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Host detection and rate of parasitism by *Acroricnus seductor* (Hymenoptera: Ichneumonidae), a natural enemy of mud-dauber wasps (Hymenoptera: Sphecidae)

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Abstract

The behavioural ecology of ichneumonid wasps that attack aculeate Hymenoptera is still largely unknown. Field observations and morphological analyses were devoted to investigate host detection and rate of parasitism by *Acroricnus seductor* (Scopoli), a natural enemy of the black and yellow mud dauber wasp *Sceliphron caementarium* (Drury). At the study site, about half of the host nests suffered parasitism by *A. seductor*. No significant difference was found between the rate of parasitism in sheltered (inside human building) and unsheltered (outside building) nests. Larger nests did not suffer a higher rate of parasitism, and larger brood cells were not more likely to be parasitized. As revealed by contents of parasitized cells, *A. seductor* appeared to act as a kleptoparasitoid, devouring spider prey and young host larvae. Analysis of video recordings obtained in the field revealed the basic behavioural sequence of host detection. *Acroricnus seductor* female taps with the antennae the host nest surface and, once a suitable host brood cell is found, inserts the ovipositor through the mud wall, possibly facilitated by the secretion of a mud-softening substance. Behavioural data, together with the presence of modified tips on the apex of female antennae and the relative thicknesses of female fore tibiae, strongly suggest that *A. seductor* uses echolocation to detect the host.

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Keywords

Cryptinae; host detection; behaviour; morphology; vibrational sounding; *Sceliphron*

Introduction

Information about host associations for Ichneumonidae attacking bees and wasps (Hymenoptera: Aculeata) is sparse and scattered, and behavioural data are even

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rarer (Casiraghi et al., 2001). Solitary wasps (Sphecidae, Crabronidae, Pompilidae and Eumeninae) are attacked by different genera of ichneumonid wasps, in particular belonging to the subfamily Pimplinae (e.g. *Perithous*, *Poemenia*, *Ephialtes*) and Cryptinae (e.g. *Acroricnus*, *Buathra*, *Cryptus*) (Casiraghi et al., 2001 and references therein; Steffan-Dwenter, 2002; Tormos et al., 2004; Loyola and Martins, 2006; Hook, 2006).

In the present paper, data on host detection behaviour and rate of parasitism by *Acroricnus seductor* (Scopoli) (Ichneumonidae: Cryptinae), a natural enemy of *Sceliphron caementarium* (Drury) (Sphecidae: Sceliphrinae), are presented.

The genus *Acroricnus* belongs to the tribe Cryptini. Although the phylogeny of this tribe is still not completely resolved, it is possible that species which attack aculeate Hymenoptera are not necessarily closely related. Some morphological traits, such as mandible shape, are presumably convergent and are related to the utilization of aculeate nests (Laurenne et al., 2006). Host shifts probably occurred in this tribe (Laurenne et al., 2006, 2009).

The genus *Acroricnus* seems to preferentially, but not exclusively, attack mud-dauber wasps of the genus *Sceliphron* (Sphecidae) (table 1). To our knowledge, five out of the 35 described species of *Sceliphron* serve as hosts to *Acroricnus* (table 1), but this value is likely to be underestimated because of a complete lack of information concerning the biology of many species of the host genus. A number of mud-daubing or wood-nesting solitary vespids were also recorded as hosts of *Acroricnus* (table 1).

Mud-dauber wasps of the genus *Sceliphron* build their multicellular aerial nests with mud (White, 1962). Nest brood cells are filled with paralyzed spiders, and a single egg is laid in each cell (Polidori et al., 2007). In some species (including *S. caementarium*), the completed nests are covered with a final, thick mud layer (Polidori et al., 2005).

Despite the long-term known association between *Acroricnus* and *Sceliphron* (Lichtenstein, 1920; Mansion, 1926; Mitchell, 1950), nothing is known on the behavioural and ecological dynamics of this antagonistic relationship. The aim of this study is to give information on the behavioural ecology of *A. seductor* associated with *S. caementarium* in Italy. We studied the rate of parasitism in a natural population, analysed the behavioural sequence of host detection by *A. seductor* and described the morphology of some structures related to this activity. We tried to find evidence of a host-detection technique, the echolocation (vibrational sounding), used by many parasitic wasps that, like *A. seductor*, attack hosts concealed under a solid substrate (Broad and Quicke, 2000; Vilhelmsen et al., 2001). While using echolocation, such wasps tap the substrate (wood, stem or soil) with the antennae and detect the position of potential hosts through the returned ‘echoes’ on the legs (Broad and Quicke, 2000). Vibrational sounding evolved under a variety of ecological conditions (types of substrates where hosts are concealed), often in situations in which the host does not produce vibrations itself (Broad and Quicke, 2000; Vilhelmsen et al., 2001).

Table 1.
Host records for species of *Acroricnus*. * The nest in this species is built with mud, but inside wide wood sticks or stems; ** this wasp resulted to have nested in old *Sceliphron* nests.

Species	Host family	Host species	Host nest type	Host prey	References
A. seductor (Scopoli)	Sphecidae	*Sceliphron caementarium* (Drury)	aerial mud-nest	spider adults and juveniles	present work, Campadelli et al. (1999)
		Sceliphron spirifex (Linnaeus)	aerial mud-nest	spider adults and juveniles	Mansion (1926), Lichtenstein (1920), Grandi (1930), Schimitschek (1944), Frilli (1966)
		Sceliphron destillatorium (Illiger)	aerial mud-nest	spider adults and juveniles	Mocsáry (1879), Coulon (1933), Schimitschek (1944), Frilli (1966), Campadelli and Pagliano (1987)
A. junceus Cresson	Vespidae	*Odynerus tigris* Saussure	aerial mud-nest	lepidopteran larvae	Champlain (1922)
A. ambulator Smith	Vespidae	*Anterhynchium flavomarginatum* (Smith)	aerial mud-nest*	lepidopteran larvae	Itino (1986)
		Anterynchium flavomarginatum micado (Kirsch)	pre-existing cavity in wood	lepidopteran larvae	Yamane (1990)
		Orancistrocerus drewseni Saussure	pre-existing cavity in wood	lepidopteran larvae	Itino (1986)

Table 1.
(Continued.)

Species	Host family	Host species	Host nest type	Host prey	References
		Orancistrocerus drewseni drewseni (Saussure)	pre-existing cavity in wood	lepidopteran larvae	Yamane (1990)
		Eumenes fraterculus Della Torre	aerial mud-nest	lepidopteran larvae	Yamane (1990)
		Eumenes rubrofemoratus Giordani Soika	aerial mud-nest	lepidopteran larvae	Yamane (1990)
		Eumenes rubronotatus Pérez	aerial mud-nest	lepidopteran larvae	Yamane (1990)
		Eumenes micado Cameron	aerial mud-nest	lepidopteran larvae	
A. cubensis (Cresson)	Vespidae	*Pachodynerus nasidens* (Latreille)	aerial mud-nest**	lepidopteran larvae	Genaro (1996a)
	Sphecidae	*Sceliphron jamaicense* (Fabricius)	aerial mud-nest	spider adults and juveniles	Genaro (1996a)
		Sceliphron assimile (Dahlbom)	aerial mud-nest	spider adults and juveniles	Genaro (1996a)
A. tricolor Mitchell		*S. caementarium*	aerial mud-nest	spider adults and juveniles	Genaro (1996b)

Female antennal tips modified into a "hammer" and enlarged subgenual organs (often suggested by swollen tibiae) in female legs, which receive the vibrational information, are expected in species using echolocation (Broad and Quicke, 2000; Vilhelmsen et al., 2001). Recently, Laurenne et al. (2009) showed that within the Cryptinae the tips of the antennae are modified into a hammer-like structure that is suitable for knocking a substrate, and that this form of echolocation seems widespread in Cryptini. These authors insinuated that *Acroricnus* uses echolocation, but did not identify which species. In addition, because the deployment of vibrational sounding may be best inferred through the analysis of female tibia in combination with the presence of modifications to the female antenna (Broad and Quicke, 2000), we analysed morphological differences of both body parts between males and females.

Materials and methods

Study area

Field observations were carried out during the summers of 2003 and 2004 near Castelleone, province of Cremona, Italy (9°46′37″E, 45°17′40″N), a small town situated 64 m above sea level. The study area was located near an abandoned and later re-naturalized sand quarry characterized by the presence of bay-oaks (*Quercus robur* L.), cornels (*Cornus sanguinea* L.) and robinia (*Robinia pseudoacacia* L.). The climate of the site is continental and characterized by rainfall of 600 to 1000 mm/year.

Host cell contents and rate of parasitism

In 2004 (16th June-3th July), 46 nests of *S. caementarium* were collected. Twenty-nine were divided in two groups according to their location outside or inside a building: "unsheltered" and "sheltered", respectively. The volume of a brood cell (computed as a cylinder) was obtained by its length and diameter, measured with a calliper to the nearest 0.1 mm.

Linear correlations were tested with the Spearman correlation test, differences between medians were tested with the Mann-Whitney test and differences between means were tested with the Aspin-Welch test because the non-homogeneity of variance did not permit the use of the Student t-test.

Behavioural observations

Observations of the activity of *A. seductor* on the nests of *S. caementarium* were carried out on the 20th, 22nd, 25th and 26th June in 2003 from 7.30 to 19.30 (solar hours); this period covered the diurnal activity of both the sphecid and the ichneumonid. A sequential scheme of the host detection behaviour was obtained from 50 minutes of video recording (video camera Sony V600E/PAL *plus* additional lens) on a single nest *plus* additional field observations. The nest from which the video was made was located under the eaves of a barn and it was not yet completed at the moment of the video recording. The video was digitized and analyzed frame-by-frame. The frames reproduced were processed with a graphical procedure (Adobe Photoshop 6.0 and Adobe Premier 7.0) to enhance the resolution.

Morphological analysis

Four ichneumonid females were captured while exploring the host nests and other four individuals (three males and one female) were obtained freshly emerged from *S. caementarium* nests. All these specimens were preserved in ethanol (70%) and analyzed by a scanning electron microscope at the Central Service for the Support to Experimental Research (SCSIE, University of Valencia). Observations were carried out by using a Hitachi S-4100 Field Emission; the work distance was 10-15 mm, at 5.0 kV. The image processing software used was EMIP 3.0 Image Processing. Photographs were taken of the tip of antennae, of sheaths and ovipositor proper and of fore tibiae. For three males and three females, the length and the width at half of the length of fore tibiae were measured under a stereomicroscope to the nearest 0.001 mm.

In the text, mean values are given ± standard deviation.

Results

Rate of parasitism

Out of 46 collected host nests, 29 included at least one parasitized brood cell. Of a total of 49 parasitized cells, 25 had *A. seductor* pupae only, 19 had the *A. seductor* pupa plus the dead host larva, and five had a live *A. seductor* larva although with a live *S. caementarium* larva. In parasitized cells we found 1-16 paralyzed spiders, in unparasitized cells we found 1-26 paralyzed spiders.

Rate of parasitism *per* nest (percentage of parasitized cells out of the total number of nests) ranged from 0% to 100% (23.6 ± 27.44% on average; $n = 29$). Mean rate of parasitism was 14.37 ± 20.16% ($n = 14$) for "unsheltered" nests and 32.22 ± 31.03% ($n = 15$) for "sheltered" nests; the medians (0 and 33.3 respectively) did not differ significantly (Mann-Whitney test: $U = 70.5$; $n_1 = 14$, $n_2 = 15$; $P = 0.12$) (fig. 1a). The volume of a parasitized cell was, on average, 1558.93 ± 355.19 mm^3 (range = 858.87-2229.37; $n = 41$) and that of an unparasitized cell was, on average, 1515.90 ± 449.83 mm^3 (range = 758.43-2752.98; $n = 109$). These average values did not differ significantly ($F = 1.6$, $P = 0.02$; Aspin-Welch test: $t = 0.61$, $df = 90.6$; $P = 0.54$). The number of cells *per* nest was positively correlated with the number of parasitized cells *per* nest in both locations (Spearman correlation test; "sheltered": $\rho = 0.57$, $n = 15$, $P = 0.032$; "unsheltered": $\rho = 0.58$, $n = 14$, $P = 0.035$) (fig. 1b-c). However, the rate of parasitism did not increase with the total number of cells (Spearman correlation test; "sheltered": $\rho = 0.27$, $n = 15$, $P = 0.32$; "unsheltered": $\rho = 0.35$, $n = 14$, $P = 0.19$).

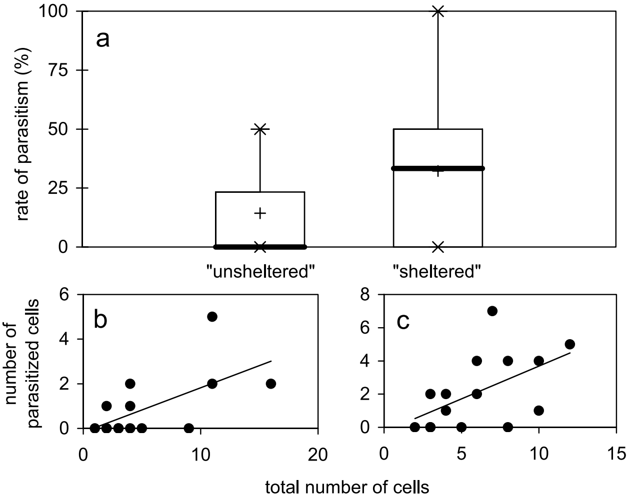

Figure 1. Parasitism of *A. seductor* in "sheltered" and "unsheltered" *S. caementarium* nests. a, difference in the percent rate of parasitism between the two groups (+ = means, × = extreme values, bold horizontal line = medians, light horizontal lines = 25% and 75% quartiles); b-c, relationship between the number of cells and the number of parasitized cells *per* nest (b, "unsheltered", c, "sheltered").

Host detection behaviour

Ichneumonid females were recorded on the host nest mostly (in 7 out of 9 cases) during the afternoon hours, in particular between 18.00 and 19.00.

The female behaviour of *A. seductor* can be summarized as follows. The wasp lands on the nest (fig. 2.1) and starts exploring, walking over the nest surface and tapping it with the antennae (fig. 2.3). The tapping activity continues whether the wasp moves across the nest, turns around (fig. 2.5) or stands motionless (fig. 2.2). Tapping activity is composed of two phases: 1) the antennae are moved forwards, extended and divaricated (fig. 3a), and 2) the antennae are moved backwards until they are close to the head (fig. 3b) by dragging the tips across the nest surface. In this latter position, the antennae tap quickly and synchronously on the nest surface. Sometimes *A. seductor* bends the metasoma tip forward and, while tapping again with the antennae, moves around exploring the nest surface by using the ovipositor sheaths (still positioned around the ovipositor proper); sheaths are maintained at an angle about 45° with respect to the substrate (fig. 2.6; fig. 3a-c). When the sheaths are pushed against the nest surface they may bend lengthwise and separate, revealing their flexibility (fig. 3d). Once a suitable point is found, the female drills into the hard mud with the ovipositor proper (fig. 2.8, fig. 3e); at this stage the sheaths are opened and moved apart making a right angle with the first and second valvulae.

Sometimes the drilling activity is associated with clockwise and anticlockwise torsion movements and with vigorous up and down movements of the abdomen (fig. 2.9; fig. 3f).

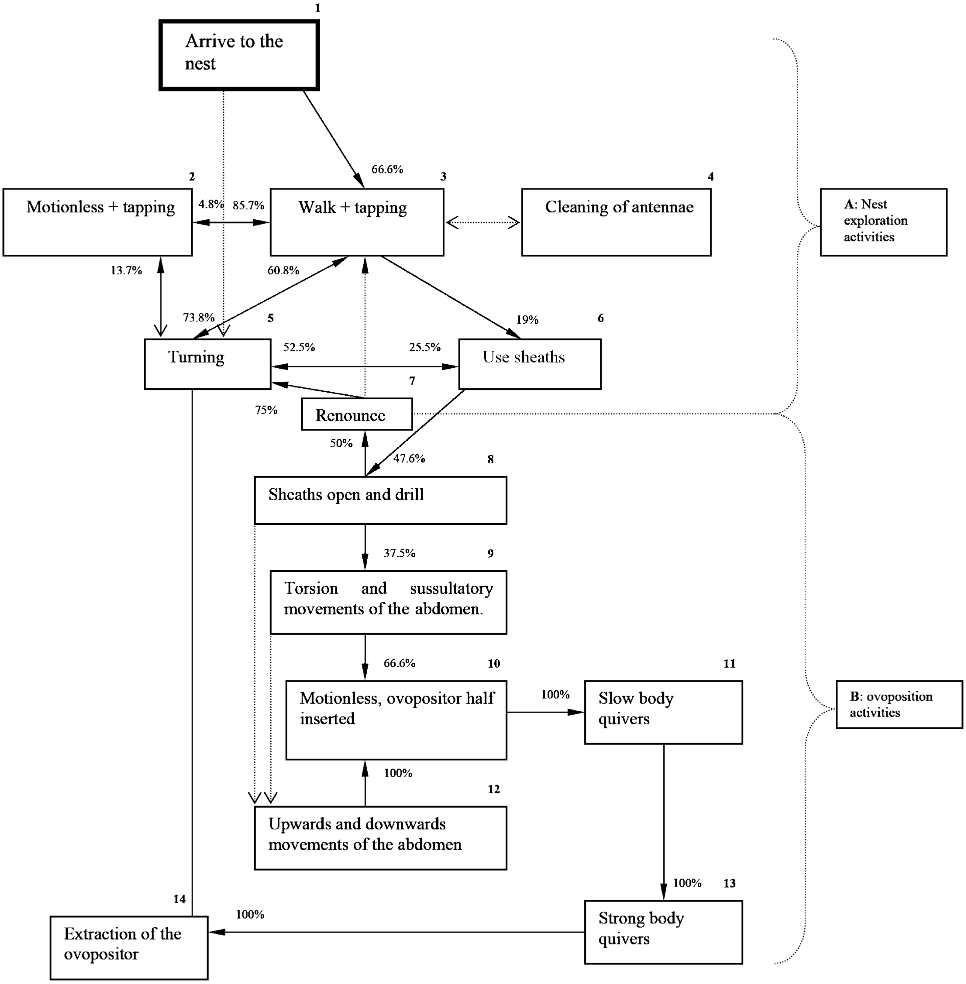

Figure 2. Ethogram of *A. seductor.* Continuous lines with bold arrow ends indicate the most frequent behavioural patterns; dashed lines with open arrows ends indicate the infrequent behaviours; brace A includes all the nest exploration activities; brace B contains the oviposition activities; percentages show the observed frequency of the event following (arrows pointing out) the previous one (contained in the box); further details in the text.

Careful analysis of video frames revealed that, during this initial drilling phase, a darker halo is formed in the nest wall around the ovipositor (fig. 3g-h). As the ovipositor penetrates deeper, this “mark” slowly disappears, reappearing again when the ichneumonid drew out the ovipositor. Such marks were still visible a few minutes after by the observer, so that it is unlikely to be an artefact of the video camera. Eventually, when the ovipositor is deeply inserted into the brood cell, the metasoma moves up and down, possibly indicating a successful insertion (fig. 2.12). At this point, the female remains motionless with the ovipositor half-inserted in the

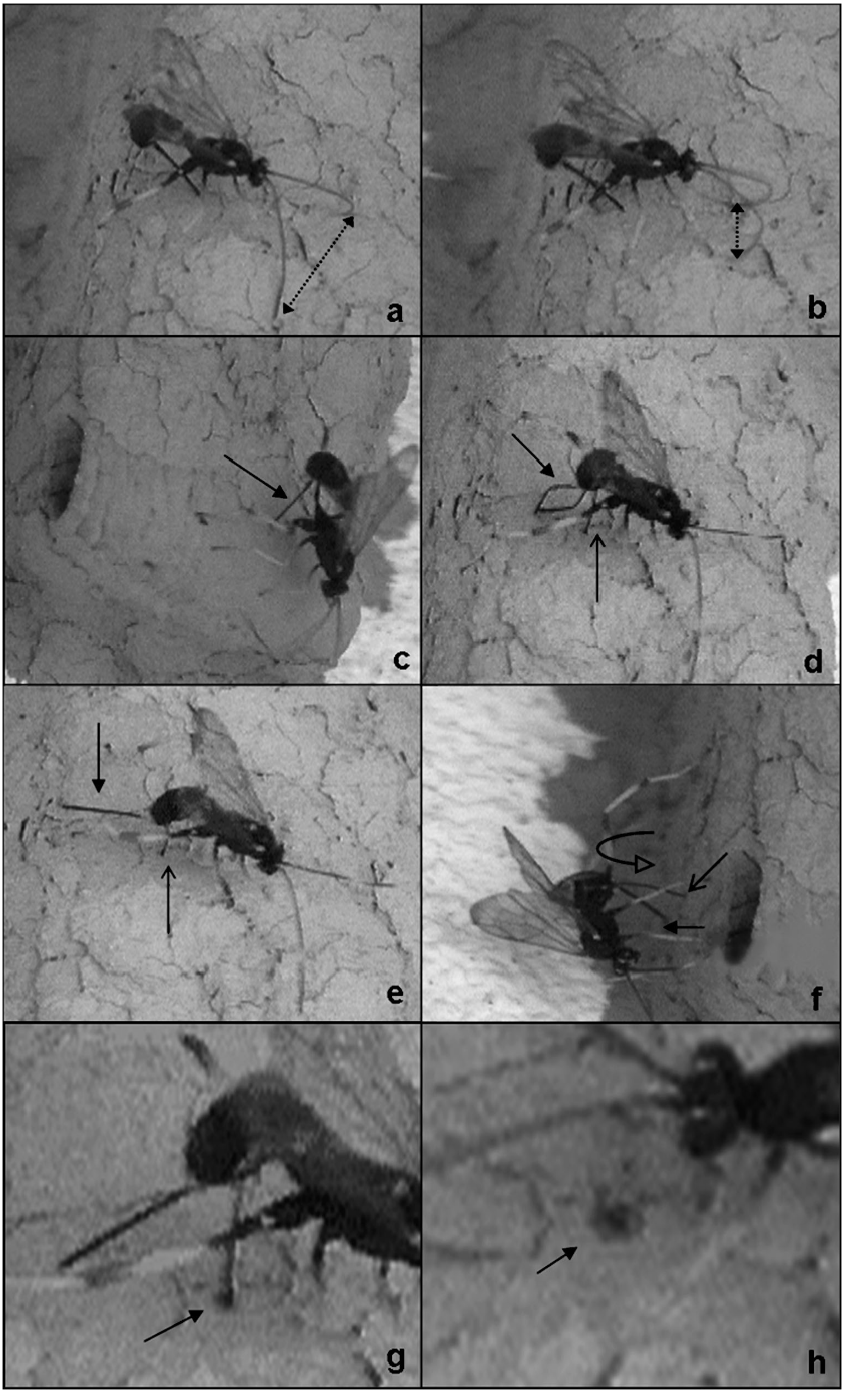

Figure 3. Parasitism by *A. seductor* on a *S. caementarium* nest: (a-b) tapping with antennae; (c-f) different phases of the oviposition; (g-h) darker halo (arrow); further details in the text.

nest (fig. 2.10), with the sheaths outstretched and perpendicular to the ovipositor. A few seconds later, the ovipositor is extracted from the cell (fig. 2.14), and the body quivers (fig. 2.11) in a more and more intense way (fig. 2.13). Then, the *A. seductor* female started new exploration activities.

Tapping, associated to movements across the nest surface and the use of sheaths, is the most time-consuming activity. The time spent by wasp with the ovipositor half-inserted into the mud varies from 15 to 55 seconds. Probably this is when oviposition takes place.

Acroricnus seductor landed on the host nest while it was away hunting for spiders or collecting mud balls. The sphecid female required on average 10 minutes catching a spider prey and during that period the ichneumonid could work undisturbed. The *A. seductor* female spent 2-10 minutes between reaching the nest and retracting the ovipositor. Only once the ichneumonid wasp was seen arriving at the nest when the host was building a new cell; in that case, the ichneumonid was immediately driven away. In two other cases a *S. caementarium* female came back to its nest and met *A. seductor*; also in this case the ichneumonid was immediately driven away.

Morphology of structures involved in host detection

In ichneumonid wasps the first and second valvulae constitute the “ovipositor proper” and the third valvulae constitute the ovipositor sheaths (Quicke et al., 1994) (fig. 4). The third valvulae are as long as the ovipositor proper and they cover and protect it.

Ovipositor sheaths (fig. 4a-b) bear sensory setae which are absent from the smooth surface of the ovipositor proper (fig. 4d). Moreover, the lateral walls of the sheaths are finely transversely subdivided by narrow furrows (fig. 4b). The ovipositor proper possesses coeloconic sensilla, whose circular depression has a diameter of about 6 μm on its distal part, and the cone in the center protruding for about 3 μm (fig. 4d, e). The basal (proximal) parts of the ovipositor proper have no conspicuous sculptures or sensilla (fig. 4f).

Scanning electron microscopic analysis showed a circular structure of approx 40 μm in diameter (fig. 5a) on the tip of the female antennae only. This is a cluster of truncate structures fused forming a smooth face. Antennae morphology differed between females and males (fig. 5a-b), the former bearing shorter and denser setae and the latter lacking the circular structure on the tip described above.

Fore tibiae of females showed some differences from those of males; in particular, they seem relatively more swollen in females (width: 0.32 ± 0.01 mm, $n = 3$), than in males (0.26 ± 0.01 mm, $n = 3$), and the ratio between width and length of fore tibiae seem higher for females (0.164 ± 0.005, $n = 3$), than in males (0.127 ± 0.003, $n = 3$) (fig. 5c-d).

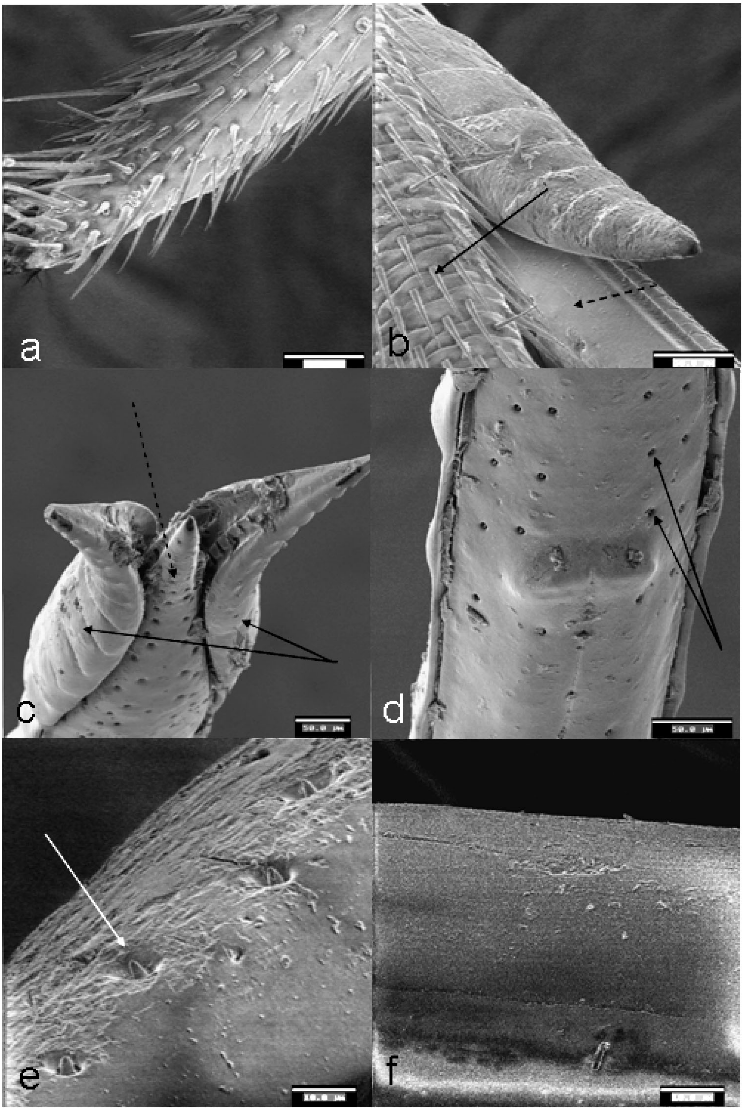

Figure 4. Scanning electron micrographs of *A. seductor* ovipositor proper and sheaths: a, sensilla on the sheaths; b-c, ovipositor's sheaths (continuous arrow) and ovipositor proper (dashed lines); d-e, receptors (arrow) on the ovipositor's distal portion; f, proximal portion of the ovipositor.

Discussion

Is A. seductor *a parasitoid or a kleptoparasite?*

The analysis of the parasitized cells shows that the host larva (dead or alive) was always at an intermediate stage of development. In the parasitized cells we never found large host larvae, prepupae or pupae. This suggests that *A. seductor* avoids cells in which the host larva is above a certain stage of development. Maybe the *A.*

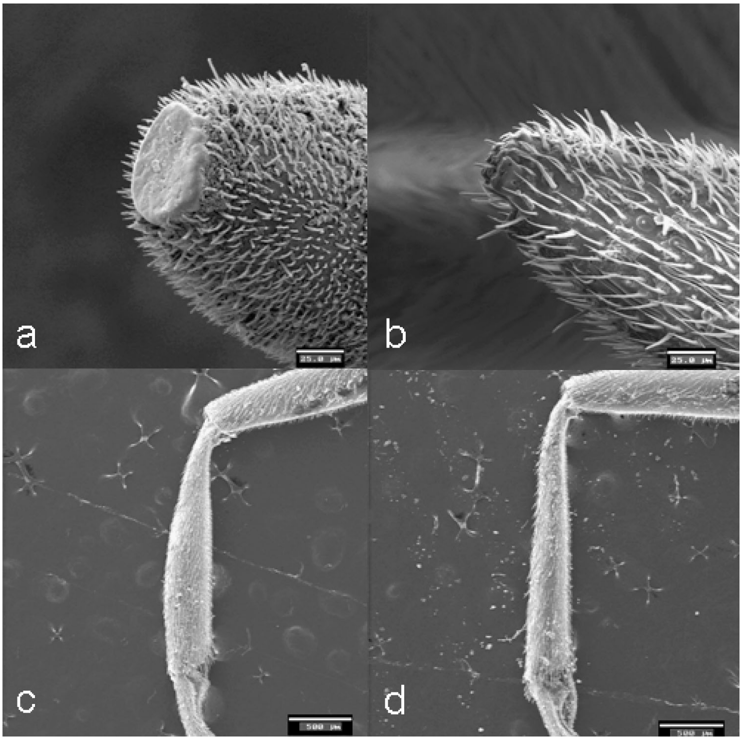

Figure 5. Scanning electron micrographs of *A. seductor* antennae and fore tibiae: a-b, tip of antenna (a: female, b: male); c-d, fore tibia (c: female, d: male).

seductor larva may not be able to feed on large hosts, possibly due to the thickness of its cuticle or because large hosts could not be quickly and entirely devoured, enabling fungal infestation. *Acroricnus seductor* larvae probably feed primarily on spider prey of the host, and, sometimes, on young host larvae. This indicates that *A. seductor* acts as a kleptoparasitoid and not simply as a parasitoid of *S. caementarium*. This contrasts to what suggested by Grandi (1930) for this species, but agrees with Itino (1986), which found that *Acroricnus ambulator* Smith was a mortality factor for eumenid wasps only at the larval stage, not at the prepupa or pupa stages. Several other members of Cryptini who attacks sphecid wasps act as kleptoparasitoids (Casiraghi et al., 2001).

Is the rate of parasitism by A. seductor *affected by nest location and size?*

The similar number of parasitized cells in sheltered and unsheltered nests supports the hypothesis that the ichneumonid females are attracted, probably by chemical stimuli (e.g. Lenteren, 1981; Vet et al., 1995), to the nests themselves rather than to seemingly appropriate sites. In contrast, at least two eusocial *Polistes* wasps seem to suffer higher rate of parasitism by ichneumonids if their paper nests are built in sheltered sites (Nelson, 1968; Rusina, 2008). Larger nests included more parasitized cells, so maybe the size of the nest could account for the probability to be attacked by the ichneumonid wasp. Cervo and Turillazzi (1996) reported that a *Polistes* social parasite selects the larger and more developed host nests from those available, and they suggest that odour concentration may be higher in larger nests, making them easier to detect than smaller ones. Anyway, new data are necessary to test this hypothesis in *A. seductor*.

In addition, larger host nests do not necessarily correspond to a greater number of suitable cells; in fact, cells are stratified in layers and deeper ones could be difficult to exploit. On the other hand, larger cells were not more likely to be parasitized by *A. seductor*. Because *A. seductor* females avoid mature and large hosts (prepupae and pupae), it is possible that host cell selection is affected by the development stage of the host rather than by the size of the cell.

Does A. seductor *use echolocation to detect the host?*

Tapping is frequently used during host detection by *A. seductor*. Tapping behaviour is a key component of the host detection through the creation of vibrational sounding ("echolocation in a solid substrate", Broad and Quicke, 2000). Vibrational sounding seems to be evolved in association with parasitism of deeply concealed hosts (Broad and Quicke, 2000): wasps would transmit vibrations into solid substrate via their antennae and, after analyzing the reflected signals, they should be able to detect the position of the potential host (Wäckers et al., 1998). This technique seems to be used also by *A. seductor*, as revealed by the "hammer" on the tip of female antennae and by the relatively thicker fore tibiae of females, which suggest that they harbour a relatively larger subgenual organ (Broad and Quicke, 2000; Vilhelmsen et al., 2001).

This results is important, considering that, despite the knowledge of such morphological adaptations for many species of Cryptini (Broad and Quicke, 2000; Laurenne et al., 2009), their association with behavioural evidence has rarely been reported in this tribe (Quicke et al., 2003; Casiraghi et al., 2001).

Echolocation by A. seductor *in relation to other cryptine wasps*

Laurenne et al. (2009) classify the types of antennal tip in Cryptinae according to the degree of the modification, ranging from unmodified, often acuminate, with simple setae at tip to being truncate with a large flat or even concave hammer area. Following such classification, the tip of female antennae of *A. seductor* resembles that of "kind 5", i.e. with cluster of short, broad, apically flattened structures virtually entirely fused so as to form a shiny, largely smooth entire face. This kind of antennal tip was recognized by Laurenne et al. (2009) for *Buathra* and *Osprynchotus*, but not for *Acroricnus*, which was assessed as the antennal tip of the kind 4, i.e. with a cluster of short, broad, apically flattened structures, but these being still largely distinct. Thus, variability in antennal tip's "hammer" may be possible inside the same genus. This is confirmed by the fact that the antennal tip observed in

Buathra by Laurenne et al. (2009) differs somehow from what observed for *Buathra tarsoleuca* Schrank, a kleptoparasitoid of *Ammophila sabulosa* L. and *Podalonia affinis* Kirby (Hymenoptera: Sphecidae) (Casiraghi et al., 2001). In *B. tarsoleuca*, in fact, the "hammer" on the tip of the antennae seems to be poorly defined, if not absent (Casiraghi et al., 2001). Apparently, *B. tarsoleuca* detects the correct position of the host egg or of the brood cell provision by the insertion of one of the antennae into the hole made previously by the ovipositor, although echolocation may be used to detect, through antennal hammering, the area to further check for the presence of the host.

The difference between *A. seductor* and *B. tarsoleuca* is particular interesting. Although the substrate protecting the resource exploited by the two ichneumonids is similar (i.e. soil and mud), the distance between the resource and the surface differs: *A. sabulosa* and *P. affinis*, the two hosts of *B. tarsoleuca*, dug burrows of about 10 cm depth in the ground, ending with a single brood cell; *S. caementarium*, instead, collects prey in brood cells separated from the outside by about 5-10 mm. This difference in host biology could account for both behavioural and morphological differences in ichneumonid host location strategy. This hypothesis agrees with what speculated through multi-species morphological comparisons: in fact, echolocation should be more successful if the object that returns the vibration signal is easily detectable, e.g. if the distance separating the source and the target of the vibrations is short (Broad and Quicke, 2000).

Another rare case of behavioural observation in support of echolocation in Cryptinae concerns *Gabunia* aff. *togoensis* Krieger (Quicke et al., 2003). In that study, the observed female was active only in sunshine in the afternoons, performing a slow to-and-fro walk along a dead tree, tapping the substrate with the antennae in a way similar to *A. seductor*. Moreover, in this species the tree surface is examined with the ovipositor sheaths in a way resembling *A. seductor* on the host mud nest. Probably females use these organs to search for existing cracks or holes to facilitate penetration of the ovipositor, as suggested in *A. seductor* also by the presence on the sheaths of sensory setae.

Coeloconic sensilla on the distal part of ovipositor have already been described in other cryptine wasps, and they seem to be mechanoreceptors (e.g. Quicke et al., 1994; Casiraghi et al., 2001). According to LeRalec et al. (1996) and Brown and Anderson (1998), species attacking deeply buried hosts possess large numbers of mechanoreceptor pegs along the length of the ovipositor shaft, while species attacking exposed hosts possess mechanoreceptors concentrated at the tip. *Acroricnus seductor* possess sensilla mostly in the distal part of the ovipositor, and, partially accordingly to this hypothesis, its host is not exposed but neither deeply concealed.

Additional interesting features of parasitism

The darker halo around the penetration point of the ovipositor (fig. 3g-h) could be caused by a fluid which exudes from the ovipositor. According to Lyngnes (1960) and Ganesalingam (1972), in the ichneumonid wasps *Ephialtes extensor* Taschenberg and *Venturia canescens* (Gravenhorst), this fluid acts as a lubricant to reduce friction of the ovipositor while boring. The same hypothesis was proposed by Le Lannic and Nénon (1999) for the wood-penetrating ovipositor of *Megarhyssa atrata* (Fabricius). Janvier (quoted in Grandi (1951)) reported *Dotocryptus macrocerus* (Spinola), a parasite of a eumenid wasp of the genus *Odynerus*, exuding from the tip of ovipositor a liquid drop that would mould the mud wall of the host nest. This could be also the case for *A. seductor*.

The tremors of the kleptoparasitoid body are probably due to the ichneumonid attempts to extract the ovipositor from the mud wall of the nest. *Sceliphron caementarium* nests are quite compact structures, probably difficult to penetrate. The same happens to *Townesia tenuiventris* (Holmgren) (Jussila, 1975), an ichneumonid wasp that parasitized *Chelostoma maxillosum* (Linnaeus), a leaf cutter bee that nests in pre-existing burrows in wood and that closes it at the end of provisioning with a solid clay plug.

These two behaviours have been rarely investigated in detail in parasitic wasps, and experimental studies devoted to their analysis will be very welcome in future researches.

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References

Broad, G.R. & Quicke, D.L.J. (2000) The adaptive significance of host location by vibrational sounding in parasitoid wasps. *P. Roy. Soc. Lond. B*, 267, 2403-2409.

Brown, P.E. & Anderson, M. (1998) Morphology and ultrastructure of sense organs on the ovipositor of *Trybliographa rapae*, a parasitoid of the cabbage root fly. *J. Insect Physiol.*, 44, 1017-1025.

Campadelli, G. & Pagliano, G. (1987) Una biocenosi in nidi di *Sceliphron destillatorium* (Hym.: Sphecidae). *Agricoltura*, 15, 39-41.

Cervo, R. & Turillazzi, S. (1996) Host nest preference and nest choice in the cuckoo paper wasp *Polistes sulcifer* (Hymenoptera: Vespidae). *J. Insect Behav.*, 9, 297-306.

Campadelli, G., Pagliano, G., Scaramozzino, P.L. & Strumia, F. (1999) Parassitoidi e inquilini di *Sceliphron caementarium* (Drury 1773) (Hymenoptera: Sphecidae) in Romagna. *Boll. Mus. Reg. Sci. Nat Torino*, 16, 225-240.

Casiraghi, M., Andrietti, F., Bonasoro, F. & Martinoli, A. (2001) A note on host detection by *Buathra tarsoleuca* (Schrank) (Hymenoptera: Ichneumonidae), a parasite of *Ammophila sabulosa* (L.) and *Podalonia affinis* (Kirby) (Hymenoptera: Sphecidae). *J. Insect Behav.*, 14, 299-312.

Champlain, A.B. (1922) Records of hymenopterous parasites in Pennsylvania. *Psyche*, 29, 95-100.

Coulon, L. (1933) Catalogue de la collection d'Hyménoptères de la famille des Ichneumonidae du Musée d'Elbeuf. *Bull. Soc. Sci. Nat. Elbeuf*, 51, 73-96.

Frilli, F. (1966) Studi sugli imenotteri icneumonidi. II. Revisione delle specie europee e mediterranee del genere *Acroricnus* Ratzeburg (Cryptinae). *Entomologica*, 2, 12-20.

Ganesalingam, V.K. (1972) Anatomy and histology of the sens organs of the ovipositor of the ichneumonid wasp, *Devorgilla canescens. J. Insect Physiol.*, 18, 1857-1867.

Genaro, J.A. (1996a) Nest parasites (Coleoptera, Diptera, Hymenopteran) of some wasps and bees (Vespidae, Sphecidae, Collectidae, Megachilidae, Anthophoridae) in Cuba. *Caribb. J. Sci.*, 32, 239-240.

Genaro, J.A. (1996b) Sobre la nidificación de *Sceliphron caementarium* y primer registro de *Trypoxylon texense* para Puerto Rico (Hymenoptera: Sphecidae). *Caribb. J. Sci.*, 32, 243-244.

Grandi, G. (1930) Contributi alla conoscenza biologica e morfologica degli Imenotteri melliferi e predatori. XI. *Boll. Lab. Ent. R. Ist. Sup. Agr. Bologna*, 3, 302-343.

Grandi, G. (1951) *Entomologia I-II.* Calderini, Bologna.

Hook, A.W. (2006) Nest, prey, and parasites of *Trigonopsis violascens* (Hymenoptera: Sphecidae) in Trinidad, West Indies. In: *Abstract conference in the 2006 ESA Annual Meeting, December 10-13, 2006, Indianapolis, IN.*

Itino, T. (1986) Comparison of life tables between the solitary eumenid wasp *Anterhynchium flavomarginatum* and the subsocial eumenid wasp *Orancistrocerus drewseni* to evaluate the adaptive significance of maternal care. *Res. Pop. Ecol.*, 28, 185-199.

Jussila, R. (1975) Observations on *Townesia tenuiventris* (Hlmgr.) (Hym., Ichneumonidae) and its hosts *Chelostoma maxillosum* (L.) (Hym., Megachilidae) and *Trypoxylon figulus* (L.) (Hym., Sphecidae). *Ann. Entomol. Fennici*, 41, 81-86.

Laurenne, N.M., Broad, G.R. & Quicke, D.L.J. (2006) Direct optimization and multiple alignment of 28S D2-D3 rDNA sequences: problems with indels on the way to a molecular phylogeny of the cryptine ichneumon wasps (Insecta: Hymenoptera). *Cladistics*, 22, 442-473.

Laurenne, N.M., Karatolos, N. & Quicke, D.L.J. (2009) Hammering homoplasy: multiple gains and losses of vibrational sounding in cryptine wasps (Insecta: Hymenoptera: Ichneumonidae). *Biol. J. Linn. Soc.*, 96, 82-102.

Le Lannic, J. & Nénon, J.P. (1999) Functional morphology of the ovipositor in *Megarhyssa atrata* (Hymenoptera, Ichneumonidae) and its penetration into wood. *Zoomorphology*, 119, 73-79.

Lenteren, J.C. Van (1981) Host discrimination by parasitoids. In: D.A. Nordlund, R.L. Johnes & W.J. Lewis (Eds.) *Semiochemicals, Dare Role in Pest Control*, pp. 153-179. Wiley, New York.

LeRalec, A., Rabasse, J.M. & Wajnberg, E. (1996) Comparative morpholgy of the ovipositor of some parasitic Hymenoptera in relation to characteristics of their hosts. *Can. Entomol.*, 128, 413-433.

Lichtenstein, J.L. (1920) Les espèces françaises du genre *Acroricnus* Ratz. *Bull. Soc. Entomol. Fr.*, 4, 71-78.

Loyola, R.D. & Martins, R.P. (2006) Trap-nest occupation by solitary wasps and bees (Hymenoptera: Aculeata) in a urban forest remnant. *Neotrop. Entomol.*, 35, 41-48.

Lyngnes, R. (1960) Shape and function of the ovipositor in the three hymenopterous species: *Ephialtes extensor* Thom. (Ichneumonidae), *Spathius exarator* L. (Braconidae) and *Plutothrix coelius* Walk. (Chalicidae). *Norsk. Entomological Tidss. Tidsskr*, 11, 122-134.

Mansion, J. (1926) Gestes dysharmoniques de la ponte de *Cryptus seductorius F. Bull. Soc. Entomol. Fr.*, 1926, 122-123.

Mitchell, R.T. (1950) The genus *Acroricnus* in America (Hymenoptera, Ichneumonidae). *Ann. Entomol. Soc. Am.*, 43, 249-261.

Mocsáry, A. (1879) Eine kleine Notiz über *Xenodocon ruficornis Först. Entomologische Nachrichten*, 5, 11.

Nelson, J.M. (1968) Parasites and symbionts of nests of *Polistes* wasps. *Ann. Entomol. Soc. Amer.*, 61, 1528-1539.

Polidori, C., Trombino, L., Fumagalli, C. & Andrietti, F. (2005) The nest of the mud-dauber wasp, *Sceliphron spirifex* (Hymenoptera: Sphecidae): an application of geological methods to structure and brood cell contents analysis. *It. J. Zool.*, 72, 153-159.

Polidori, C., Federici, M., Pesarini, C. & Andrietti, F. (2007) Factors affecting spider prey selection by *Sceliphron* mud-dauber wasps (Hymenoptera: Sphecidae) in northern Italy. *Anim. Biol.*, 57, 11-28.

Rusina, L.Yu. (2008) Reaction of parasitoids of the paper wasp *Polistes dominulus* (Christ) (Hymenoptera, Vespidae, Polistinae) to the host distribution. *Entomol. Rev.*, 88, 881-897.

Quicke, D.L.J., Fitton, M.G., Tunstead, J., Ingram, S.M. & Gaitens, P.V. (1994) Ovipositor structure and relationships within the Hymenoptera, with special reference to the Ichneumonoidea. *J. Nat. Hist.*, 28, 635-682.

Quicke, D.L.J., Leurenne, N.M., Broad, G.R. & Barclay, M. (2003) Host location behaviour and a new host record for *Gabunia* aff. *togoensis* Krieger (Hymenoptera: Ichneumonidae: Cryptinae) in Kibale Forest National Park, West Uganda. *Afr. Entomol.*, 11, 308-310.

Schimitschek, E. (1944) *Forstinsekten der Turkei und ihre Umwelt*. Verlag, Prague.

Steffan-Dwenter, I. (2002) Landscape context affects trap-nesting bees, wasps and their natural enemies. *Ecol. Entomol.*, 27, 631-637.

Tormos, J., Asís, J.D., Gayubo, S.F. & Selfa, J. (2004) Description of the final instar larvae of *Perithous septemcinctorius*, *Zatypota bohemani* and *Z. gracilis* (Hymenoptera: Ichneumonidae: Pimplinae). *J. Entomol. Sci.*, 39, 475-482.

Vet, L.E.M., Lewis, W.J. & Cardé, R.T. (1995) Parasitoid foraging and learning. In: R.T. Cardé & W.J. Bell (Eds.) *Chemical Ecology of Insects 2*, pp. 65-101. Chapman and Hall, New York.

Vilhelmsen, L., Isidoro, M., Romani, R., Basibuyuk, H.H. & Quicke, D.L.J. (2001) Host location and oviposition in a basal group of parasitic wasp: the subgenual organ, ovipositor apparatus and associated structures in the Orussidae (Hymenoptera, Insecta). *Zoomorphology*, 121, 63-84.

Wäcker, F.L., Mitter, E. & Dorn, S. (1998) Vibration sounding by the pupal parasitoid *Pimpla* (*Coccygomimus*) *turionellae*: an addition solution to the reliability-detectability problem. *Biol. Control*, 11, 141-146.

White, E. (1962) Nest-building and provisioning in relation to sex in *Sceliphron spirifex* L. (Sphecidae). *J. Anim. Ecol.*, 31, 317-329.

Yamane, S. (1990) A revision of the Japanese Eumenidae (Hymenoptera, Vespoidea). *Insect. Matsum.*, 43, 1-189.