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Secondary sexual characters and spermatophores of *Solenocera agassizii* (Decapoda: Solenoceridae), including a comparison with other solenocerid shrimp

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ABSTRACT: *Solenocera agassizii* is commercially exploited along the Costa Rican Pacific coast and represents around 30% of the country's total shrimp catch. Despite its economic importance, information on its biology is scarce. Here we describe its secondary sexual characters and spermatophores. The open thelycum is located between Sternites XIII and XIV. A pair of parallel setose projections (Sternite XIV) is distally curved in larger females (<30 mm carapace length); a disk-shaped projection (Sternite XIII) emerges from Pereopod IV and projects towards Sternite XIV, and a triangular emargination is present (Sternite XIII). The semi-open petasma with cincinnulli connecting the pleopods in mature males has sclerotized dorsolateral (DL), ventrolateral (VL) and ventromedian (VM) lobules. The VM tooth-like projections fit the VL tooth-like projections. The DL and VL lobules end in a leaf-like, less sclerotized projection and are separated by a gap. The VL lobule has a patch of spinules and a highly sclerotized costa. An elongated appendix masculina (AM) with concave margin forms a distal subtriangular lobe and has a DL margin with an aggregation of setae. The AM fits inside the appendix interna (AI) and is shorter and narrower than the AM. The spermatophore has superior (wing) and inferior (germinate body) sections. The GB ends in a triangular hook-like structure. The thelycum resembles that of *S. geijskesi*, whereas the petasma, AM and AI are similar to those of Atlantic solenocerids. The complex spermatophore resembles that of other penaeoid shrimp. According to evolutionary trends, *S. agassizii* can be considered as a less derived species within the Dendrobranchiata.

KEY WORDS: Thelycum · Petasma · Appendix masculina · Appendix interna · Spermatophore

INTRODUCTION

Many penaeoid shrimp are important fishery resources in tropical and subtropical countries (FAO 2001, 2012, Salas et al. 2011). Although penaeoid catch volumes are considerably lower than those of many other shrimp species, these decapods are highly traded due to their high market value, and are mainly exported to countries with affluent economies (FAO 2001). Diminishing catches in coastal waters have motivated the fishing industry to explore offshore and deepwater resources (Morato et al. 2006), a trend that has also been observed in Latin American shrimp fisheries (Arana et al. 2009, Wehrtmann et al. 2012). In this region, fishing activities focus on benthic and demersal invertebrates, and almost half of these resources are threatened by overexploitation (Arana et al. 2009).

One of these exploited deepwater shrimp species is the solenocerid shrimp *Solenocera agassizii* Faxon, 1893 (kolibri shrimp; local name 'camarón fidel'), which is distributed along the Pacific coast

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from Nicaragua to Peru (Holthuis 1980, Hendrickx 1995). The species is commercially fished in Costa Rica (Wehrtmann & Nielsen-Muñoz 2009, Wehrtmann et al. 2012) and Colombia (Puentes et al. 2007, INVEMAR 2009, Rodríguez et al. 2012). In Costa Rica, historical data from for *S. agassizii* are available from 1986 to 2007 (INCOPESCA, www.incopesca.go.cr/publicaciones/estadisticas.html). These data show that the highest annual landings by far were observed in 1986 (2.6×10^6 kg) (Wehrtmann & Nielsen-Muñoz 2009). Thereafter, annual landings remained under 0.5×10^6 kg, except in the years 1994, 1995, 1996 and 2005, when landings were higher but did not surpass 1.0×10^6 kg per year. *Solenocera agassizii* represents roughly 30% of all shrimp catches in the Costa Rican Pacific (Wehrtmann & Nielsen-Muñoz 2009), and despite its economic importance, information on its biology is scarce.

To the best of our knowledge, the only existing publications on *S. agassizii* describe the gonad development in females (Villalobos-Rojas & Wehrtmann 2011) and the reproductive aggregations of the species along the Pacific coast of Colombia (Rodríguez et al. 2012). Reproductive studies focusing on commercially exploited solenocerid shrimp have mainly described primary sexual characters (gonad development; e.g. Baelde 1992, Ohtomi et al. 1998, Dineshbabu & Manissery 2008, Villalobos-Rojas & Wehrtmann 2011). Conversely, descriptions of secondary sexual characters have mostly been used for taxonomy purposes in solenocerid shrimp, and are valuable for identification of species in this taxon (Pérez-Farfante & Bullis 1973, Pérez-Farfante 1977, Pérez-Farfante & Boris 1982, Pérez-Farfante & Kensley 1985, Pérez-Farfante 1988).

The petasma and the appendix masculina (AM) represent the principal sexual secondary characteristics in male penaeoid shrimps (George & Rao 1968, Dall et al. 1990, Demestre & Fortuno 1992, Bauer 1996). The petasma is a morphological modification and union of the endopods that are present on the first pair of pleopods (George & Rao 1968, Pérez-Farfante & Kensley 1997), while the AM is located on the second pair of pleopods and represents a modification of the endopod (Pérez-Farfante & Kensley 1997). The function of the petasma has been debated (Bauer 1986), and the proposed hypothesis suggests that it serves as either a sperm injection device supported by the AM or as a mechanism of attachment to and/or stimulation of the female during insemination and copulation (Bauer & Lin 1993). In contrast, the thelycum is the structure responsible for the reception and storage of sperm (usually as spermatophores), which is transferred by the male during copulation (Eldred 1958, Pérez-Farfante & Kensley 1997). This structure is located on the ventral surface of the cephalothorax and consists of modifications of the 2–3 posterior thoracic sternites (XII–XIV) (Dall et al. 1990, Pérez-Farfante & Kensley 1997). According to Pérez-Farfante & Kensley (1997), the thelycum may be classified as closed ('seminal receptacles are present') or open ('seminal receptacles are absent'); however, Pérez-Farfante & Bullis (1973) described the high morphological variability of these structures. Several authors clearly differentiate between the term 'seminal receptacle' and 'spermathecae' (Guinot & Quenette 2005, McLay & López-Greco 2011). In contrast to the spermatheca, the seminal receptacle is a structure in which fertilization can occur, and according to Guinot & Quenette (2005) is absent in most Decapoda Reptantia.

Morphological maturity of the thelycum and the petasma is essential for the successful transfer and deposition of spermatophores from the male to the female in these shrimp (Tuma 1967, Demestre & Fortuno 1992, Quinitio et al. 1993). During the development of penaeoid shrimp, the thelycum shows an increase in the number of setae and the size of its structures (Pérez-Farfante & Bullis 1973). In male penaeoid shrimp, size, degree of unification and sclerotization of the endopods of the first pleopods increase during development (Boschi & Angeluscu 1962). These morphological features are used to differentiate reproductive from immature individuals of penaeoid shrimp (Pérez-Farfante 1971, Demestre & Fortuno 1992).

Although secondary sexual characters have been described for several species of penaeoid shrimp (Boschi & Angeluscu 1962, Pérez-Farfante & Bullis 1973, Demestre & Fortuno 1992, Quinitio et al. 1993), their spermatophores have seldom been described (Heldt 1931, Burkenroad 1934, Pérez-Farfante 1975). Especially in species with an open thelycum, the spermatophore is rarely observed because it detaches easily and is lost during sampling. The description of the spermatophore can help clarify which substructures of the thelycum are important for the successful transfer/adherence of the spermatophore from the male to the female. Therefore, the objective of this study was to provide a detailed description of the secondary sexual characteristics of males and females of *S. agassizii* and compare them with other *Solenocera* species. We also provide the first description of both the spermatophore of this species and the substructures of the thelycum associated with its retention on the female.

MATERIALS AND METHODS

Samples were obtained by commercial shrimp trawlers along the Pacific continental shelf of Costa Rica (see Wehrtmann & Nielsen-Muñoz 2009, Wehrtmann et al. 2012). Specimens of *Solenocera agassizii* were collected between January 2007 and March 2010 at depths ranging from 150 to 300 m. Samples obtained in the field were transported on ice (0°C) to the laboratory at the Biology Department of the University of Costa Rica in San José, where they were stored in a freezer. In the laboratory, shrimp were sexed by the presence (males) or absence (females) of a petasma (Harán et al. 2004), and special attention was paid to females, i.e. in the search for attached spermatophores. Spermatophores attached to the female's thelycum were preserved in 75% ethyl alcohol for later description. Descriptions of the thelycum and spermatophore were made with the aid of photographs (Canon SX40 HS) and a stereomicroscope (Leica MS5; 10× magnification). For the description of the petasma, AM and appendix interna (AI), we used the same equipment, in addition to a microscope (Leica L2; 40× magnification). For each analyzed specimen, we measured: (1) carapace length (CL; from inner edge of eye orbit to outer edge of the carapace), (2) abdominal length (AL; stretched out straight, from the first abdominal segment to the tip of the telson) and (3) total length (TL = CL + AL).

To standardize vocabulary and to allow future comparisons, we followed the terminology used by Pérez-Farfante & Bullis (1973), Bauer & Cash (1991), Pérez-Farfante (1975) and Pérez-Farfante & Kensley (1997) for all descriptions.

RESULTS

A total of 78 samples of *Solenocera agassizii* were obtained from the monthly monitoring program, with a total of 11 420 specimens (5985 females and 5435 males). The females measured between 17.2 and 51.9 mm CL (mean ± SD = 31.0 ± 5.5 mm CL), whereas males ranged from 17.0 to 45.0 mm CL (29.4 ± 3.7 mm CL). A total of 22 spermatophores were found attached to female *S. agassizii* that varied from 28.5 to 46.2 mm CL (38.5 ± 4.3 mm CL) in size.

Thelycum

The thelycum of *S. agassizii* is open and has no seminal receptacles. It is located between Pereopods III and V (Sternites XIII and XIV of the cephalothorax) (Fig. 1). Sternite XIV has a pair of parallel setose projections, elongated longitudinally toward the posteroventral part of the sternite. In larger females (>30 mm CL), these projections end distally in a curve (Fig. 1A,B), extend toward the posterior part of the sternite and surpass Pereopod V; in smaller females (<30 mm CL), these structures are pointed (Fig. 1C). The posterior part of Sternite XIII has a

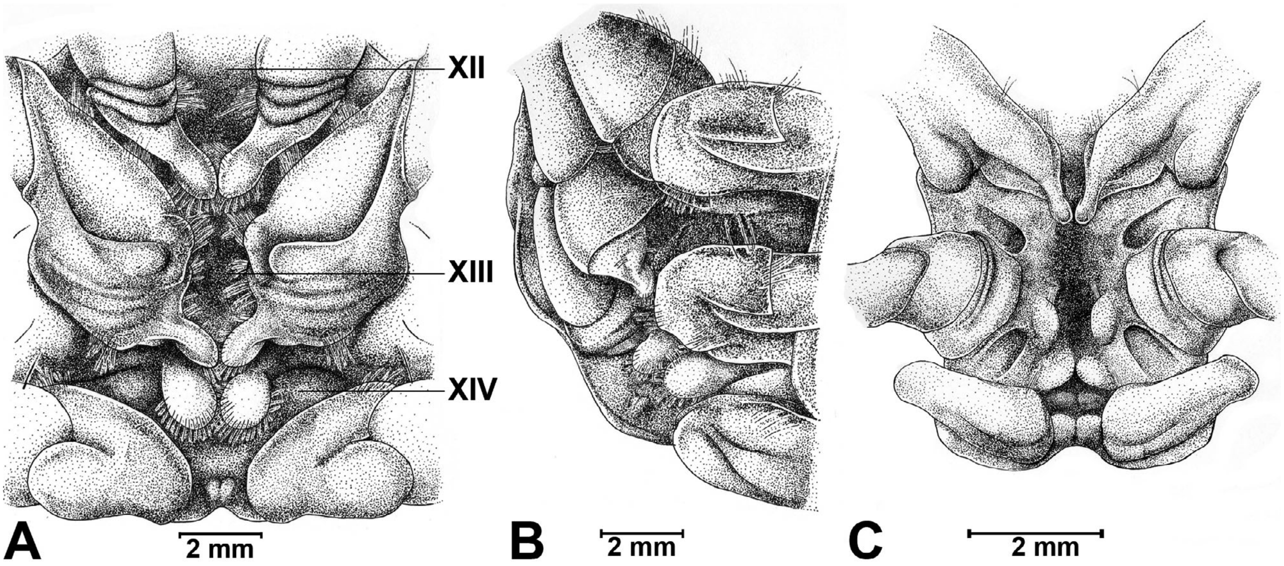

Fig. 1. Thelycum of *Solenocera agassizii*. (A) Ventral and (B) lateral view of a large female (>35.0 mm carapace length). (C) Ventral view of a smaller female (<30.0 mm LC). Sternites XII, XIII and XIV are shown in (A)

transverse setose projection, which has the shape of a disk that emerges from Pereopod IV and projects towards the anterior part of Sternite XIV. There is a triangular emargination in the anterior part of Sternite XIII. As a general rule, smaller females have fewer setae in the entire structure than larger females.

Petasma

The endopod present on the first pleopods of male *S. agassizii* has a hemipetasma; when hemipetasma are joined, they form a semi-open petasma, in which the lateral lobes are flexible but folded (Fig. 2). The pleopods are connected by cincinnulli that project from the dorsomedial margins of the endopods. The cincinnulli are disposed in rows and have a form of double hooks. In smaller shrimp, the hemipetasma can be partially (or not) (Fig. 2C) connected by the cincinnulli that are less developed (smaller and not completely formed). In mature specimens, the lateral lobes (dorsolateral and ventrolateral) and ventromedian lobules are heavily sclerotized, considerably surpassing the dorsomedian lobule, which bears the cincinnulli. The ventromedian lobule ends in 2 small tooth-like projections that fit the distal tooth-like projections of the ventrolateral lobule. A patch of small spinules is located between the ventromedian lobule and tooth-like projections. The dorso- and ventrolateral lobules are separated distally by a narrow gap. The dorso- and ventrolateral lobules end distally in a leaf-like, less sclerotized projection; a small patch of short spinules is located below the ventrolateral lobule. The ventrolateral lobule has a highly sclerotized ventral-marginal costa, which has tooth-like projections and a long plumose seta proximal to the costa.

Appendix masculina and appendix interna

The AM of *S. agassizii* shows longitudinal asymmetry (Fig. 3). It is elongated, with a strongly concave mesial margin, and its distal part forms a subtriangular lobe. The margin that delimits the dorsolateral surface is armed with a dense aggregation of setae. The AM fits inside the AI (Fig. 3).The AI is slightly shorter and narrower than the AM, and bears distally marginal setae of different sizes that together form a triangular shape.

Spermatophore

The compound spermatophore of *S. agassizii* consists of 2 subcylindrical, symmetrically opposed portions (Fig. 4). Each portion has 2 distinguishable sections: superior and inferior (germinate body). The superior section resembles a thin and translucent wing that is positioned perpendicularly to the inferior section. This winged structure comprises approximately one-fourth of the entire structure in length, and is twice as wide as the inferior section. The side of the wing that is not in contact with the thelycum has a

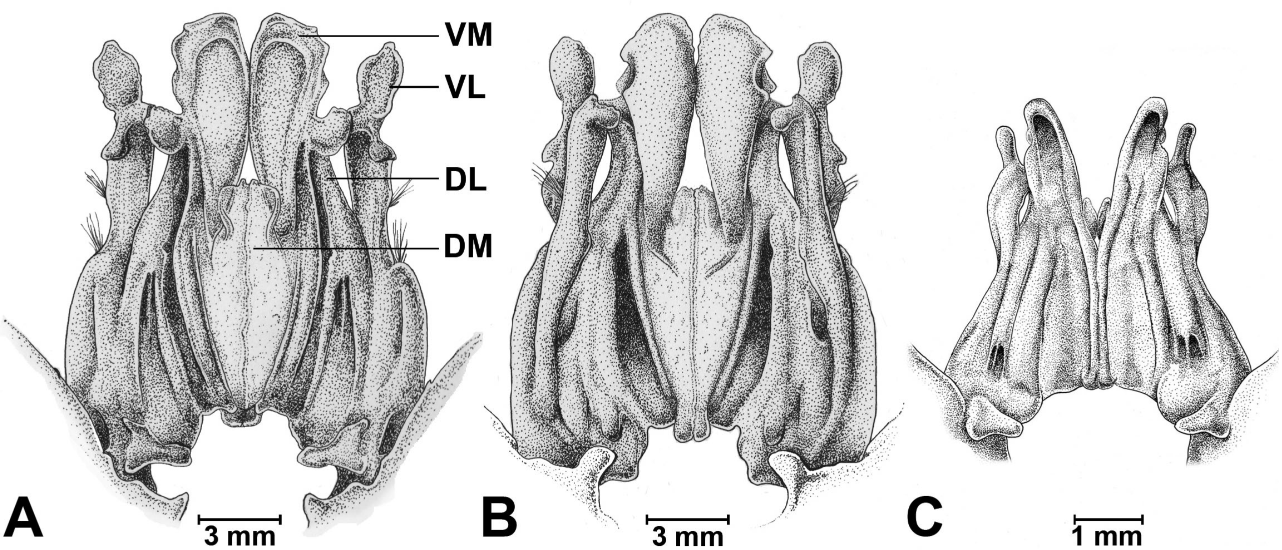

Fig. 2. Petasma of *Solenocera agassizii*. (A) Dorsal view (40.7 mm carapace length, CL). (B) Ventral view (40.7 mm CL). (C) Ventral view of a smaller male (<23.0 mm CL). VM: ventromedial lobule; VL: ventrolateral lobule; DL: dorsolateral lobule; DM: dorsomedial lobule

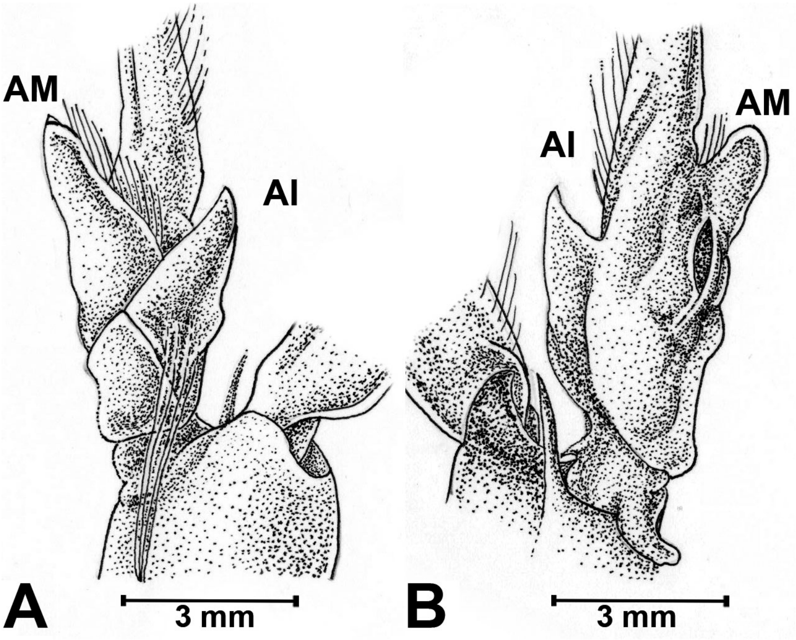

Fig. 3. Appendix masculina (AM) and appendix interna (AI) on the right second pleopod of a male of *Solenocera agassizii*. (A) Ventral view. (B) Dorsal view

small lobule, located in the junction between the wing and the inferior section of the spermatophore. The inferior portion of the spermatophore consists of 2 parallel structures with small lobules in their margins (described as 'flanges' by Pérez-Farfante & Boris 1982, Pérez-Farfante 1975); the spermatophore ends distally in a triangular hook-like structure (Fig. 4B), which can be observed in lateral view (Fig. 4C).

Regarding adhesion to the thelycum, the wing-like structure is in contact with Pereopod III, covering the coxae of these appendices almost completely. The inferior section is directed towards Pereopod V, and its distal hook-like part fits into a pair of projections on Sternum XIV (Fig. 4A).

DISCUSSION

Thelycum

Information about the morphology of secondary sexual characters of solenocerid shrimp is limited to a few species, and the thelycum of *Solenocera agassizii* is similar to that described for other American species from the genus *Solenocera* (Pérez-Farfante & Bullis 1973, Pérez-Farfante 1988, Hendrickx 1995). Unlike the descriptions for the species of *Solenocera* from Australia (Pérez-Farfante & Grey 1980) and India (Dineshbabu & Manissery 2008), the presence of paired protuberances on the anterior part of Sternite XIII in the thelyca is always mentioned for the following American species: *Solenocera acuminata* Pérez-Farfante & Bullis, 1973 (Pérez-Farfante & Bullis 1973), *S. atlantidis* Burkenroad, 1938 (Pérez-Farfante & Bullis 1973), *S. florea* Burkenroad, 1938

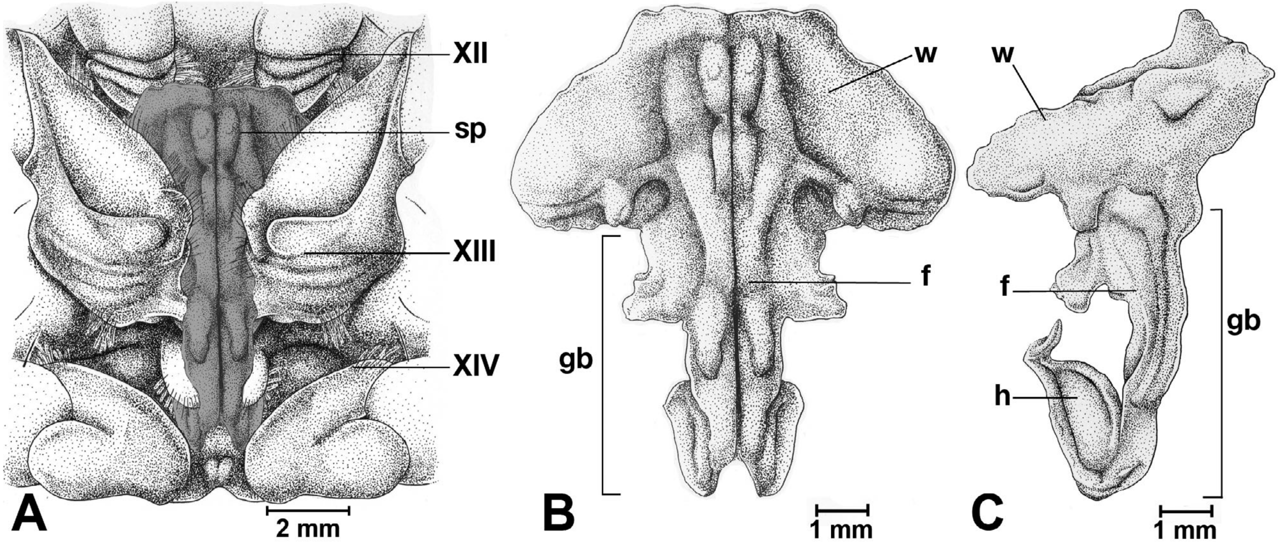

Fig. 4. Spermatophore of *Solenocera agassizii*. (A) Attached to a female. (B) Ventral view. (C) Lateral view. Sternites XII, XIII, XIV are shown in (A) sp: spermatophore; w: wing (superior section); f: flange; h: hook; gb: germinate body (inferior section)

(Pérez-Farfante 1988), *S. geijskesi* Holthuis, 1959 (Pérez-Farfante & Bullis 1973), *S. mutator* Burkenroad, 1938 (Pérez-Farfante 1988) and *S. vioscai* Burkenroad, 1934 (Pérez-Farfante & Bullis 1973). However, these protuberances can vary greatly in form and size (setose, long, subconical, flattened dorsoventrally, or roughly subreniform), and their position varies from convergent to divergent or often meeting distomesially (Pérez-Farfante & Bullis 1973). As described also for *S. vioscai* (Pérez-Farfante & Bullis 1973), these protuberances can meet or extend in parallel and contiguously in larger females of *S. agassizii*. For the structures on Sternite XIII in solenocerid shrimp, a variety of forms have been described, from beak-like, horn-like and tooth-like projections to median setose ridges and emarginations (Pérez-Farfante & Bullis 1973) (Table 1).

The thelycum of *S. agassizii* resembles those described for western Atlantic solenocerids (*S. acuminata*, *S. geijskesi*, *S. necopina* and *S. vioscai*; see Pérez-Farfante & Bullis 1973): all of these species show the presence of similar protuberances on Sternite XIV, the emargination on Sternite XIII, and the presence of setae throughout the thelycum (Pérez-Farfante & Bullis 1973). However, it should be noted that in the case of *S. agassizii*, the protuberances of Sternite XIV always terminate in a rounded end and are not pointed as in *S. acuminata*, *S. necopina* and *S. vioscai*; this structure of *S. agassizii* is most similar to the one described for *S. geijskesi* (see Pérez-Farfante & Bullis 1973). Presumably, the function of the described protuberances, emarginations and setae on the sternites is related to the adhesion and retention of the spermatophore in an open-type thelycum (King 1948, Boschi & Angeluscu 1962, Bauer 1986). Pérez-Farfante (1975) described for *Litopenaeus* spp. that variations on the coxal plates of Pereopods III, IV and V have a role in spermatophore retention. In *S. agassizii*, 3 main substructures are suggested as being responsible for the retention of the spermatophore on the thelycum: (1) the pair of projections on Sternite XIV that fit in the spermatophore's hook, (2) the transverse setose disk-shaped projection that emerges from Pereopod IV and holds the spermatophore in the central part, and (3) the setae present on Pereopod III that attach to the spermatophore's wing.

Petasma, appendix masculina and appendix interna

The morphology of male secondary sexual characters of *S. agassizii* concurs with that described for other solenocerid species: presence of a semi-open petasma on the first pleopods, and AM and AI on the second pleopods (Pérez-Farfante 1977, Pérez-Farfante & Kensley 1985) (Table 1). The developed petasma of *S. agassizii* coincides largely with that described for *S. acuminata*, *S. necopina* and *S. vioscai* (see Pérez-Farfante & Bullis 1973). Although the petasma of solenocerid shrimp initially develops as small rudimentary bud-like projections on the first pleopods (Boschi & Angeluscu 1962, Tuma 1967, Motoh & Buri 1980), the shape of the different lobes and projections constituting the organ in the developing and adult shrimp varies considerably among species (George & Rao 1968). As the endopods increase in size during ontogeny, the cincinnulli develop into double hooks and increase in number (Boschi & Angeluscu 1962, George & Rao 1968, Motoh & Buri 1980), allowing the junction of endopods in larger specimens (Eldred 1958, Sobrino & García 2007, Dineshbabu & Manissery 2008). In addition, structure calcification, increasing number of folds, and the development of distal structures have also been described as part of the petasma's development in other penaeid species (Tuma 1967, George & Rao 1968).

The function of the petasma and AM remains unclear. There are many suggested functions, mostly associated with the process of copulation (King 1948, Boschi & Angelescu 1962, Bauer 1994, Tavares & Martin 2010). Bauer (1996) mentioned that in *Sicyonia dorsalis* the petasma may temporarily connect male and female genitalia during copulation and/or adjust the position of the male genital papilla relative to the aperture of a spermatheca. Other possible functions suggested by Bauer (1986) were that the petasma (1) serves to stimulate females, (2) acts as a sensory device for males, and (3) is an indicator of male fitness, whereby females might be testing males during copulation through the detection of small alterations in the petasma. Several studies on caridean shrimp (Bauer 1996, Zhang & Lin 2004, Martínez & Dupré 2010a,b) suggested the first pair of pleopods as the responsible structure for receiving the spermatophores, while the AM supports the transfer of the spermatophores from the first pair to the sternite of the female. However, an experimental approach with the ablation of structures (Bauer 1996, Zhang & Lin 2004, Martínez & Dupré 2010a) or direct observation of copulation (Eldred 1958, Bauer 1991, 1992) is necessary to clarify the role of the petasma and AM of *S. agassizii*.

Table 1. Comparison of the principal characteristics of the secondary sexual characters described for 12 *Solenocera* species. AM: appendix masculina; AI: appendix interna; nd: not described

Species	Thelycum	Petasma	AM and AI	Reference
Solenocera agassizii Faxon, 1893	Sternite XIV with pair of parallel setose projections, elongated longitudinally in a posteroventral direction. Posterior part of Sternite XIII with transverse and setose disk-like projection that emerges from 4th pereiopod and projects to the anterior part of Sternite XIV. Triangular emargination in Sternite XIII.	Ventromedian lobule tooth-projections; dorsolateral and ventrolateral lobules end distally in leaf-like projections. All with marginal teeth and/or spinules. Plumose setae on the costae.	Elongate, mesial margin concave, distal part subtriangular, dorsolateral surface with setae. AI shorter and narrower than AM; distally marginal setae.	Present study
Solenocera acuminata Pérez Farfante & Bullis, 1973	Paired roughly conical setose protuberances on Sternite XIV; Sternite XIII with high sharp median ridge produced into a beak-like projection overhanging and anterolaterally produced into horn-like projections.	Ventromedian lobule spatulated distally, dorsolateral lobule with campanulated terminal process, ventrolateral lobule distally produced into a tongue-like lamella, all with marginal teeth and/or spinules. Plumose setae on the costae.	Elongate, mesial margin concave, distal part subtriangular, dorsolateral surface with setae. AI shorter and narrower than AM; distally marginal setae.	Pérez-Farfante & Bullis (1973)
Solenocera africana Stebbing, 1917	Subrectangular. Anterior part with arrow plate between 4th pereiopods; plates concave with central sulcus that divides and forms 2 lobes; anterior margin hidden by coxal processes of 4th pereiopods. Posterior part with concave plate between 5th pereiopods; plate with central tubercle; long setae on the anterior part; posterior thoracic ridge broadly concave medially.	Dorsomedian lobules united along more than half its length; distomedian projection broad; distal margin rounded, edge curled dorsal; distomedian tooth-like angle with setae. Ventromedian lobules shorter than dorsomedian; form mediolateral ridge that meets proximally. Elongate subtriangular dorsolateral lobule subequal to ventromedian lobule; dorsolateral lobule with distoproximal deep groove and median projection. Ventrolateral lobule narrow with subtriangular head tip; tooth-like distomedian angle.	AM anteromedian face convex, anterolateral face flat to concave; distal and outer margins with setae; posteromedian face with center tooth-like ridge. AI: thin, shorter than AM, club-shaped; half fitting into posterolateral furrow of AM; distal margin with setae.	de Freitas (1985)
Solenocera alfonso Pérez Farfante, 1981	Subquadrangular depression on Sternite XIV, also a pair of slender fusiform protuberances; Sternite XIII with high shelf divided by median slit, with anterolateral tubercles.	Ventromedian lobule with spinules, dorsolateral lobule lateral margin distally concave and with well-developed spinules with spines.	Broadening from base, dorsolaterally curved, long setae patch. AI narrower than AM; distally marginal setae.	Pérez-Farfante (1981)
Solenocera algoensis Barnard, 1946	Subrectangular, narrow concave plate between 4th pereiopods; posterior plate margin with ventrally saddle-like elevation, a midline groove, a concave process on each side and setae on the posterolateral margin. Concave plate between 5th pereiopods; sulcus with tubercles on each side, a tooth-like process on the anterolateral margin of posterior sternal process. The posterior thoracic ridge projects posterolaterally into 2 divergent horn-like structures.	Dorsomedian lobule united along less than half its length; distomedian projection broad, longer than lateral lobes. Ventromedian lobules shorter than dorsomedian lobules; forms mediolateral ridge, with papilla-like lobe with long setae. Ventrolateral club-like distal head; prominent longitudinal ridge along ventral costae; with transverse ridge on club-like distal head; ventrolateral lobule with process projecting under proximal limit of dorsolateral lobule.	Setae on mesial margin; lateral margin curved with setae; mesially, below central row of setae, is ventrally directed wall that bears short setae distally. AI: shorter than AM; rounded with setae.	de Freitas (1985)
Solenocera atlantidis Burkenroad, 1939	Paired subconical protuberances setose on Sternite XIV; Sternite XIII with convex elevation from the 4th pereiopod coxa, deeply emarginate and forming anterolaterally into horn-like projections.	Ventromedian lobule trapezoidal, dorsolateral lobule with mushroom-like terminal process both with marginal spines, ventrolateral lobule distal part subtriangular ending with a ridge. Plumose setae on the costae.	nd	Pérez-Farfante & Bullis (1973)
Solenocera australiana Pérez Farfante & Grey, 1980	Subquadrangular depression on Sternite XIV. Two pairs of setose protuberances anterior to ridge. Sternite XIII with vertical shelf bearing pair of strong setose, broad thickenings separated by median slit. Sternite XIII with setosetransverse elevation.	Ventromedian lobule and dorsolateral lanceolate lobule with spinules; ventral costae recurved bearing short spines.	AM longitudinal, dorsal ridge curved mesially; concave lateral margin with a row of long setae; and apical margin studded with row of long ones. AI strongly concave laterally, with minute spinules along distomesial margin.	Pérez Farfante & Grey (1980)

Table 1. (continued)

Species	Thelycum	Petasma	AM and AI	Reference
Solenocera choprai Nataraj, 1945	Rounded, pair of plate-like structures in 3rd pair of pereiopods. A median sternal prominence between 3rd and 4th pereiopod. Narrow vertical plates between the coxa of the 4th pereopods, with sternum as a pit. Front of pit with pair of small sternal prominences. Sternum of 5th pereiopod is broad vertical trapezoid plate.[a]	Dorsolateral, dorsomedian and distolateral lobules have spinules.[a]	AM elongate and subtriangular, ventrally concave, dorsally convex; distal margin with row of setae; circle setae surrounds flat patch on lateral margin. AI: subequal in length to AM; half fitting into concave face of AM; elongate and spoon-shaped with small oval concave mesial face and convex lateral face; distomesial margin with row of small teeth.[b]	[a]Dineshbabu & Manissery (2008), [b]de Freitas (1985)
Solenocera geijskesi Holthuis, 1959	Paired subconical setose protuberances on Sternite XIV with minute apical tubercle; Sternite XIII with plate-like structure from the 4th pereiopod produced anterolaterally into horn-like projections.	Ventromedian lobule distally broadened, dorsolateral lobule with bell-shaped terminal process, ventrolateral lobule distally narrow, all with marginal spines. Plumose setae on the costae.	nd	Pérez-Farfante & Bullis (1973)
Solenocera necopina Burkenroad, 1939	Paired subconical setose protuberances on Sternite XIV; Sternite XIII with high sharp and setose tooth-like projection, median emargination and produced anterolaterally into horn-like projections.	Ventromedian lobule trapezoidal, dorsolateral lobule subtriangular process, ventrolateral lobule with subcircular lamella all with marginal spinules. Plumose setae ventrolateral and dorsolateral lobules.	Identical to those on *S. acuminata.*	Pérez-Farfante & Bullis (1973)
Solenocera vioscai Burkenroad, 1934	Paired subconical setose protuberances on Sternite XIV; Sternite XIII with high sharp and setose beak-like projection, median emargination overhanging and produced anterolaterally into horn-like projections.	Similar to *S. acuminata.*	Similar to *S. acuminata.*	Pérez-Farfante & Bullis (1973)
Solenocera waltairensis George & Muthu, 1970	Quadrangular area with a median bald prominence in front of the two spine-covered prominences between the 5th legs; 2 small spiny papillae in front of the quadrangular area.	Similar to *S. pectinata*, but smaller spines on the lateral margins, the median and lateral lobe spines are on the distolateral margin. Process 'a' curves distally and ends in a single, lateral, hook-like spine on the median, inner side. Process 'b' with conspicuous teeth.	AI basal piece with short, blunt and finger-like projection that lacks long wavy hair near the base. The triangular, folded outer scale of distal piece longer than the flat, rectangular inner scale.	George & Muthu (1968)

Spermatophore

Descriptions of spermatophores for open-thelycum species are rare, mainly due to the difficulty of finding them attached to females (Weymouth et al. 1933, King 1948). After analyzing 5435 female *S. agassizii* and finding only 22 spermatophores, we assume that the spermatophore remains attached to the female for only a short time span. Potter et al. (1986) described the reproduction of *Metapenaeus dalli* Racek, 1957 and suggested that there would be considerable selection pressure favoring spermatophore deposition close to the moment of spawning, because spermatophore deposition can theoretically occur at any time in an open-thelycum species, but the spermatophor can easily be dislodged from the thelycum.

The descriptions of the spermatophores of other open-thelycum species such as *Litopenaeus setiferus* (see Burkenroad 1934, King 1948, Bauer & Cash 1991), *Metapenaeus mariae* (see Pérez-Farfante & Boris 1982), *Litopenaeus* spp. (see Pérez-Farfante 1975) and *Penaeus kerathurus* (see Heldt 1931) show structures similar to those found attached to female *S. agassizii*. Pérez-Farfante (1975) analyzed 5 species of *Litopenaeus* and described their spermatophores as compound structures that consist of a glutinous mass and a geminate body that can bear wings, lateral flanges, blades and/or flaps in variable dispositions. The wings have been described to be securely anchored to a groove on the sternal surface between the third and fourth pereopods of *L. setiferus* (King 1948, Pérez-Farfante 1975, Pérez-Farfante & Boris 1982, Chow et al. 1991), which coincides with our observations for *S. agassizii*. The glutinous mass is composed of adhesive and glutinous secretions (Pérez-Farfante 1975, Talbot & Beach 1989, Bauer & Cash 1991, Tavares & Martin 2010). The adhesive secretion appears to be deposited onto the spermatophore when it is ejaculated, and seems to serve to attach the spermatophore to the female's open thelycum (Talbot & Beach 1989, Bauer & Cash 1991). In contrast, the glutinous secretion (which also has adhesive properties; Talbot & Beach 1989) seems to swell in contact with water, which may assist in the accommodation of the spermatophore in the emarginations and ridges of the thelycum (Bauer & Cash 1991).

Pérez-Farfante (1975) mentioned 2 possible types of sperm exposure (related to spawning) based on observations made of several female *Litopenaeus* spp.: (1) the compound spermatophore splits, the geminate body falls or is torn off, and the sperm is exposed to the surrounding water (e.g. *L. stylirostris*, *L. schmitti* and *L. setiferus*); alternatively, (2) the compound spermatophore is still intact and attached to the female during sperm exposure, as the sperm mass protrudes anteriorly and extends onto Sternite XII. Because only complete spermatophores were found on *S. agassizii* females, it is concluded that in this species the compound spermatophore remains intact during exposure. However, a more thorough description of the male's ejaculatory duct is necessary to better understand the role and structure of the different spermatophore sections (for example, for *L. setiferus* see Bauer & Cash 1991, Chow et al. 1991).

According to Bauer (1986, 1991), there are 2 trends in the evolution of Dendrobranchiata: (1) the thelycum changes from open to closed with a median spermatheca, and more evolved species have a closed thelycum with paired spermatheca; or (2) the spermatophore is reduced from a complex, preformed external spermatophore to a simpler spermatophoric mass. Considering these evolutionary trends, *S. agassizii*, with an open thelycum and a complex spermatophore, can be considered as a less derived species within the Dendrobranchiata. This coincides with the general assumption that within solenocerids, the genus *Solenocera* approaches some morphological aspects of penaeids (Burkenroad 1983, Tavares & Martin 2010).

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