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Distal leg morphology, subgenual organs and host detection in Stephanidae (Insecta, Hymenoptera)

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The morphology of the tibia and tarsus of all legs is examined in species of two genera of Stephanidae. The subgenual organ (SGO) is examined in more detail for *Megischus* spp. The fore leg is the most modified in *Schlettererius*. In *Megischus*, the SGO of the hind leg is displaced to the middle of the tibia, which is swollen distad of it; in the female the hind tarsi are three-segmented, the basitarsomere being a composite of tarsomeres 1–3. Internally, the SGO of *Megischus* is suspended between a spine and a ridge. In the mid and hind legs, part of the tibial wall is thinner in the region of the SGO. Our observations provide circumstantial evidence that female Stephanidae detect substrate-borne vibrations when searching for hosts. The absence of antennal modification, as well as information on host stage targeted and general behaviour on the oviposition site indicates that they rely on noise made by the host rather than generate vibrations themselves, in contrast to Orussidae, a parasitoid wasp taxon that has been inferred to employ vibrational sounding. The external receptor elements – membranous pads versus tufts of setae – are not homologous in Orussidae and Stephanidae. A spine and ridge suspensorium of the SGO found in members of both families may represent a derived groundplan feature of the orussid–apocritan clade, with secondary modification or reduction in the latter group. Characters of the distal leg elements and the SGO suggest a basal position of *Schlettererius* and *Stephanus* within Stephanidae. Modifications of the hind tibia and tarsus in more derived members of the family indicate a shift in relative importance in vibration detection from the fore leg to the hind leg within the family.

Keywords: parasitoid wasps; host detection; wood-boring lifestyle

Introduction

Parasitoid wasps targeting wood-boring insects have to overcome the daunting task of detecting a host deeply concealed within a hard substrate. For some wasps, this apparently involves echolocation or vibrational sounding, i.e. detecting the host by generating vibrations and monitoring them as they are differentially reflected in the substrate. The ability to detect concealed objects (cigarette filters inside paper cylinders) has been demonstrated experimentally in *Pimpla turionellae* (Ichneumonidae; Wäckers et al. 1998). The females of many parasitoid wasps have been observed to beat the wood vigorously with the tips of the antennae, which

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might be modified for the purpose (Ichneumonidae, Broad and Quicke 2000; Orussidae, Vilhelmsen et al. 2001). The vibrations are presumably picked up by the tarsi and conveyed up the leg to the tibia, which contains the subgenual organ (SGO), a chordotonal organ usually present in the legs of winged insects (Debaisieux 1935, 1938; Yack 2004). In female *Orussus*, the SGO of the foreleg is very large, comprising upwards of 400 scolopidial sensory units (Vilhelmsen et al. 2001); smaller organs are observed in other parasitoid (Ichneumonidae: *Pimpla turionellae*; Otten et al. 2002) and non-parasitoid (Formicidae: *Camponotus ligniperda*; Menzel and Tautz 1994; Apidae: *Apis mellifera*; Schön 1911) Hymenoptera. The fore tibia of female *Orussus* is substantially modified, incorporating a thin-walled area opposite the SGO that might serve to transmit vibrations (Vilhelmsen et al. 2001).

Stephanidae is another wasp family parasitizing wood-boring insects, especially Buprestidae and Cerambycidae (Aguiar 2001, 2006a). It is a small family with worldwide distribution, comprising some 320 extant species in 11 genera (Aguiar 2004). Several observations indicate that the Stephanidae might detect vibrations in wood. Females (*Parastephanellus* sp.) have been reported to antennate intensively on a bark-free trunk before oviposition (Rodd 1951). Furthermore, numerous images published in recent monographs of Stephanidae show substantial modifications in the hind tibia and tarsus of many species (Aguiar 2001, 2006; van Achterberg 2002). These modifications include a distally swollen tibia with an inverted V-shaped depression medially and a three-segmented hind tarsus, features that are characteristic of the females of most genera of Stephanidae (van Achterberg 2002: figure 16). Moreover, van Achterberg (2002: figure 15) identified a structure in the distal part of the hind tibia of *Megischus insularis* as part of the SGO.

To investigate how Stephanidae might be able to detect vibrations in wood, we examined in more detail the legs of representatives of two stephanid genera, *Schlettererius* and *Megischus*; for the latter taxon, we produce serial sections that allow us to identify the SGO. We also conduct a brief survey of the external morphology of the legs of some additional taxa available to us for comparison. We discuss the configuration and distribution of SGOs within the Stephanidae, both in a phylogenetic and a functional context.

Material and methods

Material examined

Schlettererius cinctipes (Cresson, 1880), females, two specimens (scanning electron micrographs; SEM); *Megischus* spp., females (two specimens, Colombia, Amasonas, Amacayaku Park; two specimens, French Guyana, Regina Road, Roura-Kaw) (SEM, serial sections). The following taxa were examined from pinned specimens for the external anatomy of the legs: *Foenatopus* sp. (Thailand, Khao Fang), female; *Foenatopus* sp. (South Africa, Roodeplaat), male; *Hemistephanus collarifer* (Schletterer, 1889), female; *Megischus anomalipes* (Förster, 1855) (Italy, Sicily, Iblei Mountains and Mount Etna), females; *M. coronator* (Fabricius, 1804), female and male; *M. furcatus* (Lepeletier & Serville, 1835), female and male; *M. lieftincki* van Achterberg, 2002, female; *Parastephanellus denotatus* Aguiar, 2001, male; *P. granulatus* (Elliot, 1919), female; *P. nigricaudatus* (Sichel, 1866), females and male; *Schlettererius cinctipes*, females and male; *Stephanus serrator* (Fabricius, 1798), females and male.

Scanning electron microscopy and dry dissection

The legs were cut off at the trochanter and cleaned with ultrasound. They were transferred through a series of intermediate steps from 70% to 99.9% ethanol, which served as the transition medium for critical point drying. After critical point drying, the preparations were mounted on stubs with double-adhesive tape and coated with platinum before examination in a Jeol JSM-6335F field emission SEM unit. One hind tibia was dissected after critical point drying with scalpel, forceps and needles while partly immobilized in wax.

Serial sections

Specimens for histological investigations were initially preserved in 70–80% ethanol. Serial cross-sections of one fore, mid and hind tibia each were made from one *Megischus* sp. The specimens were embedded in Araldite® and cut at 1.5 μm with a Microm microtome (HM 360). The sections were stained with methylene blue and acid fuchsine.

Results

The results of our investigations on both external and internal features of the tibiae and tarsi of Stephanidae are presented. A more detailed description of the SGO is provided for *Megischus* spp., especially for the hind legs, where it is most developed. For the other legs, only features distinguishing it from the hind leg SGO are noted. Except when noted, descriptions apply to both sexes.

Schlettererius cinctipes
(Figures 1A–D, 2A–C)

Fore leg

The tibia is shorter than the femur; in females, a shallow lateral concavity is present in the proximal half (Figure 1A). A small dome is situated anteriorly approximately one-quarter of the total length from the base of the tibia; its microsculpture is less developed than on the surrounding cuticle (Figure 1B). The tibia gradually expands distally. The median side is more setose than the lateral side; distally, a small brush of closely placed pointed setae is present. A single modified apical tibial spur, the calcar, is situated distally; a distinct cone-shaped sensillum is present at the apex opposite the calcar. The tarsus is five-segmented and approximately 1.6 times as long as the tibia, the basitarsus comprising less than half the length of the tarsus. Tarsomere 4 is short; it bears an elongate distal flange (Figure 1C) covered with pointed setae.

Mid leg

The tibia is approximately as long as the femur; a concavity or dome is not recognizable, the tibia being of approximately equal width throughout except at its basalmost part (Figure 1D). Elongate setae are regularly distributed on the surface. Apical spurs are absent; a distinct cone-shaped sensillum is situated posteriorly at the apex. The tarsus is five-segmented and slightly shorter than the tibia. The basitarsus
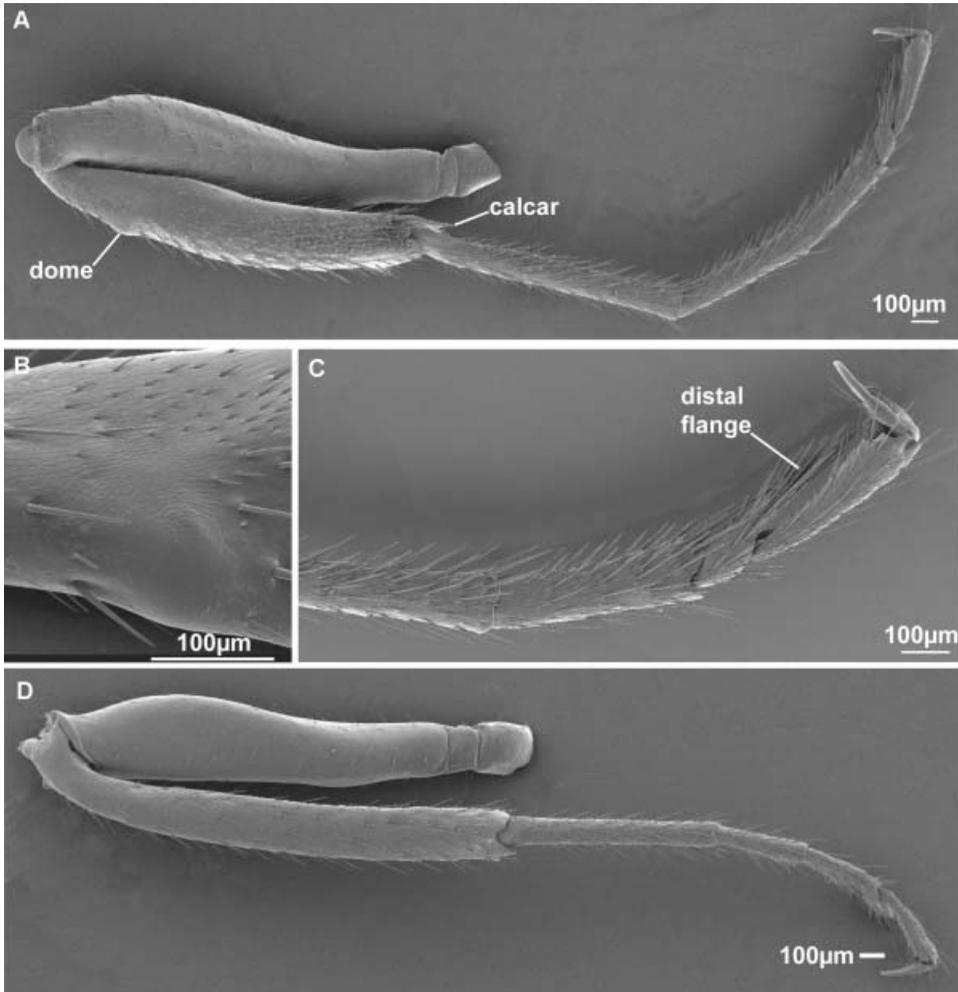
Figure 1. *Schlettererius cinctipes*, female, foreleg and mid-leg. (A) Fore leg, median view. (B) Basal part of fore tibia, median view, with dome concealing subgenual organ. (C) Fore tarsus, tarsomeres 2–5. (D) Mid leg, lateral view.

is slightly shorter than the remaining tarsomeres combined. Tarsomere 4 is short but equipped with an elongate distal flange, which is covered with pointed setae.

Hind leg

The tibia is slightly longer than the hind femur, including the trochantellus (Figure 2A), and gradually expands distally. A posterior dome and a small median depression are developed posteriorly approximately one-quarter of the total length from the base; the microsculpture of the dome is less developed than the surrounding cuticle (Figure 2B). An external longitudinal carina extends along the anterior part from the base about halfway to the apex. The tibia is more setose mesally than laterally; distally, a brush of densely placed distally swollen setae is present. A pair of
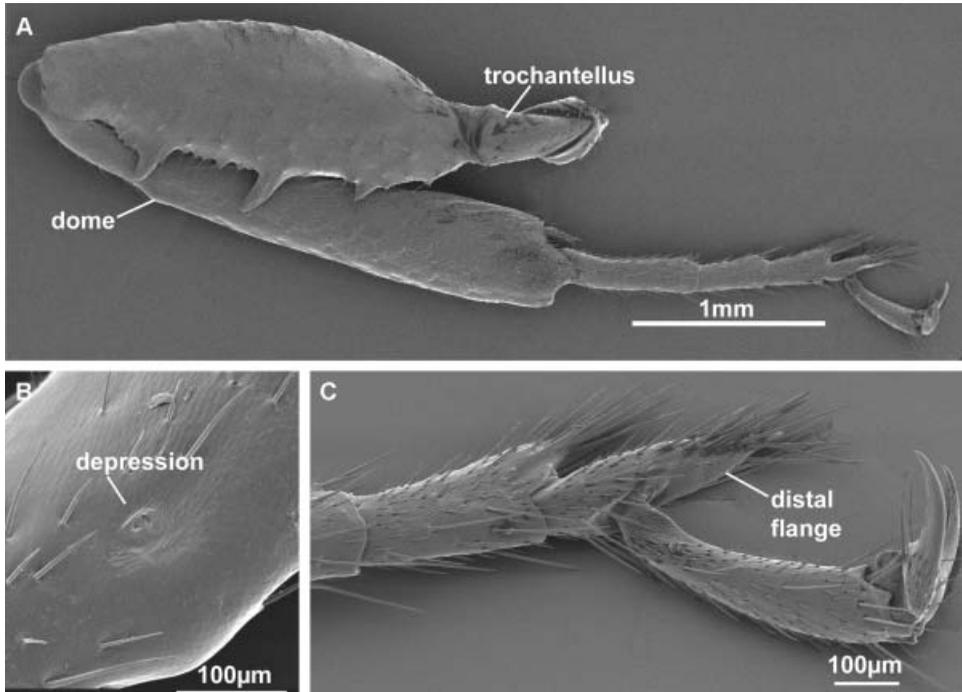
Figure 2. *Schlettererius cinctipes*, female, hind leg. (A) Hind leg, lateral view. (B) Hind tibia proximally at level of subgenual organ with dome in lower right corner, median view. (C) Hind tarsus, tarsomeres 3–5.

short apical spurs is situated on the anterior side. The tarsus is five-segmented and approximately 0.6 the length of the tibia, with the basitarsus comprising less than half of its length. Tarsomere 4 is short but an elongate distal flange is developed; the flange is covered with pointed setae (Figure 2C), which are also present distally on tarsomere 3.

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***Megischus* spp.**
(Figures 3A–D, 4A–C, 5A–F)

</div>

Fore leg

The tibia is shorter than the femur (Figure 3A). In females, it is distinctly swollen approximately one-third from its base, with an oblique depression laterally in this position (Figure 3B) and a small dome with reduced microsculpture just anterodorsad of the depression. The tibia is not expanded distad of the swelling and tapers slightly towards its apex. A row of apically expanded setae extends along the distal two-thirds of the median side. A single modified apical spur, the calcar, is present; a distinct cone-shaped sensillum is present at the apex of the tibia opposite the calcar (Figure 3B). The lateral depression on the tibia is less developed in the males, sometimes being hardly discernible.

The SGO is situated inside the proximal swelling, where the tibia is widest. It is suspended between a distinct spine (Figure 5A) laterally and a low swelling
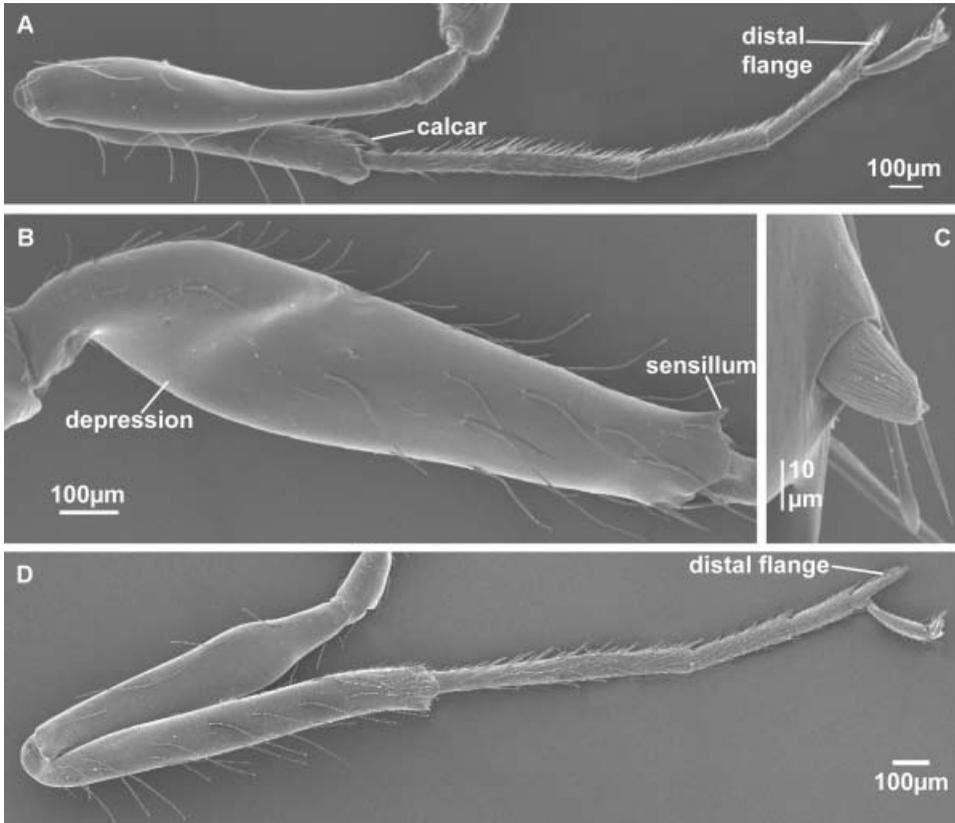
Figure 3. *Megischus* spp., female. (A) Fore leg, lateral view. (B) Fore tibia, lateral view. (C) Mid tibia, cone-shaped sensillum at apex. (D) Mid leg, lateral view.

(Figure 5B) medially on the median tibial wall. The thickness of the tibial wall is not reduced in any region except for the area around the base of the spine.

The tarsus is five-segmented in both sexes and approximately 1.7 times as long as the tibia, with the basitarsus making up less than half of its length. A slight extension with setae is present distally on tarsomere 3. Tarsomere 4 is very short, but equipped with an elongate distal flange with a dense tuft of setae at the apex (Figure 3A).

Mid leg

The tibia is slightly longer than the mid femur (Figure 3D) and of about equal width along most of its length, except for its slender base; it is, at most, slightly swollen proximally approximately one-quarter of the total length from its base; no distinct depression is present in the region of the SGO. Scattered elongate setae are present on the lateral side. Apical spurs are absent; a distinct cone-shaped sensillum is situated posteriorly at the apex (Figure 3C).

A small spine (Figures 5C and D) projects from the inner mesal wall of the tibia at the level of the swelling; the spine bends anteriorly towards its apex; opposite the spine on the inner lateral wall a low ridge is present (Figure 5C); the SGO is suspended between the spine and the ridge. The wall of the tibia posterad of the
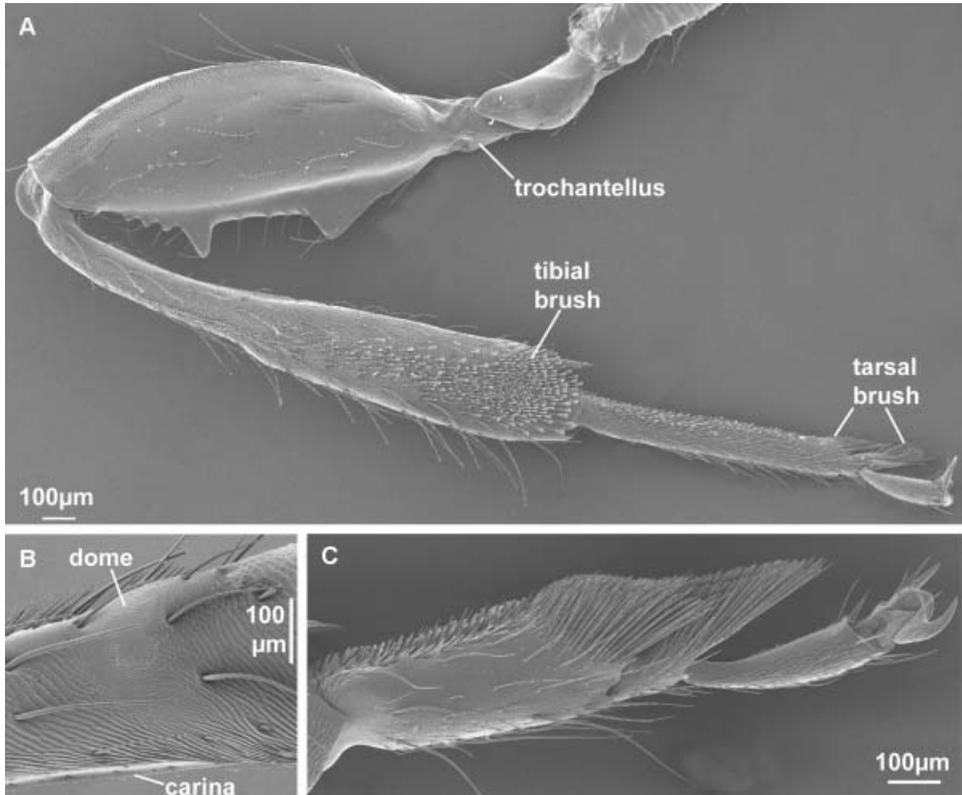
Figure 4. *Megischus* spp., female. (A) Hind leg, median view. (B) Hind tibia proximally at level of subgenual organ, lateral view. (C) Hind tarsus, tarsomeres 1–3 (different species from the one illustrated in Figure 4A).

spine and the ridge is somewhat thinner than the rest of the wall (Figures 5C and 5D, right).

The tarsus is five-segmented in both sexes and less than twice as long as the tibia, with the basitarsus making up almost half of its length. A setose extension is present distally on tarsomere 3. Tarsomere 4 is very short proximally, but an elongate distal flange with a dense tuft of setae is present at the apex (Figure 3D).

Hind leg

The tibia is distinctly longer than the femur, including the trochantellus (Figure 4A). The proximal part is slender, tubular and the walls are comparatively thick. An external longitudinal carina extends along the anterior part from the base about halfway to the apex (Figure 4B). Approximately one-third from its base, the tibia expands medially and also laterally a bit further down; the distal part appears distinctly swollen compared to the tubular proximal part. A shallow, inverted V-shaped furrow is present on the mesal side at the proximal end of the swelling. A small dome with less distinct microsculpture is present posteriorly on the tibia close to the apex of the furrow (Figure 4B). On the distal half of the mesal side of the tibia a brush composed of distally expanded setae is present; the setae are more densely
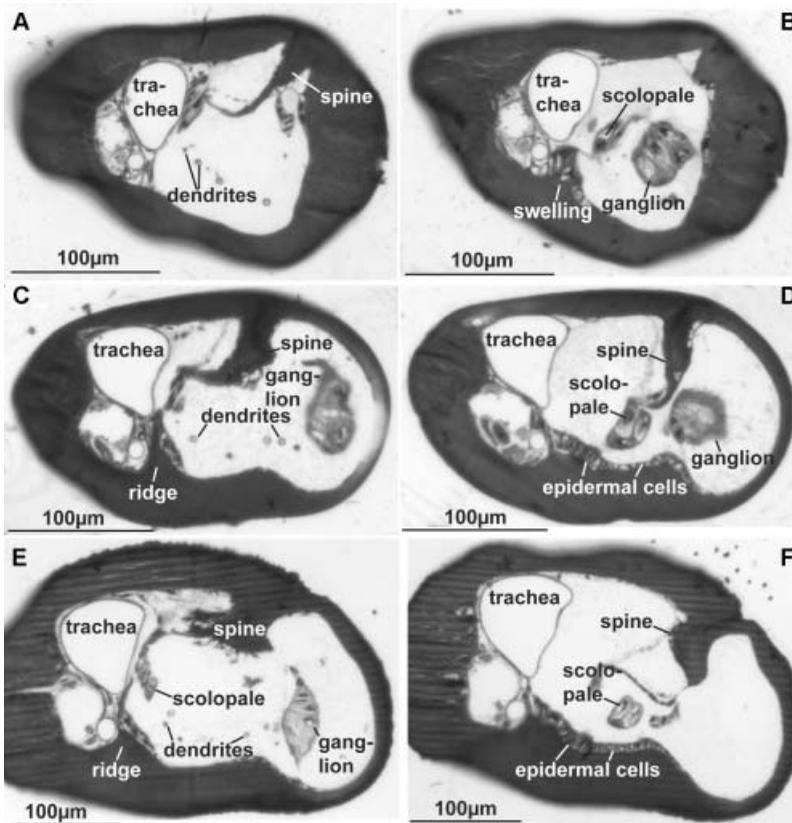
Figure 5. *Megischus* sp., female. Transverse sections of the tibiae at the level of the subgenual organ. The sections of the different legs are oriented the same way with regard to the relative positions of the trachea, the suspensorium (spine and ridge) and the subgenual organ proper for ease of comparison. (A), (B) Fore tibia, proximal and distal; lateral to the top, anterior to the right. (C), (D) Mid tibia, proximal and distal; median to the top, anterior to the left. (E), (F) Hind tibia, proximal and distal; median to the top, anterior to the left.

arranged towards the tibial apex (Figure 4A). A pair of short apical spurs is present on the anterior part of the tibia.

The SGO is situated proximally in the expanded part of the tibia, as indicated externally by the smooth dome; two tracheae, one with a small and one with a large diameter, pass along the anterior side of the SGO, and a ganglion is present posterad and slightly proximad of it (Figure 5E). The posterior wall of the tibia is distinctly thinner than the rest of the wall in the region of the SGO (Figures 5E and F, right). A distinct internal spine extends anteriorly from the median wall of the tibia (Figures 5E and F). A sheet of cap cells containing the scolopales is suspended between the spine and the opposite, lateral tibial wall (Figure 5E). A low ridge is developed anteriorly on the lateral wall, posterad of the smaller trachea. A sheet of modified epidermal cells extends posteriorly on the lateral wall of the tibia from the ridge to the thin posterior wall (Figure 5F); a direct contact of the epidermal cells with any of the cap cells was not observed. Attachment cells connecting the cap to the spine could not be identified with certainty. Slender dendrites extend between the

SGO and the ganglion posterad of it (Figure 5E). A membrane enveloping the SGO was not observed. Distad of the SGO the tarsal muscles are attached to the lateral wall of the tibia, occupying up to one-third of the tibial diameter.

The tarsus is three-segmented in the females and shorter than the tibia (Figure 4A). The basitarsus is of variable length (compare Figures 4A and C), but always at least as long as the two other tarsomeres; it bears a short lobe anteroventrally with a dense tuft of stout setae. Tarsomere 2 is very short proximally, but an elongate anteroventral flange with a dense tuft of stout setae is present adjacent to the tuft on the basitarsus (Figure 4C); together, they form a common setal brush. Tarsomere 3 is longer than tarsomere 2. In males, the hind tarsus is five-segmented and longer relative to the tibia; the basitarsus is at most slightly longer than the remaining tarsomeres combined. Tarsomere 3 and especially tarsomere 4 bear distinct distal lobes, but are not as setose as in the females.

Additional taxa examined

In general, among the additional taxa examined, tibial and tarsal structures of *Stephanus serrator* mostly resemble those of *Schlettererius cinctipes*, whereas the other taxa show more affinities with *Megischus* spp. Only the most important differences are reported here to avoid repetition.

Fore leg

A shallow concavity on the lateral side of the tibia is present in *S. serrator*, whereas a more prominent groove is developed in females of the other stephanid taxa; the groove is generally less strongly developed in males. A distinct spine situated posteriorly at the apex of the tibia could be observed in most taxa.

Mid leg

A shallow concavity approximately halfway down the median side of the tibia is present in *S. serrator*. A distinct spine situated posteriorly at the apex of the tibia could be observed in most taxa.

Hind leg

A small dome is situated approximately halfway down the posterior side of the tibia in all taxa examined. All taxa except *S. serrator* display an inverted V-shaped groove on the mesal side and the tibia is substantially swollen distad of the groove; in *S. serrator* the groove is absent and the tibia expands more gradually. The tarsus is five-segmented in *S. serrator* females and three-segmented in the females of all other species examined, with distal flanges on tarsomeres 4 and 2, respectively. Dense setal tufts are developed on the basitarsus and tarsomere 2, forming a continuous brush, in the females of all taxa except *S. serrator*.

Discussion

The fore tibia of all female Stephanidae examined display some modifications proximally, corresponding to the position of the SGO as observed in *Megischus* sp.

This suggests that they also possess a comparably specialized chordotonal organ, but further confirmation is needed. The tibia of female stephanid wasps is never as prominently altered as in Orussidae (Vilhelmsen et al. 2001), where the SGO is situated more distally in the fore tibia. However, because Orussidae is the sister group of the Apocrita, and Stephanidae is possibly the sister group of all other Apocrita (Vilhelmsen 2001, and unpublished results), it is conceivable that the modification of the fore tibia is homologous in these two taxa, albeit taken further in Orussidae. All Stephanidae retain a five-segmented fore tarsus, whereas female Orussidae have a three-segmented fore tarsus, with the elongate basitarsus consisting of the fused tarsomeres 1–3 (Vilhelmsen et al 2001; Vilhelmsen 2003). A distal spur with a thickened pad of soft cuticle is present in Orussidae, but absent in Stephanidae. Tarsomere 4 of Stephanidae bears a distal flange with a dense tuft of setae, whereas a pad is present distally on the basitarsomere in Orussidae (homologous with tarsomere 3 in Stephanidae). Both the pad in Orussidae and the tuft of setae in Stephanidae might serve the same function in vibration detection, i.e., to pick up vibrations from the substrate, but the structures are clearly not homologous in structure (membranous pad vs. setae) or topology (on inferred tarsomere 3 vs. tarsomere 4). This strongly suggests that at least the external receptor element of the sensorial system has evolved independently in both families. The pad and tufts of setae may represent autapomorphies of Orussidae and Stephanidae, respectively.

The suspensorium of the SGO in all the legs of *Megischus* is very similar to that of the fore tibia of *Orussus* (Vilhelmsen et al. 2001). In both taxa, the SGO is suspended between a distinct spine and a low ridge on the opposite side of the inner leg wall, the ridge lying close to the smaller of the tibial tracheae. The distal attachment cells (not observed with certainty in *Megischus*) attach to the spine in *Orussus*, whereas the ridge is connected to the SGO via modified epidermal cells. In contrast, other Hymenoptera where the SGO has been examined in detail do not have the spine and ridge internally: *Pimpla turionellae* (Ichneumonidae; Otten et al. 2002); *Camponotus ligniperda* (Formicidae; Menzel and Tautz 1994); *Apis mellifera* (Apidae; Schön 1911). In *P. turionellae*, the attachment cells are anchored in a pit rather than on a spine. In *A. mellifera*, the mode of operation of the SGO apparently requires it to be suspended more freely within the tibia (Kilpinen and Storm 1997). It is possible that the spine and ridge suspension is ancestral to Apocrita or an even more inclusive clade of Hymenoptera and has been secondarily modified within Apocrita, but verifying this requires examination of additional taxa.

Differences between the SGO in *Orussus* and *Megischus* occur in the development of a thin-walled area in the tibia that likely facilitates the transmission of the detected vibrations to the SGO. The thin-walled area is very prominent in the fore leg of *Orussus* (Vilhelmsen et al. 2001), but less developed in *Megischus*; in the fore leg of the latter (Figures 5A and B), it is hardly developed at all and it is also not very prominent in the other legs (Figures 5C–F). The size of the SGO in terms of the number of scolopidial sensory units is probably also different. Three to four hundred units are present in the fore tibia SGO of *Orussus* (Vilhelmsen et al. 2001), which is situated distally where the tibia is broadest. We were unable to estimate the number of units in *Megischus*. Given the position [proximally or midway (hind tibia), i.e. not in the broadest part of the tibia] and the degree of modification of the tibia externally (less than in *Orussus*), it is likely that the number of sensory units is less than in

Orussus. The size of the SGO in *Megischus* is probably more in the range of other Hymenoptera, i.e., comprising around 40 sensory units (Schön 1911; Menzel and Tautz 1994; Otten et al. 2002).

The mid tibia is the least modified in most Stephanidae. The presence of a SGO is barely indicated externally in many species. However, in *Megischus* the SGO and associated internal cuticular structures (spine, ridge) are well developed, even though not so prominent as in the hind tibia. Unfortunately, the SGO of the mid and hind tibia of *Orussus* was not examined by Vilhelmsen et al. (2001); externally, there is no obvious modification (swelling, groove, or dome) of the tibia in either sex except for the female fore tibia (unpublished observations). The cone-shaped sensillum observed at the apex of the fore and mid tibia in *Schlettererius* and *Megischus* is apparently also present in other Stephanidae. It is certainly a ground plan feature of the family, but a spine/sensillum is present at the tip of the mid tibia in Orussidae also (L. Vilhelmsen, unpublished observations); the configuration and distribution of these sensillae need to be surveyed across the entire Hymenoptera to clarify their phylogenetic significance.

Van Achterberg (2002, figure 15) provided a drawing of the interior of the distal part of the hind tibia of *Megischus insularis*, showing a cavity bordered by a convex membrane proximally that was claimed to be 'an obvious part of a subgenual organ'. Our investigations clearly show the SGO to be situated no further than midway down the hind tibia in Stephanidae. It is uncertain what was observed by van Achterberg (2002), conceivably it was part of the larger tibial trachea. The distal expansion of the hind tibia might serve to accommodate the enlarged tarsal muscles. This could also facilitate vibration detecting; an enlarged muscle may increase the pressure of the setal brush on tarsomere 1–2 against the substrate.

Within Stephanidae, the hind tibia and tarsus display considerable variation in relation to the development of the SGO and tarsal structures that might be involved in vibration detection and the distribution of these features might be phylogenetically informative. Some of this information was included in the analyses of Aguiar (2000) and van Achterberg (2002), who proposed the following basal relationships for the Stephanidae: *Schlettererius*+(*Stephanus*+remaining genera). The position of the SGO midway down the hind tibia (as indicated by the position of the smooth dome externally) might be an apomorphy for all Stephanidae except *Schlettererius*. The more proximal position of the SGO in the hind tibia of *Schlettererius* is probably plesiomorphic, because the SGO has this position in the fore and mid tibia in *Megischus* and in other insects in general (Yack 2004). The presence in the females of an inverted V-shaped furrow medially on the hind tibia, a three-segmented hind tarsus, and a prominent setal brush on tarsomeres 1–2 (Figures 4A and C; compare with Figure 2C) might be synapomorphies for all Stephanidae except *Schlettererius* and *Stephanus*.

The hind basitarsomere in *Megischus* can be inferred to correspond to tarsomeres 1–3 in *Schlettererius*, because the hind basitarsomere in *Megischus* is relatively longer than that of *Schlettererius*, and the prominent distal flange is situated on tarsomere 2 in the former and on tarsomere 4 in the latter, i.e. the penultimate tarsomere in both cases. The three-segmented hind tarsus with an elongate, composite basitarsomere has an interesting parallel in the fore basitarsus of female Orussidae (see above), which has also been suggested to be a composite structure (Vilhelmsen et al. 2001). Apparently, this represents independent

modifications, probably correlated with facilitating the detection of vibrations in wood.

Together, the modifications of the hind tibia and tarsus indicate a shift in relative importance in vibration detection from the fore to the hind leg among basal Stephanidae, even if the former still retain the ability to detect. Indeed, this arrangement could well have enhanced the overall performance by allowing comparison of variation in the reception of vibrations in different legs (Otten et al. 2002). Developing the fore and hind legs for vibration detection at the expense of the mid legs is probably the most cost-effective way of optimizing such differentiated reception. To pinpoint a source of reflected vibrations or vibrations generated by the source, it is most efficient to have the detectors (the SGOs) as widely separated as possible, especially if the source is directly underneath the wasp, i.e. in a position to be targeted by the ovipositor in the final stages of oviposition (Figure 6). Improving the SGOs in the mid leg also might not have increased the performance significantly. The reason for the SGO and the tarsi being most modified in the hind leg of most Stephanidae could be that they are the legs closest to the entry point of the ovipositor when the latter is in use (Figure 6; see also Rodd 1951, figures 1–3; Gauld and Hanson 1995, figures 4.26–4.29). This indicates that the SGOs can monitor the progress of the ovipositor and help to direct it on to the target.

Concluding remarks

Do Stephanidae employ active vibrational sounding like Orussidae (Vilhelmsen et al. 2001) and some Ichneumonidae (Broad and Quicke 2000; Otten et al. 2002)? Behavioural observations are scant, even if antennating wood has been observed
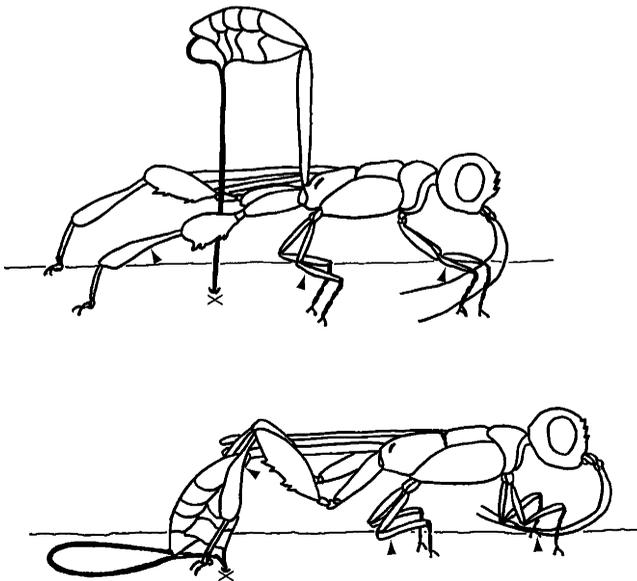

Figure 6. *Parastephanellus* sp., female ovipositing. Redrawn after Rodd (1951, figures 1 and 3). Early (top) and late (bottom) stage. X indicates the point of entry of the ovipositor into the wood, triangles the position of the subgenual organs in the different legs.

during the search for potential hosts (Rodd 1951). On the other hand, female stephanids do not have modified antennal tips for beating the substrate (unpublished observations), unlike Orussidae and some Ichneumonidae (Broad and Quicke 2000; Vilhelmsen et al. 2001). Perhaps Stephanidae employ passive vibration detection, monitoring sounds (chewing, various body movements) produced by potential hosts.

Stephanidae have been observed to search for hosts both on bark (Taylor 1967: *Schlettererius cinctipes*) and bark-free wood (Rodd 1951: *Parastephanellus* sp.; G.F. Turrisi personal observation: *Megischus anomalipes*). The latter habitat is presumably the easiest to detect vibrations through, unless the bark is tightly connected to the wood; Townes (1949) collected specimens of *Megischus bicolor* Cresson, 1865 from a dead tree where most of the bark 'still adhered tightly'(p. 367). It appears that female stephanids frequent habitats where vibration detection is feasible.

It is more difficult to decide if the stephanid females generate the vibrations themselves with the antennae or other parts of the body. Rodd (1951) observed antennation in *Parastephanellus* sp. However, females are often quite sluggish and reluctant to move when sitting on a tree trunk (Townes 1949: *Megischus bicolor*; Blüthgen 1953: *Stephanus serrator*); this sedentary habit might be interrupted by short sprints as the wasp changes its position (Jansen et al. 1988: *S. serrator*). This behaviour pattern is perhaps more in accordance with passive vibration detection, listening for sounds made by a potential host being easier from a stationary position.

In contrast, female Orussidae are highly active when searching for a suitable oviposition site, running up and down the tree trunk while antennating vigorously (Cooper 1953; Powell and Turner 1975; Ahnlund and Ronquist 2001). It would be highly desirable to know if stephanids target pupae (as can Orussidae; Ahnlund and Ronquist 2001) as well as larvae, because the former are more quiescent and hence unlikely to be detected unless vibrational sounding is employed. Parasitation of pupae is not mentioned in Aguiar (2006b), the latest compilation of stephanid biology.

It is interesting that in the Stephanidae where the females have strongly modified hind tibia and three-segmented tarsi, i.e., all except *Schlettererius* and *Stephanus*, the males also have the modifications of the hind tibia, albeit having five-segmented tarsi with less prominent setal arrangements. Obviously, the males, if they detect anything at all, are not detecting hosts.

Based on the oviposition habitat, behaviour and morphology, it seems justified to infer some kind of substrate-borne vibration detection in at least the females of Stephanidae. This is corroborated by the similarities in the structure of the tibiae and hind tarsi with the fore leg of female Orussidae, which have a similar biology. The absence of modification of the tips of the antennae for drumming, the more lethargic behaviour of stephanids in the oviposition habitat and the absence so far of any reports of targeting pupae indicate that they employ passive vibration detection rather than active vibrational sounding.

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