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Phylogeny and classification of the shrimp genera *Acetes*, *Peisos*, and *Sicyonella* (Sergestidae: Crustacea: Decapoda)

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Despite their role in marine systems, Sergestidae remain one of the most poorly understood families amongst planktonic shrimps with regard to phylogeny. Recent morphological and phylogenetic revisions of a number of sergestid genera have disentangled classificatory problems and emphasized the importance of reproductive structures for the taxonomy and phylogeny of the Sergestidae. Only three genera, *Acetes*, *Peisos*, and *Sicyonella*, remain unrevised phylogenetically. We undertook a phylogenetic analysis of these groups based on 124 morphological characters (120 binary, four multistate). Eighteen new characters were based on scanning electron microscopy studies of the clasping organ and petasma. The phylogenetic analysis revealed statistically supported monophyly of the clades *Sicyonella* and *Acetes* + *Peisos*. We combine *Peisos* and *Acetes* into a monophyletic genus *Acetes*, give emended diagnoses and keys to all species of *Sicyonella* and *Acetes*, and discuss morphological trends within these genera. We present maps of geographical distribution for all valid species of *Acetes*.

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ADDITIONAL KEYWORDS: anatomy – cladistic analysis – identification key – morphological phylogenetics – morphology – phylogenetics – taxonomy.

INTRODUCTION

Sergestid shrimps are important components of marine systems. The family Sergestidae comprises 16 pelagic genera widely distributed in the Atlantic, Indian, and Pacific Oceans (Appendix 1). These genera encompass 74 valid species, which have been recently revised (Vereshchaka, 2000, 2009; Vereshchaka, Olesen & Lunina, 2014; Vereshchaka & Lunina, 2015). In addition to these genera, the Sergestidae comprises three minor genera: *Sicyonella* with three species, *Acetes* with 14 species, and the monotypic *Peisos*. Economically, *Acetes* is one of the most important organisms in Asian and East African waters (Fig. 1D); during certain parts of the year species of *Acetes* form conspicuous aggregations near the shore, leading to an extensive fishing activity (Omori, 1975). Emended diagnoses and keys to species of *Acetes* and a review of their geographical distribution may be important for fishery planning. The genera *Sicyonella* and *Peisos* are not significant for fisheries.

All three species of *Sicyonella* were recently redescribed with the use of scanning electron microscopy (SEM; Fukuoka, Tamaki & Kikuchi, 2005), whereas the latest revision of *Acetes* was more than 40 years ago (Omori, 1975). The phylogenetic status of the monotypic *Peisos* has not been tested since the description of its only species, *Peisos petrunkevichi* (Burkenroad, 1945). The genus *Acetes* (Fig. 1A–C) was established by H. Milne Edwards (1830) for *Acetes indicus* (type by original designation). Thirteen additional species were described between 1893 (*Acetes americanus* Ortmann, 1893) and 1975 (*Acetes intermedius* Omori, 1975, and *Acetes marinus* Omori,

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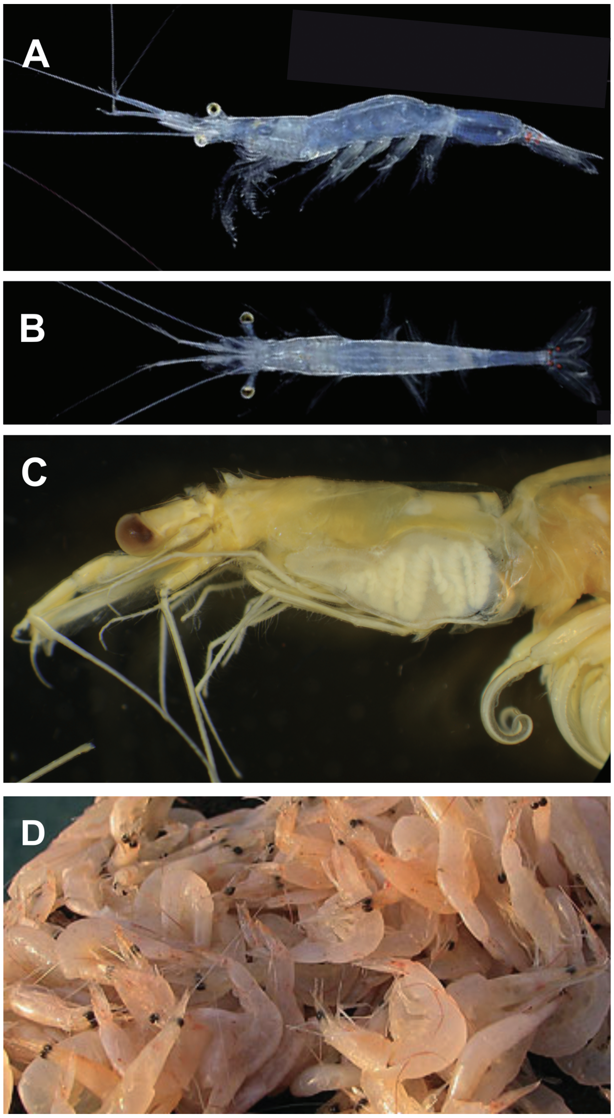

Figure 1. *Acetes japonicus in situ*, lateral (A) and upper (B) view; *Acetes paraguayensis*, allotype, ZMUC CRU-09812 in collection of the Natural History Museum of Denmark (C); *Acetes* sp. at a Indonesian fish market (D).

1975). During this period, the genera *Sicyonella* Borradaile, 1910 and *Peisos* Burkenroad, 1945 were also described.

Recent phylogenetic studies of Sergestidae using cladistic methods resulted in significant taxonomic changes both below and above the genus level (Vereshchaka *et al*., 2014; Vereshchaka & Lunina, 2015). At this stage, it is appropriate to revise the remaining minor sergestid genera, *Sicyonella*, *Acetes*, and *Peisos*, to bring the phylogenetic studies of the Sergestidae near completion.

In contrast to the other genera of Sergestidae, *Acetes*, *Peisos*, and *Sicyonella* occur in coastal and even fresh waters and have a unique set of characters compared with other sergestids. Relative to other sergestids, *Acetes* and *Peisos* have simplified mouthparts, rudimentary or absent pereopods, and a simplified petasma, etc. Conversely, *Sicyonella* is characterized by well-developed pereopods with full-sized chelae and a complete set of segments in the natatory pereopods (all pereopods are significantly reduced in the other sergestids), and an elaborated petasma, etc. It remains unclear as to which of these genera represent early branching lineages or rather terminal clades. All three genera are important for understanding the phylogeny of Sergestidae, as has been noted before (Burkenroad, 1945).

The ultrastructure of clasping and copulatory organs has been shown to be important both taxonomically and phylogenetically (Vereshchaka *et al*., 2014; Vereshchaka & Lunina, 2015). In the primitive state, these organs are simple finger-like, undivided, and lacking specialized additional structures, whereas in the derived state they demonstrate various branching, change in shape, and the presence of numerous minute structures, amongst other specializations. (Vereshchaka *et al*., 2014; Vereshchaka & Lunina, 2015). In *Acetes* and *Peisos*, the clasping and copulatory organs have been studied with the use of light microscopy only (Hansen, 1919; Omori, 1975). No comparative analysis of the morphology of the clasping and copulatory organs has been carried out between *Acetes* and *Peisos*, and *Sicyonella*.

In this paper we provide information on the ultrastructure of the clasping and reproductive organs of *Acetes* and *Peisos* with the use of SEM as the basis for a morphology-based phylogenetic analysis of these groups. Our overall goals were to test the monophyly of all three genera, to analyse their status and position within Sergestidae, to discuss morphological trends within these genera, to revise the classification of the family, and to provide a key to valid species as well as maps of their geographical distribution.

MATERIAL AND METHODS

All 14 recognized species of *Acetes*, three species of *Sicyonella*, *Peisos petrunkevichi*, and 16 type species representing all other genera of Sergestidae were included as terminals. Character state scoring for each species was derived from examination of specimens (see Appendix 1). Characters were polarized using three species representing three families of Penaeoidea, each occurring in three different types of oceanic habitats (benthopelagic, pelagic, and benthic) and therefore representing different types of morphology. The three outgroup species – all of which are type species for their genera – were *Aristeomorpha foliacea* (Aristeidae), which is benthopelagic; *Gennadas parvus* (Benthesicymidae), which is pelagic; and *Penaeus monodon* Fabricius, 1798 (Penaeidae), which is benthic.

Character state scoring for each outgroup species was derived from examination of specimens (see Appendix 1).

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

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 124 modified characters (120 binary, four multistate, amongst which 18 are new – see Appendix 2). The data matrix is presented in Appendix 3.

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

All characters were unordered (non-additive) and equally weighted; missing data were scored as unknown. Trees were generated in TNT under the 'implicit enumeration' procedure. Relative stability of clades was assessed by standard bootstrapping (sampling with replacement) with 10 000 pseudoreplicates and by Bremer support (tree bisection-reconnection algorithm, saving up to 10 000 trees up to three steps longer). We considered the clades statistically significant if they were supported either by Bremer support ≥ 3 or bootstrap values ≥ 80.

RESULTS AND DISCUSSION

Ultrastructure of sexual characters and possible homologies

As for other sergestids, the sexual structures of *Sicyonella* and *Acetes* (the clasping organ and the petasma) are well known to provide reliable information for classification (Hansen, 1919; Vereshchaka & Lunina, 2015). As not all information was available under light microscopy, SEM was used here for more detailed examination.

Serrated setae are present on the clasping organs and differ from the ordinary setae in being more robust and possessing distal serrations as seen by light microscopy (Vereshchaka, 2000, 2009). However, under SEM it can be seen that the serrated setae exhibit a complicated ultrastructure (Fig. 2). In *Acetes* and *Peisos* (except *A. americanus* and *Acetes binghami*), the serrated setae have reticulate distal parts and resemble morel mushrooms (Fig. 2A–C), whereas in *A. americanus* and *A. binghami* the setae bear longitudinal ribs (Fig. 2D). The function of these setae is uncertain but owing to their robustness they may assist in holding the female during mating and/or have chemo-/mechanoreceptory functions.

The clasping tubercle is very similar in ultrastructure to the serrated setae (Fig. 3A) and we assume that they are homologous. The clasping tubercle is most likely derived from a serrated setae of the outer male antennular flagellum. It is remarkable that *Acetes* has two tubercles; all other sergestid genera have a single one. The second tubercle may be either rudimentary (Figs 4A, C, E, 5C, 6A, 7A, C, 8C, E) or developed (Figs 5A, E, 6C, E, 7E, 8A).

Scales on the clasping organs were reported by Fukuoka *et al*. (2005) for *Sicyonella inermis* (Fig. 9A). We found similar structures in *Acetes paraguayensis* and *A. marinus* (Fig. 7A, C). Further examination of clasping organs showed that fine scales generally are present (Fig. 3A–F); they are absent only in a few species with rudimentary clasping organs (Fig. 3F). The fine scales most likely assist in clasping of the female during mating. They are absent in two species of *Sicyonella* (Fig. 9C, E) and in 13 species of *Acetes*, (Figs 4–6, 7E, 8); in these species they are replaced by two characteristic rows of serrated setae (*Sicyonella*) or by scattered pairs of robust claw-like setae (*Acetes*) that suggest an alternative clasping mechanism.

The pars media of the petasma is present in all species of *Sicyonella* (Fig. 8B, D, F) and *Acetes* except *A. marinus* (Fig. 7B). Both genera show much variation in the shape of the pars media, from being entire in *S. inermis* (Fig. 9B) and vestigial in *A. paraguayensis* (Fig. 7D) to branched in the rest of *Sicyonella* (Fig. 9D, F) and in *A. americanus* (Fig. 4D). The capitulum of the pars media in all Sergestidae, except *Acetes*, is armed with hooks visible under light microscopy (Vereshchaka, 2000, 2009; Vereshchaka *et al*., 2014). SEM shows that these hooks are squamose (Fig. 10D–F) and may form pincers in *Sicyonella* (figs 4, 10, 15 in Fukuoka *et al*., 2005) and in other sergestids (Fig. 10F). Homologies between lobes and processi in these genera have been convincingly established previously (Hansen, 1919, 1922; Vereshchaka, 2000, 2009; Fukuoka *et al*., 2005; Vereshchaka *et al*., 2014).

In *Acetes*, the capitulum of the pars media is armed with true claws (Fig. 10A–D), which are different from the squamose hooks of other sergestids (Fig. 10E–G). In *A. binghami*, *A. americanus*, and *A. petrunkevichi* (Fig. 4B, D, F), the pars media is divided and the longer branch bears tubular apical claws with serrated tips (Fig. 4D, F). These apical claws may represent a transitional state between the entire claws of *Acetes* and

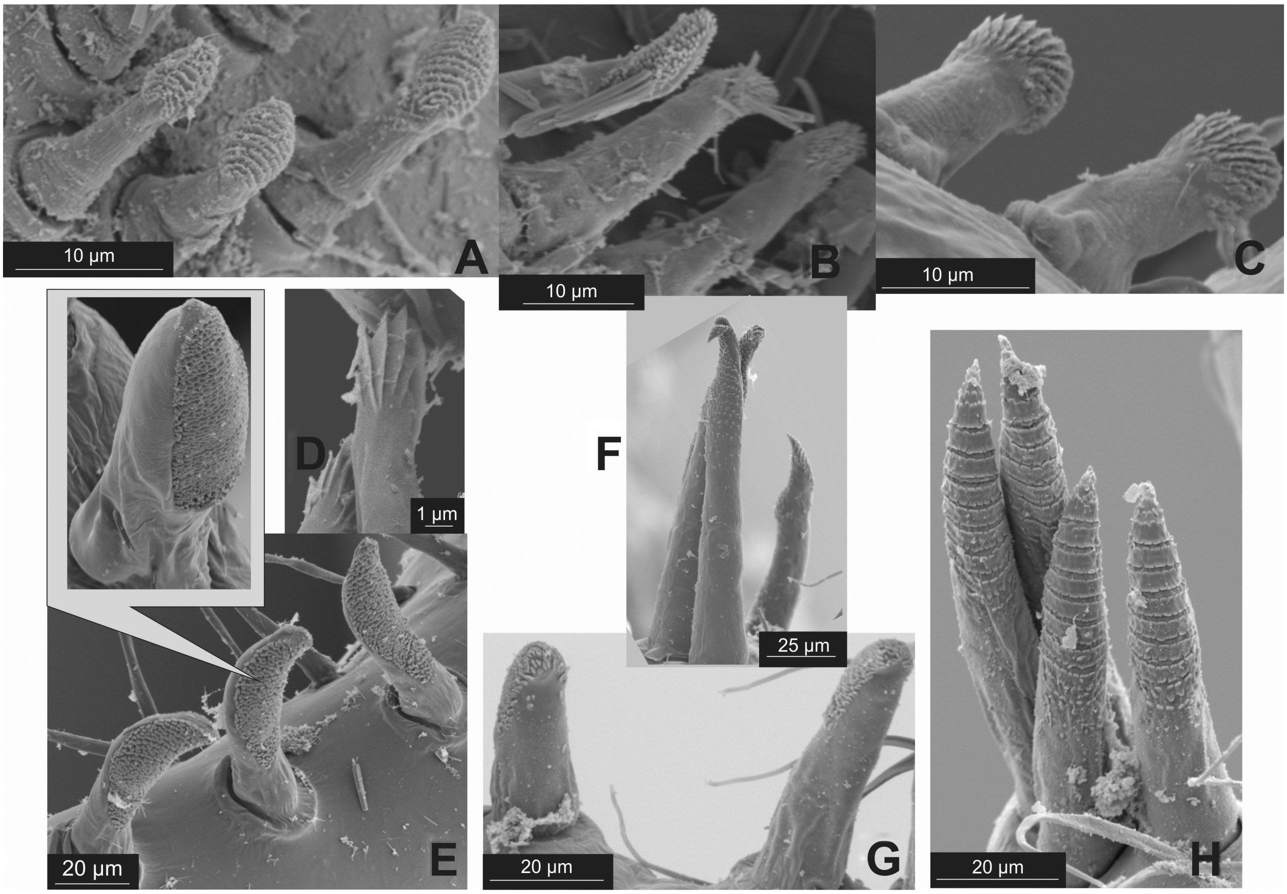

Figure 2. Sensory setae ('serrated bristles') of clasping organ (second antenna) in Sergestidae: A, *Acetes petrunkevichi*; B, *Acetes intermedius*; C, *Acetes marinus*; D, *Acetes americanus*; E, *Petalidium foliaceum*; F, *Robustosergia robusta*; G, *Challengerosergia challenger*; H, *Lucensosergia lucens*.

Peisos and the squamose hooks of other sergestids. We assume that the branches of the petasma in *A. binghami*, *A. americanus*, and *A. petrunkevichi* are nonhomologous to the lobi and processi of other sergestids. Only the processus ventralis, when present, can be recognized with certainty, owing to its characteristic position.

The pars astringens and pars externa in *Sicyonella* and *Acetes* are certainly homologous to those in other sergestid genera. In *Acetes*, the pars astringens is extraordinarily variable in morphology: It may be large, with a hook on the processus uncifer (Fig. 4B), large without a hook (Figs 5D, 6B, 7B, D, 8D, F), vestigial (Figs 5B, 7F), or absent (Figs 4D, F, 5F, 6D, F).

Supported clades

Each of analyses with *Ar. foliacea* (Analysis 1), *G. parvus* (Analysis 2), and *Pen. monodon* (Analysis 3) as outgroups retrieved nine minimal length trees, with 231, 237, and 232 steps, respectively. The topology of all three trees was identical; all supported clades are shown in Figure 11. The clade *Sicyonella* is sister to the rest of Sergestidae and received high Bremer support (4–5). Within the clade *Sicyonella*, a terminal clade *Sicyonella antennata* + *Sicyonella* received strong statistical support (8 Bremer and 98 bootstrap support). Within the rest of Sergestidae, *Acetes* is sister to the remaining genera, and received extraordinarily high Bremer (13) and bootstrap (100) support. Within the clade *Acetes*, the terminal clade *Acetes vulgaris* + *Acetes sibogae* + *Acetes intermedius* + *Acetes erythraeus* is supported statistically (4 Bremer and 79–80 bootstrap support).

The monophyly of *Sicyonella* and *Acetes* and the status of *Peisos*

Analyses 1–3, each with a different outgroup, revealed statistical support for the clade *Sicyonella*, thus suggesting its monophyletic origin. The genus is supported by the following synapomorphies, which are common for analyses 1–3 (Fig. 12): maxillula in adults

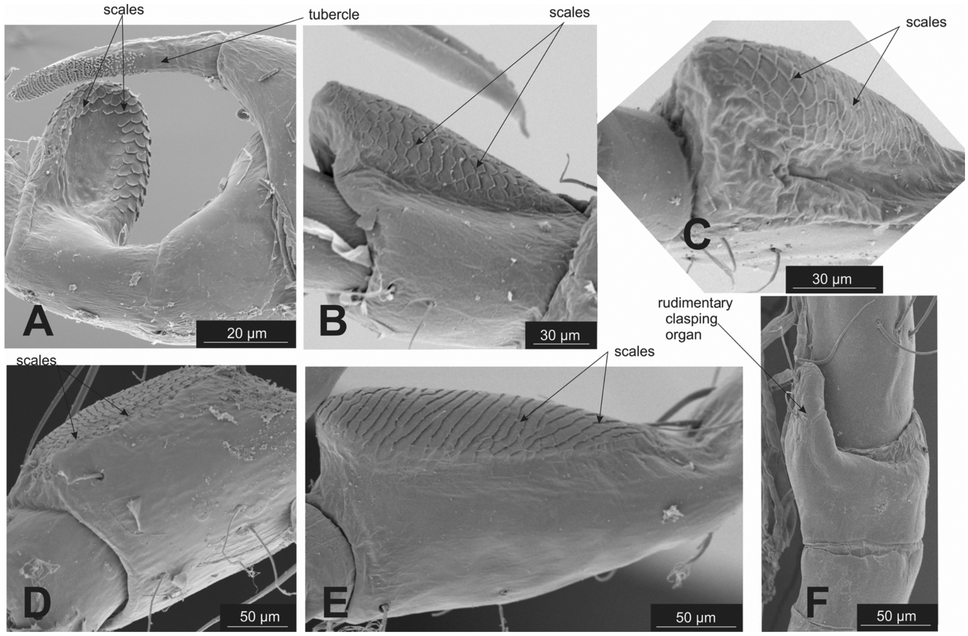

Figure 3. Tubercle and scales of the clasping organ in Sergestidae: A, *Acetes marinus*; B, *Challengerisergia challenger*; C, *Lucensosergia lucens*; D, *Robustosergia robusta*; E, *Deosergestes corniculum*; F, *Challengerosergia talismani*.

with two endites (character 29 – see Appendix 2), enlarged third maxilliped (31), and slightly reduced chela of second and third pereopods (43, 50).

Both the number of synapomorphies and the statistical robustness of the clade confirm the status of *Sicyonella* as being both monophyletic and significantly derived, justifying its taxonomic status as a separate genus.

Analyses 1–3 also revealed a very high level of statistical support for the clade *Acetes*, suggesting that this clade is also monophyletic. The clade *Acetes* without *Acetes petrunkevitchi* (= former *Peisos petrunkevitchi*) never gained robust support. We therefore combine all species of *Acetes* and the former *Peisos petrunkevitchi* into a single genus and consider *Peisos* as a junior synonym of *Acetes*. The genus is supported by the following synapomorphies, which are common for analyses 1–3: arthrobranchs on somites IX–XII absent (10, 12, 14, 15, 18), very elongated third antennular segment (24), single endite on the maxillula in adults present (29), endopod on the first maxilliped reduced or absent (30), much reduced chela on first pereopod (40), fifth pereopod in males much reduced (70), two clasping tubercles (79–80), and presence of a strong distal tooth on the fourth segment of the clasping organ (89).

TAXONOMY OF *SICYONELLA* AND *ACETES*

A key to the genera of Sergestidae is given in Vereshchaka *et al*. (2014). The results of the phylogenetic analyses provided here indicate the need for an emended diagnosis of the genera *Sicyonella* and *Acetes*.

SICYONELLA BORRADAILE, 1910

Diagnosis: Carapace and abdomen smooth, firm; labrum not much separated from antennae and eyes; rostrum acute with oblique frontal margin and two dorsal teeth; supraorbital, pterygostomial, and hepatic teeth present; sixth abdominal somite and telson in males without ventral processes; telson with four pairs of lateral spines; eyestalks not elongated, cornea well pigmented; third antennular segment without ventral processes, shorter than first segment; stylocerite present, mobile; mandible with palp; maxillula in adults with two endites; first maxilliped with three-segmented exopod and epipod; second maxilliped with epipod; third maxilliped > two times as long as first pereopod, not dimorphic sexually, dactyl four-segmented; first pereopod with ischium lacking strong movable spines and normally developed chela, fingers subequal; second pereopod with merus lacking proximal protrusion and reduced chela lacking elongated setae, fingers subequal; third pereopod with reduced chela lacking strong curved spines and elongated setae, fingers subequal; pereopods IV–V progressively decreasing in length, flat, seven-segmented, carpi and meri setose only on one margin; uropodal exopod setose at distal part 1/5 of outer margin, with small tooth by far not reaching distal end of exopod. Male clasping organ: well developed, without

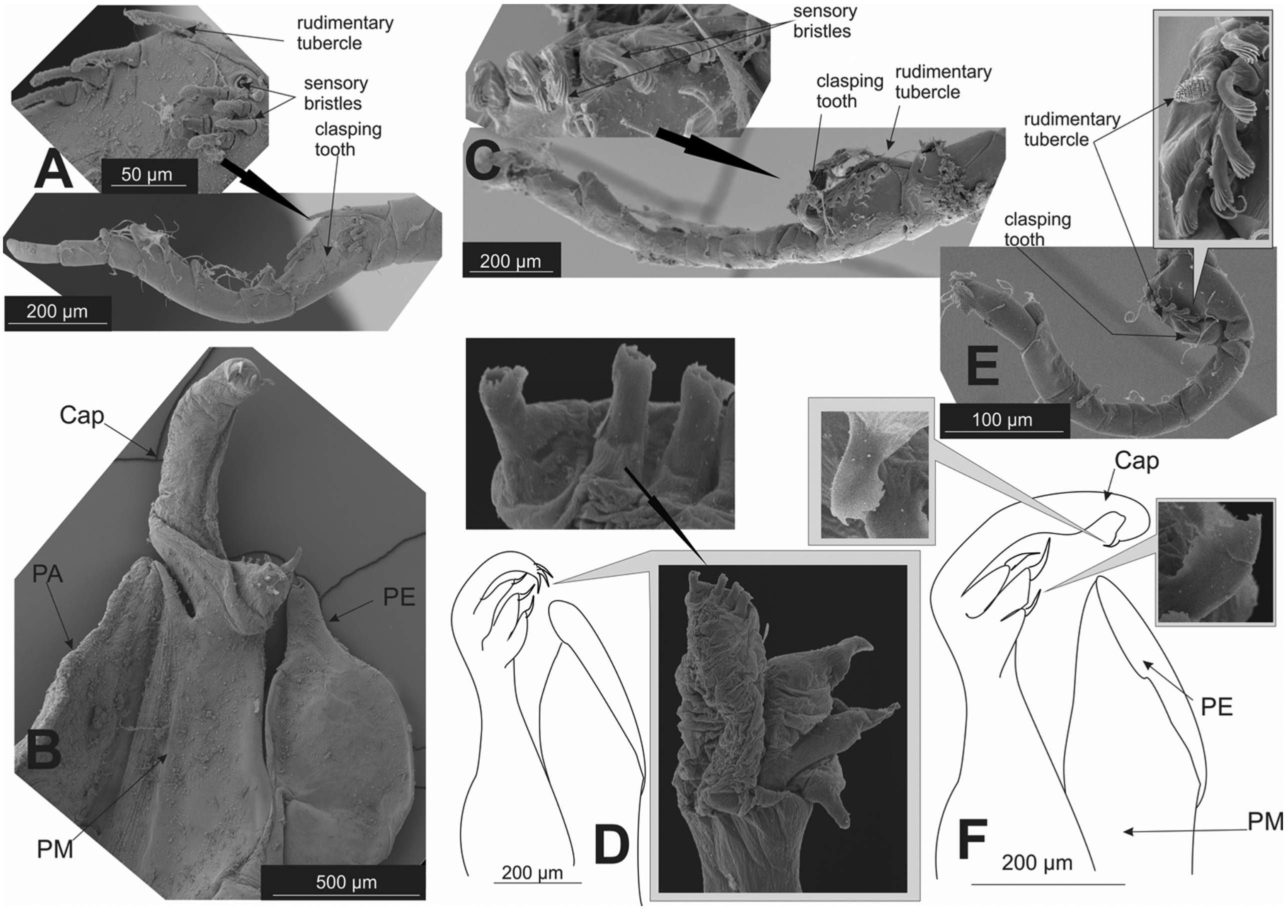

Figure 4. *Acetes petrunkevichi*: clasping organ (A) and petasma (B); *Acetes americanus*: clasping organ (C) and petasma (D); *Acetes binghami*: clasping organ (E) and petasma (F). Cap, capitulum; PA, pars astringens; PE, pars externa; PM, pars media.

clasping tubercle, bearing two contiguous rows of strong sensory setae or numerous scales. Petasma: pars astringens present, pars media developed, armed with pincers; processus uncifer developed, laminar, lacking hook. Photophores: dermal organs and organ of Pesta absent. Branchiae: podobranch on somite VIII, dendritic anterior arthrobranchs on somites IX–XIII, rudimentary posterior arthrobranchs on somites IX–XII, and dendritic posterior arthrobranchs on somite XIII.

Type species: By monotypy, *Sicyonella maldivensis* Borradaile, 1910.

Species: Sicyonella antennata Hansen, 1919, *Sicyonella inermis* (Paul'son, 1875), *Sicyonella maldivensis* Borradaile, 1910.

Remarks: Paul'son (1875) described a new species *Aphareus inermis* from the Red Sea in Russian and referred it to the family Penaeidae. Later Borradaile (1910) established a new genus *Sicyonella* for a new species, *S. maldivensis*, and, being ignorant of the Russian paper by Paul'son, was unaware that *Sicyonella* was identical to *Aphareus* Paul'son, 1875. Borradaile (1910) established a new subfamily Sicyoninae of the family Penaeidae. Calman (1913) discovered that the generic name *Aphareus* had been preoccupied by Cuvier (1830) for a fish and so proposed a new name *Aphareocaris*, also being unaware that this genus was identical to *Sicyonella* Borradaile, 1910. Hansen (1919) synonymized *Aphareocaris* with *Sicyonella* and described the latest valid species, *S. antennata*.

The excellent redescription of all valid species of *Sicyonella* by Fukuoka *et al*. (2005) with the use of SEM makes morphological comments redundant. Here we present a key to species as one was not provided in Fukuoka *et al*. (2005). Citations to illustrations that supplement the key are also given.

Acetes H. Milne Edwards, 1830

Diagnosis: Carapace and abdomen smooth, firm; labrum not much separated from antennae and eyes; rostrum acute, with oblique frontal margin; supraorbital and

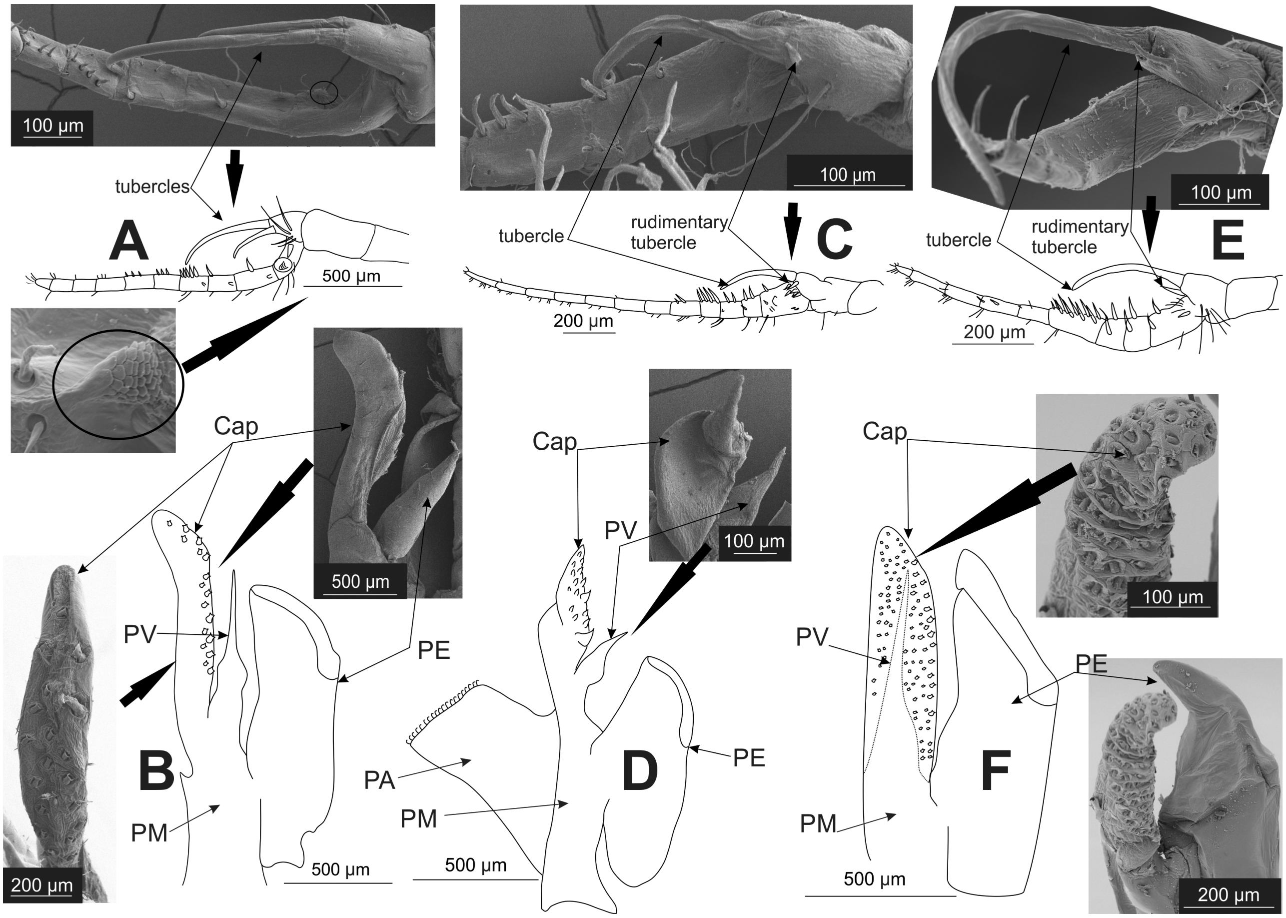

Figure 5. *Acetes chinensis*: clasping organ (A) and petasma (B); *Acetes erythraeus*: clasping organ (C) and petasma (D); *Acetes indicus*: clasping organ (E) and petasma (F). Cap, capitulum; PA, pars astringens; PE, pars externa; PM, pars media; PV, processus ventralis.

hepatic teeth present; sixth abdominal somite and telson in males without ventral processes; telson without lateral spines; eyestalks not elongated, cornea well pigmented; third antennular segment without ventral processes, longer than first segment; stylocerite present, mobile; mandible with palp; maxillula in adults with a single endite; first maxilliped with endopod and epipod; second maxilliped with epipod; third maxilliped < two times as long as first pereopod, not dimorphic sexually, dactyl subdivided; first pereopod with ischium lacking strong movable spines and reduced chela, fingers subequal; second pereopod with merus lacking proximal protrusion and much reduced chela lacking elongated setae, fingers subequal; third pereopod with much reduced chela lacking strong curved spines and elongated setae, fingers subequal; fourth pereopod in female absent or five-segmented, in male absent or three-segmented; fifth pereopod absent or three-segmented in female, absent or one-segmented (only coxa present) in male; uropodal exopod setose for distal outer margin, with small tooth by far not reaching distal end of exopod. Male clasping organ: well developed, with two developed or rudimentary clasping tubercles, no sensory bristles adjacent to clasping tubercle. Petasma: pars astringens absent or present, pars media if present armed with strong claws; pars externa developed. Photophores: dermal organs and organ of Pesta absent. Branchiae: podobranch on somite VIII, anterior arthrobranchs on somites VIII–XIII, posterior arthrobranchs absent.

Type species: By original designation, *Acetes indicus* H. Milne Edwards, 1830.

Species: Acetes americanus Ortmann, 1893, *Acetes binghami* Burkenroad, 1934, *Acetes chinensis* Hansen, 1919, *Acetes erythraeus* Nobili, 1905, *Acetes indicus* H. Milne Edwards, 1830, *Acetes intermedius* Omori, 1975, *Acetes japonicus* Kishinouye, 1905, *Acetes johni* Nataraj, 1949, *Acetes marinus* Omori, 1975, *Acetes natalensis* Barnard, 1955, *Acetes paraguayensis* Hansen, 1919, *Acetes petrunkevitchi* (Burkenroad, 1945), *Acetes serrulatus* (Krøyer, 1859), *Acetes sibogae* Hansen, 1919, *Acetes vulgaris* Hansen, 1919.

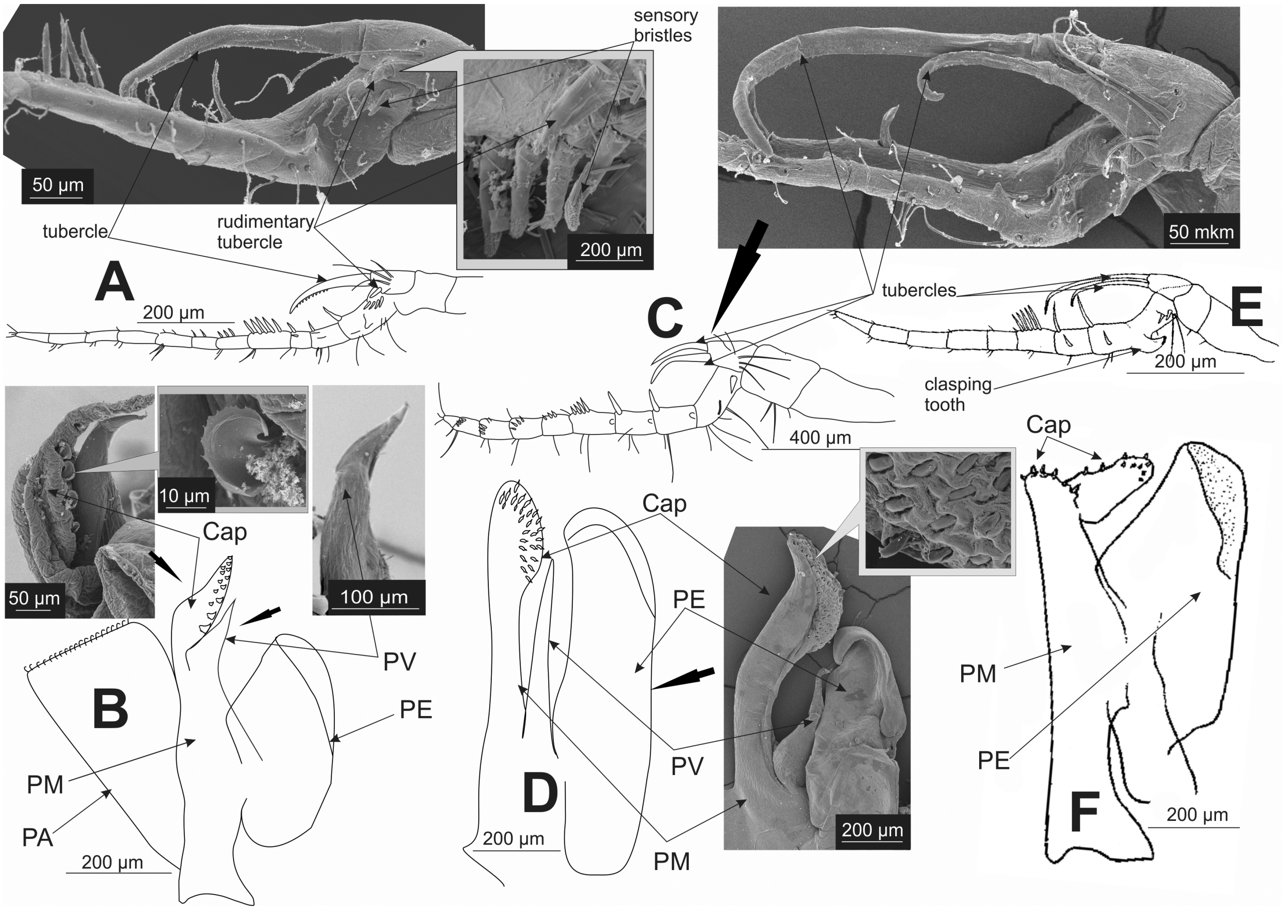

Figure 6. *Acetes intermedius*: clasping organ (A) and petasma (B); *Acetes japonicus*: clasping organ (C) and petasma (D); *Acetes johni*: clasping organ (E) and petasma (F). E and F were modified from Omori (1975). Cap, capitulum; PA, pars astringens; PE, pars externa; PM, pars media; PV, processus ventralis.

Remarks: The genus *Acetes* was established by H. Milne Edwards (1830) who described a new species, *A. indicus*, from the Ganges estuary. A comprehensive study by Omori (1975) of all valid species of *Acetes* included diagnoses and figures of all known species of the genus. This paper disentangled most of the taxonomic questions within the genus and even made it possible to identify all females, which is unique for Sergestoidea as usually only the adult males can be identified with certainty. Our SEM data on the ultrastructure of the petasma have provided hitherto-unknown morphological details and formed a basis for establishing homologies to other taxa, which is a necessity for phylogenetic studies. In the earliest available identification keys to species of *Acetes*, males and females were treated separately (e.g. Hansen, 1919), a tradition continued by Omori (1975). Below we provide a combined key for both males and females with citations for the illustrations necessary for reliable identification.

Morphological trends in *Sicyonella* and *Acetes*

Morphological analyses show that *Sicyonella* differs most clearly from the rest of Sergestidae in characters that may be associated with its occurrence at the benthopelagic shelf. These characteristics may provide additional protection, manoeuvrability, and feeding opportunities near the water–bottom interface (Vereshchaka, 1990, 1995). Some of these characters are synapomorphic (Fig. 12): two endites at the maxillulae (character 29 – see Appendix 2), enlarged third maxillipeds (31), and well-developed chelae of second and third pereopods (43, 50). Other characters (two dorsal teeth on the rostrum, pterygostomial tooth, four moveable lateral spines on the telson, a complete set of segments in fourth and fifth pereopods) may have been inherited from a common penaeid ancestor.

Most other characters within *Sicyonella* are associated with mating (male petasma and coupling struc-

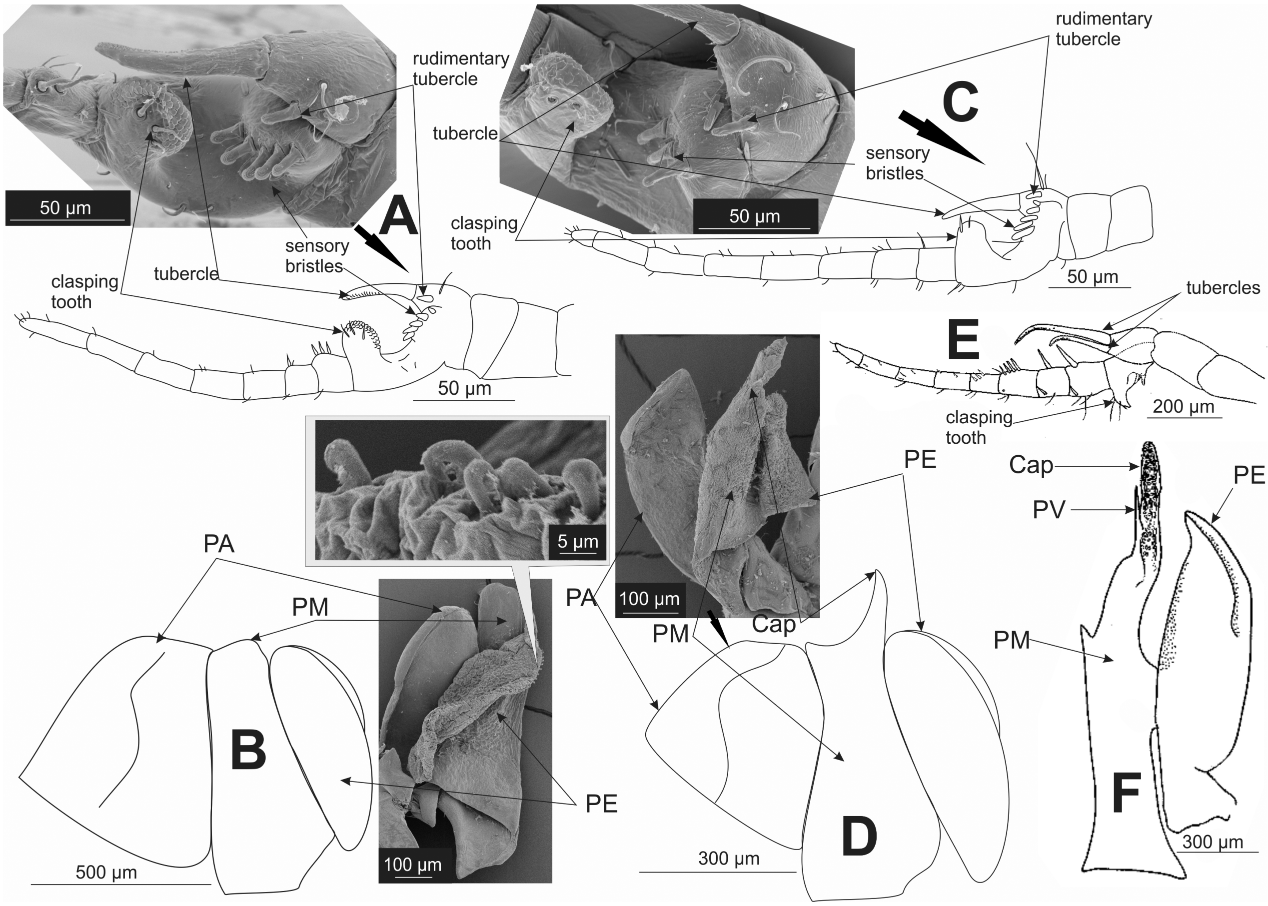

Figure 7. *Acetes marinus*: clasping organ (A) and petasma (B); *Acetes paraguayensis*: clasping organ (C) and petasma (D); *Acetes natalensis*: clasping organ (E) and petasma (F). E and F were modified from Omori (1975). Cap, capitulum; PA, pars astringens; PE, pars externa; PM, pars media; PV, processus ventralis.

tures). Hence, the species *S. inermis* is characterized by the presence of fine scales opposite the tubercle in the clasping organ (87) and by the presence of squamose hooks (100) the entire capitulum of the petasma (Fig. 12). In addition, another clade, *S. antennata* + *S. maldivensis*, is supported by a set of synapomorphies related to mating and coupling (Fig. 12): claw-like setae at the clasping organs opposite the tubercle (83), a divided capitulum of the petasma armed with squamose hooks and pincers (101, 104), well-developed lobi armatus, connectens, and terminalis (104, 107, 108–109), well-developed, elongated, twice-branched processus ventralis (110,111, 113, 114, 117, 118). The claw-like setae of the clasping organs may have a holding function. The petasmas of *S. antennata* and *S. maldivensis* are probably the most elaborate within Dendrobranchiata, with all known processi and lobi and the branched procesuss ventralis being present at the same time.

The clade *Acetes* is supported by synapomorphies related to the reduction of the branches (10, 12, 14, 15, 18), of the mouthparts (29–30), of the first chelae (40), and of the pereopods (adapted for swimming) (70). These characters, along with the general reduction in size and body compression, are probably adaptations to estuarine and freshwater shallow habitats, and to the fast reproductive cycles observed in the genus (Omori, 1975). These habitats have permanently high concentrations of oxygen, provide no possibility for extensive vertical migrations (too shallow), are productive, and in general favour short life cycles; some species have two generations in a season (Omori, 1975). Yet another set of synapomorphies is related to the presumed coupling procedure: the elongated third antennular segment (24), the presence of two clasping tubercles (79–80), and the strong distal tooth in the clasping organ (89).

All species of *Acetes*, except *A. petrunkevitchi*, show further reduction and loss of structures related to movement (fourth and fifth pereopods – Fig. 12) that may be further adaptations to shallow habitats where significant vertical migrations are impossible. Within *Acetes*, the phylogeny is based only on sexual characters, e.g. the clasping organ and the petasma (Fig. 12).

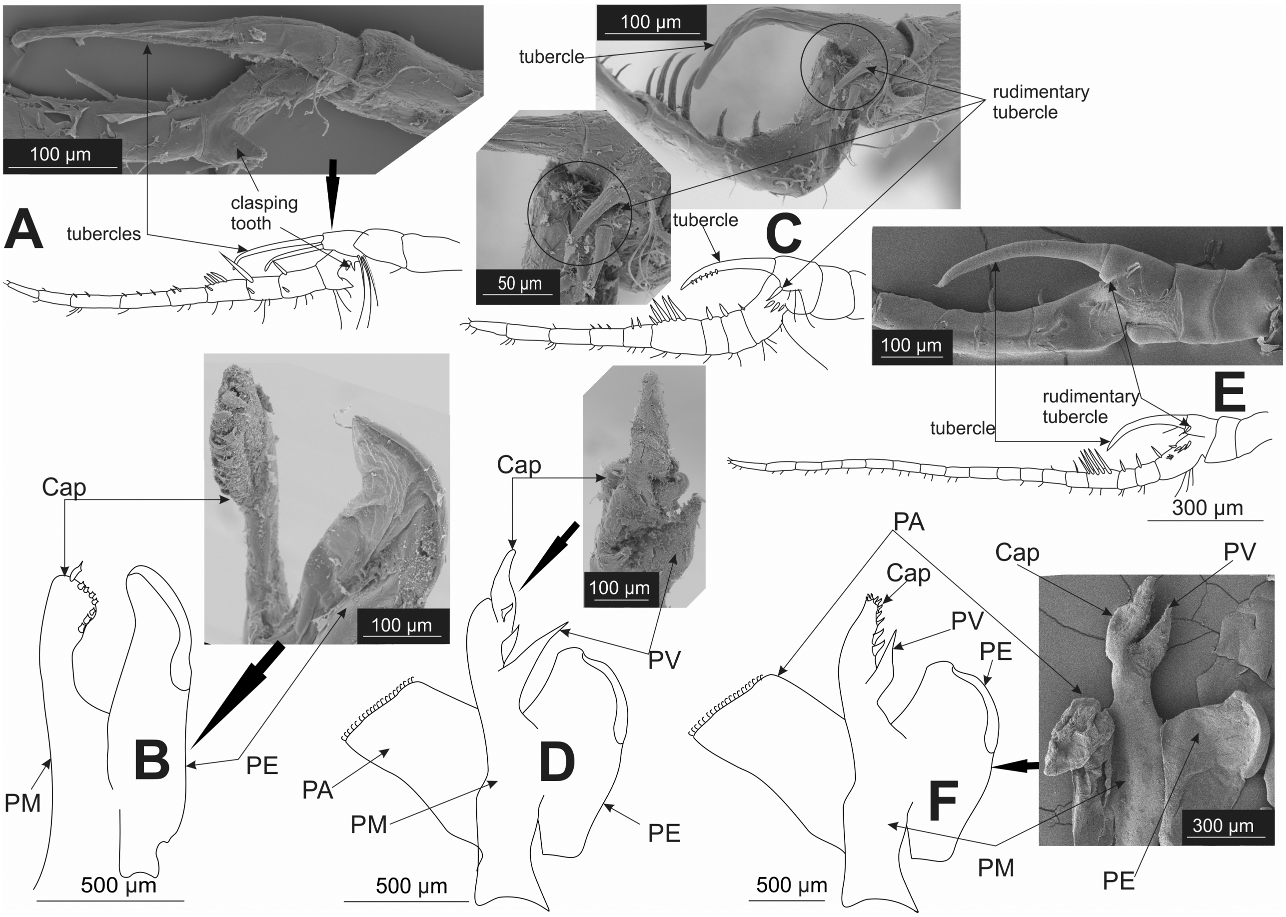

Figure 8. *Acetes serrulatus*: clasping organ (A) and petasma (B); *Acetes sibogae*: clasping organ (C) and petasma (D); *Acetes vulgaris*: clasping organ (E) and petasma (F). Cap, capitulum; PA, pars astringens; PE, pars externa; PM, pars media; PV, processus ventralis.

Omori (1975: fig. 3) manually depictured six clades of *Acetes*: (1) *A. marinus* + *A. paraguayensis*, (2) *A. erythraeus* + *A. intermedius* + *A. sibogae* + *A. vulgaris*, (3) *A. indicus*, (4) *A. serrulatus* + *A. johni* + *natalensis*, (5) *A. japonicus* + *A. chinensis*, and (6) *A. americanus* + *A. binghami*

However, our analysis supports only three of Omori's clades (Fig. 12):

1. The clade *A. marinus* + *A. paraguayensis*, which is not statistically robust but supported by the presence of fine scales on the clasping organ opposite the tubercle (87) and by the absence/strong reduction of the capitulum of the petasma (94).
2. The clade *A. americanus* + *A. binghami*, which is also not statistically robust but supported by the presence of specialized serrated setae with longitudinal ribs in the clasping organ (86).
3. The terminal clade *A. erythraeus* + *A. intermedius* + *A. sibogae* + *A. vulgaris*, which is statistically robust (Fig. 11) and supported by the following synapomorphies of the petasma: the presence of well-developed pars astringens (90, 92), additional enlarged claws on the capitulum (98), and an elongated processus ventralis (115, 117).

Most of the morphological variation within *Acetes* is seen in sexual characters, but because of substantial homoplasy, the phylogeny within the genus is hard to resolve. Like *Sicyonella*, *Acetes* is supported by synapomorphies that may be regarded as adaptations to estuarine habitats. Once adapted to such a habitat, the subsequent speciation within both genera has seemingly only been related to mating mechanisms (clasping and copulation).

Geographical remarks on the distribution of *Acetes*

The distributions of all recognized species of *Acetes* are summarized in Figure 13. The clades *A. marinus* + *A. paraguayensis* and *A. americanus* + *A. binghami* are geographically isolated from the rest of *Acetes* and occur in Central, South and North America. These clades

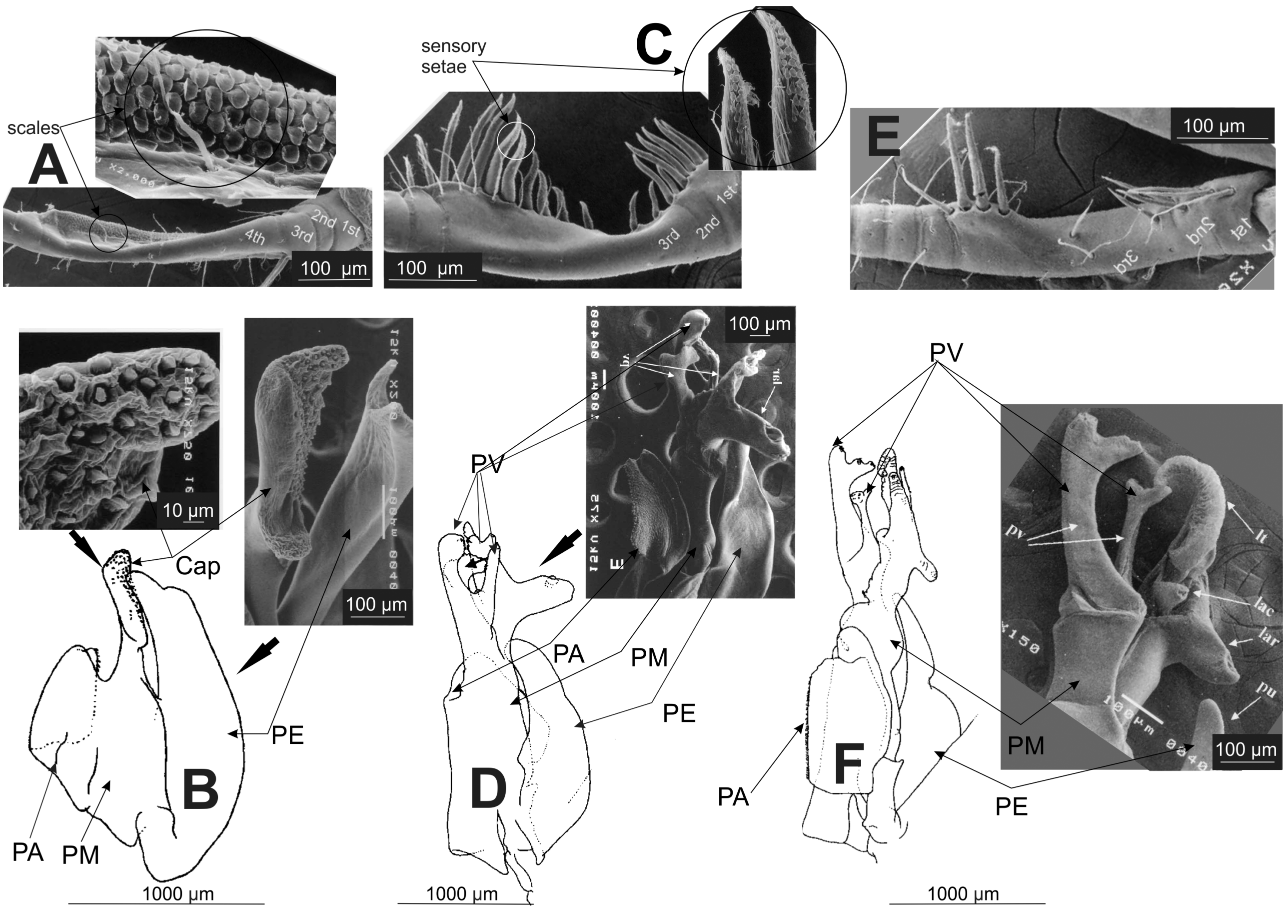

Figure 9. *Sicyonella inermis*: clasping organ (A) and petasma (B); *Sicyonella maldivensis*: clasping organ (C) and petasma (D); *Sicyonella antennata*: clasping organ (E) and petasma (F). All photos were modified from Fukuoka *et al*. (2005). Cap, capitulum; PA, pars astringens; PE, pars externa; PM, pars media; PV, processus ventralis.

originated through allopatric divergence, whereby new species arise from geographically isolated populations of the same ancestral species. One of these clades, *A. marinus* + *A. paraguayensis*, has adapted to low-salinity environments in South America and speciation within this clade reflects the degree of this adaptation: *A. marinus* lives in brackish waters, whereas *A. paraguayensis* is the only freshwater sergestid (Hansen, 1919; Omori, 1975). The second American clade, *A. americanus* + *A. binghami*, occurs in the coastal waters of North, Central, and South America and shows a parapatric distribution. The two species are geographically isolated from each other by the Isthmus of Panama, which prevents gene exchange between them.

The terminal clade of *Acetes* occurs in the Indo-West Pacific. Speciation within this clade took place allopatrically for *A. johni* and *A. erythraeus*, which are geographically isolated from the other species of *Acetes* and inhabit coastal waters of the Western Indian Ocean. The rest of the species occur along a coastal line between West India and Japan and have undergone sympatric speciation. We assume that this sympatric speciation is a likely outcome of competition for resources, when the evolution of assortative mating leads to reproductive isolation between ecologically diverging subpopulations (Dieckmann & Doebeli, 1999). Cross-breeding between sympatric species of *Acetes* is prevented by highly specialized copulatory structures, which differ greatly even between closely related species.

Figure 13 shows a number of blank areas from where *Acetes* has not yet been reported. This is probably because of a lack of sampling as the genus occurs in all well-explored coastal areas of tropical and subtropical areas. This is especially true in regard to the west coast of Africa, which contains the estuaries of big rivers such as Congo, Ebola, Gambia, Niger, Orange, and Senegal. Estuaries of these rivers would definitely be expected to harbour various species of *Acetes*.

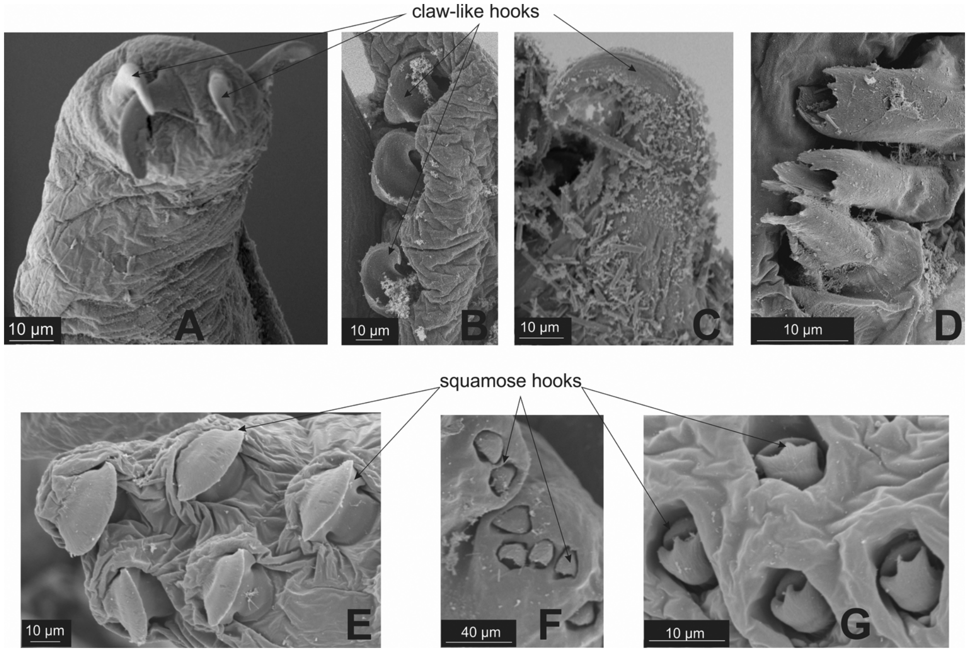

Figure 10. Armature of the capitulum of petasma in Sergestidae: A, *Acetes petrunkevichi*; B, *Acetes intermedius*; C, *Acetes sibogae*; D, *Acetes americanus*; E, *Petalidium foliaceum*; F, *Robustosergia robusta*; G, *Lucensosergia lucens*.

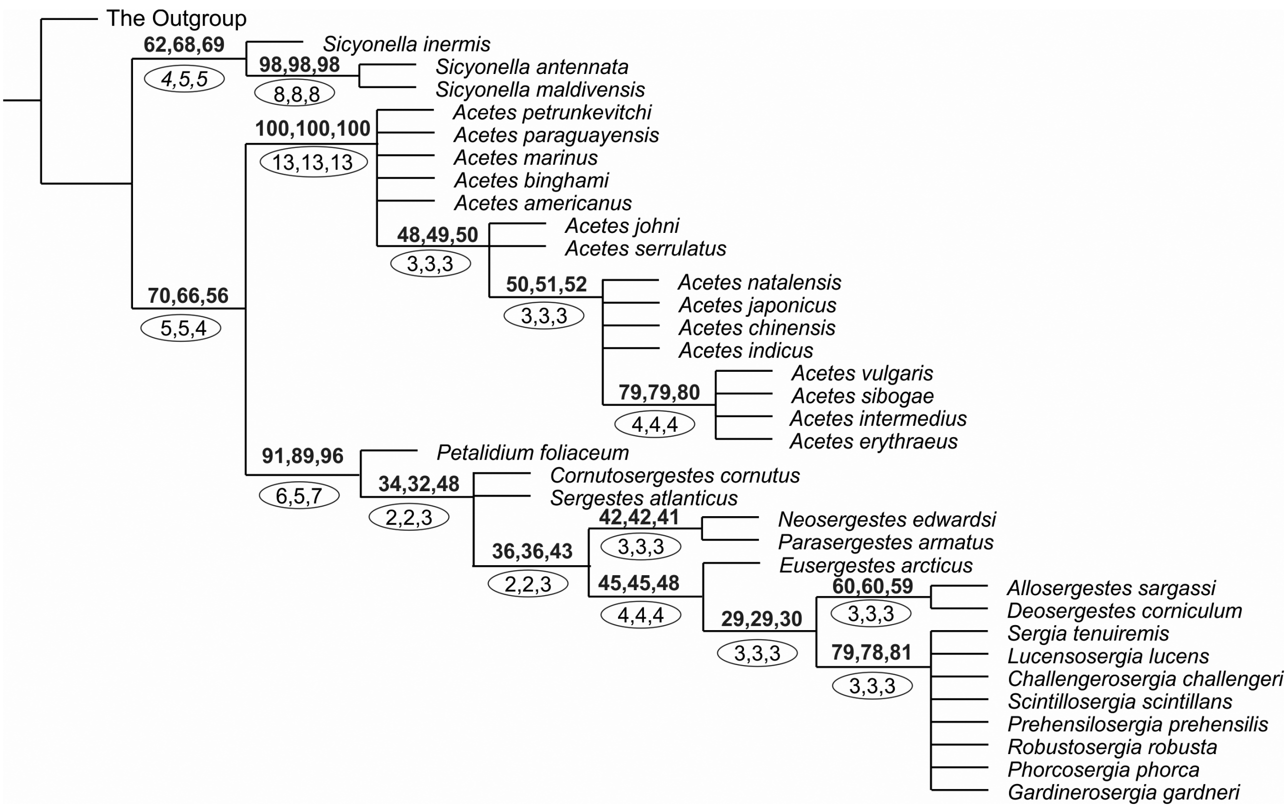

Figure 11. Supported clades of Sergestidae using three different outgroups: *Aristeomorpha foliacea* (Risso, 1827), *Gennadas parvus* Bate, 1881, and *Penaeus monodon* Fabricius, 1798. Tree topologies were identical for each analysis and so only one tree is shown. Bootstrap values for each of three analyses are separated by commas and presented above the nodes; Bremer support values for each of three analyses are separated by commas and presented below the nodes in ovals.

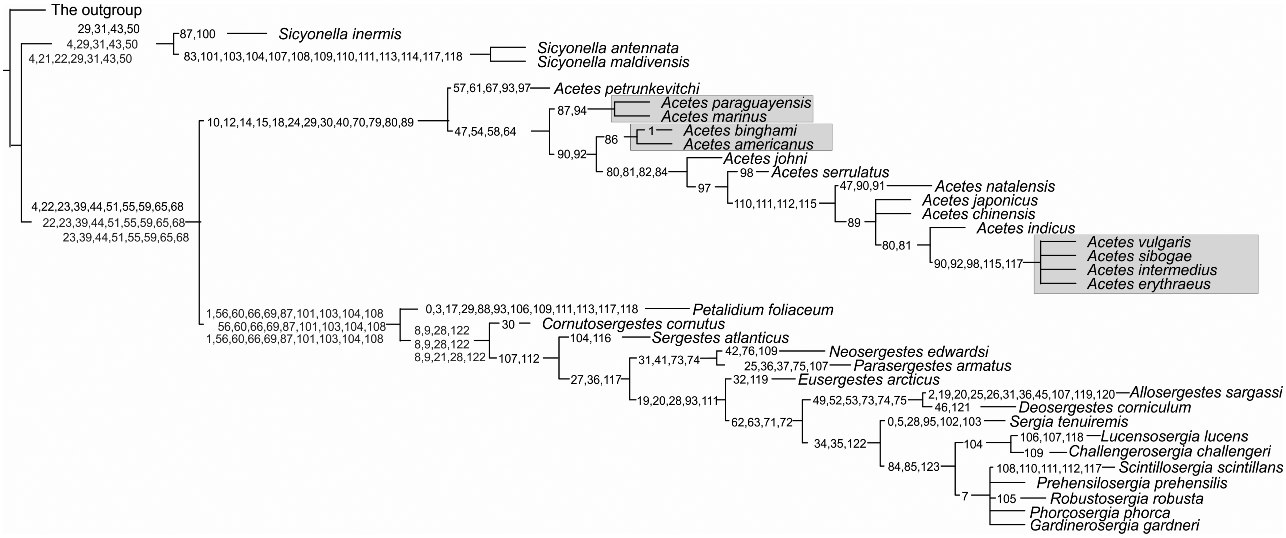

Figure 12. Strict consensus trees of Sergestidae with various outgroups: *Aristeomorpha foliacea* (Risso, 1827), *Gennadas parvus* Bate, 1881, and *Penaeus monodon* Fabricius, 1798. Tree topologies were identical for each analysis and so only one tree is shown; the nodes are marked with synapomorphies (see character list in Appendix 2). For the four cases in which synapomorphies differed amongst the analyses, the character numbers are shown in three rows, each representing one analysis. Omori's (1975) clades are marked in grey.

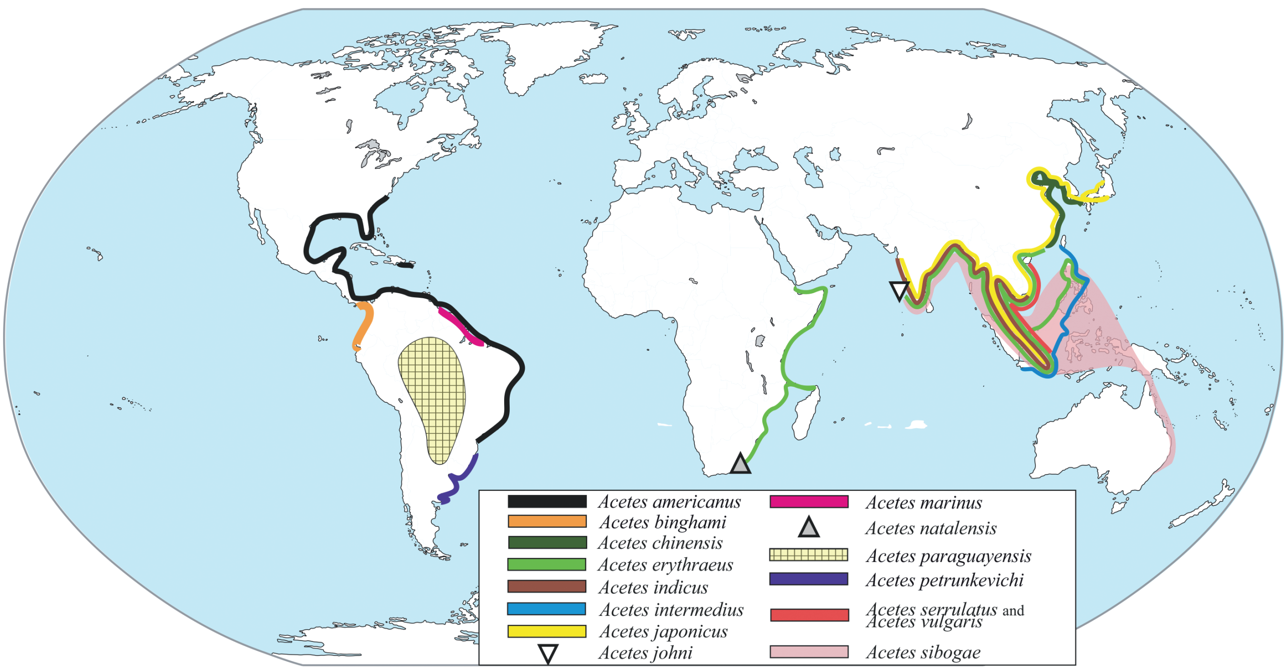

Figure 13. Provisional geographical distribution of *Acetes*. Coloured lines indicate position of estuarine habitats for each of the known species. Semitransparent coloured areas indicate species ranges of freshwater *Acetes paraguayensis* and estuarine *Acetes sibogae*.

KEY TO SPECIES OF THE GENUS *SICYONELLA*

1. Clasping organ with fine scales, without robust setae; pars media of petasma entire .... *Sicyonella inermis* (Paul'son, 1875) (Fig. 9A, B)
- Clasping organ with robust setae (Fig. 9C, E), fine scales absent; pars media of petasma divided (Fig. 9D, F) 2
2. Clasping organ with gap between contiguous rows of strong setae < 1/8 as long as third segment of outer antennular flagellum; lobus armatus of petasma nearly as large as the part including lobus inermis, lobus connectens, and lobus terminalis .... *Sicyonella maldivensis* Borradaile, 1910 (Fig. 9C, D)
- Clasping organ with gap between contiguous rows of strong setae nearly half as long as third segment of outer antennular flagellum; lobus armatus of petasma half as large as the part including lobus inermis, lobus connectens, and lobus terminalis .... *Sicyonella antennata* Hansen, 1919 (Fig. 9E, F)

KEY TO SPECIES OF THE GENUS *ACETES*

1. Rostrum without dorsal teeth .... *Acetes binghami* Burkenroad, 1934 (Fig. 4E, F)
- Rostrum with one to two dorsal teeth 2
2. Rostrum with a single dorsal tooth 3
- Rostrum with two dorsal teeth 4
3. Fourth pereopod (three or five segments) present (but reduced) .... *Acetes petrunkevitchi* (Burkenroad, 1945) (Fig. 4A, B)
- Fourth pereopod absent .... *Acetes americanus* Ortmann, 1893 (Fig. 4C, D)
4. No tooth on distal inner margin of coxa of third pereopod in female; pars astringens of petasma vestigial .... *Acetes natalensis* Barnard, 1955 (Fig. 7E, F)
- Tooth present on distal inner margin of coxa of third pereopod in female; pars astringens of petasma absent (Fig. 5B) or well developed (Fig. 5D) 5
5. Apex of telson triangular. In male, clasping organ with a single developed tubercle opposed to scattered pairs of strong, specialized setae, which are positioned without large prominence (Fig. 5E) 6
- Apex of telson rounded or truncated. In male, clasping organ with two developed tubercles (Fig. 5B) or with one tubercle opposed to a large prominence which is lacking scattered pairs of strong, specialized setae (Fig. 7A) 10
6. In female, basis of third pereopod with acute projection on inner margin. In male, pars astringens absent, no enlarged claws in addition to ordinary claws .... *Acetes indicus* H. Milne Edwards, 1830 (Fig. 5E, F).
- In female, no acute projection on inner margin of third pereopod. In male, pars astringens present, enlarged claws in addition to ordinary claws present (Fig. 6B) 7
7. Bases of first pleopods with strong, curved tooth between them 8
- No strong, curved tooth between bases of first pleopods 9
8. First segment of antennular peduncle no longer than second and third segments combined. In female, basis of third pereopod with blunt projection on distal inner margin. In male, three to five enlarged claws along outer margin .... *Acetes intermedius* Omori, 1975 (Fig. 6A, B)
- First segment of antennular peduncle longer than second and third segments combined. In female, no projection on distal inner margin of basis of third pereopod. In male, one to two enlarged claws along outer margin .... *Acetes erythraeus* Nobili, 1905 (Fig. 5C, D)
9. In female, basis of third pereopod with small projection on distal inner margin. In male, one to two enlarged claws along outer margin .... *Acetes sibogae* Hansen, 1919 (Fig. 8C, D)
– In female, no projection on distal inner margin of basis of third pereopod. In male, three enlarged claws along outer margin .... *Acetes vulgaris* Hansen, 1919 (Fig. 8E, F)
10. In female, third thoracic segment with a pair of barbs (visible in lateral view) just behind posterior teeth of coxa. In male, clasping organ with a single developed tubercle (Fig. 7A); petasma with pars astringens (Fig. 7A) 11
- In female, no barb (or not visible in lateral view) just behind posterior teeth of coxa on third thoracic segment. In male, clasping organ with two developed tubercles (Fig. 5A); petasma without pars astringens (Fig. 5B) 12
11. In female, coxa of third pereopod with small blunt tooth. In male, petasma without capitulum .... *Acetes marinus* Omori, 1975 (Fig. 7A, B)
- In female, coxa of third pereopod with large acute tooth. In male, petasma with rudimentary capitulum .... *Acetes paraguayensis* Hansen, 1919 (Fig. 7C, D)

12. In female, third thoracic segment extended posteriorly. In male, clasping organ without strong tooth opposite tubercles (Fig. 6C); petasma with PV (Fig. 6D) 13
- In female, third thoracic segment not extended posteriorly. In male, clasping organ with strong tooth opposite tubercles (Fig. 6E); petasma without PV (Fig. 6F) 14
13. Uropodal exopod with four to eight red spots. In female, posterior margin of third thoracic segment with deep incision. In male, petasma with capitulum of nearly uniform thickness .... *Acetes chinensis* Hansen, 1919 (Fig. 5A, B)
- Uropodal exopod with a single red spot. In female, posterior margin of third thoracic segment with shallow incision. In male, petasma with capitulum significantly thickened at apex .... *Acetes japonicus* Kishinouye, 1905 (Fig. 6C, D)
14. In female, anterior margin of fourth thoracic segment concave. In male, petasma with divided capitulum .... *Acetes johni* Nataraj, 1949 (Fig. 6E, F)
- In female, anterior margin of fourth thoracic segment with medial protrusion convex. In male, petasma with entire capitulum .... *Acetes serrulatus* (Krøyer, 1859) (Fig. 8A, B)

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APPENDIX 1

Terminal taxa (in alphabetical order) and sources of character scoring

BMNH, British Museum (Natural History); MNHN, Museum National d'Histoire Naturelle, Paris; SMNH, Naturhistoriska Riksmuseet, Sweden; USNM, United States National Museum; YPM, Yale Peabody Museum; ZMUC, Zoological Museum, University of Copenhagen.

No.	Species	Catalogue number
1	*Acetes carolina* Hansen, 1933	ZMUC-CRU-03106
2	*Acetes carolina* Hansen, 1933	ZMUC-CRU-03465
3	*Acetes carolina* Hansen, 1933	ZMUC-CRU-04452 (cotype)
4	*Acetes chinensis* Hansen, 1919	ZMUC-CRU-03724
5	*Acetes chinensis* Hansen, 1919	ZMUC-CRU-03725
6	*Acetes chinensis* Hansen, 1919	ZMUC-CRU-04453
7	*Acetes erythraeus* Nobili, 1905	ZMUC-CRU-04432
8	*Acetes erythraeus* Nobili, 1905	ZMUC-CRU-04433
9	*Acetes indicus* H. Milne Edwards, 1830	ZMUC CRU-04441
10	*Acetes indicus* H. Milne Edwards, 1830	ZMUC-CRU-04441
11	*Acetes indicus* H. Milne Edwards, 1830	ZMUC-CRU-04442
12	*Acetes intermedius* Omori, 1975	ZMUC-CRU-04423
13	*Acetes intermedius* Omori, 1975	ZMUC-CRU-04424
14	*Acetes japonicus* Kishinouye, 1905	ZMUC-CRU-04438
15	*Acetes japonicus* Kishinouye, 1905	ZMUC-CRU-04439
16	*Acetes marinus* Omori, 1975	ZMUC-CRU-04420
17	*Acetes marinus* Omori, 1975	ZMUC-CRU-04421
18	*Acetes paraguayensis* Hansen, 1919	ZMUC-CRU-04426
19	*Acetes paraguayensis* Hansen, 1919	ZMUC-CRU-04427
20	*Acetes serrulatus* (Krøyer, 1859)	ZMUC-CRU-04435
21	*Acetes serrulatus* (Krøyer, 1859)	ZMUC-CRU-04436
22	*Acetes sibogae* Hansen, 1919	ZMUC-CRU-04429
23	*Acetes sibogae* Hansen, 1919	ZMUC-CRU-04430
24	*Acetes vulgaris* Hansen, 1919	ZMUC-CRU-03962
25	*Acetes vulgaris* Hansen, 1919	ZMUC-CRU-04400
26	*Allosergestes sargassi* (Ortmann, 1893)	ZMUC CRU-04548
27	*Aristaeomorpha foliacea* (Risso, 1827)	ZMUC CRU-04451
28	*Challengerosergia challengeri* (Hansen, 1903)	BMNH 1903.6.6.14
29	*Cornutosergestes cornutus* (Krøyer, 1855)	ZMUC CRU–04533 (syntypes)
30	*Deosergestes corniculum* (Krøyer, 1855)	ZMUC CRU–06077 (syntypes)
31	*Eusergestes arcticus* (Krøyer, 1855)	ZMUC CRU–05590 (holotype, dissected), ZMUC CRU-04528
32	*Gardinerosergia gardneri* (Kemp, 1913)	ZMUC CRU-03726
33	*Gennadas parvus* Bate, 1881	ZMUC-CRU-04419
34	*Lucensosergia lucens* (Hansen, 1922)	ZMUC CRU-04425
35	*Neosergestes edwardsi* (Krøyer, 1855)	ZMUC CRU-04526
36	*Parasergestes armatus* (Krøyer, 1855)	ZMUC CRU–5626 (postlarva), ZMUC CRU–04507
37	*Peisos petrunkevitchi* Burkenroad, 1945	SMNH Type 2338 (holotype)
38	*Penaeus monodon* Fabricius, 1798	ZMUC-CRU-004445
39	*Petalidium foliaceum* Spence Bate, 1881	NHM 1888.22, 1888.22, 1903.6.6.16 (syntypes, damaged), ZMUC CRU-20546
40	*Phorcosergia phorca* (Faxon, 1893)	ZMUC CRU-04434
41	*Prehensilosergia prehensilis* (Bate, 1881)	BMNH 1888.2
42	*Robustosergia robusta* (Smith, 1882)	USNM 7316
43	*Scintillosergia scintillans* (Burkenroad, 1940)	ZMUC CRU-03613
44	*Sergestes atlanticus* Milne Edwards, 1830	MNHN, NA 331 (syntypes, bad condition), ZMUC CRU-04542
45	*Sergia tenuiremis* (Krøyer, 1855)	ZMUC CRU-08362
46	*Sicyonella antennata* Hansen, 1919	ZMUC ALV-1
47	*Sicyonella inermis* (Paul'son, 1875)	USNM 1026370
48	*Sicyonella maldivensis* Borradaile, 1910	ZMUC CRU-04443

APPENDIX 2

List of characters used

New characters are marked with asterisks (*)

Character no.	Character state	State no.	Reference to figure and source
Body			
0	Integument firm	0	
	Integument membranous	1	
1	Rostrum bears 2 or more dorsal teeth behind the orbital margin	0	
	Rostrum bears 0–1 dorsal teeth behind the orbital margin	1	
2	Frontal margin of rostrum oblique	0	2B, D – Vereshchaka *et al*. (2014)
	Frontal margin of rostrum vertical	1	2A – Vereshchaka *et al*. (2014)
3	Supraorbital tooth absent	0	2A–C – Vereshchaka *et al*. (2014)
	Supraorbital tooth present	1	2D – Vereshchaka *et al*. (2014)
4	Pterygostomial tooth absent	0	
	Pterygostomial tooth present	1	
5	Hepatic protrusion prominent	0	
	Hepatic protrusion inconspicuous	1	
6	Hepatic spine absent	0	
	Hepatic spine present	1	2D – Vereshchaka *et al*. (2014)
7	Hepatic barb absent	0	
	Hepatic barb present	1	2A-C – Vereshchaka *et al*. (2014)
8	Somite VIII, arthrobranch developed	0	
	Somite VIII, arthrobranch rudimentary or absent	1	
9	Somite VIII, podobranch absent	0	
	Somite VIII, podobranch present	1	
10	Somite IX, posterior arthrobranch present	0	
	Somite IX, posterior arthrobranch absent	1	
11	Somite IX, posterior arthrobranch dendritic	0	
	Somite IX, posterior arthrobranch lamellar	1	
12	Somite X, posterior arthrobranch present	0	
	Somite X, posterior arthrobranch absent	1	
13	Somite X, posterior arthrobranch dendritic	0	
	Somite X, posterior arthrobranch lamellar	1	
14	Somite XI, anterior arthrobranch present	0	
	Somite XI, anterior arthrobranch absent	1	
15	Somite XI, posterior arthrobranch developed	0	
	Somite XI, posterior arthrobranch reduced	1	
16	Somite XI, posterior arthrobranch dendritic	0	
	Somite XI, posterior arthrobranch lamellar	1	
17	Somite XII, posterior arthrobranch developed	0	
	Somite XII, posterior arthrobranch reduced	1	
18	Somite XII, posterior arthrobranch present	0	
	Somite XII, posterior arthrobranch absent	1	
19	Somite XII, posterior arthrobranch developed	0	
	Somite XII, posterior arthrobranch reduced	1	
20	Somite XII, posterior arthrobranch dendritic	0	
	Somite XII, posterior arthrobranch lamellar	1	
21	Somite XIII, posterior arthrobranch present	0	
	Somite XIII, posterior arthrobranch absent	1	
22	Telson, movable lateral spines present	0	
	Telson, movable lateral spines absent	1	
Appendages			
23	Antennule, very elongated first segment (by half or more than third segment) present	0	2E – Vereshchaka *et al*. (2014)
	Antennule, very elongated first segment (by half or more than third segment) absent	1	
24	Antennule, very elongated third segment (by half or more than first segment) present	0	2F – Vereshchaka *et al*. (2014)
	Antennule, very elongated third segment (by half or more than first segment) absent	1	
25	Stylocerite absent	0	
	Stylocerite present	1	
26	Fixed stylocerite absent	0	
	Fixed stylocerite present	1	
27	Mobile stylocerite absent	0	
	Mobile stylocerite present	1	
28	Distal tooth of scaphocerite not reaching distal end of blade	0	
	Distal tooth of scaphocerite reaching distal end of blade	1	7G – Vereshchaka *et al*. (2014)
	Distal tooth of scaphocerite overreaching distal end of blade	2	7E – Vereshchaka *et al*. (2014)

Appendix 2 *Continued*

Character no.	Character state	State no.	Reference to figure and source
29	Maxillula in adults with 4 endites	0	
	Maxillula in adults with 3 endites	1	
	Maxillula in adults with 2 endites	2	
	Maxillula in adults with a single endite	3	
30	First maxilliped with 3–4-segmented endopod	0	
	First maxilliped with 2 segmented endopod	1	
	First maxilliped with endopod rudimentary or absent	2	
31	Third maxilliped moderately developed, < 2.0 times as long as first pereopod	0	2E – Vereshchaka *et al*. (2014)
	Third maxilliped enlarged, > 2.0 times as long as first pereopod	1	2F – Vereshchaka *et al*. (2014)
32	Third maxilliped not sexually dimorphic, dactyl not modified	0	3D – Vereshchaka *et al*. (2014)
	Third maxilliped sexually dimorphic, dactyl modified in males	1	3E – Vereshchaka *et al*. (2014)
33	Third maxilliped with entire dactyl	0	
	Third maxilliped with dactyl subdivided	1	
34	Third maxilliped, dactyl subdivided into ordinary subsegments absent	0	
	Third maxilliped, dactyl subdivided into ordinary subsegments present	1	2E – Vereshchaka *et al*. (2014)
35	Third, with dactyl subdivided into specialized subsegments absent	0	
	Third maxilliped, dactyl subdivided into specialized subsegments present	1	2F – Vereshchaka *et al*. (2014)
36	Third maxilliped, dactyl consisting of 4 specialized subsegments	0	6 – Vereshchaka (2009)
	Third maxilliped, dactyl consisting of 5 specialized subsegments	1	6 – Vereshchaka (2009)
	Third maxilliped, dactyl consisting of 6 specialized subsegments	2	6 – Vereshchaka (2009)
	Third maxilliped, dactyl consisting of 7 specialized subsegments	3	6 – Vereshchaka (2009)
37	First pereopod, ischium lacking strong movable spines	0	
	First pereopod, ischium bearing strong movable spines	1	3F – Vereshchaka *et al*. (2014)
38	First pereopod with chela	0	
	First pereopod without chela	1	
39	First pereopod, normal chela (palm nearly as long as fingers) absent	0	
	First pereopod, normal chela (palm nearly as long as fingers) present	1	
40	First pereopod, reduced chela (palm > 10 times as long as fingers) absent	0	
	First pereopod, reduced chela (palm > 10 times as long as fingers) present	1	
41	Second pereopod, ischium lacking strong distally curved tooth	0	
	Second pereopod, ischium bearing strong distally curved tooth	1	3G – Vereshchaka *et al*. (2014)
42	Second pereopod, merus lacking distal protrusion	0	
	Second pereopod, merus bearing strong distally curved tooth	1	3G – Vereshchaka *et al*. (2014)
43	Second pereopod, slightly reduced chela (palm twice as long as fingers) absent	0	
	Second pereopod, slightly reduced chela (palm twice as long as fingers) present	1	
44	Second pereopod, much reduced chela (palm > 10 times as long as fingers) absent	0	
	Second pereopod, much reduced chela (palm > 10 times as long as fingers) present	1	
45	Second pereopod, fixed finger in chela rudimentary, shorter than dactyl	0	3H – Vereshchaka *et al*. (2014)
	Second pereopod, fixed finger developed, as long as dactyl	1	3I – Vereshchaka *et al*. (2014)
46	Second pereopod, chela lacking very long setae overreaching setae in tufts	0	
	Second pereopod, chela bearing very long setae overreaching setae in tufts	1	3I – Vereshchaka *et al*. (2014)
47	Third pereopod, coxa lacking mesial tooth	0	
	Third pereopod, coxa bearing mesial tooth	1	
48	Third pereopod in female, rounded basis	0	
	Third pereopod in female, basis with small projection or tooth	1	
49	Third pereopod, propodus lacking strong, curved spines proximal to tufts of setae	0	
	Third pereopod, propodus bearing strong, curved spines proximal to tufts of setae	1	3J – Vereshchaka *et al*. (2014)
50	Third pereopod, slightly reduced chela (palm three times as long as fingers) absent	0	
	Third pereopod, slightly reduced chela (palm three times as long as fingers) present	1	

Appendix 2 *Continued*

Character no.	Character state	State no.	Reference to figure and source
51	Third pereopod, much reduced chela (palm > 10 times as long as fingers) absent	0	
	Third pereopod, much reduced chela (palm > 10 times as long as fingers) present	1	
52	Third pereopod, fixed finger shorter than dactyl	0	3J – Vereshchaka *et al*. (2014)
	Third pereopod, fixed finger as long as dactyl	1	3K– Vereshchaka *et al*. (2014)
53	Third pereopod, chela lacking very long setae overreaching setae in tufts	0	
	Third pereopod, chela bearing very long setae overreaching setae in tufts	1	3J – Vereshchaka *et al*. (2014)
54	Fourth pereopod present in female	0	
	Fourth pereopod absent in female	1	
55	Fourth pereopod in female not 7-segmented	0	
	Fourth pereopod in female 7-segmented	1	
56	Fourth pereopod in female not 6-segmented	0	
	Fourth pereopod in female 6-segmented	1	
57	Fourth pereopod in female not 5-segmented	0	
	Fourth pereopod in female 5-segmented	1	
58	Fourth pereopod present in male	0	
	Fourth pereopod absent in male	1	
59	Fourth pereopod in male not 7-segmented	0	
	Fourth pereopod in male 7-segmented	1	
60	Fourth pereopod in male not 6-segmented	0	
	Fourth pereopod in male 6-segmented	1	
61	Fourth pereopod in male not 5-segmented	0	
	Fourth pereopod in male 5-segmented	1	
62	Fourth pereopod, no carpus and propodus setose along both margins	0	
	Fourth pereopod, carpus and propodus setose along both margins	1	
63	Fourth pereopod, carpus and propodus setose along one margin only	0	
	Fourth pereopod, no carpus and propodus setose along one margin only	1	
64	Fifth pereopod present in female	0	
	Fifth pereopod absent in female	1	
65	Fifth pereopod in female not 7-segmented	0	
	Fifth pereopod in female 7-segmented	1	
66	Fifth pereopod in female not 6-segmented	0	
	Fifth pereopod in female 6-segmented	1	
67	Fifth pereopod in female not 3-segmented	0	
	Fifth pereopod in female 3-segmented	1	
68	Fifth pereopod in male not 7-segmented	0	
	Fifth pereopod in male 7-segmented	1	
69	Fifth pereopod in male not 6-segmented	0	
	Fifth pereopod in male 6-segmented	1	
70	Fifth pereopod in male not consisting only of coxa	0	
	Fifth pereopod in male consisting only of coxa	1	
71	Fifth pereopod, carpus and propodus setose along both margins absent	0	
	Fifth pereopod, carpus and propodus setose along both margins present	1	
72	Fifth pereopod, carpus and propodus setose along one margin only present	0	
	Fifth pereopod, carpus and propodus setose along one margin only absent	1	
73	Uropodal exopod without outer spine	0	10 – Vereshchaka (2009)
	Uropodal exopod with outer spine	1	10 – Vereshchaka (2009)
74	Uropodal exopod, proximal segment not setose along outer margin	0	10 – Vereshchaka (2009)
	Uropodal exopod, proximal segment setose along outer margin	1	10 – Vereshchaka (2009)
75	Uropodal exopod, no proximal segment partly setose along outer margin	0	10 – Vereshchaka (2009)
	Uropodal exopod, proximal segment partly setose along outer margin	1	10 – Vereshchaka (2009)
76	Uropodal exopod, no proximal segment entirely setose along outer margin	0	10 – Vereshchaka (2009)
	Uropodal exopod, proximal segment entirely setose along outer margin	1	10 – Vereshchaka (2009)

Appendix 2 *Continued*

Character no.	Character state	State no.	Reference to figure and source
Male clasping organ			
77	Clasping tubercle absent/rudimentary	0	4B – Vereshchaka *et al*. (2014)
	Clasping tubercle present	1	4C–E – Vereshchaka *et al*. (2014)
78*	A single clasping tubercle absent	0	4C–E – Vereshchaka *et al*. (2014)
	A single clasping tubercle present	1	
79*	Two clasping tubercles (may be rudimentary) absent	0	4C–E – Vereshchaka *et al*. (2014)
	Two clasping tubercles (may be rudimentary) present	1	Figure 5A,C – present paper
80*	One rudimentary and one well-developed tubercle absent	0	
	One rudimentary and one well-developed tubercle present	1	Figure 5C – present paper
81*	Two well-developed clasping tubercles absent	0	
	Two well-developed clasping tubercles present	1	Figure 5A – present paper
82*	Claw-like setae positioned in scattered groups opposite the tubercle absent	0	
	Claw-like setae positioned in scattered groups opposite the tubercle present	1	Figure 5C – present paper
83*	Claw-like setae positioned in two contiguous rows opposite the tubercle absent	0	
	Claw-like setae positioned in two contiguous rows opposite the tubercle present	1	Figure 9C – present paper
84*	A set of serrated bristles opposite the tubercle absent	0	
	A set of serrated bristles opposite the tubercle present	1	Figure 4C – present paper
85*	Serrated bristles with reticulate distal part absent	0	
	Serrated bristles with reticulate distal part present	1	Figure 2A–C – present paper
86*	Serrated bristles with longitudinal ribs in distal part absent	0	
	Serrated bristles with longitudinal ribs in distal part present	1	Figure 2D – present paper
87*	Fine scales opposite the tubercle absent	0	
	Fine scales opposite the tubercle present	1	Figure 3A – present paper
88	A row of serrated bristles adjacent to the tubercle absent	0	
	A row of serrated bristles adjacent to the tubercle present	1	
89	Strong distal tooth or projection on the fourth segment absent	0	
	Strong distal tooth or projection on the fourth segment present	1	Figure 7A, C – present paper
Petasma			
90	Pars astringens absent	0	Figure 5B – present paper
	Pars astringens present	1	Figure 5D – present paper
91*	Vestigial pars astringens absent	0	
	Vestigial pars astringens present	1	Figure 7F – present paper
92*	Well-developed pars astringens absent	0	
	Well-developed pars astringens present	1	Figure 7B,D – present paper
93	Processus uncifer without hook	0	5C, 6D – Vereshchaka *et al*. (2014)
	Processus uncifer with a hook	1	5A,B,D – Vereshchaka *et al*. (2014)
94	Capitulum absent/vestigial	0	Figure 7B,D – present paper
	Capitulum present	1	Figure 7F – present paper
95*	No capitulum armed with strong claws	0	
	Capitulum armed with strong claws	1	Figure 10A–C – present paper
96	Divided capitulum with strong claws absent	0	
	Divided capitulum with strong claws present	1	Figure 4B,D,F – present paper
97	Entire capitulum with strong claws absent	0	
	Entire capitulum with strong claws present	1	Figure 9B – present paper
98*	Capitulum, enlarged claws in addition to ordinary claws absent	0	Figure 6D – present paper
	Capitulum, enlarged claws in addition to ordinary claws present	1	Figures 8D,F, 10C – present paper
99*	Capitulum armed with squamose hooks and pincers absent	0	
	Capitulum armed with squamose hooks and pincers present	1	Figure 10E–G – present paper
100*	Entire capitulum armed with squamose hooks and pincers absent	0	
	Entire capitulum armed with squamose hooks and pincers present	1	Figure 9B – present paper
101*	Divided capitulum armed with squamose hooks and pincers absent	0	
	Divided capitulum armed with squamose hooks and pincers present	1	Figure 9C,E – present paper
102	Capitulum with pincers, complete set of undivided lobi or processi absent	0	
	Capitulum with pincers, complete set of undivided lobi or processi present	1	

Appendix 2 *Continued*

Character no.	Character state	State no.	Reference to figure and source
103	Capitulum with pincers and significantly modified (divided or reduced) lobi/processi absent	0	
	Capitulum with pincers and significantly modified (divided or reduced) lobi/processi present	1	
104	Lobus armatus rudimentary	0	5E – Vereshchaka *et al*. (2014)
	Lobus armatus developed	1	5A-D – Vereshchaka *et al*. (2014)
105	Twisted lobus connectens and lobus terminalis absent	0	5A-E – Vereshchaka *et al*. (2014)
	Twisted lobus connectens and lobus terminalis present	1	6D – Vereshchaka *et al*. (2014)
106	Rudimentary lobus connectens absent	0	
	Rudimentary lobus connectens present	1	5C – Vereshchaka *et al*. (2014)
107	Well-developed lobus connectens absent	0	
	Well-developed lobus connectens present	1	5A,D,E – Vereshchaka *et al*. (2014)
108	Lobus terminalis absent or rudimentary	0	
	Lobus terminalis developed	1	5A-D – Vereshchaka *et al*. (2014)
109	Divided lobus terminalis absent	0	5A-D – Vereshchaka *et al*. (2014)
	Divided lobus terminalis present	1	6A – Vereshchaka *et al*. (2014)
110	Processus ventralis absent	0	5C – Vereshchaka *et al*. (2014)
	Processus ventralis present	1	5A,B,D – Vereshchaka *et al*. (2014)
111	Processus ventralis rudimentary	0	5E – Vereshchaka *et al*. (2014)
	Processus ventralis developed	1	5A,B,D – Vereshchaka *et al*. (2014)
112	Entire processus ventralis absent	0	
	Entire processus ventralis present	1	5A,B,D – Vereshchaka *et al*. (2014)
113	Divided processus ventralis absent	0	
	Divided processus ventralis present	1	9C,E – present paper
114	Twice-divided processus ventralis absent	0	
	Twice-divided processus ventralis present	1	9C,E – present paper
115	Needle-like processus ventralis absent	0	
	Needle-like processus ventralis present	1	5F – present paper
116	Triangular processus ventralis absent	0	
	Triangular processus ventralis present	1	5E – Vereshchaka *et al*. (2014)
117	Elongate processus ventralis absent	0	
	Elongate processus ventralis present	1	5B,D – – present paper
118	Processus ventralis, hooks and suckers absent	0	5A-E – Vereshchaka *et al*. (2014)
	Processus ventralis, hooks and suckers present	1	6B – Vereshchaka *et al*. (2014)
119	Processus ventralis, simple spines absent	0	5A,C,E – Vereshchaka *et al*. (2014)
	Processus ventralis, simple spines present	1	5B,D – Vereshchaka *et al*. (2014)
120	Processus ventralis, stellate spines absent	0	5A,D,E – Vereshchaka *et al*. (2014)
	Processus ventralis, stellate spines present	1	5B – Vereshchaka *et al*. (2014)
121	Processus ventralis, apical lashes absent	0	5B-E – Vereshchaka *et al*. (2014)
	Processus ventralis, apical lashes present	1	5A– Vereshchaka *et al*. (2014)
Photophores			
122	The organ of Pesta absent	0	2F – Vereshchaka *et al*. (2014)
	The organ of Pesta present	1	2E – Vereshchaka *et al*. (2014)
123	Dermal photophores absent	0	
	Dermal photophores present	1	

The character numbers also refer Figs. 12–13 and (in brackets) to the subchapters: THE MONOPHYLY OF *SICYONELLA* AND *ACETES* AND THE STATUS OF *PEISOS and* MORPHOLOGICAL TRENDS IN *SICYONELLA* AND *ACETES*.

APPENDIX 3

Data matrix

Missing data indicated by question marks (?); inapplicable data by hyphens (-)

Characters 0–40

```
                                         0 5 10 15 20 25 30 35 40
                                         | | | | | | | | |
Aristaeomorpha foliacea                  00-0101000000000000000001000000000000--0010
Gennadas parvus                          11000100010000000000000010000100000 0--0010
Penaeus monodon                          00-0001001000000000000111000000000000--0010
Acetes americanus                        00010010101-1-11-01--11011010320000--0001
Acetes binghami                          01010010101-1-11-01--110110103200000-0001
Acetes chinensis                         00010010101-1-11-01--110110103200000-0001
Acetes erythraeus                        00010010101-1-11-01--110110103200000-0001
Acetes indicus                           00010010101-1-11-01--110110103200000-0001
Acetes intermedius                       00010010101-1-11-01--110110103200000-0001
Acetes japonicus                         00010010101-1-11-01--110110103200000-0001
Acetes johni                             00010010101-1-11-01--110110103200000-0001
Acetes natalensis                        00010010101-1-11-01--110110103200000-0001
Acetes serrulatus                        00010010101-1-11-01--110110103200000-0001
Acetes sibogae                           00010010101-1-11-01--110110103200000-0001
Acetes vulgaris                          00010010101-1-11-01--110110103200000-0001
Acetes marinus                           00010010101-1-11-01--110110103200000-0001
Acetes paraguayensis                     00010010101-1-11-01--110110103200000-0001
Acetes petrunkevitchi                    00010010101-1-11-01--110110103200000-0001
Sicyonella inermis                       0001101010000000000100010101020101010 0010
Sicyonella maldivensis                   0001101010000000000100010101020101010 0010
Sicyonella antennata                     0001101010000000000100010101020101010 0010
Petalidium foliaceum                     11000010100101001101111001010100 0?00?????
Sergia tenuiremis                        1100010001010100100000110110000001 10-0100
Gardinerosergia gardneri                 0100000101010100100000110110200001 10-0100
Phorcosergia phorca                      0100000101010100100000110110000001 10-0100
Robustosergia robusta                    0100000101010100100000110110000001 10-0100
Prehensilosergia prehensilis             0100000101010100100000110110100001 10-0100
Scintillosergia scintillans              0100000101010100100000110110100001 10-0100
Challengerosergia challengeri            0100001001010100100000110110100001 10-0100
Lucensosergia lucens                     0100001001010100100000110110100001 10-0100
Deosergestes corniculum                  010000100101010010000010011010000101 20100
Eusergestes arcticus                     010100100101010010000011011010001101 20100
Sergestes atlanticus                     010100100101010010011010010120000101 40100
Cornutosergestes cornutus                010100100101010010011010010120100101 40100
Allosergestes sargassi                   011000100101010010011010000010010101 10100
Parasergestes armatus                    010000100101010010011010000020010101 01100
Neosergestes edwardsi                    010000100101010010011010011020010101 20100
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APPENDIX 3 *Continued*

Characters 41–81

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                                      41 46 51 56 61 66 71 76 81
                                      |  |  |  |  |  |  |  |  |
Aristaeomorpha foliacea               00001000000100100010000010010000100000000
Gennadas parvus                       00001000000100100010000010010000100000000
Penaeus monodon                       00001000000100100010000010010000100000000
Acetes americanus                     00011010001101000100000100000100100010110
Acetes binghami                       00011010001101000100000100000100100010110
Acetes chinensis                      00011010001101000100000100000100100010101
Acetes erythraeus                     00011010001101000100000100000100100010110
Acetes indicus                        00011011001101000100000100000100100010110
Acetes intermedius                    00011011001101000100000100000100100010110
Acetes japonicus                      00011010001101000100000100000100100010101
Acetes johni                          00011010001101000100000100000100100010101
Acetes natalensis                     00011000001101000100000100000100100010101
Acetes serrulatus                     00011010001101000100000100000100100010101
Acetes sibogae                        00011011001101000100000100000100100010110
Acetes vulgaris                       00011010001101000100000100000100100010110
Acetes marinus                        00011010001101000100000100000100100010110
Acetes paraguayensis                  00011010001101000100000100000100100010110
Acetes petrunkevitchi                 00011000001100001000100000100100100010110
Sicyonella inermis                    00101000010100100010001010010001100000000
Sicyonella maldivensis                00101000010100100010001010010001100000000
Sicyonella antennata                  00101000010100100010001010010001100000000
Petalidium foliaceum                  ??01??00?01??00100010010010010011000 0??00
Sergia tenuiremis                     00011010001100010001010001001010100011000
Gardinerosergia gardneri              00011010001100010001010001001010100011000
Phorcosergia phorca                   00011010001100010001010001001010100011000
Robustosergia robusta                 00011010001100010001010001001010100011000
Prehensilosergia prehensilis          00011010001100010001010001001010100011000
Scintillosergia scintillans           00011010001100010001010001001010100011000
Challengerosergia challengeri         00011010001100010001010001001010100011000
Lucensosergia lucens                  00011010001100010001010001001010100011000
Deosergestes corniculum               00011110101010010001010001001010011011000
Eusergestes arcticus                  00011010001100010001001001001001100011000
Sergestes atlanticus                  00011000001100010001001001001001100011000
Cornutosergestes cornutus             00011000001100010001001001001001100011000
Allosergestes sargassi                00010010101010010001010001001010011011000
Parasergestes armatus                 10011010001100010001001001001001011011000
Neosergestes edwardsi                 11011000001100010001001001001001010111000
```

APPENDIX 3 *Continued*

Characters 82–123

	82 87 92 97 102 107 112 117 122
	| | | | | | | | |
Aristaeomorpha foliacea	000000001010000000000000000000000000000000
Gennadas parvus	000000001010000000000000000000000000000000
Penaeus monodon	000000001010000000000000000000000000000000
Acetes americanus	001010010000111000000000000000000000000000
Acetes binghami	001010010000111000000000000000000000000000
Acetes chinensis	100000000000110100000000000001110010000000
Acetes erythraeus	100000001010110110000000000001110000100000
Acetes indicus	100000000000110100000000000001110010000000
Acetes intermedius	100000001010110110000000000001110000100000
Acetes japonicus	100000000000110100000000000001110010000000
Acetes johni	100000010000111000000000000000000000000000
Acetes natalensis	100000012100110100000000000001110010000000
Acetes serrulatus	100000010000110110000000000000000000000000
Acetes sibogae	100000001010110110000000000001110000100000
Acetes vulgaris	100000001010110110000000000001110000100000
Acetes marinus	001101011010000000000000000000000000000000
Acetes paraguayensis	001101011010000000000000000000000000000000
Acetes petrunkevitchi	001100011011111110000000000000000000000000
Sicyonella inermis	000001001010100001100000000000000000000000
Sicyonella maldivensis	010000001010100001010110011111011001100000
Sicyonella antennata	010000001010100001010110011111011001100000
Petalidium foliaceum	001101101011100001010110101111010001100000
Sergia tenuiremis	000001001011110001011010011011100001000000
Gardinerosergia gardneri	001101001011100001010110011011100001000001
Phorcosergia phorca	001101001011100001010110011011100001000001
Robustosergia robusta	001101001011100001010111011011100001000001
Prehensilosergia prehensilis	001101001011100001010110011011100001000001
Scintillosergia scintillans	001101001011100001010110010000000000000001
Challengerosergia challengeri	001101001011100001010100011111100001000001
Lucensosergia lucens	001101001011100001010100101011100001100001
Deosergestes corniculum	000001001011100001010110011011100001000110
Eusergestes arcticus	000001001011100001010110011011100001010010
Sergestes atlanticus	000001001010100001010100011010100010000010
Cornutosergestes cornutus	00000100101010000101011000100-000000000010
Allosergestes sargassi	000001001011100001010110001011100001011010
Parasergestes armatus	000001001010100001010110001010100001000010
Neosergestes edwardsi	000001001010100001010110011110100001000010