flexible integuments without causing large wounds.

The arrangement of sense organs, especially of mechanoreceptors, on first and second valvulae also appears to be related to host characteristics. Species attacking hosts concealed in plant substrates, such as the eucoilids, parasitoids of larval *Drosophila*, have the largest number of mechanoreceptors over the valvulae. Such sensilla probably enable them to locate their hosts while probing the substrate.

The host of aphid hyperparasitoids is contained within the body of a dead or living aphid and only a small space has to be probed by the female to locate the host. Mechanoreceptors in these wasps tend to concentrate at the tip, even if sensilla also occur proximally on the valvulae. Concentration of mechanoreceptors at the tips of the valvulae is even more pronounced in parasitoids attacking free, exposed hosts as in mealybug parasitoids, aphidiines, and oophagous parasitoids. However, degree of localization depends upon that portion of the ovipositor penetrating the host. In mealybug parasitoids and in oophagous species, the ovipositor is deeply driven into the host, and mechanoreceptors are concentrated apically but occur over about one-third of valvular length. In aphidiines in which only the tip of the ovipositor penetrates the host, sense organs occur only at the tip. *Aphelinus abdominalis* may seem to be an exception but the small campaniform sensilla occurring on that part of the valvulae not penetrating the host could function in detection of egg movement down its shaft.

Sense organs on the third valvulae also seem to be adaptive. In females of some species (eucoilids, charipids, and *Aphelinus abdominalis*) almost no sensilla occur on these valvulae and the third valvulae never touch the host or substrate. In all other examined species, these valvulae contact the host integument, either before or after egg-laying, and numerous sensilla can be found. Certain aphidiines have a rich supply of sense organs on the third valvulae and their egg-laying behaviour includes examination of the host cuticle with the tips of these valvulae.

Although there is great uniformity in basic structure of the ovipositor in parasitic Hymenoptera, there is also much variation among species. This study shows that some ovipositor traits appear to be associated with host characteristics important for the parasitization process. Indeed, species belonging to the same family but parasitizing different types of host can have very different features on their ovipositors. Conversely, species belonging to different families or superfamilies but parasitizing the same type of host often show adaptive convergence.

Finally, morphological study of ovipositor characteristics related to host characteristics could provide data on the evolution of host exploitation (i.e. ectoparasitism to endoparasitism, primary to secondary parasitism) and on progressive host radiation in parasitic Hymenoptera, at the level of species, instars, and habitats.

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References

Altner, H. 1977. Insect sensillum specificity and structure: An approach to a new typology. Vol. **VI**, pp. 295–303 *in* Le Magnen, J., and P. MacLeods (Eds.), Olfaction and Taste. Information Retrieval, London.

Altner, H., and L. Prillinger. 1980. Ultrastucture of invertebrate chemo-thermo and hygroreceptors and its functional significance. *International Review of Cytology* **67**: 69–139.

Austin, A.D. 1990. Revision of the enigmatic Australasian genus *Miropotes* Nixon (Hymenoptera: Braconidae: Microgastrinae), with comments on the phylogenetic importance of the female ovipositor system. *Systematic Entomology* **15**: 43–68.

Austin, A.D., and T.O. Browning. 1981. A mechanism for movement of eggs along insect ovipositors. *International Journal of Insect Morphology and Embryology* **10**: 93–108.

Bronner, R. 1985. Anatomy of the ovipositor and oviposition behavior of the gall wasp *Diplolepis rosae* (Hymenoptera: Cynipidae). *The Canadian Entomologist* **117**: 849–858.

Copland, M.J.W. 1976. Female reproductive system of the Aphelinidae (*Hymenoptera: Chalcidoidea*). *International Journal of Insect Morphology and Embryology* **5**: 151–166.

Copland, M.J.W., and P.E. King. 1971. The structure and possible function of the reproductive system in some Eulophidae and Tetracampidae. *The Entomologist* **104**: 4–28.

——— 1972*a*. The structure of the female reproductive system in the Pteromalidae (Chalcidoidea: Hymenoptera). *The Entomologist* **105**: 77–96.

——— 1972*b*. The structure of the female reproductive system in the Eurytomidae (Chalcidoidea: Hymenoptera). *Journal of Zoology* **166**: 185–212.

——— 1972*c*. The structure of the female reproductive system in the Torymidae (Hymenoptera: Chalcidoidea). *Transactions of the Royal Entomological Society of London* **124**: 191–212.

Copland, M.J.W., P.E. King, and D.S. Hill. 1973. The structure of the female reproductive system in the Agaonidae (Chalcidoidea: Hymenoptera). *Journal of Entomology (A)* **48**: 25–35.

Fergusson, N.D.M. 1988. A comparative study of the structures of phylogenetic importance of female genitalia of the Cynipoidea (Hymenoptera). *Systematic Entomology* **13**: 13–30.

Gibbons, J.R.H. 1979. A model for sympatric speciation in *Megarhyssa* (Hymenoptera: Ichneumoidae): Competitive speciation. *American Naturalist* **114**: 719–741.

Heatwole, H., and D.M. Davis. 1965. Ecology of three sympatric species of parasitic insects of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae). *Ecology* **46**: 140–150.

Keil, T.A., and R.A. Steinbrecht. 1984. Mechanosensitive and olfactory sensilla of insects. Vol. **2**, pp. 477–516 *in* King, R.C., and H. Akai (Eds.), Insect Ultrastructure. Plenum, New York, NY. 624 pp.

Lebart, L., A. Morineau, and N. Tabard. 1977. Techniques de la description statistique. Dunod, Paris. 351 pp.

Le Ralec, A. 1991. Les Hyménoptères parasitoïdes: Adaptations de l'appareil reproducteur femelle. Morphologie et ultrastructure de l'ovaire, de l'oeuf et de l'ovipositeur. Thèse de Doctorat de l'Université de Rennes I, France. 117 pp.

Livingstone, D., and M.H.S. Yacoob. 1986. Natural enemies and biologies of the egg parasitoids of Tingidae of southern India. *Uttar Pradesh Journal of Zoology* **6**: 1–21.

Mackauer, M. 1961. Die Gattungen der Familie Aphidiidae und ihre Verwandtschaftliche Zuornung. *Beitraege zur Entomologie* **11**: 792–803.

Matsuda, R. 1976. The Hymenoptera. pp. 373–396 *in* Matsuda, R. (Ed.), Morphology and Evolution of the Insect Abdomen. Pergamon Press, New York, NY. 534 pp.

McIver, S.B. 1975. Structure of cuticular mechanoreceptors of arthropods. *Annual Review of Entomology* **20**: 381–397.

——— 1985. Mechanoreception. pp. 71–132 *in* Kerkut, G.A., and L.J. Gilbert (Eds.), Comprehensive Insect Physiology, Biochemistry and Pharmacology. Vol. VI. Pergamon Press, Oxford. 673 pp.

Quicke, D.L.J., L.C. Ficken, and M.G. Fitton. 1992. New diagnostic ovipositor characters for Doryctine wasps (Hymenoptera, Braconidae). *Journal of Natural History* **26**: 1035–1046.

Quicke, D.L.J., M.G. Fitton, and S. Ingram. 1992. Phylogenetic implications of the structure and distribution of ovipositor valvilli in the Hymenoptera (Insecta). *Journal of Natural History* **26**: 587–608.

Quicke, D.L.J., M.G. Fitton, J.R. Tunstead, S. Ingram, and P.V. Gaitens. 1994. Ovipositor structure and relationships within the Hymenoptera, with special reference to the Ichneumonoidea. *Journal of Natural History* **28**: 635–682.

SAS Institute Inc. 1990. SAS/STAT User's Guide. Release 6.07 Edition, Vol. 1. SAS Institute Inc., Cary, NC. 890 pp.

Scudder, G.G.E. 1971. Comparative morphology in insect genitalia. *Annual Review of Entomology* **16**: 379–406.

Smith, E.L. 1968. Biosystematics and morphology of Symphyta. I. Stemgalling *Euura* of the California region and a new female genitalic nomenclature. *Annals of the Entomological Society of America* **61**: 1389–1407.

——— 1969. Evolutionary morphology of external insect genitalia. I. Origins and relationships to other appendages. *Annals of the Entomological Society of America* **62**: 1051–1079.

——— 1970*a*. Hymenoptera. pp. 156–170 *in* Tuxen, S.L. (Ed.), Taxonomist's Glossary of Genitalia in Insects. Munksgaard, Copenhagen. 284 pp.

——— 1970*b*. Evolutionary morphology of the external insect genitalia. 2. Hymenoptera. *Annals of the Entomological Society of America* **63**: 1–27.

Snodgrass, R.E. 1933. Morphology of the insect abdomen. II. The genitalia ducts and the ovipositor. *Smithsonian Miscellaneous Collections* **89**: 1–148.

Städler, E. 1984. Contact chemoreception. pp. 3–35 *in* Bell, W.J., and R.T. Cardé (Eds.), Chemical Ecology of Insects. Chapman & Hall Ltd., London. 524 pp.

Vet, L.E.M., and J.J.M. Van Alphen. 1985. A comparative functional approach to the host detection behaviour of parasitic wasps. 1. A qualitative study on Eucoilidae and Alysiinae. *Oikos* **44**: 478–486.

Vu Quang Con, and Nguyen Van San. 1987. Effectiveness of egg parasites (Hymenoptera) depending of the parasites abdomen structure and on the type of egg-batches in lepidopteran rice pests. *Zoologicheokij Zhurnal* **66**: 60–65.

Zacharuk, R.Y. 1980. Ultrastructure and function of insect chemosensilla. *Annual Review of Entomology* **25**: 27–47.

——— 1985. Antennae and sensilla. Vol. **6**, pp. 1–69 *in* Kerkut, G.A., and L.I. Gilbert (Eds.), Comprehensive Insect Physiology, Biochemistry and Pharmacology. Pergamon Press, Oxford. 673 pp.

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