BRILL

JOURNAL OF CRUSTACEAN BIOLOGY, 34(5), 618-628, 2014

Journal of Crustacean Biology

STERNAL SPINES IN PENAEID POSTLARVAE (DECAPODA: PENAEIDAE): LIFE-PHASE-SPECIFIC AND SYSTEMATICALLY SIGNIFICANT?

James G. Ditty *

National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, 4700 Avenue U, Galveston, TX 77551, USA

ABSTRACT

Our ability to identify and discriminate postlarvae of penaeids below family level remains poor due to phase brevity and a lack of taxonomic characters. Whether sternal spines are unique and taxonomically significant to postlarvae has not been resolved. I describe number and placement of spines in *Parapenaeus* sp. Smith, 1885, and a specimen tentatively identified as *Xiphopenaeus kroyeri* (Heller, 1862) from the Gulf of Mexico; review information for penaeids worldwide; and evaluate the significance of sternal spines as a life-phase specific taxonomic character and to penaeid systematics. To date, sternal spines have been described for 14 of 32 genera and 26 species. Most taxa share one of two common sternal formulas: either $0 + 0 + 0 + 1 + 0$, or $0 + 0 + 0 + 1 + 1$. Only *Metapenaeopsis* Bouvier, 1905, and the tentative *Xiphopenaeus kroyeri* have a pair of spines on at least the first-two sternal plates, and only *Metapenaeopsis* and *Litopenaeus* Pérez-Farfante, 1969, contain members with different sternal formulas. I suggest that differences among taxa in shape of the sternal plates may be an unrecognized taxonomic character. Sternal spines are not life-phase specific and do not reflect lower-level systematic relationships within Penaeidae regardless of generic nomenclature applied. The unusual length, shape, and reverse orientation of the spine on plate five in species of *Parapenaeus*, and presence of an elongate ventromedian spine on one or more pleomeres in *Parapenaeus* and *Funchalia* Johnson, 1868, supports molecular and morphological data that Penaeidae may be paraphyletic. While generally ineffective as a stand-alone taxonomic character, differences in number, placement, and orientation of sternal spines, i.e., the 'sternal pattern'; knowledge of geographic distributions; and, perhaps differences in sternal plate shape should be included in the suite of characters used to discriminate and identify penaeids during the postlarva phase.

KEY WORDS: developmental plasticity, *Parapenaeus*, penaeid diversity, sternal plate shape, sternal spine patterns

DOI: 10.1163/1937240X-00002261

INTRODUCTION

Penaeidae Rafinesque, 1815 contains at least 25 genera and 225 species or subspecies worldwide (Tables 1, 2). The seven new genera proposed by Sakai and Shinomiya (2011) from within *Parapenaeopsis* Alcock, 1901, elevate the total to at least 32 genera (De Grave and Fransen, 2011). Of known species, about 77% occur only in the Indo-Pacific, 9% occur only in the Western Atlantic and 7% occur only in the Eastern Pacific. Here, I follow the taxonomy of Pérez-Farfante and Kensley (1997) and McLaughlin et al. (2005) despite ongoing debate about the sub-generic or generic classification of some members of Penaeidae (Dall, 2007; Flegel, 2007; McLaughlin et al., 2008; Ma et al., 2011).

Members of Penaeidae occupy estuarine, shelf, and oceanic waters over 500-m deep (Holthuis, 1980) with many species important commercially and as prey for fishes and other marine organisms. Dall et al. (1990a) characterize the complex life cycle of penaeids into one of four types. Type 1 remain in low salinity estuaries throughout life and includes most species of *Metapenaeus* Wood-Mason, 1891. Type 2 spawn offshore and early life stages (ELS) move into estuaries to develop and grow before returning offshore to enter the adult population, e.g., *Farfantepenaeus* Burukovsky, 1997; *Litopenaeus* Pérez-Farfante, 1969; and, *Xiphopenaeus kroyeri* (Heller, 1862). Type 3 shrimp prefer higher salinity estuarine and coastal areas, e.g., *Rimapenaeus* Pérez-Farfante and Kensley, 1997, and, some species of *Metapenaeopsis* Bouvier, 1905. Type 4, e.g., *Funchalia* Johnson, 1868, some species of *Metapenaeopsis*, *Parapenaeus* Smith, 1885, and *Penaeopsis* Bate, 1881, remain offshore throughout life (Dall et al., 1990a).

Complex life cycles often require unique traits that differ from previous and succeeding life stages of the same species; represent adaptations to the planktonic environment; and, permit exploitation of resources other than those utilized by the adult (Anger, 2006). The penaeid life cycle includes a pelagic larva phase, short transitional 'postlarva' phase, and benthic juvenile-adult (Dall et al., 1990a; Anger, 2006), except the entirely pelagic *Funchalia* and *Pelagopenaeus* Pérez-Farfante and Kensley, 1997. The term 'postlarva' is frequently used incorrectly to refer to all life stages from termination of the mysis phase through onset of sexual maturity (Dall et al., 1990b). More appropriately, the 'postlarva' (Gurney, 1942; Harvey et al., 2002), 'megalopa' (Williamson, 1969; Kurata, 1970), or 'decapodid' phase (Kaestner, 1970; first postlarva only, Felder et al.,

* E-mail: Jim.Ditty@NOAA.gov

© The Crustacean Society, 2014. Published by Brill NV, Leiden

Table 1. Distribution of penaeid genera whose sternal spine pattern has been described for one or more taxa. [1] Assignment of postlarvae to *Penaeopsis* by Burkenroad (1934a) is tentative. [2] Assignment to *Xiphopenaeus* is tentative.

Genus	Min. no. of species	Hemisphere		Isobath (m)			References
		West	East	Within 75	75-200	Beyond 200	
Atypopenaeus Alcock, 1905	5		X	X			Holthuis (1980)
Farfantepenaeus Burukovsky, 1997	8	X		X	X		Holthuis (1980); Spivak (1997); Felder et al. (2009)
Fenneropenaeus Pérez-Farfante, 1969	6		X	X	X		Holthuis (1980)
Litopenaeus Pérez-Farfante, 1969	5	X		X			Holthuis (1980); Spivak (1997); Felder et al. (2009)
Marsupenaeus Tirmizi, 1971	1		X	X			Holthuis (1980)
Megokris Pérez-Farfante and Kensley, 1997	9		X	X			Holthuis (1980)
Melicertus Rafinesque, 1814	8		X	X	X		Holthuis (1980)
Metapenaeopsis Bouvier, 1905	76	X	X	X	X	X	Holthuis (1980)
Metapenaeus Wood-Mason, 1891	30		X	X	X		Holthuis (1980); Spivak (1997)
Parapenaeus Smith, 1885	17	X	X		X	X	Holthuis (1980); Spivak (1997); Felder et al. (2009)
Penaeopsis Bate, 1881	7[1]	X	X		X	X	Holthuis (1980); Paramo and Saint-Paul (2012)
Penaeus Fabricius, 1798	3		X	X			Holthuis (1980)
Trachysalambria Burkenroad, 1934a	9		X	X	X		Holthuis (1980)
Xiphopenaeus Smith, 1869	1[2]	X		X			Holthuis (1980); Spivak (1997); Felder et al. (2009)

Table 2. Distribution of penaeid genera whose sternal spines have not been described. [1] Restricted to Southwest Atlantic; [2] entirely pelagic; [3] isobath information unavailable; [4] restricted to Southeast Atlantic; [5] count includes seven new genera partitioned from within *Parapenaeopsis* by Sakai and Shinomiya (2011); [6] restricted to Eastern Pacific; [7] Caribbean only.

Genus	Min. no. of species	Hemisphere		Isobath (m)			References
		West	East	Within 75	75-200	Beyond 200	
Artemesia Bate, 1888	1	X[1]		X			Holthuis (1980); Spivak (1997)
Funchalia Johnson, 1868	5	X[2]	X			X	Hopkins et al. (1994)
Heteropenaeus De Man, 1896	1		X[3]				
Macropetasma Stebbing, 1914	1		X[4]	X			Holthuis (1980)
Parapenaeopsis Alcock, 1901	21[5]	X	X	X	X		Holthuis (1980); Sakai and Shinomiya (2011)
Pelagopenaeus Pérez-Farfante and Kensley, 1997	1	X[2]	X	X	X	X	Burkenroad (1936)
Protrachypene Burkenroad, 1934a	1	X[6]		X			Holthuis (1980)
Rimapenaeus Pérez-Farfante and Kensley, 1997	6	X		X	X		Holthuis (1980); Felder et al. (2009)
Tanypenaeus Pérez-Farfante, 1972	1	X[7]			X		Pérez-Farfante (1972)
Trachypenaeopsis Burkenroad, 1934a	3	X	X	X			Almeida et al. (2007); Crosnier et al. (2007); Felder et al. (2009)
Trachypenaeus Alcock, 1901	1		X	X			Holthuis (1980)

1985) generally consists of three to six transitional stages between the late pelagic larva and recently settled juvenile when propulsion switches from thoracic to pleopodal, chelae on the first-three pereiopods become functional (Dall et al., 1990b; Anger, 2006), and transition to the adult body form begins (Felder et al., 1985). I use the term 'postlarva' here, and restrict its usage to this transitional life-phase.

Postlarvae remain difficult to identify below family level due to phase brevity and a lack of taxonomic characters (Felder et al., 1985; Dall et al., 1990b). Characters traditionally used to identify and discriminate 'postlarvae' and early juveniles include: scaphocerite shape and lateral spine length; number of rostral teeth; carapace, pleonal and furcal spination patterns (Cook, 1966; Dall et al., 1990b; Calazans, 1993); presence or absence of spinules in the adrostral and epigastric regions, and along the dorsal carina of the sixth pleomere (Ringo and Zamora, 1968; Cabrera-Jimenez, 1983); antennule morphology (Cabrera-Jimenez and Gil-R.-S., 1991); relative length of antennular flagellum segments (Motoh and Buri, 1981; Calderón-Pérez et al., 1989; Ditty, 2011); and, chromatophore patterns (Motoh and Buri, 1981). None of the aforementioned characters, however, are restricted to the postlarva phase.

Post-mysis stages of many penaeids have spines ventrally along the cephalothorax (Burkenroad, 1934a), a character possibly unique to postlarvae (Jackson et al., 1989). Heldt (1938) first mentioned and illustrated sternal spines in reared *Melicertus kerathurus* (Forskål, 1775). Later, Jackson et al. (1989) described spine number and placement in reared *Atypopenaeus formosus* Dall, 1957 and *Metapenaeopsis palmensis* (Haswell, 1879); examined and compared sternal spine placement in several species of *Metapenaeus*, *Penaeus* Fabricius, 1798, and *Megokris granulosus* (Haswell, 1879), which Jackson et al. (1989) label *Trachypenaeus* Alcock, 1901 from the Indo-Pacific; and developed the sternal spine formula to describe number and placement of spines on each thoracic plate. Pérez-Farfante and Kensley (1997) subsequently elevated five sub-genera of *Penaeus* to generic level, i.e., *Farfantepenaeus*, *Fenneropenaeus* Pérez Farfante, 1969, *Litopenaeus*, *Marsupenaeus* Tirmizi, 1971 and *Melicertus* Rafinesque, 1814, and partitioned *Trachypenaeus* into four genera, i.e., *Megokris* Pérez-Farfante and Kensley, 1997, *Rimapenaeus*, *Trachypenaeus*, and *Trachysalambria* Burkenroad, 1934a, which obscured the potential significance of sternal spines as a life-phase specific character.

Identification of reliable life-phase specific taxonomic characters for accurate discrimination of targeted taxa is essential for ecological and behavioral studies of ELS, development of aquaculture techniques, and acquisition of early life history information for stock management purposes (Anger, 2006). Shrimp stocks depend on the annual supply of new recruits for replenishment. Fluctuations in oceanographic conditions due to global warming, ocean acidification, and other environmental perturbations that can alter physiological processes, behaviors, dispersal and recruitment pathways, and habitat use patterns of ELS may adversely impact the population dynamics of shrimp and necessitate alternate management strategies (Ramirez-Rodriguez et al., 2003; Cury et al., 2008).

The significance of sternal spines in penaeid taxonomy and systematics remains poorly understood. My objectives were to: describe number and placement of sternal spines in *Parapenaeus* sp. and a specimen tentatively identified as *Xiphopenaeus kroyeri* from the Gulf of Mexico; review information for penaeids worldwide; evaluate the significance of sternal spines as a life-phase specific taxonomic character; and, determine whether sternal spines provide insight into family relationships and penaeid diversity.

Materials and Methods

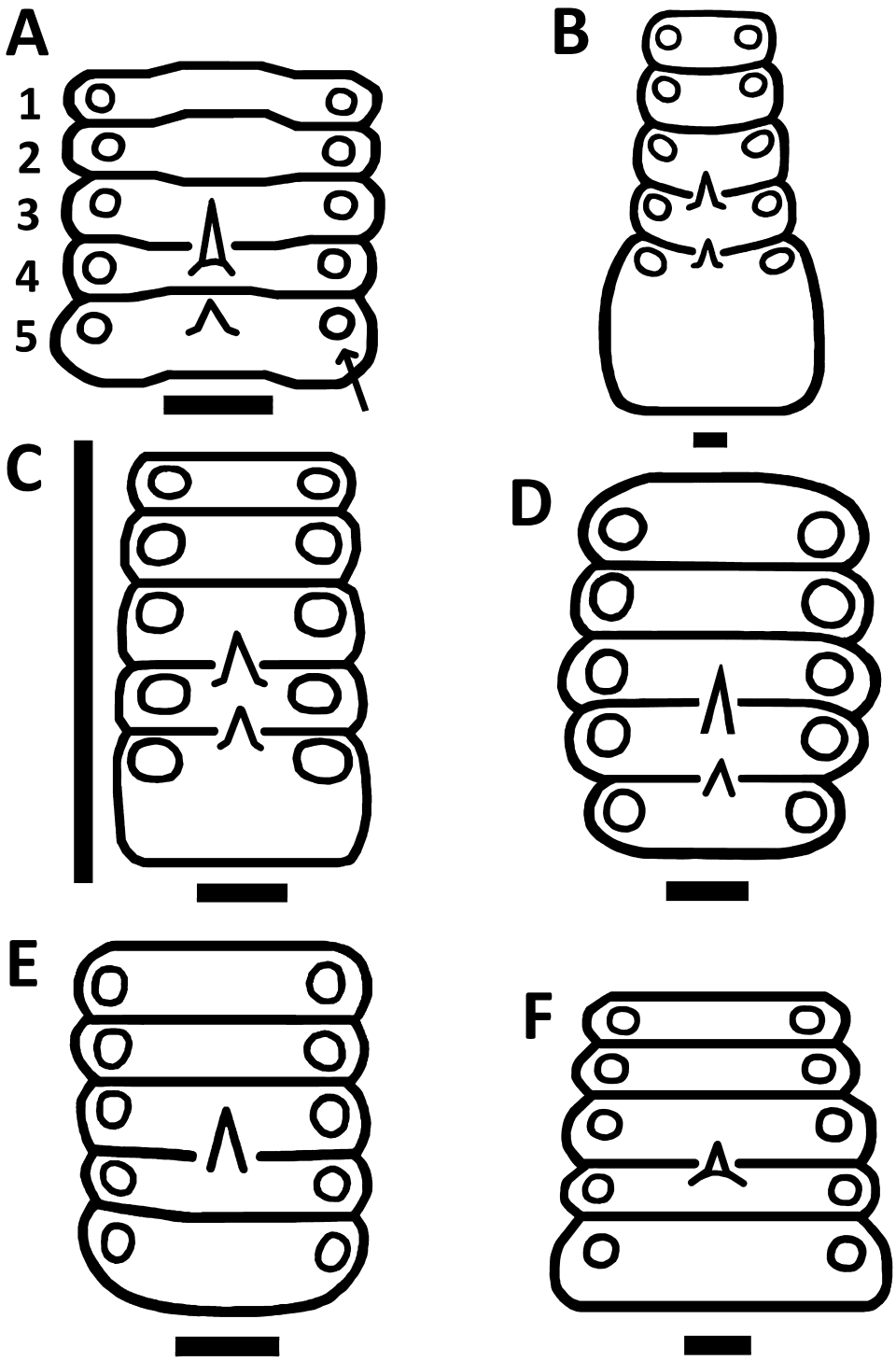
I examined sternal spine number and placement in *Parapenaeus* sp. ($n = 4$ myses, 3-5 dorsal teeth (DT); 3 postlarvae, 5 DT), *Farfantepenaeus aztecus* (Ives, 1891) ($n = 13$; 3-6 DT), *Farfantepenaeus duorarum* (Burkenroad, 1939) ($n = 9$; 3-6 DT), *Litopenaeus setiferus* (Linnaeus, 1767) ($n = 8$; 3-5 DT), *Melicertus kerathurus* ($n = 1$; 2 DT), and a postlarva tentatively identified as *Xiphopenaeus kroyeri* ($n = 1$; 4 DT). Rostral tooth counts exclude the epigastric tooth. *Farfantepenaeus aztecus*, *Farfantepenaeus duorarum*, *Litopenaeus setiferus* and the tentative *Xiphopenaeus kroyeri* were collected by hand-net, drop trap, or benthic sled along western Louisiana and south Texas, or with a 0.5-m plankton net (0.500-mm mesh) in a tidal pass into Galveston Bay. The species identity of *Farfantepenaeus aztecus* and *Farfantepenaeus duorarum* had previously been verified with a multiplex Polymerase Chain Reaction (PCR) assay, which targeted the 16S rRNA mitochondrial gene (Alvarado Bremer et al., 2010). The specimen assigned to *Xiphopenaeus kroyeri* was identified by characters described in Kurata (1970) after an unsuccessful attempt to molecularly verify the identity due to preservation history. I used characters from Paulinose (1979) and Dall et al. (1990b) to confirm the generic identity of *Parapenaeus*, and characters from Heldt (1938) to identify a specimen of *Melicertus kerathurus* collected in waters of the northeastern Atlantic off Portugal.

Sternal spines are located on one or more plates along the ventral surface of the cephalothorax between pereiopods (Fig. 1A). Plates are numbered one through five toward the pleon (Fig. 1A) following Jackson et al. (1989). By comparison, Kitani (1993a) numbers the plates four through eight, and Pérez-Farfante and Kensley (1997) number the plates 10 through 14. Following the numbering system of Jackson et al. (1989), a sternal formula of $0 + 0 + 0 + 1 + 1$ indicates that plates one through three lack spines, while plates four and five have one spine each (Fig. 1A).

Number, placement, orientation, and length of sternal spines can differ among taxa, which I call the 'sternal pattern.' Sternal spines are located near the body midline in taxa with one spine on a given plate, and on each side of the body midline in taxa with two spines on a given plate. Spines located on the same plate are comparable in length, but spine length often differs among plates (Fig. 1). I used a digital camera coupled to a stereo-zoom microscope to document spine placement, length, and orientation, and shape of the sternal plates for taxa I examined. Sternal spines are re-illustrated here for *Litopenaeus setiferus* and *Farfantepenaeus aztecus* because diagrammatic illustrations in Ditty (2011) are not to scale, and depict differences in sternal plate shape(s) inaccurately. Sternal spines generally range in total length from about 0.01 to 0.1 mm and may require a biological stain to enhance definition, but are easiest to observe in cleared and stained specimens (Jackson et al., 1989).

Results and Discussion

Postlarvae of most penaeids share one of two common sternal formulas: $0 + 0 + 0 + 1 + 1$ or $0 + 0 + 0 + 1 + 0$ (Table 3). *Atypopenaeus formosus*, *Marsupenaeus japonicus* (Bate, 1888) and most former members of the '*Penaeus*' complex, i.e., *Farfantepenaeus*, *Fenneropenaeus*, *Melicertus* and *Penaeus*, have a longer spine on plate four and shorter spine on plate five (Fig. 1A-D). *Metapenaeus* and members of the former '*Trachypenaeus*' complex, e.g., *Megokris* and *Trachysalambria*, have a spine on plate four only (Table 3; Fig. 1E-F). Species of *Litopenaeus* also have a spine on plate four (Fig. 1G), except *Litopenaeus occidentalis* (Streets, 1871), which has a spine on plates four and five (Kitani,



1996) like *Farfantepenaeus*, *Fenneropenaeus*, *Melicertus*, and *Penaeus* (Table 3).

The sternal spine pattern in the tentative *Xiphopenaeus kroyeri* differs from that described for other penaeids. *Xiphopenaeus kroyeri* has a pair of spines on each of the first-three sternal plates, i.e., 2 + 2 + 2 + 0 + 0, which become progressively smaller and more widely-spaced from plates one to three (Table 3, Fig. 1H). Species of *Metapenaeopsis* from the Indo-Pacific have a pair of spines on the first and second plates, and may have a single spine on plates four and five (Table 3; Fig. 1I-K). To date, only the tentative *Xiphopenaeus kroyeri* has a pair of spines on the first-three sternal plates.

Myses and postlarvae of *Parapenaeus* sp. have a slender, elongate, posteroventrally-directed spine near the posterior margin of plate five, i.e., 0 + 0 + 0 + 0 + 1 (Fig. 1L), which differs in length, shape, and orientation from sternal spines described for other penaeid genera (Fig. 1A-

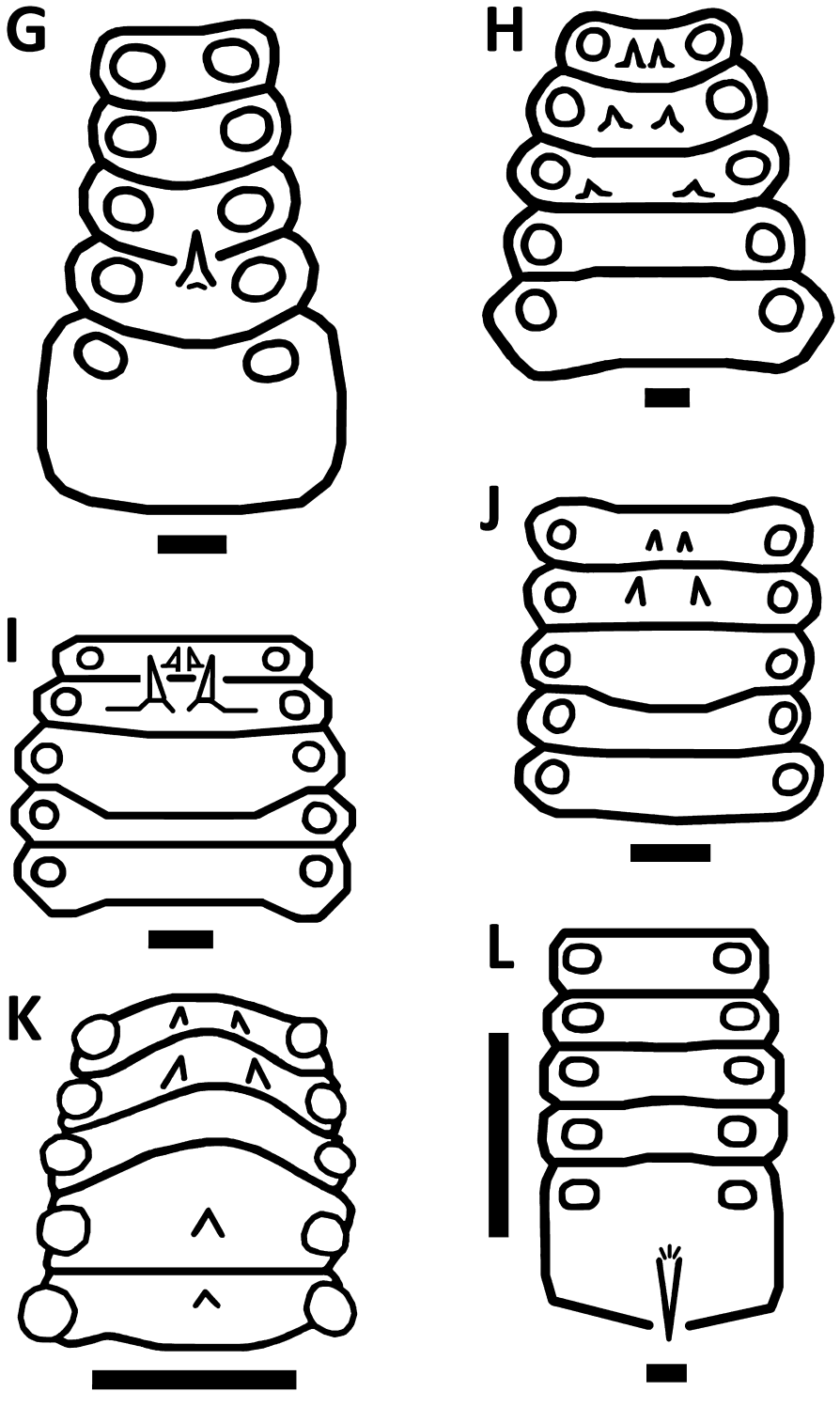


Fig. 1. Number and placement of sternal spines in postlarvae of 12 penaeid taxa. Sternal spines are located on one or more plates along the ventral surface of the cephalothorax between pereiopods. Sternal plates are numbered from one through five toward the pleon. Arrow indicates circular base of the pereiopods, which were removed for clarity. A, *Atypopenaeus formosus*; B, *Farfantepenaeus aztecus*; C, *Melicertus kerathurus*; D, *Penaeus semisulcatus*; E, *Metapenaeus ensis*; F, *Megokris granulosus*; G, *Litopenaeus setiferus*; H, tentative *Xiphopenaeus kroyeri*; I, *Metapenaeopsis palmensis*; J, *Metapenaeopsis barbata*; K, *Metapenaeopsis dalei*; L, *Parapenaeus*. Images are rescaled to standardize the horizontal measurement unit. Horizontal scale bar represents 0.1 mm. Vertical scale bar represents 0.5 mm and applies only to images C and L. Note considerable difference in size of postlarvae of some taxa based on width of the sternum. Images A, F and I from Jackson et al. (1989; Fig. 15C-E), with F labeled *Trachypenaeus* in Jackson et al. (1989); B-C, G-H and L are originals; D from Ronquillo et al. (2006; Fig. 11R); E from Ronquillo and Saisho (1993; Fig. 11Q); J from Ronquillo and Saisho (1997; Fig. 8N); and K from Choi and Hong (2001; Fig. 11I, original sub-figure mislabeled). Images are reproduced with kind permission of the publishers through Rightslink®: CSIRO Publishing (Collingwood, VIC, Australia), Oxford University Press (Oxford, UK) and Springer-Verlag with permission from Springer Science + Business Media (Berlin, Germany). Other images are reproduced with permission of NOAA Fisheries.

Table 3. Sternal spines in penaeid postlarvae. Each plate is associated with one of the five pereiopods. [1] Some species have a spine on plates four and five. [2] Describes spine placement for three unverified species. [3] Describes spine placement for two species tentatively assigned to *Penaeopsis*. [4] Tentatively assigned to *Xiphopenaeus kroyeri*.

Taxon	Sternal plate number and spine placement					References
	1	2	3	4	5	
Atypopenaeus formosus Dall, 1957	0	0	0	1	1	Jackson et al. (1989)
Farfantepenaeus aztecus (Ives, 1891)	0	0	0	1	1	Jackson et al. (1989); Ditty (2011)
Farfantepenaeus brevirostris (Kingsley, 1878)	0	0	0	1	1	Kitani (1994, 1997a)
Farfantepenaeus californiensis (Holmes, 1900)	0	0	0	1	1	Kitani (1993a, 1994)
Farfantepenaeus duorarum (Burkenroad, 1939)	0	0	0	1	1	Ditty (2011)
Fenneropenaeus indicus (H. Milne Edwards, 1837)	0	0	0	1	1	Jackson et al. (1989)
Fenneropenaeus merguiensis (De Man, 1888)	0	0	0	1	1	Jackson et al. (1989)
Litopenaeus occidentalis (Streets, 1871)	0	0	0	1	1	Kitani (1994, 1996, 1997b)
Litopenaeus setiferus (Linnaeus, 1767)	0	0	0	1	0	Jackson et al. (1989); Ditty (2011)
Litopenaeus stylirostris (Stimpson, 1874)	0	0	0	1	0	Jackson et al. (1989); Kitani (1994)
Litopenaeus vannamaei (Boone, 1931)	0	0	0	1	0	Jackson et al. (1989); Kitani (1993b)
Marsupenaeus japonicus (Bate, 1888)	0	0	0	1	1	Jackson et al. (1989)
Megokris granulosus (Haswell, 1879)	0	0	0	1	0	Jackson et al. (1989)
Melicertus kerathurus (Forskal, 1775)	0	0	0	1	1	Heldt (1938); this study
Melicertus latisulcatus (Kishinouye, 1896)	0	0	0	1	1	Jackson et al. (1989)
Melicertus longistylus (Kubo, 1943)	0	0	0	1	1	Jackson et al. (1989)
Melicertus plebejus (Hess, 1865)	0	0	0	1	1	Jackson et al. (1989)
Metapenaeopsis barbata (De Haan, 1844)	2	2	0	0	0	Ronquillo and Saisho (1997)
Metapenaeopsis dalei (Rathbun, 1902)	2	2	0	1	1	Choi and Hong (2001)
Metapenaeopsis palmensis (Haswell, 1879)	2	2	0	0	0	Jackson et al. (1989)
Metapenaeus affinis (H. Milne Edwards, 1837)	0	0	0	1	0	Hassan (1981)
Metapenaeus ensis (De Haan, 1844)	0	0	0	1	0	Ronquillo and Saisho (1993)
Metapenaeus moyebi (Kishinouye, 1896)	0	0	0	1	0	Kurata and Pusadee (1974)
Parapenaeus Smith, 1885	0	0	0	0-1[1]	1	Pearson (1939); Paulinose (1979)[2]; this study
Penaeopsis Bate, 1881	0	0	0	1	1	Burkenroad (1934a)[3]
Penaeus esculentus Haswell, 1879	0	0	0	1	1	Jackson et al. (1989)
Penaeus monodon Fabricius, 1798	0	0	0	1	1	Jackson et al. (1989)
Penaeus semisulcatus De Haan, 1844	0	0	0	1	1	Jackson et al. (1989); Ronquillo et al. (2006)
Trachysalambria curvirostris (Stimpson, 1860)	0	0	0	1	0	Ronquillo and Saisho (1995)
Xiphopenaeus kroyeri (Heller, 1862)	2	2	2	0	0	This study [4]

L). *Parapenaeus* sp. also has a feeble, slender, elongate, posterioventrally-curved median spine on pleomere one, and a feeble, shorter, gently-curved, more ventrally-directed spine on pleomere two. Illustrations of ELS of *Parapenaeus* sp. collected off the U.S. Atlantic and Gulf coasts (Pearson, 1939; Figs. 50-53) and *Parapenaeus longirostris* (Lucas, 1846) from the North Atlantic and Mediterranean Sea (Stephensen, 1923, Fig. 10; Gurney, 1942, Fig. 55) display sternal and pleonal spines in lateral view. Species of *Parapenaeus* from the Indo-Pacific have an elongate spine on sternal plates four and five, or plate five only, and have a ventromedian spine on the first-two to four (Paulinose, 1979), or rarely all pleomeres (Gurney, 1942).

Sternal spines have not been described for *Funchalia*. Species of *Funchalia*, however, have an elongate ventromedian spine on the first-three or four pleomeres (Gurney, 1924; Paulinose, 1974; Lindley et al., 2001) with the spine on the first-two pleomeres curved slightly forward rather than backward as in species of *Parapenaeus*. In addition, young of *Funchalia* have posteriorly directed 'spinules' along the ventrolateral margins of the sixth pleomere (Gurney, 1924; Paulinose, 1974; Lindley et al., 2001) not reported to date for other penaeid genera. The unusual length, shape, and reverse orientation of the spine on plate five in species of *Parapenaeus*, and the presence of a slender, elongate, ventromedian spine on two or more pleomeres in *Parapenaeus* and *Funchalia* that other penaeids lack support molecular and morphological data that Penaeidae may be paraphyletic (Tavares et al., 2009; Tavares and Martin, 2010).

Information on number and placement of sternal spines in species of *Penaeopsis* is problematic. The identity of post-mysis stages assigned to '*Penaeopsis*' by Burkenroad (1934a) has not been molecularly verified, but Burkenroad notes that wild-caught '*Penaeopsis serratus*' Bate, 1881, and '*Penaeopsis challengeri*' De Man, 1911, have "an anteriorly-directed median spine on sternites XIII and XIV," i.e., $0 + 0 + 0 + 1 + 1$. Penaeid ELS labeled '*Penaeopsis*' by Gurney (1924, 1943) and Paulinose (1973) are misidentified and do not mention sternal spines (Jackson et al., 1989; Chong and Sasekumar, 1994; Ronquillo and Saisho, 1997; Choi and Hong, 2001). Myses in Gurney (1924; Fig. 9 labeled *Parapenaeus*; Fig. 10 labeled *Penaeopsis*) have a denticulate anterioventral carapace margin consistent with a species of *Metapenaeopsis* (Chong and Sasekumar, 1994; Ronquillo and Saisho, 1997). Feathered setae along the telson in the first postlarva of what Gurney (1943; Fig. 43) refers to as

mostly '*Penaeopsis goodei*,' now *Metapenaeopsis goodei* (Smith, 1885), also resembles a species of *Metapenaeopsis* (Chong and Sasekumar, 1994; Choi and Hong, 2001). The combination of a denticulate anterioventral carapace margin in myses and a furcal spine count of 7 + 1 + 7 in the second and third mysis-stages and first postlarva of what Paulinose (1973) calls *Penaeopsis rectacuta* (Bate, 1881) suggest a species of *Metapenaeopsis*.

In general, taxa whose sternal spines remain undescribed have little commercial-value due to their relatively small size or deep-water distribution. In addition, some taxa have very restricted regional distributions, e.g., *Protrachypene* Burkenroad, 1934a; occur only in deeper offshore waters, e.g., *Pelagopenaeus*, *Tanypenaeus* Perez-Farfante, 1972; or, are poorly known, e.g., *Heteropenaeus* De Man, 1896, *Pelagopenaeus*, and *Trachypenaeopsis* Burkenroad, 1934a (Table 2). *Artemesia longinaris* Bate, 1888, *Macropetasma africana* (Balss, 1913), and several species of *Parapenaeopsis* have been reared, but number and placement of sternal spines has not been described. The seven proposed new genera from within *Parapenaeopsis* have no effect on information presented here because sternal spines have not been described for any species of *Parapenaeopsis*.

Sternal spine patterns may help discriminate postlarvae of some penaeids in regions with relatively few taxa, but should not be used as a stand-alone taxonomic character for several reasons. First, most penaeids share one of two common sternal patterns (Table 3). Second, subjective differences in relative spine length between adjacent plates can be misleading due to optical parallax, i.e., spine base and tip not in same optical plane. When looking down at the sternal plates, spines appear relatively shorter than when viewed from the side due to their diagonal orientation relative to the body axis. Third, spine length changes over time. Spines become progressively smaller and gradually disappear in most taxa as postlarvae transition to the juvenile life-phase. 'Shorter' spines also disappear before 'longer' spines; therefore, a sternal formula of 0 + 0 + 0 + 1 + 1 can become 0 + 0 + 0 + 1 + 0 after loss of the shorter spine on plate five. Finally, timing of character acquisition and loss can vary with feeding history, rearing conditions, water temperatures, and genotype (Hartnoll, 1982; Williamson, 1982; Anger, 2006). Genetics restrict most developmental events to a narrow window of time, but environmental conditions can interact with genotype to modify timing of character appearance or loss (Anger, 2006). Therefore, when penaeids acquire and lose characters like sternal spines can vary seasonally, between populations, and with changes in environmental conditions. Jackson et al. (1989) suggest that sternal spines may be unreliable as a taxonomic character for postlarvae with more than four DT. I suggest that the range varies from about three to five DT depending on taxon, developmental plasticity, and other factors that can affect the rate of molting, e.g., food availability, water temperatures, environmental conditions.

The effect of developmental plasticity and changes in environmental conditions on timing of acquisition and loss of transitory characters like sternal spines should not be overlooked. One reviewer expressed concern that *Farfantepenaeus duorarum* collected in Florida Bay during July and postlarvae reared from known parentage with three to five DT had a spine on plate four only, while wild-caught postlarvae with three to five DT collected during November had a spine on plate four only, or a spine of reduced length on plates four and five. Variability in timing of sternal spine loss is not surprising given geographic and seasonal differences in morphology of *Farfantepenaeus duorarum* across the Gulf of Mexico (Ditty and Alvarado Bremer, 2011). Populations of *Farfantepenaeus duorarum* along the U.S. Atlantic and Gulf coasts display high haplotype and nucleotide diversity consistent with the possibility of different ecological populations (McMillen-Jackson and Bert, 2004). Discrete ecological populations of the same species are an increasingly common pattern in the Gulf of Mexico normally associated with barriers like the Mississippi River that restrict gene flow (Felder and Staton, 1994).

Sternal spines are not restricted to the postlarva phase. Mysis-stages, juveniles and adults of some penaeids can have sternal spines. First-stage myses of *Melicertus kerathurus* have rudimentary spines (Heldt, 1938), as do 25-35% of second-stage myses of *Litopenaeus vannamei* (Boone, 1931), *Farfantepenaeus brevirostris* (Kingsley, 1878) and *Farfantepenaeus californiensis* (Holmes, 1900), and third-stage myses of *Litopenaeus occidentalis* (Kitani, 1993a, b, 1996, 1997a, b). In addition, mysis-stages of *Parapenaeus* sp. have a spine on one or more sternal plates (Pearson, 1939; Paulinose, 1979). Some species of *Litopenaeus* and *Farfantepenaeus* with six DT from the eastern Pacific (Kitani, 1993a, b, 1996, 1997a, b) and *Farfantepenaeus aztecus* collected during spring and fall in the northern Gulf of Mexico with up to 6 − 7 + 1 rostral teeth, which may be early juveniles, can also have a vestigial spine on plate four (Ditty, 2011). Additionally, juveniles and adults of some species of *Metapenaeopsis* have prominent spines along the sternum. A juvenile *Metapenaeopsis* sp. (5.3 mm carapace length (CL)) from Florida Bay had a sternal formula of 0 + 2 + 0 + 1 + 1. Larger juveniles and adults of *Metapenaeopsis* sp. no longer had the spine on plates four and five, but retained the pair on plate two (M. Criales, personal communication, April 2014). Juvenile (6.0-6.5 mm CL) *Metapenaeopsis mineri* Burkenroad, 1934a, from the Eastern Pacific also have a pair of spines on plate two (Burkenroad, 1934a).

Characters used to identify when the postlarva phase terminates are often subjective because postlarvae essentially represent the morphologically under-developed juvenile (Anger, 2006). Large, setose, functional pleopods; functional chelae on the first three pereiopods with short bristles terminally; antennules with segmented flagella; and, lack of a supraorbital spine often found in myses distinguish the mysis phase and first postlarva of most taxa (Dall et al., 1990c). Dall et al. (1990b) use number of rostral teeth, body length, and a change in telson shape and number of furcal spines to identify when the postlarva phase terminates. However, body length and attainment of the adult complement of rostral teeth are generally inadequate metrics to delimit the phase because rates of growth and development can vary with environmental conditions (Paulinose, 1979; Anger, 2006). In addition, what defines a 'countable' rostral tooth varies among authors. Loss of the characteristic squarish telson profile and

a reduction in furcal spine count may be 'better' traits to distinguish the postlarva from early juvenile.

I suggest that differences in sternal plate shape may be an unrecognized taxonomic character. I base my suggestion on apparent differences in height, width, and contour of individual plates in former members of '*Penaeus*' (Fig. 1B-D, G), and between *Metapenaeopsis palmensis*, *Metapenaeopsis barbata* (De Haan, 1844), and *Metapenaeopsis dalei* (Rathbun, 1902) (Fig. 1I-K). My observation is preliminary because plates are incompletely developed in postlarvae and authors do not describe how they determine plate shape for illustration purposes and may have interpreted and depicted plate characteristics differently. Nevertheless, based on a standardized horizontal scale of 0.1 mm, differences in overall width of the sternal plates may help discriminate some taxa (Fig. 1A-L). The relationship between sternal spine length and plate height, however, cannot be used as a basis for taxonomic identification because spine length changes over time and the height of individual plates can differ among taxa.

The evolutionary origin of sternal spines is unknown. Characters like sternal spines can develop independently in different taxa as a secondary adaptation to the pelagic environment (Felder et al., 1985) and may be common in aquatic organisms with planktonic ELH stages (Williamson, 1982; Felder et al., 1985; Anger, 2006). Little information exists on genital development in penaeids, but species like *Metapenaeus affinis* (Milne Edwards, 1837) and *Litopenaeus setiferus* incorporate the spine on plate(s) four and/or five into the sternal wall after the last postlarva stage. After modification, plates four and/or five eventually develop into the thelycum of females (Burkenroad, 1934b; Heldt, 1938; Hassan, 1981; Dall et al., 1990c).

Sternal spines do not reflect lower-level systematic relationships within Penaeidae regardless of generic nomenclature applied because most taxa share one of the two common sternal formulas (Table 3). Recall that only *Metapenaeopsis*, and perhaps *Litopenaeus*, contain species with different sternal formulas. A molecular study of species of *Metapenaeopsis* from the Indo-Pacific identified two clades based on presence (*Metapenaeopsis barbata* and *Metapenaeopsis palmensis*) or absence (*Metapenaeopsis dalei*) of stridulating ridges along the carapace (Tong et al., 2000). Members of each clade also differed in the distribution of adults, e.g., shallow versus deeper-water species or vertical depth distribution, structure of genitalia (Crosnier, 1994a, b), and sternal spine pattern in postlarvae (Table 3; Fig. 1I-K). Tong et al. (2000) suggest that deeper water Indo-Pacific species of *Metapenaeopsis* diverged from shallow-water forms during the Pleistocene Epoch when sea-level was 50-150 m lower than today. Colonization of deep waters by shallow water species as Tong et al. (2000) suggest are consistent with ecological and morphological diversification in *Metapenaeopsis* as revealed by the different sternal patterns. Note that most taxa with one of the two common sternal patterns, e.g., species of *Metapenaeus* and former members of '*Penaeus*' and '*Trachypenaeus*' (Table 3), generally occur over the inner shelf and in estuarine habitats. If Tong et al. (2000) are correct, other speciose genera with members that occupy a wide range of ecological habitats like *Parapenaeopsis* should also contain species with different sternal configurations.

Whether sternal spines reflect higher-level systematic relationships within Penaeoidea is unclear. Reared ELS and preliminary information on ELS of other penaeoid families appear consistent with the suggestion of Burkenroad (1934b) that mysis and early post-mysis stages of Penaeidae and Sicyoniidae Ortmann, 1898, have spines along the sternum that members of Benthesicymidae Wood-Mason, 1891 and Solenoceridae Wood-Mason, 1891 lack. For example, reared *Sicyonia carinata* (Brunnich, 1768) have a single, long, ventromedian spine on plate four (Heldt, 1938; Fig. 124). Juvenile and adult *Sicyonia* Milne Edwards, 1830, also have a long spine on plate four (Huff and Cobb, 1979), or plates four and five, and some species have a pair of spines near the posterior margin of plate one (De Freitas, 1984). Few members of other penaeoid families have been reared, but *Gennadas elegans* (Smith, 1882), *Pleoticus muelleri* (Bate, 1888), and *Solenocera membranacea* (Risso, 1816) apparently lack sternal spines (Heldt, 1938; Iorio et al., 1990). Although characters like sternal spines can evolve independently in different taxa due to convergent evolution, phylogenetic analyses based on morphology support a close relationship between sicyoniids and penaeids (Tavares et al., 2009).

In summary, reliable discrimination of closely related taxa requires traits with high diagnostic power that reduce the subjectivity often found in taxonomic identifications. Sternal spines do not meet that criterion because postlarvae of most penaeids share one of two common sternal patterns (Table 3). Moreover, when sternal spines disappear varies among taxa and with feeding history, environmental conditions, water temperatures, and genotype. Sternal spines do not reflect lower-level systematic relationships regardless of generic nomenclature applied and are not life-phase specific because mysis-stages, juveniles, and adults of some penaeids can have spines along the sternum. Sternal spines should not be used as a stand-alone taxonomic character. However, knowledge of the number and placement of spines; the geographic distribution of adults; and, perhaps differences in sternal plate shape or overall dimensions of the sternum should be included in the suite of characters used to identify and discriminate penaeids during the postlarva phase.

ACKNOWLEDGEMENTS

Thanks to Dr. Antonina dos Santos, Instituto Português do Mar e da Atmosfera, Lisbon, Portugal, for providing a postlarva of *Melicertus kerathurus* collected off Portugal, and to Carley Knight, University of Southern Mississippi and NOAA's Pascagoula Laboratory for myses and postlarvae of *Parapenaeus* sp. from the Gulf of Mexico. Thanks to Dr. Geoffrey Matthews (retired), formerly of NOAA's Galveston Laboratory, and to Shawn Hillen and Juan Salas of NOAA's Galveston Laboratory who participated in sample collection, and to NOAA's Southeast Fisheries Science Center for funding support. Thanks also to Juan Salas for illustrating the sternal pattern for *Litopenaeus setiferus*, *Farfantepenaeus aztecus*, *Melicertus kerathurus*, *Parapenaeus* sp. and tentative *Xiphopenaeus kroyeri*. Images were reproduced by kind permission of the publishers through Rightslink®: CSIRO Publishing (Marine and Freshwater Research); Oxford University Press (Journal of Plankton Research); Springer (Hydrobiologia) with permission from Springer Science + Business Media; and courtesy of NOAA Fisheries (Fishery Bulletin). Views and opinions expressed here are those of the author and do not necessarily reflect those of NOAA Fisheries.

REFERENCES

Alcock, A. 1901. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the Royal Indian marine survey ship "Investigator": i-vi, 1-286, pls. 1-3. Indian Museum, Calcutta.

———. 1905. A revision of the genus *Peneus*, with diagnoses of some new species and varieties. Annals and Magazine of Natural History 16: 508-532.

Almeida, A. O., P. A. Coelho, and L. E. A. Bezerra. 2007. Further record of *Trachypenaeopsis mobilispinis* (Rathbun) (Decapoda, Penaeidae) from Brazilian coastal waters. Crustaceana 80: 379-383.

Alvarado Bremer, J. R., J. G. Ditty, J. Turner, and B. L. Saxton. 2010. Molecular species identification of commercially important penaeid shrimp from the Gulf of Mexico using a haplotype-specific multiplex PCR assay. Biochemical Systematics and Ecology 38: 715-721.

Anger, K. 2006. Contributions of larval biology to crustacean research: a review. Invertebrate Reproduction and Development 49: 175-205.

Balss, H. 1913. Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen sud Afrika. Decapode Crustaceen. Denkschriften der Medizinische-Naturwissenschaftlichen Gesellschaft zu Jena 15: 105-110.

Bate, C. S. 1881. On the Penaeidea. Annals and Magazine of Natural History (5) 8: 169-196, pls. 11-12.

———. 1888. Report on the Crustacea Macrura collected by the H.M.S. Challenger during the years 1873-1876. Report on the scientific results of the voyage of the H.M.S. Challenger during the years 1873-1876. 24: 1-942, pls. 1-150.

Boone, L. 1931. Anomuran, Macruran Crustacea from Panama and Canal Zone. Bulletin of the American Museum of Natural History 63: 137-189.

Bouvier, E.-L. 1905. Sur les Pénéides et les Sténopides recueillis par les expéditions francaises et monégasques dans l'Atlantique oriental. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 140: 980-983.

Brunnich, M. T. 1768. Ichthyologia Massiliensis, sistens piscium descriptiones eorumque apud incolas nomina. Accedunt Spolia Maris Adriatica: 1-110. Hafniae et Lipsiae, apud Rothii viduam et Proft.

Burkenroad, M. D. 1934a. Littoral Penaeidea chiefly from the Bingham Oceanographic Collection, with a revision of *Penaeopsis* and descriptions of two new genera and eleven new American species. Bulletin of the Bingham Oceanographic Collection, Yale University 4: 1-109.

———. 1934b. The Penaeidea of Louisiana with a discussion of their world relationships. Bulletin of the American Museum of Natural History 68: 61-143.

———. 1936. The Aristaeinae, Solenocerinae and pelagic Penaeidae of the Bingham Oceanographic collection. Bulletin of the Bingham Oceanographic Collection, Yale University 5: 1-151.

———. 1939. Further observations on Penaeidae of the northern Gulf of Mexico. Bulletin of the Bingham Oceanographic Collection, Yale University 6: 1-61.

Burukovsky, R. N. 1997. Selection of the type species for *Farfantepenaeus* Burukovsky, 1972 (Crustacea: Decapoda: Penaeidae). Proceedings of the Biological Society of Washington 110: 154.

Cabrera-Jimenez, J. A. 1983. Characters of taxonomic value of the postlarvae of the shrimp *Penaeus* (*Farfantepenaeus*) *brevirostris* Kingsley (Decapoda Natantia), of the Gulf of California, Mexico. Crustaceana 44: 292-300.

———, and B. G. Gil-R.-S. 1991. Morfologia del camoron postlarval *Penaeus* (*Litopenaeus*) *vannamei* con formula rostral 3/0: Organizacion y quetotaxia de la antenula. Anales del Instituto de Biologia, Universidad Nacional Autonoma de Mexico (Zoologia) 62: 41-56.

Calazans, D. 1993. Key to the larvae and decapodids of genera of the infraorder Penaeidea from the southern Brazilian coast. Nauplius, Rio Grande 1: 45-62.

Calderón-Pérez, J. A., E. Macias-Regalado, F. A. Abreu-Grobois, and S. Rendon-Rodriguez. 1989. Antennular flagella: a useful character for distinguishing subgenera among postlarval shrimp of the genus *Penaeus* (Decapoda) from the Gulf of California. Journal of Crustacean Biology 9: 482-491.

Choi, J. H., and S. Y. Hong. 2001. Larval development of the kishi velvet shrimp, *Metapenaeopsis dalei* (Rathbun) (Decapoda: Penaeidae), reared in the laboratory. Fishery Bulletin (U.S.) 99: 275-291.

Chong, V. C., and A. Sasekumar. 1994. Larval development of the fiddler shrimp, *Metapenaeopsis stridulans* (Alcock, 1905) (Decapoda: Penaeidae) reared in the laboratory. Journal of Natural History 28: 1265-1285.

Cook, H. L. 1966. A generic key to the protozoan, mysis, and postlarval stages of the littoral Penaeidae of the northwestern Gulf of Mexico. Fishery Bulletin (U.S.) 65: 437-447.

Crosnier, A. 1994a. Crustacea Decapoda: Les *Metapenaeopsis* indo-ouest-pacifiques avec un appareil stridulant (Penaeidae). Deuxieme partie, pp. 255-337. In, A. Crosnier (ed.), Resultats des Campagnes MUSORSTOM. Vol. 12. Mémoires du Muséum national d'Histoire naturelle, Paris.

———. 1994b. Crustacea Decapoda: Les *Metapenaeopsis* indo-ouest-pacifiques sans appareil stridulant (Penaeidae). Descrition de deux especes nouvelles, pp. 339-349. In, A. Crosnier (ed.), Resultats des Campagnes MUSORSTOM. Vol. 12. Mémoires du Muséum national d'Histoire naturelle, Paris.

———, A. Machordom, and M.-C. Boisselier-Dubayle. 2007. Les espèces du genre *Trachypenaeopsis* (Crustacea, Decapoda, Penaeidae). Approches morphologiques et moléculaires. Zoosystema 29: 471-489.

Cury, P. M., Y.-J. Shin, B. Planque, J. M. Durant, J.-M. Fromentin, S. Kramer-Schadt, N. C. Stenseth, M. Travers, and V. Grimm. 2008. Ecosystem oceanography for global change in fisheries. Trends in Ecology and Evolution 23: 338-346.

Dall, W. 1957. A revision of the Australian species of Penaeinae (Crustacea Decapoda: Penaeidae). Australian Journal of Marine and Freshwater Research 8: 136-231.

———. 2007. Recent molecular research on *Penaeus* sensu lato. Journal of Crustacean Biology 27: 380-382.

———, B. J. Hill, P. C. Rothlisberg, and D. J. Staples. 1990a. Chapter 8. Life Histories, pp. 283-332. In, J. H. S. Blaxter and A. J. Southward (eds.), The Biology of the Penaeidae. Advances in Marine Biology 27. Academic Press, San Diego, CA.

———, ———, ———, and ———. 1990b. Chapter 3. Taxonomy, pp. 55-126. In, J. H. S. Blaxter and A. J. Southward (eds.), The Biology of the Penaeidae. Advances in Marine Biology 27. Academic Press, San Diego, CA.

———, ———, ———, and ———. 1990c. Chapter 2. Morphology, pp. 7-54. In, J. H. S. Blaxter and A. J. Southward (eds.), The Biology of the Penaeidae. Advances in Marine Biology 27. Academic Press, San Diego, CA.

De Freitas, A. J. 1984. The Penaeoidea of southeast Africa. V – The Family Sicyoniidae. Investigational Report Oceanographic Research Institute, South Africa No. 60: 1-12.

De Grave, S., and C. H. J. M. Fransen. 2011. Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). Zoologische Mededelingen 85: 195-589.

De Haan, W. 1844. Crustacea. In, P. F. von Siebold (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-xxxi, ix-xvi, 1-243, pls. A-J, L-Q, 1-55. Lugduni-Batavorum, Leiden.

De Man, J. G. 1888. Report on the podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson F.R.S., Superintendent of the Museum. The Journal of the Linnean Society (Zoology) 22: 1-312, pls. 11-19.

———. 1896. *Heteropenaeus longimanus* nov. gen. n. sp., eine neue Penaeide aus der Java-See. Zoologischer Anzeiger 19: 111-113.

———. 1911. Family Penaeidae. The Decapoda of the Siboga Expedition. Part I. Siboga Expedition, Monograph 39a: 1-131, pls. 1-10.

Ditty, J. G. 2011. Young of *Litopenaeus setiferus*, *Farfantepenaeus aztecus* and *F. duorarum* (Decapoda: Penaeidae): a re-assessment of characters for species discrimination and their variability. Journal of Crustacean Biology 31: 458-467.

———, and J. R. Alvarado Bremer. 2011. Species discrimination of postlarvae and early juvenile brown shrimp (*Farfantepenaeus aztecus*) and pink shrimp (*F. duorarum*) (Decapoda: Penaeidae): coupling molecular genetics and comparative morphology to identify early life stages. Journal of Crustacean Biology 31: 126-137.

Fabricius, J. C. 1798. Entomologia Systematica emendata et aucta, secundum classes, ordines, genera, species adjectis synonimis locis observa-

tionibus descriptionibus. Tom. II. Supplementum Entomologiae Systematicae: 1-572. Hafniae, Copenhagen.

Felder, D. L., F. Álvarez, J. W. Goy, and R. Lemaitre. 2009. Chapter 59: Decapoda (Crustacea) of the Gulf of Mexico, with comments on the Amphionidacea, pp. 1019-1104. In, D. L. Felder and D. K. Camp (eds.), Gulf of Mexico Origin, Waters and Biota. Vol. 1, Biodiversity. Texas A&M University Press, College Station, TX.

———, and J. L. Staton. 1994. Genetic differentiation in trans-Floridian species complexes of *Sesarma* and *Uca* (Decapoda: Brachyura). Journal of Crustacean Biology 14: 191-209.

———, J. W. Martin, and J. W. Goy. 1985. Patterns in early postlarval development of decapods, pp. 163-225. In, A. M. Wenner (ed.), Crustacean Growth: Larval growth. Crustacean Issues 2. A. A. Balkema, Rotterdam.

Flegel, T. W. 2007. The right to refuse revision in the genus *Penaeus*. Aquaculture 264: 2-8.

Forskål, P. 1775. Descriptiones animalium, avium, amphibiorum, piscium, insectorium, vermium, quae in itinere orientali observavit, 1-19, i-xxxiv, 1-164, one map. Hafniae (Copenhagen).

Gurney, R. 1924. British Antarctic (Terra Nova) Expedition, 1910. Crustacea. Part IX. Decapod larvae. British Museum Natural History Report 8: 37-202.

———. 1942. Larvae of Decapod Crustacea. Crustacea Issue 129: 1-306. The Ray Society, London.

———. 1943. The larval development of two penaeid prawns from Bermuda of the genus *Sicyonia* and *Penaeopsis*. Proceedings of the Zoological Society of London Series B: Biological Sciences 113: 1-16.

Hartnoll, R. G. 1982. Growth, pp. 111-196. In, L. G. Abele (ed.), The Biology of Crustacea. Vol. 2: Embryology, Morphology and Genetics. Academic Press, San Diego, CA.

Harvey, A. W., J. W. Martin, and R. Wetzer. 2002. Chapter 17 Phylum Arthropoda: Crustacea, pp. 337-369. In, C. M. Young, M. A. Sewell, and M. E. Rice (eds.), Atlas of Marine Invertebrate Larvae. Academic Press, San Diego, CA.

Hassan, H. 1981. The genital organs and their development in *Metapenaeus affinis* (Decapoda, Penaeidae) studied through rearing them in the laboratory. Hydrobiologia 78: 49-58.

Haswell, W. A. 1879. On the Australian species of *Penaeus* in the Macleay Museum, Sydney. Proceedings of the Linnean Society of New South Wales 4: 38-44.

Heldt, J. H. 1938. Reproduction of the decapod crustaceans of the peneid family. Annales de l'Institut Océanographique, Monaco XVIII: 31-206.

Heller, C. 1862. Beitrage zur naheren Kenntnis der Macrouren. Sitzungsberichte der mathematisch-naturwissen-schaftlichen Classe der Kaiserlichen Akademie der Wissenschaften (Wien) 45: 389-426.

Hess, W. 1865. Beiträge zur Kenntnis der Decapoden-Krebse Ost-Australiens. Archiv fur Naturgeschichte, Berlin 31: 127-173.

Holmes, S. J. 1900. Synopsis of California stalk-eyed Crustacea. Occasional Papers of the California Academy of Sciences 7: 1-262.

Holthuis, L. B. 1980. FAO Species Catalogue. Vol. 1 – Shrimps and Prawns of the World. An annotated catalogue of species of interest to fisheries. FAO Fisheries Synopsis 125: 1-271. FAO, Rome.

Hopkins, T. L., M. E. Flock, J. V. Gartner, Jr., and J. J. Torres. 1994. Structure and trophic ecology of a low latitude midwater decapod and mysid assemblage. Marine Ecology Progress Series 109: 143-156.

Huff, J. A., and S. P. Cobb. 1979. Penaeoid and Sergestoid shrimps (Crustacea: Decapoda). Memoirs of the Hourglass Cruises, Florida Department of Natural Resources, Marine Research Laboratory 5: 1-102.

Iorío, M. I., M. A. Scelzo, and E. E. Boschi. 1990. Desarrollo larval y postlarval del langostino *Pleoticus muelleri* Bate, 1888 (Crustacea, Decapoda, Solenoceridae). Scientia Marina 54: 329-341.

Ives, J. E. 1891. Crustacea from the northern coast of Yucatan, the harbor of Vera Cruz, the west coast of Florida and the Bermuda Islands. Proceedings of the Academy of Natural Sciences of Philadelphia 43: 176-207.

Jackson, C. J., P. C. Rothlisberg, R. C. Pendrey, and M. T. Beamish. 1989. A key to genera of the penaeid larvae and early postlarvae of the Indo-West Pacific region, with descriptions of the larval development of *Atypopenaeus formosus* Dall and *Metapenaeopsis palmensis* Haswell (Decapoda: Penaeoidea: Penaeidae) reared in the laboratory. Fishery Bulletin (U.S.) 87: 703-733.

Johnson, J. Y. 1868. Descriptions of a new genus and a new species of macrurous decapod Crustaceans belonging to the Penaeidae, discovered at Madeira. Proceedings of the Zoological Society of London 1867: 895-901.

Kaestner, A. 1970. Invertebrate Zoology. Crustacea. Volume III, pp. 1-523. John Wiley & Sons, New York.

Kingsley, J. S. 1878. Notes on the North American Caridea in the museum of the Peabody Academy of Science at Salem, Mass. Proceedings of the Academy of Natural Sciences of Philadelphia 1878: 89-98.

Kishinouye, K. 1896. Note on a Japanese *Penaeus* and its classification. Zoological Magazine, Tokyo 8: 372-374.

Kitani, H. 1993a. Morphology of postlarvae of the yellowleg shrimp *Penaeus californiensis*. Nippon Suisan Gakkaishi 59: 217-221.

———. 1993b. Morphology of postlarvae of the whiteleg shrimp *Penaeus vannamei*. Nippon Suisan Gakkaishi 59: 223-227.

———. 1994. Identification of wild postlarvae of the penaeid shrimps, genus *Penaeus*, in the Pacific coast of Central America. Fisheries Science 60: 243-247.

———. 1996. Larval development of western white shrimp *Penaeus occidentalis* reared in the laboratory. Fisheries Science 62: 883-891.

———. 1997a. Larval development of the crystal shrimp *Penaeus* (*Farfantepenaeus*) *brevirostris* under laboratory conditions. Fisheries Science 63: 218-227.

———. 1997b. Postlarval morphology of the western white shrimp *Penaeus occidentalis* (Crustacea: Penaeidae). Revista de Biologia Tropical 45: 627-630.

Kubo, I. 1943. Diagnosis of a new species of the genus *Penaeus*. Suisan Kenkyusi 38: 200-201.

Kurata, H. 1970. Studies on the life histories of decapod crustacea of Georgia: Part III. Larvae of decapod Crustacea of Georgia. Unpublished report, University of Georgia Marine Science Institute, Sapelo Island: i-iv, 122-274, pls. 1-105.

———, and V. Pusadee. 1974. Larvae and early postlarvae of a shrimp, *Metapenaeus burkenroadi*, reared in the laboratory. Bulletin of the Nansei Regional Fisheries Research Laboratory (Thailand) 7: 69-84.

Lindley, J. A., F. Hernández, J. Scatllar, and J. Docoito. 2001. *Funchalia* sp. (Crustacea: Penaeidae) associated with *Pyrosoma atlanticum* (Thaliacea: Pyrosomidae) off the Canary Islands. Journal of the Marine Biological Association of the United Kingdom 81: 173-174.

Linnaeus, C. 1767. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 12th Edition. Holmiae 1: 1-1056.

Lucas, H. 1846. Histoire naturelle des animaux articulés. Première partie. Crustacés, Arachnides, Myriapodes et Hexapodes. In, Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Sciences Physique, Zoologie I: i-xxxv, 1-403, pls. 1-8. Imprimerie Nationale, Paris.

Ma, K. Y., T.-Y. Chan, and K. H. Chu. 2011. Refuting the six-genus classification of *Penaeus* s.l. (Dendrobranchiata, Penaeidae): a combined analysis of mitochondrial and nuclear genes. Zoologica Scripta 40: 498-508.

McLaughlin, P. A., D. K. Camp, M. V. Angel, E. L. Bousfield, P. Brunel, R. C. Brusca, D. Cadien, A. C. Cohen, K. Conlan, L. G. Eldredge, D. L. Felder, J. W. Goy, T. Haney, B. Hann, R. W. Heard, E. A. Hendrycks, H. H. Hobbs III, J. R. Holsinger, B. Kensley, D. R. Laubitz, S. E. LeCroy, R. Lemaitre, R. F. Maddocks, J. W. Martin, P. Mikkelsen, E. Nelson, W. A. Newman, R. M. Overstreet, W. J. Poly, W. W. Price, J. W. Reid, A. Robertson, D. C. Rogers, A. Ross, M. Schotte, F. R. Schram, C.-T. Shih, L. Watling, G. D. F. Wilson, and D. D. Turgeon. 2005. Common and scientific names of aquatic invertebrates from the United States and Canada: Crustaceans. American Fisheries Society, Special Publication 31. American Fisheries Society, Bethesda, MD, 545 pp.

———, R. Lemaitre, F. D. Ferrari, D. L. Felder, and R. T. Bauer. 2008. A reply to T. W. Flegel. Aquaculture 275: 370-373.

McMillen-Jackson, A. L., and T. M. Bert. 2004. Genetic diversity in the mtDNA control region and population structure in the pink shrimp *Farfantepenaeus duorarum*. Journal of Crustacean Biology 24: 101-109.

Milne Edwards, H. 1830. Description des genres *Glaucothoe*, *Sicyonie*, *Sergeste* et *Acete*, de l'ordre des Crustacés Décapodes. Annales des Sciences Naturelles (1) 19: 333-352.

———. 1837. Histoire naturelles des crustaces', comprenant l'anatomie, la physiologie et la classification de ces animaux 2. Librairie encyclopédique de Roret, Paris, 532 pp.

Motoh, H., and P. Buri. 1981. Identification of postlarvae of the genus *Penaeus* appearing in shore waters. Researches on Crustacea 11: 86-94.

Ortmann, A. E. 1898. Gliederfüssler: Arthropoda, pp. 1057-1168, pls. CIX-CXVI. In, A. Gerstäecker (ed.), Dr. H. G. Bronn's Klassen und Ordnun-

gen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild. C. F. Winter'sche Verlagshandlung, Leipzig.

Paramo, J., and U. Saint-Paul. 2012. Spatial structure of the pink speckled deep-sea shrimp *Penaeopsis serrata* (Bate, 1881) (Decapoda, Penaeidae) during November-December 2009 in the Colombian Caribbean Sea. Crustaceana 85: 103-116.

Paulinose, V. T. 1973. Developmental stages of *Penaeopsis rectacuta* Bate (Decapoda: Penaeidae) from the Indian Ocean, pp. 97-110. In, Indian Ocean Biological Centre Handbook. Vol. 5.

———. 1974. Decapod Crustacea from the International Indian Ocean Expedition: the species of *Funchalia* (Penaeidae) and their post-larvae. Journal of Natural History 8: 433-443.

———. 1979. Decapod Crustacea from the International Indian Ocean Expedition (Larval and post-larval stages of *Parapenaeus* Smith (Penaeinae)). Journal of Natural History 13: 599-618.

Pearson, J. C. 1939. The early life histories of some American Penaeidae, chiefly the commercial shrimp *Penaeus setiferus* (Linn.). Bulletin of the Bureau of Fisheries 49: 1-73.

Pérez-Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*. Fishery Bulletin (U.S.) 67: 461-591.

———. 1972. *Tanypenaeus caribeus*, a new genus and species of the shrimp family Penaeidae (Crustacea, Decapoda) from the Caribbean Sea. Bulletin of Marine Science of the Gulf and Caribbean 22: 185-195.

———, and B. Kensley. 1997. Penaeoid and Sergestoid Shrimps and Prawns of the World. Keys and Diagnoses for the Families and Genera. Memoires du Museum National d'History Naturelle, Paris 175: 1-233.

Rafinesque, C. S. 1814. Précis des découvertes et travaux somiologiques de Mr. C. S. Rafinesque-Schmaltz entre 1800 et 1814; ou choix raisonné de ses principales découvertes en zoologie et en botanique, pour servir d'introduction à ses ouvrages futurs: 1-55. Royale Typographie Militaire, Palerme.

———. 1815. Analyse de la Nature ou Tableau de l'univers et des corps organisés: 1-224. Palerme.

Ramirez-Rodriguez, M., F. Arreguin-Sanchez, and D. Lluch-Belda. 2003. Recruitment patterns of the pink shrimp *Farfantepenaeus duorarum* in the southern Gulf of Mexico. Fisheries Research 65: 81-88.

Rathbun, M. J. 1902. Japanese stalk-eyed crustaceans. Proceedings of the United States National Museum 26: 23-55.

Ringo, R. D., and G. Zamora, Jr. 1968. A penaeid postlarval character of taxonomic value. Bulletin of Marine Science 18: 471-476.

Risso, A. 1816. Histoire naturelle des crustacés des environs de Nice. A la Librairie grecque-latine-allemande, Paris: 1-175, pls. 1-3.

Ronquillo, J. D., and T. Saisho. 1993. Early developmental stages of greasyback shrimp, *Metapenaeus ensis* (De Haan, 1844) (Crustacea, Decapoda, Penaeidae). Journal of Plankton Research 15: 1177-1206.

———, and ———. 1995. Early developmental stages of southern rough shrimp, *Trachypenaeus curvirostris* (Stimpson, 1860) (Decapoda, Penaeidae) reared in the laboratory. Crustaceana 68: 833-863.

———, and ———. 1997. Larval development of *Metapenaeopsis barbata* (De Haan, 1844) (Crustacea: Decapoda: Penaeidae). Marine and Freshwater Research 48: 401-414.

———, ———, and R. S. McKinley. 2006. Early developmental stages of the green tiger prawn, *Penaeus semisulcatus* De Haan (Crustacea, Decapoda, Penaeidae). Hydrobiologia 560: 175-196.

Sakai, K., and S. Shinomiya. 2011. Preliminary report on eight new genera formerly attributed to *Parapenaeopsis* Alcock, 1901, sensu lato (Decapoda, Penaeidae). Crustaceana 84: 491-504.

Smith, S. I. 1869. Notice of the Crustacea collected by Prof. C. F. Hartt on the coast of Brazil in 1867. Transactions of the Connecticut Academy of Arts and Sciences 2: 1-41.

———. 1882. Reports on the results of dredging, under the supervision of Alexander Agassiz, along the east coast of the United States, during the summer of 1880, by the U.S. Coast Survey steamer "Blake," Commander J. R. Bartlett, U.S.N., commanding. Bulletin of the Museum of Comparative Zoology at Harvard College 10: 1-108, pls. 1-16.

———. 1885. On some genera and species of Penaeidae, mostly from recent dredgings of the United States Fish Commission. Proceedings of the United States National Museum 8: 170-190.

Spivak, E. D. 1997. The crustacea decapoda in the southwestern Atlantic (25°-55°S): distribution and life cycles. Investigaciones Marinas Valparaiso 25: 69-91.

Stebbings, T. R. R. 1914. South African Crustacea. Part VII of S. A. Crustacea, for the Marine Investigations in South Africa. Annals of the South African Museum 15: 1-55, pls. 1-12.

Stephensen, K. 1923. Decapoda-Macrura, excl. Sergestidae. (Penaeidae, Pasiphaeidae, Hoplophoridae, Nematocarcinidae, Scyllaridae, Eryonidae, Nephropsidae, Appendix). Report of the Danish Oceanographical Expeditions 1908-10. Vol. II. Biology: 1-85.

Stimpson, W. 1860. Prodromus descriptionis animalium evertebratorum, quae in expeditione ad oceanum Pacificum septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VIII. Crustacea macrura. Proceedings of the Academy of Natural Sciences of Philadelphia: 91-116.

———. 1874. VI. – Notes on North American Crustacea in the museum of the Smithsonian Institution. No. III Annals of the Lyceum of Natural History of New York 10: 92-136.

Streets, T. H. 1871. Catalogue of Crustacea from the Isthmus of Panama collected by J. A. McNeil. Proceedings of the Academy of Natural Sciences of Philadelphia 23: 238-243.

Tavares, C., and J. W. Martin. 2010. Chapter 63: Suborder Dendrobranchiata Bate, 1888, pp. 99-164. In, F. R. Schram, J. C. von Vaupel Klein, M. Charmantier-Daures, and J. Forest (eds.), Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Brill, Leiden.

———, C. Serejo, and J. W. Martin. 2009. A preliminary phylogenetic analysis of the Dendrobranchiata based on morphological characters, pp. 261-279. In, J. W. Martin, K. A. Crandall, and D. F. Felder (eds.), Crustacean Issues 18: Decapod Crustacean Phylogenetics. CRC Press, Boca Raton, FL.

Tirmizi, N. M. 1971. *Marsupenaeus*, a new subgenus of *Penaeus* Fabricius, 1798 (Decapoda, Natantia). Pakistan Journal of Zoology 3: 193-194.

Tong, J. G., T. Y. Chan, and K. H. Chu. 2000. A preliminary phylogenetic analysis of *Metapenaeopsis* (Decapoda: Penaeidae) based on mitochondrial DNA sequences of selected species from the Indo-West Pacific. Journal of Crustacean Biology 20: 541-549.

Williamson, D. I. 1969. Names of larvae in the Decapoda and Euphausiacea. Crustaceana 16: 210-213.

———. 1982. Larval morphology and diversity, pp. 43-110. In, L. G. Abele (ed.), The Biology of Crustacea. Vol. 2: Embryology, Morphology and Genetics. Academic Press, San Diego, CA.

Wood-Mason, J. 1891. Phylum Appendiculata. Branch Arthropoda. Class Crustacea. In, J. Wood-Mason and A. Alcock (eds.), 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 1890-91. Annals and Magazine of Natural History (6) 8: 269-286.

RECEIVED: 24 December 2013.
ACCEPTED: 30 June 2014.