

Planktonic stages of *Processa macrodactyla* (Decapoda: Caridea: Processidae) reared in the laboratory

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Two ovigerous females of the processid shrimp *Processa macrodactyla* were caught in April 1997 at 13 m depth in coastal waters of Rota, Cádiz Bay, south-western Spain (36°36'N 6°18'W). Rearing was terminated after nine zoeal stages, when larvae moulted to the first juvenile instar. Descriptions of the appendages of every instar have been made so as to: (1) compare the larval morphology with that of other previously described known species in the genus *Processa* (*P. canaliculata*, *P. edulis*, *P. elegantula*, *P. modica*, *P. nouveli*); and (2) with those larvae not ascribed to a certain species in order to facilitate the specific identification of unknown collected planktonic larvae. When describing *P. macrodactyla* some characters remained, with few exceptions, invariable in their setation form ZI to ZIV or ZV, to then change and maintain until the last zoeal stage. This can be due to intermediate moults, with the result that some larvae unite the characters of Stages ZIV and ZV and others those of ZV and ZVI.

INTRODUCTION

The caridean genus *Processa* comprises numerous small shrimps spread worldwide, of which ten species are recorded within European waters (d'Udekem d'Acoz, 1999): *Processa edulis* Risso, 1816, *Processa modica* Williamson, 1979, *Processa nouveli* Al-Adhub & Williamson, 1975, *Processa canaliculata* Leach, 1815, *Processa elegantula* Nouvel & Holthuis, 1957, *Processa macrophthalma* Nouvel & Holthuis, 1957, *Processa acutirostris* Nouvel & Holthuis, 1957, *Processa robusta* Nouvel & Holthuis, 1957, *Processa macrodactyla* Holthuis, 1952 and *Processa intermedia* Holthuis, 1951. *Processa edulis* was subdivided by Nouvel & Holthuis (Nouvel & Holthuis, 1957) into three subspecies: *P. edulis edulis*, distributed in the Mediterranean, and *P. edulis crassipes* and *P. edulis arcassonensis* recorded in the Atlantic. Williamson & Rochanaburanon, 1979, proposed *P. modica* divided into *P. modica carolii* from the Mediterranean and south-west Atlantic coasts of Spain and the Atlantic subspecies *P. modica modica*. The species *P. nouveli* is considered with the subspecies *P. nouveli nouveli* in the Mediterranean and *P. nouveli holthuisi* in the Atlantic (Al-Adhub & Williamson, 1975). *Processa acutirostris* is only found in the Mediterranean and *P. intermedia* occurs in Atlantic waters, while *P. canaliculata*, *P. elegantula*, *P. robusta* and *P. macrophthalma* are recorded from Atlantic waters as well as in the western Mediterranean Sea (d'Udekem d'Acoz, 1999). Finally, *P. macrodactyla* appears on the south Atlantic coasts of Spain (González-Gordillo & Rodríguez, 2000) and the Alboran Sea (García Raso & Casanova, 1985).

The larval morphology of these species is scarcely known since only partial descriptions of zoeal stages are available for *P. edulis* (Gurney, 1923 as *P. canaliculata*: Z1–Z4 from plankton specimens; Lebour, 1936: Z8 from plankton samples; Kurian, 1956: Z1–Z7 from plankton samples; Fincham & Williamson, 1978 as *P. edulis crassipes*: Z6 from plankton samples; Barnich,

1996 as *P. edulis edulis*, from plankton samples); *P. modica* (Fincham & Williamson, 1978 as *P. modica modica*: Z5; Williamson & Rochanaburanon, 1979 as *P. modica modica*: Z1–Z7 from plankton samples; Barnich, 1996 as *P. modica carolii*: Z8 from plankton samples), *P. nouveli* (Gurney, 1923 as *P. canaliculata*: Z5–Z9 from plankton specimens; Kurian, 1956 as *P. canaliculata*: Z1, Z5, Z6 from plankton specimens; Fincham & Williamson, 1978 as *P. nouveli holthuisi*: Z1, Z6; Williamson & Rochanaburanon, 1979 as *P. nouveli holthuisi*: Z1–Z9 from laboratory cultures; Barnich, 1996 as *P. nouveli nouveli*, from plankton samples), *P. canaliculata* (Lebour, 1936: Z1–Z5, Z8, Z9 from laboratory and plankton specimens; Fincham & Williamson, 1978: Z6) and for *P. macrodactyla* (González-Gordillo & Rodríguez, 2000: Z1, hatched in the laboratory). For the other species of the genus no accurate larval descriptions are available. Other larval descriptions of processid species have been made from specimens collected in plankton samples from European waters although, at the present time, they remain unclassified as *Processa ?elegantula*, *Processa* sp.1, and *Processa* sp.2 (Barnich, 1996); *Processa EM4* and *Processa EM7* (Williamson, 1967); *Processa EM5* and *Processa EM6* (Williamson, 1967; dos Santos, 1999); and *Processa EFSL11* (dos Santos, 1999).

In this paper, the complete larval development of *P. macrodactyla* was reared in the laboratory in order to describe and compare it with that of congeneric species with known larvae so as to facilitate the specific identification of unknown planktonic larvae.

MATERIALS AND METHODS

Two ovigerous shrimp were caught in April 1997 with a benthic trawl at 13 m depth in coastal waters of Rota, Cádiz Bay, south-western Spain (36°36'N 6°18'W). The specimens were maintained in a 2-l glass beaker,

Table 1. *Setation and other characteristics of zoeal stages of Processa macrodactyla. Setal groups on successive segments are separated by a comma and groups of setae on the same segment, or on different lobes of the same endite, are separated by a plus sign (+). Carapace length in millimetres.*

Features	Stages				
	Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V
Carapace length	0.56 ±0.011	0.61 ±0.017	0.70 ±0.036	0.80 ±0.055	0.84 ±0.027
Antennule					
peduncle	naked	2p	1c+4p,1e+7p	1c+8p,1e+8p	1c+11p,3e+4p
endopod	as long seta	as long seta	as long seta	as long seta	as long seta
exopod	1p+1s+3a	1s+3a	1s+3a	1s+3a	1s+3a
Antenna					
peduncle	1c	1c	1c	1c	1c
endopod	rows of spinules	rows of spinules	rows of spinules	rows of spinules	no spinules
exopod	9p+1j+2p	9p+1j+2p	12p+1j+1p	13p+1j+1p	14p+1j+1p
Maxillule					
coxal endite	2e+5d	2e+5d	2e+5d	2e+6d	8e
basial endite	5t	7t	8t	8t	10–11t
endopod	2e,3e	3e,3e	3e,3e	3e,3e	3e,3e
Maxilla					
coxal endite	(10p)+(1p+3e)	(11p)+(2p+2e)	(11p)+(2p+2e)	(11p)+(2p+2e)	(12p)+(2p+2e)
basial endite	(1p+3e)+(1p+3e)	(1p+4e)+(1p+4e)	(1p+4e)+(1p+4e)	(1p+4e)+(1p+4e)	(1p+5e)+(1p+5e)
endopod	3e+2e+1e+3e	3e+2e+1e+3e	3e+2e+1e+3e	3e+2e+1e+3e	3e+2e,1e+1e+2e
scaphognathite	3p+2p	5p+2p	7p+2p	11p+2p	17p
First maxilliped					
coxa	6p	9p	9p	9p	9p
basis	2p+10e	2p+12e	1p+13e	1p+13e	1p+15e
endopod	3e,1e,2e,1e+3e	3e,1e,2e,1e+3e	3e,1e,2e,1e+3e	3e,1e,2e,1e+3e	3e,1e,2e,1e+3e
exopod	1n+3n	1n+4n	1n+4n	1n+4n	2n+4n
Second maxilliped					
coxa	2p	2p	2p	2p	2p
basis	1e+2e+3e+3e	1e+2e+3e+3e	1e+2e+3e+3e	1e+2e+3e+3e	1e+2e+3e+3e
endopod	3e,2e,2e,1p+4e	3e+1p,1p,0,2e,1e+5e	3e+1p,1p,0,2e,1e+5e	3e+1p,1p,0,2e,1e+5e	3e+1p,1p,0,2e,1e+5e
exopod	1n+1s+2n	1n+1s+4n	1n+1s+4n	2n+4n	2n+4n
Third maxilliped					
coxa	0	0	0	0	1e
basis	1e+1e+2e	1e+1e+2e	1e+1e+2e	1e+1e+2e	1e+1e+2e
endopod	2e,0,2e,1e+3e	2e,0,0,2e,1e+3e	2e,0,0,2e,1e+3e	2e,0,0,2e,1e+3e	2e,0,0,3e,1e+4e
exopod	2n+3n	2n+4n	2n+4n	2n+4n	2n+4n
First pereopod	biramous bud	biramous bud			
coxa			0	0	0
basis			1p+1p+1p	1p+1p+1p	1p+1p+1p
endopod			2e,1e,0,2e,1e+3e	2e,1e,0,2e,1e+4e	2e,1e,1e,3e,4e+1d
exopod			2n+4n	2n+4n	2n+4n
Second pereopod	absent	absent			
coxa			0	0	0
basis			0	1e+1e+2e	1e+1e+2e
endopod			2e,1s+3e	2e,0,0,2e,1s+3e	2e,1e,1e,2e,2e+3e
exopod			2n+4n	2n+4n	2n+4n
Third pereopod	absent	absent	absent	biramous bud	
coxa					0
basis					1e
endopod					1e+1e+2e
exopod					1n+4n
Fourth pereopod	absent	absent	absent	biramous bud	biramous bud
Fifth pereopod	absent	absent	absent	absent	absent
Abdomen					
somites	0,0,0,0,2b	0,0,0,0,2b	0,0,0,0,2b,0	0,0,0,0,2b,0	0,0,0,0,2b,0
Pleopods	absent	absent	absent		absent
Uropods	absent	absent			
endopod			2s	6p	10–12p
exopod			6p	9p	18–19p
Telson	7d+7d	8d+8d	(1p+7d)+(1p+7d)	(1p+5d)+(1p+5d)	(3p+5d)+(3p+5d)

(Continued)

Table 1 (Cont.). *Setation and others characteristics of zoeal stages of Processa macrodactyla.*

Features	Stages			
	Zoea VI	Zoea VII	Zoea VIII	Zoea IX
Carapace length	1.20 ±0.031	1.51 ±0.017	1.57 ±0.010	1.64 ±0.008
Antennule				
peduncle	1c+19p,5e+4p	1c+24p,9p	1c+24p,9p	1c+27p,9p
endopod	0,2s+1p	0,1s,2s+1p	0,3s,1s,5e	1e,6e,2e,5e
exopod	1s+3a	3e,3e,3e	3p+4p,3p,3e	2p+3p+4p+2s,5p+2s,4e
Antenna				
peduncle	1c	1c	1c	1c
endopod	0,5s	6-segmented	8-segmented	8-segmented
exopod	17p+1j+3p	22p+1j+5p	22p+1j+5p	23p+1j+5p
Maxillule				
coxal endite	1s+8d	2e+10d	2e+10d	2e+10d
basial endite	1s+12t	4s+12t	4s+12t	6s+12t
endopod	3e,3e	3e,3e	3e,3e	3e,3e
Maxilla				
coxal endite	(16p)+(2p+3e)	(16p)+(2p+3e)	(16p)+(2p+3e)	(16p)+(2p+3e)
basial endite	(1p+6e)+(1p+6e)	(1p+6e)+(1p+6e)	(1p+6e)+(1p+6e)	(1p+6e)+(1p+6e)
endopod	3e+2e,1e+1e+2e	3e+2e,1e+1e+2e	3e+2e,1e+1e+2e	3e+2e,1e+1e+2e
scaphognathite	27p	43p	43p	48p
First maxilliped				
coxa	10p	10p	10p	10p
basis	1p+19e	1p+19e	6p+17e	26e
endopod	3e+1p,1e+1p,2e,1e+3e	3e+1p,1e+1p,2e,1e+3e	3e+1p,1e+1p,2e,1e+3e	3e+1p,1e+1p,2e,1e+3e
exopod	1p+2n+4n	1p+2n+4n	1p+2n+4n	1p+2n+4n
Second maxilliped				
coxa	2p	2p	2p	2p
basis	1e+2e+3e+3e	1e+2e+3e+3e	1e+2e+3e+3e	1e+2e+4e+3e
endopod	3e+1p,2e+1p,1p,3e,1e+6e	3e+1p,2e+1p,1p,3e,6e+1d	3e+1p,2e+1p,1p,4e,6e+1d	3e+1p,2e+1p,1p,4e,6e+1d
exopod	1n+2n+4n	2n+2n+4n	2n+2n+4n	2n+2n+4n
Third maxilliped				
coxa	1e	1e	1e	1e
basis	1e+1e+2e	1e+1e+2e	1e+1e+2e	1e+1e+2e
endopod	2e,1e,2e,7e,1e+4e	2e,1e+2e,3e,12e,4e+1d	2e,3e,4e,12e,4e+1d	4e,7e,5e,15e,4e+1d
exopod	2n+2n+4n	1s+2n+2n+4n	1s+2n+2n+4n	1s+2n+2n+4n
First pereopod				
coxa	1p	1p	1p	1p
basis	1p+1p+1p	1p+1p+1p	1p+1p+1p	1p+1p+1p
endopod	2e,1e,2e,5e,4e+1d	2e,4e,4e,11e,8e+1d	2e,4e,4e,11e,8e+1d	2e,7e,4e,14e,9e+1d
exopod	2n+2n+4n	1n+2n+2n+4n	2n+2n+2n+4n	1-2n+2n+2n+4n
Second pereopod				
coxa	0	0	0	0
basis	1e+1e+2e	1e+1e+2e	1e+1e+2e	1e+1e+2e
endopod	2e,1e,1e,4e,5e+1d	3e,2e,3e,6e,6e+1d	3e,2e,3e,6e,6e+1d	3e,2e,3e,6e,6e+1d
exopod	2n+2n+4n	2n+2n+2n+4n	2n+2n+2n+4n	2n+2n+4n
Third pereopod				
coxa	0	0	0	0
basis	1e+1e+2e	1e+1e+2e	1e+1e+2e	1e+1e+2e
endopod	2e,2e,2e,5e,3e+1d	4e,4e,4e,12e,7e+1d	4e,4e,4e,12e,7e+1d	5e,7e,7e,13e,7e+1d
exopod	1n+2n+4n	2n+2n+4n	2n+2n+4n	2n+2n+4n
Fourth pereopod				
coxa	0	0	0	0
basis	1e+1e	1e+2e	1e+1e+2e	1e+1e+2e
endopod	2e,1e,2e,5e,2e+1d	3e,4e,4e,8e,7e+1d	4e,5e,6e,12e,7e+1d	4e,7e,8e,16e,7e+1d
exopod	4n	2n+4n	2n+4n	2n+4n
Fifth pereopod				
coxa	0	0	0	0
basis	1e+2e	1e+2e	1e+1e+2e	1e+1e+2e
endopod	2e,1e,1e,4e,1e+2e+1d	2e,1e,3e,7e,7e+1d	3e,4e,4e,11e,7e+1d	4e,8e,6e,16e,7e+1d
Abdomen				
somites	0,0,0,0,2b,1b	0,0,0,0,2b,1b	0,0,0,0,2b,1b	0,0,0,0,2b,1b
Pleopods	small buttons	biramous buds	biramous buds	biramous buds
Uropods				
endopod	17-18p	46-48p	36-38p	31p+13e
exopod	26-28p	38-39p	36-39p	42p+7e
Telson	(3s+5d)+(3s+5d)	(3s+5d)+(3s+5d)	(3s+5d)+(3s+5d)	(3s+5d)+(3s+5d)

a, aesthetasc; b, abdominal spine; c, spine; d, plumodenticulate seta; e, sparsely plumose seta; j, spiny projection; n, plumose natatory seta; p, plumose seta; s, simple seta; t, plumodenticulate cuspidate setae.

Table 2. Morphological differences in described larval stages of the European species of the genus *Processa*.

	<i>P. macrodactyla</i>	<i>P. canaliculata</i>	<i>P. edulis crassipes</i>	<i>P. edulis edulis</i>	<i>P. modica modica</i>	<i>P. modica carolii</i>	<i>P. novaei holthuisi</i>	<i>P. novaei novaei</i>
Authors	Present study	(1)	(1), (2)	(3), (4)	(5)	(3), (5)	(2), (5), (7)	(3), (7)
Carapace denticles	4	5-8	0-2	4	4	5	3-4	3-6
Length rostrum: frontal lobe ratio	>1	>1	<1	<1	=1	=1	ZII-ZIII: =1 ZIV-ZIX: >1	=1
Spine on stylocerite of antennula in ZVIII	Present	Present (3)				Present (3)		Present (3)
Pterygostomian spine	Marginal	Marginal	Submarginal	Small	Long submarginal	Very long	Short almost marginal	Short
Endopod of maxillule	2, 3 (ZI)	?	2, 3	?	2, 3	?	1+2, 3	
Exopodal seta of maxillule	1+2, 3 (ZII-ZIX)	?	ZI-ZIII	?	ZI-ZIII	?	ZI-ZIII	?
Endopod of maxilla	always present	?	?	?	2-4+2+1+1+2	?	2+2+1+1+2	?
Median abdominal spines on somite	6 (from ZVI)	no	no	no	3	3	no	no
Paired abdominal spines on somite	5, 6	4, 5	5	5	5	5	5	5
No. of zocal stages	9	8-9	8	8	7	9	9	9
Geographical distribution in European waters*	Eastern Atlantic Mediterranean	Eastern Atlantic Mediterranean	Eastern Atlantic	Mediterranean	Eastern Atlantic	South-eastern Spain Mediterranean	Eastern Atlantic	Mediterranean
	<i>Processa ?elegantula</i>	<i>Processa</i> sp.1	<i>Processa</i> sp.2	<i>Processa</i> EM4	<i>Processa</i> EM5	<i>Processa</i> EM6	<i>Processa</i> EM7	<i>Processa</i> EFSL11
Authors	(3)	(3)	(3)	(9)	(7), (9)	(7), (9)	(9)	(7)
Carapace denticles	5	3-4	6-7	0	4	9	3-6	5-6
Length rostrum: frontal lobe ratio	>1	No (3)	>1		=1	>1		=1
Spine on stylocerite of antennula in ZVIII	Present (3)	Short	No (3)	Slightly submarginal	Markedly submarginal	Almost marginal	Marginal or almost marginal	Long
Pterygostomian spine	Long	Short	Long	?	?	?	?	?
Endopod of maxillule	?	?	?	?	?	?	?	?
Exopodal seta of maxillule	?	?	?	?	?	?	?	?
Endopod of maxilla	?	?	?	?	?	?	?	?
Median abdominal spines on somite	no	no	no	?	no	no	no	no
Paired abdominal spines on somite	5	5	5	5	5	5	5	5
No. of zocal stages	8	8	8	?	9	9	9	9
Geographical distribution in European waters**	Mediterranean French coast	Mediterranean French coast	Mediterranean French coast	Israel coast	Israel coast Portuguese coast	Israel coast Portuguese coast	Israel coast	Portuguese coast

Authors: (1) (Lebour, 1936); (2) (Gurney, 1923); (3) (Barnich, 1996); (4) (Kurian, 1956); (5) (Williamson & Rochanaburanon, 1979); (6) (Fincham & Williamson, 1978); (7) (dos Santos, 1999); (8) (Smaldon, 1993); (9) (Williamson, 1967). *, Geographical distribution for adult specimens (d'Udekem d'Acoz, 1999). **, Geographical distribution refers to larval stages according to the location where collected.

Table 3. Time of appearance of pereopods and phase of development in described zoeal stages of genus *Processa*.

	<i>P. macrodactyla</i> (Present study)	<i>P. modica modica</i> (Williamson & Rochanaburanon, 1979)	<i>P. canaliculata</i> (Lebour, 1936)	<i>P. edulis crassipes</i> (Gurney, 1923) (Lebour, 1936)	<i>P. nouveli holthuisi</i> (Williamson & Rochanaburanon, 1979)
Zoea I	1P bud	1P bud	?	1P bud	?
Zoea II	1P bud	1P functional 2P bud 3P bud 4P bud 5P bud	1P functional	1P functional 2P bud 3P bud 4P bud 5P bud	1P functional
Zoea III	1P functional 2P functional	1P functional 2P bud 3P bud 4P bud 5P bud	1P functional 2P functional	1P functional 2P functional 3P bud 4P bud 5P bud	1P functional 2P functional
Zoea IV	1P functional 2P functional 3P bud 4P bud	1P functional 2P functional 3P bud 4P bud 5P bud	1P functional 2P functional 3P functional	1P functional 2P functional 3P functional 4P bud 5P bud	1P functional 2P functional 3P functional 4P functional? 5P functional?
Zoea V	1P functional 2P functional 3P functional 4P bud	1P functional 2P functional 3P functional 4P bud 5P bud	1P functional 2P functional 3P functional 4P functional 5P functional?	1P functional 2P functional 3P functional 4P functional 5P bud	1P functional 2P functional 3P functional 4P functional 5P functional?
Zoea VI–IX ⁽¹⁾	1P functional 2P functional 3P functional 4P functional 5P functional	1P functional 2P functional 3P functional 4P functional 5P functional	1P functional 2P functional 3P functional 4P functional 5P functional	1P functional 2P functional 3P functional 4P functional 5P functional	1P functional 2P functional 3P functional 4P functional 5P functional

⁽¹⁾, there are no ZVIII and ZIX zoeal stages for *P. modica*; neither ZIX zoeal stage for *P. edulis*.

containing well-aerated filtered natural seawater (36 salinity) until hatching. No food was added. Females released larvae 48 h and 72 h after their collection in a total amount of approximately 2000 and 500 larvae, respectively. After hatching, actively swimming larvae were transferred to 1-l glass bottles with aeration at constant temperature (22°C ± 1) and fed with *Artemia* nauplii. The water was changed daily, and larvae were checked for evidence of moulting. Each time the water was renewed, 3–4 larvae were preserved in 4% formalin. Rearing was terminated when larvae moulted to the first juvenile instar.

Descriptions of different instars were based on at least ten specimens of each larva. The appendages were dissected in water, mounted in Faure's liquid and drawn using an interference phase microscope with camera lucida. General recommendations proposed by Clark et al. (1998) for standardization in larval descriptions were followed. Carapace length (CL) was measured from the anterior margin of eyes to the posterior carapace margin. The sizes given are the arithmetic mean ± 95% confidence intervals. Other drawings of different parts of larval stages are available. Contact authors if needed.

RESULTS

The complete planktonic development of *Processa macrodactyla* took place through nine zoeal stages. At 22°C ± 1 and 36 salinity the juvenile stage appeared 23 days after hatching. The major features of each larval stage and changes in appendage setation follow. Details of

the type and distribution of setae and other features are given in Table 1. Table 2 shows the main morphological differences between described larvae of the genus *Processa* and those of which only partial descriptions have been made without assigning a certain species. Table 3 shows the time of appearance of pereopods and the presence of exopods. The first larval stage of *Processa macrodactyla* previously described by González-Gordillo & Rodríguez (2000) is added here to make comparison easier.

Processa macrodactyla Holthuis, 1952 (Figures 1–3, Tables 1–3)

Previous description: Zoea I (González-Gordillo & Rodríguez, 2000: 95, figures 3–4, table 1)

General morphology of zoeal stages

Carapace (Figures 1A,C,D & 2D). Flattened, with pterygostomial spine present and four small teeth on anteroventral margin. Mediodorsal tubercle on anterior part of carapace in first two stages and on anterior and posterior parts of carapace in subsequent stages. Rostrum absent in first stage but this and supraorbital spine appearing from second stage on. Eyes stalked from second larval stage.

Antennule (Figure 3F,I): slender with unsegmented peduncle in two first stages. Endopod as a long plumose seta.

Antenna (Figure 3G,H): endopod unsegmented, elongated and tapering spine process bearing a row of minute

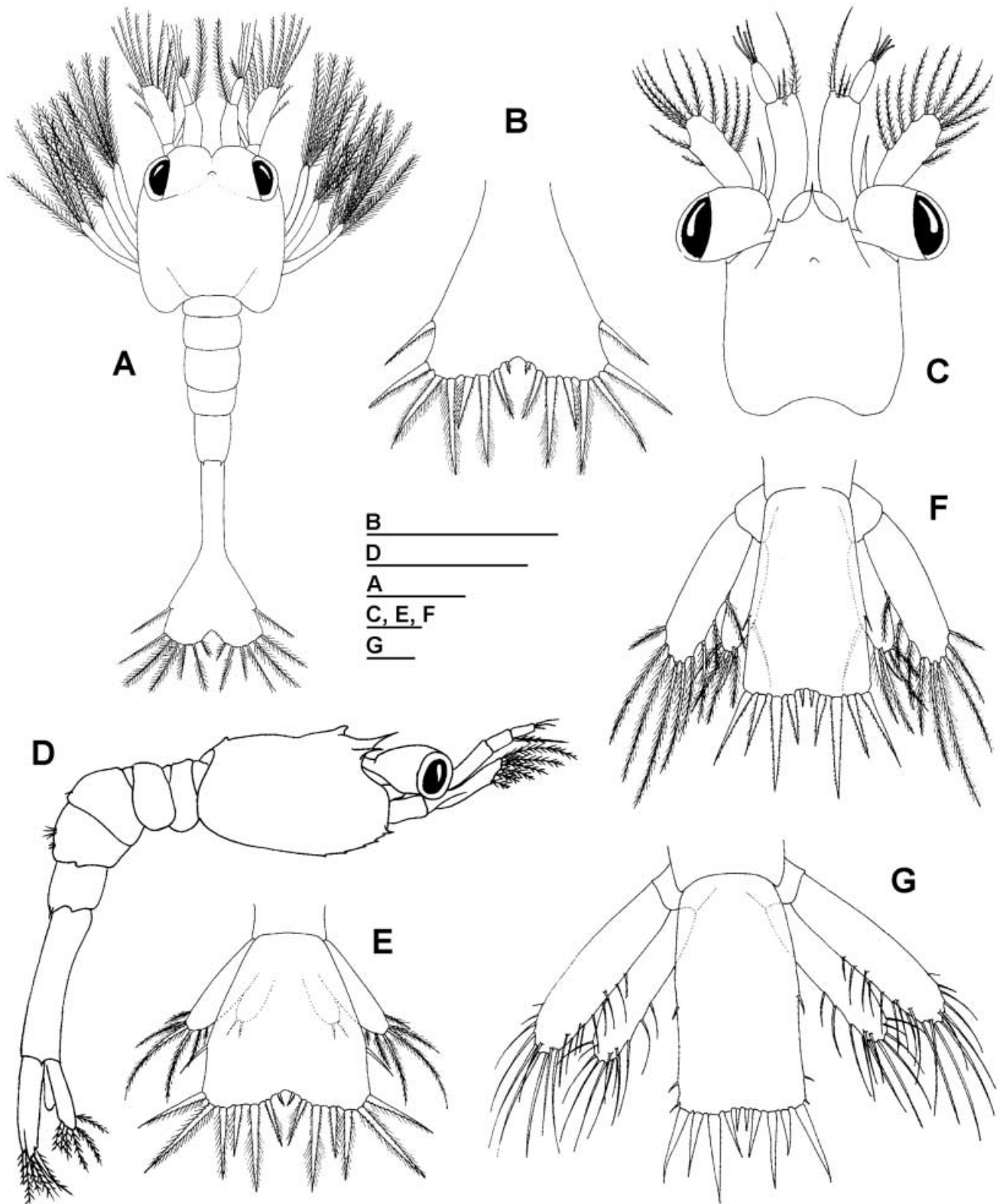


Figure 1. *Processa macrodactyla*. (A) Zoea I: dorsal view; (B–C) Zoea II: (B) telson; (C) cephalothorax dorsal view; (D–E) Zoea III: (D) lateral view; (E) uropods and telson; (F) Zoea IV: uropods and telson; (G) Zoea V: uropods and telson. Scale bars: A, 250 μm ; B, D, 500 μm ; C, E–G, 100 μm .

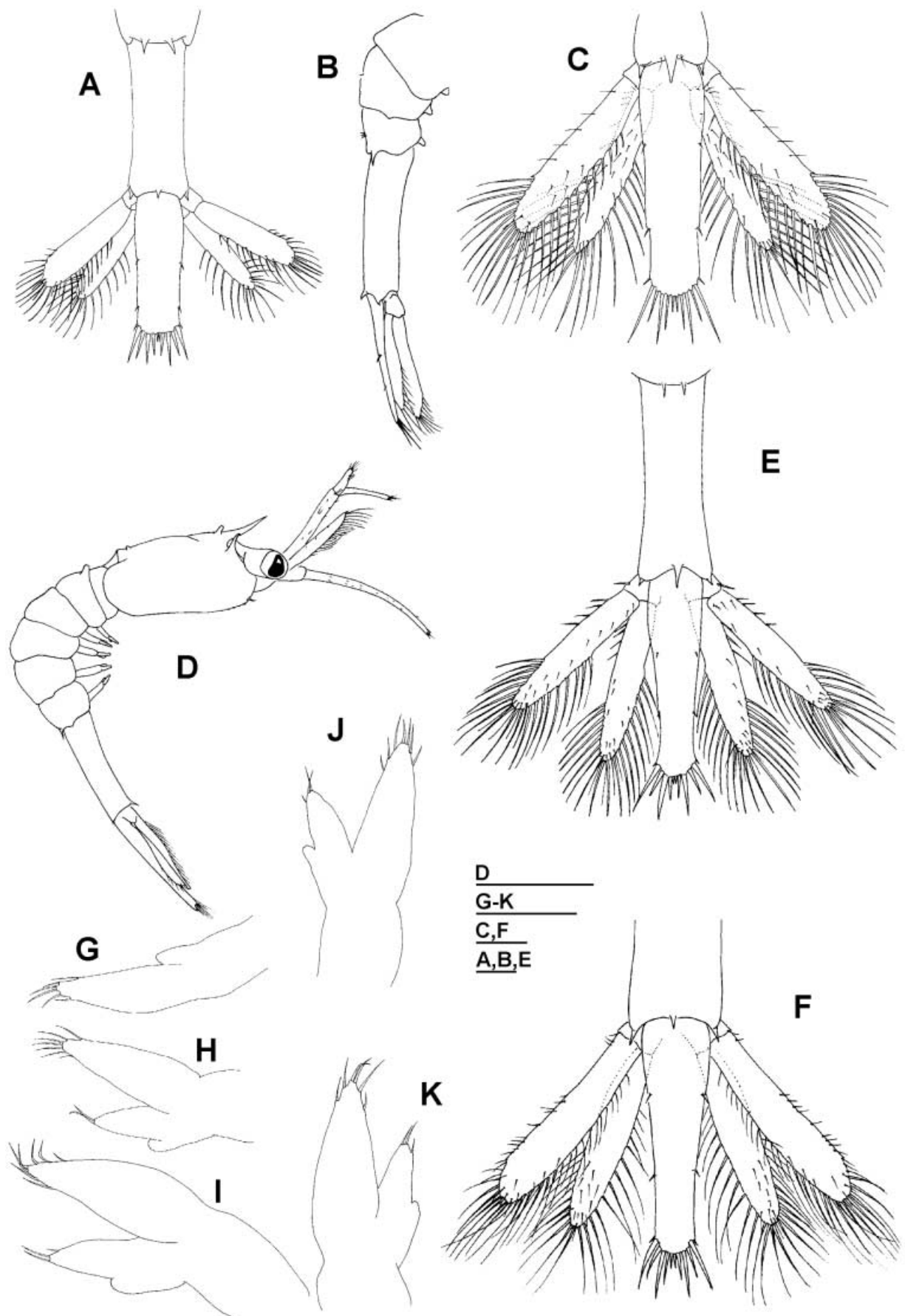


Figure 2. *Processa macrodactyla*. (A–B) Zoea VI: (A) uropods and telson; (B) lateral view of abdomen; (C) Zoea VII: uropods and telson; (D–E) Zoea VIII: (D) lateral view; (E) uropods and telson; (F–K) Zoea IX: (F) uropods and telson; (G) first pleopod; (H) second pleopod; (I) third pleopod; (J) fourth pleopod; (K) fifth pleopod. Scale bars: A–C, E–K, 200 μ m; D, 1 mm.

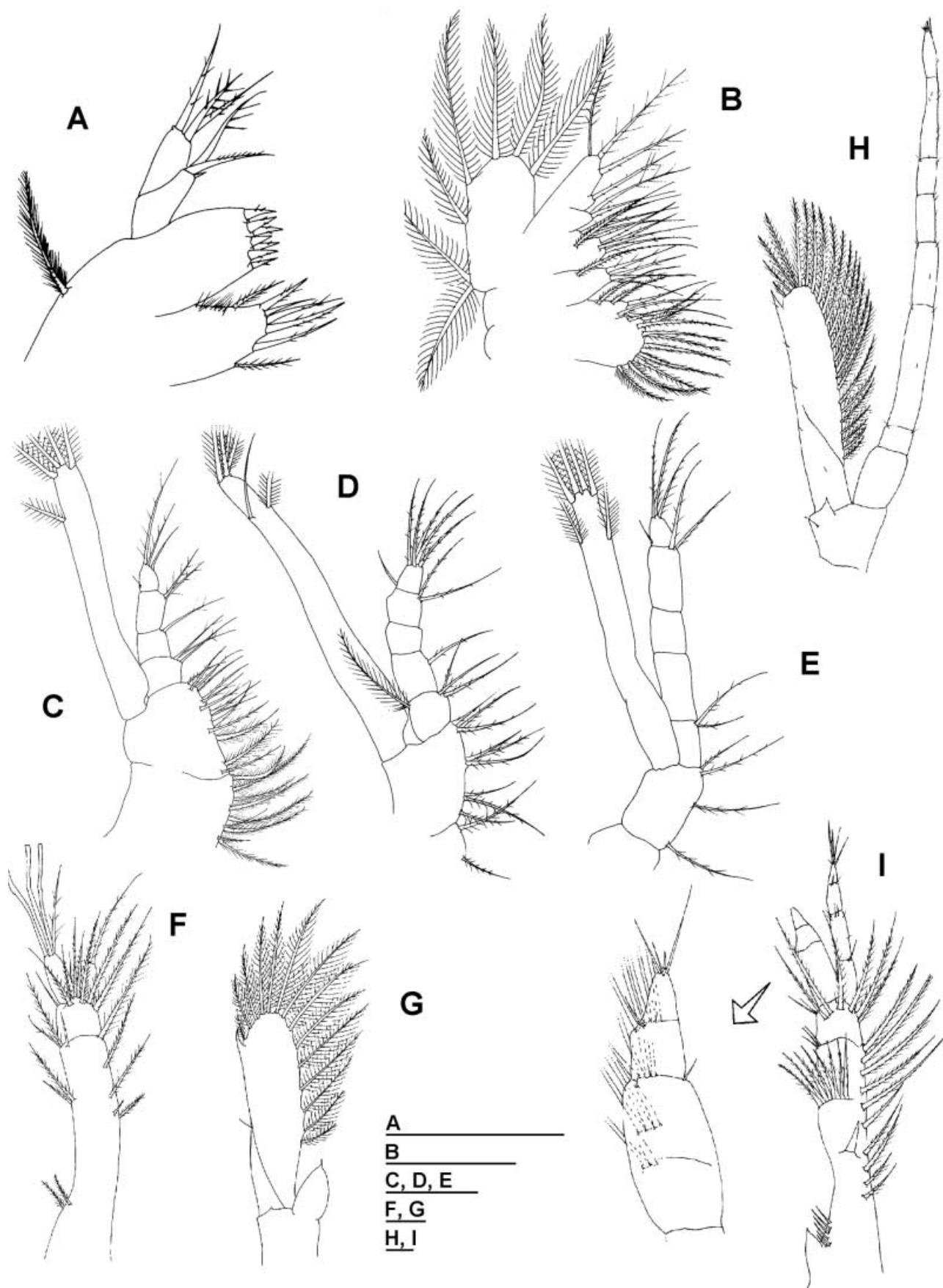


Figure 3. *Processa macrodactyla*. (A–E) Zoea II: (A) maxillule; (B) maxilla; (C) first maxilliped; (D) second maxilliped; (E) third maxilliped; (F–G) Zoea V: (F) antennule; (G) antenna; (H–I) Zoea IX: (H) antenna; (I) antennule. Scale bars: 100 μm .

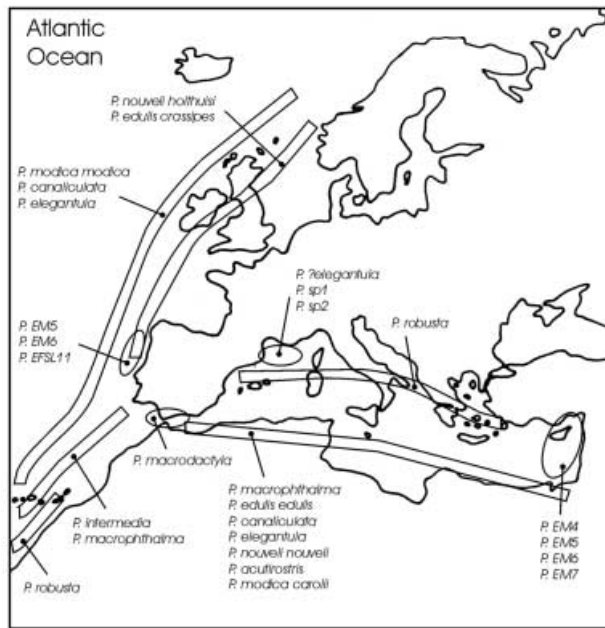


Figure 4. European distribution of recorded *Processa* species.

spines in first five stages, and not extending beyond middle of exopod. In subsequent stages the endopod is segmented and exceeds middle of exopod. Exopod unsegmented and broad.

Mandible: palp absent.

Maxillule (Figure 3A): endopod 2-segmented with number of setae unchanged from second zoeal stages. Exopod present as a long plumose seta.

Maxilla (Figure 3B): coxal and basal endites bilobed. Endopod unsegmented and tetralobed, setation unchanged.

First maxilliped (Figure 3C): endopod 4-segmented extending beyond middle of exopod. Exopod unsegmented.

Second maxilliped (Figure 3D): endopod 4-segmented, extending beyond middle of exopod. Exopod unsegmented.

Third maxilliped (Figure 3E): coxa naked. Endopod 4-segmented as long as exopod in four first stages and exceeding the length of exopod in subsequent stages. Exopod unsegmented.

Pereiopods: progressive development throughout zoeal stages. First to fifth pereiopods fully functional from sixth stage. First to fourth pereiopods biramous, fifth pereiopod uniramous. First and second right pereiopods with cheliped-like form from seventh zoeal stage.

Abdomen (Figures 1A,D & 2B,D): five somites and telson in two first stages, sixth additional somite in subsequent stages. Somite 4 bears a dorsal tuft of short setae. Somite 5 with a pair of small dorsal spines.

Pleopods (Figure 2G–K): present as small buttons in sixth larval stage; biramous buds in seventh stage.

Uropods (Figures 1E,F,G & 2A,C,E,F): present from third zoeal stage.

Telson (Figures 1B,E,G & 2A,C,E,F): broad posteriorly, with a median cleft in four first stages and almost rectangular shaped in subsequent stages. Tapering towards posterior end in last stage. Central pair of setae smallest.

DISCUSSION

The larval morphology of the studied species *Processa macrodactyla* is a typical example of larvae belonging to the Infraorder Caridea, presenting carapace laterally flattened and telson flattened with usually seven (Zoea I) or eight (later zoeae) setae on each half margin, and without median spine (dos Santos & González-Gordillo, 2004). Other characteristic features can also be useful to distinguish between families. Larvae of the family Processidae have been compared with those of Pandalidae, Hippolytidae and Crangonidae as they seem to be closer to each other than to other families. In Pandalidae, as in Processidae, the distance between bases of antennules is higher than the width of each antennule, but the presence of an unsegmented antennal exopod and an untoothed-rostrum are distinctive characters of processid larvae. Hippolytidae larvae differ from Processidae larvae in two main characters: (1) the distance between bases of antennules is lower than the width of each antennule; and (2) the presence of an anal spine since the first stage of development. Crangonidae shares with Processidae an unsegmented antennal exopod and the presence of a subchelate first pereiopod in later stages. However, they differ in the form of the endopod of antennule that is long and thin in Processidae, and in the absence of supraorbital spines in all larval stages of Crangonidae. In addition to the differences in the larval morphology, the long series of development and its structure in Processidae is completely different from that shown by Crangonidae.

The larval stages of *P. macrodactyla* share with its species congeners the following characters: the dorso-lateral spines on the fifth abdominal somite (Lebour, 1936); the absence of rostrum in Zoea I and its short-size presence in later stages; the presence of an anal spine in later zoeal stages (Williamson & Rochanaburanon, 1979); the presence of a pair of supraorbital spines from the second zoeal stage on; the presence of a pterygostomian spine (Williamson & Rochanaburanon, 1979); the presence of functional maxillipeds from Stage I on (dos Santos, 1999); when present, the fifth pereiopod has the same size as the other pereiopods and lacks exopod; and finally, telson without a deep central invagination (dos Santos & González-Gordillo, 2004). In contrast, other features that remain unchanged throughout the development of *P. macrodactyla*, such as the number of denticles on the ventral carapace margin, the presence of exopodal seta in the maxillule, and the setation of the endopod of the maxillule and maxilla, can be used to distinguish it from other congeneric species (Table 2).

The number of carapace denticles is a common feature often used by other authors to distinguish between the larvae of the species of the genus *Processa*. It presents 4 in *P. macrodactyla* and 5–8 in *P. canaliculata*. It also differs between subspecies: it is 0–2 in *P. edulis crassipes* while 4 in *P. edulis edulis* and 5 in *P. modica caroli* but 4 in *P. modica modica*. It was said to be 3 in *P. nouveli holthuisi* (Williamson & Rochanaburanon, 1979) and 3 or 4 in *P. nouveli nouveli* (Barnich, 1996), but dos Santos, 1999 noted 3 or 4 for the first subspecies and 3–6 for the second one. With regard to what has been previously stated, specimens with more than four carapace denticles were considered to be *P. nouveli nouveli* in such a way that this species could have

been overestimated while *P. nouveli holthuisi* could have been underestimated (dos Santos, 1999). For this reason, when referring to carapace denticles it is important to take into account the geographical distribution (see Figure 4), the place where samples come from and larval size in each stage.

The length or location of pterygostomial spine and the ratio between rostrum length and frontal lobe have also been used by some authors in order to try to clarify larval identification, as they are features that remain invariable, or almost invariable, along the larval development. Also the presence or absence of a spine on the stylocerite of the antennule has been used to identify between adult species of *Processa* (Smaldon, 1993) as well as some undetermined *Processa* species. The setation of the endopod of maxillule in the first stage of *P. macrodactyla* is 2, 3, as in *P. modica modica* and *P. edulis crassipes* (not described in the text of Gurney, 1923 but drawn) and it changes for the successive stages to 1+2, 3, as in *P. nouveli holthuisi*. The exopodal seta of maxillule is always present in *P. macrodactyla* but it is only observed in the three first zoeal stages of *P. modica modica*, *P. edulis crassipes* and *P. nouveli holthuisi*. The 5-lobed endopod of maxilla only shows differences between species in the setation of the proximal lobe, bearing two setae in *P. nouveli holthuisi*, three setae in *P. macrodactyla* and 2–4 setae in *P. modica modica*. The remaining features of the appendages shown in *P. macrodactyla*, as the setation of the coxa and the basis of maxillipeds and pereopods, cannot be compared with those from the other species mentioned because no descriptions are available.

Known morphological differences between larval stages of different *Processa* are also based on the presence or absence of abdominal spines. All of the described species have a pair of dorso-lateral spines on somite V, which is a common characteristic in this genus. *Processa canaliculata* has another pair of dorso-lateral spines on the fourth abdominal segment which may be much reduced but is always present (Lebour, 1936). *Processa modica* is the only species compared presenting a small median dorsal spine on abdominal somite 3 and another one on somite 6, similar in length to those on somite 5, present from Stage III (Williamson & Rochanaburanon, 1979), which definitely characterizes this species. It is peculiar of *P. macrodactyla* also to show a median abdominal spine on somite 6 from Zoea VI.

Relative to the total zoeal number of the larval series nine stages are described for *P. modica carolii*. In previous descriptions seven zoeal stages were assigned to *P. modica modica* showing this as a distinguishing feature between *P. modica* subspecies since they are not always morphologically distinct (Williamson & Rochanaburanon, 1979). The zoeal stages are eight or nine for *P. edulis* and *P. canaliculata*, while nine for *P. nouveli*. In the present study, also nine zoeal stages were found for *P. macrodactyla*. As mentioned by Lebour (1936) the larvae of *P. canaliculata* and *P. edulis crassipes* from the inshore plankton moulted to the decapodit stage after ZVIII, whereas larvae from the offshore plankton moulted only after ZIX to the decapodit so as to improve their chances of reaching the coast again. Barnich (1996), points out that this could be the reason why ZIX stages of *Processa* can miss when taken from coastal plankton samples. According to Lebour, the post-larvae reared from ZVIII stages are smaller and less

developed than those from ZIX stages (Barnich, 1996). Also Gurney (1923) pointed out the same, as well as the fact that one stage may represent more than one moult. In this way, it can be observed from the results obtained for *P. macrodactyla*, an outstanding change in the setation between an early zoeal stage group (ZI to ZIV–V) and a later zoeal stage group (ZV–VI to ZIX). The main changes in the setation are referred to the endopod and exopod of the antennule, peduncle and endopod of the antenna, coxal endite of the maxillule, coxal and basal endites of the maxilla, coxa and endopod of the first maxilliped, endopod of the second maxilliped, coxa, endopod and exopod of the third maxilliped, coxa of the first pereopod, endopod and exopod of the second pereopod, basis of the third pereopod, pleopods and telson. These characters remain, with few exceptions, invariable from ZI to ZIV or ZV, to then change and maintain until the last zoeal stage. It has not been noticed in other species of the genus so it might not exist, or otherwise it might have been omitted owing to incomplete descriptions. Some characters of Zoea V are shared with previous stages, while others are found in more developed stages. This is in accordance with a combinatorial moulting situation, where morphological mechanisms are accelerated or retarded resulting in an instar exhibiting heterochrony in its anatomical features. Similarly, Gurney (1923) describing *P. nouveli holthuisi* pointed out that there is a considerable variation among the specimens of this ZV stage and there might be in some cases, intermediate moults during Stage V with the result that some larvae unite the characters of Stages ZIV and ZV, and others those of ZV and ZVI.

There are a few larval forms of *Processa* which some authors could not ascertain to a species level. Williamson (1967) described some larvae from the eastern Mediterranean. One of them is *Processa EM4* which, according to the number of carapace denticles and the location of pterygostomial spine, is tempting to ascribe to *P. edulis crassipes*. However, the geographical distribution rejects this possibility as Nouvel & Holthuis (1957) mentioned this subspecies to appear only in Atlantic waters (Figure 4). On the other hand, Barnich (1996) also referred to these *Processa EM4* when citing new larvae called *Processa* sp.1 collected along French Mediterranean coasts. These are found to be very similar to *Processa EM4* with the only obvious difference being the absence of carapace denticles in *Processa EM4* and the presence of 3–4 denticles in *Processa* sp.1. However, we consider this a relevant feature in a way that *Processa* sp.1 can be considered more alike, between known larval species, to *Processa edulis edulis*. Nevertheless, the description given is insufficient to certainly designate a known species larvae. Barnich (1996) also described *Processa* sp.2, with no matching descriptions between these and known *Processa* larvae. Even though the larvae of *P. robusta*, *P. acutirostris*, *P. elegantula* and *P. macrophthalma* are unknown up to now their adults occur in the same area where both *Processa* sp.1 and *Processa* sp.2 were sampled. Williamson (1967) also mentioned larvae he called *Processa EM5*, giving morphological features but being unable to find resemblances with other larval species. Later, dos Santos (1999) collected these larvae in the Portuguese coasts (North Atlantic). dos Santos (1999) considered the possibility of

ascribing this *Processa EM5* to *P. macrophthalma* as this species was already cited along Portuguese coasts by Neves (1973) and the adults are found to live in both areas where larvae were collected. Another partial description made by Williamson (1967) is *Processa EM6* and it was reviewed by dos Santos (1999). dos Santos (1999) mentioned *P. intermedia* as the only unknown larvae to occur in Portuguese coasts. But the adult stage of this species has not been found in the eastern Mediterranean (d'Udekem d'Acoz, 1999) where *Processa EM6* was first sampled. Otherwise, *P. elegantula* is distributed both along the Atlantic coasts and in the Mediterranean. Hence, according to Barnich (1996) *Processa EM6* could be ascribed as *P. elegantula* despite some morphological differences. Williamson (1967) ascribed the *Processa EM7* larvae observed in eastern Mediterranean to *P. canaliculata* after Bourdillon-Casanova (1960), observations supported by the high abundance of this species in the area. Still, no additional pair of spines on somite 4 is punctuated on *Processa EM7* and the given size of the last zoea differs greatly between the two species. Barnich (1996) corresponded *Processa EM7* with *P. nouveli nouveli*, with which it is more alike. Later, dos Santos (1999) found in Portuguese waters larvae similar to those of *Processa EM7*, and these were also referred to as *P. nouveli nouveli* (A. dos Santos, personal communication). Finally, dos Santos (1999) collected in the same area larvae of *Processa* named as *Processa EFSL11* which was not ascribed to any species with larval development known along Portuguese coasts or European waters. Nevertheless, *P. intermedia*, with unknown larval development, included in its distribution the south coasts of Portugal, being able to correspond the larvae of *Processa EFSL 11* to those of *P. intermedia*. Yet, the possibility that more unknown *Processa* species can be recorded is something to bear in mind (dos Santos, 1999).

The time of appearance of the pereopods in the larval development and the presence of exopods are also important taxonomic characters to identify shrimp larvae. In Table 3 the presence of pereopods and phase of development are listed (bud/functional) in each larval stage of those *Processa* species where they are described. With regard to this feature, *P. macrodactyla* and *P. modica modica* are the species with the slowest pereopodal development while the fastest are *P. canaliculata*, *P. edulis crassipes* and *P. nouveli holthuisi*. In *P. macrodactyla*, the first pereopod is functional only from Zoea III on, at the same time as the second one, while in the other species the first pereopod is functional from Zoea II. The third pereopod is only functional from Zoea V on in *P. macrodactyla* and *P. modica modica* while *P. canaliculata*, *P. edulis crassipes* and *P. nouveli holthuisi* already show a functional fourth pereopod. The full development of the pereopods in the studied processid species is achieved in Zoea VI. Taking this into account, we can easily distinguish the five early larval stages of *Processa* from the later stages and even differentiate between species of the genus. On the other hand, *P. modica modica* and *P. edulis crassipes* are the species with shorter larval series (usually seven and eight zoeal stages, respectively) and it is precisely these species that show all pereopods (as buds, mainly) from Zoea II on. In contrast, the full appearance of the pereopods (including buds) in the other species is only observed from Zoea V on. It is possible that the reduction of the number of zoeal stages in the

larval development involves a premature appearance of all pereopods at once. Gurney (1942) also pointed out that the abbreviation of the larval life tends to the suppression of the exopods on the pereopods. This feature is observed in *P. modica modica*, which is the unique species without exopods on the fourth pereopod.

It appears to be typical of the Caridea type of development that: (1) their moults are gradual, often associated with little or no change in size, morphology, and biomass; and (2) both the number of instars within a larval phase and the morphological characters of an instar vary intraspecifically (Anger, 2001). This is what makes it difficult to discover characters which are of real systematic importance in a way that each larval stage can be distinguished by a combination of characters shared by most instars (dos Santos & González-Gordillo, 2004). Furthermore, it has been observed how *Processa* species do not necessarily pass through every development stage. Some may be omitted while other stages are represented by more than one moult (Gurney, 1923). In this way, it has been found to be appropriate to give a table (Table 2) more than an identification key as it includes morphological characters that otherwise can be ignored while being useful for the correct identification of *Processa* larvae. When *P. macrodactyla* is being identified, the characters shown in Table 1 can be useful to determine its zoeal stage.

We wish to thank Dr Antonina dos Santos for constructive comments that improved the initial manuscript. This research was partially supported by post-doctoral fellowships (SFRH/BPD/1596/2000) from the Ministério da Ciência e da Tecnologia (FCT), Portugal, and by Research Program 'Ramón y Cajal' from the Ministerio de Educación y Ciencia, Spain.

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Submitted 19 May 2005. Accepted 28 September 2005.