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Comparative morphology of the thelycum of the planktonic shrimp genus *Lucifer* (Crustacea: Decapoda: Luciferidae) and its significance in taxonomy

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Abstract Adult females of all seven species of *Lucifer* are distinguished by each thelycum including the atrium and the processes of the terminal thoracic sternite. The thelyca of all seven species are described and illustrated in detail. A key to females of *Lucifer* is provided for the first time. This study made it possible to distinguish between females of closely related species: *L. faxoni* and *L. chacei*, *L. penicillifer* and *L. intermedius*, and *L. typus* and *L. orientalis*. In *L. chacei*, the terminal thoracic sternite has a median process, which does not develop at all in the other six species. In *L. penicillifer* the atrium is partitioned by a central membrane, which does not develop at all in the other six species. The opening in the atrium in *L. orientalis* is the longest among all seven species.

Key words: Taxonomy, Crustacea, *Lucifer*, thelycum, atrium, epiplankton, ghost shrimp

Introduction

The planktonic shrimps of the genus *Lucifer* are small, 6-15 mm in total length. This genus includes the following seven species in the tropical and subtropical waters of the oceans: *Lucifer hanseni*, *L. faxoni*, *L. chacei*, *L. penicillifer*, *L. intermedius*, *L. typus*, *L. orientalis*.

The structure of the petasma (male sexual organ) has hitherto been considered to be the important character to distinguish species of *Lucifer* (Hansen, 1919; Bowman, 1967). Although the female sexual organ, the thelycum, has been described and illustrated by many authors over the past century (Dohrn, 1871; Semper, 1872; Brooks, 1882; Bate, 1888; Rosenstadt, 1896; Kishinouye, 1928; Burkenroad, 1934; Bowman, 1967; Hartnol, 1968; Squire, 1990; Omori, 1992), insufficient attention has been paid to the structure of the thelycum as a taxonomic character. One exception is the study by Hayashi and Tsumura (1981) who distinguished between females of *L. penicillifer* and *L. intermedius* under a scanning electron microscope. Thus, the taxonomy of the females of *Lucifer* is far from complete due to weak knowledge of interspecific morphological differentiation.

I have examined in detail the thelyca of all seven species. This study revealed that the thelycum exhibits specific morphological characters. Moreover it proves to be a reliable diagnostic character to distinguish females of *Lucifer* under light microscope. This paper aims to provide detailed descriptions and illustrations of the thelyca of all species of *Lucifer*, and a key to species based on thelycum morphology of females.

Materials and methods

Specimens of *Lucifer* were available from samples collected with a NORPAC net from various localities (Table 1). Off northwestern Honshu, both *L. intermedius* and *L. penicillifer* were collected. However, in the other localities only one species were collected (see Hashizume and Omori, 1998). They were preserved in 5-10% formalin-sea water or 70% ethanol-distilled water. Prior to microscopic observations, adult specimens were cleared in heated 5% potassium hydroxide distilled water or 15-50% glycerin-distilled water, because the dead specimens are opaque as a whole. The thelycum could then be viewed from the lateral side with a compound microscope (Nikon Eclipse E200) or a stereo microscope (Nikon SMZ800) equipped with a drawing tube (Figs. 1A, 1B). The

Table 1. List of materials examined.

Species	Locality	Date	Latitude	Longitude	Collector	Total length
L. hanseni	Labuan, Java, Indonesia	11 May. 1993	06°15.0'S	105°50.0'E	Dr. Mulyadi	6.1-10.0 mm (N=20)
L. faxoni	Off Freeport, Gulf of Mexico	10 May. 1994	26°59.5'N	092°59.9'W	R/V Shoyo-Maru	9.3-12.8 mm (N=10)
L. chacei	Kaneohe Bay, Oahu Is., Hawaii	8 Nov. 1989	21°26'N	157°47'W	Dr. T. Clark	7.0-14.2 mm (N=20)
	Bonin Is.	16 Jun. 1995	27°55'N	142°13.0'E	Dr. K. Fukuoka	
L. penicillifer	Perusian Gulf	21 Jan. 1993	26°44.9'N	051°23.0'E	R/V Umitaka-Maru	9.0-13.7 mm (N=20)
L. intermedius	Off northwestern Honshu	4 Oct. 1994	39°32'N	142°19'E	R/V Iwate-Maru	8.0-15.5 mm (N=20)
L. typus	Off Western Australia	4 Aug. 1994	33°00.0'N	031°00.3'E	R/V Shoyo-Maru	8.2-12.2 mm (N=20)
L. orientalis	Off Peru	14 Mar. 1966	08°47'S	081°20'W	Anton Bruun	9.5-12.7 mm (N=10)

compressed body and extremely narrow thoracic sternum of *Lucifer* makes it difficult to observe the thelycum from the ventral side. Consequently, a horizontal slice of the ventral part of the thorax was removed by a razor (see Figs. 1A, 1C) and the thelycum from the ventral side could be easily observed.

For confirmation, I have examined fresh specimens of five species (*L. hanseni, L. penicillifer, L. intermedius, L. typus* and *L. orientalis*) collected by a NORPAC net with a large cod-end off Banda and nearby in Tateyama harbor in Chiba Prefecture, Japan (35°00'N, 139°45'E) during September - November of 1994 and of 1995.

Basic structure of thelycum (Fig. 1)

The thelycum is an external seminal receptacle lying on the posterior part of the thoracic sternum and formed by outgrowths from the last and next to the last thoracic somites (Figs. 1A, 1B). The thelycum of *Lucifer* consists of the terminal thoracic sternite, the coxae of the third pereopods (P3), the atrium (Atr) and the spermatheca (Spt). The atrium (Atr) is a chitinous pouch formed by a median depression of the terminal thoracic sternite between the basal conjunctions (BP3) of the third pereopods. The atrium is connected to the paired, saclike spermatheca at its innermost (proximal) part (IAt) by paired seminal ducts (SD). Between both of the BP3, the atrium has a opening (OAt), which is covered by a pair of lamellar-shaped processes (LPT) on the terminal thoracic sternite (Fig. 1C). In one species the central membrance (CAT) develops in the cavity of the atrium. The terminal thoracic sternite has a median process (MET) on the posterior end in all species and also a smaller median process (MPT) on the anterior part in one species. Additionally, several setae (SP3) are located proximally on the mesial margin of the coxa of the third pereopod. When present, the neck of the spermatophore is inserted into the atrium (see Semper, 1972), nevertheless, it appears that females of *Lucifer* do not retain the spermatophore for long periods of time (Hashizume, unpublished).

Description

Lucifer hanseni Nobili, 1905 (Figs. 2A, 3A)

Atr narrow in median part, then abruptly curved anteriorly and nearly horizontal at innermost part, situated beneath Spt; cuticular of Atr weakly sclerotized; OAt medium in length, placed partly beyond posterior edge of coxa of P3; CAT not developed (Figs. 2A, 3A). BP3 reaching mid-length of depth of Atr in lateral view (Fig. 2A). LPT slender, semicircular and slightly angulated, covered distal half of depth of Atr as well as lateral margin of OAt (Figs. 2A, 3A); mesial margin of LPT weakly chitinous, without hairs (Fig. 3A). MPT not developed; MET low (Figs. 2A, 3A).

Lucifer faxoni Borradaile, 1915 (Figs. 2B, 3B)

Atr narrow in distal one-third, then abruptly curved anteriorly, situated beneath Spt; cuticular of

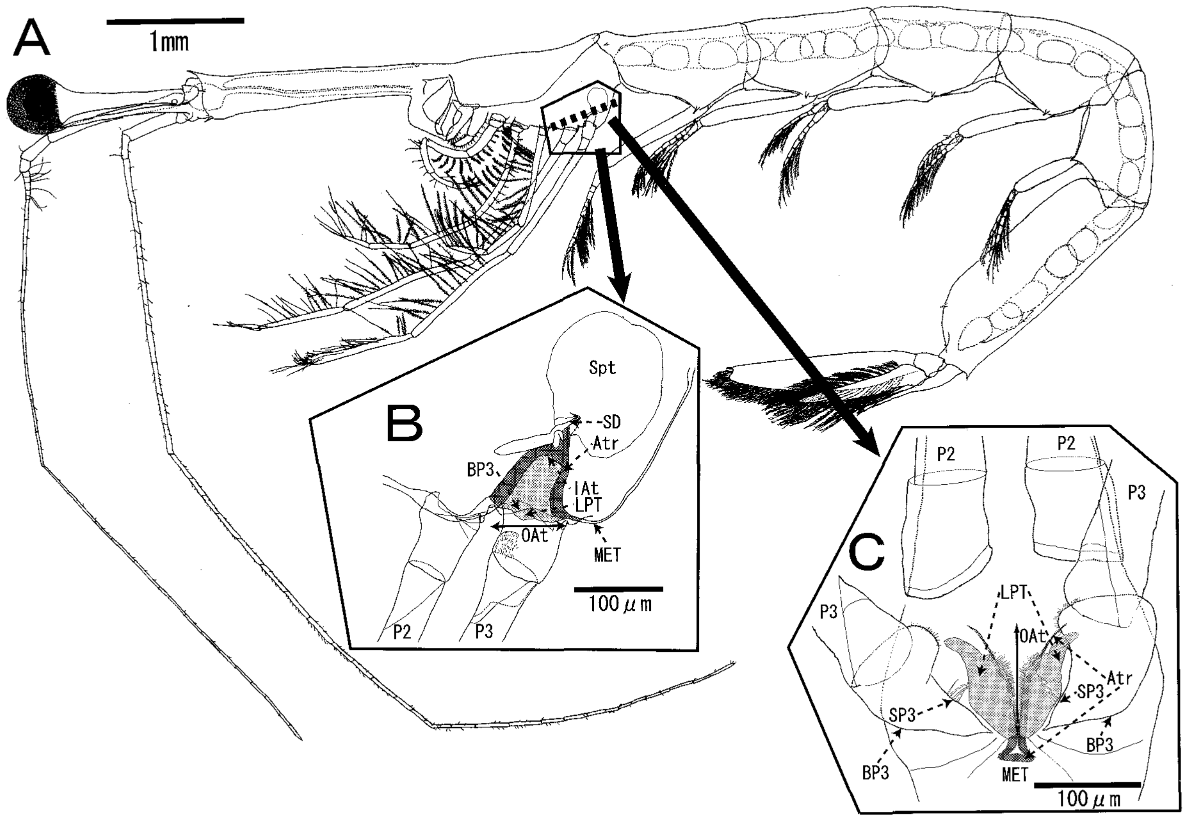

Fig. 1 *Lucifer typus*, showing morphological characters as here defined. A, whole animal; B, left lateral view of thelycum; C, ventral view of thelycum. Abbreviations are: Atr, atrium; BP3, basal conjunction of coxa of third pereopod; IAt, innermost (proximal) part of atrium; LPT, lamellar-shaped process on terminal thoracic sternite; MET, median process on posterior end of terminal thoracic sternite; OAt, opening in atrium; P2, second pereopod; P3, third pereopod; SD, seminal duct; SP3, setae on mesial margin of coxa of third pereopod; Spt, spermatheca. Maximal length of OAt is shown with double arrowed solid line. In 1B, LPT as well as anterior and posterior margin of cuticular of Atr are colored with light and dark shadow, respectively. In 1C, LPT as well as ventral and lateral margin of cuticular of Atr are colored with light and dark shadow, respectively. The halftone shadow is an overlap of LPT and cuticular of Atr.

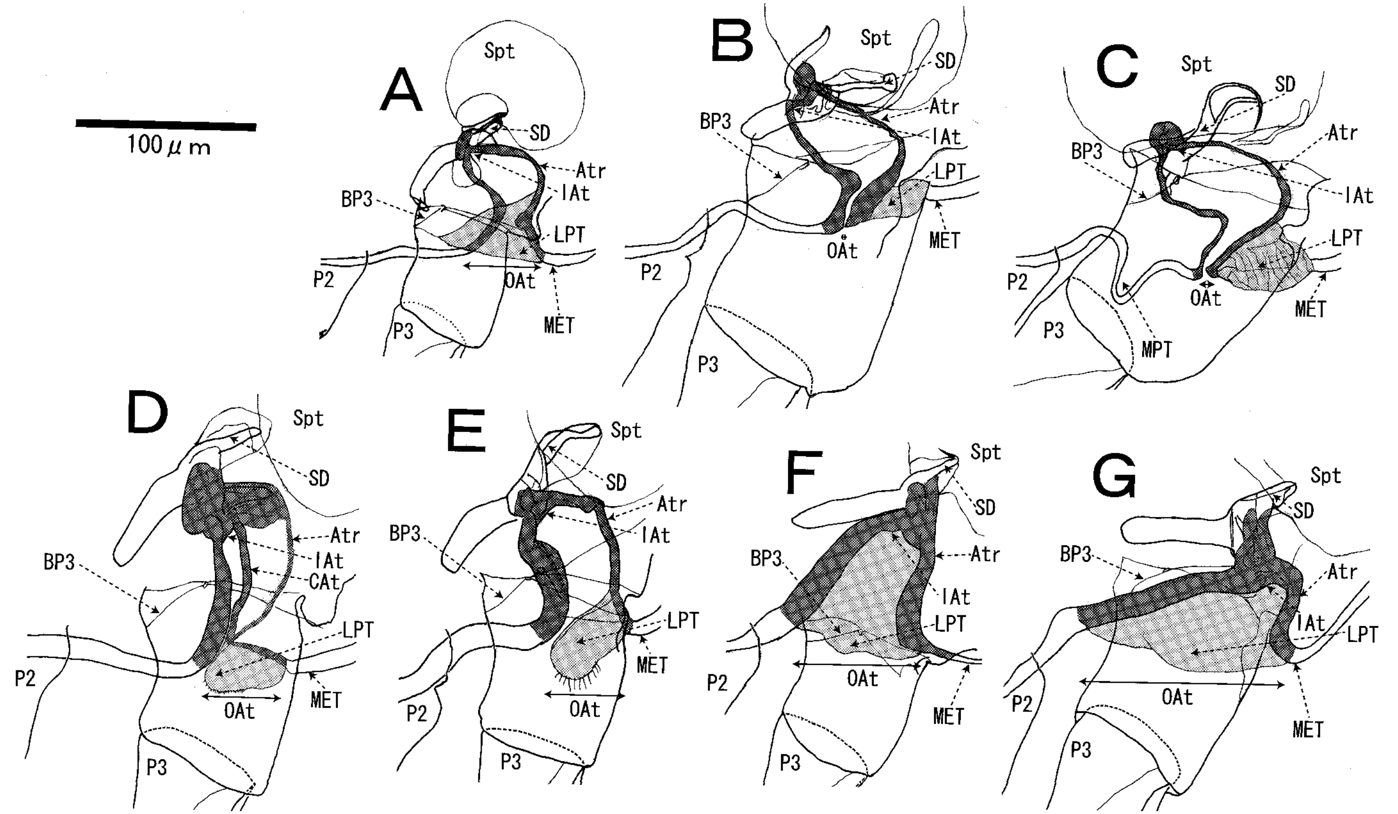

Fig. 2 Left lateral view of the thelyca of *Lucifer*. A, *L. hanseni*; B, *L. faxoni*; C, *L. chacei*; D, *L. penicillifer*; E, *L. intermedius*; F, *L. typus*; G, *L. orientalis*. Abbreviations are: Atr, atrium; BP3, basal conjunction of coxa of third pereopod; CAt, central membrane of atrium; IAt, innermost part of atrium; LPT, lamellar-shaped process on terminal thoracic sternite; MET, median process on posterior end of terminal thoracic sternite; MPT, median process on terminal thoracic sternite; OAt, opening in atrium; P2, second pereopod; P3, third pereopod; SD, seminal duct; Spt, spermatheca. Maximal length of OAt is shown with double arrowed solid line. LPT as well as anterior and posterior margin of cuticular of Atr are colored with light and dark shadow, respectively.

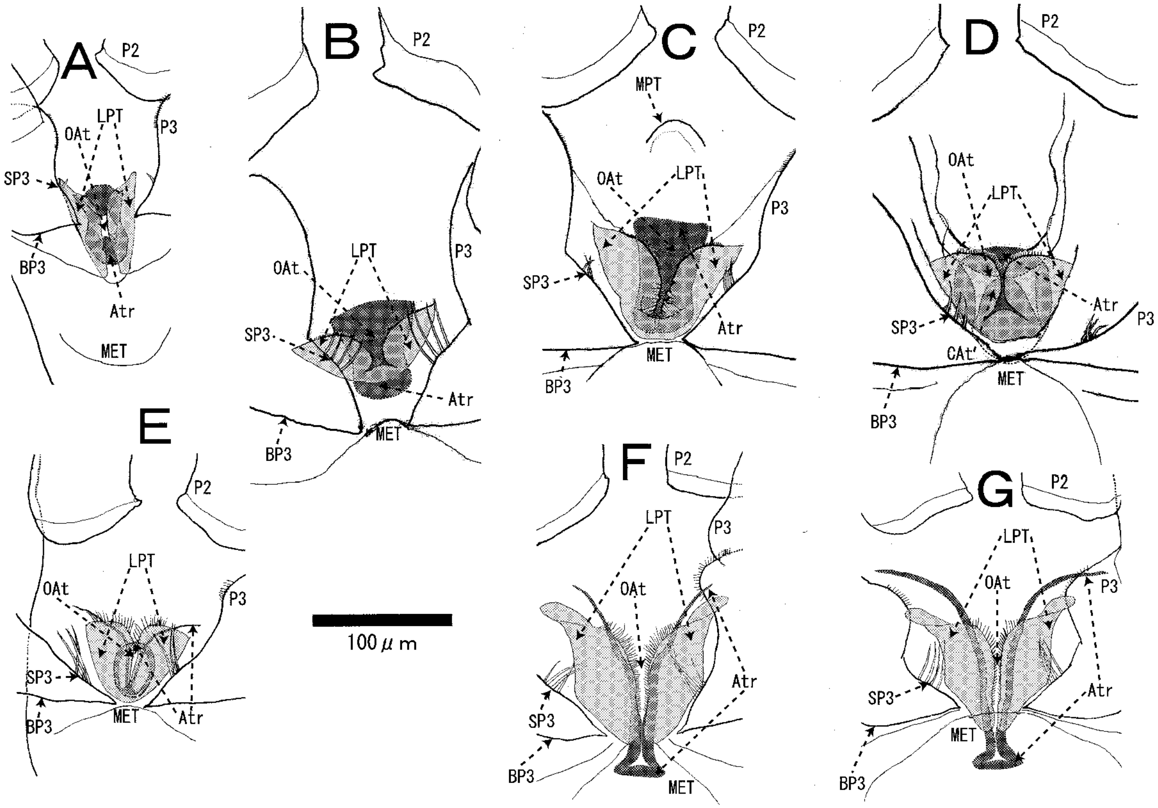

Fig. 3 Ventral view of the thelyca of *Lucifer*. A, *L. hanseni*; B, *L. faxoni*; C, *L. chacei*; D, *L. penicillifer*; E, *L. intermedius*; F, *L. typus*; G, *L. orientalis*. Abbreviations are: Atr, atrium; BP3, basal conjunction of coxa of third pereopod; CAt, central membrane of atrium; LPT, lamellar-shaped process on terminal thoracic sternite; MET, median process on posterior end of terminal thoracic sternite; MPT, median process on terminal thoracic sternite; OAt, opening in atrium; P2, second pereopod; P3, third pereopod; SP3, setae on mesial margin of coxa of third pereopod. LPT as well as ventral and lateral margin of cuticular of Atr are colored with light and dark shadow, respectively. The halftone shadow is an overlap of LPT and cuticular of Atr. Abbreviations as in Figure 2.

Atr sclerotized at distal one-third; OAt considerably short and like a slit, placed in line with coxa of P3; CAT not developed (Figs. 2B, 3B). BP3 reaching mid-length of depth of Atr in lateral view (Fig. 2B). LPT slender and semicircular, covered almost distal half of posterior part of Atr as well as slightly lateral margin of OAt; mesial margin of LPT considerably chitinous, with many short hairs (Figs. 2B, 3B). MPT not developed; MET high, moderately angulated at distal end, then gradually sloping posteriorly (Figs. 2B, 3B).

Lucifer chacei Bowman, 1967 (Figs. 2C, 3C)

Atr narrow in distal one-third, then abruptly curved anteriorly and nearly horizontal at innermost part, situated beneath Spt; cuticular of Atr slightly sclerotized; OAt very short and like a slit, placed in line with coxa of P3; CAT not developed (Figs. 2C, 3C). BP3 reaching mid-length of depth of Atr in lateral view (Fig. 2C). LPT slender and semicircular, covered distal half of posterior part of Atr as well as slightly lateral margin of OAt; mesial margin of LPT slightly chitinous with many short hairs; posterior part of LPT slightly thick, considerably wrinkled and chitinous (Figs. 2C, 3C). MPT conical and slightly angularly, situated nearly in front of OAt (Figs. 2C, 3C). MET high, somewhat rounded at distal end, then gradually sloping posteriorly (Figs. 2C, 3C).

Lucifer penicillifer Hansen, 1919 (Figs. 2D, 3D)

Atr considerably narrow in distal one-fourth, then little gradually curved anteriorly, situated anterior to Spt; cuticular of Atr sclerotized at anterior part as well as innermost part; OAt partitioned by CAt, placed in line with coxa of P3; maximal length of OAt approximately half times of depth of Atr; CAT considerably developed (Figs. 2D, 3D). BP3 reaching mid-length of depth of Atr in lateral view (Fig. 2D). LPT broad and semicircular, covered distal one-fifth of Atr as well as almost entirely OAt; mesial margin of LPT considerably chitinous, with many short hairs (Figs. 2D, 3D). MPT not developed; MET high, somewhat rounded at distal end, then gradually sloping posteriorly (Figs. 2D, 3D).

Lucifer intermedius Hansen, 1919 (Figs. 2E, 3E)

Atr long in distal part, then gradually curved anteriorly, situated anterior to Spt; cuticular of Atr sclerotized anteriorly; OAt broadly oval, placed in line with coxa of P3; maximal length of OAt approximately half times of depth of Atr; CAT not developed (Figs. 2E, 3E). BP3 reaching mid-length of depth of Atr in lateral view (Fig. 2E). LPT rounded triangularly, covered distal one-fifth of Atr as well as almost entirely OAt; mesial margin of LPT slightly chitinous, with many long hairs (Figs. 2E, 3E). MPT not developed; MET high, moderately angulated at distal end, then gradually sloping posteriorly (Figs. 2E, 3E).

Lucifer typus (H. Milne-Edwards, 1837) (Figs. 2F, 3F)

Atr long in distal part, then gradually curved posteriorly, situated anterior to Spt; cuticular of Atr considerably sclerotized; OAt long, almost placed in line with coxa of P3; maximal length of OAt subequal to depth of Atr; CAT not developed (Figs. 2F, 3F). BP3 little reaching OAt in lateral view (Fig. 2F). LPT slender and semicircular, slightly angulated, covered completely depth of Atr as well as greater area of OAt; mesial margin of LPT considerably chitinous, with very many long hairs (Figs. 2F, 3F). MPT not developed; MET high, moderately angulated at distal end, then gradually sloping posteriorly (Figs. 2F, 3F).

Lucifer orientalis Hansen, 1919 (Figs. 2G, 3G)

Atr long in distal part, then gradually curved posteriorly, situated anterior to Spt; cuticular of Atr considerably sclerotized; OAt considerably long, almost placed in line with coxa of P3; maximal length of OAt almost twice times of depth of Atr; CAT not developed (Figs. 2G, 3G). BP3 extending IAt in lateral view (Figs. 2G, 3G). LPT slender and semicircular, slightly angulated, covered entirely depth of Atr as well as almost posterior half of OAt; mesial margin of LPT considerably chitinous, with many long hairs (Fig. 3G). MPT not developed; MET considerably high, semicircular at distal end, then gradually sloping posteriorly (Figs. 2G, 3G).

Females of *Lucifer* can be identified with the following key.

Key to species of the genus *Lucifer* based on thelycum morphology

1.	Maximal length of OAt subequal or longer than depth of Atr ···	2 (=Group A by Hansen, 1919)
1.	Maximal length of OAt shorter than depth of Atr ·················	3 (=Group B by Hansen, 1919)
2.	Maximal length of OAt subequal to maximal depth of Atr ···························	*Lucifer typus*
2.	Maximal length of OAt twice as long as maximal depth of Atr ·················	*Lucifer orientalis*
3.	Atr abruptly curved anteriorly and situated beneath Spt ···	4
3.	Atr gradually curved anteriorly and situated anterior to Spt ···································	6
4.	OAt placed partly beyond posterior edge of coxa of P3. ···························	*Lucifer hanseni*
4.	OAt placed in line with coxa of P3 ···	5
5.	Terminal thoracic sternite with MPT ··	*Lucifer chacei*
5.	Terminal thoracic sternite without MPT ···	*Lucifer faxoni*
6.	Atr with CAt ··	*Lucifer penicillifer*
6.	Atr without CAt ··	*Lucifer intermedius*

Discussion

The present study proves that the thelycum represents a species specific character in *Lucifer* morphology, particularly in the form of the atrium and processes on the terminal thoracic sternite. Species group B (=*L. hanseni, L. faxoni, L. chacei, L. penicillifer and L. intermedius*) by Hansen (1919) has a short opening in the atrium and the atrium is curved anteriorly. While species group A (=*L. typus and L. orientalis*) has a long opening in the atrium and the atrium is curved posteriorly. The thelycum of *L. hanseni* is similar to that of *L. faxoni* and *L. chacei,* because these species have an atrium that is abruptly curved anteriorly and situated beneath the spermatheca. Moreover, the structure of lamellar-shaped process on the terminal thoracic sternite of *L. penicillifer* is similar to that of *L. intermedius.* In the present study the thelycum morphology leads to reliable identification under a light microscope between females of closely related species: *L. faxoni* and *L. chacei, L. penicillifer* and *L. intermedius,* and *L. typus* and *L. orientalis.* In *L. hanseni* the posterior half of the opening in the atrium extends beyond the posterior edge of the coxa of the third pereopod, however, the opening in the atrium is placed in line with the coxa of the third pereopod in the other six species. In *L. chacei,* the terminal thoracic sternite has a median process, which does not develop at all in the other six species. In *L. penicillifer,* the atrium is partitioned by a central membrane, which does not develop at all in the other six species. Furthermore, the opening in the atrium in *L. orientalis* is the longest among all seven species. These morphological differences among the thelycum of female *Lucifer* can be observed more easily in fresh specimens than in preserved specimens, since freshly caught specimens are transparent.

The atrium was first defined by Burkenroad (1934) and called the spermathecal canal by Hartnol (1968). Bowman (1967) called the spermatheca and the median process on the anterior part of terminal thoracic sternite the seminal receptacle and ventral process, respectively. Additionally, the posterior end of the terminal thoracic sternite is called the sternal plate of the last thoracic segment by Hayashi and Tsumura (1981).

Various body characteristics have been considered useful in distinguishing the females of *Lucifer* by Hansen (1919), Petit (1973) and Omori (1992). These are: the antennule, the eye, the exopod of the uropod (Hansen, 1919), the shape of a notch between the 4th and 5th abdominal segments (Petit, 1973), along with the extension of the rostrum length (Omori, 1992). To confirm this, I have examined many females of *Lucifer* collected from various localities, and, as a consequence, the usefulness of these characters is diminished, because the occurrence of unseparable intermediate forms is frequently noted between closely related species (Hashizume, unpublished). Thus, the thelycum is concluded at this time to be one of the key characters that allow reliable identification for adult females of *Lucifer.*

The opening in the atrium is comparatively long in *L. orientalis* and *L. typus,* and is longer in the former than in the latter. It, however, is distinctly shorter in *L. faxoni* and *L. chacei.* Correspondingly, the male sexual organ (petasma) of *L. orientails* is considerably thicker than that of *L. typus.* The petasma of *L. faxoni* and *L. chacei* are slender and spine-like (Hansen, 1919; Bowman, 1967). It is interesting to discuss the morphological relationships of female and male sexual organs (see Eberhard, 1985). The opening in the atrium extends partly beyond the posterior edge of the coxa of the third pereopod in *L. hanseni,* while it is usually placed in line with the coxa of the third pereopod in the other six species. It is necessary to remember that only *L. hanseni* releases eggs into the sea, while the other species hold their egg masses by the third pereopod (Hashizume and Omori, 1998).

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