

New Anatomical Evidence from the Male Asian Citrus Psyllid (Hemiptera: Liviidae) Invokes Controversy Over the Accepted Function of Some Male Reproductive Organs in Psylloidea

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Abstract

Males of many Psylloidea are known to possess a characteristic structure at the functional hub of their reproductive apparatus, between afferent and efferent passage of seminal fluid. The structure is a squat, cylindrical endoskeleton consisting of two sections. Classical authors named them as ‘sperm pump’ and ‘ejaculatory duct’, based on superficial resemblance to a spring-loaded, thimble-shaped cylinder, encircled by smooth, vertical columns interpreted to be muscles which, when contracted, compress the cylinder and affect seminal fluid discharge. The discovery of numerous spherules of unknown composition and function in and around the columns of the Asian citrus psyllid male genitalia invoked rigorous scrutiny of the classical literature for evidence to support its claims, and determined that the grounds for vetting the structure as a sperm pump were fully teleological. This paper raises several objections to modern acceptance of this classical interpretation, presenting them as problematic, thought-provoking, and sometimes controversial anatomical features. The two sections are herein called ‘drum’ and ‘spout’. As an endoskeleton, the sections are an invagination of the exoskeleton and therefore cannot receive seminal fluid into their hollow. A phallus is identified inside an aedeagal tube, indicating that it is the ejaculatory duct—the tube, drum, and spout are considered its housing. A sheath envelopes the drum and is directly continuous with the spout hypodermis, another problematical feature raising the question of whether it is detached from adherence to the drum cuticles. Also, there are four afferent tubes but only two openings in the drum to receive their seminal fluids.

Key words: psyllids, genitalia, terminology

The male internal reproductive organ complex of approximately 175 species from all eight extant families of the Hemipteran superfamily Psylloidea (Cicero et al. unpublished; Mathur 1975, Glowacka 1987, Brown and Hodkinson 1988) is known to possess an endocuticular structure that classical authors called the ‘sperm pump’ (Speyer 1929 for *Cacopsylla* (=Psylla) *mali* (Schmidberger) (Hemiptera: Psyllidae)), ‘ejaculatory pump’ (Saunders 1921 for *C. mali*), or ‘piston-shaped organ’ (Witlaczil 1885 for *Baeopelma* (=Psylla) *foersteri* (Flor) (Hemiptera: Psyllidae)). Synonymies are taken from Ouvrard (2019).

These terms were derived from several features observed and sketched by the early histologists from which they concluded a sperm pumping functionality—it is an endocuticular structure, it occurs in males only, it has a thimble-shaped anterior half (then referred to as a ‘pump’ or ‘piston’), connate to a spout-shaped posterior half (then referred to as the ‘ejaculatory duct’). The thimble-shape owes to a hollow, cylindrical core (‘the cylinder’) between, and perpendicular to, an apical

plate and a basal plate of wider diameters. Judging from Saunders’ (1921) emphasis, the most convincing feature leading to their conclusion is the numerous columns (‘columns’) that attach to, and vertically span the space between, the apical plate ‘overhang’ and the basal plate ‘underhang’. Their smooth surfaces, discrete columnar shapes and circumferential positions were, to them, evincive of muscle masses.

Schlee (1969: 102) made intensive effort to analyze the pumping mechanism, and, on identifying transverse, chitinous rings (‘*Versteifungsringen*’) around the inner surface of the cylinder, envisioned them as inflexion sites upon which the interstitial cuticle can fold inward, thus compressing the length of the cylinder. Zucht (1972: 1975) interpreted the rings as elastic chitin spirals, which restore the original shape when the muscle contraction subsides: *Der dünnwandige Zylinder ist innen durch elastische Chitinspiralen ausgesteift, die bei Nachlassen der Muskelkontraktion die ursprüngliche Gestalt wieder herstellen.*

Schlee (1969: 102, Abb. 12) described and sketched the apical plate as having two large openings through which the sperm passes. The presence of two openings has been validated by the use of micro-computed tomography (Alba-Alejandre et al. 2018: 16, f. 5l). Schlee indicated (p. 102; p. 103, Abb. 13) that a gland is attached to the center of the inner surface of the apical plate such that it partially blocks the two openings but leaves room enough for semen to flow around it and into the pump capacity and ejaculatory duct interior: *Das Sperma tritt durch zwei große Öffnungen in der Oralwand in die Pumpe ein und gelangt im Pumpraum zwischen dessen Wandungen und die Außenwand der „Pumpendrüse“*. Zucht (1972: 193, Abb.18a, ERö) agreed with this interpretation.

The above observations, and the observation that the ‘pump’ occupies an overtly central position in the semen-stream between the afferent duct lumina of the seminal vesicles and the efferent ‘ejaculatory duct’, left no question that when deployed, the apparently muscular columns compress the thimble longitudinally to discharge the semen.

Collectively, all these observations and interpretations were so seductive as to result in time-honored usage of the term ‘sperm pump’ and acceptance of its inferred function. To date (Alba-Alejandre et al. 2018), this function has not been questioned even though no ultrastructural studies have been undertaken to identify the cell types, tissue types, and cuticle infrastructure involved in pursuit of proof of function. These shortcomings, relative to the rigor that modern studies require, cast doubt on their claims. With study of the descriptive text and supportive evidence in free translations of the German papers, their analyses are herein viewed as fully teleological. The intention of this paper is to provide thought-provoking discussion by presenting new evidence that the function of the structure in question is far more complex, and in some cases controversial.

Snodgrass (1935) made a distinction between ‘internal’ and ‘external’ genitalia. Internal genitalia other than the ‘sperm pump’, namely the gonads, seminal vesicle, and accessory glands, are dealt with in another paper (Cicero et al. unpublished). According to his definitions, the external genitalia consists of the aedeagus, parameres, proctiger, and other associated structures. Because of the terminological problems created with study of the many variations among insects, application of these terms to psyllids is also fraught with shortcomings. This paper presents new evidence that will serve to clarify the relationship between terminology and function of the structures called ‘aedeagus’, ‘intromittent organ’, ‘phallus’, and ‘ejaculatory duct’ of the broader Psylloidea.

Methods

Male internal reproductive organ complexes ($n = 14$) were dissected in 0.01 M Na⁺ K⁺ PBS (Sambrook et al. 1989) from the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera, Liviidae, ACP), fixed in 4% formaldehyde, 0.5% glutaraldehyde in PBS, rinsed in PBS, dehydrated in a graded ethanol series (25%, 50%, 75%, 95%, 100%), critical point dried, and viewed with an Hitachi SU5000 Schottky field emission scanning electron microscope (SEM) (Hitachi America, Tarrytown, NY).

Numerous mating pairs of ACP ($n = 3$) were obtained by using methods modified from Wenninger and Hall (2007). Newly emerged adults were sexed and isolated in pairs on *Citrus* seedlings in inverted plastic cups with two mesh-covered holes at the top and a petri dish floor at the bottom. After 4–5 d, males mounted females and were given 10–15 min following initiation of copulation. The cups were then placed in a 0°C freezer for 24–36 h. Pairs were submerged in retail grade mineral oil for 36 h, then taken to the dissecting microscope stage and slowly teased away from each other to examine the

in copula configuration. All pairs except three separated during manipulation, leaving the three to observe and photograph.

Males were submerged in mineral oil, external genitalia were cut from the body, and then the aedeagus was dissected out for photographing under a compound microscope.

Results

The endocuticular structure of male ACP was consistent in gross habitus with that of the species referred to by prior authors as the ‘sperm pump’. Viewable aspects in Fig. 1A and B agreed with Fig. 2A, confirming that it consisted of anterior and posterior sections. The anterior section is herein called the ‘drum’ (Figs. 1Ac, Bc and 2Bp; replacing ‘pump’ in Fig. 2Ab) and the posterior section is herein called the ‘spout’ (Figs. 1Am, Bm and 2Bq; replacing ‘ejaculatory duct’ in Fig. 2Ad). The cylinder was the interior aspect of the thimble-shaped drum, spanning the space between apical and basal plates (Figs. 1Bn and 2Bo), leaving an ‘overhang’ and an ‘underhang’ (Fig. 2Bl, r). The drum/spout complex occupied a central position in the semen-stream between the afferent duct lumina of the seminal vesicle body (Fig. 1Aa, b, Ba) and the spout.

The apparently noncuticular aspects of the drum/spout complex were the columns, the sheath, and the phallus. Each of the columns were attached apically and basally to, respectively, the apical plate overhang and the basal plate underhang, and all were circumferentially arranged around the cylinder (Fig. 1Aj). A sheath enveloped the drum, including the columns (Figs. 1Ae and 2Aj, Bj), and this membrane was continuous with the hypodermal cell layer lining the posterior surface of the basal plate and the spout (Figs. 1Af, m and 2Ak, Bk, x).

By SEM, the drum of two of the 14 specimens contained numerous, uniformly spherical objects between the columns and the sheath (Fig. 1Ad), between the posterior basal plate surface and its hypodermis (Fig. 1Al), and between the spout cuticle and its hypodermis (Fig. 1Ak, l, m). Their origin could not be determined from the available micrographs, but many of them rolled out freely through a rip in the sheath when manipulated to mount on an SEM stub.

ACP males possessed a hollow, hinged, thinly cylindrical, tweezer-shaped, sclerotic tube between the parameres (Fig. 3A) that housed a phallus (Fig. 1C). The tube was divided into basal and apical sections by a hinge. Figure 3B showed that the hinge of the sclerotic tube allowed for the apical section to extend to a correct position. Figure 3C, D showed that the sclerotic tube was almost fully inserted during copulation.

Discussion

The Drum/Spout Complex

The early authors drew sketches of the drum/spout complex with and without the columns, but none reported observation of spherules in dissections of their subject psyllids. According to their sketches, the columns are the only structures that occur in the space between the sheath and the cylinder. None of their sketches indicate any openings which might allow accessory gland fluid (Fig. 1Ag) to flow into space external to the cylinder *in vivo*. If this information is correct, it suggests that the columns, sheath cells, and hemolymph are the only available sources of the substance the spherules are made of.

Recent findings (Cicero et al. unpublished) proved that the columns are indeed muscles, and that the spherules, or the material they are composed of, do originate from inside the sarcomeres. The uniform geometry of the spherules suggests that they might have

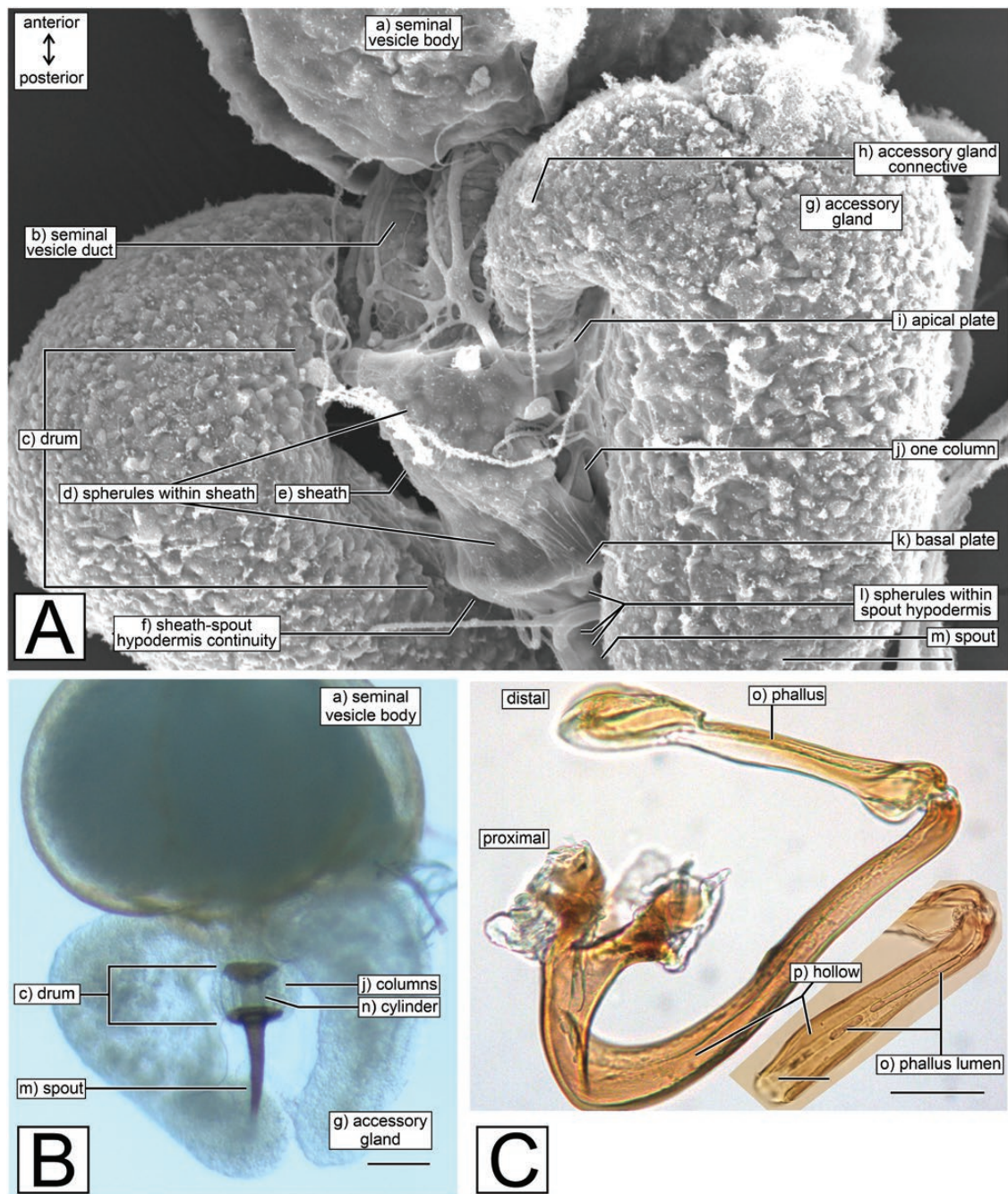


Figure 1. Some components of the reproductive apparatus of the male Asian citrus psyllid, *Diaphorina citri*. Gonads and vasa were removed. (A) SEM of the so-called 'sperm pump', herein referred to as the drum/spout complex. A large number of spherules (d) of approximately equal size occur between the sheath (e) and the columns (j). They also occur between the basal plate/spout hypodermis and their cuticles (k, l, m). It is not clear in this micrograph whether sheath (e) continues around the apical plate rim (i) to line the anterior apical plate surface between the ducts and connectives (b, h). Line = 50 μ m. (B) Light micrograph showing the central cuticular cylinder (n), not visible in (A). Line = 100 μ m. (C) Aedeagus with phallus (o) passing through its hollow (p). Line = 50 μ m. Right, higher magnification. The dissection media, mineral oil, has replaced some of the luminal contents, adding contrast. Line = 25 μ m.

been a liquid lipid or lipid derivative which artifactually rounded and solidified during processing.

The early authors presented no proof of an anteroposterior compressibility of the drum cuticle other than the position of the (then) putative muscular columns and the transverse lines, the latter interpreted as coils of a spring (Fig. 2Ag₁, g₂, Bn). Contraction/extension of the muscles would be directly exerted on the apical plate overhang and basal plate underhang to which they are attached, and these plates may, alternatively, have the flexibility that would fulfill

a functional interpretation of the muscles as a contractile tissue. The controversy invoked with this thought is the inapparent reason for the columns to contract if their attachment sites do not affect a pumping action.

Other muscles may be associated with the seminal vesicle body, which would fulfill the suggestion that pressure is needed to discharge the seminal fluid. In summary, the conclusion that the drum/spout complex is a sperm pumping appliance is, by these points and those below (*The Invagination Hollow*), rendered unwarranted at this time.

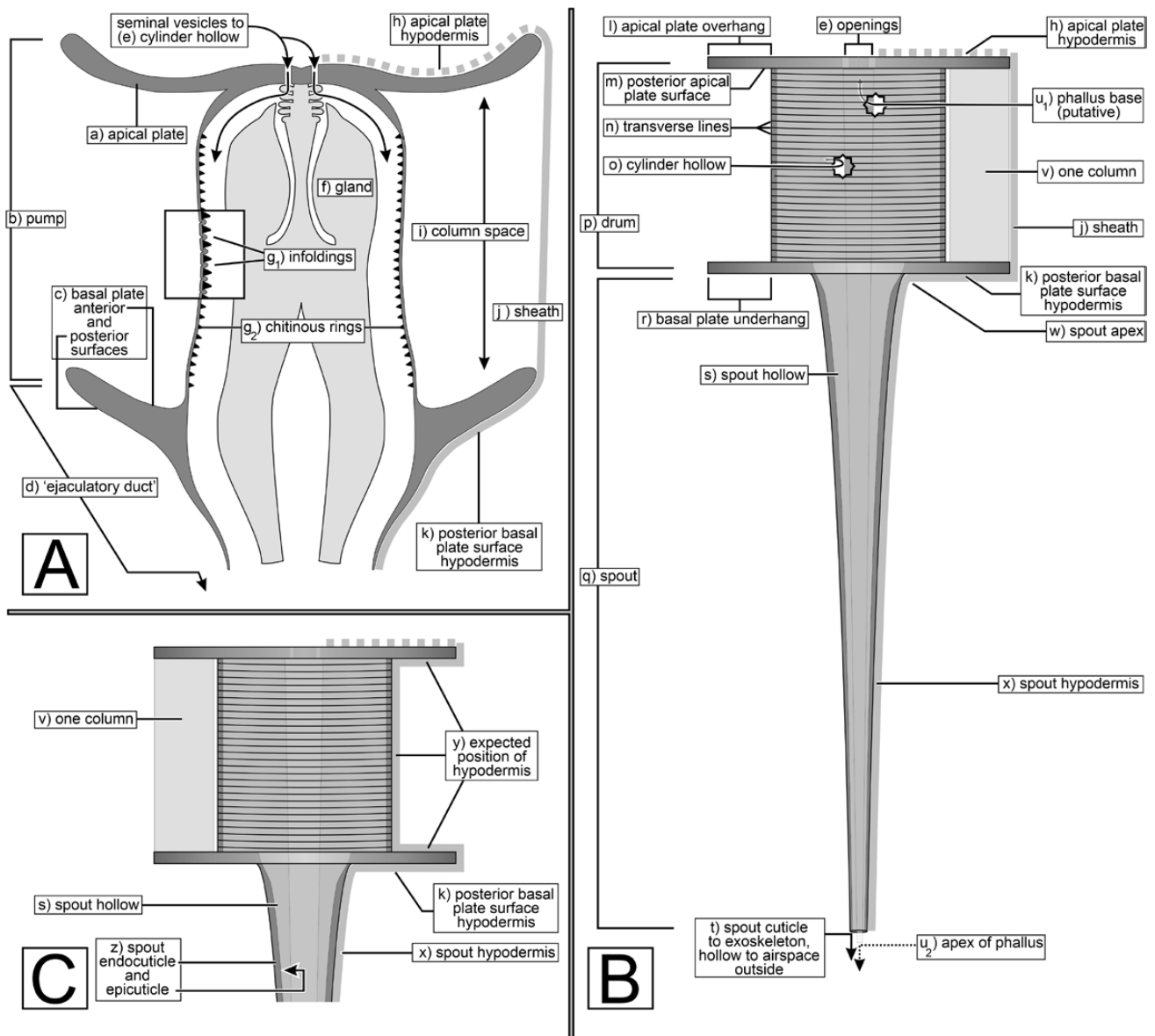


Figure 2. Interpretations of the controversial appliance known in prior literature as the ‘sperm pump’. Continuation of the sheath is not drawn in on the left side (cf. Fig. 1Ae, f). (A) Modified from Schlee (1969: Abb. 13). A back-flow regulation gland (f) was perceived to be attached to the inner apical surface of the cylinder, and seminal fluid was thought to pass through two openings (e) and around the gland (arrows) to fill the hollow of the cylinder and ‘ejaculatory duct’ interior (d). Columns, not drawn in (i), were thought to be muscles which, when contracted, compressed the cylinder by folding its cuticle inward between chitinous rings (g_1 , g_2). (h) The presence of an apical plate hypodermis is not clear in Fig. 1A1. (B) A model of the male ACP drum/spout complex based on SEM and light microscopy. The base of the phallus (u_1) has not been verified to be attached to the inner posterior apical plate surface (m). Note that the sheath (j) is positioned outside the cylinder (cf. Fig. 1Ae, f) and does not undergo a cuticle even though it transitions directly into the basal plate and spout hypodermis (k, x). (C) A model illustrating the problematical position of the sheath in (j) (B). It is continuous with the posterior basal plate surface hypodermis and spout hypodermis (k, x), but this hypodermal continuity is expected to be continuous with the anterior basal plate and outer cylinder surfaces also (y). If this is the case, then the identity of the sheath is unaccounted for. (z) The spout epicuticle is interior while the aedeagus epicuticle is exterior (cf. Fig. 3b).

The Sheath

Characterization of the sheath is controversial because, although the drum/spout complex is an endoskeleton, it is not directly associated with a cuticle even though it is continuous with the hypodermis associated with the posterior basal plate surface and spout cuticles (Figs. 1Ae, f, k, and 2Bk, x). Its continuity with the apical plate is not clear in Figure 1A. This configuration is in conflict with ‘cuticular continuity’ (Cicero et al. 2015: 752, f. 7Cn, Do and below, *The Invagination Hollow*)—a tenet that represents an aspect of basic cuticle physiology, which asserts that continuity be maintained around all outer surfaces of the body and all inner surfaces

of invaginations so that apical membranes of the epidermal cells of the exoskeleton and hypodermal cells of the endoskeleton are not exposed. Accordingly, the hypodermis of the basal plate posterior surface is expected to round its rim, underly its anterior surface, continue anteriorly to underly the cylinder surface, and thence along the apical plate surfaces (Fig. 2Cy), rendering the sheath unaccounted for. A second controversy is invoked with the observation that the spherules also appear between the spout hypodermis and its cuticle (Fig. 1A1), suggesting that the hypodermis is detached. This may be artifactual, or it may reflect an unknown, *in vivo* functionality that allows the putative lipid to reach the spout’s outer cuticle surface.

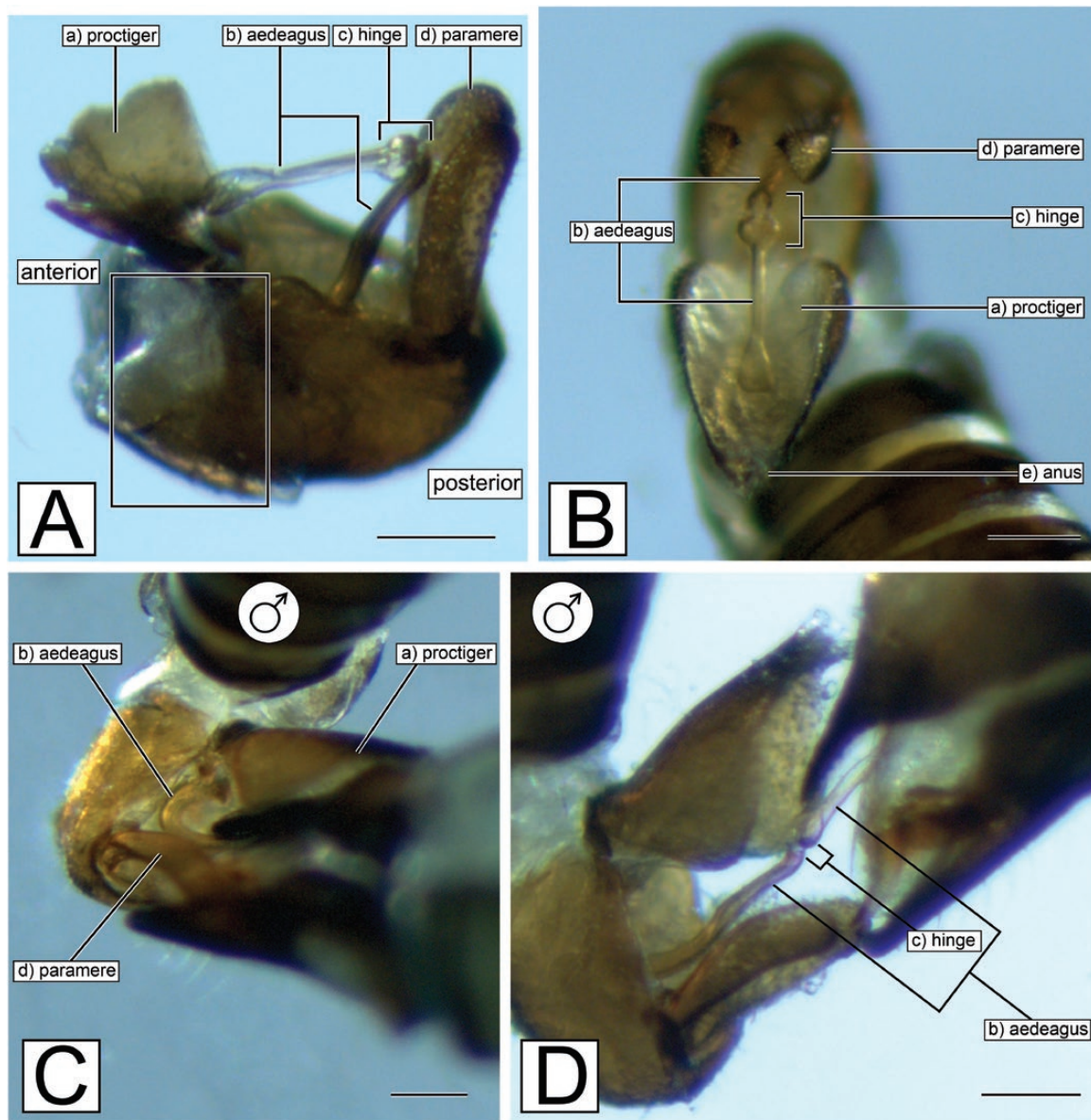


Figure 3. Male ACP external genitalia and copulatory configuration. Lines = 100 μm . (A) Genitalia dissected free from the body. Lateral view. Proctiger (a) was dissected away to expose the spoon-shaped apex of the sclerotic tube (b) which, verified in Fig. 1C to house a phallus, is correctly the aedeagus rather than the ‘ejaculatory duct’ (see text, *The Aedeagus*). (c) Aedeagus is hinged. Inset—rectangle identifies a block of the external genitalia between eighth abdominal segment and the attachment of the aedeagus. Its complexity is not elucidated, but since the spout epicuticle is interior (cf. Fig. 2Cz) while the aedeagal cuticle is exterior, a juxtaposition of cuticle laminae passes through it (see text, *The Aedeagus*). (B) Dorsal view. In this specimen, the proctiger (a) and the apical segment of the aedeagus (b) was reflexed anteriorly into a correct position. (C) Aedeagus (b) is nearly fully intromitted. (D) Copulatory pair teased away from each other to clearly show the intromitting aedeagus (b).

The Aedeagus

In the revised edition of Torre-Bueno’s glossary of entomology (Torre-Bueno 1962), Nichols (1989) expanded Torre-Bueno’s definition of ‘aedeagus’ to a full page, listing the variations of this structure from insect order to order. Since the variation vastly outweighs the number of coined terms commonly used to describe certain component parts of the male genitalia—aedeagus, intromittent organ, ejaculatory duct, phallus—it is understandable that these terms have been variously and inconsistently applied by prior authors. Another reason for this inconsistency is that the authors used a homological approach but did not attempt to ascertain proof of function to guide their usage of the terms. The homological

approach, generally used to fix terminology of genital components across the board (Snodgrass 1935), is beyond the scope of this forum. Instead, it is the intention here to use proof of function where possible by relying on some basic physiological tenets that characterize and distinguish ‘aedeagus’ from the other terms for their application to male Psylloidea.

A ‘duct’ is herein understood to be a cellular tube with a lumen through which media traverses. A well-characterized example is the salivary duct (Ammar 1986, Cicero and Brown 2012). Confirmation of a phallus (Fig. 1Co) inside the hollow (Fig. 1Cp) of the hinged sclerotic tube (Fig. 3Ab) of ACP indicates that it carries the semen-stream and is the ejaculatory duct, while the sclerotic tube is its

housing. The phallus + sclerotic tube, then, would be the aedeagus. [Figure 3Cb](#) confirms that the sclerotic tube also enters the female rather than being topically applied to the vaginal orifice thereby relying on the phallus to extend further. As such, the aedeagus is also the intromittent organ. The resting position and copulatory position of the phallus apex are unknown, but serial cross-sectioning or computed tomography combined with a systemic stain such as osmium tetroxide or BAPC (branched amphiphilic peptide capsules, [Sukthankar et al. 2014](#)) can ascertain them.

The presence of a phallus inside the sclerotic tube is evidence that the phallus continues anteriorly and interiorly into the spout. The spout is by that reasoning the internal sclerotic housing for the phallus, not the ‘ejaculatory duct’. As explained in the next Section (*The Invagination Hollow*), the phallus very likely attaches to the inner apical plate surface to receive seminal fluid directly from the seminal vesicles. The ‘gland’ of prior authors ([Fig. 2Af](#)) is probably an elaboration of the attachment.

The Invagination Hollow

The exterior (hemolymph-side) surface of the cylinder/spout cuticle is certainly endocuticular ([Fig. 2Cz](#)). The interior surfaces of the cylinder/spout cuticle are therefore epicuticular ([Fig. 2Cz](#)), and the drum/spout complex is actually an invagination of the exoskeleton. As an invagination, the space inside the cylinder and spout is a continuous ‘hollow’ and the hollow must eventually open to the outside air ([Fig. 2Bt](#)). This tenet, and the presence of a phallus, argues against the interpretation of earlier authors that the seminal fluid, discharged from the seminal vesicle ducts and passed through the two apical plate openings ([Fig. 2Ae, Be](#); ‘foramina’, [Alba-Alejandre et al. 2018](#): 7, f. 5j; ‘beiden Einströmöffnungen’, [Schlee 1969](#): 102, Abb. 12), empties into the cylinder interior, from which it is ‘pumped’ through the ‘ejaculatory duct’ (the spout) to the female. The limitations of resolution inherent in their microscopy did not allow for identification of the ‘gland’ ([Fig. 2Af](#)) to be a continuous phallic tube that, although unproven, appears to extend from the apical plate ([Fig. 2Bu₁](#)), through the spout ([Fig. 2Bu₂](#)), and thence through the aedeagus ([Fig. 3b](#)) to reach the female. This continuity can certainly be verified by TEM.

Further, and more problematical, is the observation that media from four afferent tubes, two from the seminal vesicle body and two from the accessory glands ([Fig. 1Aa, b, g, h](#)), pass through only two openings in the apical plate. The functional configuration of the openings that pass four media streams and integrates them into two efferent streams, or perhaps even one, might also be elucidated by TEM. General adult specimens would be advisable for such a study because their soft cuticles would better facilitate ultramicrotomy.

The phallus negotiates its pathway through a complex ‘block’ of cuticle between the spout and the base of the aedeagus ([Fig. 3A](#), inset). [Zucht \(1972](#): 172, Abb. 1) and [Tremblay \(1965\)](#) attempted to map this complex, but their study overlooked the juxtaposition of the two overcoating epicuticles. The spout epicuticle ([Fig. 2Cz](#)) lines the interior spout hollow while the aedeagus epicuticle ([Fig. 3](#)) lines the exterior. This observation needs to be examined for possible configurations that may violate the tenet of cuticular continuity, but strict adherence to the tenet asserts that the epicuticle of the aedeagal tube must round its apical rim and continue anteriorly and interiorly through the ‘block’ to become the spout epicuticle and cylinder epicuticle. This can also be confirmed with electron microscopy and computed tomography.

Future research directions are best facilitated by establishing precise terminology for the components of complex insect organ

systems. Since the homological approach invokes the unintended consequence of diverse interpretations, a functional approach is far more desirable for the broader audiences, especially when generic terminology is implemented in place of homological terms ([Cicero et al. 2015](#)) and animation is used to facilitate learning ([Cicero et al. 2019](#)).

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References Cited

- Alba-Alejandre, I., W. B. Hunter, and J. Alba-Tercedor. 2018. Micro-CT study of male genitalia and reproductive system of the Asian citrus psyllid, *Diaphorina citri* Kuwayama, 1908 (Insecta: Hemiptera, Liviidae). *PLoS ONE*. 13: e0202234. doi:10.1371/journal.pone.0202234
- Ammar, E.-D. 1986. Ultrastructure of the salivary glands of the planthopper, *Peregrinus maidis* (Ashmead) (Homoptera: Delphacidae). *Int. J. Insect Morphol. Embryol.* 15(5/6): 417–428. doi:10.1016/0020-7322(86)90034-6
- Brown, R. G., and I. D. Hodkinson. 1988. Taxonomy and ecology of the jumping plant-lice of Panama (Homoptera: Psylloidea). *In* J. Lyneborg (ed.) *Entomograph* vol. 9. E. J. Brill/Scandinavian Science Press Ltd. Leiden, The Netherlands. doi:10.1002/mmnd.19890360431
- Cicero, J. M., and J. K. Brown. 2012. Ultrastructural studies of the salivary duct system in the whitefly vector *Bemisia tabaci* (Aleyrodidae: Hemiptera). *Ann. Entomol. Soc. Am.* 105(5): 701–717. doi:10.1603/AN12030
- Cicero, J. M., P. A. Stansly, and J. K. Brown. 2015. Functional anatomy of the oral region of the potato psyllid (Hemiptera: Psylloidea: Trioziidae). *Ann. Entomol. Soc. Am.* 108(5): 743–761. doi: 10.1093/asea/sav059
- Cicero, J. M., J. Alba-Tercedor, W. B. Hunter, L. M. Cano, S. Saha, L. A. Mueller, and S. J. Brown. 2019. An animated correspondence of Asian citrus psyllid stylets to the model for biogenesis of potato psyllid stylets. https://citrusgreening.org/microtomography/cicero_stylet_2018. Last viewed, May 24, 2019. doi:10.6084/m9.figshare.7591049
- Glowacka, E. 1987. The structure of male reproductive system in certain species of Carsidaridae (Homoptera, Psylloidea). *Acta Biol. Silesiana.* 6: 66–80.
- Mathur, R. N. 1975. Psyllidae of the Indian subcontinent. Indian Council of Agricultural Research, New Delhi, India.
- Nichols, S. W. 1989. The Torre-Bueno glossary of entomology. NY Entomological Society, New York. doi:10.1163/187631290X00238
- Ouvrard, D. 2019. Psyllist - The world Psylloidea database. <http://www.hemiptera-databases.com/psyllist> - Last viewed, 25 May 2019. doi:10.5519/0029634
- Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989. *Molecular cloning: A laboratory manual*, 2nd ed. Cold Spring Harbor Laboratory Press, New York, NY.
- Saunders, L. G. 1921. The anatomy of *Psyllia mali* Schmidberger. Ph.D. dissertation, McGill University, Montreal, QC, Canada.
- Schlee, D. 1969. Sperma-Übertragung (und andere merkmale) in ihrer bedeutung für das phylogenetische system der Sternorrhyncha (Insecta, Hemiptera). *Phylogenetische studien an Hemiptera. I. Psylliformes (Psyllina und Aleyrodina) als monophyletische gruppe.* *Z. Morphol. Tiere.* 64: 95–138. doi: 10.1007/BF00391783
- Snodgrass, R. E. 1935. *Principles of insect morphology*. McGraw-Hill, New York. doi:10.4039/Ent67183-8
- Speyer, W. 1929. *Der Apfelblattsauger Psylla mali* Schmidberger. *Monographien zum Pflanzenschutz*, Springer, Berlin.

- Sukthankar, P., L. A. Avila, S. K. Whitaker, T. Iwamoto, A. Morgenstern, C. Apostolidis, K. Liu, R. P. Hanzlik, E. Dadachova, and J. M. Tomich. 2014. Branched amphiphilic peptide capsules: cellular uptake and retention of encapsulated solutes. *Biochim. Biophys. Acta.* 1838: 2296–2305. doi: 10.1016/j.bbame.2014.02.005
- Torre-Bueno, J. R. de la. 1962. *A glossary of entomology*, 3rd ed. Brooklyn Entomological Society, New York.
- Tremblay, E. 1965. Studio morfo-biologico sulla *Trioza tremblayi* Wagner (Homoptera-Homoptera, Psyllidae). *Boll. Lab. Entomol. Agraria.* 23: 37–138.
- Wenninger, E. J., and D. G. Hall. 2007. Daily timing of mating and age at reproductive maturity in *Diaphorina citri* (Homoptera: Psyllidae). *Fla. Entomol.* 90(4): 715–722. doi: 10.1653/0015-4040(2007)90[715:DTOMAA]2.0.CO;2
- Witlaczil, E. 1885. Die anatomie der Psylliden. *Z. Wissen. Zool.* 42: 569–638.
- Zucht, B. von. 1972. Bau und entwicklung der äußeren genitalorgane bei psyllinen (Homopteren). *Zool. Jahrb. Abt. Anat. Ontog. Tiere.* 89: 167–231.