

Studies on the larval development of northeastern Atlantic and Mediterranean Porcellanidae (Decapoda, Anomura). I – Redescription of the larval stages of *Porcellana platycheles* (Pennant, 1777) reared under laboratory conditions

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ABSTRACT: The complete larval development is described for *Porcellana platycheles* (Pennant) reared under laboratory conditions. The development consists of two zoeal stages and one megalopa. At 20 °C and 35 ‰ salinity, the megalopa appeared 17–18 days after hatching. Survival was 56 % from hatching to the megalopa stage. The morphological features of the zoeal and megalopa stages of *P. platycheles* are compared with those of other species of *Porcellana*, and a key of the known zoeal stages of the genus is given.

INTRODUCTION

The family Porcellanidae is represented in northeastern Atlantic waters and the Mediterranean Sea by four species belonging to two genera: *Pisidia longimana*, *Pisidia longicornis*, *Pisidia bluteli* and *Porcellana platycheles*. The distribution range of *P. platycheles*, a very common crab in Iberian waters, extends along the Atlantic coast from the Shetland Islands to Cape Blanco, and along all the coast of the Mediterranean Sea (Zariquiey, 1968). The species is ovigerous throughout the year in the Iberian Peninsula. It is found mainly on rocky intertidal substrata in the infralittoral zone between 1 to 3 m depths.

With regard to larval development, the existing descriptions of the larval stages of the genus *Porcellana* are still hardly conclusive. Most of the previous descriptions referring to *Porcellana* larvae are too insufficiently detailed to allow comparisons of the zoeae with those of the other species of porcellanids, and consequently many of these larvae have probably been erroneously attributed to *Porcellana*. The complete sequential larval development in laboratory culture is restricted to *P. sigsbeiana* (Gore, 1971); Sankolli (1967) and Brooks & Wilson (1881) have described only the first stage of *P. ornata* and *P. sayana*, respectively. The larval stages have been studied most intensively in *P. platycheles*, but

the illustrations thereto have been incomplete and the descriptions too brief. Couch (1843) reared larvae from eggs, but his confusing account does not allow a clear definition of this species. Bate (1868) figured, in less detail, a zoea that he identified as *P. platycheles*. Williamson (1915) mentioned larvae obtained from plankton in the North Sea and described and drew briefly several appendages. Webb (1921) gave a sketch of the general form and described the colouration and the structure of mouthparts. Lebour (1943) described the zoeal stages from first zoeae obtained directly by hatching and from zoeae collected from the plankton at Plymouth, but the descriptions of the appendages were not given. Le Roux (1961) reared larvae of *P. platycheles* from eggs in laboratory conditions for the determination of developmental time, but he did not mention the features of the mouthparts. Thus, the knowledge of the features of zoeal stages is incomplete and almost unknown for *P. platycheles*.

The purpose of this paper is to complete the description of the larval life history of *P. platycheles*, based on larvae reared from eggs in the laboratory, in order to facilitate the identification of the different stages from plankton samples and to distinguish them from others of the genus *Porcellana* as described by previous authors.

MATERIAL AND METHODS

Two ovigerous females were collected from the intertidal zone at Santa María del Mar (Cádiz) and El Portil (Huelva), southwestern Iberian Peninsula, on May 1993 and October 1994, and were maintained in seawater – filled aquarium until hatching. When hatching occurred, 100 larvae were distributed and then placed in twenty glass compartments, each with 40 ml of natural seawater (35 ‰). The remainder were transferred to 500-ml glass bowls, without complementary ventilation. The trays and mass culture dishes were kept at 20°C ± 1°C. Water was changed daily, and larvae were fed daily with freshly hatched nauplii of *Artemia*. Moulting and mortality in a culture were recorded every day. Dead larvae were fixed with 4 % Formalin, and preserved in 70 % ethanol. The appendages were dissected in seawater and mounted in lactophenol. These were drawn with an interference phase microscope and camera lucida. Descriptions were based on 10 zoea I larvae, 8 zoea II larvae and 8 megalopae. In zoeae, total length was measured from the tip of the rostral spine to the tips of the posterior spines; carapace length was measured from the anterior margin of the eye to the point of insertion of the posterior carapace spines, and carapace width was measured across the widest part of the carapace. The description of colouration is based on living or freshly fixed animals. The spent females and complete larval series have been deposited in the Museo Nacional de Ciencias Naturales, Madrid (Spain) (no. 20.04/402).

RESULTS

Rearing data

Under laboratory conditions, *Porcellana platycheles* hatches as a prezoa (Fig. 2B), lasting, at most, about 1.5 hours. Then it passes through two subsequent zoeal stages to megalopa. *P. platycheles* reaches the megalopal stage after 17-18 days of rearing, the first zoeal stage during 6-9 days and the second zoeal stage 11-20 days. Survival of first zoea

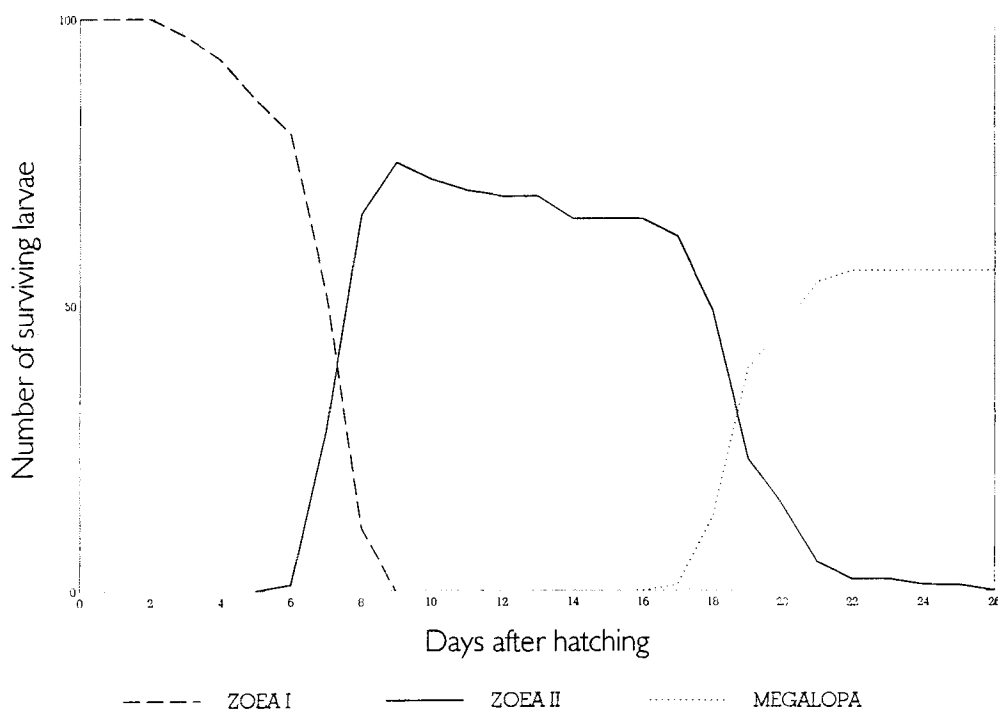


Fig. 1. Relationship between larval survival and moulting time of *Porcellana platycheles* reared at 20 °C and 35 ‰ S in the laboratory

was 79 %, while survival of second zoea was 76 %. Total survival percentage is 56 % from hatching to the megalopa stage. The developmental time of the larval stages is drawn in Figure 1. Measurements of the carapace, rostrum and posterior spines for the three larval stages are presented in Table 1.

Description of larval stages

Zoea I

Total length 8.22 ± 0.55 mm; range 7.08 - 9.08; N = 15.

Duration: 6–9 days.

Carapace (Fig. 2A, C) typical porcellanid zoea. One elongated rostral spine about 4.5 length of the carapace, curved upward, armed with encircling rows of tiny spinules at its tip. Two posterior spines about double the length of the carapace, both covered ventrally with a single row of minute spinules. Antero-dorsal surface of the carapace with three pairs of fine hairs. Eyes sessile at this stage.

Abdomen composed of five somites, with no pleopods ventrally. Fourth and fifth somites with stout posterolateral spines.

Table 1. Measurements (mm) of the carapace, rostrum and posterior spines in the larvae of *Porcellana platycheles*

	Carapace length	Carapace width	Rostrum length	Posterior spines
ZOEA I				
Range	0.83–1.16	0.58–0.75	4.00–5.75	2.00–2.50
Mean	1.04	0.67	4.98	2.23
Standard deviation	0.09	0.05	0.47	0.15
No. examined	21	18	15	19
ZOEA II				
Range	1.00–1.50	0.66–0.83	4.33–6.58	1.50–2.91
Mean	1.22	0.76	5.53	2.40
Standard deviation	0.18	0.05	0.60	0.30
No. examined	21	14	17	18
MEGALOPA				
Range	1.15–1.34	0.91–1.06		
Mean	1.26	0.97		
Standard deviation	0.05	0.04		
No. examined	14	14		

Telson (Fig. 3A) broadly triangular, bearing a strong spine on each posterolateral border which are accompanied by a small sparsely plumose seta. Five pairs of long and plumose processes and one pair of small setae in central prominence. Two very slender setules found on dorsal surface of telson. An anal spine present on ventral surface.

Antennule (Fig. 4A) unsegmented bearing 3 aesthetascs, similar in length, and 3 setae on distal portion.

Antenna (Fig. 4D) biramous. Basal segment with 1 stout setae. Endopodite bearing a hair-like spine on outer margin. Exopod exceeding that of endopodite, with 3 spines.

Maxillule (Fig. 5D). Coxal endite with 10 sparse setae. Basal endite with 6 spinous processes and 5 sparse setae. Endopodite unsegmented, with 2 terminal, 1 subterminal plumose seta and several fine hairs on outer margins.

Maxilla (Fig. 5A). Coxal endite bilobed with 8 and 7 setae on proximal and distal lobes, respectively. Basal endite bilobed with 9 and 10 plumodenticulate setae on distal and proximal lobes, respectively. Unsegmented endopodite bearing 4 terminal, 2 subterminal and 3 long setae below latter. Scaphognathite with 6 setulate plumose setae fringing outer margin plus 1 long, apical plumose seta. Fine hairs occurring along margins of the coxal and basal lobes' joint, as illustrated.

Maxilliped I (Fig. 6A). Coxopodite armed with 2 ventral setae. Basipodite setae 1 + 2 + 2 + 3 on inner margin progressing distally. Setation on first to fourth segment of endopodite is 3, 4, 5, 11, plus one seta dorsally on distal segment near its base, and fine hairs on the same side of segments one, two and three. Exopodite 2-segmented with 4 natatory setae.

Maxilliped II (Fig. 6D). Coxopodite naked. Basipodite with 1 + 2 ventral setae. Endopodite 4-segmented with 2, 3, 3, 9 setae progressing distally plus one seta dorsally

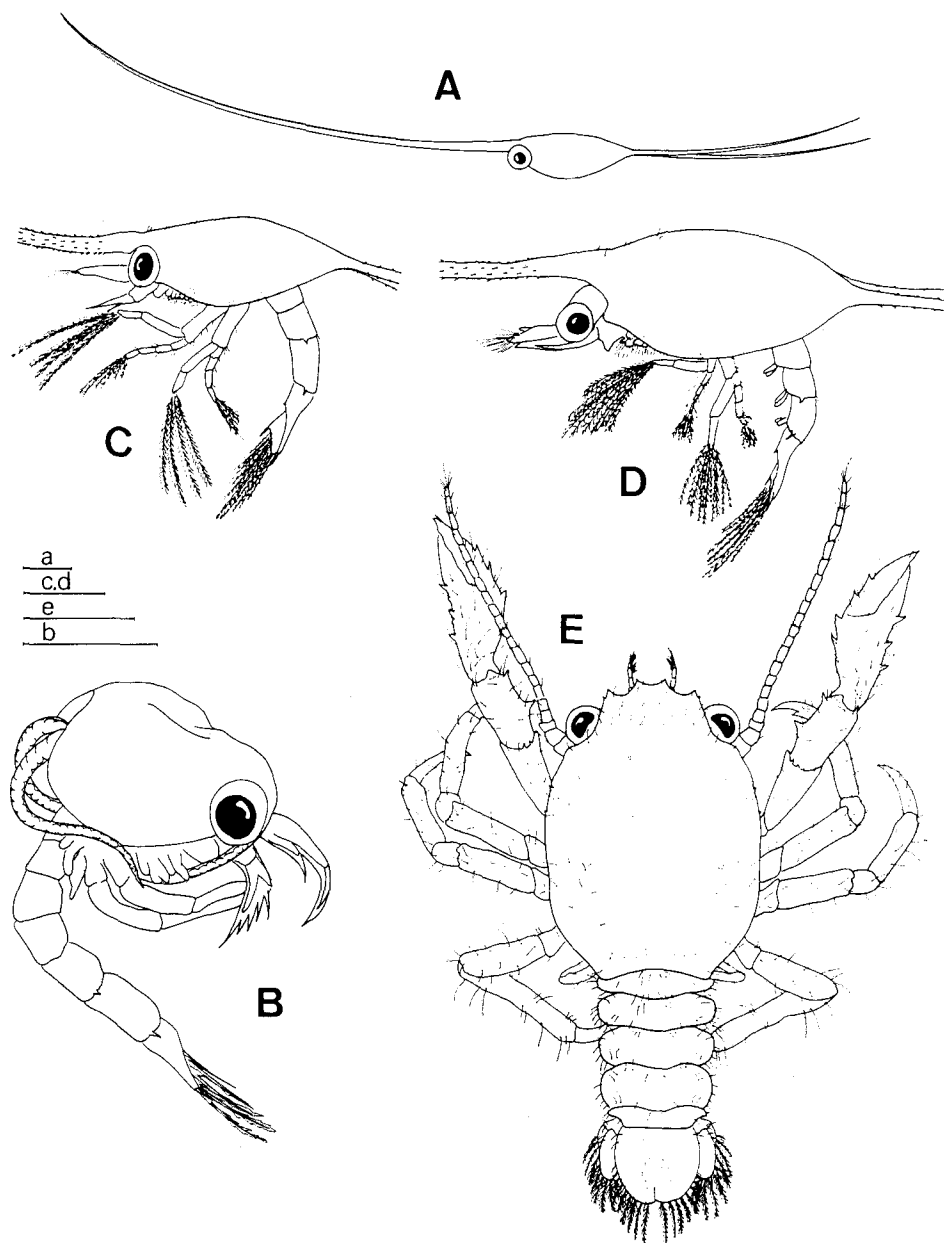


Fig. 2. *Porcellana platycheles*. A: Zoea I, carapace in lateral dorsal view; B: Prezoea; C: Zoea I; D: Zoea II; E: Megalopa. Scale bar: 500 μ m

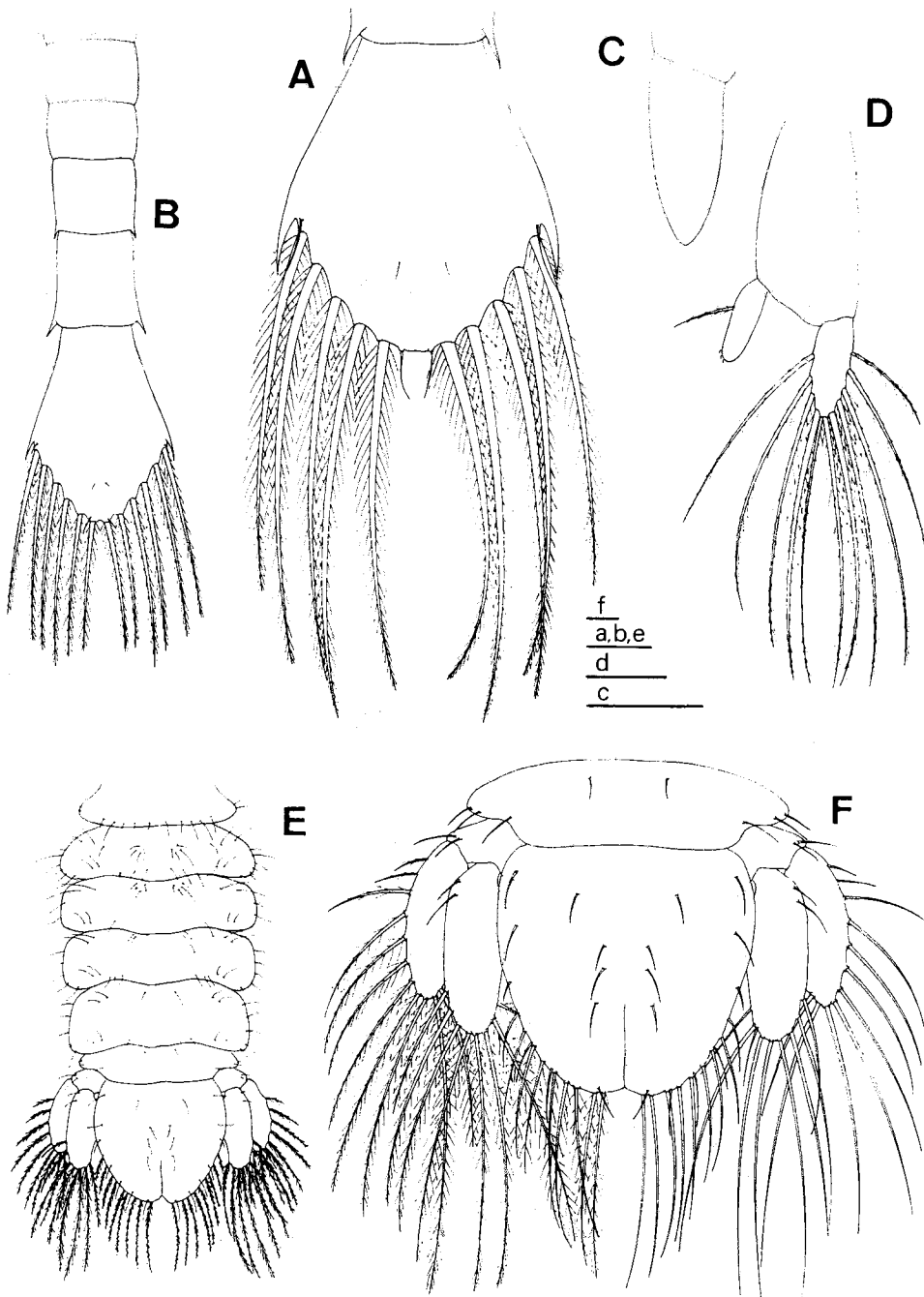


Fig. 3. *Porcellana platycheles*. A: Zoea I, telson; B: Zoea II, abdomen; C: Zoea II, pleopod; D: Megalopa, pleopod; E: Megalopa, abdomen; F: Megalopa, telson. Scale bar: 100 μ m (A, C, D); 200 μ m (B, E, F)

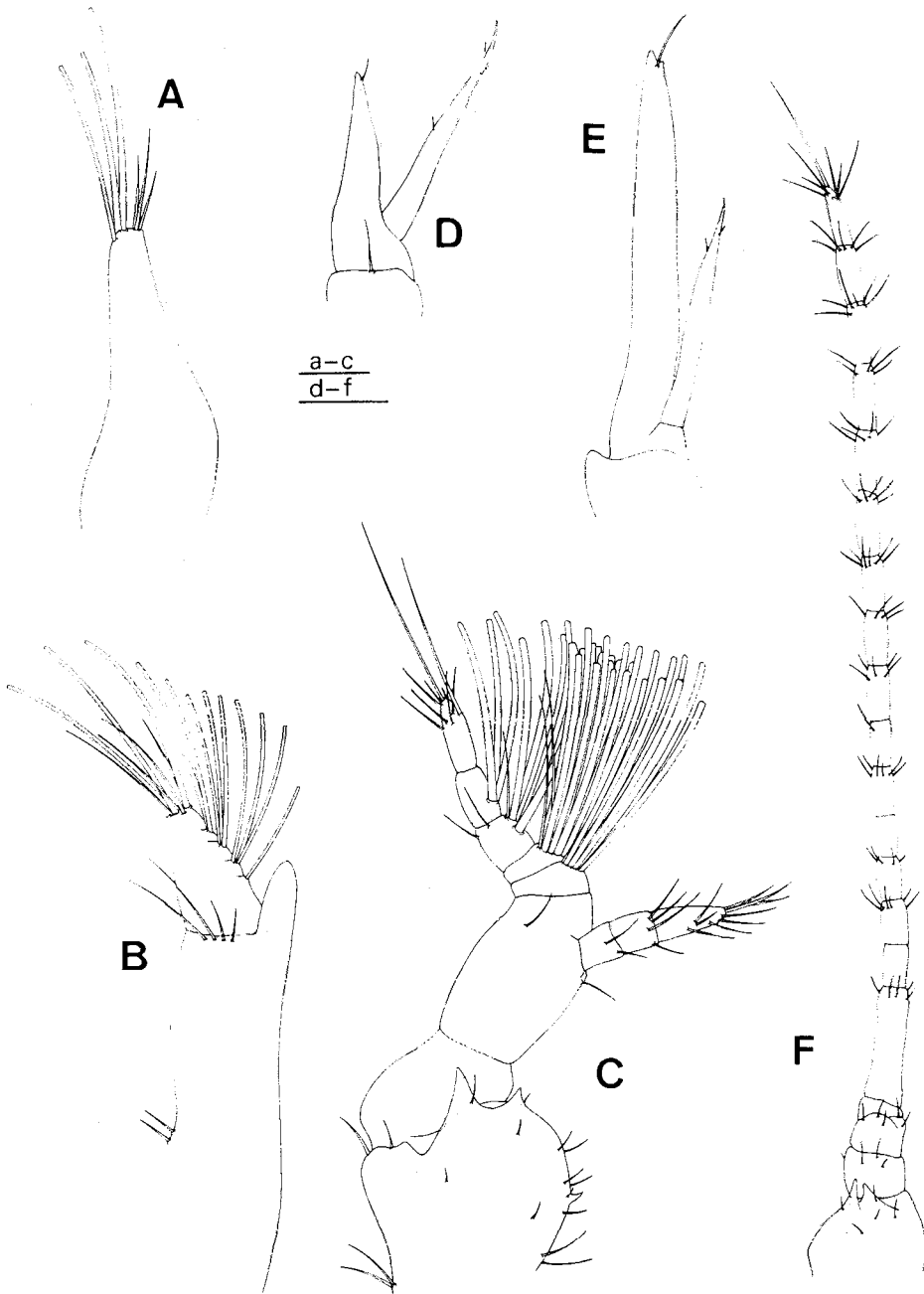


Fig. 4. *Porcellana platycheles*. A: Zoea I, antennule; B: Zoea II, antennule; C: Megalopa, antennule; D: Zoea I, antenna; E: Zoea II, antenna; F: Megalopa, antenna. Scale bar: 100 μ m

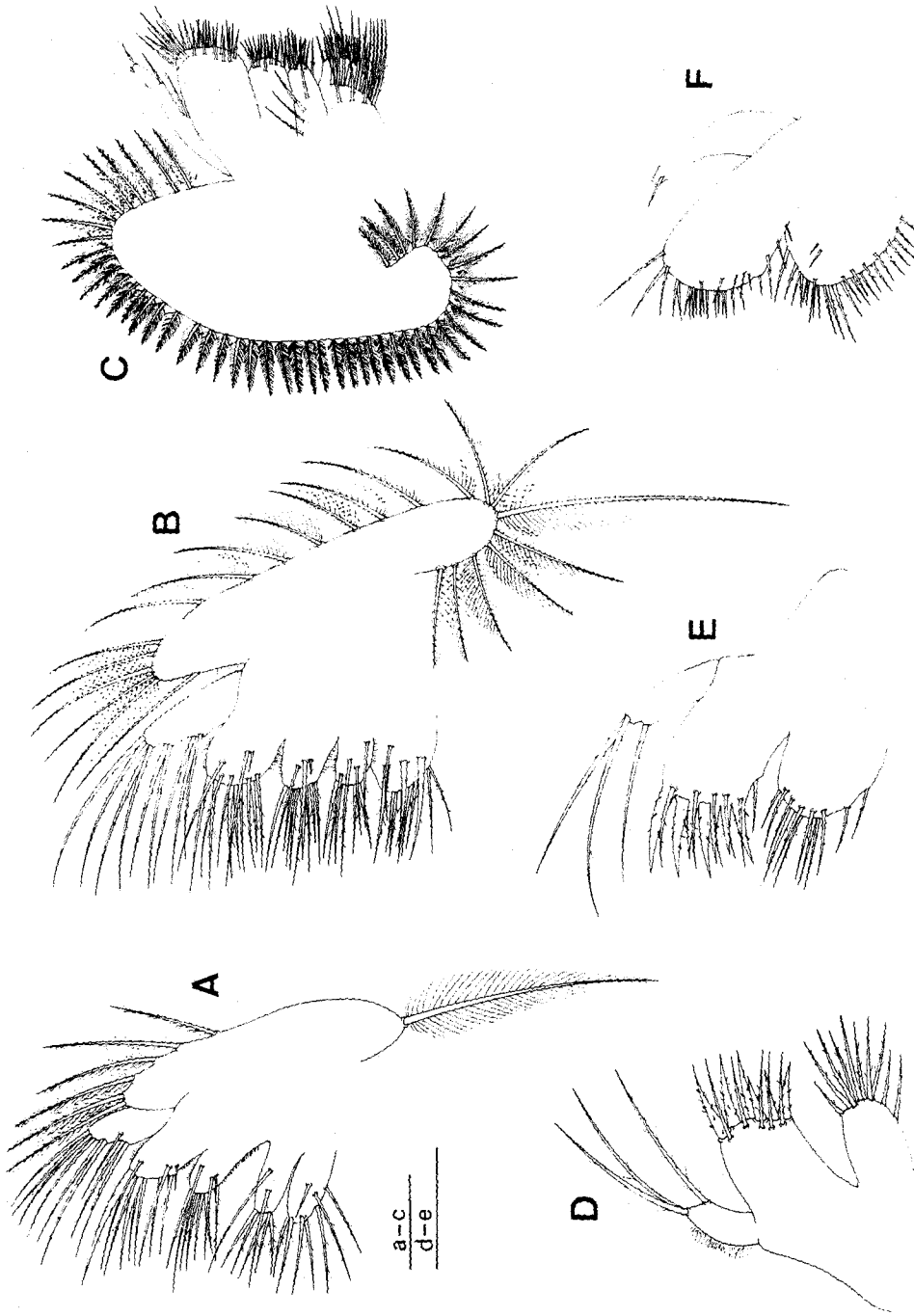


Fig. 5. *Porcellana platycheles*. A: Zoea I, maxilla; B: Zoea II, maxilla; C: Megalopa, maxilla; D: Zoea I, maxillule; E: Zoea II, maxillule; F: Megalopa, maxillule. Scale bar: 100 μ m

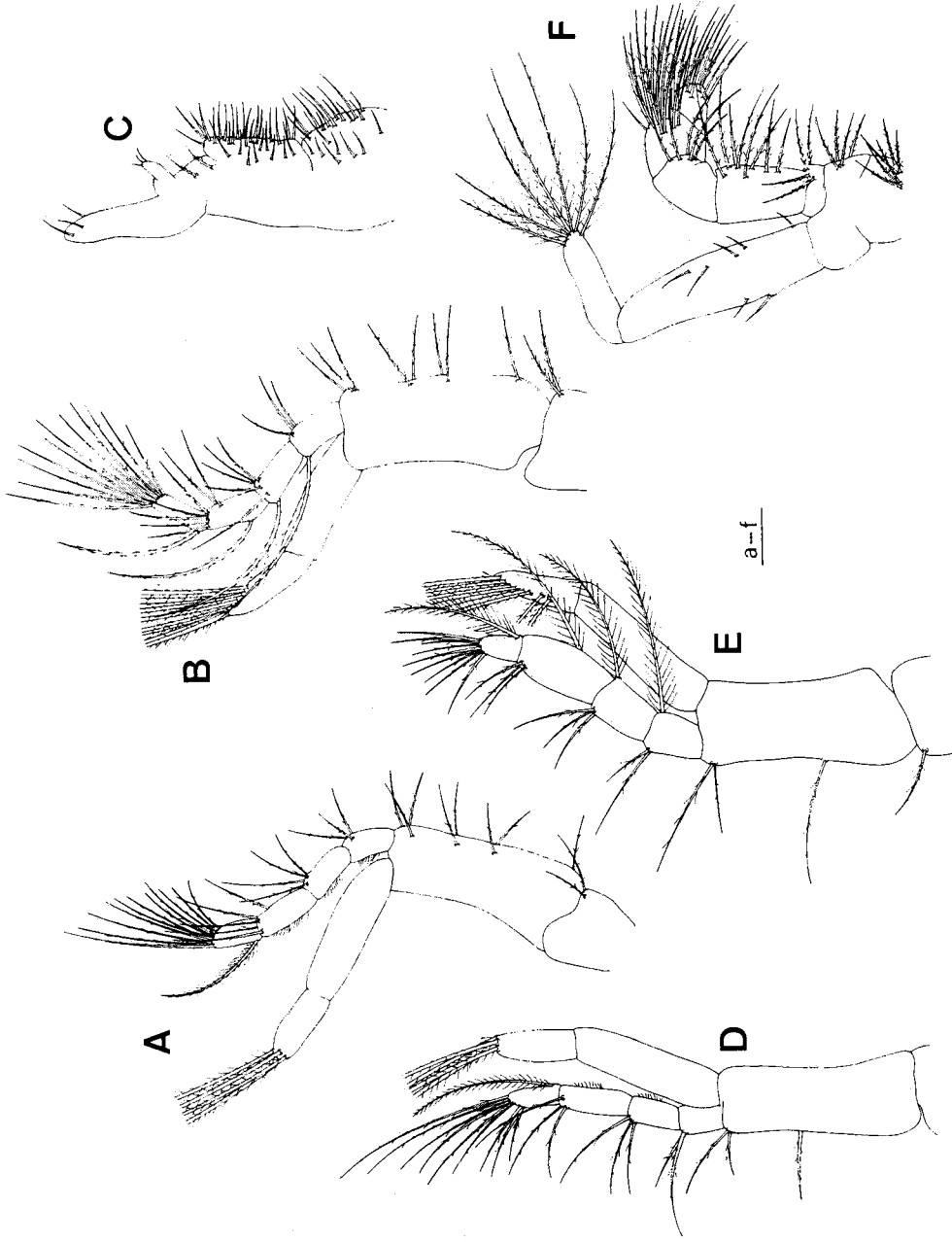


Fig. 6. *Porcellana platycheles*. A: Zoea I, first maxilliped; B: Zoea II, first maxilliped; C: Megalopa, first maxilliped; D: Zoea I, second maxilliped; E: Zoea II, second maxilliped; F: Megalopa, second maxilliped. Scale bar: 100 μ m

on distal segment near its base and long, fine hairs on same side of segments two and three. Exopodite as in maxilliped I.

Maxilliped III (Fig. 7A) as rudimentary bud, naked.

Pereiopods undeveloped buds without segmentation. Pleopods absent in this stage.

Zoea II

Total length 9.26 ± 0.85 mm; range 8.41–11.00; N = 14.

Duration: 11–20 days.

Carapace (Fig. 2D) similar in shape to zoea I but more inflated with rostral spine almost straight. Armature of rostral and posterior spines similar to zoea I. Eyes now mobile.

Abdomen (Fig. 3B) five-segmented with pleopod buds (Fig. 3C) present on all somites except first. Posterolateral borders of somites fourth and fifth bearing stout spines.

Telson with similar setation as stage I but with additional seta on central prominence of telson plate. Two small setae on dorsal surface.

Antennule (Fig. 4B) biramous. Protopodite with 2 small setae near basal swelling and 4 simple setae distally. Endopodite bud emerging from protopod, naked. Exopodite with 1 + 3 + 3 + 2 + 3, aesthetascs progressing distally, plus 4 apical plumose setae.

Antenna (Fig. 4E) with endopodite longer than exopodite and bearing 1 subterminal seta. Exopodite with 2 slender spinules.

Maxillule (Fig. 5E). Coxal endite with 12 sparsely plumose setae. Basal endite with 6 submarginal setae and 7 massive processes. Endopodite unsegmented with 1 subapical and 2 apical long setae in the distal segment.

Maxilla (Fig. 5B). Coxal endite with 19 sparsely plumose setae; 11 on proximal lobe and 8 on distal lobe. Basal endite with 11 and 13 setae on proximal and distal lobes, respectively. Endopodite as in Stage I. Scaphognathite fringed with 21 plumose setae around margin, plus 1 distal longer seta.

Maxilliped I (Fig. 6B). Coxopodite armed with 2 ventral setae. Basipodite setae unchanged. Endopodite with 3, 5, 7, on inner margin of the first, second and third segment, respectively, 11 terminal setae in the distal segment and 1 long seta on outer margin of each segment. Fine dorsal setules absent. Exopodite 2-segmented with 12 natatory setae.

Maxilliped II (Fig. 6E). Coxopodite with 1 ventral seta. Basipodite bearing 1 + 2 setae on inner margin as stage I. Endopodite setation unchanged, but with additional long dorsal setae in the segment I, II and III. Fine dorsal setules absent. Exopodite 2-segmented with 10 terminal and 2 subterminal natatory setae.

Maxilliped III (Fig. 7B) show an exopodite two-segmented with 4 apical plumose setae on distal segment.

Pereiopods developing as stage processes with evidence of chelation on first pair. Pleopods as small buds on segment 2 to 5.

Megalopa

Carapace length 1.26 ± 0.05 mm; range 1.15–1.34; N = 14.

Carapace (Fig. 2E) crablike, longer than wide, with 2 small lateral spines and with few scattered hairs. Frontal region produced, projecting just beyond eyes, beneath which antennules are visible, with small setae dorsally and armed with four strong teeth, as

shown. Outer orbital angle with several hairs, in which might appear 1 small tooth. Eyes stalked.

A b d o m e n (Fig. 3E) six-segmented with setae placed as shown. Segments II-V bearing biramous pleopods (Fig. 3D) ventrally.

T e l s o n flat plate (Fig. 3F), without spines but with 9 pairs of long setae plus 5 pairs of short setae interspersed on its posterior margin, and 6 pairs of small setae on dorsal surface. Uropods biramous, well developed. Protopodite with 2 setae on outer margin. Endopodite with 2 proximal short setae plus 8 distal long setae. Exopodite bearing 13 marginal setae.

A n t e n n u l e (Fig. 4C). Peduncle 3-segmented. Basal segment inflated with 2 teeth on anterior surface and with many setae, as drawn. Second segment bare. Third segment bearing 2 medial setae. Lower flagellum 3-segmented with 2, 4, 9 setae progressing distally. Upper flagellum 5-segmented with setal formula 8a, 16a + 2s, 5a + 3s, 3a, 9s, (a = aesthetasc; s = seta) respectively, placed on rows as shown, and 2 denticulate processes on the proximal segment.

A n t e n n a (Fig. 4F). Peduncle 3-segmented with 5, 4, 5, setae respectively. Flagellum (= endopod) with 17 segments bearing 1-6 setae around distal margin of each segment, placed as shown, except for first, third and sixth segments. Terminal segment with 7 apical setae.

M a x i l l u l e (Fig. 5F). Coxal endite with 25 marginal setae and 2 submarginal small setae. Basal endite bearing 26 setae and spines. Endopodite reduced to single lobe with 1 slender subterminal seta.

M a x i l l a (Fig. 5C). Endites densely covered with setae and spines. Coxal endite with 4 + 12 + 10 long setae disposed in three rows on the proximal lobe, progressing distally, and 4 basal setae and 9 marginal setae on the distal lobe. Basal endite bearing 15 setae on the proximal lobe and with 28 setae on the distal lobe. Endopodite unsegmented bearing 3 sparsely setose setae and 2 small setae hooked on tip. Scaphognathite, about 50 soft plumose setae around outer margin.

M a x i l l i p e d I (Fig. 6C). Coxal endite with 8 medial setae and 12 marginal long setae. Basal endite with 28 setae placed uniformly. Endopodite and exopodite unsegmented, bearing 2 medial plus 3 apical setae and 3 subterminal setae, respectively.

M a x i l l i p e d II (Fig. 6F). Coxopodite bearing 6 setae on ventral margin. Basipodite with 4 ventral setae. Endopodite with 5 distinct segments bearing 4, 8, 5, 30, 14, long setae, placed as shown. Exopodite 2-segmented with 5 setae on inner margin and 2 setae on outer margin, in the proximal segment, and 7 plumose long setae in the distal segment which is constricted in the medial region.

M a x i l l i p e d III (Fig. 7C). Endopodite 5-segmented, those of segments ischium and merus with medial edges developed into distinct lobelike projection on inner margin and with stout teeth. All segments profusely setose. Short exopodite 5-segmented, extending to half of second endopodal segment, with 1, 2, 1, 0, 2, setae on segments, progressing distally.

Cheliped well developed (Fig. 7E), covered with numerous setae. Merus with 2 apical teeth. Carpus with 2 sharp teeth on inner margin and 1 apical tooth. Propodus with 3 teeth on outer margin and 2 teeth on inner margin. Dactylus with 2 marginal teeth. Walking legs densely setose. Fifth pereopod chelate (Fig. 7D), bearing numerous setae. Propodus with 4 serrated scythelike setae plus other setae. Dactylus with a long terminal seta plus other setae.

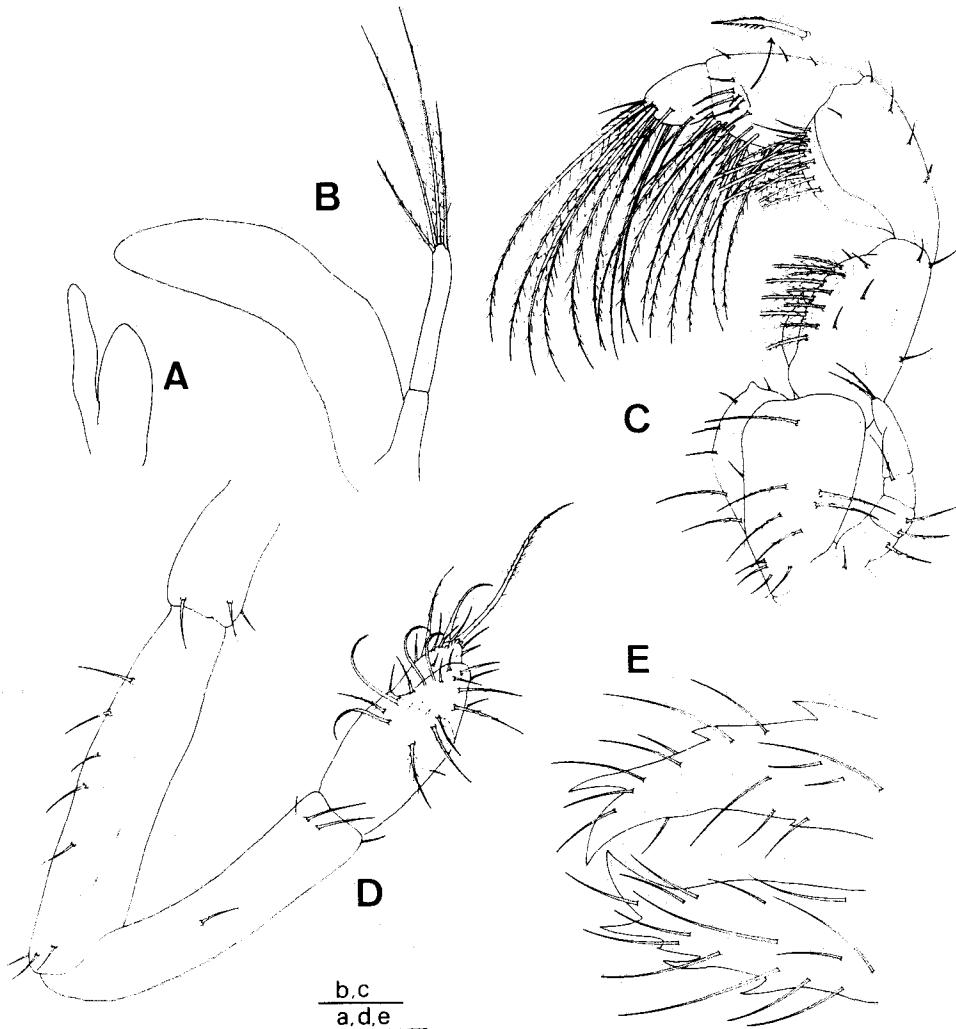


Fig. 7. *Porcellana platycheles*. A: Zoea I, third maxilliped; B: Zoea II, third maxilliped; C: Megalopa, third maxilliped; D: Megalopa, fifth pereiopod; E: Megalopa, detail of first pereiopod. Scale bar: 100 μ m

DISCUSSION

The larvae of Porcellanidae are easily recognizable in the plankton as their rostrum extends to form a very long spine, and the carapace is produced backwards into two spines no smaller in size.

The first description of a larval stage in the Porcellanidae family was made by Thompson (1835) and ascribed to the genus *Porcellana*. Since then, numerous reports have described larval developments of Porcellanidae, although it is remarkable that no com-

plete account of its transformation has ever been given clearly, except for *Porcellana sigsbeiana* (Gore, 1971). Lebour (1943) made an important contribution to the knowledge of the larval morphology of Porcellanidae with the elaboration of a first classification of the known genera. She distinguished two distinct groups according to the shape of the telson: *Petrolisthes*-group and *Porcellana*-group. The former group includes the species which show the fifth long seta of telson on the central prominence during the first stage, a central tooth being added to this prominence at the second stage; this group is represented by the genera *Petrolisthes*, *Pachycheles*, *Megalobrachium* and *Neopisoma*. Larvae belonging to the *Porcellana*-group are characterized by showing at the first stage the fifth long seta of telson situated outside the central prominence and a sixth seta on the prominence in stage II. This group includes the genera *Porcellana*, *Pisidia*, *Polyonyx* and *Euceramus*.

In the northeastern Atlantic Ocean and Mediterranean Sea this family is represented by two genera, *Pisidia* and *Porcellana*; descriptions of the larvae of these are available for *Pisidia longicornis* and *Porcellana platycheles* only. Zoeae of both species differ from each other in that in *Pisidia longicornis* the two ventral denticles located close to the base of the posterior spines of the carapace are larger than in *Porcellana platycheles*. Another distinguishing feature is that the third long seta of the telson bears at its distal end hook-like curved denticles, which do not appear in *P. platycheles*. As to the megalopa stage, whereas in *P. platycheles* there are two teeth in the central lobe, in *P. longicornis*, at least four are apparent.

In all the *Porcellana* species whose larval stages are known, the most characteristic difference of the zoeal stages is the location of lateral spines in abdominal somites. These occur in somites II, III, IV and V of *P. sigsbeiana*, in IV and V of *P. platycheles*, and in V of *P. ornata* (Brooks & Wilson [1881] do not mention this feature for *P. sayana*). Another significant difference is the setal formulae of the basipodite of first maxilliped. While in *P. platycheles* and *P. sigsbeiana* 1 + 2 + 2 + 3 setae appear on inner margin, *P. ornata* shows 2 + 2 + 3 + 3 setae, and *P. sayana* 2 + 1 + 1 + 3 setae. Additional features are summarized in Table 2.

A number of features are common to all *Porcellana* species. At the first stage the exopodite of the antennula shows 3 aesthetascs, the endopodite bears 1 hair-like spine, the scaphognathite of the maxilla has 5–7 soft plumose setae and a long posterior plumose process, and the coxopodite of the second maxilliped is devoid of setae. Furthermore, the telson bears 5 pairs of plumose setae plus 2 pairs of fine hairs. These features confirm that *Porcellana* belongs to the *Porcellana*-group, as proposed by Lebour (1943). Throughout the development of *Porcellana* the setal formula of the basipodite of the second maxilliped remains unchanged. Nevertheless, in the present study the females collected in El Portil (Huelva) had a third seta at their distal end, a feature that may reflect intraspecific variations between populations of Huelva and Cádiz.

Table 2. Some morphologically different features in the zoeal larvae of *Porcellana platycheles*, *P. sigsbeiana*, *P. ornata* and *P. sayana*

	<i>P. platycheles</i> (present study)	<i>P. sigsbeiana</i> (Gore, 1971)	<i>P. ornata</i> (Sankolli, 1967)	<i>P. sayana</i> (Brooks & Wilson, 1881)
ZOEA I				
Lateral spines on abdominal somites	0,0,0,2,2	0,2,2,2,2	0,0,0,0,2	no data
Distal hooks in 3rd telson long seta	no	no	present	no data
Exopodite antennule *	3a + 3s	3a + 3s	3a + 3s	3a + 4s
Exopodite antenna	3	1	6 - 7	0
Endopodite maxillule	1 + 2	(1 - 2) + 2	1 + 3	0 + (2-3)
Endopodite maxilla	3 + 2 + 4	3 + 2 + 4	3 + 2 + 4	1 + 1 + 2
First maxilliped	2	2	1	1
coxopodite	1 + 2 + 2 + 3	1 + 2 + 2 + 3	2 + 2 + 3 + 3	2 + 1 + 1 + 3
basipodite	3,4,(2 + 3),(11 + 1)	3,3,(1 + 2),(7 + 1)	3,2,(3 + 2),(7 - 8 + 1)	3,3,,(1 + 2),(7 + 1)
endopodite	2,3,3,(9 + 1)	3,3,3,(7 + 1)	2,2,(1 + 2),(5 + 1)	2,2,2,(5 + 1)
Endopodite second maxilliped				
ZOEA II				
Antenna exopodite	2	1	no data	no data
Scaphognathite maxilla	21 + 1	22 - 24 + 1	no data	no data
Endopodite first maxilliped	(3 + 1),(5 + 1),(7 + 1),(11 + 1)	(3 + 1),(3 + 1),(3 + 1),(9 + 1)	no data	no data
Endopodite second maxilliped	(2 + 1),(3 + 1),(3 + 1),(9 + 1)	(3 + 1),(3 + 1),(3 + 1),(9 + 1)	no data	no data
Exopodite third maxilliped	4	6	no data	no data

* a: aesthetascs; s: spines

A key is provided distinguishing the different species of *Porcellana* of which the larval development is known.

- 1a. Endopodite, four segments of first maxilliped with 11 terminal setae and the same of the second maxilliped with 9 terminal setae. . . . *Porcellana platycheles*.
- b. These characters not combined. 2
- 2a. Antennule, exopodite with 3 aesthetascs plus 3 simple setae; maxilla endopodite with 3 + 2 + 4 setae; scaphognathite with at least 6 marginal plumose setae plus 1 long apical plumose seta. 3
- b. Antennule, exopodite with 3 aesthetascs plus 4 simple setae; maxilla endopodite with 1 + 1 + 2 setae; scaphognathite with 5 marginal plumose setae plus 1 long apical plumose seta. *Porcellana sayana*.
- 3a. First maxilliped coxopodite armed with 2 setae and the basipodite with 1 + 2 + 2 + 3 progressing distally. *Porcellana sigsbeiana*.
- b. These characters not combined. *Porcellana ornata*.

With regard to megalopa morphology, only the description of *P. sigsbeiana* is available. Its larvae have 3 strong teeth in the rostrum, whereas those of *P. platycheles* show 4. However, the rare descriptions of *Porcellana* megalopae do not afford sufficient morphological features to be able to define the interspecific differences.

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