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USAGE OF THE TERMS *THELYCUM* AND *SPERMATHECA* IN THE REPRODUCTIVE MORPHOLOGY OF THE DECAPODA, WITH SPECIAL REFERENCE TO THE PENAEOIDEA

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ABSTRACT

A recent proposal (Tavares and Secrétan, 1993) for restricted usage of the terms *thelycum* and *spermatheca* in the Decapoda is discussed. Although the term *thelycum* has been most commonly utilized to signify the female genital area in penaeoid shrimps, the proposal does not address or include some of the pertinent evidence from the extensive literature on penaeoid systematics and reproductive morphology. The suggested limited definition of *thelycum* is not considered justifiable given the vast diversity in spermatophore structure, attachment, and storage in penaeoids or other decapods. The view that the *thelycum* is formed from only one thoracic sternite is hardly tenable, because the literature on penaeoid shrimps clearly shows that two and sometimes three thoracic sternites are involved in spermatophore attachment or storage, the main criterion of the proposal for function of a *thelycum*. It is noted herein that the *thelycum* of penaeoid females may serve (a) for either temporary attachment or prolonged storage of spermatophores or (b) as an area of genital contact with the male, which leads to the apertures of paired internalized seminal receptacles or spermathecae; sperm-free male accessory substances may or may not be deposited on that area. A rigid, limited application of the term *spermatheca* to only one variation of sperm or spermatophore storage structure (that derived from intersegmental phragmata) is hardly acceptable given the generalized meaning of the term (=sperm storage) and the considerable variation in such structures in the Decapoda.

Tavares and Secrétan (1993) recently attempted to unambiguously define the terms *thelycum* and *spermatheca* in the decapod Crustacea. However, their treatment of the problem has overlooked some of the literature on reproductive morphology and systematics of the penaeoid shrimps, a group with which the term *thelycum* is most closely associated and used (e.g., Andrews, 1911; Burkenroad, 1934a, b, 1936; Heldt, 1938; Kubo, 1949; Pérez Farfante, 1969, 1971a, b, 1975, 1977, 1980, 1982, 1985, 1988). In this paper, restricted usage of these terms proposed by Tavares and Secrétan (1993) is discussed, and rejection of their proposition is suggested for several reasons given below.

Historical Overview

Thelycum has been traditionally and most frequently used by systematists and workers in decapod reproductive morphology as a term for the genital area of penaeoid females, the area of the posteroventral cephalothorax involved with spermatophore attachment and/or storage. Bate (1888: v) proposed the term thelycum, apparently derived from the Greek word for "woman-like" or "like a female," and he defined "thelycum" as a "Structure on the ventral surface of the pereion peculiar to females" in the "Crustacea Macrura." In reference to reproductive morphology of the Decapoda, Calman (1909: 290) stated "In addition to the internal receptacula seminis mentioned above, an external organ having apparently the same function is found in certain Decapods. It is best known in the Penaeidae, where it has been named the *thelycum* and affords characters of systematic importance." In an early review of sperm transfer in decapods, Andrews (1911: 419) referred to "A peculiar receptacle known as the 'thelycum' is found in certain prawns, the Penaeidae." Kubo (1949: 110), in his classic work on the morphology and systematics of Japanese penaeids, more thoroughly explained that "The thelycum consists of a series of prominences, depressions or grooves, plates and sacs raised from sternites of the sixth to eighth thoracic segments." Due to the remarkable morphological diversity of the female genital area of penaeoids, reflecting the concomitant diversity of the form of penaeoid spermatophores, with both external attachment and internalized storage, the limits and definitions of structures and processes constituting a thelycum have been quite variable.

Bauer (1986), in a short comparative review on reproductive morphology of decapods, and in a review of penaeoid reproductive morphology (Bauer, 1991), dealt with the variable application of *thelycum* (and other terms) by using a working definition, i.e., one made for the purposes of those papers. Bauer (1986: 314), in order to compare female genitalia among different decapod taxa, stated: "I use *thelycum* **here** to describe any *external* modifications of the female posterior thoracic sternites or coxae related to sperm transfer and storage. Thelyca may thus serve for the attachment of an external spermatophore or may lead into or surround openings to spermathecae when the latter are present." (Boldface added).

Since Tavares and Secrétan (1993) also proposed restricted usage of the term *spermatheca*, some introductory remarks about that term are appropriate as well. The etymology of the word *spermatheca* (Greek *sperma* = seed, semen; *theke* = box, case, cup) indicates its common usage in decapod crustaceans and other arthropods, i.e., an *enclosed space* (of various anatomical structure and position) where sperm and/or spermatophores are deposited and stored. In making comparisons among decapod females, Bauer (1986) considered any invagination of the exoskeleton in which sperm-bearing material is stored after copulation as a spermatheca (synonymous with seminal receptacle but not thelycum). Bauer (1991: 192–193), in a review of reproductive morphology of penaeoid shrimps, modified the use of *seminal receptacle* (=sperm receptacle = spermatheca) to "any enclosed space" in which sperm or spermatophores are stored.

Proposed Usage of *Thelycum* and *Spermatheca*

Tavares and Secrétan (1993) have criticized past usage of the terms *thelycum* and *spermatheca* and have proposed new, restricted definitions, based on specific morphological criteria. Both *thelycum* and *spermatheca* are considered separate categories of *seminal receptacles*, designated by Tavares and Secrétan (1993: 133) as spermatophore storage structures in which "the place of storage of the spermatophores is not connected to the ovary." The distinction between the two types, according to Tavares and Secrétan (1993: 134), is that "*Thelycum* is a structure derived from sternal modifications **always of a single segment.** It can be on the sixth, seventh or eighth thoracic sternite and can be either an invagination or an evagination. *Spermatheca* is a structure always derived from two adjacent segments, that is, a split between the plates of the intersegmental phragmae. One plate of this phragma is derived from sternite 8 and the other from sternite 7. The spermatheca always involves these two segments except, as far as we know, in the penaeioid genera *Gennadas* and *Bentheogennema* in which the spermatheca is derived from the intersegmental phragmae 7/6. The spermatheca is always paired in the peditreme crabs and unpaired in the 'macrurans'." (Boldface added).

Discussion of and Arguments against a Restricted Application of the Term *Thelycum*

The restricted definition of the term *thelycum* proposed by Tavares and Secrétan (1993) is not supported by arguments or evidence given in their paper. According to these workers, the *thelycum* is derived from "sternal modifications always of a *single segment.*" (Italics added). However, as documented by an extensive literature on penaeoid reproductive morphology (e.g., Calman, 1909; Andrews, 1911; Burkenroad, 1934a, b, 1936; Heldt, 1938; Kubo, 1949; Pérez Farfante, 1969, 1971a, b, 1975, 1977, 1980, 1982, 1985, 1988; Bauer, 1991; Bauer and Lin, 1993), the modifications of posterior thoracic sterna for attachment and/or storage of spermatophores usually *occur in more than one segment* in females of penaeoid shrimps. In the "open thelycum" species of *Penaeus* (*Litopenaeus*), workers such as Andrews (1911, figs. 1, 2), Burkenroad (1934a, figs. 5, 6), and Pérez Farfante (1969, figs. 11, 18; 1975, figs. 4, 7, 11, 15, 18) showed that modifications to receive the external spermatophore involved sternites of thoracic segments 7 and 8 (=body segments 13 and 14). The disposition of spermatophores on the female is a key issue in delimiting the female genital area or thelycum in *Penaeus* spp. with open thelyca, and spermatophores have been observed on thelyca of females and clearly illustrated in

several such *Penaeus* (*Litopenaeus*) spp. by Pérez Farfante (1975, figs. 1C, 2, 5, 8, 12, 13, 16, 19), as well as on females of some species of Solenoceridae (Pérez Farfante, 1977, figs. 35, 41, 62), a group in which females also have open thelyca. Pérez Farfante (1975: 471–472, fig. 5) clearly showed that the spermatophore was attached to thoracic sternite 6, as well as sternites 7 and 8, in *Penaeus* (*Litopenaeus*) *occidentalis* Streets, and thus modifications of all three posterior thoracic sternites compose the thelycum in this species.

Tavares and Secrétan (1993) gave "*Aristeus* sp." as an example of a penaeoid in which the female has a thelycum derived from a single sternite, that of the seventh thoracic segment. Photographs of a ventral and a dorsal view of the sternal skeleton of an "*Aristeus* sp." (fig. 2) were shown in which an external evagination on thoracic sternite 7 was labeled as the thelycum. No observations or literature citations are given by Tavares and Secrétan on the actual disposition of spermatophores on the ventral surface of female *Aristeus* that might support this designation of a thelycum. Yet Orsi Relini and Tunesi (1987: 463–464) clearly explained in their description of the spermatophores and thelycum of *Aristeus antennatus* (Risso) that the spermatophores are attached to and cover the sternal surfaces of *thoracic segments 7 and 8* of inseminated females. Thus, the only original (but incomplete) observation made by Tavares and Secrétan of a penaeoid thelycum supposedly derived from just one thoracic sternite is not correct.

In "closed thelyca" species, spermatophores and/or accessory male secretions may be enclosed in a space principally situated on the eighth thoracic segment of females (Burkenroad, 1934a; Heldt, 1938; Pérez Farfante, 1971a; Bauer, 1991). However, as Andrews (1911, figs. 3, 5) first showed, sternal modifications of the seventh as well as the eighth thoracic segments contribute to formation of the enclosed space where the sperm and associated accessory materials are stored in *Penaeus duorarum* Burkenroad ("*Penaeus brasiliensis*"). Pérez Farfante (1969, e.g., figs. 3c, d, 26, 27, 47, 48, 66, 76) has illustrated the double segment nature of the thelyca in females of several such species of *Penaeus* with a "closed thelycum." In several other penaeoid taxa, elements from both thoracic sternites 7 and 8 contribute to a median genital area where sperm-free male products are deposited and which leads to the openings of paired, invaginated, internalized seminal receptacles, e.g., *Trachypenaeus* spp. (Burkenroad, 1934a: 97–99, fig. 10; Pérez Farfante, 1971a: 639–642, figs. 5, 6; Bauer and Lin, 1993, figs. 16–27), *Xiphopenaeus kroyeri* (Heller) (Burkenroad, 1934a: 103–104, fig. 12), *Protrachypene precipua* Burkenroad (Burkenroad, 1934b: 47–48, fig. 11) and *Parapenaeus* spp. (Burkenroad, 1934a: 109; Pérez Farfante, 1982: 193–194, figs. 4, 5; personal observations).

Penaeus japonicus Bate is a penaeoid species that was given by Tavares and Secrétan as one of their examples of a decapod with a thelycum which, by their definition, is derived from only one sternite of the female. However, it is clear from the detailed descriptions of the thelycum and spermatophores of this species by Hudinaga (1942, plates XVI, XVII) and especially Tirmizi (1958), neither of whom was cited by Tavares and Secrétan, that not only thoracic sternite 8 but also thoracic sternite 7 is involved in spermatophore attachment and storage. Tirmizi (1958: 232) directly stated that the thelycum "consists of a triangular projection, the anterior plate, on the seventh thoracic sternite and a sac or pouch-like structure on the eighth." In her paper, Tirmizi described and illustrated how both sternites are involved in holding the sperm sacs and accessory wings of the spermatophores.

Tavares and Secrétan (1993) also included in their definition of "thelycum" that it is a spermatophore *storage* organ. The definition of the word *storage* is that something is deposited or saved for future use. How long must a spermatophore be affixed to the female in order to qualify as being stored? Tavares and Secrétan gave the genus *Atya* as an example of a caridean genus in which females have a thelycum, as they defined it, without original observations, descriptions, or citations of work on spermatophore storage in this genus. In carideans in which actual observations on spermatophore deposition and spawning have been reported, spermatophores are attached externally, but are soon used within a short time, since

spawning and fertilization of eggs occur soon after mating: within a few minutes in *Heptacarpus pictus* (Stimpson) (Bauer, 1976) and *H. paludicola* Holmes (Bauer, 1979); within 12 hours in *Palaemon elegans* Rathke (=*Leander squilla* (L.)) (Höglund, 1943), from a few hours to 24 h in *Macrobrachium* spp. (Lee and Fielder, 1982; Chow *et al.*, 1982). In some of the "open thelyca" penaeids, such as *Penaeus* (*Litopenaeus*) *vannamei* Boone, mating and spermatophore transfer take place just before spawning (Yano *et al.*, 1988), so that sperm is utilized in fertilization of eggs very soon (within two hours) after spermatophore deposition. It is doubtful that these examples of temporary spermatophore attachment in carideans and penaeids constitute "storage." For this reason, Bauer (1986, 1991) used "thelycum" as a structure which could serve either for attachment of spermatophores or for long term spermatophore storage.

One last difficulty with restricted definitions of *thelycum* is presented by the penaeoid genus *Sicyonia*. The sternites of thoracic segments 7 and especially 8 are highly modified in females and have been collectively termed a "thelycum" by penaeoid systematists (Burkenroad, 1934a: 122; Kubo, 1949: 114–115; especially Pérez Farfante, 1985: e.g., 5, 8, 14 and figs. 6, 11, 12). However, no sperm or spermatophoric material is ever stored or attached to that area. The male reproductive tract produces only sperm in a nonspecialized seminal fluid without any other male accessory secretion (Bauer, 1991, 1992). Sperm is stored in paired seminal receptacles invaginated into the cephalothorax (Pérez Farfante, 1985, fig. 7; Bauer, 1991) (paired spermathecae, as defined by Tavares and Secrétan, see below). In *Sicyonia* spp., the thelycum is the female genital area surrounding the apertures to the seminal receptacles where male genital orifices and copulatory appendages make contact during copulation and sperm transfer (Bauer, 1991, 1992).

The complete internalization of sperm storage and reduction of spermatophores to a liquid sperm mass without male accessory substances probably represents an advanced condition in the Penaeoidea (Bauer, 1991), and Burkenroad (1983) suggested that sicyoniids are advanced in the Penaeoidea on other grounds. It is not unreasonable to assume that ancestral stocks from which sicyoniids were derived were taxa in which the function of the thelycum for spermatophore attachment or storage was reduced (Bauer, 1991), as in penaeids such as *Trachypenaeus* spp., where only a sperm-free male accessory substance occurs in or on the thelycum (Burkenroad, 1934a; Pérez Farfante, 1971a; Bauer and Lin, 1993). Thus, even in the absence of sperm or spermatophore attachment or storage, application of the term *thelycum*, used in the conventional sense of penaeoid systematics, to the female genital area of *Sicyonia* seems justifiable.

Discussion of and Arguments against Restricted Application of the Term *Spermatheca*

Tavares and Secrétan (1993) proposed restriction of the term *spermatheca* to a type of seminal receptacle that is derived from intersegmental phragmata (lamellate invaginations of the cuticle, Secrétan, 1980). Such receptacles are found in females of various penaeoid genera, none of which are given as examples by Tavares and Secrétan, such as *Trachypenaeus*, *Parapenaeus*, *Xiphopenaeus*, and *Sicyonia* (Burkenroad, 1934a: 98, 103–104, 109, 122; Pérez Farfante, 1971a, fig. 6; 1982, fig. 5; 1985, fig. 7; Bauer, 1986, 1991; Bauer and Lin, 1993, fig. 22). In females of these taxa, paired cuticular invaginations between thoracic segments 7 and 8 project inside the cephalothorax, and sperm or spermatophores are stored there. Tavares and Secrétan (1993: 134) stated that a *spermatheca* is "always paired in the peditreme crabs and *unpaired* in the 'macrurans'." (Italics added). It is not clearly stated what is meant by "macrurans" in the text and in fig. 1 of the Tavares and Secrétan article, but, since the spermatheca of some penaeoid genera is mentioned, the intentional or inadvertent inclusion of penaeoids in the term "macrurans" (with regard to an unpaired spermatheca) is implied. Tavares and Secrétan (1993: 134) stated that the penaeoid genera *Bentheogennema* and *Gennadas* have a "spermatheca," but the paired nature of their "sperm receptacles" (Burkenroad, 1936: 59, 63, fig. 50) (=seminal receptacles = spermathecae) was never recognized or specified anywhere in the article for these or any other penaeoid genera. One

unfamiliar with the literature on penaeoid reproductive morphology might well be led to the conclusion that penaeoid spermathecae of this type are unpaired. However, they are paired.

Except for diagrammatic representations of a spermatheca in a "macruran" and in a "peditreme brachyuran crab," Tavares and Secrétan (1993) supported the proposed morphological origin of their "spermatheca" only with a single photographic observation on the sternal skeletons of *Nephrops norvegicus* (L.) and two brachyuran species, but gave no supporting evidence from original observations or published studies on reproductive morphology for penaeoids. Without such evidence, their statement on the anatomical formation of this type of "spermatheca" must remain a hypothesis, albeit a reasonable one, to be tested by anatomical and histological observations on the ontogeny of this structure in different taxa.

The problem of defining *spermatheca* as in Tavares and Secrétan (1993) is further complicated in penaeoid shrimps, such as several species of *Trachypenaeus*, by the fact that sperm may be stored in paired intersegmental invaginations ("spermatheca" sensu Tavares and Secrétan) but in addition an accessory male substance lacking sperm ("sperm-free male secretion" of Burkenroad, 1934a; "glutinous material" of Pérez Farfante, 1971; "plug substance" of Bauer and Lin, 1993, figs. 17–21) is located in the enclosed median pocket (thoracic sternite 8) that leads to the apertures of the seminal receptacles (spermathecae). Bauer and Lin (1993) suggested various roles for this material in the insemination and sperm storage process (during insemination, it pushes sperm packets into the "spermathecae"; prevents backflow of sperm from the latter; serves as a mating plug preventing copulations by other males; indirectly contributes to correct direction of flow when sperm is released during later spawning and fertilization of eggs). One interpretation of this situation is that the plug material is part of the spermatophore, in which case the median pocket is a thelycum according to the definition by Tavares and Secrétan. If so, these *Trachypenaeus* spp. would have both a *thelycum* and a *spermatheca* (actually paired) in the sense of Tavares and Secrétan (1993) for whom the two spermatophore-storing structures could not cooccur, by definition, in the same species. Another possible interpretation is that the accessory male secretion is not a spermatophore material (the numerous sperm packets transferred to the seminal receptacles are the actual spermatophores; Bauer and Lin, 1993). Thus, these sternal modifications of the genital area would not be termed a *thelycum*, although described in that sense for many years by systematists and reproductive morphologists. A similar space in penaeids, such as *Penaeus aztecus* Ives and related species, contains *both* sperm masses *and* male accessory secretions. Obviously, the variation in female genital morphology and in the structure and mode of storage of sperm and male accessory materials in penaeoids makes the restricted nomenclature suggested by Tavares and Secrétan confusing and without real utility.

Although I primarily focus here on the penaeoid shrimps, I have some comments about the use of *spermatheca* in brachyuran crabs. The distinction that Tavares and Secrétan made between the two types of sperm-storing structures in brachyurans [one type not associated with the ovary, as in the Dromiacea and Archaeobrachyura (classification used from Bowman and Abele, 1982); the other type at least partially derived from the oviduct, as in other Brachyura] has already been clearly made by the classic works of Hartnoll on brachyuran reproductive morphology (Hartnoll, 1968, 1975), papers not cited by Tavares and Secrétan (1993). It is implied by Tavares and Secrétan that the distinction between the two morphological types of spermathecae in brachyurans was not made in Bauer (1986), although it quite clearly was. Both Hartnoll (1968, 1975) and Bauer (1986) employed the generally used term "spermatheca" for both types of sperm-storage structures, although clearly discriminating between them. There are certainly morphological grounds to support proposals for restricted and specialized terms to differentiate between these two types of seminal receptacles or spermathecae in the Brachyura, as Tavares and Secrétan (1993) have done. However, previous detailed work (Hartnoll, 1968, 1975) on these structures in brachyurans should not be ignored.

Conclusions

Usage of the term *thelycum* proposed by Tavares and Secrétan (1993) is rejected principally because their definition restricts its morphological origin to one thoracic sternite, when clearly this is not the case in penaeoid shrimps, the group in which the term has been most extensively used in systematics and in studies on reproductive morphology. In addition, the diverse and variable nature of spermatophore attachment and sperm storage in penaeoids makes narrow usage of *thelycum* untenable and without obvious utility. The *thelycum* in penaeoids is the female genital area, i.e., modifications of female thoracic sternites 7 and 8 (sometimes including thoracic sternite 6) which, depending on the penaeoid taxon, may serve for temporary attachment or prolonged storage of spermatophores, an area where male accessory substances but not sperm are deposited, or as an area of genital contact with the male during copulation and sperm transfer which leads to or opens into internalized spermathecae. Thus, the penaeoid thelycum may or may not serve in sperm storage and it may or may not serve as a spermatheca or seminal receptacle. In some penaeoid genera, females may have, in addition to the thelycum, paired cuticular invaginations into the cephalothorax for sperm storage, i.e., internalized seminal receptacles or spermathecae.

It is suggested that the term *spermatheca* (=seminal receptacle) should be retained in its general sense, i.e., any enclosed space related to extended storage of sperm or spermatophores. The difficulty in a rigid, limited definition of a term such as *spermatheca* is similar to that of development of a uniform nomenclature for a term such as *spermatophore* (Mann, 1984), given the diversity in size, shape, and number of substances composing a spermatophore in different groups, especially among the Decapoda.

Terminology should increase communication and understanding among scientists and in comparative work should serve in identification of homology and homoplasy in studies on the evolution and phylogeny of a group. A complex nomenclature for genital morphology may be necessary to fulfill those objectives, given the diversity of genitalia and spermatophores in the Decapoda. However, the proposals of Tavares and Secrétan (1993) for usage of the terms *thelyca* and *spermatheca* do not appear to accomplish these goals, especially when the penaeoid decapods are considered.

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