PRESENCE OF ABDOMINAL APPENDAGES IN FEMALES OF CAPRELLA EQUILIBRA SAY, 1818 (PERACARIDA, AMPHIPODA): IS METACAPRELLA MAYER, 1903 A VALID GENUS?

BY

J. M. GUERRA-GARCÍA and M. ROS
Laboratorio de Biología Marina, Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Avda Reina Mercedes 6, E-41012 Sevilla, Spain

ABSTRACT

Detailed morphological studies of the caprellid abdomen are necessary to understand the evolution of this group. According to the diagnosis of the genus Caprella, the abdomen of males is provided with a pair of uni- or bi-articulate appendages and a pair of lobes, and females only have the pair of lobes and lack appendages. However, during a monitoring study of Caprella equilibra in southern Spain, we found that 7% of the females were provided with abdominal appendages, revealing that there is intraspecific variation of the female abdomen, even in the same population. The intrageneric and even intraspecific evidence of morphological variation of the abdominal appendages in Caprella and Metacaprella indicates that the external morphology of these appendages is not an ontogenetically and morphologically stable character to diagnose a genus. Consequently, this study supports the evidence that the abdominal appendage is a polymorphic and symplesiomorphic character in Caprella and Metacaprella, and that Metacaprella is not a valid genus.

RESUMEN

El estudio morfológico detallado del abdomen de los caprélidos es necesario para entender la evolución de este grupo. Según la diagnosis del género Caprella, el abdomen del macho está provisto de un par de apéndices uni o bi-articulados y un par de lóbulos, y las hembras poseen el par de lóbulos pero carecen de apéndices. Durante un estudio de seguimiento de Caprella equilibra en el sur de España, encontramos que el 7% de las hembras presentaron apéndices abdominales, revelando la existencia de variabilidad intraespecífica en el abdomen de la hembra, incluso en la misma población. Las evidencias de variabilidad morfológica intragenérica, e incluso intraespecífica, en los apéndices abdominales de Caprella y Metacaprella indican que la morfología externa de estos apéndices no es un carácter estable ontogenéticamente ni morfológicamente. Por tanto, este estudio indica que el apéndice abdominal sería un carácter polimórfico y simplesiomórfico en Caprella y Metacaprella y que Metacaprella no sería un género válido.
INTRODUCTION

The Caprellidea (Crustacea, Malacostraca, Peracarida) comprise more than 400 described species (J. M. Guerra-García, unpubl.) and the genus Caprella Lamarck, 1801 is the most important, including around 50% of the total number of species (Guerra-García & Tierno de Figueroa, 2009).

Traditionally, Caprellidea have been considered a suborder of the order Amphipoda, classified into five families (Caprellidae, Caprogammaridae, Cyamidae, Paracercopidae, Phitisicidae) (Vassilenko, 1974; Takeuchi, 1993). Laubitz (1993) considered three additional families (Caprellinoididae, Pariambidae, and Protellidae) and her classification in eight families instead of five has been adopted subsequently by most authors (Ito et al., 2008, 2011). However, Guerra-García (2002a), in a review of the characters of the families Pariambidae and Protellidae, found multiple inconsistencies and suggested to adopt, while the phylogeny and higher classification of the caprellids are still under debate, the minimum number of families, following Takeuchi (1993). The studies of Vassilenko (2006) seem to lend support to Takeuchi (1993) more than to Laubitz (1993) concerning the phylogeny of Caprellidea. Myers & Lowry (2003) have recently proposed a new phylogeny and classification for the suborder Corophiidea Leach, 1814. Based on the hypothesis of the evolution of different feeding strategies, the Corophiidea are divided into two infraorders, the Corophiida and the Caprellida. In their new classification, the superfamily Caprelloidea contains five families: Caprellidae, Caprogammaridae, Cyamidae, Dulichiidae, and Podoceridae, and the Caprellidae are subdivided into three subfamilies: Caprellinae, Paracercopinae, and Phitisicinae. According to this approach, Caprelloidea would be a superfamily instead of a suborder.

The general characteristics of the Caprellidea include a slender and cylindrical body, fusion of the head and pereonite 1, rudimentary coxae, two or three pairs of gills, brood plates on pereonites 3 and 4, reduced or absent pereopods 3 and 4 in most cases, and a degenerated abdomen and abdominal appendages (Ito et al., 2008). These characteristics, especially the abdomen structure, are highly divergent from the body plan of other malacostracan crustaceans; therefore, caprellids are of great interest for understanding the morphological evolution in crustaceans. In spite of this, the phylogenetic relationships among the Caprellidea are poorly understood. Most of the caprellid families have reduced or absent pereopods 3 and 4, and the pleon is greatly reduced in size, without segmental structure, and bearing only one to three pairs of vestigial appendages. However, there are two families that do not show the above-mentioned typical caprellid body plan. The Caprogammaridae have an elongated and segmented pleon with pleopods, but pereopods 3 and 4 are rudimentary as in other caprellids (Takeuchi & Ishimaru, 1991), while the Phitisicidae possess well-developed six-articulate pereopods 3 and 4 but a reduced
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abdomen lacking developed pleopods. Consequently, the unique character status of these families implies that there has been either a reacquisition or multiple losses of both pereopods and pleon within the Caprellidea lineages (Ito et al., 2011). It is generally accepted that Caprellidea derived from Gammaridea (cf. Myers & Lowry, 2003; Ito et al., 2008), which are characterized by well developed pereopods 3 and 4, and by the presence of a pleon. Takeuchi (1993) suggested that the Caprellidea could be polyphyletic: the Phtisicidae could have evolved from a different ancestor than the Caprogammaridae and other caprellids, and he suggested a podocerid-like ancestor for the line Caprogammaridae-Caprellidae. Laubitz (1993) also suggested the possibility of polyphyly but with a different approach, with one lineage (provided with mandibular molar) including the Caprogammaridae, Pariambidae, Protellidae, and Caprellidae, derived from the Corophioidea, and another lineage (without mandibular molar), including Phtisicidae, Caprellinoididae, Cyamidae, and Paracercopidae, derived from the Leucothoidea. The idea of two major lines of evolution seems also to be supported by a recent study of Guerra-García & Tierno de Figueroa (2009) based on an analysis of digestive contents in 62 caprellid species. However, the recent morphological cladistic analysis of the Corophioidea showed that Caprellidea would be monophyletic (Myers & Lowry, 2003). Ito et al. (2008) conducted the first molecular study based on 18S rRNA and their results also indicated that the Phtisicidae and other caprellid families form a monophyletic clade. However, a close phylogenetic relationship between Corophioidea and Caprellidea was not definitively supported by Ito et al. (2008). Given their complicated morphological evolution, Ito et al. (2011) suggested the possibility of Caprellidea as an exception to Dollo’s law (evolution is irreversible, once a complex morphological character is lost in the course of evolution, it never reappears). In this sense, the ancestral state reconstruction based on the obtained molecular phylogeny suggested that once lost, pereopods 3 and 4 were regained in the Phtisicidae, while the pleon was regained in the Caprogammaridae, while the possibility of independent losses could not be excluded.

Taking into account the difficulties in clarifying the phylogenetic position of the Caprellidea, detailed morphological studies of the caprellid abdomen could help to understand the complicated evolution of this group of crustaceans.

MATERIAL AND METHODS

During a monitoring study of the population of Caprella equilibra Say, 1818 in La Línea harbour, Córdiz, southern Spain (36°09′35.6″N 5°21′27.2″W), summer 2011, we collected abundant females for abdomen examination. To observe the abdomen more clearly, we immersed the specimens in Hertwig’s liquid (consisting
of 270 g chloral hydrate, 19 ml chloridric acid 1 N, 150 ml distilled water, and 60 ml glycerin) heated in an oven at 65°C for approximately 3 hours (Guerra-García & Tierno de Figueroa, 2009). A total of 75 female abdomens were carefully examined.

RESULTS AND DISCUSSION

The abdomen in the genera *Caprella* and *Metacaprella*

According to the diagnosis of the genus *Caprella* (see McCain, 1968; Krapp-Schickel, 1993), the abdomen of males is provided with a pair of uni- or bi-articulate appendages and a pair of lobes, and females only have the pair of lobes and lack the appendages (fig. 1A, C, D). The abdomen is located in the seventh (last) pereonite in both males and females. The appendages could be remnants of pleopods, although it cannot be excluded that they could correspond to extremely reduced uropods. It seems that these appendages are used as copulatory papillae and are inserted during copulation into the female’s genital openings (fig. 1B, E) which are located ventrally on the posterior end of the fifth pereonite (Lim & Alexander, 1986).

Mayer (1903), taking into consideration that the females of some species of *Caprella* had also two small appendages, suggested the possibility of splitting the genus *Caprella*, and tentatively proposed the genus *Metacaprella* for *Caprella anoma*la Mayer, 1903 and *Caprella kennerlyi* Stimpson, 1864, based on the presence of a pair of abdominal appendages in the female. This genus *Metacaprella*, provisionally established by Mayer (1903), was subsequently adopted by Dougherty & Steinberg (1953), who designated *M. kennerlyi* as the type species of the genus. Although several authors questioned the validity of this genus (McCain, 1968; Laubitz, 1970), most of them have maintained the genus in their faunal studies (Laubitz, 1970, 1972; Vassilenko, 1974; Arimoto, 1976). Mori (1999), in an interesting revision of the ontogeny of the abdominal appendages, concluded that the abdominal appendage is considered to be a polymorphic and symplesiomorphic character in *Caprella* and *Metacaprella*, and he did not recognize the genus *Metacaprella* as a valid genus. Sakaguchi (1989) and Takeuchi (1989) described the postmarsupial development of several species of the genus *Caprella* (*Caprella scaura* Templeton, 1836, *Caprella danilevskii* Czerniavskii, 1868, *Caprella okadai* Arimoto, 1930, and *Caprella generosa* Arimoto, 1977), reared in the laboratory. In all these species, all the hatchlings and early juveniles had paired abdominal appendages bearing single apical setae. The appendages grew larger in males becoming one- or two-articulate, whereas they were reduced in females with only an apical seta as a vestigial structure. Lang et al. (2007) also remarked the presence
Fig. 1. A, typical abdomen (pereonite 7) in male and female of the genus *Caprella* [refigured from Guerra-García et al., 2006 (*C. penantis* Leach, 1814)]; B, female genital openings (pereonite 5) of *Caprella* [refigured from Guerra-García, 2002b (*C. septentrionalis* Krøyer, 1838)]. C, D, SEM images (ventral and frontal) of male abdomen of *Caprella* [modified from Sturaro & Guerra-García, 2011 (*C. tavolarenensis* Sturaro & Guerra-García, 2011)]; E, SEM image of female genital openings of *Caprella* [modified from Sturaro & Guerra-García, 2011]. P, pereonite.
of tiny appendages in all juveniles of the species *C. equilibra*. Mori (1999) pointed out that, although the postmarsupial development of *Metacaprella* species had not been extensively studied, the morphological features of the abdominal appendages in juveniles are almost identical to those of *Caprella*.

On the other hand, intra-generic variations in the morphology of abdominal appendages exist in both *Caprella* and *Metacaprella* (cf. Mori, 1999). The appendages of adult males of *Caprella* can be one- or two-articulate, while in the females they can be completely reduced or be present as a pair of setae, as a vestigial structure. In *Metacaprella*, the appendages can be small and unsegmented or relatively large and incompletely two-articulate. Furthermore, Mori (1999) pointed out the existence of intraspecific morphological variation in females of *C. danilevskii*. Those from Japanese waters have only a pair of vestigial setae on the abdomen (Takeuchi, 1989), whereas those from the western North Atlantic and the Mediterranean have a pair of small abdominal appendages (McCain, 1968; Krapp-Schickel, 1993). Recently, Guerra-García et al. (2006) studied specimens of *C. danilevskii* from Colombia and found only vestigial setae on the abdomen, similar to those in Japanese specimens. Guerra-García (2004) described the species *Caprella traudlae* Guerra-García, 2004 from Australia, and found small appendages in females of this *Caprella* species, similarly to *C. danilevskii*.

The abdomen in *Caprella equilibra*

The abdomen of *C. equilibra* has traditionally been described as a typical abdomen for the genus (see McCain, 1968; Krapp-Schickel, 1993): males are provided with a pair of appendages and a pair of lobes, and females only have the pair of lobes and lack the appendages. However, after examination of 75 females collected from La Línea harbour, Southern Spain, we found 5 females provided with abdominal appendages (fig. 2). Apart from the appendages, these females were morphologically similar to the normal females. Consequently, the present study reveals that there is an intraspecific variation in the female abdomen, even in the same population. Previously, this intraspecific variation had been reported among populations of *C. danilevskii* separated by thousands of kilometers. The intrageneric, and even intraspecific evidence of morphological variation of the abdominal appendages in *Caprella* and *Metacaprella* indicates that the external morphology of these appendages is not an ontogenetically and morphologically stable character, sufficient to diagnose a genus. Because characters that appear earlier in the ontogeny are considered to be ancestral and those appearing later derived (Eldredge & Cracraft, 1980; Mori, 1999), the presence of abdominal appendages in the adult female of *Metacaprella* is not an autapomorphy of the genus, but a symplesiomorphy of the species assigned to the genus (Mori, 1999).
Fig. 2. Details (optical microscope) of female abdomens (ventral view) in Caprella equilibra Say, 1818, from La Línea harbour, Cádiz, southern Spain. A, normal abdomen (93% of the total number of females examined); B, abdomen with appendages (7% of the total number of females).
Our observations in *C. equilibra* support the evidence reported by Mori (1999) that the abdominal appendage is a polymorphic and symplesiomorphic character in *Caprella* and *Metacaprella*. Therefore, we agree with Mori (1999) that the establishment of the genus *Metacaprella* only on the basis of a plesiomorphic character should be avoided.

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