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Comparative Study of the Skeletal Parts of the Sting Apparatus in Some Sphecid species from Saudi Arabia (Hymenoptera: Sphecidae)

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A b s t r a c t : A comparative morphological study of the skeletal parts of the sting apparatus in some sphecid species representing five subfamilies is presented. For most of the species discussed, the different sclerites are being described and illustrated for the first time. It was found that the various structures are of great use for taxonomy not only at the subfamily level but also among the genera and species. Most of the structures were also found to be correlated with their function, according to the type of the prey and the nature of the prey activity.

The scanning electron microscope study of certain sclerites, particularly the gonostyli and lancet shafts, has revealed the presence of sensory structures in the former and of different barb shapes in the latter, which are of considerable interest. The sensory structures vary in shape, density and distribution among the species studied.

K e y w o r d s : Sting morphology, Sphecidae, Aculeata, Hymenoptera.

Abbreviations

| | |
|----------|--------------------------------|
| BL | basal lobe of gonostylus |
| DB..... | dorsal bar of spiracular plate |
| DL..... | distal lobe of gonostylus |
| Fu..... | furcula |
| Go | gonostylus |
| HP | hair plate |
| LS..... | lancet shaft |
| OP | oblong plate |
| QP | quadrate plate |
| SB | sting base |
| SEM..... | scanning electron microscope |
| SP..... | spiracular plate |
| SS..... | sting shaft |
| TP..... | triangular plate |
| Va..... | valve |

Introduction

It has been found that the sting of the Aculeata is homologous with that of other hymenopterans. However, it is modified for stinging rather than for egg-laying, which is considered as diagnostic for the Aculeata (QUICKE et al. 1999). Morphological studies of the aculeate sting apparatus have been made by a number of authors (for review see BORDAS 1895; SNODGRASS 1933; OESER 1961; SCUDDER 1961; MATSUDA 1976; SMITH 1969, 1970, 1972)

As aculeate solitary wasps, the venom apparatus of the Sphecidae is well-known to be a defensive system against attack (STEINER 1976). The sclerites that formed the ovipositor lost their association with the reproductive system and became mainly a mechanism of defence (ROBERTSON 1968). Females also use their stings to paralyse a host (STEINER 1976; RATHMAYER 1978), and this illustrates their predatory behaviour. The morphology of the sphecid sting apparatus varies widely not only between subfamilies but also among genera and species (MASCHWITZ & KLOFT 1971), and these variations may be correlated with the different ways in which they paralyse their hosts as well as the degree of host body sclerotization (RADOVIC 1985). However, many functional aspects are still in need of further study.

The most important studies dealing with the morphology of the sphecid sting apparatus are those by BORDAS 1895; PAWLOWSKY 1927; D'ROZARIO 1940; OESER 1961; OLBERG 1961; ROBERTSON 1968; MASCHWITZ & KLOFT 1971; MATSUDA 1976; RADOVIC 1967, 1985; RICHARDS 1977; RATHMAYER 1961, 1978; KASPARYAN 1980; GONZALEZ & HERMANN 1985; HERMANN & GONZALEZ 1986; RADOVIC & SUSIC 1997; GADALLAH 2001, PACKER 2003.

The present paper presents a comparative morphological study of the skeletal parts of the stinging apparatus of some sphecid species (16 species representing five subfamilies). The specimens were collected from different areas in the western region of Saudi Arabia. For most of them, the sclerites are being described and illustrated for the first time, and they are clearly of importance for taxonomy among genera and species. A scanning electron microscope study (SEM) of certain parts, particularly the tip of the gonostyli and the lancet shaft, has shown several kinds of sensory structures in the former and of barb shapes in the latter which are of considerable interest.

Material and Methods

The skeletal parts of the sting apparatus in 16 sphecid species representing 5 subfamilies were studied. The specimens were collected from different areas of the western region of Saudi Arabia (including Jeddah, Taif, and Hadasham). The collected specimens were identified, and then dissected from the gaster in 70% ethyl alcohol under a binocular stereomicroscope, using fine forceps and pins. The dissected parts were cleaned of their muscles to obtain a clear view of the different sclerites, by immersing them in a mixture of lactic acid, glycerol, and 40 % formaldehyde in the ratio 10: 2: 0.4 cl (RADOVIC & HURD 1980) for 2-3 days, depending on the degree of sclerotization of the different parts in the various species. This was followed by dehydration through a series of ethyl alcohols up to 70% concentration. The different parts were then placed in a concave slide with few drops of glycerol and examined under a binocular microscope at different ma-

gnifications. After examination, the specimens were preserved in small vials containing ethyl alcohol and a few drops of glycerol to keep them soft for any subsequent examination. Measurements were made using an ocular micrometer. Drawings were made using camera lucida.

For SEM studies, the gonostyli and lancet shafts of some representative species were cleaned and dried, and then coated in a vacuum with palladium-gold. Photographs were taken at different magnifications.

Sphecid classification and nomenclature follow BOHART & MENKE (1976). The terminology of the sting apparatus sclerites is based on HERMANN & GONZALEZ (1986).

Results

The sclerotized parts of the sting apparatus of the following 16 species representing 5 subfamilies were studied: *Ammophila insignis egregia* MOCSARY, *Prionyx viduatus* (CHRIST) (Sphecinae); *Oxybelus lamellatus* OLIVIER (Crabroninae); *Gastrosericus wallii* SPINOLA, *Larra anathema* (ROSSI), *Parapiagetia odontostoma* (KOHL), *Tachysphex schmiedeknechti* KOHL, and *Tachytes comberi* TURNER (Larrinae); *Bembix arenaria* HANDLIRSCH, *Bembix oculata* LATREILLE, *Bembecinus bytinskii* DE BEAUMONT, *Hoplisoides ferrugineus* (SPINOLA), and *Stizus savignyi* SPINOLA (Bembicinae); *Cerceris* sp., *Philanthus coarctatus* SPINOLA, and *Philanthus triangulum* (FABRICIUS) (Philanthinae). All the species studied were found to possess the typical structure of an aculeate sting apparatus. The sting apparatus is found in the sting chamber formed by the sixth gastral segment (SNODGRASS 1956). The degree of sclerotization of the different parts depends to a large extent upon the size of the individuals. In all the species studied, the gonostyli and sting were found to be the most heavily sclerotized parts.

The paired spiracular plates (SP) conceal the posterior two-thirds of the quadrate plates (QP). Each possess two distinct lobes (= lamina spiracularis, PACKER 2003) within which a spiracle (sp) could be seen at about the centre, with an associated trachea. The two lobes are joined by a thin bridge-like dorsal bar (DB). The overall shape of SP varies considerably in the different species studied (figs 1-14).

The oblong plates (OP) are in the form of thin elongate bone-shaped structures. They are either straight along their lengths or may be slightly convex outwardly and curved ventro-medially, weakly sclerotized. They articulate proximally with the ventral side of the triangular plate (TP) and distally with the gonostylus (Go). They possess basidorsally at their point of articulation with the TP a number of sensory hairs (trichoid sensilla, as named by HERMANN & DOUGLAS 1976) in a hair plate (HP). The shape of the oblong plates as well as the number of trichoid sensilla were found to differ among the species studied (figs 15-30).

Triangular plates (TP) are triangular in shape, and are relatively small in all the species studied. They give rise to the first ramus (Ra_1) in the basal region and to the lancet shaft (LS) at the apex. Each possesses two posterior angles; the dorsal angle articulates with the QP and the ventral angle with the OP. Triangular plates are very similar in shape and size in all the species studied.

The ovipositor sheath or gonostylus (Go) is strongly sclerotized, two-segmented in most of the species studied, with a basal lobe (BL) and a distal lobe (DL) (except in all the

philanthines studied, in which it is one-segmented). The length of the BL differs from that of the DL, as will be discussed later (figs 31-46). Both segments of Go have setae which vary greatly in size, shape and distribution. A cluster of sensory structures could also be seen at the tip of the distal lobe. These structures are best seen by scanning electron microscope (SEM) (see scanning micrographs).

The paired lancet shafts (LS) are long, thin, and pointed at apex. Their dorsal surfaces bear a pair of symmetrical valves proximally (Va, named valvilli by QUICKE et al. 1992). They are housed by the sting base. The paired LS are either smooth along their lengths (fig. 65) or may have one or more weak barbs or teeth that are restricted to the apical half (figs 62, 63, 64, 66, 67). The number of such teeth, when present, varies among the species studied. The lancets are positioned ventrally on the sting shaft (SS) which is strongly sclerotized in all the species studied.

Basally, the sting shaft expands laterally and dorsally into a swollen sting base (SB). Two projections (= processus medianus, PACKER 2003) could be seen at the anterior margin of the sting base, which serve as the points of articulation receiving the ventral arms of the furcula (Fu) (figs 68-71). The furcula (Fu) is an inverted Y-shaped sclerite that articulates with the anterodorsal part of SB. The stem of the Y has been called the dorsal arm and the two other arms of the furcula are the ventral arms (HERMANN & CHAO 1983). The tips of the ventral arms each articulate with one of the sting base projections. Laterally, a strong flange could be seen from the dorsal arm that receives an extensive supply of muscles from the paired oblong plates. The furcula is very variable in shape, depending on the degree of curvature of the ventral arms as well as the length of the dorsal arm in relation to that of the ventral ones (figs 47-61).

In Sphecinae:

Two species were studied: *Ammophila insignis egregia*, and *Prionyx viduatus*. In *Prionyx* the two lobes are oval, elongated, with normal DB (fig. 1), while in *Ammophila* the two lobes of SP are relatively large and rounded, with very thin DB (fig. 2). The number of trichoid sensilla on the basidorsal part of OP is different, being 15 in *Ammophila* and 25 in *Prionyx* (figs 15, 16).

The gonostylus, as in most of the sphecid species studied, is 2-segmented, and BL is longer than DL (1.5 mm and 1.0 mm long respectively) in *Ammophila* sp. (fig. 32). The reverse is the case in *Prionyx* (5.5 mm and 6 mm long respectively) (fig. 31). The tip of DL is densely covered with sensory pores (photo 1).

The lancet shafts (LS) in both genera have very slightly rounded barbs instead of the normal toothed barbs near its tip (photo 2). The sting is very slightly curved to straight in both of the species studied. The furcula (Fu) is relatively large here. It is relatively long, with short ventral arms in *Ammophila* that are curved gently ventro-medially (fig. 47). In *Prionyx*, the ventral arms of the furcula are relatively longer, and deeply concave ventro-medially (fig. 48).

In Larrinae:

Five species were studied: *Gastrosericus waltlii*, *Larra anathema*, *Parapiagetia odontostoma*, *Tachysphex schmiedeknechti* and *Tachytes comberi*.

It was found that the DB of SP has antero-lateral projections in three of these (*Gastrosericus waltlii*, *Larra anathema*, and *Tachysphex schmiedeknechti*) (figs 4, 6).

The number of trichoid sensilla on the OP ranges from 15 to 20 among the species studied (figs 17-21). In all of them, the gonostylus is 2-segmented, and DL is longer than BL (except in *Tachytes*) (0.9 mm and 0.6 mm respectively in *Gastrosericus wallii*; 1.5 mm and 1.0 mm in *Parapiagetia odontostoma*; 2.7 mm and 2.0 mm in *Larra anathema*; and 1.5 mm and 1.2 mm in *Tachysphex schmiedeknechti*) (figs 33-36). In *Tachytes*, DL is equal in length to BL (2mm.) (fig. 37). The distribution of sensory bristles along the length of Go varies among the species studied (photos 3-6).

The lancet shaft (LS) is smooth in both *Larra anathema* and *Gastrosericus wallii*, but has 3-4 weak barbs at the lancet tips in the remaining species (figs 62, 63; photo 7). The sting is straight to slightly curved in *Parapiagetia odontostoma* and *Tachysphex schmiedeknechti*, and strongly curved in the remaining species.

The furcula (Fu) is very peculiar in shape in *Gastrosericus wallii* (fig. 49), appearing as if formed from 2 separate sclerites that are connected at base by a membrane at the point of articulation with the sting base. It is robust and V – rather than Y-shaped, with a short dorsal arm and small lumen between the ventral arms and the base of the sting shaft in both *Parapiagetia odontostoma* and *Tachytes comberi*, in which the dorsal flange is greatly reduced in size (figs 51, 53).

In Crabroninae:

One species was studied: *Oxybelus lamellatus*. The DB of SP has a small rounded membranous process medio-ventrally (fig. 7). The basidorsal area of OP has 10 trichoid sensilla. The Go, as in most of the species studied, is 2-segmented, and DL is slightly longer than BL (0.6 mm and 0.5 mm respectively); the BL is narrow at base, widening to the junction between it and the DL. A very few short fine hairs could be seen externally at the distal part of BL. The tip of DL is very peculiar in shape as revealed by the SEM (photo 8), being slightly notched, and covered with a few sensory bristles as well as sensory pores. No spiny process could be seen, as was described by Radovic (1985) for *Oxybelus victor*.

The lancet shaft (LS) is smooth, without barbs or teeth (fig. 67). The sting is strongly curved along its length.

In Bembicinae:

Five species were studied: *Bembix arenaria*, *B. oculata*, *Bembecinus bytinskii*, *Hoplisoides ferrugineus*, and *Stizus savignyi*. The SP lobes differ in shape and size among the species studied, but have the same shape in the two *Bembix* species; DB with a weak membranous process medio-ventrally (figs 8, 10). In *Hoplisoides ferrugineus*, the DB projects antero-laterally (not rounded as in the two *Bembix* species), with a relatively larger membranous process medio-ventrally (fig. 9); relatively broad in *Stizus savignyi*, but without such a membranous process medio-ventrally (fig. 11).

The number of the trichoid sensilla varies among the species studied, being 30 in *Bembix* species and *Bembecinus bytinskii*, 12-15 in *Hoplisoides ferrugineus*, and 33-35 in *Stizus savignyi* (figs 23-27). As in most of the Sphecidae studied, the gonostylus is 2-segmented, whilst in all cases (except *Hoplisoides ferrugineus*) DL is relatively shorter than BL (2.0 mm and 2.2 mm respectively in *Bembix oculata*; 1.8 mm and 2.0 mm in *Bembix arenaria*; 1.1 mm and 1.4 mm in *Bembecinus bytinskii*; 4.0 mm and 4.4 mm in *Stizus savignyi* respectively, while it is 1.25 mm and 1.0 mm in *Hoplisoides ferrugineus*). The

tip of DL is densely covered with differently shaped sensory bristles that vary in density and distribution among the bembicines studied (photos 9-12).

The lancet shaft (LS) in all studied species smooth except in the two *Bembix* species and *Bembecinus*. In *Bembix* 2 broad barbs are found dorsally, forming a line parallel to the longitudinal axis of the lancet as revealed by the SEM and scattered sensilla of different shapes could be seen at the tip of the sting shaft in each one (photo 13). The sting is deeply curved in all the species studied.

In Philanthinae:

Three species were studied: *Cerceris* sp., *Philanthus coarctatus*, and *Philanthus triangulum*. In *Philanthus* species, the SP lobes are obviously large, quadrate in shape, with very thin DB (figs 13, 14); there is a medio-ventral membranous area in *P. triangulum* (fig.13). These lobes are elongated, kidney-shaped, with a very thin simple DB in *Cerceris* sp. (fig. 12).

The trichoid sensilla in the basidorsal area of the OP vary in number (figs 28-30), being 15 in *P. coarctatus*, 20 in *Cerceris* sp., and 25 in *P. triangulum*. In all of the philanthines studied, the Go is one-segmented (2.0 mm long in *Philanthus triangulum*; 1.3 mm long in *Philanthus coarctatus*; and 1.1 mm long in *Cerceris* sp.), with a deep apical incision ventrally (figs 44-46). It is parallel-sided along most of its length and angulated distally in *P. triangulum*, and densely covered with numerous fine hairs along its length (fig. 45). The SEM study revealed a dense covering of long sensory bristles as well as sensory pores between, which extend along the whole length of the Go (photos 15, 16).

The lancet shaft (LS) is provided with four weak barbs near the tip in *P. coarctatus*, three in *Philanthus triangulum*, whilst it is smooth in *Cerceris* sp. (fig. 65). The sting is deeply curved in *Philanthus* species, straight in *Cerceris*.

Discussion

As an aculeate solitary wasp, the function of the sphecid sting apparatus is mainly to paralyse a host (STEINER 1976; RATHMAYER 1978), and it is used in defence only when attacked (STEINER 1976). It is clear from the present study as well as from previous studies (examples see GONZALEZ & HERMANN 1985; RADOVIC 1985; HERMANN & GONZALEZ, 1986; RADOVIC & SUSIC 1997; GADALLAH 2001) that modifications in the different sclerites of the sting are correlated with its function in securing a host and with the way in which the sting is inserted into different loci in the host. These modifications are also dependent on the degree of sclerotization of the host body as well as the activity of the host, whether it is a slow-moving insect or a swift flier (RADOVIC 1985). Since the behaviour of some of these wasps is still in need of further study, some of the characters described above may only be of use in their taxonomy at present.

The spiracular plates are said to be the only large components of the gas exchange system found in the sting apparatus (PACKER 2003). The dorsal bar connecting them prevents independent movement of the two lobes. The two lobes are found to be separated in all bees and a few apoid wasps, and are joined only by a membrane (HAZELTINE 1967; MELO 1999).

The paired oblong plates (OP) partially envelop the sting base dorsally and laterally, thus

masking it. They are thought to have been derived from the subcoxa, coxa, and coxosternite of the 8th gastral segment (SMITH 1970). They serve to support the basal part of the gonostylus (Go), and provide points of origin for several muscles that function in protracting and retracting the lancet shafts (LS) as well as in sting deflection (HUNT & HERMANN 1970). The sensory trichoid sensilla (as named by HERMANN & DOUGLAS 1976) form a hair plate (HP) on the basidorsal part of the oblong plate, at the point of articulation with the triangular plate. They are said to be of the mechanoreceptor type (QUICKE et al., 1999). They receive stimuli during sting deflection, since they are found just anterior to the fulcral point of the sting (HERMANN & MULLEN 1974), and are probably involved in detecting the position and movements of the triangular plates (TP) relative to the oblong plates (QUICKE et al. 1999).

The gonostylus (Go) is derived from the posterior parts of the 9th gonocoxites. As in most aculeates, most of the species studied have 2-segmented gonostyli. Their function is to protect the sting, and they may also be involved in sensing the environment (HUNT & HERMANN 1970; QUICKE et al. 1999). The base of the Go has been shown to be involved in the secretion of an alarm pheromone in honey bee workers (CASSIER et al. 1994). Scanning electron microscope study of the species studied reveals the presence of various kinds, shapes and numbers of sensory bristles and pores clustered at the tip of the Go which appear to be absent in bees (PACKER 2003). They are said to be mechanoreceptors (BLUM & HERMANN 1978; LE RELAC et al. 1996). A one-segmented gonostylus is very rare within Sphecidae (RADOVIC 1985), but was found mainly in all the philanthines under study. This character can be used to separate this group from the others. The tip of the gonostylus in the Philanthinae is very peculiar in having an inner deep incision at apex. This incision may result from its function of securing the prey which may be impaled on the sting during transport (RADOVIC 1985), as the prey consists mostly of very active fliers of the superfamily Apoidea (as in *Philanthus* species).

In all the species studied, the proximal end of the lancet shafts (LS) support two large, symmetrical valves (Va, named valvilli by QUICKE et al. 1992). These valves are said to be an auxiliary structure which aids many stinging Hymenoptera in evacuating the venom (HUNT & HERMANN 1970). As the lancet shafts move alternately back and forth, the valve on each lancet forces venom out through the sting shaft (SS), so that they form the pistons of a force pump for venom (QUICKE et al. 1999). The paired lancet shafts (LS) function primarily in the stinging by the action of the valves (Va). They are either entirely smooth along their lengths, or they may be furnished with nodulated barbs or weak teeth near to their tips. This may be correlated with their function during stinging in relation to the kind of body sclerotization of their prey (RADOVIC 1985), or it may taken as a useful phylogenetic and taxonomic character (see WAHL & SHARKEY 1993; WAHL & GAULD 1998; GADALLAH 2001). Species in which the lancet shaft is smooth are those in which the prey is heavily sclerotized, as in the case of *Gastrosericus walilii* and *Larra anathema* (Larrinae) which provision their nests exclusively with Gryllids and Gryllotalpids (HONORÉ 1942; BOHART & MENKE 1976; RADOVIC 1985); *Stizus* species (Bembicinae) which provision their nests with grasshoppers and mantids (BOHART & MENKE 1976; KROMBEIN 1984); *Cerceris* species (Philanthinae) which take adults of different families of Coleoptera (WILLIAMS 1919; JAFFUEL & PIRION 1926; SCULLEN & WOLD 1969; EVANS & MATTHEWS 1970).

Those species in which the lancet shafts are furnished with some teeth are probably taking more weakly sclerotized prey. Examples of this are *Ammophila* species, which prefer hairless lepidopterous caterpillars and hymenopterous sawfly larvae (BOHART & MENKE 1976); *Bembix* species, which use muscoid dipterans as prey (BOHART & MENKE

1976; RADOVIC 1985); *Philanthus* species, which provision their nests with highly vagile bees of various apoid families (BEAUMONT 1954; EVANS 1955; EVANS & LIN 1959; RADOVIC 1985), but sometimes also with wasps of the families Vespidae, Sphecidae, Chrysididae, and Ichneumonidae (EVANS & LIN 1959; EVANS 1966); *Bembecinus*, with leaf hoppers and other Homoptera (BOHART & MENKE 1976).

The degree of curvature of the stings depends to a large extent on the degree of activity of the prey (RADOVIC 1985). It has been found that the prey of Sphecids that possess a strongly descendent powerful sting are very good fliers and are stung while in flight, being attacked on the venter (RADOVIC 1985; HERMANN & GONZALEZ 1986). Examples of this are *Bembix* and *Oxybelus* (on Muscoidea), and *Philanthus* (on Apoidea). However, in some sphecids which have a strongly descendent sting, the prey is less active. In such cases, the sting curvature may be attributed to the underground habit of the prey (RADOVIC 1985). Examples of this are *Larra anathema*, *Gastrosericus waltlii* and *Tachytes comberi* which attack large and powerful orthopterans that are found underground: since the host venter is close to the substrate, it would be difficult for the wasp to sting its host on the venter unless the sting is strongly curved (HERMANN & GONZALEZ 1986). On the other hand, sphecids that possess straight stings are found to prey on slow-moving or less active, non-flying prey. They sting their prey in situ (RADOVIC 1985). Examples are *Ammophila* (which attack slow-moving caterpillars; BOHART & MENKE 1976); *Prionyx* (on grasshoppers; BOHART & MENKE 1976); *Tachysphex* (on Phasmatidae; PULAWSKI 1971, 1988); and *Cerceris* (on coleopteran adults such as the less vagile Curculionidae, WILLIAMS, 1919; JAFFUEL & PIRION 1926; SCULLEN & WOLD 1969; EVANS & MATTHEWS 1970).

The furcula (Fu) in all the species studied is relatively large, Y- or V-shaped. It is very important in sting manipulation (HERMANN 1968, 1969). It has a well developed antero-dorsal flange that receives a strong supply of muscles from the oblong plates (HERMANN & BLUM 1967). This heavy supply of muscles as well as its strong articulation with the sting base indicate that it is of great significance in sting depression and rotation, which facilitate the site selection and insertion (HERMANN & CHAO 1983).

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Zusammenfassung

Eine vergleichende morphologische Studie des Stachelapparats einiger Grabwespen aus fünf Unterfamilien wird vorgestellt. Für die meisten der gehandelten Arten ist dies die erste Beschreibung und Darstellung dieser Bauweise. Es zeigte sich, dass die verschiedenen Strukturen nicht nur auf Ebene der Unterfamilie, sondern auch in der Gattungs- und Arttaxonomie Relevanz besitzen. Es wurden auch funktionsmorphologische Zusammenhänge hinsichtlich des Jagdverhaltens abgeleitet.

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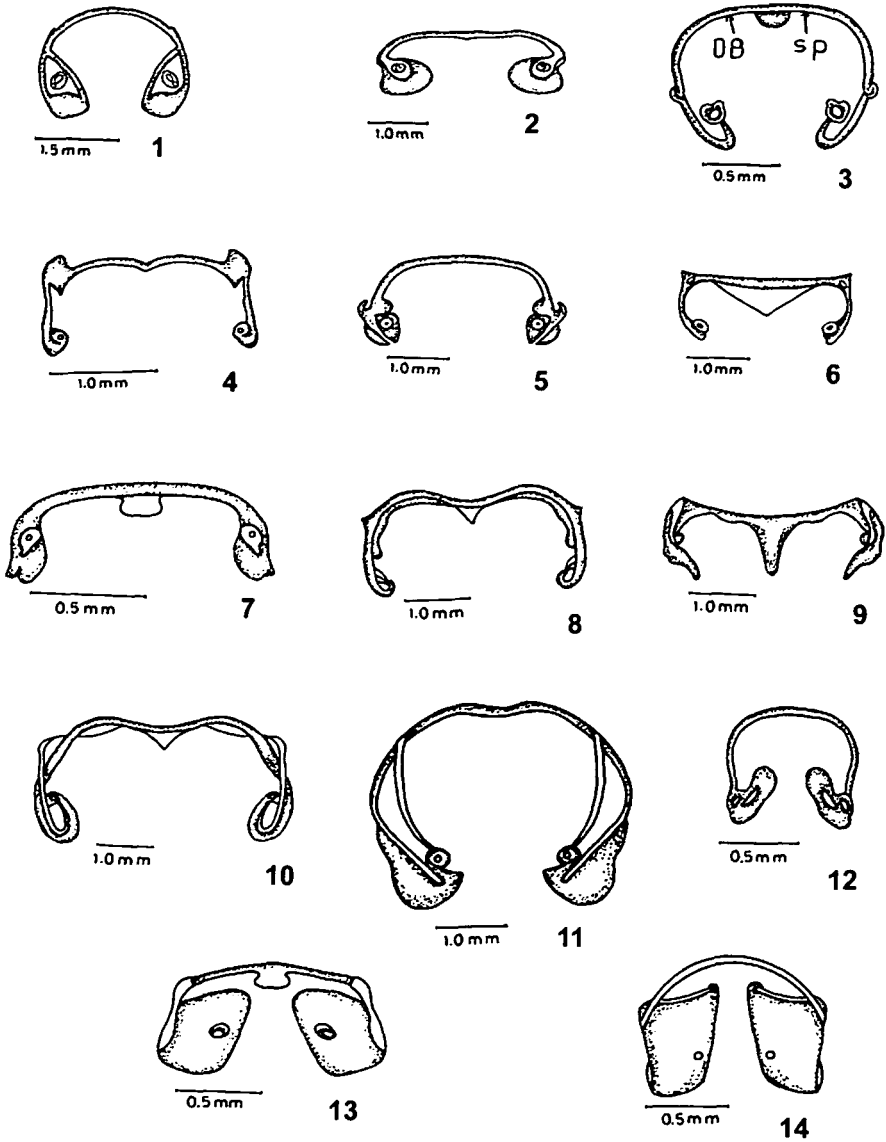
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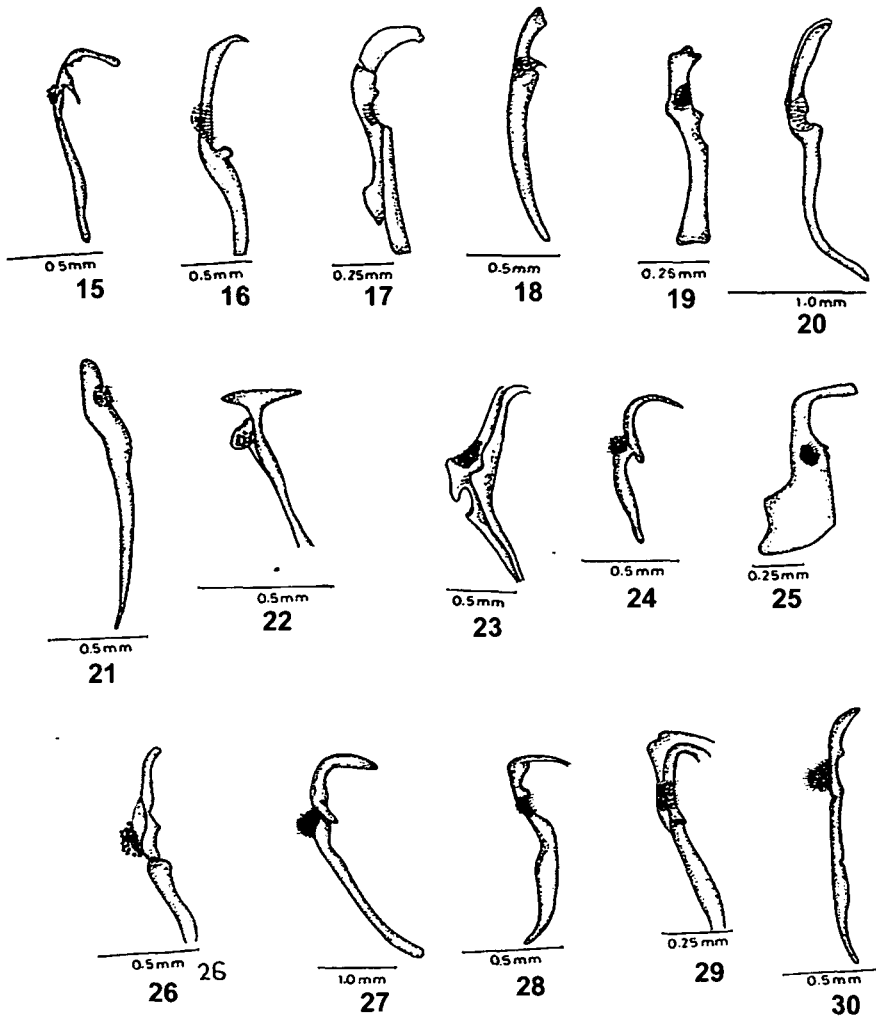
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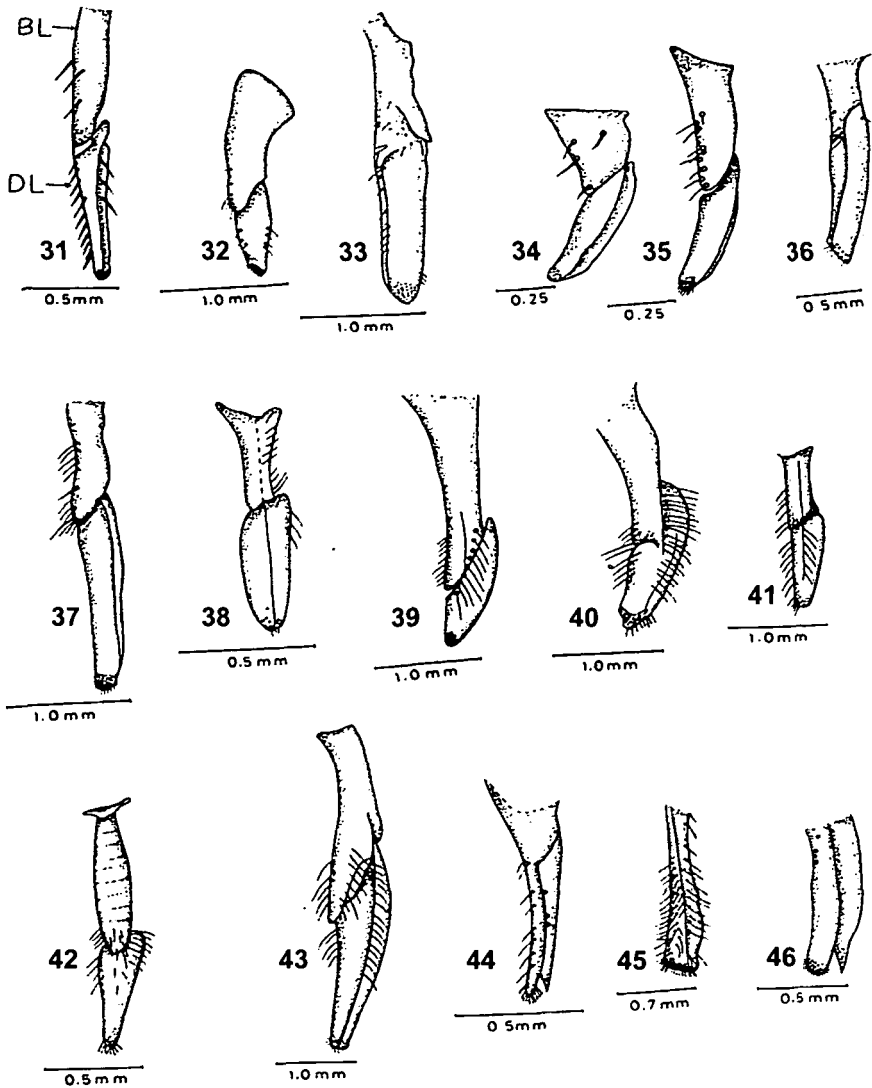
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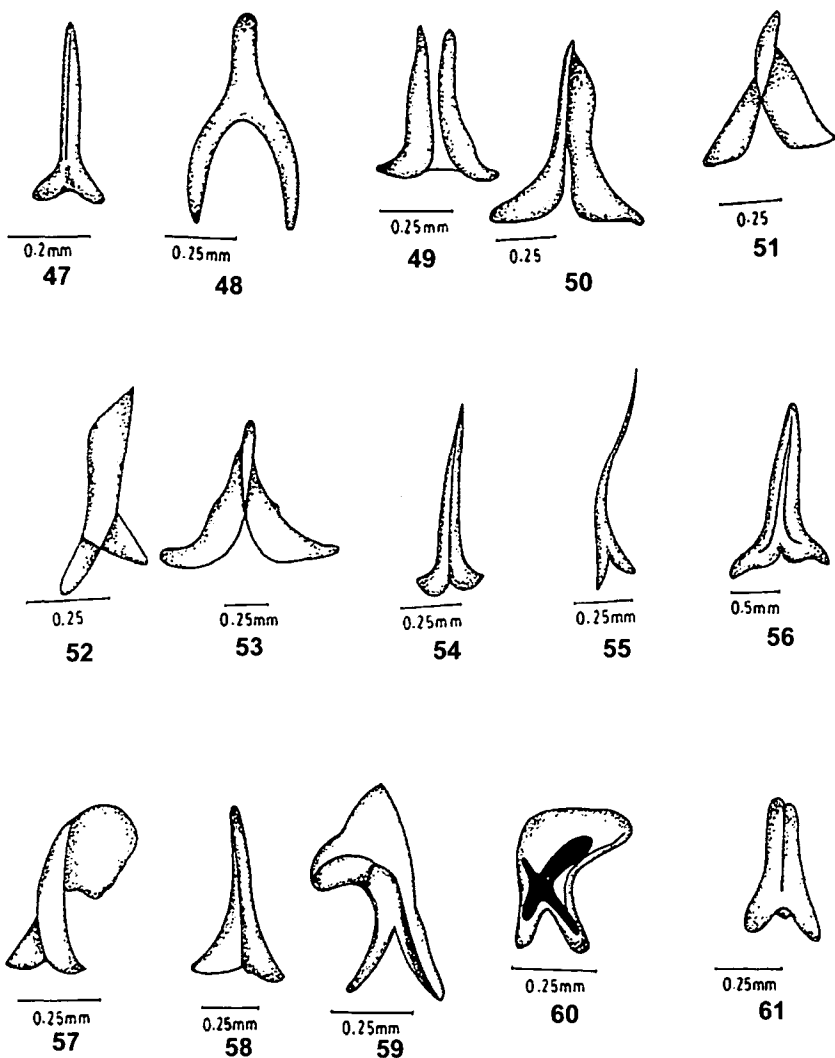
Figs 1-14. Spiracular plates (SP) in the studied sphecid species. 1 - *Prionyx viduatus*; 2 - *Ammophila insignis egregia*; 3 - *Parapiagetia odontostoma*; 4 - *Gastrosericus waltlii*; 5 - *Tachytes* sp.; 6 - *Tachysphex schmiedeknechti*; 7 - *Oxybelus lamellatus*; 8 - *Bembix oculata*; 9 - *Hoplisoides ferrugineus*; 10 - *Bembix arenaria*; 11 - *Stizus savignyi*; 12 - *Cerceris* sp.; 13 - *Philanthus triangulum*; 14 - *Philanthus coarctatus*.



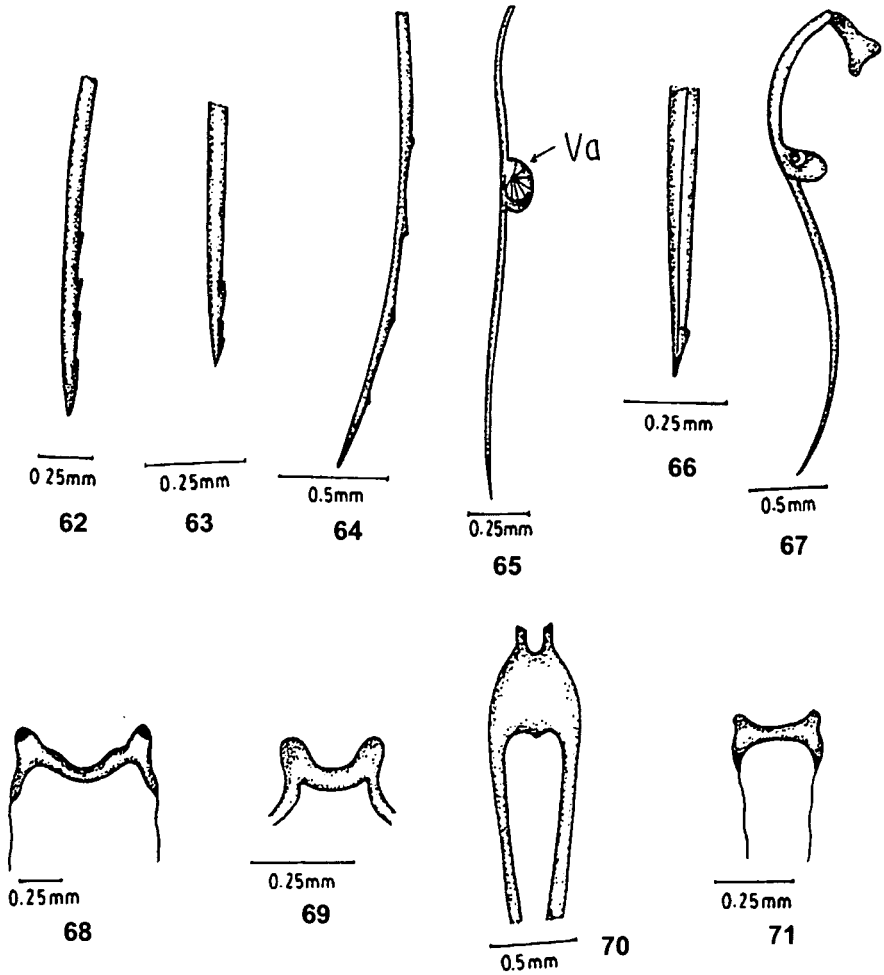
Figs 15-30. The oblong plates (OP) of the studied sphecid species: 15 - *Ammophila insignis egregia*; 16 - *Prionyx viduatus*; 17 - *Gastrosericus wallii*; 18 - *Tachysphex schmiedeknechii*; 19 - *Parapiagetia odontostoma*; 20 - *Larra anathema*; 21 - *Tachytes* sp.; 22 - *Oxybelus lamellatus*; 23 - *Bembix arenaria*; 24 - *Hoplisoides ferrugineus*; 25 - *Bembecinus bytinskii*; 26 - *Bembix oculata*; 27 - *Stizus savignyi*; 28 - *Philanthus coarctatus*; 29 - *Cerceris* sp.; 30 - *Philanthus triangulum*.



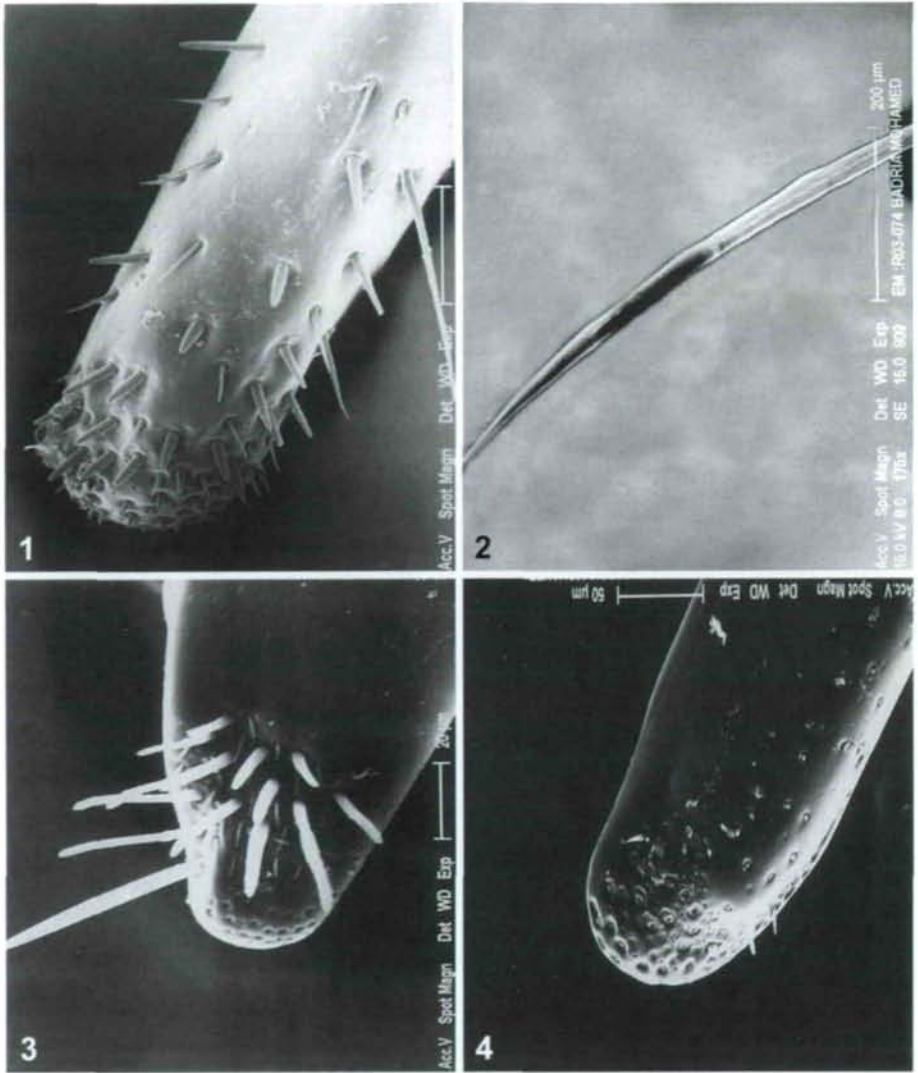
Figs 31-46. Gonostylus (Go) of the studied species: 31 - *Prionyx viduatus*; 32 - *Ammophila insignis egregia*; 33 - *Larra anathema*; 34 - *Gastrosericus wallii*; 35 - *Tachysphex schmiedeknechti*; 36 - *Parapiagetia odontostoma*; 37 - *Tachytes* sp.; 38 - *Oxybelus lamellatus*; 39 - *Bembix oculata*; 40 - *Bembix arenaria*; 41 - *Hoplisoides ferrugineus*; 42 - *Bembecinus bytinskii*; 43 - *Stizus savignyi*; 44 - *Cerceris* sp.; 45 - *Philanthus triangulum*; 46 - *Philanthus coarctatus*.



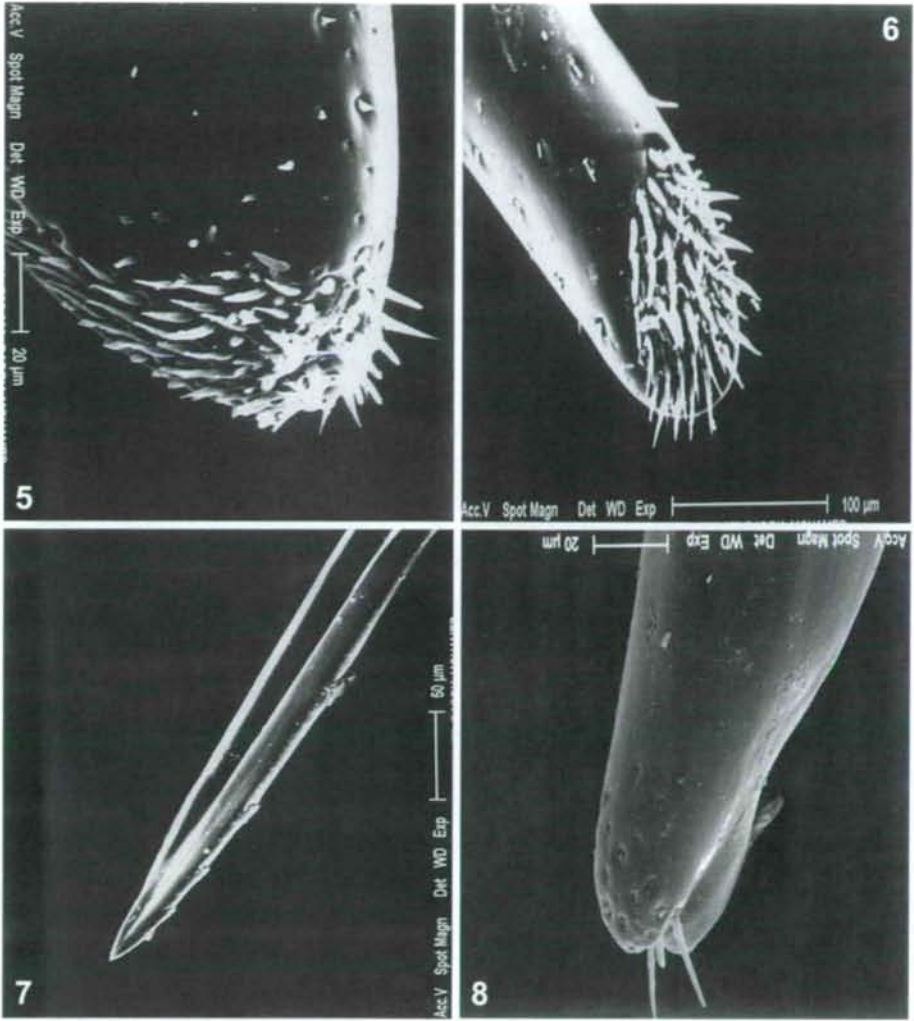
Figs 47-61. Furcula (Fu) of the studied sphecid species: 47 - *Ammophila insignis egregia*; 48 - *Prionyx viduatus*; 49 - *Gastrosericus waltlii*; 50 - *Tachysphex schriedeknechti*; 51 - *Parapiagetia odontostoma*; 52 - *Larra anathema*; 53 - *Tachytes* sp.; 54 - *Oxybelus lamellatus*; 55 - *Bembix arenaria*; 56 - *Stizus savignyi*; 57 - *Hoplisoides ferrugineus*; 58 - *Bembecinus bytinskii*; 59 - *Philanthus triangulum*; 60 - *Philanthus coarctatus*; 61 - *Cerceris* sp.



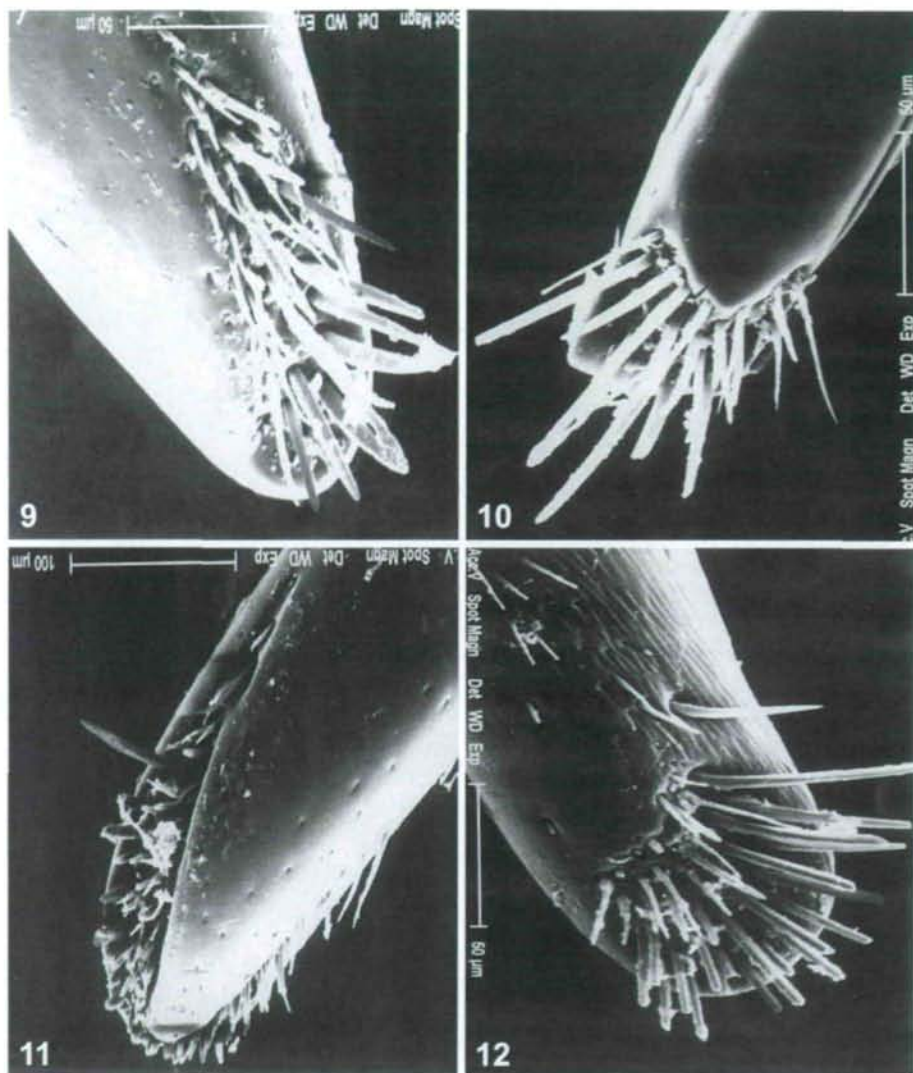
Figs 62-67. Lancet shaft (LS) of some sphecid species: 62 - *Tachytes* sp.; 63 - *Parapiagetia odontostoma*; 64 - *Prionyx viduatus*; 65 - *Cerceris* sp.; 66 - *Bembecinus bytinskii*; 67 - *Oxybelus lamellatus*. Figs 68-71. Sting base (SB) of some sphecid species: 68 - *Larra anathema*; 69 - *Gastrosericus waltlii*; 70 - *Bembix arenaria*; 71 - *Parapiagetia odonostoma*.



Photos 1-4: 1 – Gonostylus tip of *Prionyx viduatus*. 2 – Lancet Shaft of *Prionyx viduatus*. 3 – Gonostylus tip of *Gastrosericus waltlii*. 4 – Gonostylus tip of *Larra anathema*.

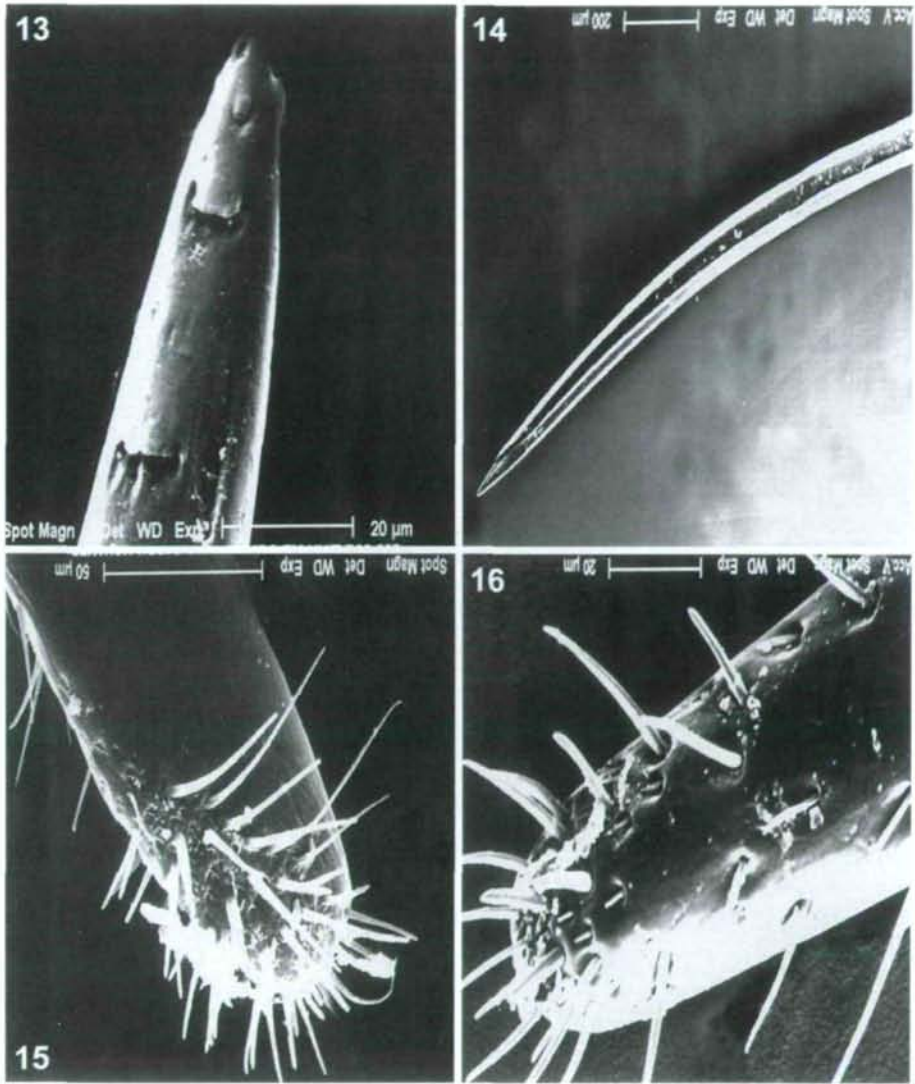


Photos 5-8. Gonostylus tip of *Parapiagetia odontostoma*. 6 – Gonostylus tip of *Tachytes* sp. 7 – Tip of Lancet shaft of *Tachytes* sp. 8 – Gonostylus tip of *Oxybelus lamellatus*.



Photos 9-12. Gonostylus tip of *Bembix* sp. 10 – Gonostylus tip of *Bembecinus bytinskii*. 11 – Gonostylus tip of *Hoplisoides ferrugineus*. 12 – Gonostylus tip of *Stizus savignyi*.

1412



Photos 13-16. Tip of lancet shaft of *Bembix arenaria*. 14 – Tip of lancet shaft of *Stizus savigni*. 15 – Gonostylus tip of *Philanthus coarctatus*. 16 – Gonostylus tip of *Cerceris* sp.

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