

External Morphology of *Tagosodes orizicolus* (Homoptera: Delphacidae) Revealed by Scanning Electron Microscopy

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ABSTRACT A comprehensive analysis of the ultrastructure of the delphacid rice pest *Tagosodes orizicolus* (Muir) was undertaken using scanning electron microscopy to resolve taxonomic problems in the distinction of females and nymphs from other specimens commonly found in rice fields of tropical America. This research includes a detailed description of female genitalia and the ultrastructural variations observed during nymphal development. Ultrastructure of the mouthparts, specifically the stylets; and the genitalia of the male are also described. Important ultrastructural details were revealed, such as the presence of microtrichia and sensillae, which are not clear when observed by light microscopy. The adults have numerous sensillae; immatures have bell-shaped chemoreceptors along the dorsal area, structures that are absent in the adult stage. Strong differences were observed between the first instar and older nymphs, such as stamen-like setae, wider frons, convex clypeus observed in the first and second instars; whereas conical eyes and an oar-shaped legs were observed only in the first instar.

KEY WORDS *Tagosodes orizicolus*, delphacid, ultrastructure, sensilla, genitalia, mouthparts

THE DELPHACIDAE is the largest and most studied family of planthoppers, consisting of >20,000 species classified in 300 genera and 19 families (Wilson et al. 1994). Most delphacids have monocots as host plants, particularly grasses and sedges. Their host preferences, phloem-feeding habits, oviposition behavior, and ability to transmit viruses have contributed to their status as severe pests of important crops like rice, corn, sugarcane, and other cereals (Wilson et al. 1994). The family is readily identified by the possession of a movable spur at the apex of each metatibia (Wilson and Claridge 1991).

Of the several delphacids that are important pests of rice, *Tagosodes orizicolus* (Muir) (known previously as *Sogata orizicola* Muir) is distributed in all rice growing areas of tropical America, including Mexico, the Caribbean, and Central and South America (Morales and Niessen 1985). It is monophagous, causing severe feeding and oviposition damage to its host plant, and is the vector of the rice hoja blanca tenuivirus (*Rhbv*).

Males are yellow-brown with frons, clypeus, genae and forewings darkly marked, and the females are paler, with a yellow dorsal stripe. The species is sexually dimorphic: males are 2–3 mm in length, and the females are larger (3–5 mm). Metamorphosis is hemimetabolous (paurometabolus) with five instars. The male genitalia, especially the aedeagus, parameres,

and shape of the diaphragm are important features in species identification (Wilson and Claridge 1991).

The objective of this work was to determine the ultrastructure of the external morphology of males, females, and nymphs of this species, highlighting details of the cephalic capsule, thorax, abdomen, and male and female genitalia. Although the general morphology of delphacids has been described (O'Brien and Wilson 1985), a comprehensive study of *T. orizicolus* is necessary to resolve some difficulties in the identification of females and nymphs of this species from other delphacid specimens collected in rice fields because the diagnostic traits in the keys are given only for males (Asche and Wilson 1990).

Materials and Methods

Insects were collected from colonies maintained in an insectary and kept under controlled temperature (15–20°C), light, and humidity (70–80%). Several measurements (thoracic length, body width, and body length) were made in 15 male and female specimens as well as in nymphs from the first to fifth instar. Each of 10 males, females and nymphs (first to fifth instars) of *T. orizicolus* were fixed in a solution of 2% glutaraldehyde and 2.5% paraformaldehyde in a 0.1 M sodium phosphate buffer, pH 7.4. They were vacuum treated in a hypodermic needle and were left overnight at 4°C (Karnovsky 1965, Kozuka 1989). The samples were washed with 0.1 sodium phosphate, pH 7.4, and were postfixed in 2% osmium tetroxide in a 0.1 M pH 7.4 phosphate buffer for 2 h at room temperature. Later, they were dehydrated in a 30–100% ethanol gradient for 15 min at each concentration. This was followed by three changes in terbutylic al-

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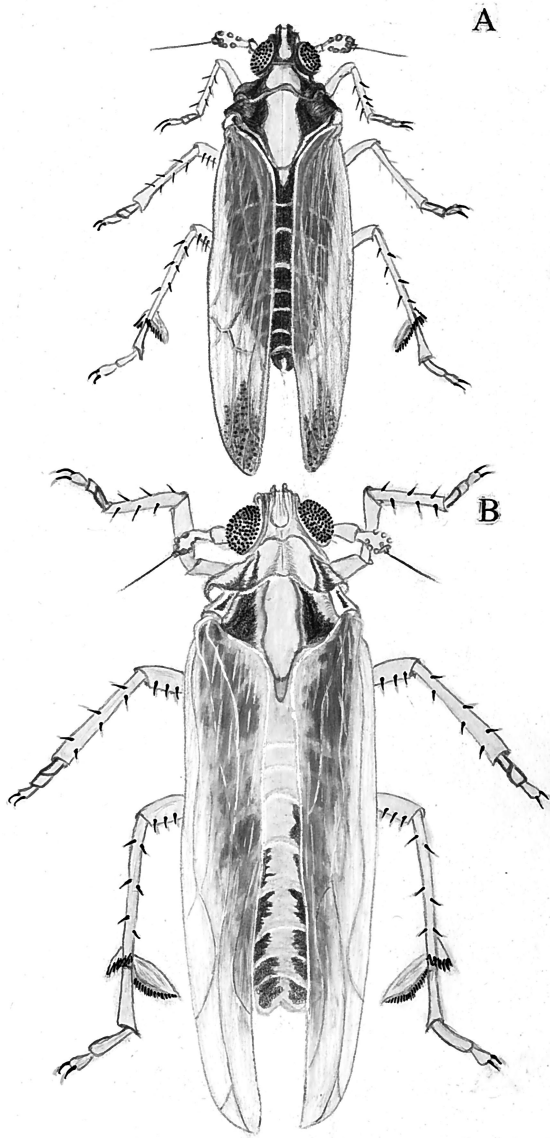


Fig. 1. Dorsal view of the male (A) and female (B) of *Tagosodes orizicolus*.

cohol and the samples were dried by sublimation in a VFD-20 desiccator for 1 h.

Once dried, the samples were placed on aluminum bases with double-sided carbon adhesive tape and were covered with 20 nm of platinum in an ion coater. The samples were later observed under a scanning electron microscope, using magnifications from 200 to 2,500 \times .

Results

General Morphological Description of *T. orizicolus* Adults. The adults are dorsoventrally flattened with tectiform wings (Figs. 1 and 6A). They are characterized by having a movable spur at the distal end of the

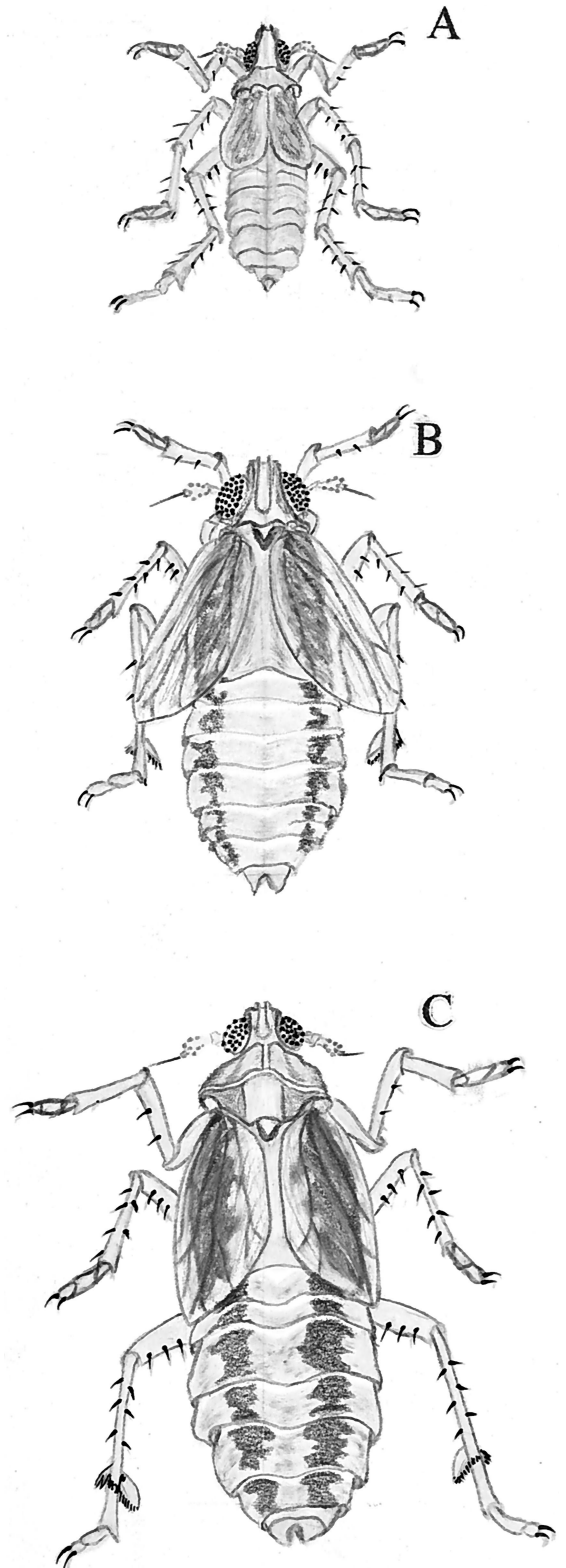


Fig. 2. Dorsal view of the nymphs of *Tagosodes orizicolus*: second instar (A), third instar (B), and fifth instar (C).

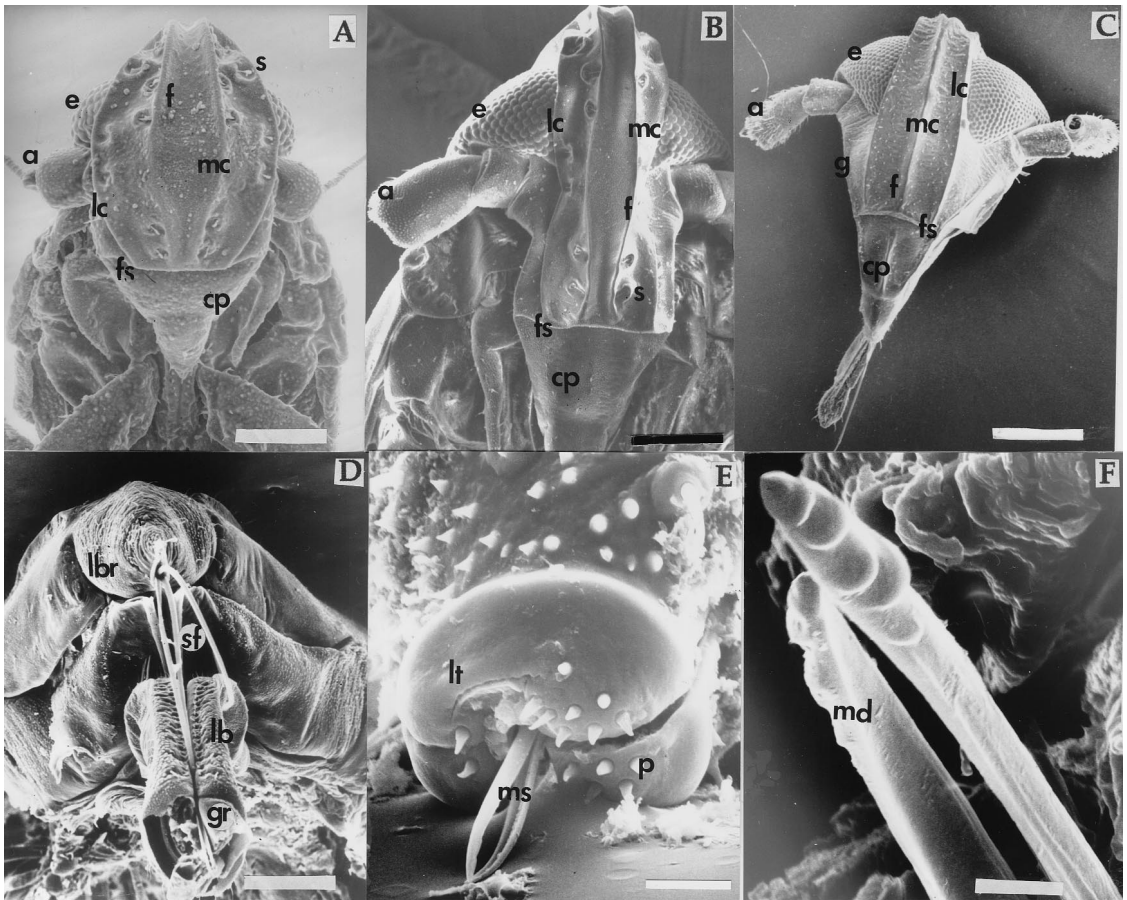


Fig. 3. Frontal view of the head of the first instar (A), fifth instar (B), male adult (C), and details of the highly modified mouthparts of *Tagosodes orizicolus* (D, E, and F). Median carinae (mc), lateral carinae (lc), frons (f), clypeus (cp), frontoclypeal suture (fs), bell-shaped sensillae (s), compound eye (e), antenna (a) and the gena (g), stylet fascicle (sf), mandibular stylets (md), maxillary stylets (ms), labrum (lbr), subcylindrical labium (lb), labial tip (lt) and papillae (p). Bars: A = 136 μ m, B = 142 μ m, C = 166 μ m, D = 70 μ m, E = 8 μ m, F = 3 μ m.

hind tibia (Figs. 1 and 7B). The length of the male is 2.17 ± 0.13 mm, thoracic length is 0.57 ± 0.01 mm, and the width is 0.49 ± 0.06 mm. The male body is brown overall with a yellow stripe from the vertex to the scutellum, with a dark apical spot on the forewings. The frons is dark with three longitudinal yellow stripes that correspond to the median and lateral carinae. The legs and antennae are also yellowish (Fig. 1A). The length of the female is 2.77 ± 0.15 mm, thoracic length is 0.71 ± 0.07 mm, and the width is 0.60 ± 0.07 mm. The female body is yellow with dark brown stripes laterally from the mesothorax to the abdomen, leaving a paler longitudinal dorsal stripe that extends from the vertex to the end of the abdomen. The forewings lack an apical spot (Fig. 1B).

General Morphological Description of *T. orizicolus* Nymphs. The nymphs pass through five instars, the first instar length is 0.68 ± 0.17 mm, thoracic length is 0.08 ± 0.05 mm, and the width is 0.05 ± 0.12 mm. The body is transparent white, with large red conical eyes. The pronotum, mesonotum, and metanotum are clearly observed (Fig. 6C). The wing pads are not well

developed and do not obscure the metanotum (Fig. 6C). The legs are flattened and resemble an oar (Fig. 7A). The second instar is yellowish, the wing pads are partially developed, and there is no evident tibial spur (Fig. 2A). Length is 0.82 ± 0.23 mm, thoracic length is 0.09 ± 0.12 mm, and the width is 0.13 ± 0.06 mm. The third instar is yellow with two slender dorsal stripes. The wing pads are more fully developed and partially obscure the metanotum (Fig. 2B). The coxa, femur, tibia, and tarsus are well developed, and the spur is obvious (Fig. 2B). The length is 1.72 ± 0.27 mm, thoracic length is 0.37 ± 0.12 mm, and the width is 0.34 ± 0.14 mm. The fourth instar length is 2.08 ± 0.29 mm, thoracic length is 0.45 ± 0.08 mm, and the width is 0.34 ± 0.14 mm. The fifth instar length is 2.10 ± 0.25 mm, thoracic length is 0.47 ± 0.07 mm, and the width is 0.40 ± 0.10 mm. The longitudinal dorsal stripes of the fourth and fifth instar are darker. The metanotum is completely covered by the wing pads. The mesonotum is evident and starts to show the V-shape of the scutellum, the tibial spur is clearly observed (Fig. 2C). All instars bear distinctive rows of pits on the frons

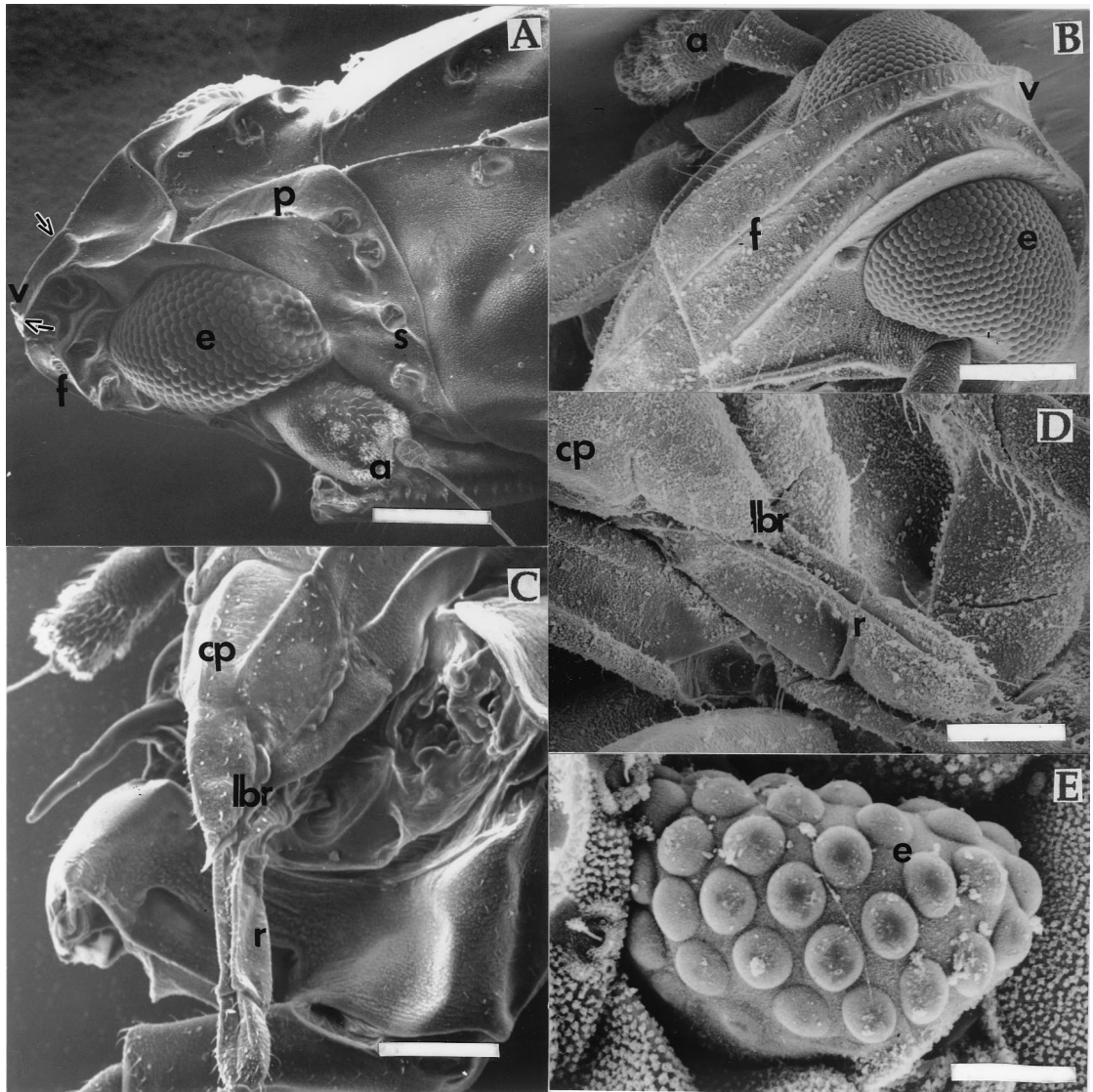


Fig. 4. Lateral view of different features of the head and mouthparts of a female adult (B and C), first (E), and fourth instar (A and D) of *Tegosodes orizicolus*. Vertex (v), frons (f), lateral carinae (arrow), transverse carinae (arrow), compound eye (e), antenna (a), pronotum (p), bell-shaped sensillae (s), clypeus (cp), labrum (lbr), and rostrum (r). Bars: A = 142 μ m, B = 250 μ m, C = 133 μ m, D = 136 μ m, E = 0.27 mm.

(Fig. 3 A and B), and laterally on the abdomen (Fig. 6 B–D), which the adults lack (Fig. 6E).

Cephalic Capsule. The cephalic capsule of the first and second instar has two longitudinal median carinae, two lateral carinae, and the clypeus has no evident central carina (Fig. 3A). It also shows a wider frons that bears numerous sensillae with setae that resemble the stamens of some flowers (Fig. 8C). The frons shows a strong frontoclypeal suture. The frons of the third, fourth, and fifth instars has two longitudinal median carinae and two lateral carinae, a slender frontoclypeal suture, and a clypeus with no evident central carina (Fig. 3B). The adult has a single central carina and two lateral carinae on the frons; a strong central

carina is also present on the clypeus (Fig. 3C). The gena, the region between the lateral border of the frons and the compound eye, is well developed in the adult (Fig. 3C). In nymphs, the vertex and the frons are separated by a lateral and transverse carina (Fig. 4A), whereas the adult shows a continuous frons and vertex (Fig. 4B). The vertex in the adult is limited in the rear by the pronotum, to the sides by the large compound eyes, and to the front by the frons (Fig. 4B). The compound eyes of the adult are rounded with closely grouped ommatidia (Fig. 4B). The eyes of a first instar are conical and have fewer and more dispersed ommatidia (Fig. 4E). The mouthparts of *T. orizicolus* consist of the labrum, labium, and four

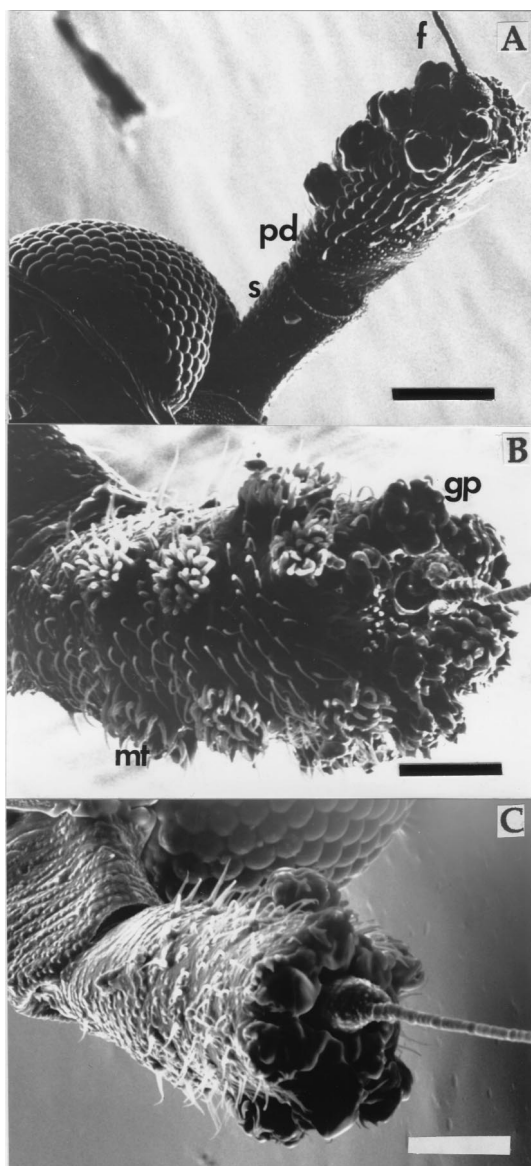


Fig. 5. Views of *Tagosodes orizicolus* antennae. (A) Scape (s), pedicel (pd) and flagellum (fl). (B and C) Microtrichiae (mt) and glandular protuberances (gp). Bars: A = 13 μ m, B = 46 μ m, C = 46 μ m.

stylets (Fig. 3D). Attached to the distal part of the clypeus is the labrum, located anterior to the labium.

The modified labium or proboscis (also known as rostrum or beak) is three-segmented and is much longer in adults (Fig. 4C) than in nymphs (Fig. 4D). The distal segment has abundant papillae and the medium and proximal segments have fewer (Fig. 4C). The first labial segment is partially obscured by the overlapping clypellus (Fig. 4C). The labium forms a deep groove that contains the maxillary and mandibular stylets (Fig. 3D). The labial tip is rosette-shaped, bears multiple papillae and the stylet fascicle emerges from its central opening (Fig. 3E). The stylet fascicle

is formed by two mandibular stylets that surround and envelop two curved maxillary stylets, which are tightly held together to form the food canal (Figs. 3D and E). The distal part of the maxillary stylets is sharp (Fig. 3E), and the mandibular stylet tip has abundant protrusions (Fig. 3F). The latter are possibly specialized to pierce plant tissues while probing. The antennae are composed of three well-developed segments: the scape, pedicel, and a terminal flagellum (Fig. 5A). The pedicel is complex and densely covered with microtrichiae and glandular terminal bulges (Fig. 5B). The flagellum has a central position in the distal region of the antenna and its base is enlarged (Fig. 5C).

Thorax. The thorax of fourth and fifth instars shows the wing pads, which cover most of the thorax. The pronotum is reduced and overlaps laterally with the pleural sclerites (Fig. 6B). In Fig. 6B the vertex in the upper part of the head, pronotum, subpentagonal mesonotum, and the bell-shaped sensillae are evident. In the fourth and fifth instars and adults the metanotum is not evident due to the overlapping of the mesonotum and wing pads or wings (Fig. 6A and B), whereas first, second, and third instars do not have well-developed wing pads, clearly exposing the metanotum (Fig. 6C). The pronotum, mesonotum, and metanotum of the first instar are clearly seen (Fig. 6C). Also, notice the multiple sensillae distributed along the head, thorax, and abdomen (Fig. 6C).

In adults, the distal part of the metatibia is enlarged forming a crown (Fig. 7B) with a movable apical spur, a diagnostic structure of the family Delphacidae. The spur has a saw on its internal edge with serrated structures containing numerous setae forming disorganized rows. The third tarsal segment displays a pair of apical claws (Fig. 7D) with a central arolium and multiple rows of sensorial papillae. The shape of the leg of the first instar shows different features from the leg of the adult and older nymphs (Fig. 7A). The hind leg of a third instar shows tarsal segments I, II, and III, the spur is not completely developed, and the tibia is not broadened forming a crown (Fig. 7C). In adults, the hind wings are entirely covered by the fore wings and their venation is reduced in comparison to other hoppers (Fig. 6A). Major features of the fore wings include microtrichia distributed along the wing forming organized rows (Fig. 8A) and an apical spot that is present only in males (Fig. 1A).

Abdomen. The abdomen is elongated and laterally flattened with eight evident segments. The superior and terminal appendices, the anal style, forms a small corrugated barrel in the adult (Figs. 9A and 10A). In immature stages, the last abdominal segment does not present this differentiated barrel (Fig. 6D). Nymphs have lateral rows of bell-shaped sensillae, which have a central seta (Fig. 8B and C), probably with chemosensory function. This seta has a peculiar stamen-like shape in the first instar (Fig. 8C). The sensillae of the third, fourth, and fifth instars are found on a sculptured tegument with a rugose appearance (Fig. 8B), whereas the tegument observed in the first and second

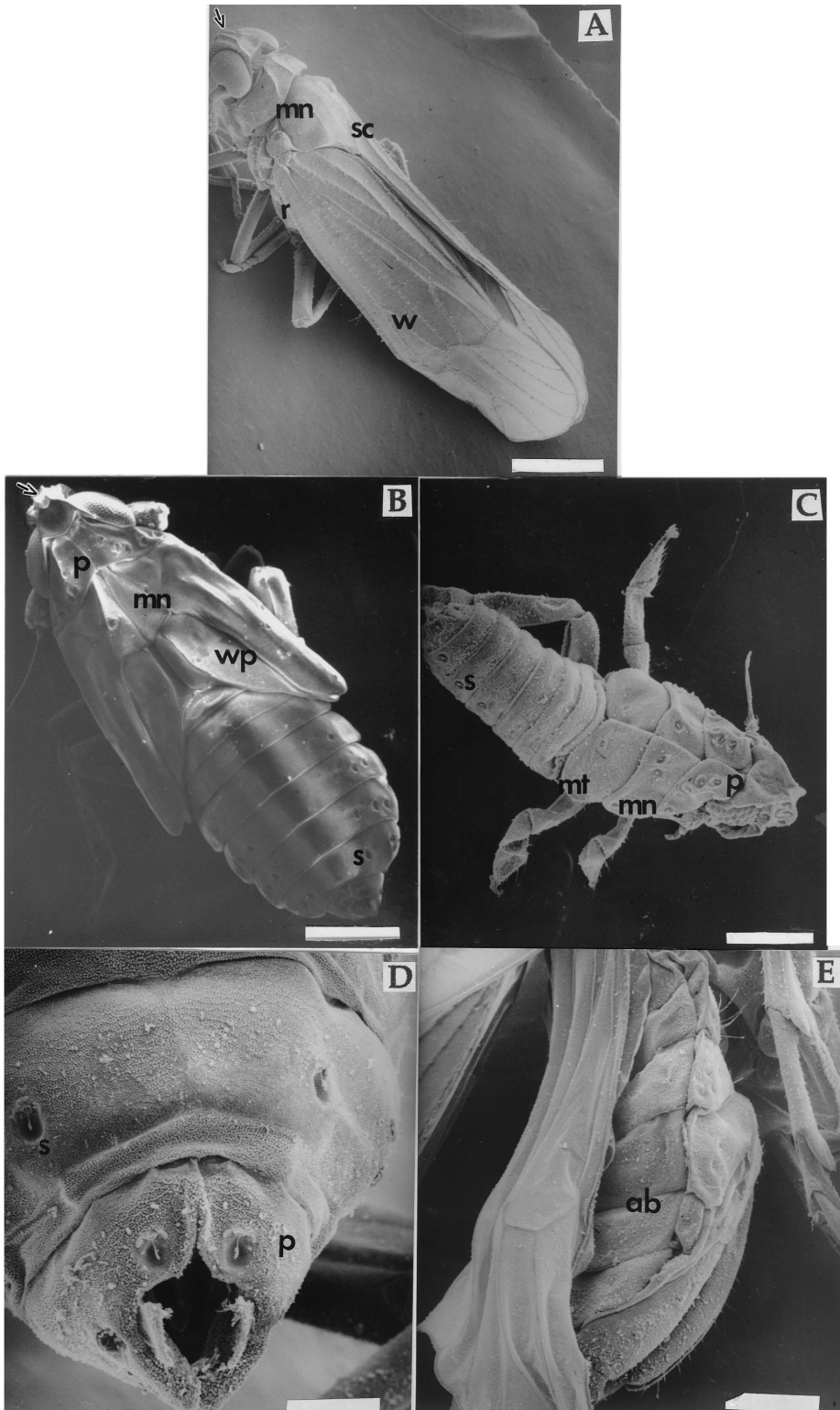


Fig. 6. Thorax of *Tagosodes orizicolus* female adult (A), fifth instar (B), first instar (C) and dorsal view of the caudal section of the abdomen of a second instar (D) and a female adult (E). Pronotum (p), mesonotum (ms), metanotum (mn), multiple sensillae (s), vertex (arrow), bell-shaped sensillae (s), wing pads (wp), scutellum (sc), wings (w), abdomen (ab). Bars: A = 10 mm, B = 400 μ m, C = 231 μ m, D = 150 μ m, E = 0.50 mm.

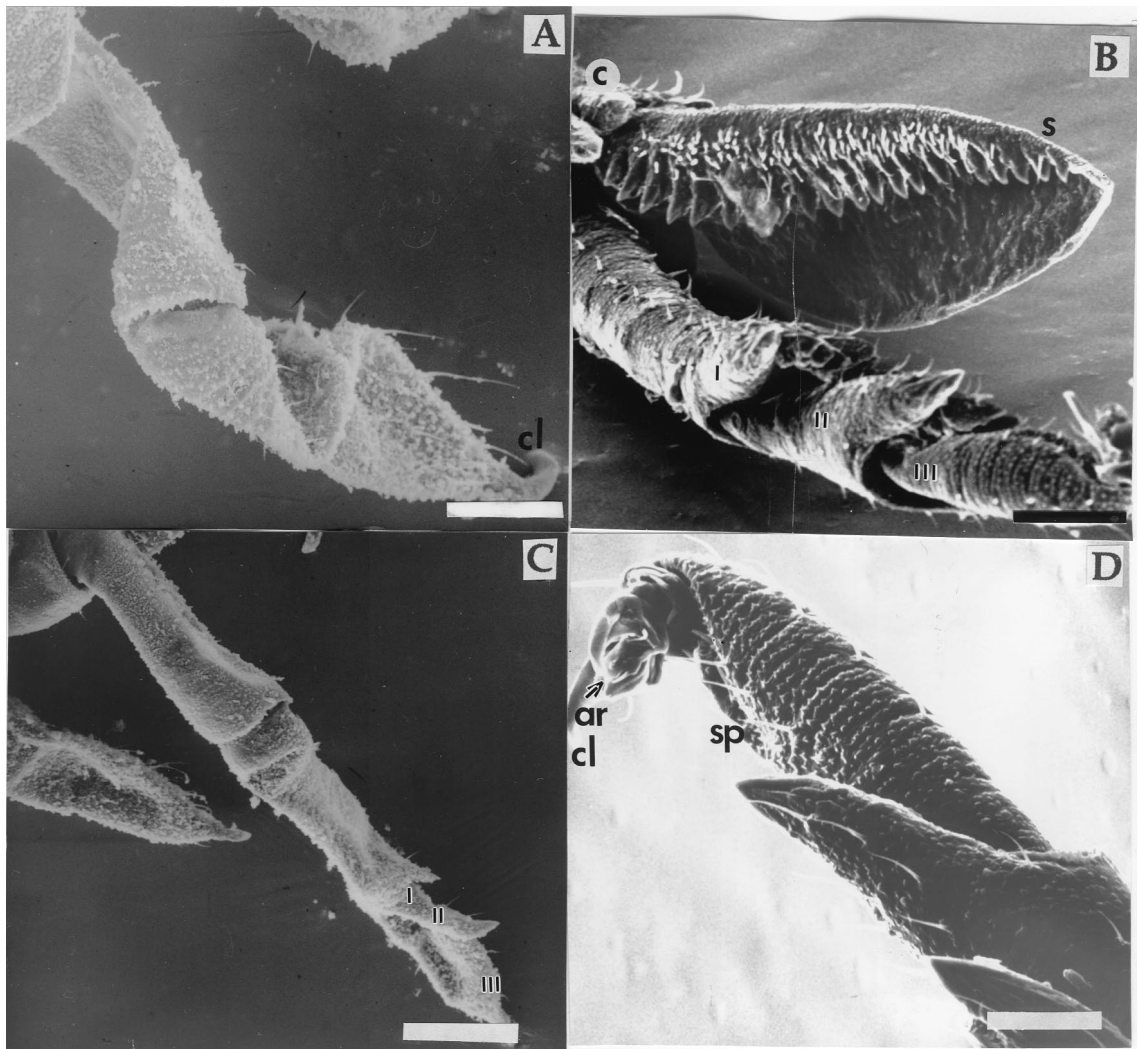


Fig. 7. Terminal part of the hind leg of *Tagosodes orizicolus* first (A), third (C) instar, and adult (B and D). Tarsal segments (I, II, III), claws (cl), crown (c), spur (s), central arolium (ar) (arrow), and multiple sensorial papillae (sp). Bars: A = 60 μm , B = 19 μm , C = 100 μm , D = 34 μm .

instars is more sponge-like (Fig. 8C). These sensillae are not present in adults.

Male Genitalia. Male genitalia provide numerous diagnostic characteristics for species identification. The ninth segment of the abdomen forms the pygofer, a capsule that contains several elements of the male genitalia. A modification in the phallobase divides the pygofer in two chambers, into which the aedeagus retracts (Fig. 9A). Diagnostic features of this species are the V-shaped structure at the midpoint of the diaphragm (Fig. 9B), the sclerotized aedeagus, which is a simple more or less straight tube, with a thickened base and a narrower distal end (Fig. 9C), and the characteristically shaped parameres (Fig. 9A and D). The gonopore, located in the apical end of the aedeagus (Fig. 9B and C), has a series of short, strong teeth on its ventral part.

Female Genitalia. Below the female anal tube, valvulae I, II, and III are found. The latter is the outermost and most developed, which corresponds to the pygofer (Fig. 10A). Valvulae I are strongly associated with valvulae II (Fig. 10B and D) and have a scale-like ornamentation (Fig. 10C and D). Valvulae II are fused, giving rise to a true ovipositor (Fig. 10B and D). The sclerotized ovipositor is sword-shaped and has a series of teeth on the ventral region (Fig. 10B) forming a serrated edge. Valvulae III have a corrugated ultrastructure (Fig. 10C).

Discussion

The external morphology, size, and coloration of *T. orizicolus*, as well as adult sexual dimorphism are useful in determining the identity of samples collected in

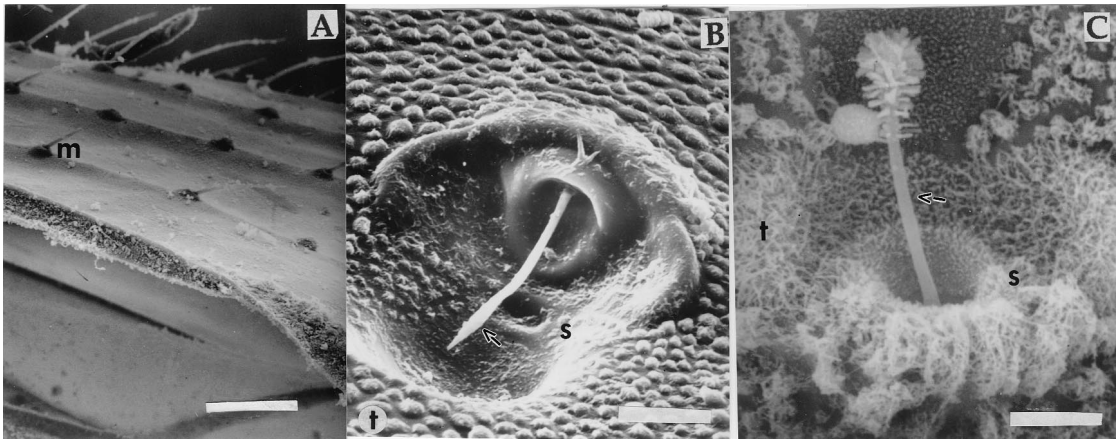


Fig. 8. Details of the microtrichiae in the wing of a male adult (A) and bell shaped sensillae of the fifth (B) and first instars (C), both bell shaped sensillae (s) inserted in different teguments. Microtrichiae (m), tegument (t) and setae (arrow). Bars: A = 100 μm , B = 15 μm , C = 136 μm .

rice fields. But a comprehensive analysis of the ultrastructure of males and particularly females and nymphs is needed to solve difficulties in the identification of specimens, because small delphacids belonging to *Tagosodes* species resemble *Sogatella* species in coloration and external appearance. These difficulties are mostly because their separation is mainly based on small differences in male genitalia (Asche and Wilson 1990).

In a previous investigation (Oliva 1998), numerous delphacid species (*Nilaparvata serrata* Caldwell, *Chionomus havanae* Muir & Giffard, *Toya propinqua* Fieber, *Caenodelphax teapae* Fowler, *Sogatella kolophon* Kirkaldy, and *Tagosodes cubanus* Crawford, among others) were commonly found on rice fields in Costa Rica. Because females and nymphs of *T. orizicolus* are difficult to distinguish from specimens of the above species, information that enhances the identification of females and immatures stages of *T. orizicolus* is needed.

The male genitalia have provided critical diagnostic features useful in determining the identity of collected samples and further separation of species. The pygofer, aedeagus, and parameres are the most frequently used diagnostic structures in the majority of species. The 10th and 11th segments of the abdomen of the male seem to be modified appendages of the anal tube or claspers, which are support structures used by the male during copulation.

Although traditionally the female genitalia have been of little interest in species classification, some European researchers have found useful features, especially in delphacids. Some of these diagnostic female structures include the valves and their serrated edges, and the width of the ovipositor. The serrated edges and the ensiform sclerotized structure of the ovipositor are features specialized for inserting eggs into plant tissues. A mated female lays an average of 10 eggs per day with an average total production of 161 eggs. Eggs are laid in a cluster in a slit cut by the ovipositor in the aerenchyma of the midrib of the rice

leaf blade or in the leaf sheath. The number of eggs per cluster varies, tending toward a multiple of seven; they are slightly curved, 0.6–0.8 mm long, and white (McMillian 1963).

It is of great interest to know the differences between the nymphal stages and the adults to see which characters of the species are maintained or modified during development. Some of these differences in *T. orizicolus* are the stamen-like setae present on the sensillae of the first and second instar, modified as a hair-like structure in older nymphs, and absent in the adult stage. Another difference is the conical eye with a small number of oval ommatidia of the first nymphal stage compared with the rounder eyes with many hexagonal ommatidia of older nymphs and adults.

The wider frons and convex clypeus with a shorter rostrum are other differences characterizing the first instars. Differences can also be noticed in the legs, where the oar-shaped leg of the first instar differs from the legs of older instars and adults. This peculiar oar shape may be useful as a flotation device. Nymphs are sedentary and usually found on the lower portion of the plant and they tend to move around the stem of the plant or drop to the water when disturbed. Older stages (mostly male adults) are found higher up on the plant and are inclined to fly when disturbed.

Many structures that are not clearly observed by light microscopy are mostly associated with mechanoreception. For example, the microtrichiae and glandular terminal bulges in the pedicel of the antenna apparently have a chemoreceptor function (O'Brien and Wilson 1985). All planthopper nymphs show bell-shaped sensillae and a few of them retain these pits as adults. They are present mostly on the cephalic capsule and the segments of the abdomen (O'Brien and Wilson 1985). These sensillae, observed in older nymphs as a plain seta and in younger nymphs as a more branched structure, are projections of the cuticle, possibly articulated with the body wall. One or more nerve cells are usually associated with each seta (Chapman 1971).

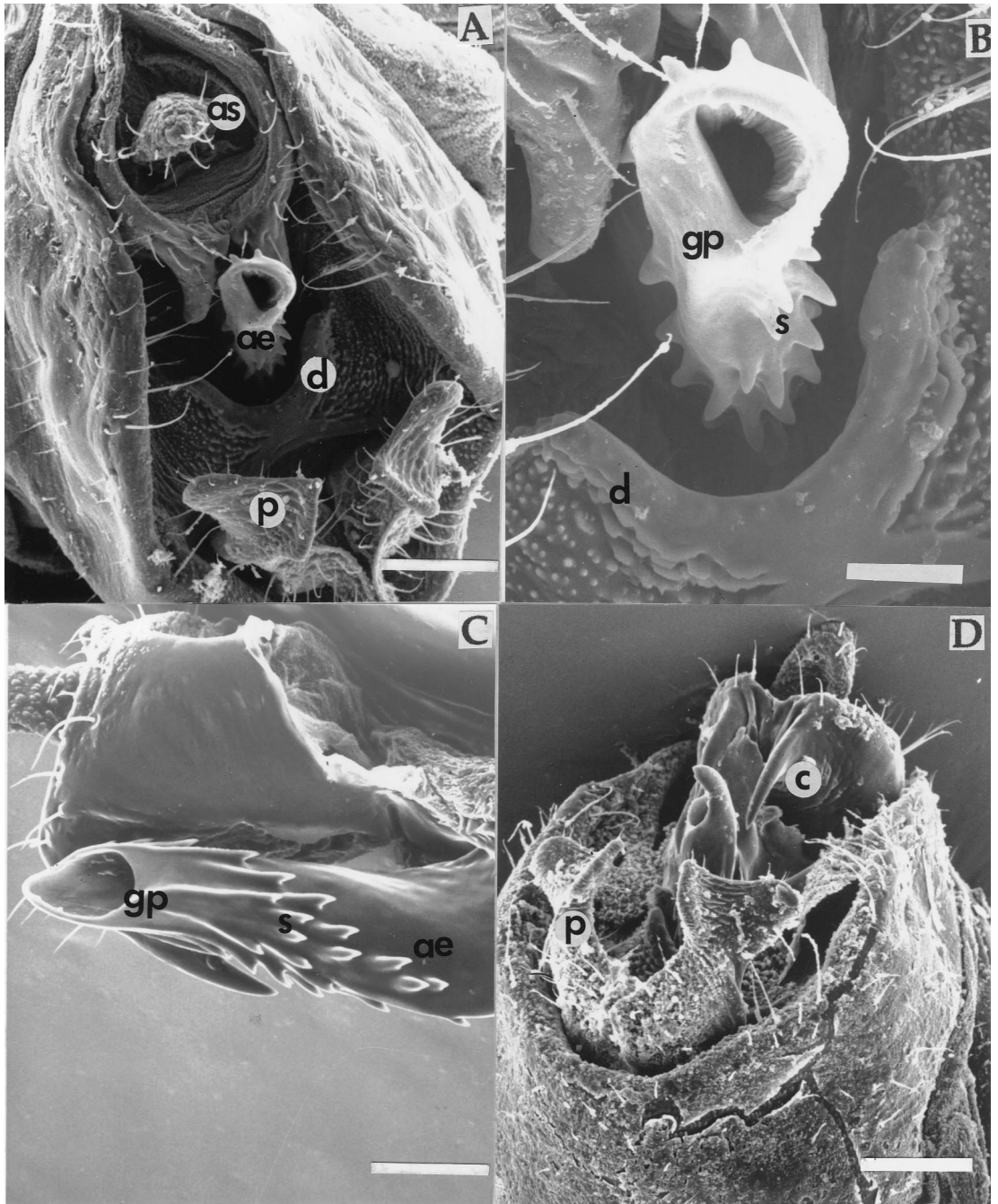


Fig. 9. Details of the female genitalia of *T. orizicolus*. In figure (A) observe the pygofer (p), anal style (as), the valvula I (VI), valvula III (VIII) and ovipositor (o). (D and C) The corrugated ultrastructure and scale-like ornamentation of VII and VIII. The sword-shaped sclerotized ovipositor (o) is observed in B. Bars: A = 185 μm , B = 9 μm , C = 27 μm , D = 12 μm .

Adults of *T. orizicolus*, like many members of the Fulgoroidae, have a continuous frons and vertex without evident separation. Nevertheless, nymphs of *T. orizicolus* do have a clear separation between the frons and vertex. The carinae of the vertex seem to be of a different origin from those of the frons.

The mouthparts of *T. orizicolus* are similar to those described by Backus (1985) for the delphacid *Nilaparvata lugens* (Stål). The sharp end of the maxillary stylets and the abundant protrusions of the mandibular stylets are structures specialized to pierce plant tissues while probing and ingesting plant fluids. The

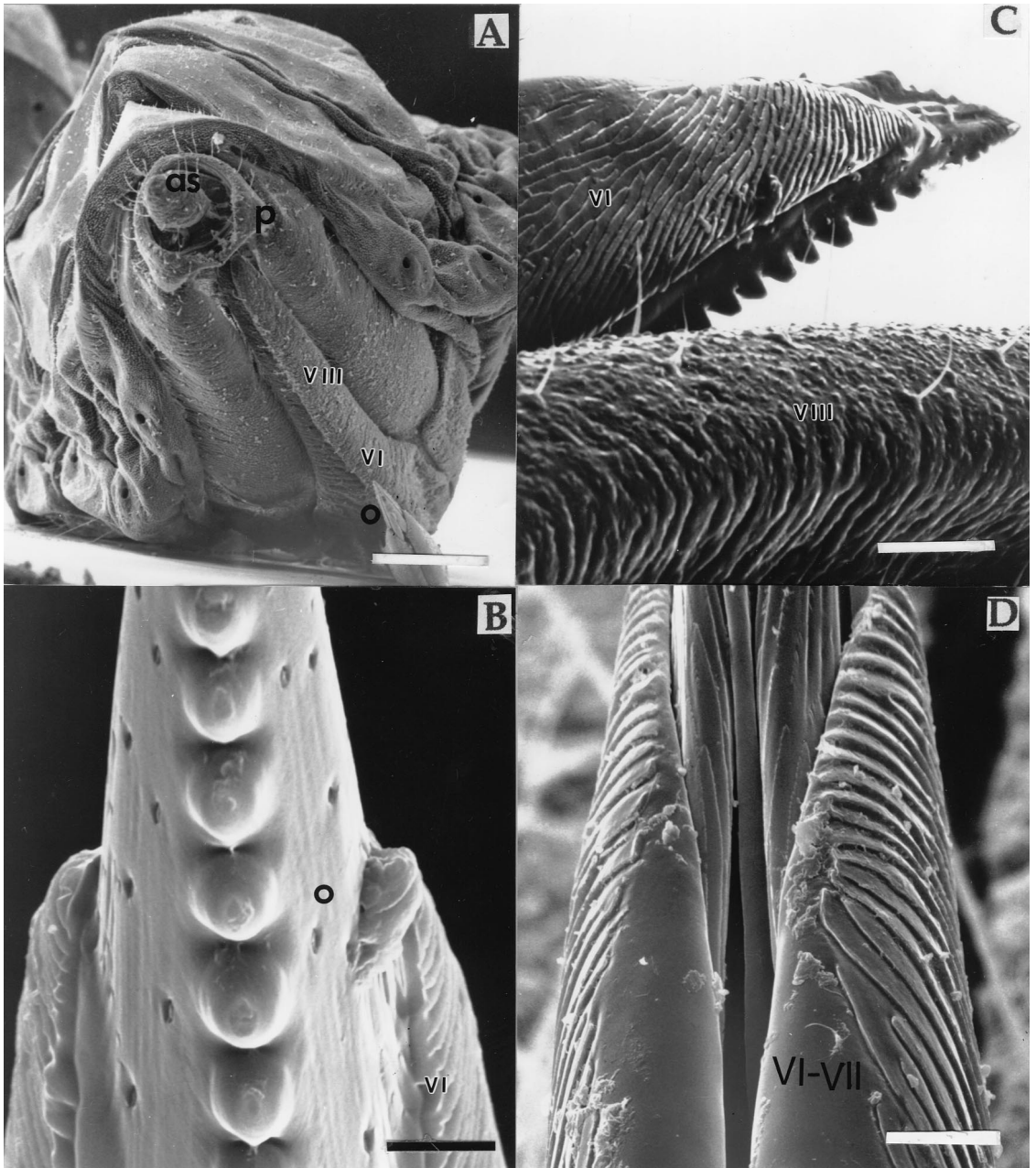


Fig. 10. Details of the male pygofer. In figure (A) observe the aedeagus (ae), anal style (as), parameres (p) and diaphragm (d). (B and C) Sclerotized aedeagus and the gonopore (gp) with a series of short, strong spines (s) on its ventral part. The claspers (c) are observed in D. Bars: A = 66.5 μ m, B = 62 μ m, C = 57 μ m, D = 91 μ m.

modified labium or proboscis bears papillae on the distal segment; these papillae are chemosensory structures and their glandular and nerve terminals have stimuli receptors for nutritional fluids (Snodgrass 1935). The labial tip, with its rosette shape, bears multiple sensillae, apparently associated with host plant surface exploration and probing of the plant (Denno and Perfect 1994). The tip of the labium is repeatedly appressed to the plant surface to explore the

surface. This behavior is usually accompanied by secretion of a drop of saliva at the tip of the stylets. This saliva solidifies around the stylets and forms a stylet sheath. The insect appresses its labium to the surface and inserts its stylets through this drop into the plant tissues. Generally, hoppers insert their mandibular stylets only a short distance into the leaf, while the maxillary stylets push through and beyond the mandibular stylets. Once a suitable tissue has been located,

the insect begins ingesting plant fluids and eventually finishes its probing by retracting the stylets from the plant (Backus 1985).

Being an hemimetabolous (paurometabolous) insect, fully developed and functional wings only occur in adults of *T. orizicolus*. In immature stages the wings are visible as external pads. The venation of delphacids is considerably reduced in comparison to other families of planthoppers. In the hind wings, venation is moderately reduced but much reticulation is present.

Although considerable work based on descriptions of the male genitalia of *T. orizicolus* has been done, little is known about female genitalia. In this research we concluded that there are important diagnostic female structures that are helpful in the identification of female specimens of this species. Nymphal morphology and ultrastructure in this species are other themes that have not been widely studied. In this article the first instar was described in detail and major ultrastructural changes were observed in comparison to the second, third, fourth, and fifth instars. Research aimed at studying ultrastructural characteristics, including mouth parts, structures involved in mechanoreception, and genitalia can resolve taxonomic problems in distinguishing different stages of delphacid species found in rice fields in tropical America.

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References Cited

- Asche, M., and M. R. Wilson. 1990. The Delphacid genus *Sogatella* and related groups: a revision with special reference to rice-associated species (Homoptera: Fulgoroidea). *Syst. Entomol.* 15: 1–42.
- Backus, E. A. 1985. Anatomical and sensory mechanisms of leafhopper and planthopper feeding behavior, pp. 163–190. *In* L. R. Nault and J. G. Rodríguez [ed.], *The leafhoppers and planthoppers*. Wiley, New York.
- Chapman, R. F. 1971. *The insects: structure and function*. Elsevier, New York.
- Denno, R. F., and T. J. Perfect. 1994. Evolutionary patterns of host plant use by delphacid planthoppers and their relatives, pp. 7–113. *In* R. F. Denno and T. J. Perfect [eds.], *Planthoppers: their ecology and management*. Chapman & Hall, New York.
- Karnovsky, M. J. 1965. A formaldehyde-glutaraldehyde fixative of high osmolarity for use in electron microscopy. *J. Cell Biol.* 27: 137.
- Kozuka, Y. 1989. *Laboratory manual for transmission electron microscope specimen preparation*. Centro de Investigación en Biología Celular y Molecular, San Jose, Universidad de Costa Rica.
- McMillian, W. W. 1963. Reproductive and mating behaviour of *Sogatia orizicola* (Homoptera: Delphacidae). *Ann. Entomol. Soc. Am.* 330–334.
- Morales, F. J. and A. Niessen. 1985. Rice hoja blanca virus. Description of plant viruses. No. 299. Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
- O'Brien, L. B., and S. T. Wilson. 1985. Planthopper systematics and external morphology. *In* L. R. Nault and J. G. Rodríguez [ed.], *The leafhoppers and planthoppers*. Wiley, New York.
- Oliva, M. 1998. Fluctuación poblacional de delphacidos y su ámbito de poaceas hospederas asociadas al arroz en Liberia, Guanacaste. M.S. thesis, Universidad Nacional Facultad de Ciencias de la Tierra y el Mar, Escuela de Ciencias Agrarias.
- Snodgrass, R. E. 1935. *Principles of insect morphology*. McGraw-Hill, New York.
- Wilson, M. R., and M. F. Claridge. 1991. *Handbook for the identification of leafhopper and planthopper of rice*. CAB, Wallingford, UK.
- Wilson, M. R., and M. F. Claridge. 1994. Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. Chapman & Hall, New York.

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