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Morphology of the larval stages of *Macropodia czernjawskii* (Brandt, 1880) (Decapoda, Brachyura, Inachidae) reared in the laboratory

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ABSTRACT

The complete larval development of *Macropodia czernjawskii* (Brandt, 1880), is described and illustrated for the first time. Larvae were reared in the laboratory and development consisted of two zoeal stages and a megalopa. The main difference in the zoeal stages is the absence of lateral spines on the telson furcae, which allow it to be distinguished from the remaining species of *Macropodia* as well as from the zoeae of most majoids.

INTRODUCTION

The spider crab genus *Macropodia* Leach, 1814, is represented in the northeastern Atlantic and Mediterranean waters by nine species: *M. czernjawskii* (Brandt, 1880), *M. deflexa* Forest, 1978, *M. intermedia* Bouvier, 1940, *M. linaresi* Forest & Zariquiey-Álvarez, 1964, *M. longipes* (Milne-Edwards & Bouvier, 1899), *M. longirostris* (Fabricius, 1775), *M. parva* Noort & Adema, 1985, *M. rostrata* (Linnaeus, 1761), and *M. tenuirostris* (Leach, 1814). *Macropodia czernjawskii* is found in the Eastern Atlantic and Mediterranean Sea (D'Udekem d'Acoz 1999), where it inhabits rocky intertidal pools and bottoms with algae at depths of 0.3-80 m (García Raso 1984; Zariquiey-Álvarez 1968).

The complete larval development reared in the laboratory is known for only four species of *Macropodia*: *M. tenuirostris* (Salman 1981), *M. rostrata* (Ingle 1982, 1992), *M. longipes* (Guerao & Abelló 1997) and *M. parva* (González-Gordillo & Rodríguez 2001). Lebour (1927, 1928) had previously described the larval development of *M. deflexa* (as *M. egyptia*), *M. tenuirostris* (as *M. longirostris*), and *M. rostrata*, but descriptions and illustrations were brief and incomplete. The first zoea of *M. linaresi* was described by Guerao *et al*. (1998).

The complete larval development (two zoeal stages and the megalopa) of *M. czernjawskii* is herein described and illustrated in detail and compared with the known development of other species of the genus.

MATERIAL AND METHODS

One ovigerous individual of *Macropodia czernjawskii* was collected by hand from intertidal pools off El Chato beach (Cadiz, southwestern Spain) (36^{o} 28’ 30’’ N 06^{o} 15’ 40’’ W), on 10 September 1999. The ovigerous crab was placed in an aquarium containing filtered and well-aerated sea water at a salinity of 32 ± 1 ‰ and keep at 26 ± 1°C. A total of 417 zoeae hatched on 17 September, the 300 most actively swimming zoeae were transferred to 2 L glass bottles (150 ind. L^{-1}) with aeration, and constant temperature (25 ± 1°C) for mass culture. Zoea I larvae were fed with a mix of rotifer *Brachionus plicatilis* (Müller, 1786) (fed with *Nannochloropsis gaditana* Lubián, 1982) and nauplii of *Artemia* sp., and from ZII to first crab with only fresh nauplii of *Artemia* sp. All reared larvae were maintained under the same constant conditions of temperature and salinity mentioned above. Seawater was changed daily, and culture was checked daily for exuviae and dead larvae and it was finished when all megalopae moulted to the first crab instar. Exuviae and specimens of all stages were fixed in 4% neutral formalin for later examination.

For an easier microscopic observation of larval structures and setation a digestion-stain procedure (adjustment of that described by Landeira *et al*. 2009) was carried out. Entire specimens were first placed for 10 minutes in a watch glass with 2 ml of heated lactic acid. Immediately after, 3 drops of Clorazol Black stain (0.4 g Clorazol Black powder dissolved in 75 ml 70% Ethanol) were added to the heated solution. The specimen was removed from the solution after 5-10 minutes and placed on a slide with lactic acid before proceeding with the dissection of the mouthparts.

Drawings and measurements were made using a Wild MZ6 and Zeiss Axioskop compound microscope with Nomarski interference, both equipped with a *camera lucida*. All measurements were made by using an ocular micrometer. Descriptions and measurements of different larval stages were based on at least 10 specimens of each stage, but due to the exceptional feature found in the telson (absence of lateral spines on the furcae), 30 additional zoea I, and 25 zoea II, were also checked for only this character. Description and figures are arranged according to the standards proposed by Clark *et al*. (1998).

Measurements taken in zoeal stages were: rostro-dorsal length (RDL) measured from frontal margin to tip of dorsal spine; cephalothorax length (CL) measured from frontal margin (between the eyes) to posterolateral cephalothoracic margin; cephalothoracic dorsal spine length (DSL) distance from base to tip of dorsal spine; antenna length (AL) from base of the antennal peduncle to tip of the spinous process. For the megalopa, cephalothorax length (CL) measured from the frontal to posterior margin of cephalothorax; cephalothorax width (CW) as the cephalothorax maximum width.

The parental female and complete larval series have been deposited in the Museo Nacional de Ciencias Naturales (MNCN) under accession number MNCN 20.04/867 (parental female), MNCN 20.04/867 (Zoeae I), MNCN 20.04/8678 (Zoeae II) and MNCN 20.04/8679 (Megalopae).

RESULTS

The larval development of *M. czernjawskii* consists of two zoeal stages and a megalopa. At 25 ± 1°C and 32 ± 1 ‰ salinity the larval development is completed in a minimum of 8 days (appearance of the first crab). The duration and survival of each larval stage is show in Fig. 1. The first zoeal stage is described in detail, and only the main differences in subsequent stages are noted.

Description of larvae

First zoea

(Figs. 2A, B, H; 3A, D; 4A, D; 5A, D; 7A, D)

Size: RDL = 1.152 ± 0.03; CL = 0.569 ± 0.05 mm; DSL = 0.688 ± 0.09 mm; AL = 0.607 ± 0.05 mm, N= 10.

Cephalothorax (Figs. 2A, B, H): Globose and smooth with well-developed dorsal spine, slightly curved backward; rostral and lateral spines absent; anteromedian ridge present; dorsomedian tubercle absent; pair of anterodorsal and posterodorsal simple setae; posterolateral margin with densely plumose "anterior seta", two sparsely plumose setae and minute denticles; eyes sessile.

Antennule (Fig. 3A): Uniramous, unsegmented and conical, endopod absent; exopod with 4 terminal aesthetascs (two long and two shorter) and 1 simple seta.

Antenna (Fig. 3D): Biramous, spinuous process of protopod very long with two rows of distal spinules; unsegmented and short endopod; exopod slightly shorter than protopod, with 2 medial simple setae and distal spinules.

Mandible: Incisor and molar process developed, irregularly dentate; palp absent.

Maxillule (Fig. 4A): Coxal endite with 7 plumodenticulate setae; basial endite with 4 terminal setae (3 cuspidate, 1 plumodenticulate), 2 subterminal plumodenticulate setae and 1 proximal plumose seta; endopod 2-segmented with 0, 3 sparsely plumose setae; epipodal and exopodal seta absent.

Maxilla (Fig. 4D): Coxal endite not bilobed with 7 plumodenticulate setae; basial endite bilobed with 5 + 4 plumodenticulate setae; unsegmented endopod not bilobed, with 4 setae (3 sparsely plumose, 1 distal simple shorter); exopod (scaphognathite) with 9 marginal plumose setae plus one stout plumose process.

First maxilliped (Fig. 5A): Epipod present without setae. Coxa without setae; basis with 9 medial sparsely plumodenticulate setae arranged as 2+2+2+3; endopod 5-segmented, longer than exopod, with 3, 2, 1, 2, 5 (4 terminal + 1 subterminal) sparcely plumodenticulate setae; exopod 2-segmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 5D): Coxa without setae; basis with one sparcely plumodenticulate seta; endopod 3-segmented, with 0, 0, 4 setae, (2 subterminal + 2 terminal); exopod 2-segmented with 4 terminal plumose natatory setae.

Third maxilliped: Present as biramous buds.

Pereiopods: Present as incipient buds, cheliped bilobed.

Pleon (Fig. 7A, D): Five somites; somite I without setae; somite II-V with pair of minute simple setae on posterodorsal margin; somite II with pair of forwardly directed dorsolateral processes, somites III-V with long and terminally acute posterolateral processes.

Pleopods: Incipient pleopods bud on somites II-V.

Telson (Fig. 7A): Bifurcated, with deep median cleft; 2 pairs of 3 serrulate setae on posterior margin, medial setae longest; telson furcae without spines, and distally spinulate.

Second zoea

(Figs. 2C, D; 3B, E; 4B, E; 5B, E; 7B, E)

Size: RDL = 1.030 ± 0.07; CL = 0.606 ± 0.01 mm; DSL = 0.576 ± 0.08 mm; AL = 0.684 ± 0.05 mm, N=10.

Cephalothorax (Figs. 2C, D): Anteromedian ridge more pronounced than zoea I; 3 pairs of anterodorsal simple setae; well developed supraocular process; eyes stalked and movable.

Antennule (Fig. 3B): Exopod terminally with 6 terminal aesthetascs (3 long, 3 shorter) and 1 simple seta.

Antenna (Fig. 3E): Endopod more elongated.

Mandible: Palp bud present.

Maxillule (Fig. 4B): Basial endite with 5 terminal setae (3 cuspidate, 2 plumodenticulate), 2 subterminal plumodenticulate setae and 1 proximal plumose seta; exopodal seta present.

Maxilla (Fig. 4E): Basial endite with 5 + 5 sparsely plumodenticulate setae; endopod now with fourth seta sparsely plumose and of the same length of the rest; scaphognathite (exopod) with 18 plumose marginal setae.

First maxilliped (Fig. 5B): Exopod with 6 terminal plumose natatory setae.

Second maxilliped (Fig. 5E): Basis without setae; exopod with 6 terminal plumose natatory setae.

Pleon (Figs. 7B, E): Posterolateral spines more elongated.

Pleopods (Figs. 7B, E): Biramous more elongated, endopod buds present.

Megalopa

(Figs. 2E-G; 3C, F, G; 4C, F; 5C, F, G; 6A-D; 7C, F)

Size: CL = 0.833 ± 0.045 mm; CW = 0.631 ± 0.035 mm; N= 10

Cephalothorax (Figs. 2E, G): Longer than broad, with small rostrum, directed ventrally; each protogastric region with dorsally directed blunt process with pair of plumose setae; one tubercle on mesogastric region and on posterodorsal margin; prominent long spine present on cardiac region; four pairs of simple setae on frontal region as drawn.

Antennule (Fig. 3C): Peduncle 3-segmented, without setae; unsegmented endopod without setae; exopod 2-segmented, proximal segment with 1 and distal segment with 4 aesthetascs.

Antenna (Fig. 3F): Peduncle 3-segmented with 1, 0, 1 setae respectively, proximal segment with stout ventrally directed process; flagellum 4-segmented with 0, 4, 0, 3 setae respectively.

Mandible (Fig. 3G): Palp unsegmented with one terminal simple seta.

Maxillule (Fig. 4C): Basial endite with 7 terminal setae (4 cuspidate, 3 plumodenticulate), 5 subterminal sparsely plumodenticulate setae and 1 proximal plumose seta; endopod reduced, unsegmented and without setae.

Maxilla (Fig. 4F): Coxal endite with 5 terminal plumose setae; basial endite bilobed with 3 + 5 sparsely plumodenticulate setae; endopod unsegmented and without setae; exopod with 18-20 marginal plumose setae plus 1 small simple seta on each lateral surface.

First maxilliped (Fig. 5C): Epipod without setae; coxal endite with 6 plumose setae; basial endite with 7 sparsely plumodenticulate setae; endopod reduced, unsegmented and without setae; exopod 2-segmented, with 4 plumose setae on distal segment.

Second maxilliped (Fig. 5F): Epipod present, without setae; protopod without setae. Endopod 4-segmented with 0, 1 (plumose), 2 (1 simple and 1 plumodenticulate), and 4 (plumodenticulate) setae; exopod 2-segmented, with 4 terminal plumose setae on distal segment.

Third maxilliped (Fig. 5G): Epipod with 1 terminal long seta; protopod with 1 simple seta; endopod 5-segmented, with 7, 3, 3, 7, 4 setae respectively; exopod 2-segmented with 4 plumose setae on distal segment.

Pereiopods (Figs. 6 A-D): Cheliped with a small proximal ventral tubercle on merus; pereiopods II-V slender and setose, with dactyl terminally acute; ischium of pereiopods II-III with prominent curved hook-shape spines. Setation as illustrated.

Sternum (Fig. 2 F): Setation as shown in the illustration.

Pleon (Figs. 7C, F): Five somites, somite VI absent; somite I without setae; somite II with one pair of posterodorsal simple setae; somite III with two pairs of posterodorsal simple setae; somite IV-V with one pair posterodorsal of 3 simple setae.

Pleopods (Fig. 6E): Present on somites II-V; endopods with 2 cincinuli; exopods with 8 long plumose natatory setae.

Telson (Figs. 7C, F): Longer than broad without setae.

DISCUSSION

The Majoidea is one of the most species-rich groups of Brachyura and has more than 900 species (Ng *et al*. 2008; De Grave *et al*. 2009). Although these many species inhabit different marine habitats and have a diversity of adaptations as well as a wide variety of zoeal and megalopal forms, they share a set of larval characters that distinguish them from the rest of the brachyuran superfamilies: only two zoeal stages, the scaphognathite of the zoea I has at least nine marginal plumose setae and the apical stout process is greatly reduced, zoea II with developed pleopods (Rice 1980; Van Dover *et al*. 1982), megalopa lacking sensory setae on the dactylus of the fifth pereiopods, uropods may be absent, and when present, they have no more than eight setae and the antennal flagellum never more than five segments (Rice 1988).

Several works have used larval features to study the phylogeny and familial relationships of Majoidea (Rice 1980, 1988; Clark & Webber 1991; Marques & Pohle 1998, 2003; Pohle & Marques 2000). With respect to Inachidae, these studies agree in considering the family to be monophyletic when *Macrocheira kaempferi* (Temminck, 1836) and *Stenorhynchus* Lamarck, 1818 are removed. Some of these authors even consider Inachidea as the most derived majoid family. Recent studies (Hultgren *et al.* 2009; Hultgren & Stachowicz 2008) combined larval morphology data and molecular evidence to also support the monophyly of Inachidae, but as inachid species are poorly represented in these analyses it is not possible to reach definitive conclusions at present. In general, the molecular results are congruent with those derived from larval morphology in the rest of the majoid families.

Inachidae consists of 204 species in 37 genera (Ng et al. 2008; De Grave *et al*. 2009), but larval data are only available for 26 species (12 genera). Therefore, it is currently too early to define larval features that characterize this family, which is made even more difficult since the known data indicate that there are strong intergeneric differences (see Oh & Ko 2011). Some of this larval morphological evidence has led authors to suggest removing species like *Platymaia wyvillethomsoni* Miers, 1886 and *Ergasticus clouei* A. Milne-Edwards, 1882, from Inachidae (Oh & Ko 2011; Guerao & Abelló 2007). Therefore, new larval descriptions of genera without larval data, and new molecular analyses that represent a wider number of inachid genera are needed to shed light on the real familial composition and phylogenetic relationships.

Macropodia comprises 17 valid species, of which nine inhabit northeast Atlantic and Mediterranean waters. There is currently larval data for only six species, all of them belonging to this Atlanto-Mediterranean group. As it has been previously pointed out (Guerao & Abelló 1997; González-Gordillo & Rodríguez 2001) the morphology of the larval stages of the genus *Macropodia* is very similar among the different species. It is therefore not easy to find consistent characters that can be used to distinguish them. First, the morphometry can be compared (data shown in Table 1). Although differences are obvious, especially between the largest (*M. tenuirostris*) and the smaller larvae (*M. czernjaswkii*), these kinds of differences have to be considered with care due to the latitudinal (temperature) effect on size, as previously demonstrated in other species (*Metacarcinus magister* (Dana, 1852), as *Cancer magister*, Shirley *et al*. (1987)). In the present study this is clear for *M. rostrata*, which shows differences between the larvae from the U.K. and those from SW Spain (see Table 1). Even in larvae collected from the same area, these measurements need to be carefully analyzed since there are also data that correlate larval intraspecific differences in size with parental female size (Sato & Suzuki 2010), and differences that depend on the season of the year (Pardo *et al*. 2009). More interesting are differences in ratios, for example between the DSL and CL, which makes it possible to see which larvae have a long dorsal cephalothoracic spine, and not just obtain an absolute measure. In this case, while the zoea I of *M. rostrata* from the U.K. has the longest DS (1.3-1.4 mm), it is the zoea I of *M. linaresi* that has the highest DSL/CL ratio (1.98-2.0) (see Table 1).

Table 2 summarizes the main morphological and meristic features that differ among *Macropodia* larval stages. Other minor differences (especially in the number of setae) are not listed because they may be more related to the size of the larvae rather than being a remarkable difference. According to these data, three main groups can be distinguished: The first comprises *M. rostrata*, *M. parva* and *Macropodia* S13, and is characterized by antennal morphology of the zoeae with a rounded tip of the protopod, and exopod and protopod without spinules, the megalopae without a cheliped isquial spine and only one small tubercle in the merus of the cheliped. *Macropodia tenuirostris* and *M. longipes* form a second group that is characterized by the antenna of zoeae having protopod and exopod spinulated with acute tips, and megalopae with one spine on the isquium and two well-developed spines on the merus of the cheliped. *Macropodia linaresi* can be included in this group but only based on features of the zoea I, because there are currently no data on the zoea II and megalopa. The third group is represented solely by *M. czernjawskii*. It shows intermediate characters, sharing the antennal morphology of the zoeae of *M. tenuirostris, M. longipes* and *M. linaresi*, and the spinulation of the cheliped of the megalopa of *M. rostrata* and *M. parva*. However, it does have a particular trait that distinguishes it from other *Macropodia* zoeae: the absence of a lateral spine on the telson furcae. This character is really exceptional in Majoidea, as all known zoeae in this superfamily have at least one pair of well-developed lateral spines on the telson furcae, with only a few exceptions: four species of *Doclea* Leach, 1815 (see Krishnan & Kannuandi 1988) that do not have spines on the telson furcae, and *Pyromaia tuberculata* (Lockington, 1877) that only has a pair of small dorsal spines (see Fransozo & Negreiros-Fransozo 1997; Luppi & Spivak 2003). *Macropodia* has been defined, within inachids, as the most derived genus due to reduction in number of segments, appendages and setation, for example, the setation of the endopods of maxillule (0, 3), maxilla (2+2) and the second maxilliped (0, 0, 4), among others. This absence of spines on the telson furcae could be in line with this characteristic, and more larval descriptions of the remaining species of this genus are necessary in order to confirm this.

Within each group mentioned above, separations can be made as follows: the zoea I of *M. linaresi* has a long, straight dorsal spine of the carapace, which is shorter and slightly curved distally in *M. tenuirostris* and *M. longipes*. Differences between these two last species are more difficult to find. In the zoeal stages the only differences are the antennules formula (see Table 2), the setation of the scaphognathite of the maxilla of zoea II (which could be related to size), and two dorsal setae on abdominal somite 1 that are present in *M. tenuirostris* and absent in *M. longipes*. There are evident differences in the overall morphology of the megalopa, as the cardiac spine of the cephalothorax is more than twice as long as the protograstic spines, and the first segment of the antennal peduncle does not have setae in *M. longipes,* while in *M. tenuirostris* the megalopa cardiac and protograstic spines have a similar length, and one setae is present in the first segment of the antennal peduncle. Likewise, differences between the larval stages of *M. rostrata* and *M. parva* are not easy to observe. In this case there are additional difficulties due to differences reported in *M. rostrata* larvae from different geographical origins. Starting with this intraspecific variability in *M. rostrata*, two main groups can be separated based on the presence or absence of exopodal seta on the maxillule of zoea II: larvae from the Isle of Man and Plymouth (Ingle 1982) as well as from S. Torpes Bay (SW Portugal) (described by Paula (1987) as *Macropodia* S13) have exopodal seta; and larvae from Carthage-Salammbo (Tunisia) (Ingle 1982) and San Pedro River (SW Spain) (unpublished material from larvae reared by AR) do not have exopodal seta. Other features for making comparisons are confusing due to inaccuracies between the original description by Ingle (1982) and a posterior re-description (Ingle 1992). For example, in his first work Ingle (1982) only described one medial seta on the exopod of the antenna of zoea I, and that the megalopa had setation of the antennal peduncle 0, 0, 1; however, later in his 1992 description he described the antennal exopod of the zoea I as having two medial setae, and 1, 0, 1 setae on the antennal peduncle of the megalopa. Although Paula (1987) initially attributed the larvae described as *Macropodia* S13 to *M. linaresi*, *M. tenuirostris* or *M. longipes*, it should actually be identified as *M. rostrata* based on the zoeal antennal morphology. Alternatively, these larvae could belong to *M. longirostris* or *M. intermedia*, which are two other species present in the area and for which there are currently no larval data. The minor differences with respect to *M. rostrata* from the U.K. are the same as those of the larvae from SW Spain (see Table 2), and are therefore presumably related to intraspecific variability due to geographical origin.

$There are no significant differences when the larval stages of *M. rostrata* and *M. parva* are compared (see Table 2), because re-examination of the larval stages of several specimens of *M. parva* deposited at the Instituto de Ciencias Marinas (accession number MJ/2000-3) showed that some differential characters, such as the presence of one seta at the basis of the second maxilliped of zoea II and two dorsal setae on the telson of the megalopa, described by González-Gordillo & Rodríguez (2001) were absent in the re-examined larvae. Therefore, this could be a mistake in the original description or a less frequent feature. These characters are in any case not useful for characterizing these larvae.

González-Gordillo & Rodríguez (2001) suggested that *M. rostrata* and *M. parva* could be subspecies due to strong homogeneity in the larval morphology, and the similar morphological characteristics of adults, which even coexist in the same habitat in the Gulf of Cádiz. In addition, D´Udekem d´Acoz (1999) questioned the validity of *M. parva* due to the inaccurate description of the species, which is mainly based on small specimens. Initial data from an ongoing work on the molecular phylogeny of *Macropodia* suggest that *M. rostrata* and *M. parva* should be considered as the same species due to similar sequences of the mitochondrial genes 16S and Cox1 (Marco-

Herrero *et al*. unpublished data). Therefore, the slight differences observed in larval stages (see Tables 1, 2) should be attributed to intraspecific variability.

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LITERATURE CITED

Clark, P. F., Calazans, D. K. & Pohle, G. W. (1998) Accuracy and standardization of brachyuran larval descriptions. *Invertebrate Reproduction and Development*, 33, 127–144.

Clark, P. F. & Webber, W. R. (1991) A redescription of *Macrocheira kaempferi* (Temminck, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura). *Journal of Natural History*, 25, 1259–1279.

D'Udekem d'Acoz, C. (1999) *Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales* *adjacentes au nord de 25°N.* (Vol. 40). Paris, Muséum National d'Histoire Naturelle, 383 pp.

De Grave, S. (2009) A classification of living and fossil genera of Decapod Crustaceans. *The Raffles Bulletin of Zoology,* 21, 1–109.

Fransozo, A. & Negreiros-Fransozo, M. L. (1997) Larval Stages of *Pyromaia tuberculata* (Lockington, 1877) (Decapoda, Majidae, Inachinae) reared in the Laboratory. *Crustaceana,* 70, 304–323.

García Raso, J. E. (1984) Brachyura of the coast of Southern Spain (Crustacea, Decapoda). *Spixiana,* 7, 105–113.

González-Gordillo, J. I. & Rodríguez, A. (2001) The complete larval development of the spider crab, *Macropodia parva* (Crustacea, Decapoda, Majidae) from laboratory culture. *Invertebrate Reproduction and Development,* 39, 135–142.

Guerao, G. & Abelló, P. (1997) Larval Development of the Spider Crab *Macropodia longipes* (Brachyura: Majidae: Inachinae). *Journal of Crustacean Biology,* 17, 459–471

Guerao, G., Abelló, P. & Torres, P. (1998) Morphology of the first zoea of the spider crab *Macropodia linares*i (Brachyura, Majidae, Inachinae). *Societat d'Historia Natural de les Balears,* 41, 13–18.

Guerao, G. & Abelló, P. (2007) The first zoea of *Inachus aguiarii*, *Inachus communissimus* and *Ergasticus clouei* (Decapoda, Brachyura, Majoidea) with implications for the systematics of the family Inachidae. *Zootaxa*, 1429, 55–68.

Hultgren, K. M., Guerao, G., Marques, F. & Palero, F. (2009) Assessing the contribution of molecular and larval morphological characters in a combined phylogenetic analysis of the superfamily Majoidea. *In:* J. W. Martin, K. A.

Crandall & D. L. Felder (Eds), *Decapod Crustacean Phylogenetics*. Crustacean Issues, pp. 437–455.

Hultgren, K. M. & Stachowicz, J. J. (2008) Molecular phylogeny of the brachyuran crab superfamily Majoidea indicates close congruence with trees based on larval morphology. *Molecular Phylogenetics and Evolution,* 48, 986–996.

Ingle, R. W. (1982) Larval and post-larval development of the slender-legged spider crab, *Macropodia rostrata* (Linnaeus) (Oxyrhyncha: Majidae: Inachinae) reared in the laboratory. *Bulletin of the British Museum of Natural History (Zoology),* 42, 207–225.

Ingle, R. W. (1992) *Larval stages of northeastern Atlantic crabs: An illustrated key* (Vol. 1st edition), Chapman & Hall (London & New York) 363 pp.

Krishnan, T. & Kannupandi, T. (1988) Larval Development of the Spider Crab *Doclea gracilipes* Stimpson, 1857 (Decapoda: Brachyura: Majidae) Reared in the Laboratory. *Journal of Crustacean Biology,* 8, 420–429.

Landeira, J. M., Lozano-Soldevilla, F. & González-Gordillo, J. I. (2009) Morphology of first seven larval stages of the striped soldier shrimp, *Plesionika edwardsii* (Brandt, 1851) (Crustacea: Decapoda: Pandalidae) from laboratory reared material. *Zootaxa*, 1986, 51–66.

Leach, W. E. (1815) *The zoological miscellany; being descriptions of new or interesting animals*. (Nodder and Son, London), **2**: 1-154 + 8 (unnumbered) pages. Atlas (1814): pls. 61-120.

Lebour, M. V. (1927) Studies of the Plymouth Brachyura. I. The Rearing of Crabs in Captivity, with a Description of the Larval Stages of *Inachus dorsettensis*, *Macropodia longirostris* and *Maia squinado*. *Journal of the Marine Biological Association of the United Kingdom (New Series),* 14, 795–821.

Lebour, M. V. (1928) The Larval Stages of the *Plymouth* Brachyura. *Proceedings of the Zoological Society of London,* 98, 473–560.

Luppi, T. A. & Spivak, E. D. (2003) Postembryonic development of *Pyromaia tuberculata* (Lockington, 1877): a review of larval and postlarval morphology. *Scientia Marina,* 67, 201–214.

Marques, F. & Pohle, G. (1998) The use of structural reduction in phylogenetic reconstruction of decapods and a phylogenetic hypothesis for 15 genera of Majidae: testing previous larval hypotheses and assumptions. *Invertebrate Reproduction and Development,* 33, 241–262.

Marques, F. & Pohle, G. (2003) Searching for larval support for majoid families (Crustacea: Brachyura) with particular reference to Inachoididae Dana, 1851. *Invertebrate Reproduction and Development,* 43, 71–82.

Ng, P. K. L., Guinot, D. & Davie, P. J. F. (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *The Raffles Bulletin of Zoology,* 17, 1–286.

Oh, S. M. & Ko, H. S. (2011) The zoeal development of *Platymaia wyvillethomsoni* Miers, 1886 (Crustacea: Decapoda: Majoidea: Inachidae) described from laboratory reared material. *Invertebrate Reproduction and Development*, 1–9.

Pardo, L. M., Ampuero, D. & Veliz, D. (2009) Using morphological and molecular tools to identify megalopae larvae collected in the field: the case of sympatric Cancer crabs. *Journal of the Marine Biological Association of the United Kingdom,* 89, 481–490.

Paula, J. (1987) Planktonic stages of brachyuran crabs from the South-Western Iberian coast (Crustacea, Decapoda, Brachyura). *Journal of Natural History*, 21, 717–756.

Pohle, G. & Marques, F. (2000) Larval stages of *Paradasygyius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae. *Proceedings of the Biological Society of Washington*, 113, 739–760.

Rice, A. L. (1980) Crab zoeal morphology and its bearing on the classification of the Brachyura. *The Transactions of the Zoological Society of London*, 35, 271–372.

Rice, A. L. (1988) The megalopa stage in majid crabs, with a review of spider crab relationships based on larval characters. *In:* Fincham (Ed), *Aspects of Decapod Crustacean Biology*. Zoological Society of London, pp. 27–46.

Salman, S. (1981) Larval development of *Macropodia tenuirostris* (Leach) (Crustacea, Brachyura, Majidae), reared in the laboratory. *Journal of Natural History*, 15, 931–938.

Sato, T. & Suzuki, H. (2010) Female size as a determinant of larval size, weight, and survival period in the coconut crab, *Birgus latro*. *Journal of Crustacean Biology*, 30, 624–628.

Shirley, S. M., Shirley, T. C. & Rice, A. L. (1987) Latitudinal variation in the Dungeness crab, *Cancer magister*: zoeal morphology explained by incubation temperatures. *Marine Biology,* 95, 371–376.

Van Dover, C. L., Factor, J. R. & Gore, R. H. (1982) Developmental Patterns of Larval Scaphognathites: An Aid to the Classification of Anomuran and Brachyuran Crustacea. *Journal of Crustacean Biology*, 2, 48–53.

Zariquiey-Álvarez R. (1968) Crustáceos decápodos ibéricos. *Investigación Pesquera*. 32, 1–510.

[FIGURE CAPTIONS]

FIGURE 1. Rearing records of *Macropodia czernjawskii* (Brandt, 1880) reared at 25 ± 1°C and 32 ± 1 ‰ salinity. ZI, zoea I; ZII, zoea II; M, megalopa; CI, first crab.

FIGURE 2. *Macropodia czernjawskii* (Brandt, 1880). Zoea I, cephalothorax, A: lateral view; a: posterolateral margin detail; B: frontal view. Zoea II, cephalothorax, C: lateral view; D: frontal view. Megalopa, E: dorsal view; F: sternum; G: lateral view of cephalothorax.

FIGURE 3. *Macropodia czernjawskii* (Brandt, 1880). Antennule, A: zoea I; B: zoea II; C: megalopa. Antenna, D: zoea I; E: zoea II; F: megalopa. Mandible, G: megalopa.

FIGURE 4. *Macropodia czernjawskii* (Brandt, 1880). Maxillule, A: zoea I; B: zoea I; C: megalopa. Maxilla, D: zoea I; E: zoea II; F: megalopa.

FIGURE 5. *Macropodia czernjawskii* (Brandt, 1880). First maxilliped, A: zoea I; B: zoea II; C: megalopa. Second maxilliped, D: zoea I; E: zoea II; F: megalopa. Third maxilliped, G: megalopa.

FIGURE 6. *Macropodia czernjawskii* (Brandt, 1880). Megalopa, A: Cheliped, with detail of tubercle on merus; B: detail of distal part of propodus and dactylus; C: second pereiopod; D: fourth pereiopod; E: Pleopod.

FIGURE 7. *Macropodia czernjawskii*(Brandt, 1880). Abdomen, dorsal view, A: zoea I; B: zoea II; C: megalopa. Abdomen, lateral view, D: zoea I; E: zoea II; F: megalopa.

Table 1. Morphometric differences between larval stages of the *Macropodia* species with larval data known. Abbreviations: CL, cephalothorax length; DSL, dorsal spine of the cephalothorax length; AL, antenna length; ZI, zoea I, ZII, zoea II; nd, no data;[1] *M. rostrata* larvae from San Pedro River (SW Spain) were obtained from an ovigerous female collected in August 1999;[2] larvae from plankton samples attributed to *M. linaresi*, *M. tenuirostris* or *M. longipes*. All data in mm.

		Zoeal stages								**Megalopa**		
		CL		**DSL**		**DSL/ CL**		**AL**				
Species (reference)	**Origin**	**ZI**	**ZII**	**ZI**	**ZII**	**ZI**	**ZII**	**ZI**	**ZII**	**CL**	**CW**	**CL/CW**
M. tenuirostris (Salman 1981)	Isle of Man (U.K.)	0.98	1.19	1.14	0.89	1.16	0.74	0.9-1.0	1.05	1.14	0.98	1.16
M. tenuirostris (Ingle 1982)	Isle of Man (U.K.)	0.9-1.0	1.1-1.2	1.0-1.1	nd	1.11	nd	0.9-1.0	1.1-1.2	1.5	nd	nd
M. rostrata (Ingle 1982)	Isle of Man (U.K.)	0.7-0.8	0.8-0.9	1.3-1.4	1.1-1.2	1.85-1.75	1.9-1.3	1.2	1.3-1.4	1.2-1.3	nd	nd
M. rostrata[1] (present study)	San Pedro River (SW Spain)	0.66	0.78	1.03	0.9	1.56	1.15	0.87	0.95	0.98	0.76	1.3

M. longipes (Guerao&Abelló 1997)	Delta EbroRiver (W Mediterranean)	0.75-0.77	0.9	0.90-0.94	0.80-0.82	1.2	0.88-1.1	0.80-0.83	0.87-0.89	1.1-1.15	0.78-0.82	1.40-1.41
M. linaresi (Guerao *et al.* 1997)	Cape La Nao (W Mediterranean)	0.60-0.63	-	1.20-1.25	-	2-1.98	-	0.64-0.66	-	-	-	-
M. parva (González-Gordillo & Rodríguez 2000)	El Chato beach (SW Spain)	0.63	0.85	0.60	0.92	0.95	1.08	0.61	0.81	1.0	0.78	1.28
M. czernjawskii (present study)	El Chato beach (SW Spain)	0.57	0.61	0.69	0.58	1.21	0.95	0.60	0.68	0.83	0.63	1.31
Macropodia S13(2) (Paula 1987)	S. Torpes Bay (SW Portugal)	0.74	0.79	1.15	1.19	1.55	1.51	nd	nd	1.09	nd	nd

Table 2. Main morphological and meristic differences between larval stages of the *Macropodia* species with larval data known. Abbreviations: Pp, Posterodorsal protuberance; Sl, slightly; Pt, protopod tip; s, setation; ss, simple setae; es, exopodal seta; sp., spine; (1) 0,1+2 in SW Spain zoea I; (2) absent in SW Spain and Tunisia zoeae II; (3)1, 0, 1 setae in SW Spain and Ingle´s 1992 description of megalopae; (4)according to Paula (1987) no difference respect to Ingle´s (1982) description of *M. rostrata*; (5) data from SW Spain larvae; other abbreviations and references as in Table 1.

Species	***M. tenuirostris***	***M. longipes***	***M. linaresi***	***M. rostrata***	***M. parva***	***Macropodia* S13**	***M. czernjawskii***
Zoea I							
Cephalothorax Pp	present	present	present	absent	absent	absent	absent
Dorsal spine	Sl curved distally	Sl curved distally	Straight	Straight	Sl curved distally	Sl curved distally	Sl curved distally
Antennule s	4a, 1ss	3a, 2ss	3a, 2ss	2a, 2ss	4a, 1ss	nd	4a, 1ss
Antenna Pt	acute	acute	acute	rounded	rounded	rounded	acute
Antennal protopod	spinulated	spinulated	spinulated	not spinulated	not spinulated	not spinulated	spinulated 2 rows
Maxillule endopod s	0, 1+2	0, 1+2	0, 1+2	0, 3(1)	0, 3	0, 1+2	0, 3

Telson furcae	spinulated	spinulated (minute spinules)	spinulated (minute spinules)	spinulated (very minute spinules)	spinulated (very minute spinules)	nd	spinulated (minute spinules)
Telson lateral spines	present	present	present	present	present	present	absent
Zoea II							
Cephalothorax Pp	present	present	-	absent	absent	absent	absent
Dorsal spine	straight	Sl curved distally	-	curved	curved	straight	curved
Maxillule es	present	present	-	present [(2)]	absent	present	present
Pleonal somite 1 s	2	0	-	0	0	0	0
Megalopa							
Antennal peduncle s	1, 0, 1	0, 0, 1	-	0, 0, 1 [(3)]	1, 0, 1	0, 0, 1[(4)]	1, 0, 1
Cheliped isquium sp.	1	1		0	0	0[(4)]	0
Cheliped merus sp.	2	2	-	1 (minute)	1 (minute)	1 (minute)[(4)]	1 (minute)
Sternal plate s	nd	nd	-	6 [(5)]	6	nd	28

Pleonal somite 5 s	2+2	2+2	-	1+2+2+1	3+3	2+2	3+3