SPIXIANA	40	2	181–184	München, Dezember 2017	ISSN 0341–8391

A specimen of the snapping shrimp *Alpheus pontederiae* de Rochebrune, 1883 with symmetric chelipeds

(Decapoda, Caridea, Alpheidae)

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Soledade, G. O., Oliveira, M. V. & Almeida. A. O. 2017. A specimen of the snapping shrimp *Alpheus pontederiae* de Rochebrune, 1883 with symmetric chelipeds (Decapoda, Caridea, Alpheidae). Spixiana 40(2): 181–184.

The first pair of pereiopods is very asymmetric in the snapping shrimps of the genus *Alpheus* Fabricius, 1798. The major chela of this pair of appendages is extremely very well developed, with fingers modified for snapping production, whereas the minor chela has slender fingers often used for handling, feeding, and digging. The objective of this study is to report the rare finding of a specimen of *Alpheus pontederiae* de Rochebrune, 1883 from Niger Delta, Nigeria, with two minor symmetric chelipeds. Three alternative hypotheses are raised to explain the symmetry observed.

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Introduction

Alpheid shrimps are a highly diverse taxon of decapod crustaceans, with more than 600 species distributed in 47 genera (see De Grave & Fransen 2011). In snapping shrimps of the family Alpheidae Rafinesque, 1815, the first pair of pereiopods is very asymmetric, and such asymmetry originates in the juvenile phase (Young et al. 1994). The major chela of this pair of appendages is extremely very well developed, with fixed and mobile fingers of a rather peculiar morphology (tooth-cavity system). The chela produces a snapping sound which is one of the most audible sounds in the environments where these animals live (see Versluis et al. 2000, Anker et al. 2006). This cheliped is used for prey capture and in agonistic interactions (Nolan & Salmon 1970). Functional snapping claws evolved only once within Alpheidae (Anker et al. 2006), in a highly speciose clade (~75 % of alpheid species) that includes the genera *Alpheus* Fabricius, 1798, *Metalpheus* Coutière, 1908, *Pomagnathus* Chace, 1937, *Racilius* Paul'son, 1875, and *Synalpheus* Spence Bate, 1888. It is believed that the snapping claw facilitated the extensive radiation undergone by these shrimps (see Anker et al. 2006). The minor chela has slender fingers, which are not modified for sound production, and are often used for handling, feeding, and digging (Govind et al. 1988).

In *Alpheus*, the most speciose alpheid genus with more than 300 described species (see De Grave & Fransen 2011, Almeida et al. 2014), the snapping claw may develop in either side of the body. However, few species of *Alpheus* have been investigated concerning this matter and no one-side handedness (predominance of the snapping claw on one side

of the animal's body) was found in these studies (Dawes 1934, Young et al. 1994, Soledade et al. in prep.). Reversion in the position of the first cheliped after autotomy has been observed in a few species of *Alpheus* (Wilson 1903, Dawes 1934, Govind et al. 1988, Young et al. 1994, Pereira et al. 2014). In these cases, the loss of the major cheliped is followed by the regeneration into a minor cheliped, while the original minor cheliped develops into a new major cheliped (Wilson 1903, Shin-Iké 1956, Govind et al. 1988, Young et al. 1994). On the other hand, the loss of the minor cheliped results in the regeneration into another minor cheliped (Wilson 1903, Shin-Iké 1956, Govind et al. 1988). In addition to the two conditions mentioned above, the loss of both chelipeds may result in regeneration without asymmetry reversal (Wilson 1903, Shin-Iké 1956). According to Wilson (1903), asymmetry reversal may decrease the delay in the development of this appendage – which is of extreme relevance for these shrimps – as an existing structure is used as the foundation of the new large chela.

Alpheus pontederiae de Rochebrune, 1883 inhabits estuaries in the western Atlantic (Venezuela to Paraná, Brazil) and eastern Atlantic (Senegal to Congo) (Christoffersen 1984, Soledade & Almeida 2013). The species is part of a non-related group of snapping shrimps in which the males' minor chelae is ornamented with balaeniceps-type setae. During the course of a taxonomic study involving *A. pontederiae*, we found a male specimen from Niger Delta, Nigeria, with two symmetric minor chelipeds. The objective of this study is to report this rare finding as well as proposing hypotheses for the anomaly observed.

Material and methods

The material was found during the examination of a batch containing 13 males and 13 females from Nigeria, deposited in the crustacean collection of the Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands (Niger Delta, between Brass and Port Harcourt, coll. H.J.G. Beets, V–VIII.1960, RMNH. Crus.D.15531). The identification of the material analysed here as *A. pontederiae* is based on a set of morphological characteristics such as orbital hoods unarmed (Fig. 1A,B); fingers of minor chela with balaeniceps-type setae (Fig. 1C–E); third and fourth pereiopods with spiniform setae on ventrolateral surface of ischium; dactylus of third and fourth pereiopods subspatulate; uropodal exopod with two sharp teeth on posterolateral margin, one on each side of spiniform setae (Fig. 1F) (see Christoffersen 1984, Soledade & Almeida 2013). Illustrations were made under a stereomicroscope equipped with a camera lucida.

Results

The specimen measured 8.6 mm in carapace length. The general aspect of the carapace, abdomen, cephalic appendages, and other appendages was considered normal and in accordance with the species' typical morphology (Fig. 1A,B,F). The two minor chelipeds had the characteristic morphology of *A. pontederiae*, i.e., with balaeniceps-type setae on the fingers (Fig. 1C–E). The two chelipeds had similar article proportions. However, the left chela (length = 10.1 mm, width = 2.2 mm) (Fig. 1E) was slightly longer than the right (length = 9.5 mm, width = 1.8 mm) (Fig. 1D). The pollex of the right chela was slightly laterally curved and shorter than the dactylus, suggesting a previous injury (Fig. 1C,D).

Discussion

Reports of the occurrence of this type of anomaly are extremely rare in alpheids. The presence of two major chelipeds was verified in few individuals of *Alpheus angulosus* McClure, 2002 (McClure 1996, as *Alpheus angulatus*) and *Alpheus armillatus* H. Milne Edwards, 1837 (Darby 1939, as *Crangon armillatus*). This feature was also found in a species of *Synalpheus* Spence Bate, 1888 (misidentified by Hickman & Zimmerman 2000, see Anker et al. 2006), as well as in an individual of *Athanas ornithorhynchus* Banner & Banner, 1973 (Marin et al. 2004). Individuals of *Alpheus rugimanus* A. Milne-Edwards, 1878 and *Alpheus galapagensis* Sivertsen, 1933 with two minor chelipeds were reported by Coutière (1899) and Anker et al. (2006), respectively.

The mechanisms inducing symmetry in natural populations are unknown, but experimental studies attempted to identify them (e.g., Wilson 1903, Dawes 1934, Shin-Iké 1956, Mellon & Stephens 1978, Govind et al. 1988, Young et al. 1994, Pereira et al. 2014). Experiments carried out with *Alpheus heterochaelis* Say, 1818 showed the neural control of asymmetry reversal (Wilson 1903, Young et al. 1994). The complete suture of the contralateral nerve of the minor cheliped, followed by the intentional removal of the major cheliped, resulted in the symmetry of the chelipeds, i.e., in the development of a second major cheliped (Wilson 1903, Mellon & Stephens 1978, Govind et al. 1988, Young et al. 1994). This type of lesion-mediated symmetry of nerve endings was also observed in *Alpheus armillatus* under experimental conditions (Mellon & Stephens 1978). In experiments with *Alpheus rapax* Fabricius, 1798, removal of both chelipeds in individuals with a total length smaller and larger than 8 mm resulted in the

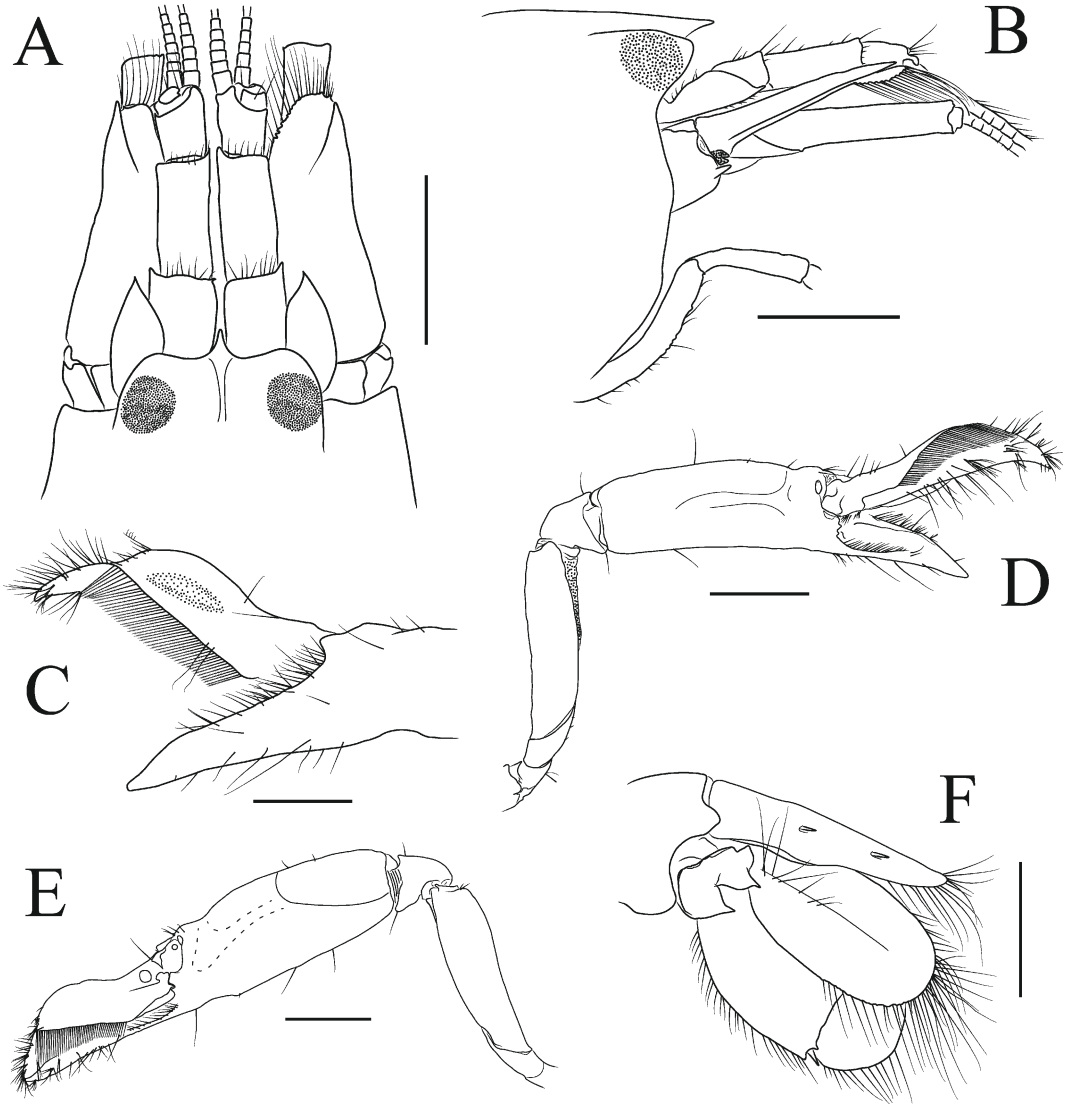

Fig. 1. *Alpheus pontederiae* de Rochebrune, 1883. Male with symmetric minor chelipeds from Niger Delta, Nigeria (RMNH.Crus.D.15531). **A.** Frontal region and cephalic appendages, dorsal view; **B.** frontal region and cephalic appendages, lateral view; **C.** detail of right cheliped, mesial view; **D.** right cheliped, lateral view; **E.** left cheliped, lateral view; **F.** telson and uropods, lateral view. Scale bars: 2 mm.

regeneration of two minor chelipeds and asymmetry reversal, respectively (Shin-Iké 1956).

Three alternative hypotheses can be raised to explain the symmetry observed in the specimen of *A. pontederiae*: (i) the symmetry developed in the juvenile phase due to an inhibition of the developmental mechanism which would result in a typical major chela in one of the chelipeds; (ii) the symmetry was generated in the adult phase after autotomy of the major cheliped (after a predator attack or agonistic encounter with a conspecific), followed by non-differentiation of the minor cheliped into a new major cheliped; (iii) the individual autotomized the major cheliped and was captured while at the onset of the asymmetry reversal process. The complete regeneration of a new major cheliped requires three moults (Wilson 1903, Mellon & Stephens 1978, Pereira et al. 2014). Following the first moult after

autotomy, the new cheliped has an intermediate condition between a major and minor chela (Mellon & Stephens 1978, Pereira et al. 2014). Mellon & Stephens (1978) observed this condition in three snapping shrimps, *A. armillatus*, *Alpheus californiensis* Holmes, 1900, and *A. heterochaelis*. In *A. angulosus*, the snapping ability was recovered after the first moult; however, the snaps produced by the new chela might not have been functionally equivalent to that of a fully developed major chela (Pereira et al. 2014). In the specimen of *A. pontederiae*, the chelipeds are very similar in form, i. e., they are not in an intermediate condition between major and minor chelae. Thus, the hypotheses (i) and (ii) seem to be the most plausible in explaining the asymmetry observed. However, the slight deformity observed in the pollex of the right chela might indicate a previous injury due to predator attack or agonistic interaction, reinforcing the hypothesis (ii) as the most satisfactory in this case.

Acknowledgements

The authors are indebted to Dr. Charles Fransen and Ms. Karin van Dorp (Netherlands Centre for Biodiversity Naturalis, Leiden) for lending the material examined. We thank Patricia S. dos Santos for laboratorial support; GOS thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a PhD scholarship; MVO thanks Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) for a Master scholarship; and AOA thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a Research scholarship support (305939/2015-7).

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