



A phylogeny-based revision of the family Luciferidae (Crustacea: Decapoda)

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Received 3 August 2015; revised 19 November 2015; accepted for publication 19 January 2016

Luciferidae is a family of peculiar and widely distributed shrimps with an unclear systematic position and uncertain internal phylogeny. We undertook a phylogenetic analysis of Luciferidae based on 169 morphological characters (147 binary, 22 multistate). Several characters were based on scanning electron microscopy studies of the reproductive organs (e.g. petasma). All seven recognized species of Luciferidae were included as well as 17 additional species representing all other genera of Sergestoidea. Characters were polarized using three outgroups of the superfamily Penaeoidea, occurring in three different types of oceanic habitat. The phylogenetic analysis revealed monophyly of Luciferidae and the presence of two terminal robust clades within the family, which we treat as separate genera, *Lucifer* and ***Belzebub* gen. nov.** Morphological trends within Luciferidae are discussed, and diagnoses and keys to genera and all species are given.

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doi: 10.1111/zoj.12398

ADDITIONAL KEYWORDS: classification – new genera – phylogenetics – revision – taxonomy.

INTRODUCTION

Species of Luciferidae are amongst the most peculiar shrimps in the world because of their aberrant appearance (Fig. 1), which includes a much compressed body, reduced appendages and branchia, and a curious copulatory organ. The systematic position of Luciferidae within Dendrobranchiata remains uncertain. After its description (Thompson, 1829), *Lucifer* was separated from the other sergestid shrimps and established as the type genus for a separate family, Luciferidae De Haan, 1849. Later, the status of the group was lowered to the subfamily level, Luciferinae Bate, 1888; and kept as such for a long time (e.g. Hansen, 1919). However, most recent carcinologists have considered Luciferidae as a monotypic family within the superfamily Sergestoidea Dana, 1852 (Burkenroad, 1983; Williams, 1984; Squires, 1990; Perez-Farfante & Kensley, 1997; De Grave & Fransen, 2011).

The family comprises seven species, six of which [*Lucifer faxoni* Borradaile, 1915; *Lucifer hanseni* Nobili, 1905; *Lucifer intermedius* Hansen, 1919; *Lucifer orientalis* Hansen, 1919; *Lucifer penicillifer* Hansen, 1919; *Lucifer typus* H. Milne Edwards, 1837 (in H. Milne Edwards, 1834–1840)] were described in detail in the monographic study by H. J. H. Hansen (1919) and later by Petit (1973) and Naomi *et al.* (2006); a seventh species, *Lucifer chacei* Bowman & McCain, 1967; was later established for Pacific specimens of *L. faxoni*. The current knowledge of the morphology and phylogeny of Luciferidae is in the same state as it was a century ago, which is unfortunate as many species are highly abundant and play a significant role in epipelagic ecosystems (Woodmansee, 1966; Bowman & McCain, 1967; Zimmerman, 1973; Lee, Omori & Peck, 1992; Antony, 2005; Teodoro *et al.*, 2012). Recent studies of several genera in the sister family Sergestidae (Vereshchaka, Olesen & Lunina, 2014; Vereshchaka & Lunina, 2015) yielded a data matrix with 150 morphological characters and resulted in the establishment of eight new sergestid genera. This matrix has been used

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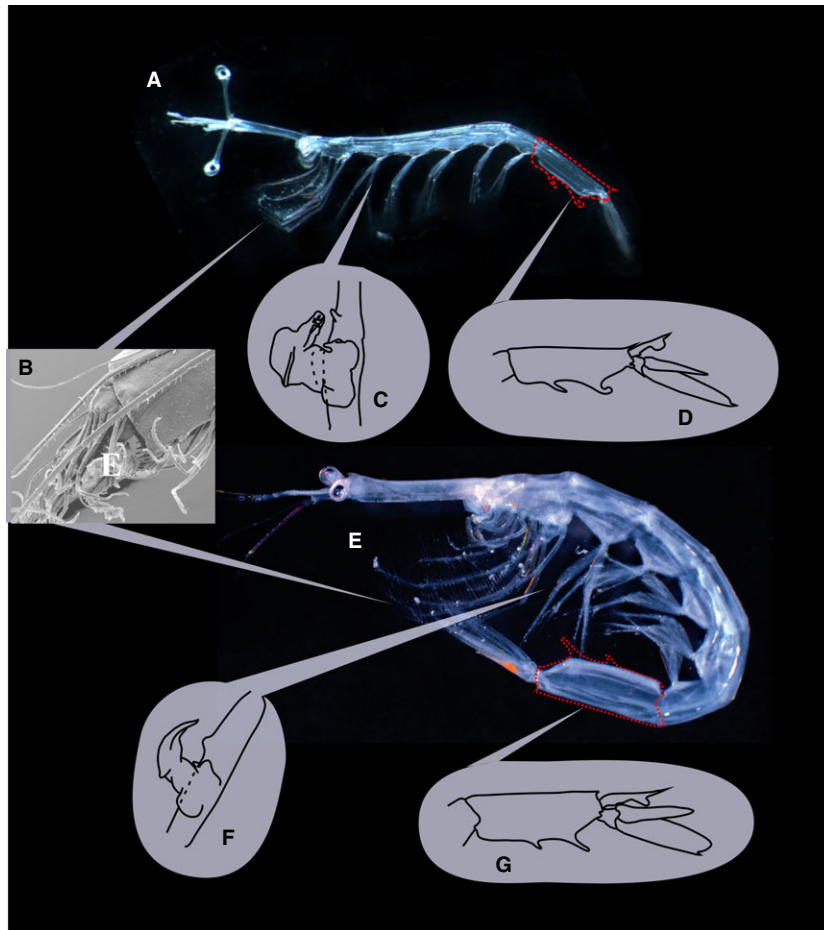


Figure 1. General view of females of *Lucifer typus* H. Milne Edwards, 1837 (A) and *Belzebub hanseni* (Nobili, 1905) comb. nov. (E). Red dotted line indicates shape of sixth abdominal segment and telson in males. Inset images are: subchela of third pereopod (B), petasmas in males (C and F), and sixth abdominal segment and telson in males (D and G).

in the present paper as a basis for a phylogenetic analysis and a revision of the classification of Luciferidae. Compared with Sergestidae, species of Luciferidae are small and appear simplified and specialized in morphology, so restudy of the morphology of many species was required in order to accommodate them in the Sergestidae matrix used by Vereshchaka *et al.* (2014).

MATERIAL AND METHODS

MATERIAL

The material used for this study is from the extensive collections of pelagic invertebrates from the Danish 'Dana I' (1920–22) and 'Dana II' (1928–30) Expeditions stored at the Natural History Museum of Denmark (formerly 'Zoological Museum, University of Denmark'). The work involved sorting and identification of the museum's collection of Luciferidae; individuals were then selected for further study by scanning electron microscopy (SEM).

SCANNING ELECTRON MICROSCOPY

Prior to treatment for SEM, relevant parts (such as the petasma) of selected specimens were dissected in order to expose important structures for further study. The material was dehydrated in a graded ethanol series, critical point dried, mounted, and coated with a mixture of platinum and palladium following standard procedures (e.g. Olesen, Richter & Scholtz, 2003). The SEM used was a JEOL JSM-6335F (with a field emission gun). The images were processed and arranged in standard graphical software such as CorelDraw X7 and various Adobe programs.

TERMINAL TAXA FOR PHYLOGENETIC ANALYSIS

Suborder Dendrobranchiata comprises two superfamilies, Penaeoidea Rafinesque, 1815; with six families, and Sergestoidea Dana, 1852; with two families (Luciferidae and Sergestidae). The ingroup

in this study consisted of all seven recognized species of Luciferidae (Appendix S1). In order to test the monophyly of Luciferidae in a wider context, representatives (the type species) of all other genera of Sergestoidea were also included (17 in total; see Appendix S1).

As outgroups we tested three species representing three families of Penaeoidea, each occurring in three different types of oceanic habitat (benthopelagic, pelagic, and benthic) and therefore representing different types of morphology. The three species – all of which are type species of their genera – are *Aristeomorpha foliacea* (Aristeidae), which is benthopelagic; *Genadas parvus* (Benthescymidae), which is pelagic; and *Penaeus monodon* (Penaeidae), which is benthic. Character state scoring for each species was derived from examination of specimens (see Appendix S1).

MORPHOLOGICAL CHARACTERS

We used the data matrix of Vereshchaka & Lunina (2015) as a basis for this work. The character states are figured in Vereshchaka (2000, 2009), Vereshchaka *et al.* (2014), and Vereshchaka & Lunina (2015). We used 169 modified characters (22 new – see Appendix S2). The data matrix is presented in Appendix S3.

Data were handled and analysed under maximum parsimony settings using a combination of programs: WINCLADA/NONA, NDE (Nexus Data Editor), and TNT (Nixon, 1999; Goloboff, Farris & Nixon, 2000).

ANALYTICAL METHODS

All characters were unordered (non-additive) and equally weighted; missing data were scored unknown; the score given for each state (i.e. 0, 1, 2) implies nothing about order in a transformation series (Ahyong, 2009). Trees were generated in TNT using the ‘traditional search’ options. The search parameters were set to the following: memory set to hold 1 000 000 trees; swapping algorithm was tree bisection-reconnection (TBR) with 1000 trees to save per replication zero-length branches collapsed; suboptimal trees set to be filtered out. Relative stability of clades was assessed by standard bootstrapping (sample with replacement) with 10 000 pseudoreplicates and by Bremer support (algorithm TBR, saving up to 10 000 trees up to three steps longer).

We considered the clades statistically significant if they were supported either by bootstrap values ≥ 80 or Bremer ≥ 3 .

RESULTS AND DISCUSSION

Luciferidae are characterized by the absence (branchia, pereopods IV–V) or reduction (mouthparts,

first and second pereopods) of numerous external characters (Perez-Farfante & Kensley, 1997). Only a few organs (e.g. third pereopod and petasma) show complex structures and SEM was used to restudy these characters in detail.

ULTRASTRUCTURE OF SELECTED CHARACTERS AND POSSIBLE HOMOLOGIES

Third pereopod

This pereopod is modified into a peculiar chela-like (‘subchela’) structure formed of the dactyl bearing eight to nine claws of similar size, which, in a claw-like manner, opposes a part of the propodus (Fig. 2B, C). The subchela is covered by numerous setae, which vary in size and structure. The structure of pereopod III is similar in all seven studied species. The third pereopod in Luciferidae shows superficial similarity to that of the genera *Allosergestes* and *Deosergestes* of Sergestidae (Fig. 2A). As in these sergestid genera (Vereshchaka, 2009), the distal part of the propodus in Luciferidae is armed with robust, claw-like teeth and tufts of specialized setae, which may have sensory or grooming function. The dactyl is much reduced in Luciferidae, *Allosergestes*, and *Deosergestes*. In *Allosergestes* and *Deosergestes*, the propodus and dactyl are arranged as a true chela, although much specialized, whereas in Luciferidae they instead form a subchela.

Petasma, general structure

The petasma is positioned on the inner side of the basipod of the first pleopod. In all species examined it projects forward and slightly distally (Figs 3B, 4A, 5A, 6A, 7B, 8B, C, 9B). The basal part of the petasma (‘palm’ in Fig. 8C) is broad and robust, probably acting as a ‘hand’ during spermatophore transfer. The distal part of the petasma is narrow and partly folded (‘first finger’ in Fig. 8C), and is adjacent to a protuberance of the frontal margin of the basipod (‘thumb’ in Fig. 8C); these parts probably act like a first finger and a thumb, respectively (using the human hand as analogy). The distal part of the petasma has a characteristic morphology, which is very important for species identification.

Undoubtedly, the petasma of Luciferidae is homologous to that of other Sergestoidea. In contrast to them, the pars astrigens (the part joining the two parts into one unit) is absent in Luciferidae, but the other specialized parts are present, meaning that possible homologies can be established.

Sheath of the petasma

The distal part of the petasma (‘first finger’) consists of a kind of sheath enclosing a chitinized element. The sheath is not completely closed but has a slit on

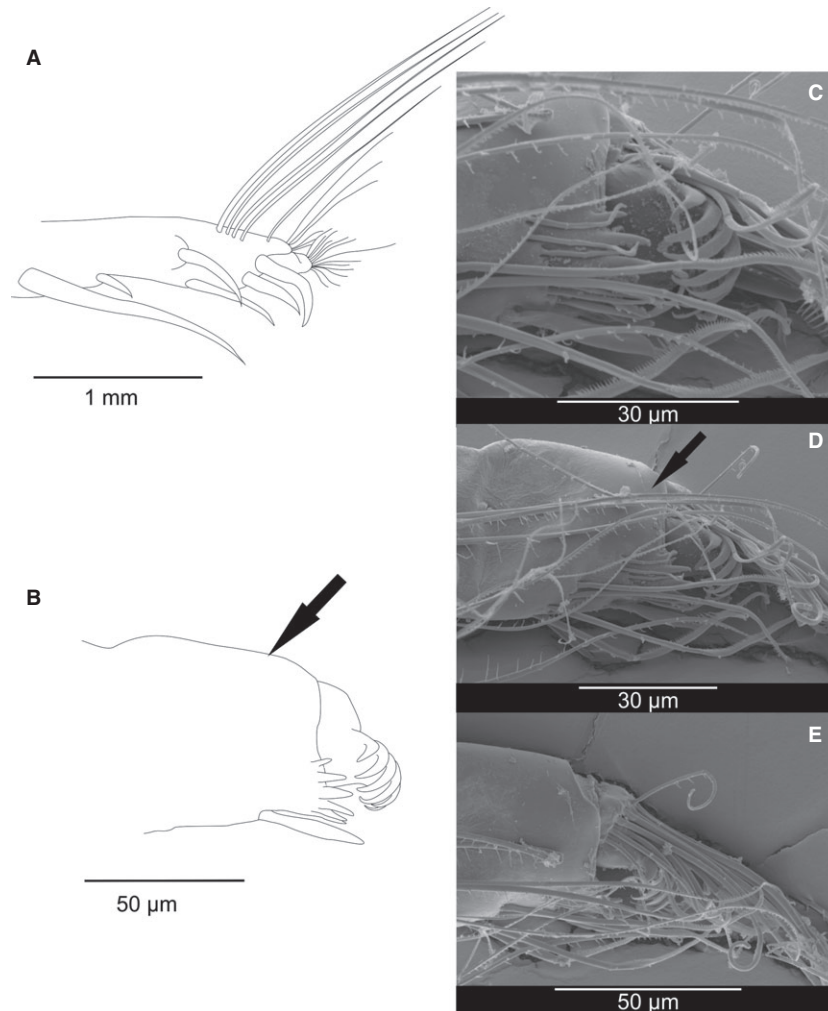


Figure 2. Chela of third pereopod in *Deosergestes corniculum* (A) and *Belzebug penicillifer* (Hansen, 1919) comb. nov. (B, C–E, scanning electron micrographs). Arrows point at same morphological structures.

the inner side (Fig. 7D); the sheath bears a special locking structure at the tip (Fig. 7D, G), probably preventing untimely opening. The inner side of the sheath may bear a hook as in *L. typus* (Fig. 3D–F) or be smooth and unarmed as in all other species (Fig. 7D). We recognize two different sheath types:

1. Wide, with a deep apical lacuna (Figs 3A, 4D), entirely covered with continuous chitinous ribs (Figs 3A, 4B, D), without additional friction structures at the apex. The sheath is not supported by additional ribs. This type is characteristic for *L. typus* and *L. orientalis*.
2. Narrow, tapering, without visible lacuna (Figs 7D, 8E), with apical chitinous structures, which may be arranged either in transverse rows of ridges (Fig. 5D) or in longitudinal rows of fine scales (Figs 6C, 8I). In addition to these ‘friction’ structures, there are one to three apical plate-like

protrusions (Figs 5D, 6E, 7F, 8I, 9A) and fine setae (Figs 7F, 8E). The sheath is supported by an additional strong, chitinized rib (Fig. 8G, H). This type is characteristic for *Belzebug intermedius*, *Belzebug faxoni*, *Belzebug hanseni*, *Belzebug chacei*, and *Belzebug penicillifer*.

Hansen (1919) failed to recognize the homology of the sheath in *Lucifer* and other sergestoids. In his description of *L. typus*, he misinterpreted a strong hook of the petasma of this species. Having used light microscopy, Hansen (1919) considered the hook as a separate structure of unknown origin inside the sheath. In fact, the hook is a part of the sheath and very similar to the hooks on the processus uncifer observed in several sergestid genera (compare Fig. 10B and E). We thus suggest a homology between the sheath and the processus uncifer of the other Sergestoidea.

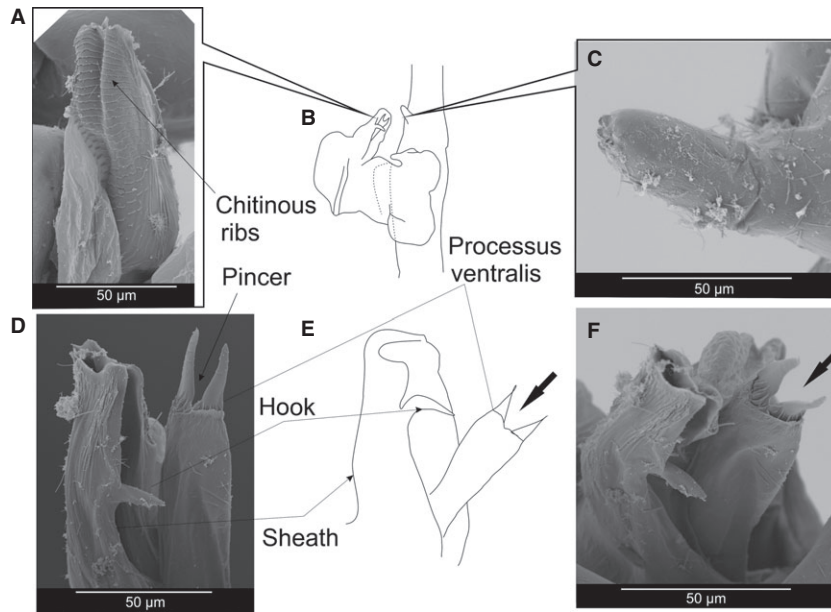


Figure 3. Petasma of *Lucifer typus* H. Milne Edwards, 1837: inner view of the sheath (A, scanning electron micrograph), general structure (B), ‘thumb’ on the uropodal basipod (C, scanning electron micrograph), lateral view of the sheath and processus ventralis (D, scanning electron micrograph, E), apical view of the sheath and processus ventralis (F, scanning electron micrograph). Arrows point at same morphological structures.

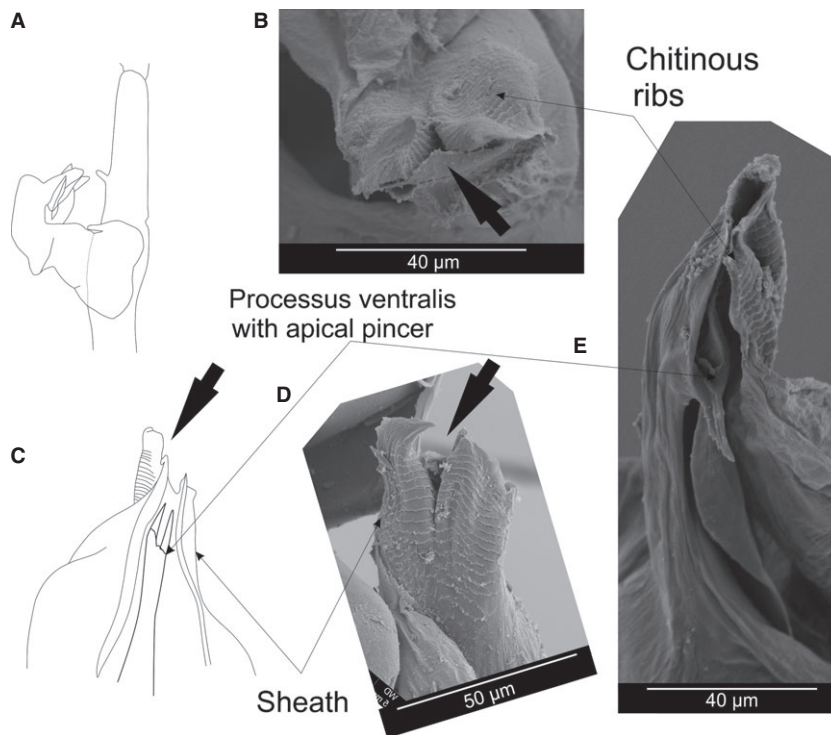


Figure 4. Petasma of *Lucifer orientalis* Hansen, 1919: general structure (A), apical view of the sheath (B, scanning electron micrograph), lateral view of the sheath and the processus ventralis (C, E, scanning electron micrographs), inner view of the sheath (D, scanning electron micrograph). Arrows point at same morphological structures.

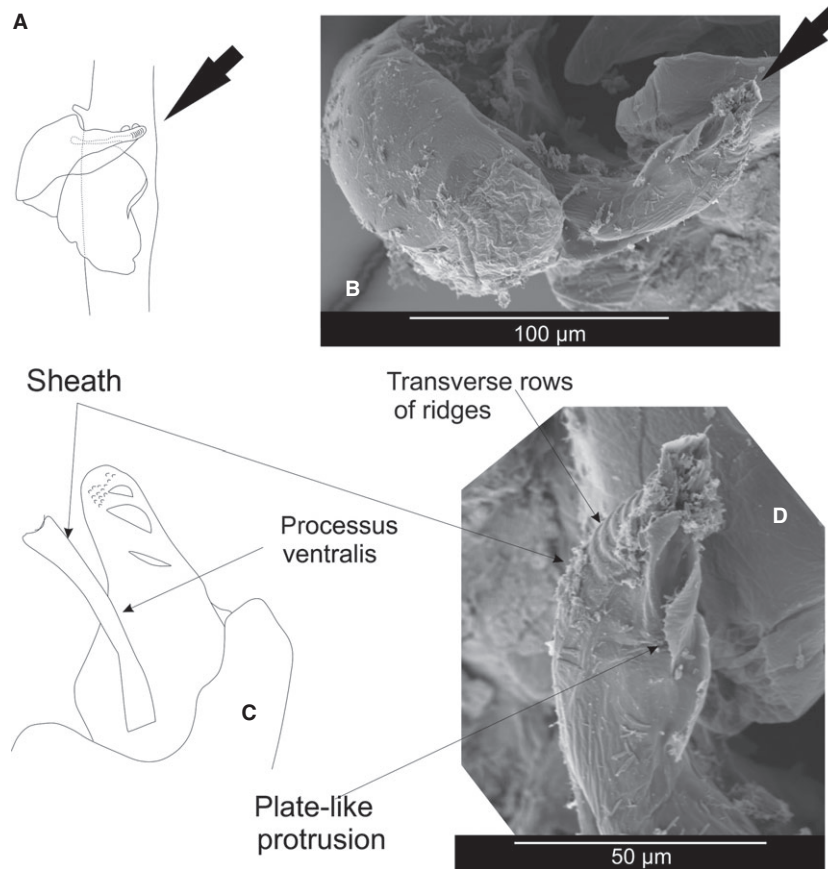


Figure 5. Petasma of *Belzebug intermedius* (Hansen, 1919) comb. nov.: general structure (A), apical view of the sheath (B, scanning electron micrograph), lateral view of the sheath and the processus ventralis (C, D, scanning electron micrographs). Arrows point at same morphological structures.

The inner chitinized element of the petasma

The sheath is semitransparent and the general structure of the inner chitinized element can be seen in light microscopy. The ultrastructure of this element, however, is visible only with the use of SEM and locating it is partly a matter of chance as only in rare cases the sheath partly opens as a result of the drying procedure. In *L. typus* and *L. orientalis*, this element is wide, smooth, and bears two apical lashes shaped as a pincer (Figs 3D, F, 4E). In the other species, this element is nearly spiniform and bears 'friction' structures (Fig. 8E) and minute setae laterally (Figs 7D, G, 8D). In *B. penicillifer*, the inner element bears an apical brush of long setae (Fig. 6E, F).

Hansen (1919) was the first to consider the inner chitinized element as a homologue to the processus ventralis of the other sergestids. The SEM data obtained here confirm his hypothesis: the terminal portion of the chitinized element in *L. typus* and *L. orientalis* bears a pincer that is identical to the structures found in *Deosergestes* (compare Fig. 10H and I) but fewer in number (two instead of six or

more). In other species of Luciferidae, the processus ventralis lacks terminal lashes and is acicular in shape; a similar reduced state is found in some species of the genus *Acetes*.

The overall homologies between the petasmas of Luciferidae and Sergestidae are shown in Fig. 10 along with a hypothetical transitional state not actually present in any recent species. In Luciferidae, the pars astrigens is lost, the processus ventralis is the only part of the pars media left, and the processus uncifer (pars externa) is folded and rolled around the pars media (processus ventralis).

RESULTS OF PHYLOGENETIC ANALYSES

Analysis 1 with *A. foliacea* as outgroup retrieved ten minimal length trees of 254 steps in length (Fig. 11A). The most basal sergestoid clades are *Sycionella* followed by *Petalidium*. The clade *Petalidium* is followed by two sister clades: (1) *Peisos* + *Acetes* + Luciferidae and (2) the rest of Sergestidae (15 genera of the former *Sergestes* and *Sergia*). The clades received Bre-

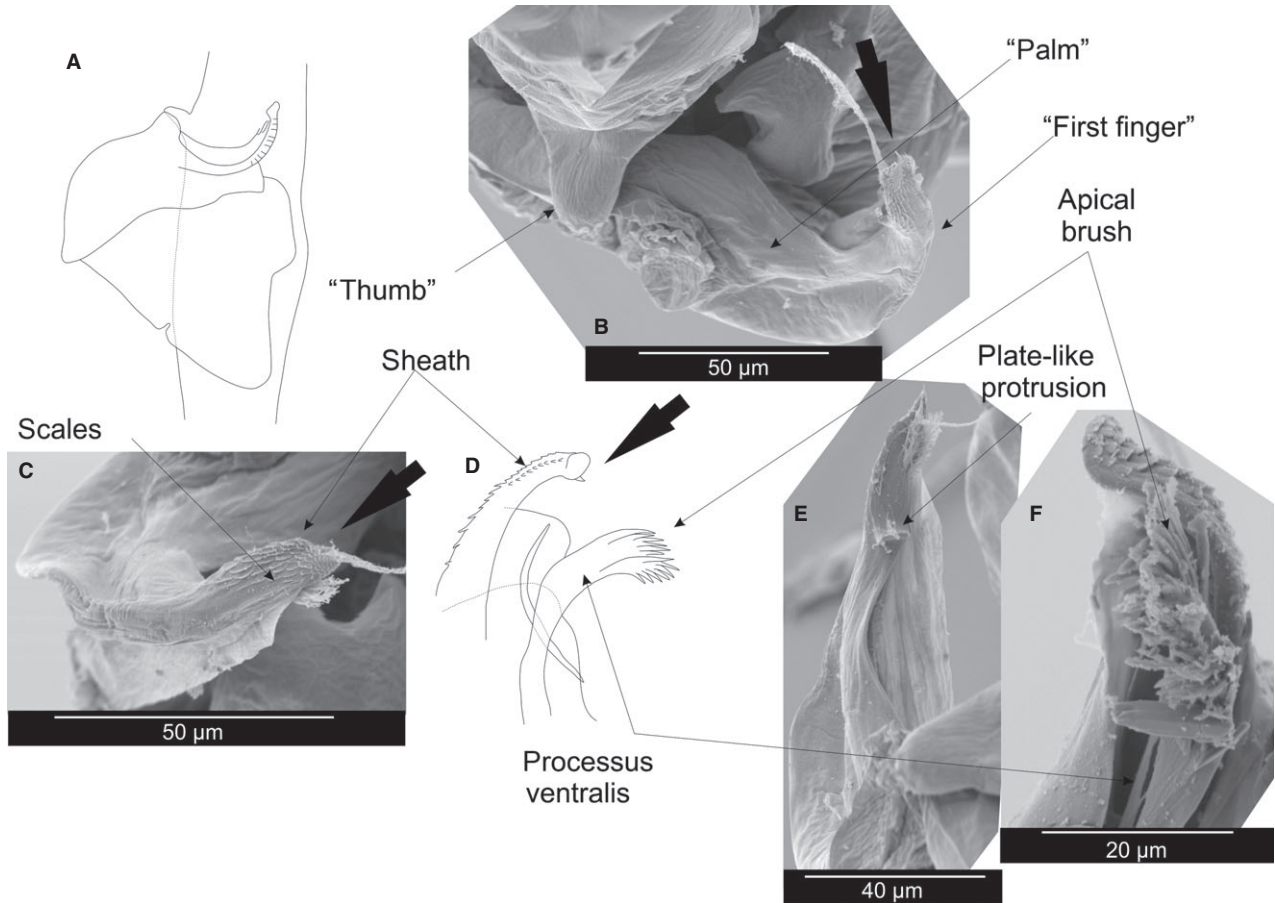


Figure 6. Petasma of *Belzebug penicillifer* (Hansen, 1919) comb. nov.: general structure (A), apical view of the petasma (B, scanning electron micrograph), apical view of the sheath (C, scanning electron micrograph), lateral view of the sheath and the processus ventralis (D, E, scanning electron micrographs), apex of the processus ventralis (F, scanning electron micrograph). Arrows point at same morphological structures.

mer supports of 5 and 6, respectively; the latter also received a bootstrap support of 85. Within the former clade, there is a terminal group Luciferidae with a bootstrap support of 100 and Bremer support of 25; this group is sister to *Acetes* and split into two clades. Both clades are robust as both received a Bremer support of 4 and bootstrap support of ≥ 90 .

Analysis 2 with *G. parvus* as outgroup retrieved ten minimal length trees of 259 steps in length (Fig. 11B). The tree topology was similar to that of Analysis 1. The only minor difference concerns lesser bootstrap supports for 15 genera of the former *Sergestes* and *Sergia*. The terminal group Luciferidae with the two sister clades *L. orientalis* + *L. typus* and *B. hanseni* + *B. chacei* + *B. faxoni* + *B. penicillifer* + *B. intermedius* received the same Bremer and bootstrap supports as in Analysis 1.

Analysis 3 with *Pen. monodon* as outgroup retrieved 30 minimal length trees of length 257 steps (Fig. 11C). The tree topology was again generally

similar to those of Analyses 1 and 2 but *Petalidium* has jumped further up in the tree. Bremer supports of the clades (1) *Peisos* + *Acetes* + Luciferidae and (2) 15 genera of the former *Sergestes* and *Sergia* are the same as in Analyses 1 and 2. The terminal group *Lucifer* with the two sister clades *L. orientalis* + *L. typus* and *B. hanseni* + *B. chacei* + *B. faxoni* + *B. penicillifer* + *B. intermedius* again received the same levels of Bremer and bootstrap support as in Analyses 1 and 2.

THE MONOPHYLY OF LUCIFERIDAE AND THE STATUS OF TWO TERMINAL CLADES (*LUCIFER* AND *BELZEBUB* GEN. NOV.)

Analyses 1–3 with the three different outgroups all revealed a very high level of support for the clade Luciferidae, thus confirming its monophyletic origin. The analyses revealed the following synapomorphies for Luciferidae (synapomorphy numbers can be found in Appendix S2):

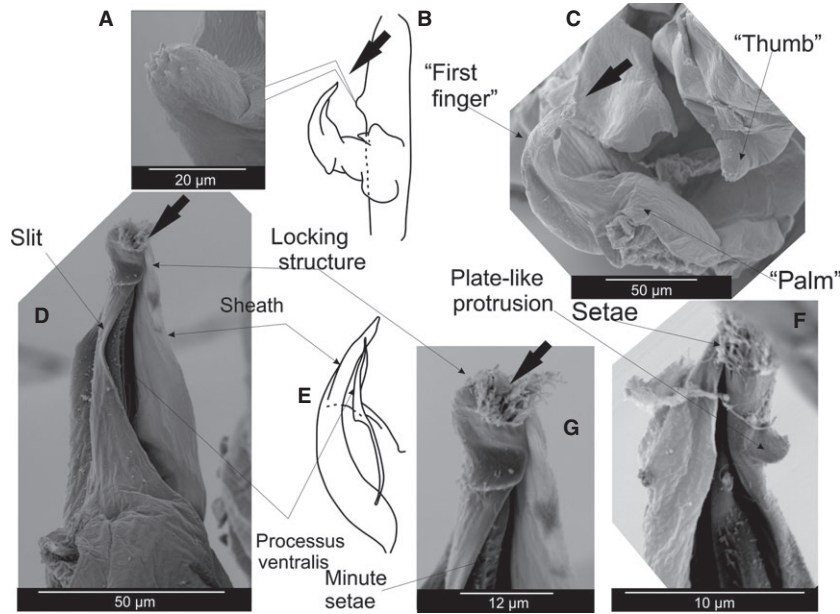


Figure 7. Petasma of *Belzebug hanseni* (Nobili, 1905) comb. nov.: ‘thumb’ (A, scanning electron micrograph), general structure (B), apical view of the petasma (C, scanning micrograph), lateral view of the sheath and the processus ventralis (D, scanning electron micrograph, E), apex of processus ventralis and the sheath (F, G, scanning electron micrographs). Arrows point at same morphological structures.

- (1) separation of the labrum from the antennae and eyes;
- (5) presence of a pterygostomial tooth on the carapace;
- (10, 14, 22, 27) absence of anterior arthrobranchia on somites IX–XIII;
- (31) presence of two ventral processes on the sixth abdominal somite in males;
- (34, 36) presence of two movable lateral spines and a conspicuous distoventral protuberance on the telson;
- (42) absence of a ventral flagellum on the antennules in males;
- (43) absence of a stylocerite;
- (45) presence of a robust distal tooth on the scaphocerite overreaching the end of the blade;
- (46) absence of a mandibular palp;
- (47) presence of two endites of the maxillula in adults;
- (48, 49) absence of epipod and exopod on the first maxilliped;
- (51) absence of epipod on the second maxilliped;
- (54) dactyl of the third maxilliped entire;
- (58, 62) absence of chela of the first and second pereopods;
- (68, 69, 71, 72) presence of strong curved spines and very long, specialized setae on the propodus, subchela with fixed finger shorter than dactyl of the third pereopod;
- (81) absence of the fifth pereopod in males;

- (86) outer spine of the uropodal exopod in females nearly reaching distal end of the exopod;
- (89) absence of male clasp organ; and
- (100) absence of pars astrigens of the petasma.

Both the number of synapomorphies and the statistical robustness of the clade confirm the status of Luciferidae as being highly derived, justifying its taxonomic status as a separate family. The family has traditionally been considered as monotypic, as it comprises a single genus, *Lucifer* (e.g. Perez-Farfante & Kensley, 1997). However, our analyses show that the clade Luciferidae consists of two distinct sister clades, each of which have high Bremer support (4) and high bootstrap values (≥ 90). Here we treat these two clades as separate genera: *Lucifer* and ***Belzebug* gen. nov.** (see diagnoses for both genera below).

Lucifer, which contains *L. typus* and *L. orientalis*, is supported by the following synapomorphies:

- (37, 38) sexually dimorphic eyes (larger in males) with eyestalks elongated, subconical, and nearly reaching end of the scaphocerite;
- (103, 108) processus unifer of the petasma transformed into a sheath with wide tip not supported by chitinous ribs and armed with transverse ribs along entire inner margin;
- (141) presence of the apical pincer-like structure on the processus ventralis of petasma.

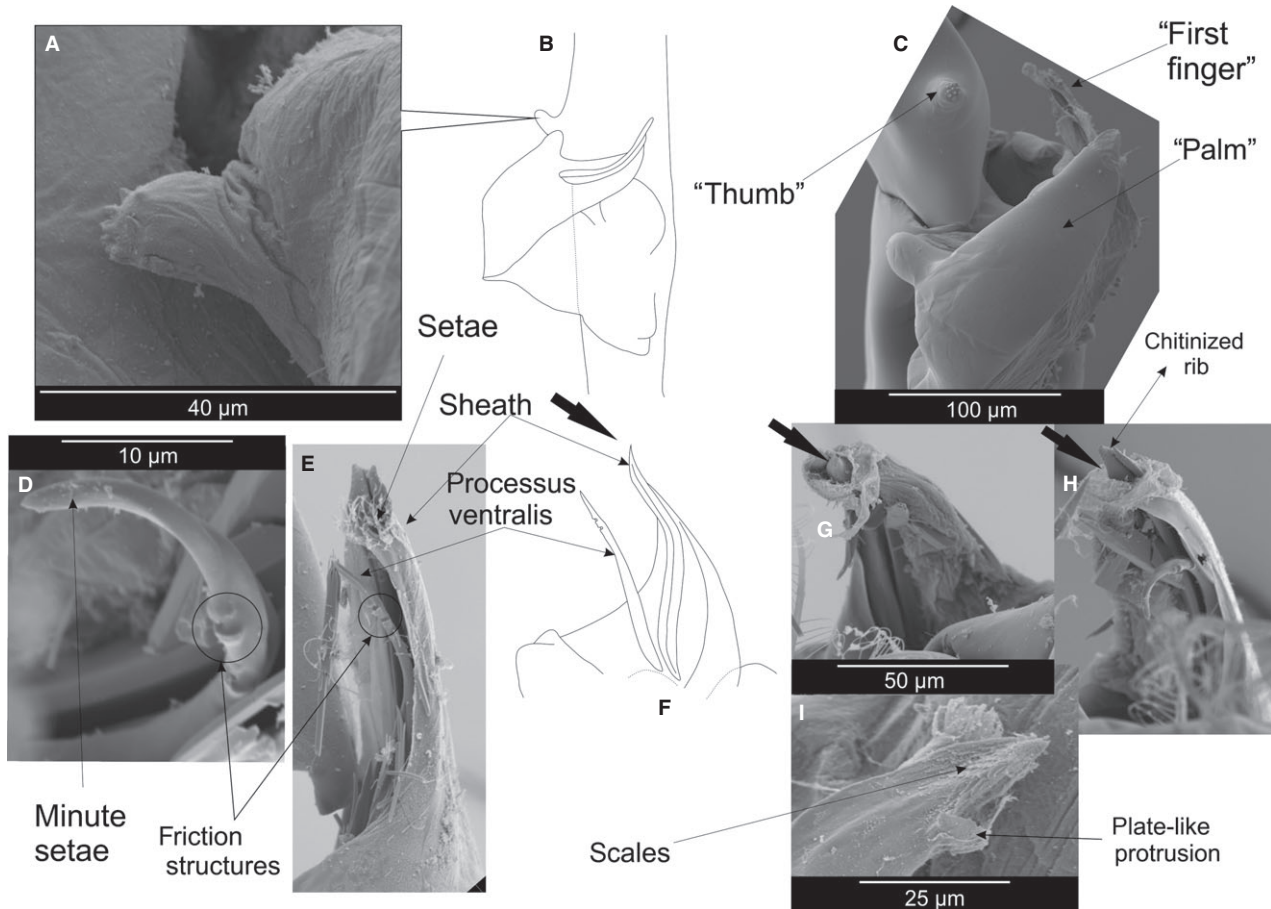


Figure 8. Petasma of *Belzebug faxoni* (Borradaile, 1915) comb. nov.: ‘thumb’ (A, scanning electron micrograph), general structure (B), apical view of the petasma (C, scanning electron micrograph), lateral view of the sheath and the processus ventralis (D, scanning electron micrograph, E, scanning electron micrograph, F), distal part of the sheath with apical scales (G–I, scanning electron micrographs). Arrows point at same morphological structures.

***Belzebug* gen. nov.**, which contains *B. chacei*, *B. faxoni*, *B. hanseni*, *B. intermedius*, and *B. penicillifer*, is supported by the following synapomorphies:

- (104, 106) processus uncifer of the petasma transformed into a narrow sheath with entire tip supported by a chitinous rib and bearing terminal setae and plate-like structures in addition to transverse structures at the tip;
- (107, 109) processus uncifer of the petasma apically armed with fine ‘friction’ structures and plate-like protrusions.

TAXONOMY

FAMILY LUCIFERIDAE DE HAAN, 1849

Synonyms: Luciferinae Bate, 1888; Leuciferinae Ortman, 1898; Leuciferidae Barnard, 1950.

Emended diagnosis: Rostrum short, acute, oblique; carapace compressed laterally, with postorbital, pterygostomial, and hepatic teeth, labrum widely separated from antennae and eyes; sixth abdominal somite in male bearing two ventral processes; telson with two pairs of lateral spines, strong ventral protuberance present in male. Antennules without ventral flagellum and clasping organ, mandible and maxillae lacking palp; first maxilliped lacking epipod and exopod; second maxilliped lacking epipod; first and second pereopods without chelae; third pereopod with subchela, distal end of propodus bearing strong, curved teeth and serrated setae; fourth and fifth pereopods absent in both sexes. Genital aperture unpaired in both sexes. Photophores: dermal organs and organ of Pesta absent. Petasma: pars astrigens absent, pars externa developed, transformed into a sheath around long, entire processus ventralis. Branchiae: absent.

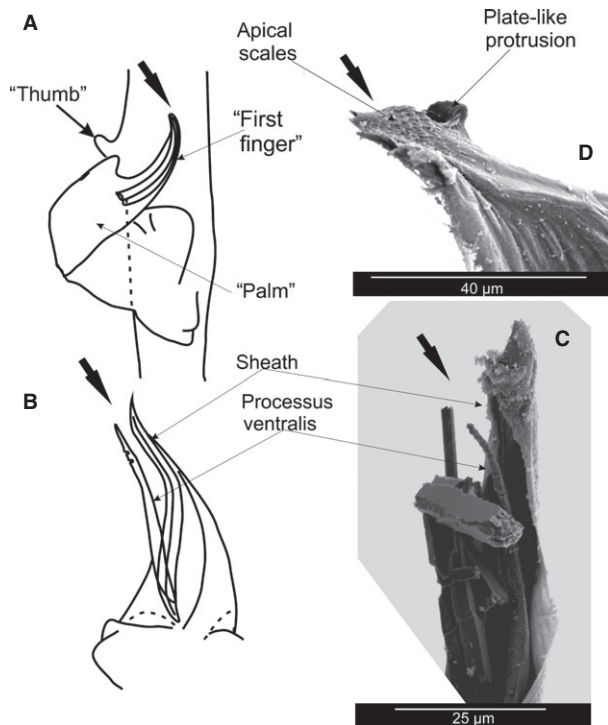


Figure 9. Petasma of *Belzebug chacei* (Borradaile, 1915) comb. nov.: general structure (A), lateral view of the sheath and the processus ventralis (B, D, scanning electron micrographs), distal part of the sheath and the processus ventralis (C, scanning electron micrograph). Arrows point at same morphological structures.

KEY TO SPECIES OF THE FAMILY LUCIFERIDAE

1. Posterior ventral process on sixth male abdominal somite curved, not tapering, apically obtuse (Fig. 1D). Eyestalks elongated, conical, nearly reaching end of scaphocerite (Fig. 1A). Petasma: sheath wide, entirely armed with transverse chitinous ribs along inner margin, without additional plate-like structures (Figs 3A, 4D); processus ventralis lamellar, with apical pincer (Fig. 3D, E)*Lucifer* Thompson, 1829.
- Posterior ventral process on sixth male abdominal somite nearly straight, tapering, apically subacute (Fig. 1G). Eyestalks of moderate length, subcylindrical, not reaching end of scaphocerite (Fig. 1E). Petasma: sheath narrow, tapering, supported by strong chitinous ribs, armed with apical scales or of ridges, with additional plate-like structures (Figs 5C, 6B); processus ventralis spiniform, without apical pincer (Fig. 9D)*Belzebug* gen. nov.

GENUS *LUCIFER* THOMPSON, 1829

Synonyms: *Lucifer* Thompson, 1829 [partim]; *Leucifer* H. Milne Edwards, 1837 [partim].

Emended diagnosis: Posterior ventral process on sixth male abdominal somite curved, not tapering, apically obtuse. Eyestalks elongated, conical, eyes sexually dimorphic, nearly reaching end of scaphocerite; stylocerite absent; scaphocerite with distal tooth overreaching end of blade; third maxilliped with entire dactyl, not sexually dimorphic; uropodal exopod with proximal segment not setose along outer margin. Petasma: pars externa transformed into a wide sheath not supported by strong chitinous rib; sheath armed with transverse rows of minute scales, without additional pincer-like structures; processus ventralis lamellar, with apical pincer, lacking lateral friction structures.

Type species: *Lucifer typus* H. Milne Edwards, 1837.

Species: *Lucifer typus* H. Milne Edwards, 1837; *L. orientalis* Hansen, 1919.

Remarks: Correspond to the species group A of *Lucifer* (Hansen, 1919). The genus is easily distinguished from the sister genus *Belzebug* by its long, conical eyestalks and sexually dimorphic (larger in males) eyes. Males also differ in (1) the posterior ventral process on the sixth abdominal somite, which is curved, not tapering, obtuse at the end (instead of nearly straight, tapering, almost acute at the end in *Belzebug*) and (2) the sheath of the petasma, which is wide and unsupported (instead of narrow and supported by a strong chitinous rib in *Belzebug*).

Etymology: From the Latin 'lux' (genitive 'lucis') meaning 'light' and 'ferre' meaning 'carry'; an allusion to the luminescence that this species produces.

Distribution: Oceanic genus, panoceanic distribution.

KEY TO SPECIES OF THE GENUS *LUCIFER*

1. Second pair of lateral spine on telson positioned just above or slightly posterior to margin of ventral processus. Petasma: sheath with prominent hook, apically sinuous but entire (Fig. 3D–G)*L. typus* H. Milne Edwards, 1837.
- Second pair of lateral spine on telson positioned slightly anterior to margin of ventral processus. Petasma: sheath without hook, apically trilobed (Fig. 4C, D) *L. orientalis* Hansen, 1919.

LUCIFER TYPUS H. MILNE EDWARDS, 1837 (FIG. 3A–G)

Synonyms: *Leucifer reynaudii* H. Milne Edwards, 1837; *Leucifer typus* H. Milne Edwards, 1837; *Leu-*

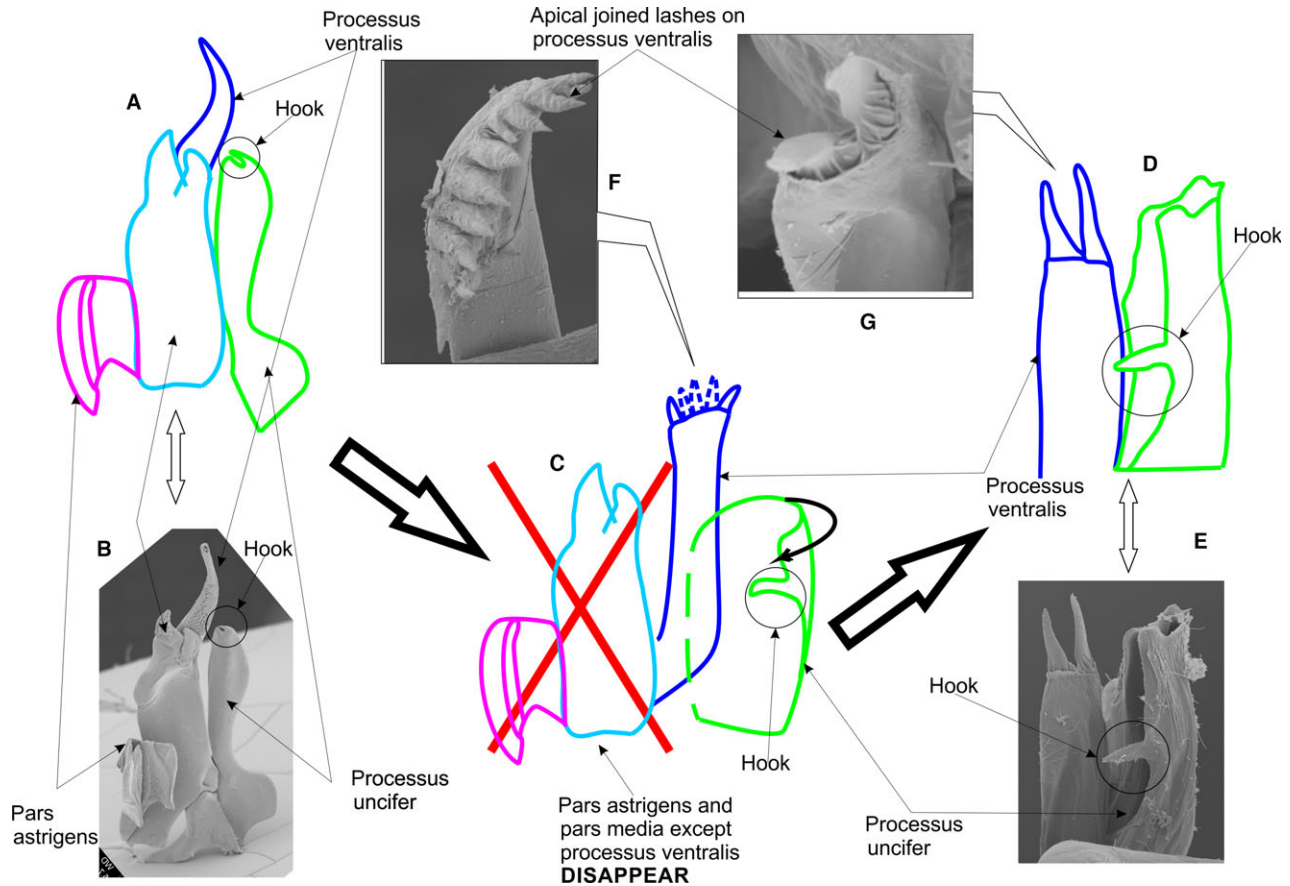


Figure 10. Homologies in the petasma of Luciferae and Sergestidae. Petasma in *Lucifera lucens* (Hansen, 1922), schematic structure (A) and scanning electron micrograph (B); a hypothetical Sergestoidea with transitional states (C); *Lucifer typus* H. Milne Edwards, 1837, schematic structure (D) and scanning electron micrograph (E); distal parts of the processus uncifer with joined lashes in *Deosergestes corniculum* (Krøyer, 1855) (F) and *Lucifer typus* (G). Arrows point at same morphological structures.

cifer pacificus Dana, 1852; *Leucifer uracanthus* Steindachner, 1861; *Lucifer acestra* Dana, 1852 [partim]; *Lucifer acicularis* Dana, 1852 [partim]; *Lucifer batei* Borradaile, 1915; *Lucifer bonitensis* Borradaile, 1915; *Lucifer clausi* Borradaile, 1915; *Lucifer zybrantsii* Philippi, 1857.

Diagnosis: Ventral processes on sixth abdominal segment in male subequal; ventral process on telson large, with swollen part directed downward and slightly forward; second pair of lateral spines on telson positioned just above or slightly posterior to margin of ventral processus. Eystalks very slender, eyes in male larger than in female; outer spine of uropodal exopod nearly reaching distal end of exopod in both sexes. Petasma: sheath with prominent hook branching from a sheath, apically sinuous, nearly entire, armed with transverse chitinous ridges (Fig. 3A) from basal to distal part; processus

ventralis with two terminal lashes joined as a pincer.

Remarks: Only males may be identified with certainty. The prominent hook on the sheath of the petasma is the most significant diagnostic character of this species; this hook can be seen in light microscopy. *Lucifer typus* is the only species of *Lucifer* known from the Atlantic.

Etymology: From the Latin 'typus' meaning 'type'.

Geographical distribution (Fig. 12): North-east Pacific, off Baja California and Gulf of California to north of 4°N; off Newfoundland; north-west Atlantic off USA; Sargasso Sea; Brazil; north-east Atlantic; Mediterranean; south-east Atlantic off Cape of Good Hope; east coast of South Africa; Bay of Bengal; around India; East and South China Seas; Philippines; Malaysia; Queensland, Australia; eastern Central Pacific; Coral Sea.

LUCIFER ORIENTALIS HANSEN, 1919 (FIG. 4A–D)

Diagnosis: Ventral processes on sixth abdominal segment in male subequal; ventral process on telson large, with swollen part directed downward and slightly forward; second pair of lateral spines on telson positioned slightly anterior to margin of ventral process. Eystalks very slender, eyes in male larger than in female; outer spine of uropodal exopod nearly reaching distal end of exopod in both sexes. Petasma: sheath without hook, apically trilobed, armed with transverse chitinous ridges from basal to distal part; processus ventralis with terminal pincer.

Remarks: Only males may be identified with certainty. The absence of the hook on the sheath of the petasma (visible in light microscopy) and the presence of the trilobed (not entire) apex on the sheath both distinguish this species from *L. typus*.

Etymology: From the Latin 'orientalis' meaning 'Eastern', as the species lives in the Indo-Pacific, east of the Atlantic Ocean from where the closely related *L. typus* was initially described.

Geographical distribution (Fig. 12): East coast of South Africa; Red Sea; around India; Indonesia; Malaysia to South China Sea; Philippines; eastern Central Pacific Ocean.

BELZEBUB GEN. NOV

Synonym: *Lucifer* Thompson, 1829 [partim].

Diagnosis: Posterior ventral process on sixth abdominal somite in male nearly straight, tapering, apically subacute. Eystalks of moderate length, subcylindrical, eyes not dimorphic sexually, not reaching end of scaphocerite; stylocerite absent; scaphocerite with distal tooth overreaching end of blade; third maxilliped with entire dactyl, not sexually dimorphic; uropodal exopod with proximal segment not setose along outer margin. Petasma: pars externa transformed into a narrow, tapering sheath supported by strong chitinous rib; sheath armed with apical scales or ridges and with plate-like structures; processus ventralis spiniform, without apical pincer.

Type species: By present designation, *B. hanseni* (Nobili, 1905).

Species: *Belzebub chacei* (Bowman, 1967); *B. faxoni* (Borradaile, 1915); *B. hanseni* (Nobili, 1905); *B. intermedius* (Hansen, 1919); *B. penicillifer* (Hansen, 1919).

Remarks: Corresponds to the species group B of *Lucifer* (Hansen, 1919). The genus is easily distinguished from its sister genus *Lucifer* by medium-sized, subcylindrical eystalks and eyes that are not sexually dimorphic. Males also differ in having a nearly straight posterior ventral process on the sixth abdominal somite and in the shape and armature of the sheath and processus ventralis of the petasma.

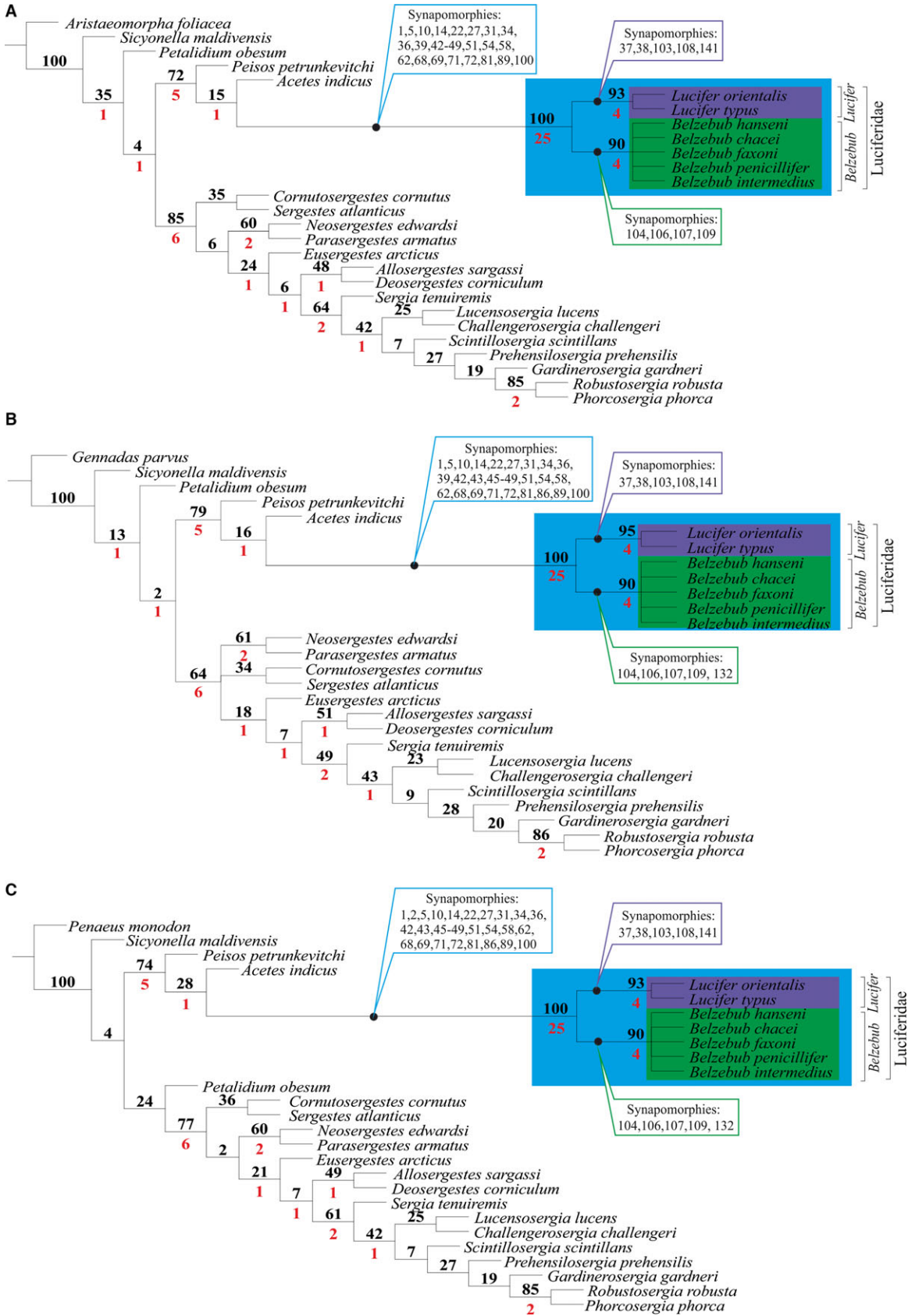
Etymology: From the Hebrew 'ba'al' meaning 'lord' and 'z'bhubb' meaning 'fly'. We chose the Old English transliteration because it is shorter than the Greek 'beelzeboub'. 'Belzebub' is sometimes referred to as another name for the devil, so by this name we allude to the close relationship between this genus and *Lucifer*, another well-known synonym of the word 'devil' (but note that *Lucifer* actually was intended to mean 'light-bearer' in this context).

Distribution: Neritic genus, panoeceanic distribution.

KEY TO SPECIES OF **BELZEBUB GEN. NOV.**

1. Petasma: sheath bottle-shaped, with distal transverse rows of ridges, plate-like structures large and fringed (Fig. 5C, D)
B. intermedius (Hansen, 1919) comb. nov.
- Petasma: sheath subconical, with distal longitudinal rows of fine scales, plate-like structures small, with entire margins (Fig. 7F) 2
2. Petasma: processus ventralis bearing a dense brush of long terminal setae (Fig. 6D–F)
B. penicillifer (Hansen, 1919) comb. nov.
- Petasma: processus ventralis with short, scattered lateral setae only, without dense brush of terminal setae (Figs 7F, 8D) 3
3. Outer tooth of uropodal exopod far from reaching distal end of exopod; petasma: processus ventralis setose along medial part (Fig. 7G, F) *B. hanseni* (Nobili, 1905) comb. nov.
- Outer tooth of uropodal exopod nearly reaching distal end of exopod; petasma: processus ventralis setose along distal part (Fig. 8D) 4
4. Atlantic species *B. faxoni* (Borradaile, 1915) comb. nov.

Figure 11. Strict consensus trees of Sergestoidea with (A) *Aristeomorpha foliacea* (Risso, 1827) as outgroup, with (B) *Gennadas parvus* Bate, 1881; as outgroup, and with (C) *Penaeus monodon* Fabricius, 1798; as outgroup. Bootstrap values are indicated above the nodes and Bremer support below (red font). The clade Luciferidae is in blue, two terminal robust clades of Luciferidae are in green and purple.



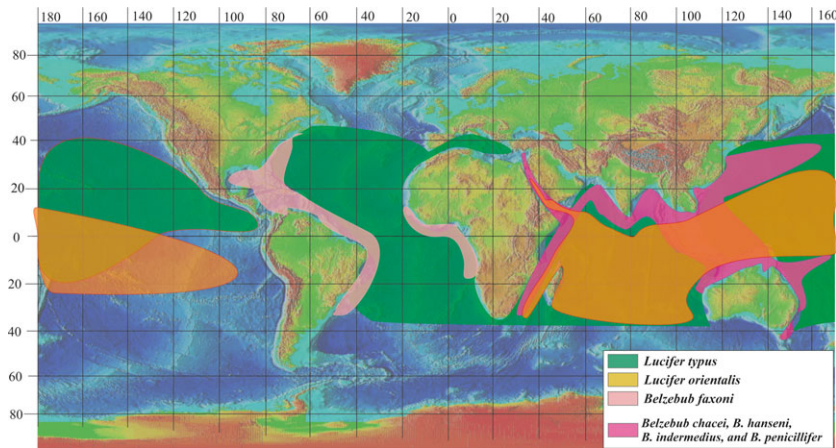


Figure 12. Provisory macroscale geographical distribution of species of *Lucifer* and *Belzebug*. Based upon Dana Expedition data, Hansen (1919), Bowman & McCain (1967), Omori (1977), Lee *et al.* (1992), Perez-Farfante & Kensley (1997), Antony (2005), Ma, Xu & Zhou (2009), Xu (2010), and Teodoro *et al.* (2012).

- Indo-Pacific species *B. chacei* (Bowman & McCain, 1967) comb. nov.

***BELZEBUB INTERMEDIUS* (HANSEN, 1919) COMB. NOV. (FIG. 5A–C)**

Synonym: *Lucifer intermedius* Hansen, 1919.

Diagnosis: Anterior ventral process on sixth abdominal segment in male shorter than posterior process; ventral process on telson of medium size, with swollen part directed downward and slightly backward; outer spine of uropodal exopod nearly reaching distal end of exopod in both sexes. Petasma: sheath without hook, bottle-shaped, with distal transverse rows of ridges, plate-like structures large and fringed; processus long and narrow.

Remarks: Only males can be identified with certainty. The bottle-shaped (not subconical) sheath, transverse rows of ridges and large, fringed, plate-like structures at the apex of the sheath all distinguish *B. intermedius* from all other species of the genus and family. The ultrastructure of the processus ventralis remains unknown.

Etymology: From the Latin ‘intermedius’ meaning ‘intermediate’, an allusion to the transitional set of morphological characters between the two species groups *sensu* Hansen (1919) of the former *Lucifer*.

Geographical distribution (Fig. 12): Gulf of Oman; around India; Indonesia; Malacca Straits; East China Sea; Changjiang estuary to Japan.

***BELZEBUB PENICILLIFER* (HANSEN, 1919) COMB. NOV. (FIG. 6A–E)**

Synonym: *Lucifer penicillifer* Hansen, 1919.

Diagnosis: Anterior ventral process on sixth abdominal segment in male slightly shorter than posterior process; ventral process on telson of medium size, with swollen part directed downward and slightly backward; outer spine of uropodal exopod nearly reaching distal end of exopod in both sexes. Petasma: sheath without hook, subconical, with distal longitudinal rows of fine scales, plate-like structures small, with entire margins; processus long and narrow, bearing a dense brush of long terminal setae.

Remarks: Only males may be identified with certainty. The dense brush of long setae at the tip of the processus ventralis of the petasma distinguishes *B. penicillifer* from all other species of the genus and family.

Etymology: From the Latin ‘penicilla’ meaning ‘brush’, an allusion to the unique brush-like morphology of the processus ventralis.

Geographical distribution (Fig. 12): South-east coast of South Africa; east African coast; Bay of Bengal; around India; Malaysia; Indonesia; South China Sea; East China Sea; Philippines; Hong Kong; Japan; northern Australia.

***BELZEBUB HANSENI* (NOBILI, 1905) COMB. NOV. (FIG. 7A–G)**

Synonyms: *Lucifer Hanseni* Nobili, 1905; *Lucifer hanseni* Borradaile, 1916; *Lucifer inermis* Borradaile, 1915.

Diagnosis: Anterior ventral process on sixth abdominal segment in male much shorter than posterior process; ventral process on telson of medium size; outer spine of uropodal exopod nearly reaching distal end of exopod in male but is much shorter in females (by far not reaching distal end

of exopod). Petasma: sheath without hook, subconical, with distal longitudinal rows of fine scales, plate-like structures small, with entire margins; processus long, needle-like, finely setose along medial part, without a dense brush of long terminal setae.

Remarks: The outer tooth of the uropodal exopod, which is far from reaching (nearly reaching in the other Luciferidae) the distal end of exopod, distinguishes females of *B. hanseni* from all other species of the genus and family. The processus ventralis is very similar to that in *B. faxoni* and *B. chacei*, but differs in the position of the fine lateral setae (medial in *B. hanseni* and apical in *B. faxoni* and *B. chacei*).

Etymology: Named after Dr Hans J. H. Hansen, a Danish carcinologist.

Geographical distribution (Fig. 12): Madagascar; Red Sea; around India; South China Sea, East China Sea; Changjiang estuary; Victoria, Australia, Tasmania, South Pacific Ocean. This species has been recently reported from the Mediterranean coast of Israel, which probably has resulted from a recent invasion through the Suez Canal, rather than the species having gone undetected in the intervening period (De Grave, Einav & Galil, 2012).

***BELZEBUB FAXONI* (HANSEN, 1919) COMB. NOV.**
(FIG. 8A–G)

Synonyms: *Lucifer affinis* Borradaile, 1915; *Lucifer typus* Faxon, 1878; *Lucifer faxoni* Borradaile, 1915; *Lucifer Faxonii* Hansen, 1919.

Diagnosis: Anterior ventral process on sixth abdominal segment in male slightly shorter than posterior process; ventral process on telson of medium size, with swollen part directed downward and slightly backward; outer spine of uropodal exopod nearly reaching distal end of exopod in both sexes. Petasma: sheath without hook, subconical, with distal longitudinal rows of fine scales, plate-like structures small, with entire margins; processus long, needle-like, finely setose along distal part, without a dense brush of long terminal setae. Atlantic species.

Remarks: Only males can be identified with certainty. This species is very similar, if not identical, to *B. chacei* (see remarks on *B. chacei* below). Both species differ from all other species of the genus and family in having subconical sheath enclosing spiniform processus ventralis bearing only sparse lateral setae in the distal part.

Etymology: Named after Dr Walter Faxon, an American ornithologist and carcinologist.

Geographical distribution (Fig. 12): Western Atlantic from Long Island Sound to Rio de Janeiro; Gulf of

Mexico; Caribbean Sea; Bermuda; eastern Atlantic off Senegal and Congo.

***BELZEBUB CHACEI* (BOWMAN & MCCAIN, 1967)**
COMB. NOV. (FIG. 9A–D)

Synonym: *Lucifer chacei* Bowman & McCain, 1967.

Diagnosis: Anterior ventral process on sixth abdominal segment in male slightly shorter than posterior process; ventral process on telson of medium size, with swollen part directed downward and slightly backward; outer spine of uropodal exopod nearly reaching distal end of exopod in both sexes. Petasma: sheath without hook, subconical, with distal longitudinal rows of fine scales, plate-like structures small, with entire margins; processus long, needle-like, finely setose along distal part, without a dense brush of long terminal setae. Indo-Pacific species.

Remarks: In the description of *B. chacei*, Bowman & McCain (1967: 269) wrote: “*L. chacei* is so similar to *L. faxoni* that it is possible that their generic divergence is at the subspecific rather than specific level”. Bowman & McCain (1967: 270) suggested four diagnostic characters: (1) eyes slightly shorter in *B. chacei*, (2) rostrum slightly shorter in *B. chacei*, (3) ventral process of telson broader in *B. chacei*, and (4) sheath of petasma curved in *B. chacei* and straight in *B. faxoni*. We did not find the first three characters reliable owing to variation and resulting subjectivity in use. The fourth character (curvature of the sheath) may vary significantly in form depending on the view point of the observer and therefore is of uncertain value. We also failed to find any reliable diagnostic character in the ultrastructure of the petasma, the organ that shows significant differences amongst all other species of Luciferidae. However, we adopt a conservative approach and consider *B. chacei* as a valid species but highlight the need for future research, preferably with the use of molecular methods.

Etymology: Named after Dr Fenner A. Chace, Jr., an American carcinologist.

Geographical distribution (Fig. 12): East coast of South Africa; Madagascar; around India; Indonesia to Hawaii; Tahiti.

MORPHOLOGICAL TRENDS IN LUCIFERIDAE

Analyses 1–3 show that the clade Luciferidae differs from the closely related *Acetes* and the more basally placed *Sicyonella* and *Petalidium* in the reduction or absence of numerous morphological characters. Some structures are reduced: the number of movable lateral spines on the telson (two left on each side), endites of the maxillula (two left), entire

(not subdivided and elongated) dactyl of the third maxilliped. Many structures are absent: all arthrobranchia, the ventral flagellum on the antennules along with the male clasping organ, the stylocerite of the first antennae, the mandibular palp, the epipods and exopods of the first and second maxillipeds, the chela of the first and second pereopods, and the fifth pereopods in both sexes. It is interesting to note that many of these structures are also absent or incompletely developed in many sergestid larvae. Additional characters shared between Luciferidae and Sergestoidea larvae include: a wide separation of the labrum from the antennae and eyes, the presence of a pterygostomial tooth on the carapace (Hansen, 1919; Vereshchaka, 2000, 2009). We therefore suggest a neotenic origin of Luciferidae.

Alongside with a general minimization in size, Luciferidae has adopted a new ecological niche that is reflected in a set of synapomorphies related to a new type of feeding and other behavioural strategies. Luciferids are carnivorous and the third pereopods are adapted to catching small planktonic crustaceans on which the shrimps feed (Lee *et al.*, 1992). The morphological adaptations (synapomorphies) of the third pereopod for carnivorous feeding involve the presence of robust, curved spines all over the limb, very long specialized setae on the propodus, and a very specialized subchela (68, 69, 71, 72 see numbers of characters in Appendix S2).

Another phylogenetic trend relates to reproduction. The presence of ventral processes on the sixth abdominal somite and on the telson in the male (31, 36) may indicate an alternative mechanism of male–female coupling in Luciferidae. In other Sergestoidea clasping take place using structures on the anterior part of the body (clasping organ on the male antennula), but in Luciferidae structures on the posterior body part may be involved. Such a ‘hindbody’ clasping mechanism is further supported by the presence of a greatly elongated outer spine on the uropodal exopod in both sexes (86). Such a putative different clasping posture in Luciferidae would imply a different mechanism for spermatophore transfer, which could explain the greatly variable petasma structure in the family. Amongst the unique features of the petasma in Luciferidae is the lack of a pars astrigens (100). The function of a pars astrigens is probably to unite the left and right side petasmas so that they can operate as a single organ during spermatophore transfer. In Luciferidae, where a pars astrigens is lacking, the right and left side petasmas may operate as two independent hand-like structures using the ‘thumb’, ‘first finger’, and ‘palm’ to oppose each other during spermatophore handling. The polarization of a number of other characters indicates that the coupling mecha-

nisms in *Lucifer* and *Belzebub* have been subject to much evolution. In *Lucifer*, the pars astrigens of the petasma has been drastically modified into a wide sheath entirely armed with transverse chitinous ribs enclosing the processus ventralis (103, 108), whereas the latter has got an apical pincer (141). Other synapomorphies of *Lucifer*, such as the elongate eyestalks and the sexually dimorphic eyes (37, 38), may also be related to mating. In *Belzebub*, the pars astrigens of the petasma has been transformed into a narrow sheath supported by chitinous ribs and apically armed with terminal setae, fine scales, and plate-like structures (104, 107, 109). This sheath covers the processus ventralis, which is lacking apical pincer but bearing lateral friction structures (132).

ACKNOWLEDGEMENTS

These studies were supported by the Russian Foundation for Basic Research (grant number 15-04-08228), the Danish Carlsberg Foundation, and the Presidium Programs 3P and 22P of the Russian Academy of Sciences.

REFERENCES

- Ahyong ST. 2009.** The polychelidan lobsters: phylogeny and systematics (Polychelida: Polychelidae). In: Martin JW, ed. *Decapod crustacean phylogenetics*. Los Angeles, CA: Natural History Museum of L. A. County, 369–396.
- Antony G. 2005.** Occurrence and distribution of the planktonic shrimps of the genus *Lucifer* in the EEZ of India. *Journal of the Marine Biological Association of India* **47**: 20–30.
- Barnard KH. 1950.** Descriptive catalogue of South African decapod crustacea. *Annals of the South African Museum* **38**: 1–837.
- Bate CS. 1881.** On the Penaeidea. *Annals and Magazine of Natural History* **5**: 169–196.
- Bate CS. 1888.** Report on the Crustacea *Macrura* dredged by HMS Challenger, Zoology 23. 942.
- Borradaile LA. 1915.** Notes on Carides. *Annals and Magazine of Natural History* **15**: 205–213.
- Bowman TE. 1967.** The planktonic shrimp, *Lucifer chacei* sp. nov., (Sergestidae: Luciferinae), the Pacific Twin of the Atlantic *Lucifer faxoni*. *Pacific Science* **21**: 266–271.
- Bowman TE, McCain JC. 1967.** Distribution of the planktonic shrimp, *Lucifer*, in the Western North Atlantic. *Bulletin of Marine Science* **17**: 660–671.
- Burkenroad MD. 1983.** Natural classification of Dendrobranchiata, with a key to recent genera. In: Schram ER, ed. *Crustacean Phylogeny*. Crustacean. Rotterdam: A A Bakelma, pp. 279–290.
- Dana JD. 1852.** Conspectus crustaceorum, etc. Conspectus of the Crustacea of the exploring expedition under Capt. C. Wilkes, USA. *Proceedings of the Academy of Natural Sciences of Philadelphia* **6**: 6–28.

- De Grave S, Franssen CHJM. 2011.** *Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda)*. Leiden: NCB Naturalis.
- De Grave S, Einav R, Galil BS. 2012.** Recent records of the Indo-Pacific species, *Lucifer hanseni* Nobili, 1905 (Crustacea; Decapoda; Luciferidae) from the Mediterranean coast of Israel. *BioInvasions Records* **1**: 115–118.
- De Haan W. 1833–1850.** Crustacea. In: von Siebold PF, ed. *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suspecto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit: i–xxxix, ix–xvi, 1–243, Plates A–J, L–Q, 1–55. Lugduni-Batavorum.*
- Fabricius JC. 1798.** *Entomologia systematica emendata et aucta: supplementum*. Hafniae: Proft et Storch, 1–572.
- Goloboff P, Farris S, Nixon K. 2000.** *TNT: tree analysis using new technology*. Available at: <http://www.lillo.org.ar/phylogeny/tnt/>
- Hansen HJ. (1919).** *The Sergestidae of the Siboga expedition*. 1–65.
- Lee WY, Omori M, Peck RW. 1992.** Growth, reproduction and feeding behavior of the planktonic shrimp, *Lucifer faxoni* Borradaile, off the Texas coast. *Journal of Plankton Research* **14**: 61–69.
- Ma Z, Xu Z, Zhou J. 2009.** Effect of global warming on the distribution of *Lucifer intermedius* and *L. hanseni* (Decapoda) in the Changjiang estuary. *Progress in Natural Science* **19**: 1389–1395.
- Milne Edwards Y. 1837.** *Histoire Naturelle des Crustacés comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux*, Vol. 2, 532.
- Naomi TS, Geetha A, George RM, Jasmine S. 2006.** Monograph on the planktonic shrimps of the genus *Lucifer* (Family Luciferidae) from the Indian EEZ. *Central Marine Fisheries Research Institute Bulletin* **49**: 1–54.
- Nixon K. 1999.** The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* **15**: 407–414.
- Nobili G. 1905.** Diagnoses préliminaires de 34 espèces et variétés nouvelles, et de 2 genres nouveaux de Décapodes de la Mer Rouge. *Bulletin du Muséum d'Histoire Naturelle* **6**: 393–411.
- Olesen J, Richter S, Scholtz G. 2003.** On the ontogeny of *Leptodora kindtii* (Crustacea, Branchiopoda, Cladocera), with notes on the phylogeny of the Cladocera. *Journal of Morphology* **256**: 235–259.
- Omori M. 1977.** Distribution of warm water epiplanktonic shrimps of the genera *Lucifier* and *Acetes* (Macrura, Penaeidea, Sergestidae). Proc. Symp. Warm Water Zooplankton. Spl. Publ., Goa: NIO, 1–12.
- Ortmann A. 1898.** Gliederfüssler: Arthropoda. In: Bronn's Klassen und Ordnungen des Tierreichs. 5(2) Crustacea, Malacostraca - [Systematik]: 1057–1168.
- Perez-Farfante I, Kensley B. 1997.** Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera. *Editions du Museum national d'Histoire naturelle* **1997**: 233.
- Petit D. 1973.** Données sur la morphologie et la croissance chez le genre *Lucifer* (Decapodes Sergestidae): *L. intermedius*, *L. penicillifer*, *L. hanseni*, *L. chacei*, *L. faxonii*. *Cahiers ORSTOM. Série Océanographie* **11**: 207–227.
- Rafinesque CS. 1815.** *Analyse de la Nature ou Tableau de l'Univers et des corps organisés*. Palerme, 1–224.
- Squires HJ. 1990.** Decapod Crustacea of the Atlantic Coast of Canada. *Canadian Bulletin of Fisheries and Aquatic Science* **221**: 1–532.
- Steindachner F. 1861.** Vorläufige Mittheilung über *Leucifer uracanthus* n. sp., *Ophianoplus sarsii* n. sp., und über äusseren Kiemen-Anhänge der Protopterus-Arten. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* **11**: 365–366.
- Teodoro SDSA, Negreiros-Fransozo ML, Simões SM, Lopes M, Costa RCD. 2012.** Population ecology of the planktonic shrimp *Lucifer faxoni* Borradaile, 1915 (Crustacea, Sergestoidea, Luciferidae) of the southeastern coast of Brazil. *Brazilian Journal of Oceanography* **60**: 245–253.
- Thompson JV. 1829.** Zoological researches, and illustrations; or, natural history of nondescript or imperfectly known animals, in a series of memoirs, illustrated by numerous figures. Memoir 3. On the luminosity of the Ocean, with description of some remarkable species of luminous animals (*Pyrosoma pigmaea* and *Sapphirina indicator*) and particularly of the four new genera, *Noctiluca*, *Cynthia*, *Lucifer* and *Podopsis*, of the Shizopoda, 30.
- Vereshchaka A. 2000.** The genus *Sergia*: taxonomy, systematics, and distribution. “Galathea” Report 19, 207.
- Vereshchaka A. 2009.** The genus *Sergestes*: taxonomy, systematics, and distribution. “Galathea” Report 22, 137.
- Vereshchaka AL, Lunina AA. 2015.** Phylogeny and taxonomy of the enigmatic genus *Petalidium* (Decapoda, Sergestidae), with biological remarks. *Zoological Journal of the Linnean Society* **174**: 459–472.
- Vereshchaka A, Olesen J, Lunina A. 2014.** Global diversity and phylogeny of pelagic shrimps of the former genera *Sergestes* and *Sergia* (Crustacea, Dendrobranchiata, Sergestidae), with definition of eight new genera. *PLoS ONE* **9**: e112057.
- Williams AB. 1984.** *Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida*. Washington, DC: Smithsonian Institution Press, 550.
- Woodmansee RA. 1966.** Daily vertical migration of *Lucifer*, planktonic numbers in relation to solar and tidal cycles. *Ecology* **47**: 847–850.
- Wood-Mason J, Alcock A. 1891.** Natural history notes from H.M. Indian marine survey steamer ‘Investigator’, Commander R.F. Hoskyn, R.N., commanding. Series II, No. 1. On the results of deep-sea dredging during the season 1890–1891. *Annals and Magazine of Natural History* **XLVI**: 268–286.
- Xu ZL. 2010.** Determining optimal temperature and salinity of *Lucifer* (Dendrobranchiata: Sergestoidea: Luciferidae) based on field data from the East China Sea. *Plankton and Benthos Research* **5**: 136–143.
- Zimmerman ST. 1973.** The transformation of energy by *Lucifer chacei* (Crustacea, Decapoda). *Pacific Science* **27**: 247–259.

SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article.

Appendix S1. Included taxa with museum information.

Appendix S2. List of characters used. New or revised characters are marked with asterisks (*).

Appendix S3. Data matrix. Missing data indicated by question marks (?); inapplicable data by hyphens (-).