The secret life of deep-sea shrimps: ecology and evolution clues from the larval description of *Systellaspis debilis* (Caridea: Oplophoridae)

Cátia Bartilotti [Corresp., Equal first author, 1] , **Antonina Dos Santos** [Equal first author, 1]

[1] IPMA, Lisboa, Portugal

Corresponding Author: Cátia Bartilotti
Email address: cbartilotti@ipma.pt

Currently there are 21 shrimp species in the northeastern Atlantic and Mediterranean Sea which are considered to belong to the superfamily Oplophoroidea, but the larval development is unknown for most of them. The complete larval development of *Systellaspis debilis* (A. Milne-Edwards, 1881), here described and illustrated, is the first one to have been successfully reared in the laboratory, consisting of four zoeal and one decapodid stages. The zoeae were found to be fully lecithotrophic, which together with the females' lower fecundity, are probably evolutionary consequences of the species mesopelagic habitat.

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5 Cátia Bartilotti & Antonina dos Santos

7 IPMA, Av. Dr. Alfredo Magalhães Ramalho, 6, 1495-165, Algés, Portugal

9 Corresponding Author:

10 Cátia Bartilotti

11 IPMA, Av. Dr. Alfredo Magalhães Ramalho, 6, 1495-165, Algés, Lisboa, Portugal

12 Email address: cbartilotti@ipma.pt

14 ## Abstract

15 Currently there are 21 shrimp species in the northeastern Atlantic and Mediterranean Sea which
16 are considered to belong to the superfamily Oplophoroidea, but the larval development is
17 unknown for most of them. The complete larval development of *Systellaspis debilis* (A. Milne-
18 Edwards, 1881), here described and illustrated, is the first one to have been successfully reared in
19 the laboratory, consisting of four zoeal and one decapodid stages. The zoeae were found to be
20 fully lecithotrophic, which together with the females' lower fecundity, are probably evolutionary
21 consequences of the species mesopelagic habitat.

23 ## Introduction

24 *Systellaspis debilis* is a mesopelagic shrimp belonging to the family Oplophoridae, occurring in
25 the Atlantic and Indian Oceans (*e.g. Lunina, Kulagin & Vereshchaka, 2018*). Even though a lot is
26 known about the mesopelagic community and its function in marine ecosystems, much remains
27 unknown, especially for the crustacean species. However, oplophorid shrimps and their larvae
28 gained attention recently with the application of molecular techniques to the phylogenetic
29 systematic studies of Caridea. Wong *et al*. (*2015*) provided the molecular data to support the
30 resurrection of the family Acanthephyridae by Chan *et al*. (*2010*), retrieving two major clades
31 within the Oplophoroidea, the Oplophoridae and the Acanthephyridae. Recently, *Lunina,*

32   *Kulagin & Vereshchaka* (*2018*) presented the most comprehensive phylogenetic analyses for this
33   group to date, using morphological and molecular data, showing four robustly supported species
34   groups within the genus *Systellaspis*.

35   Seventy years earlier, Gurney & Lebour (*1941*) suggested oplophorid species two groups
36   according to the size of the eggs and the number of zoeal stages in the life cycle: the first group
37   including the genera *Oplophorus*, *Systellapis*, *Ephyrina* and *Hymenodora* having large lipid-
38   filled eggs and five or fewer zoeal stages, and the second group, with the genera *Acanthephyra*,
39   *Meningodora* and *Notostomus* having small eggs and nine or more planktotrophic stages.
40   Previously Kemp (*1907*) noticed that *S. debilis* had much larger eggs and their newly hatched
41   larvae were more developed than those of *Acantephyra purpurea*. The egg size is an important
42   aspect of the life history of marine organisms, with large eggs generally reflecting an increased
43   maternal investment (e.g. *Moran & McAlister, 2009*).

44   Of the 16 valid species of Oplophoridae Dana, 1852, only two larval sequences collected
45   from plankton have been described: five zoeal stages and one decapodid for *Oplophorus*
46   *spinosus*, and, four zoeal stages and one decapodid for *Systellaspis debilis*, both by Gurney &
47   Lebour (*1941*). *S. debilis* first zoeal stage is described as having a small rostrum, eyes large and
48   sessile, all pereopods and pleopods present as buds, a broad telson with a small median indent
49   with 7+7 spines fringed with spinules, and the uropods visible under integument (*Gurney &*
50   *Lebour, 1941*). The second stage is presented as having eyes stalked, the peduncle of the
51   antennule 3-segmented, the telson with 8+8 spines and free uropods. Regarding the third larval
52   stage, Gurney & Lebour (*1941*) described it as having the rostrum shorter than the antennal
53   scaphocerite with ten small dorsal teeth, the flagellum of the antennule long, the first and second
54   pereopods chelate, and the uropods reaching the convex distal margin of a parallel-sided telson
55   (*Gurney & Lebour, 1941*). No intermediate stage was described between the second and the
56   third zoea, but it was registered that the second zoea corresponds to a normal third zoeal stage of
57   a caridean larvae (*Gurney & Lebour, 1941*). Finally, some figures of a possible fourth zoeal stage
58   and the description of the "Post-larval 1", which corresponds to nowadays decapodid stage, with
59   the thorax still full of yolk, are presented (*Gurney & Lebour, 1941*).
60   Gathering information on the biological traits for mesopelagic species is difficult, since
61   their capture and live maintenance under laboratory conditions are problematic. However, larval
62   development under laboratory conditions for morphological purposes can be a useful way to
63   acquire knowledge on feeding traits and development patterns. Throughout the adult phase of the
64   life-cycle, during the oogenesis the energy for partially or entirely food-independent larval
65   development is stored as egg yolk, establishing the degree of lecithotrophy or planktotrophy (*e.g.*
66   *Anger, 2001*). Therefore, full lecithotrophy and planktotrophy are extremes in a continuum: full
67   lecithotrophy corresponds to high yolk stores that allow no feeding during the development of
68   the larvae, and planktotrophy corresponds to larvae that need to feed during their development
69   (*e.g. Anger, 2001*).

70   The present work aims to describe the complete larval development of *Systellaspis*
71   *debilis* from laboratory reared material, comparing it with the previous description available for
72   the species, and, presenting information on the development pattern of the larvae. Also, we
73   discuss the implications of the lecithotrophy and planktotrophy of the larvae on the ecology and
74   evolution of the oplophorid shrimps.
75

76   **Materials & Methods**

77   **Specimen collection and larval culture**
78   The ovigerous females of *Systellaspis debilis* were collected in two different research surveys
79   carried out by Instituto Português do Mar e a Atmosfera, I.P. (IPMA, former IPIMAR) off the
80   southwest and southern coasts of Portugal, in August 2010 and June 2011 onboard of RV
81   Noruega, as a by-catch of the plankton sampling (Bongo net, with 90 cm of diameter aperture,
82   and 500 μm of mesh size) and the crustacean bottom trawls (field permit approval by IPMA,
83   Oceanographic Survey MedEx- 02060810, and Nephrops Survey Offshore Portugal- 02030611,
84   respectively). A total of thirteen ovigerous females were obtained in both years. All females were
85   captured dead, each carrying between a minimum of two and a maximum of twelve eggs (Table
86   1) that were immediately and carefully removed from the pleopods and transferred to 200 ml
87   glass beakers with aerated autoclaved seawater. Following Company & Sardà (*1997*), three
88   stages of egg development were defined: the early stage (1), with intense colour and no other
89   pigmentation visible; the middle stage (2), an egg with a more pale colour and with an embryo
90   having a slight eye pigmentation; and the late stage (3), an egg almost without colour and with an
91   embryo with the eye pigmentation well visible and developed. In stages 2 and 3, the heartbeat
92   was checked in order to know if the embryo was alive. Once at the laboratory, the elliptical eggs
93   were measured on the major and the minor axes, corresponding respectively to its length and
94   width, under a binocular microscope with a micrometer lens. Once at the laboratory, the elliptical
95   eggs were measured on the major and the minor axes, corresponding respectively to its length
96   and width, under a binocular microscope with a micrometer lens. The eggs were kept in
97   autoclaved seawater with a salinity of 35± 1, a temperature of 18± 1 ºC, a photoperiod of 12 h
98   light: 12 h dark, and weak aeration. The eggs were checked daily until hatching. Once hatched,
99   the larvae were separated with the aid of a glass pipette and transferred to a 30 ml glass beaker,
100   to be individually reared with constant weak aeration. During rearing, the larvae were kept in
101   exactly the same conditions. The water was changed daily, and the larvae checked for the
102   evidence of molting (presence of exuviae in the bottom of the culture recipient). In experiments
103   carried out in 2010, a high hatching efficiency *Artemia* sp. (250000 nauplii.g^{-1} of product)
104   prepared following Sorgeloos, Dhert & Candreva (*2001*), were provided daily at a density of 10
105   nauplii.ml^{-1}. No decrease in the density of *Artemia* was verified, leading us to suppose that these
106   were nonfeeding larvae. Since it was observed that the larval cycle was completed, the
107   experience was repeated in 2011 without food. In both years, the experiments finished with the

108 larvae reaching the decapodid and juvenile stages, which were fixed in 4% borax buffered
109 formaldehyde along with the exuviae for later morphological analysis.
110
111 Larval drawings and measurements
112 Drawings and measurements were made following the method described in detail by Bartilotti,
113 Salabert & dos Santos (*2016*). The long plumose setae on the exopods of maxillipeds, and on the
114 pleopods and uropods were drawn truncated, and the setules from setae were omitted from
115 drawings when necessary. The number of examined specimens per stage (N) is referred in the
116 description. Measurements taken were: total length (TL), corresponding to the distance from the
117 tip of the rostrum to the posterior end of telson; carapace length (CL), measured from the tip of
118 rostrum to the posterior margin of the carapace; and rostrum length (RL), corresponding to the
119 distance from the tip of rostrum to the eye socket (except in zoea I where it was not measured).
120 Ten specimens of first to third zoeal stages, seven specimens of fourth zoeal stage, and six
121 specimens of decapodid stage were measured. The larval series has been deposited in IPMA-
122 Instituto Português do Mar e da Atmosfera, in Lisbon, Portugal (IPIMAR/O/Sd/01/2011).
123

Results

125 Rearing the larvae of *Systellaspis debilis*
126 Under laboratory conditions the larvae hatched with a high amount of bright red yolk, stored in
127 the pereon and observed throughout all the development (Figure 1). Hatching occurred three to
128 forty days after the collection of the eggs (Table 1). During the larval rearing, both zoea and
129 decapodid, stood still, floating most of the time, and swimming only as a response to an external
130 stimulus (e.g. tactile stimuli with an autoclaved glass pipette).
131   In 2010 rearing experiments, no feeding behavior was observed, and the larvae went
132 through the entire larval cycle using their yolk. Therefore, no food was provided in the 2011
133 rearing experiments, but the decapodid stage was successfully achieved, after the 4 zoeal stages.
134 Thus, we conclude that this species has a full lecithotrophic development. Considering the two
135 years of experiments, with an average duration of 28.23$\pm$ 1.48 days after hatching, the zoeae
136 were able to molt and grow, going through the metamorphosis to the decapodid. The duration of
137 the successive stages was 4- 6 days for stage I, 5- 8 days for stages II and III, 8- 11 days for stage
138 IV. After 12 days, two of the decapodid stage larvae were able to molt, one in 2010 and another
139 in 2011, reaching the first juvenile stage without food.
140
141 Description of the complete larval development of *Systellaspis debilis*
142 Under laboratory conditions at 18$\pm$ 1 ºC of temperature, four zoeal stages and one decapodid
143 were identified, and are described in detail.
144
***145 Systellaspis debilis* (A. Milne-Edwards, 1881)**
146 (Figures 2-7)

147
148 *First zoea*
149 Dimensions: TL= 9.35- 10.01 mm; CL= 3.19- 3.52 mm; N= 5.
150   Carapace (Figs 2A, 2B, 2C): rostrum small, down turned; eyes compound and sessile;
151 pterigostomian spine present, followed by 8- 9 very small denticles.
152   Antennule (Fig 2D): peduncle unsegmented, with 1 terminal plumose seta and short outer
153 flagellum with 1 plumose seta and 2 shorter+ 1 longer aesthetascs terminally.
154   Antenna (Fig 2E, 2F): protopod unsegmented, with a small strong distal papposerrate
155 seta; endopod less than half the length of the scaphocerite, apically with 1 plumose seta;
156 scaphocerite unsegmented, broad, with 24- 26 plumose setae and 1 small spine on apex.
157   Mandibles (Fig 2G): slightly asymmetrical, with undifferentiated molar and incisive
158 processes; palp present.
159   Maxillule (Fig 2H): coxal endite with 1- 2 small spines, basial endite with 1 small spine;
160 endopod unsegmented with 1 short simple seta at half the length, 1 spine subterminally and 2
161 plumose setae terminally.
162   Maxilla (Fig 2I): coxal endite bilobed with 2 simple+ 2- 3 plumose setae, basial endite
163 bilobed with 1 simple and 1 plumose+ 2 simple and 1 plumose setae; endopod unsegmented
164 bearing 2+ 1+ 1+ 3 plumose setae; scaphognathite with 8- 10 marginal plumose setae, and one
165 long distal stout setose process.
166   First maxilliped (Fig 2J): coxa with 2- 3 simple setae; basis with 7- 8 simple setae;
167 endopod 4-segmented with 1, 1, 1+ 1, 1+ 3 plumose setae; exopod unsegmented, bearing 2
168 shorter plumose setae subterminally and 3 plumose setae terminally; epipod present.
169   Second maxilliped (Fig 2K): coxa with 1 simple seta; basis with 3- 4 simple setae;
170 endopod 5-segmented with 2, 1, 0, 1 and 3 simple terminal setae; exopod unsegmented, bearing
171 2 subterminal and 3 terminal plumose setae; epipod present.
172   Third maxilliped (Fig 2L): coxa unarmed; basis with 2- 3 simple setae; endopod 5-
173 segmented with 1- 2, 1, 0, 1- 2 and 3 simple setae; exopod unsegmented, bearing 2 subterminal
174 and 3 terminal plumose setae.
175   First to fifth pereopods (Fig 2M): biramous buds, with pleurobranchs present;
176 photophores present on the fifth pair of pereopods.
177   Pleon (Fig 2A, 2N): 5 pleomeres, without setae or spines, fifth pleomere with a rounded
178 pleura.
179   Pleopods (Fig 2A, 2O): present as biramous buds; photophores present on first and
180 second pleopods.
181   Uropods: absent.
182   Telson (Fig 2N, 2P): triangular, broader posteriorly, with a small median indent, with
183 7+7 setae, the inner 5 plumose and the outer 2 plumose on proximal axis only.
184
185 *Second zoea*
186 Dimensions: TL= 10.34- 11.00 mm; CL= 3.52- 3.85 mm; RL= 0.66- 0.88; N= 5.

187   Carapace (Figs 3A, B): eyes stalked, with the ocular peduncle reaching half the length of
188   the antennal peduncle; rostrum triangular, as long as the eyes; pterigostomian spine followed by
189   8- 9 small denticles.
190   Antennule (Fig 3C): peduncle 3-segmented, with 1 small spine positioned at about two
191   thirds of the length of the first segment+ 3 plumose setae along the inner margin+ 7- 8 plumose
192   setae distributed on distal outer margin, second segment with 2 plumose setae along the inner
193   margin+ 5- 6 plumose setae distributed on distal outer margin, and distal segment with 1
194   plumose seta on inner margin+ 1short plumose and 1 simple setae on outer margin+ 6- 7
195   plumose setae distally; inner flagellum 2-segmented, first segment naked and distal segment
196   bearing 1 simple seta distally; outer flagellum unsegmented with 2 aesthetascs at one third of the
197   length of the segment+ 2 aesthetascs at two thirds of the length of the segment+ 1 simple seta
198   terminally.
199   Antenna (Fig 3D): protopod unsegmented with a small strong simple spine; 2-segmented
200   endopod longer than half the length of the scaphocerite, shorter basal segment naked, terminal
201   longer segment with 1 plumose seta distally; scaphocerite with 30- 31 plumose setae and 1
202   strong spine on apex.
203   Mandibles (Fig 3E): palp enlarged in size, otherwise unchanged.
204   Maxillule (Fig 3F, 3G, 3H): coxal endite with 1- 3 spines, basial endite with 1 spine;
205   endopod unchanged.
206   Maxilla (Fig 3I): coxal endite bilobed with 2- 3 simple+ 1 spine and 2- 3 plumose setae
207   distributed as illustrated; basial endite bilobed with 1 plumose seta and 1+ 1 spines, 1 simple and
208   1 plumose setae; endopod unsegmented bearing 2+ 1+ 1+ 3 plumose setae; scaphognathite with
209   10- 13 marginal plumose setae, and one long distal stout setose process.
210   First maxilliped (Fig 3J): coxa with 1 small spine and 1 plumose seta; basis with 2 small
211   spines and 4-6 plumose setae distributed as illustrated; endopod 4-segmented with 1 plumose
212   seta on inner margin and 1 plumose seta on outer margin, 1 plumose seta, 1 simple and 1
213   plumose setae, and 1+ 3 plumose setae; exopod unsegmented, bearing 2 shorter setae
214   subterminally and 4 long terminal plumose setae; epipod unchanged.
215   Second maxilliped (Fig 3K): coxa with 1- 2 plumose setae; basis with 3- 4 plumose setae;
216   endopod 5-segmented with 1, 1, 0, 0- 1, and 1+3 plumose setae; exopod unsegmented bearing 2
217   shorter setae subterminally and 4 long terminal plumose setae; epipod unchanged.
218   Third maxilliped (Fig 3L): coxa unarmed; basis with 2- 3 plumose setae; endopod 5-
219   segmented with 1, 1, 0, 2, and 3 plumose setae; exopod unsegmented, bearing 2 subterminal and
220   4 terminal plumose setae.
221   First to fifth pereopods (Fig 3M): first pereopod endopod and exopod bearing one small
222   simple seta apically, otherwise unchanged besides size.
223   Pleon (Fig 3A): unchanged besides size.
224   Pleopods (Fig 3A, N): biramous buds enlarged in size; photophores present on first to
225   third pleopods.
226   Uropods: absent, but already visible under telson integument.

227   Telson (Fig 3O): with a very small median indentation, now with 8+8 setae, the inner 7
228   plumose and the outer plumose on proximal axis only.
229
230   *Third zoea*
231   Dimensions: TL= 10.45- 11.00 mm; CL= 3.63- 3.96 mm; RL= 0.77- 0.88; N= 6.
232   Carapace (Figs 4A, 4B): pterigostomian spine followed by 8- 9 small denticles on lateral
233   antero-ventral margin.
234   Antennule (Fig 4C): peduncle 3-segmented, basal segment with 1 spine positioned at half
235   the length of the segment, 1- 2 plumose setae on inner margin, 1 small plumose seta on the
236   stylocerite, and 9- 12 plumose setae distributed on distal outer margin; second segment with 2
237   plumose setae along the inner margin and 5- 7 plumose setae distributed on distal outer margin;
238   distal segment with 2+ 2 plumose setae along inner margin, 6 short plumose and 4 plumose setae
239   on distal outer margin; inner flagellum 4-segmented, first and second segments naked, distal
240   segment bearing 2 simple subterminal+ 1 plumose terminal setae; outer flagellum 4-segmented
241   with 1, 3, and 3 aesthetascs in the first three segments, and 1+ 1 simple setae terminally.
242   Antenna (Fig 4D): protopod unsegmented with a strong spine; 2-segmented endopod
243   longer than three quarters of the length of the scaphocerite, shorter basal segment naked, terminal
244   longer segment with 2- 3 very small simple setae terminally; scaphocerite with 32- 34 plumose
245   setae and 1 strong spine on apex.
246   Mandibles (Fig 4E): palp enlarged in size, otherwise unchanged.
247   Maxillule (Fig 4F, 4G, 4H): coxal endite with 3 very small spines, basial endite with 4- 5
248   spines; 2-segmented endopod, proximal segment with 1 simple seta, distal segment with 1 spine
249   subterminally and 2 plumose setae terminally.
250   Maxilla (Fig 4I): coxal endite bilobed with 3- 4+ 3 simple and plumose setae distributed
251   as illustrated, basial endite bilobed with 2- 3+ 3- 4 simple and plumose setae; endopod
252   unsegmented bearing 2+ 1+ 1+ 3 plumose setae; scaphognathite with 15- 17 marginal plumose
253   setae, microtricha as illustrated, and one long distal stout setose process.
254   First maxilliped (Fig 4J): coxa with 2 simple setae; basis with 7- 8 simple and plumose
255   setae distributed as illustrated; endopod 4-segmented with 1+ 1 plumose setae on inner margin
256   and 1 plumose seta on outer margin, 1 plumose seta, 1 simple and 1 plumose setae, and 1 shorter
257   subterminal+ 3 longer terminal plumose setae; exopod unsegmented, bearing 2 shorter setae
258   subapically and 4 long terminal plumose setae; epipod enlarged in size.
259   Second maxilliped (Fig 4K): coxa with 1- 2 plumose setae; basis with 4- 5 plumose setae;
260   endopod 5-segmented with 2, 1, 0- 1, 1+ 1, and 1+ 2 plumose setae; exopod unsegmented
261   bearing 2 shorter setae subapically and 4 long terminal plumose setae; epipod enlarged in size.
262   Third maxilliped (Fig 4L): coxa unarmed; basis with 3- 4 plumose setae; endopod 5-
263   segmented with 1- 2, 1, 0, 1+1, and 3 plumose setae; exopod unsegmented, bearing 2 subterminal
264   and 4 terminal plumose setae.
265   First to fifth pereopods (Fig 4M): first pereopod endopod 5-segmented, subchelate, with
266   internal distal margin of propodus produced forward to about one-third of dactylus, with 1+ 1

267   simple setae distally on terminal segment, and exopod unsegmented bearing 2 simple setae
268   apically; second to fifth pereopods endopod 5-segmeted bearing 1- 2 very small simple setae
269   terminally, and exopod unsegmented with 1- 2 very small simple setae terminally; photophores
270   present on the fifth pair of pereopods.
271   Pleon (Fig 4A): first to fifth pleomeres unchanged; sixth pleomere separated from the
272   telson with 6 pairs of small simple setae distributed as figured.
273   Pleopods (Fig 4A, 4N, 4O, 4P, 4Q, 4R, 4S): enlarged in size; first pleopod endopod
274   rudimentary, bud-like, and exopod with 1 small spine subterminally and 2 small spines
275   terminally; second to fifth pleopods endopod rudimentary, bud-like, and exopod with 2 small
276   spines terminally. Photophores present on first to fourth pleopods.
277   Uropods (Fig 4A, 4T, 4U, 4V): biramous; endopod small with 2- 3 short plumose seate
278   apically; exopod well developed shorter than the posterior margin of telson, with 12- 14 marginal
279   plumose setae and 2- 3 plumose setae on ventral margin.
280   Telson (Fig 4A, 4T): separated from the sixth pleomere, with 8+ 8 setae.
281
282   *Fourth zoea*
283   Dimensions: TL= 10.80- 11.28 mm; CL= 3.84- 4.00 mm; RL= 0.80- 1.04; N= 4.
284   Carapace (Figs 5A, 5B): three luminous organs on eye; rostrum extending beyond the
285   eyes, with 9- 10 dorsal teeth and 2 very small ventral teeth; pterigostomian spine followed by 7-
286   9 very small spines on lateral ventral margin.
287   Antennule (Fig 5C): peduncle 3-segmented, basal segment with 1 spine positioned at two
288   thirds of the length of the segment, 2- 3 plumose setae on inner margin, 2 small plumose setae on
289   the stylocerite, and 11- 13 plumose setae distributed on distal outer margin; second segment with
290   2- 3 plumose setae along the inner margin and 6- 7 plumose setae distributed on distal outer
291   margin; distal segment with 8 subterminal plumose+ 6 terminal plumose setae distributed as
292   illustrated; inner flagellum 6-segmented, first to third segments naked, third and fourth segments
293   with 2- 3 simple setae, and terminal segment with 3- 4 simple setae; outer flagellum 5-segmented
294   respectively with 1 aesthetasc, 2+ 3 aesthetascs, 3 aesthetascs, 1 simple seta, and 2- 3 simple
295   setae.
296   Antenna (Fig 5D): protopod unsegmented with one strong simple seta on the inner
297   margin and one strong spine on the outer margin; endopod measuring almost one and a half
298   times the length of the scaphocerite, with 18 segments each bearing 0- 4 very small simple setae
299   terminally; scaphocerite now with 35- 36 plumose setae and 1 strong spine on apex.
300   Mandibles (Fig 5E): incisor and molar processes as illustrated; palp enlarged in size,
301   unsegmented.
302   Maxillule (Fig 5F): coxal endite with 6- 7 spines, basial endite with 7- 8 spines; 2-
303   segmented endopod, proximal segment with 1 simple seta, distal segment with 1 spine
304   subterminally and 2 plumose setae terminally.
305   Maxilla (Fig 5G): coxal endite bilobed with 5- 6+ 3 simple and plumose setae distributed
306   as illustrated; basial endite bilobed with 3- 4+ 3- 4 simple and plumose setae; endopod

307   unsegmented bearing 2+ 1+ 1+ 3 plumose setae; scaphognathite with 17- 20 marginal plumose
308   setae, and two distal stout setose processes.
309   First maxilliped (Fig 5H): coxa with 2 simple setae; basis with 8- 9 simple and plumose
310   setae distributed as illustrated; endopod 4-segmented with 1+ 1 plumose setae, 1+ 1 plumose
311   setae, 1+ 1 plumose setae, and 1 shorter subterminal+ 3 longer terminal plumose setae; exopod
312   unsegmented, bearing 2 shorter setae subapically and 4 long terminal plumose setae; epipod
313   enlarged in size.
314   Second maxilliped (Fig 5I): coxa with 1- 2 plumose setae; basis with 5- 6 plumose setae;
315   endopod 5-segmented with 2, 1, 0- 1, 2, and 1+ 2 plumose setae; exopod unsegmented bearing 2
316   shorter setae subapically and 4 long terminal plumose setae; epipod enlarged in size.
317   Third maxilliped (Fig 5J): coxa unarmed; basis with 3- 4 plumose setae; endopod 5-
318   segmented with 1- 2, 1, 0, 2, and 3 plumose setae, and a luminous organ on the 4th segment
319   (propodus); exopod unsegmented, bearing 2 subterminal and 4 terminal plumose setae.
320   First pereopod (Fig 5K): functional, coxa unarmed; basis with 3 simple setae; endopod
321   subchelate, 5-segmented, ischium, merus and carpus with 1, 1- 2, 1 simple setae respectively, as
322   illustrated; distal margin of the propodus produced forward to about one-third of dactylus
323   bearing 1- 2 simple setae+ 1 spinous process, dactylus with 1 simple seta+ 1 spinous process;
324   exopod unsegmented, bearing 2 subterminal and 4 terminal plumose setae; pleurobranch
325   developed.
326   Second pereopod (Fig 5L): functional, coxa unarmed; basis with 1 simple seta; endopod
327   subchelate, 5-segmented, ischium, merus and carpus with 1, 1- 2, and 0 simple setae
328   respectively, distal margin of the propodus produced forward to about one-third of dactylus
329   bearing 1 simple seta+ 1 spinous process, dactylus with 1 simple seta+ 1 spinous process;
330   exopod unsegmented, bearing 2 subterminal and 4 terminal plumose setae; pleurobranch
331   developed.
332   Third pereopod (Fig 5M): functional, coxa unarmed; basis with 1 simple seta; endopod 5-
333   segmented, ischium, merus, carpus and propodus with 1, 0- 1, 1, 2 simple setae, dactylus with 1
334   simple seta+ 1 spinous process; a luminous organ on the carpus; exopod unsegmented, bearing 2
335   subterminal and 4 terminal plumose setae; pleurobranch developed.
336   Fourth pereopod (Fig 5N): functional, coxa unarmed; basis with 1 simple seta; endopod
337   5-segmented, ischium, merus, carpus and propodus with 0- 1, 1, 1, 2 simple setae, dactylus with
338   1 simple seta+ 1 spinous process; a luminous organ on the carpus; exopod unsegmented, bearing
339   4 terminal plumose setae; pleurobranch developed.
340   Fifth pereopod (Fig 5O): functional, coxa unarmed; basis naked; endopod 5-segmented,
341   ischium, merus, carpus and propodus with 0, 0, 0, 1 simple seta, dactylus ending in a spinous
342   process; a luminous organ on the carpus; exopod unsegmented, bearing 2 small terminal simple
343   setae; pleurobranch developed.
344   Pleon (Fig 5A, 5P, 5Q, 5R): first to third pleomeres unchanged; fourth pleomere with a
345   posteromedial spine; fifth pleomere with a posteromedial spine and a spine on the pleura; sixth
346   pleomere with a pair of lateral spines.

347   Pleopods (Fig 5A, 5S): protopod naked; first pleopod endopod naked and exopod with 2
348 small spines; second to fiffth pleopods endopods and exopods with 2 small spines distally,
349 appendix interna as bud, present from second to fifth pleopods. Photophores present on first to
350 fifth pleopods.

351   Uropods (Fig 5T): protopod without setae; endopod with 2- 3 short plumose setae
352 medially on outer margin and 14- 16 plumose setae along distal and inner margins; exopod, with
353 1 small spine on apex followed by 20- 22 plumose setae along distal and inner margin, and 2- 3
354 plumose setae on ventral margin.

355   Telson (Fig 5T): with a median spine on posterior margin, followed by 5 pairs of strong
356 plumose processes on the posterior end being the fourth pair plumose only on the inner margin, 2
357 pairs of outer spines, and 1 pair of lateral spines; almost rectangular shaped.

358

359 *Decapodid*

360 Dimensions: TL= 11.77- 12.10 mm; CL= 4.40- 4.62 mm; RL= 1.10- 1.32; N= 4.

361   Carapace (Fig 1, 6A, 6B, 6C): eyestalk with ocellus on medio-distal portion, and three
362 luminous organs; rostrum shorter than scaphocerite with 9- 10 dorsal teeth and 2- 3 small ventral
363 teeth; antennal spine present, and pterigostomian spine followed by 10- 11 small spines on lateral
364 ventral margin.

365   Antennule (Fig 6H): peduncle 3-segmented, basal segment with 1 spine positioned at two
366 thirds of the length of the segment, 3- 5 plumose setae on inner margin, 1- 2 small plumose setae
367 on the stylocerite, and 11- 13 plumose setae distributed on distal outer margin; second segment
368 with 2- 3 plumose setae along the inner margin and 6- 8 plumose setae distributed on distal outer
369 margin; distal segment with 7- 9 subterminal plumose+ 7- 8 terminal plumose setae distributed
370 as illustrated; inner flagellum 10- 11 segments each with 0- 5 simple setae; outer flagellum 10-
371 11 segments, first three segments with 1 aesthetasc, 2+ 3 aesthetascs+ 1 simple seta, and 3+ 3
372 aesthetascs, fourth to last segment naked to 3 simple setae distally.

373   Antenna (Fig 6I): protopod 2-segmented, distal segment with one simple seta and one
374 strong spine; endopod longer than the scaphocerite, with 33- 36 segments each bearing 0- 5 very
375 small simple setae terminally; scaphocerite now with 39- 41 plumose setae, 1 strong spine on
376 apex, and 1- 2 simple setae distributed along outer margin.

377   Mandibles (Fig 6J): palp 2-segmented, proximal segment with 2 plumose setae, distal
378 segment with 2 simple+ 4 plumose setae; incisor process with about ten to 12 strong serrated
379 teeth, molar process as illustrated.

380   Maxillule (Fig 6K): coxa with 10- 12 simple and papposerrate setae; basis with 15- 17
381 cuspidate and papposerrate setae; 2-segmented endopod, proximal segment with 1 longer
382 subterminal and 1 shorter terminal outer plumose setae, distal segment with 2 plumose setae
383 terminally.

384   Maxilla (Fig 6L): coxal endite bilobed with 6- 7+ 3 setae; basial endite bilobed with 5- 6+
385 6- 7 setae; endopod unsegmented bearing 1+ 1+ 1 and 3 plumose setae terminally;
386 scaphognathite with 21- 23 marginal plumose setae.

387   First maxilliped (Fig 6M): coxa with 3- 4 setae; basis with 12- 13 papposerrate setae;
388   endopod 3-segmented, with 1+ 1, 1, 1+ 3 papposerrate setae distributed as figured; exopod with
389   9- 10 short plumose setae on outer margin, 3 terminal plumose setae and 1 shorter plumose seta
390   subapically on inner margin; epipod bilobed.
391   Second maxilliped (Fig 6N): coxa with 1 plumose seta; basis with 5- 7 plumose setae;
392   endopod 5-segmented with 1- 2+ 1, 1+ 1, 0- 1, 6- 7, and 10- 11 plumose setae; exopod
393   unsegmented bearing 2 setae subapically and 4 long terminal plumose setae; epipod enlarged in
394   size.
395   Third maxilliped (Fig 6O, 6P): coxa unarmed; basis with 3- 4 plumose setae; endopod 5-
396   segmented with 4- 5 plumose setae, 1 spine+ 6- 7 plumose setae, 5- 6 plumose setae, 8- 10
397   plumose setae, and 2 spines+ 2 simple setae distributed as illustrated, and a luminous organ on
398   the 4th segment (propodus); exopod unsegmented, bearing 2 subterminal and 4 terminal plumose
399   setae.
400   First pereopod (Fig 7A, 7B): coxa naked, basis with 3- 5 plumose setae; endopod sub-
401   chelate, 5-segmented, ischium, merus and carpus with 8- 9, 4- 5 and 2- 4 simple and plumose
402   setae distributed as illustrated, propodus produced beyond half the length of the dactylus bearing
403   5- 7+ 4- 6 simple setae distributed as illustrated and 2 spines distally, dactylus with 2- 4 simple
404   setae and 2 spines distally; exopod unsegmented, bearing 2 subterminal and 4 terminal plumose
405   setae; pleurobranch developed.
406   Second pereopod (Fig 7C, 7D): coxa naked, basis with 2- 3 plumose setae; endopod sub-
407   chelate, 5-segmented, ischium, merus and carpus with 4- 6, 4- 5 and 3- 4 simple and plumose
408   setae distributed as illustrated, propodus produced half the length of the dactylus bearing 4- 5+ 3-
409   2 simple setae distributed as illustrated and 2 spines distally; dactylus with 3- 5 simple setae and
410   2 spines distally; exopod unsegmented, bearing 2 subterminal and 4 terminal plumose setae;
411   pleurobranch developed.
412   Third pereopod (Fig 7E, 7F): coxa naked; basis with 1- 2 plumose setae; ischium, merus,
413   carpus and propodus with 1- 3, 3- 4, 2- 3 and 4- 5 simple and plumose setae arranged as figured,
414   luminous organ present on carpus; dactylus with 3- 5 simple setae and 2 spines distally; exopod
415   unsegmented, bearing 2 subterminal and 4 terminal plumose setae; pleurobranch developed.
416   Fourth pereopod (Fig 7G): coxa naked; basis with 2 plumose setae; ischium, merus,
417   carpus and propodus with 2- 3, 1- 2, 2- 3 and 5- 6 simple and plumose setae arranged as figured,
418   luminous organ present on carpus; dactylus with 3- 4 simple setae and 1 spine distally; exopod
419   unsegmented, bearing 2 subterminal and 4 terminal plumose setae; pleurobranch developed.
420   Fifth pereopod (Fig 7H, 7I): coxa naked; basis with 1- 2 plumose setae; ischium, merus
421   and carpus with 1- 2, 1- 2 and 4- 5 simple and plumose setae arranged as figured; propodus with
422   1 stout plumose seta at two thirds of the length of the segment and 5- 6 plumose and simple setae
423   distributed, luminous organ present on carpus; dactylus with 1- 2 simple setae subterminally and
424   4 stout simple setae distally; exopod short, measuring less than one third of the length of the
425   endopod, bearing 4 terminal plumose setae; pleurobranch developed.

426   Pleon (Figs 1, 6A, 6D, 6E, 6F, 6G): third to fifth pleomeres with a posteromedial spine,
427   being the one on somite 3 strong, the one on somite 4 slightly upturned, and the one on somite 5
428   which also bears a lateral spine, acute; sixth pleomere with a pair of lateral spines. Photophores
429   present on the base of each pair of pleopods, close to their insertion in the pleon.
430   First pleopod (Fig 6A, 7J, 7K): basipodite naked; endopod with 2 subterminal plumose
431   setae and 2 cincinulli, exopod with 15- 16 plumose setae
432   Second pleopod (Fig 6A, 7L, 7M): basipodite smooth; endopod with 10- 11 plumose
433   setae and the small *appendix interna* which presents 2 cincinulli, exopod with 16- 17 plumose
434   setae.
435   Third pleopod (Fig 6A, 7N, 7O): basipodite smooth; endopod with 10 plumose setae and
436   the small *appendix interna* which presents 2 cincinulli; exopod with 14- 15 plumose setae.
437   Fourth pleopod (Fig 6A, 7P, 7Q): basipodite smooth; endopod with 9- 10 plumose setae
438   and the small *appendix interna* which presents 2 cincinulli; exopod with 14- 15 plumose setae.
439   Fifth pleopod (Fig 6A, 7R, 7S): basipodite smooth; endopod with 8- 9 and the small
440   *appendix interna* which presents 2 cincinulli; exopod with 13- 14 plumose setae.
441   Uropods (Fig 7T): protopod unarmed; endopod with 19- 20 plumose setae along inner
442   and distal margins, 4- 5 sparsely plumose setae along outer margin and 2- 5 sparsely plumose
443   setae distributed on ventral margin; exopod with 24- 25 plumose setae along inner and distal
444   margins, 2- 3 sparsely plumose setae along outer margin and 2- 4 sparsely plumose setae
445   distributed on ventral margin.
446   Telson (Fig 7T): parallel-sided, presents a slightly convex distal margin with a short
447   median spine, 2 pairs of small lateral spines and 6 pairs of processes distally (the first pair is the
448   shortest, the second pair the longest, and the second to the sixth are plumose); small anal spine
449   now present.
450

451   ## Discussion
452   **Morphology of the larval cycle of *Systellaspis debilis* and larval characters for the**
453   **Oplophoridae**
454   The complete larval development of *Systellapis debilis* described in present study has four zoeae
455   and one decapodid, which adds a zoea to the, until now known larval sequence for this species.
456   The Gurney & Lebour (*1941*) description, based on a sequence of larval stages from plankton of
457   Bermuda waters, presents a larval cycle of three zoea and a post-larval stage (=decapodid).
458   However, Gurney & Lebour (*1941*) indicate that the second zoeal stage has a telson with 8+8
459   posterior processes and free uropods, whereas the results from this study shows that the uropods
460   are visible through the telson integument but not free. In fact, Gurney & Lebour had concluded
461   that the second zoea corresponded to a normal third stage (*Gurney & Lebour, 1941*).
462   Nonetheless, after a detailed morphological comparison between present work and Gurney &
463   Lebour (*1941*) *S. debilis* larval descriptions, we found only minor differences, which concerns
464   the setation of some appendages and the dimensions of the larvae. When comparing the first
465   zoea, the maxilla previously described lacks detail in the coxal and basial lobes with 2+0 and

466   1+1 small setae, which are ornamented with 2+ 2- 3 and 2+ 3 setae in the coxa and basis,
467   respectively. The telson is described as having the uropods under its integument, which in the
468   present work are visible only in the second zoeal stage.
469   The second zoea described in present study was not previously observed by Gurney &
470   Lebour (*1941*). For the third zoeal stage, the only difference between the two descriptions is in
471   the number of setae of the scaphognathite of the maxilla that presents 15- 17 marginal plumose
472   setae and 1 long distal stout setose process, instead of 13 marginal plumose processes as in
473   Gurney & Lebour (*1941*) description. The fourth zoeal stage now presented slightly differs from
474   the Gurney & Lebour (*1941*) third stage, by the presence of two very small ventral teeth in the
475   rostrum, and the more setae found in the maxillule and in the maxilla. Gurney & Lebour also
476   compare the third larval stage with a specimen taken at Bermuda (*Gurney & Lebour, 1941*),
477   considering that probably it is a fourth stage. Comparing this specimen with the fourth zoeal
478   stage obtained in present study, we conclude that it differs in the flagellum of the antenna, which
479   is longer than the exopod, and in the telson that is slightly wider at the posterior end, with a
480   straight posterior margin (*Gurney & Lebour, 1941*).
481   We agree with Gurney & Lebour (*1941*) probable explanation for the observations made
482   that there is some variation in the number of stages after the second zoea, also because the
483   characters of the telson agree well with those described in present study for the fourth zoeal
484   stage. Besides this, Gurney & Lebour describe another probable larval stage four, collected in the
485   Discovery station 281 (see Fig 6A-C in Gurney & Lebour, 1941), different from the one
486   described in the present study for the decapodid stage. Gurney & Lebour (*1941*) stage four
487   presents 6 ventral teeth in the rostrum, the carapace has an anterior ventral margin slightly
488   serrated, the maxillule, maxilla and first maxilliped are figured, and the telson is described as
489   more slender, presenting a long median spine. The author then compares this larval form with
490   the one described in Kemp (*1907*), hypothesizing that both correspond to the same stage,
491   possibly of a different species or of an intermediate stage between the last zoeal stage and the
492   first decapodid. When compared with the fourth zoea described by us, they differ in the number
493   of ventral teeth of the rostrum and in the form of the telson, which in the present study is
494   rectangular shaped with a median spine with the same size of the other telson posterior process.
495   Regarding the endopod of the maxillule of the specimen collected in the Discovery station 281
496   (*Gurney & Lebour, 1941*), it seems unsegmented, which is segmented in the fourth zoea
497   described here; also, the endopod of the maxilla possess only 3 setae which in the present
498   description has 2+ 1+ 1+ 3 plumose setae. The larvae described by Gurney & Lebour (*1941*)
499   presents a first maxilliped similar to the one observed for a decapodid stage, with a 3-segmented
500   endopod, the exopod with plumose setae along the outer margin, and, the epipod bilobed,
501   whereas the fourth zoea described here presents a first maxilliped typical of a zoeal stage, with a
502   4-segmented endopod, the exopod with plumose setae terminally, and, a small epipod. Therefore,
503   since the Discovery station 281 larvae described by Gurney & Lebour (*1941*) has a telson and the
504   first maxilliped similar to those of the decapodid stage, and the endopods of both, the maxillule

505 and maxilla, are different in shape and number of setae, we consider that, probably, it belongs to
506 a different Oplophorid species.

507   It is recognized that the number of stages can be a consequence of the genetic differences
508 between regionally separated populations (*e.g. Anger, 2001*), of the energy content of larvae at
509 hatching as a proxy for the Per Offspring Investment (POI, *e.g. Oliphant & Thatje, 2013*), or of
510 the environmental conditions such as the temperature (*e.g. Oliphant, Hauton & Thatje, 2013*).
511 The plasticity in the number of larval stages is common for shrimps, and results published to date
512 show that temperature, salinity and food affect the moult cycle, and can produce intermediate
513 forms (e.g. different morphs of *Nauticaris magellanica* from the third zoeal stage on, as
514 described in *Wehrtmann & Albornoz, 2003*). Likewise, besides the morphological plasticity,
515 different populations of the same species can have larval cycles with a different number of stages
516 (e.g. populations of *N. magellanica* from the Argentine waters- Atlantic ocean- and the Chilean
517 waters- Pacific ocean- differed in the number of stages, size, setation of thoracopods, and
518 development of pereopods, as described in *Thatje & Barcadirt, 2000*). Back to 1941, Gurney and
519 Lebour (*1941*) were already aware of this, indicating that the differences observed between the
520 Bermuda and the Discovery specimens might be due to the individual variation in the degree of
521 development between the two populations. This plasticity is more common for long larval series
522 than for short ones(*e.g. Anger, 2001*), where the critical periods related with quantity and quality
523 of energy affect the moult cycle (*e.g. Wehrtmann & Albornoz, 2003*). The larval cycle of
524 *Systellaspis debilis* has been shown here to be fully lecitorophic, and possibly less variation is
525 expected for this group of species, since the changes in the energy requirements throughout
526 development are already provided for in the strongly enhanced yolk stores.

527   Gurney's decapodid, described as "post-larval 1" (*Gurney & Lebour, 1941*) is smaller in
528 size when compared with those obtained in present study, but shows a longer rostrum with 13
529 dorsal teeth and 8 small ventral teeth and, the telson illustrated seems to be more developed. On
530 the other hand, Coutiére (*1906*) presented a larval form that can be considered as a decapodid
531 stage, having a total length of 11 mm (see Fig 2A, in *Coutiére, 1906*), the rostrum shorter than
532 the scaphocerite, with the same number of dorsal teeth and a smaller number of ventral teeth (13
533 and 3 respectively). The distribution of the luminous organs and of the photophores is in
534 agreement in all three descriptions. Both authors (*Coutiére, 1906*; and *Gurney & Lebour, 1941*)
535 mention that the pereon is full of yolk, as observed in the present study.
536   Gurney & Lebour (1941) stated that the morphological larval characters for *Systellaspis*
537 and *Oplophorus* are very similar, reflecting a closer relation between both genera. Besides the
538 presence of the luminous organs, the two larval series differ on the antennal scaphocerite which
539 in *Oplophorus spinosus* has a stout apical spine from first stage on, a small exopod on pereopod
540 5, and a reduced ocular pappila. It is also stated, that probably the mouthparts remain not
541 functional due to the mass of yolk observed in the body (*Gurney & Lebour, 1941*), an
542 assumption in agreement with our observations. Considering present knowledge, we conclude
543 that species of the family Oplophoridae will, most probably, have a larval cycle of four to five

544 zoeae. The first zoea will have the exopod of the antenna unsegmented, will present buds for all
545 pereopods and pleopods, which will be biramous in all pereopods, the pereon will be full of yolk
546 through all larval development. The telson is broad presenting a small median spine on posterior
547 margin, in the last stage of zoea.
548
549 **Lecithotrophy in *Systellaspis debilis* larvae and its implications on the ecology and evolution**
550 **of oplophorids**
551 We propose that the larval phase of *S. debilis* is full lecithotrophic, due to the findings within
552 this study showing that the complete larval development, from the first zoea to decapodid, and
553 first juvenile stage, occurred without feeding. Full lecithotrophy has been described as a probable
554 evolutionary consequence of living in a habitat with ecological and physiological constraints
555 (*e.g. Anger, 2001*), similar to the one where this species lives. This is mostly known for decapods
556 inhabiting extreme habitats such as land locked species (e.g. *Benzie, 1982* for *Caridina*
557 *mccullochi*; *Couret & Wong, 1978* for *Halocaridina rubra*; and *Rodríguez & Cuesta, 2011* for
558 *Dugastella valentina*, three atyid shrimps respectively with five, four, and two non feeding zoeal
559 stages; and *González-Gordillo, Anger & Schubart, 2010* for *Sesarma windsor* and *Metopaulias*
560 *depressus*, two sesarmid crabs with two non feeding zoeal stages). For species living in extreme
561 habitats the evolutionary selection pressures are related with scarcity of food, temperature
562 variation, and high salinity gradients. In some cases subsequent to the full lecithotrophy in one or
563 more larval stages, facultative lecithotrophy is possible due to the quantity of yolk still stored in
564 the pereon (*e.g. Anger, 2001*). A clear example of this pattern was described for a freshwater
565 atyid with abbreviated development and parental care, *Dugastella valentina* (Crustacea,
566 Decapoda, Caridea), whose first, second and third juvenile stages are facultative lecithotrophs
567 (*Rodríguez & Cuesta, 2011*). Observing the pereon of the juvenile stage of *S. debilis*, is possible
568 to state that it is full of yolk, leading to the supposition that maybe, similarly to what was
569 previously observed in the obligate lecithotroph *D. valentina*, also *S. debilis* juveniles could be
570 facultative lecithotrophs (*Rodríguez & Cuesta, 2011*).
571   Gurney & Lebour (1941) separated the oplophorids in two distinct groups according to
572 the size of the eggs: the large eggs genera *Ephyrina*, *Hymenodora*, *Oplophorus* and *Systellaspis*,
573 versus the small eggs genera *Acanthephyra* and *Notostomus*. The authors related the size of the
574 eggs with the number of zoeal stages in the larval cycle predicting that species with small eggs
575 would have a long larval cycle, and the ones with large eggs will have a short larval cycle of no
576 more than five zoeal stages (*Gurney & Lebour, 1941*). The females of *S. debilis* observed in the
577 present study carried between 2 to 12 very large eggs (Table 1), supporting that prediction.
578 Consequently, knowing that the species *Hymenodora glacialis* and *Oplophorus spinosus* besides
579 the size of the eggs shared other characteristics such as the presence of pereopods and pleopods
580 from the first zoeal stage (*Gurney & Lebour, 1941*), we hypothesize that most probably these
581 species will have a fully lecithotrophic larval development as well.

582   Gaten & Herring (*1995*) hypothesized that the larvae of species of the genera
583 *Oplophorus*, *Systellaspis*, *Ephyrina* and *Hymenodora*, with large eggs (k-strategists), showing an

584   extended parental care or enhanced female energy investment in a reduced number of offspring,
585   occur at depths of 200 m or more. Contrasting with these, the species of the genus *Acanthephyra,*
586   produce large numbers of larvae (r-strategists, investing in a high number of eggs), are
587   distributed at depths of 200 m or upper. In fact, the larvae of *S. debilis* are rare in the plankton of
588   the euphotic zone (up to 200 m depth) as shown in e.g. Dos Santos (*1999*), Torres *et al*. (*2014*)
589   and Pochelon *et al*. (*2017*). Therefore they probably inhabit in deeper layers of the water column,
590   restricting their dispersion, skipping the need and search for food in an oligotrophic environment
591   such as the mesopelagic zone. This might be a strategy acquired to enhance the survival of the
592   species, stabilizing the evolutionary trajectory imposed, and in accordance with the recent
593   evidence of cryptic speciation in *S. debilis* (Atlantic *vs*. Pacific and Indian Oceans, as the recent
594   results by *Lunina, Kulagin & Vereshchaka, 2018*, seem to demonstrate).
595   Considering that the phylogenetic reconstructions are very effective for tracing character
596   evolution and major life-history adaptations, a greatly reduced dependence of a vulnerable free
597   living larva on planktonic food sources, is treated as a derived character, i.e. an advanced trait in
598   evolution (*e.g. Anger 2001*), and an increase in maternal investment is considered a crucial step
599   in the shift to non-feeding lecithotrophic development (*e.g. Strathmann 1978*). Considering the
600   recent phylogenetic reconstructions, Bracken *et al*. (*2009*) suggested the polyphyly of the
601   Oplophoridae, and Chan *et al*. (*2010*) recommended to consider the two families, Oplophoridae
602   and Acanthephyridae. Later, Wong *et al*. (*2015*) phylogenetic analyses to trace the evolution of
603   bioluminescence within the oplophorids, resulted in a two major clades topology, strongly
604   supporting the monophyly of the first clade, the family Oplophoridae (Bayesian analysis- BAY-
605   posterior probabilities and Maximum Likelihood- ML- bootstrap values displayed of 100/100).
606   The authors considered that the emergence of photophores, also occurred later in the evolution,
607   and was restricted to the first clade. The lecithotrophy observed for the oplophorids seems to be
608   similar to what has been stated for the sesarmid crabs (*e.g. González-Gordillo, Anger &*
609   *Schubart, 2010*), where the planktotrophy- lecithotrophy dichotomy appears to show the
610   evolutionary radiation from the marine to the terrestrial environment, with the percentage of
611   increased yolk storage, allowing respectively planktotrophy, facultative lecithotrophy or full
612   lecithotrophy. Therefore, the oplophorid shrimps seem to be good candidates to study the
613   evolutionary correlation between the two developmental pattern extremes in the mesopelagic
614   environment: the planktotrophy in the larvae of the Acanthphyridae *versus* the full lecithotrophy
615   of the Oplophoridae.
616   Enhanced yolk reserves constitute a strategy to reduce the nutritional vulnerability of the
617   newly hatched 1arvae (*e.g. Anger, 2001*). Accordingly, considering a probable evolutionary trend
618   towards a shortening of the planktotrophic larval phase (*e.g. Strathmann, 1978*), it is accepted
619   that the tendency towards lecithotrophy is associated with a decrease in the number of larval
620   stages (4- 5 zoeal stages; *e.g. Anger, 2001*). An abbreviated larval development similar to the one
621   observed for *S. debilis* in the present study was already recorded for the larvae of *Pasiphaea*
622   *japonica* (family Pasiphaeidae; *Nanjo & Konishi, 2009*), hence both species hatch with the
623   pereopods and pleopods as buds, and complete their larval cycle with four full lecithotrophic

624   zoeal stages. But other developmental patterns are observed in the nature, describing different
625   evolutionary trajectories. Recently, Hernández-Ávila, Cambon-Bonavita & Pradillon (*2015*),
626   while studying the larvae of the alvinocaridids, concluded that the observed undeveloped
627   mouthparts and the large amount of lipid reserves strongly support the occurrence of primary
628   lecithotrophy. Though, the alvinocaridids larvae undeveloped mouthparts are combined with the
629   lack of pereopods and pleopods, suggesting lecithotrophy only in the first zoea, a stage that can
630   last 70 days. The authors suppose that the combination of undeveloped mouthparts with the
631   absence of pereopods and pleopods in the newly hatched zoeae, suggests lecithotrophy, in an
632   extended larval development (with more that 4- 5 stages), defining a life history model consistent
633   with a wide dispersal strategy in the oligotrophic environment where these species live
634   (hydrothermal vents and/ or cold seeps).
635

Conclusions

637   Present work paramount the need for more larval descriptions of representatives of the
638   superfamily Oplophoroidea, but also of other mesopelagic species, in order to elucidate the
639   general patterns of development in its two families, understanding the taxonomic significance of
640   different life history strategies and, clarifying the phylogeny of this group. The complete larval
641   development of *Systellapis debilis* is described from laboratory reared material. The four zoeal
642   and one decapodid stages were found to be full lecithotrophic. Considering the previous
643   descriptions for the Oplophoridae, which larval cycle consists of four to five zoeae, we propose
644   as larval characters for this family: the exopod of the antenna unsegmented from the first zoea,
645   all pereopods and pleopods present as buds from the first zoea, exopods in all pereopods, the
646   telson broad with a small median spine on posterior margin in the last zoeal stage, and the pereon
647   full of yolk through all the larval development, suggesting a full lecithotrophic development. The
648   full lecithotrophy pattern is a probable evolutionary consequence of living in the mesopelagic
649   zone, and seems to be an ecological adaptation of this species to this extreme environment.
650   Knowing that the larvae of *S. debilis* are rare in the plankton of the euphotic zone, they inhabit
651   the deeper layers of the water column. Due to the yolk-based development, the larval survival is
652   enhanced in the mesopelagic oligotrophic zone, as there is no search for food. Considering the
653   phylogenetic analyses published to date and the observations made in present study, we consider
654   that similarly to what has been stated for some land locked crabs, also the oplophorid shrimps,
655   can be a good model to study the lecithotrophy vs planktothrophy extremes in the mesopelagic
656   environment.
657

Acknowledgements

659   The specimens used in present study were collected and reared under appropriate permits and
660   approved ethics guidelines.

661

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741

742   **Figures**
743   **Figure 1-** *Systellaspis debilis*, decapodid, yolk stored in the pereon.
744
745   **Figure 2-** *Systellaspis debilis*. First zoea: (A) total animal, lateral view. (B) detail of rostrum,
746   dorsal view. (C) detail of carapace anterior ventral margin. (D) antennule. (E) antenna. (F) detail
747   of antennal protopod seta. (G) mandibles. (H) maxillule. (I) maxilla. (J) first maxilliped. (K)
748   second maxilliped. (L) third maxilliped. (M) first to fifth pereopods. (N) pleopods. (O) pleon with
749   telson. (P) telson. Scale bars: 0.05 mm (F-G); 0.1 mm (A- E, H- P).
750
751   **Figure 3** – *Systellaspis debilis*. Second zoea: (A) total animal, lateral view. (B) detail of carapace
752   anterior ventral margin. (C) antennule. (D) antenna. (E) mandibles. (F) maxillule. (G) detail of
753   maxillule coxal endite. (H) detail of maxillule basial endite. (I) maxilla. (J) first maxilliped. (K)
754   second maxilliped. (L) third maxilliped. (M) first to fifth pereopods. (N) pleopods. (O) telson.
755   Scale bars: 0.05 mm (G- H); 0.1 mm (A- F, I- L, O); 1 mm (M- N).
756
757   **Figure 4** – *Systellaspis debilis*. Third zoea: (A) total animal, lateral view. (B) detail of carapace
758   anterior ventral margin. (C) antennule. (D) antenna. (E) mandibles. (F) maxillule. (G) detail of
759   maxillule coxal endite. (H) detail of maxillule basial endite. (I) maxilla. (J) first maxilliped. (K)
760   second maxilliped. (L) third maxilliped. (M) first to fifth pereopods. (N) pleopods. (O) detail of
761   first pleopod exopod posterior margin. (P) detail of second pleopod exopod posterior margin. (Q)
762   detail of third pleopod exopod posterior margin. (R) detail of fourth pleopod exopod posterior
763   margin. (S) detail of fifth pleopod exopod posterior margin. (T) telson and uropods. (U) detail of
764   uropods. (V) detail of uropods endopod posterior margin. Scale bars: 0.05 mm (G- H, O- S, V);
765   0.1 mm (A- F, I- N, T- U).
766
767   **Figure 5** – *Systellaspis debilis*. Fourth zoea: (A) total animal, lateral view. (B) detail of rostrum.
768   (C) antennule. (D) antenna. (E) mandibles. (F) maxillule. (G) maxilla. (H) first maxilliped. (I)
769   second maxilliped. (J) detail of propodus posterior end and dactylus of third maxilliped. (K) first
770   pereopod. (L) second pereopod. (M) third pereopod. (N) fourth pereopod. (O) fifth pereopod. (P)
771   detail of fourth pleomere posteromedial margin. (Q) detail of fifth pleomere posterior margin. (R)
772   detail of sixth pleomere posterior margin. (S) pleopods. (T) telson and uropods. Scale bars: 0.1
773   mm (A, C- O); 1 mm (B, P- R, S- T)..
774
775   **Figure 6** – *Systellaspis debilis*. Decapodid: (A) total animal, lateral view. (B) detail of rostrum.
776   (C) detail of carapace anterior ventral margin. (D) detail of third pleomere posteromedial margin.
777   (E) detail of fourth pleomere posteromedial margin. (F) detail of fifth pleomere posterior margin.
778   (G) detail of sixth pleomere posterior margin. (H) antennule. (I) antenna. (J) mandibles. (K)
779   maxillule. (L) maxilla. (M) first maxilliped. (N) second maxilliped. (O) third maxilliped. (P)
780   detail of propodus and dactylus of third maxilliped. Scale bars: 0.1 mm (A, D- P); 1 mm (B- C).
781

782 **Figure 7** – *Systellaspis debilis*. Decapodid: (A) first pereopod. (B) detail of propodus and dactylus
783 of first pereopod. (C) second pereopod. (D) detail of propodus and dactylus of second pereopod.
784 (E) third pereopod. (F) detail of propodus and dactylus of third pereopod. (G) fourth pereopod. (H)
785 fifth pereopod. (I) detail of propodus and dactylus of fifth pereopod. (J) first pleopod. (K) first
786 pleopod *appendix interna* posterior margin, detail of cincinulli. (L) second pleopod. (M) second
787 pleopod *appendix interna* posterior margin, detail of cincinulli. (N) third pleopod. (O) third
788 pleopod *appendix interna* posterior margin, detail of cincinulli. (P) fourth pleopod. (Q) fourth
789 pleopod *appendix interna* posterior margin, detail of cincinulli. (R) fifth pleopod. (S) fifth pleopod
790 *appendix interna* posterior margin, detail of cincinulli. (T) telson and uropods. Scale bars: 0.05
791 mm (K, M, O, Q, S); 0.1 mm (A- J, L, N, P, R, T).

792 **Tables**
793 **Table 1-** Sampled females used in present study, per date of collection; number of eggs; stage of
794 the eggs- defined as early stage (1), with intense colour and no other pigmentation visible,
795 middle stage (2), with a more pale colour and an embryo having a slight eye pigmentation, and,
796 late stage (3), almost without colour and with an embryo with the eye pigmentation well visible
797 and developed (adapted from *Company & Sardà, 1997*); size (length, corresponding to the major
798 axis distance x width, corresponding to the minor axis distance, in mm) and volume of the eggs;
799 number of hatchings; and date of hatching.
Figure 1

Decapodid, yolk stored in the pereon.

Systellaspis debilis , decapodid, yolk stored in the pereon.

Figure 2

First zoea.

Systellaspis debilis . *First zoea: (A) total animal, lateral view . (B) detail of rostrum, dorsal view . (C) detail of carapace anterior ventral margin . (D) antennule . (E) antenna . (F) detail of antennal protopod seta . (G) mandibles . (H) maxillule . (I) maxilla . (J) first maxilliped . (K) second maxilliped . (L) third maxilliped . (M) first to fifth pereo pods . (N) pleopods . (O) pleon with telson . (P) telson. Scale bars: 0.05 mm (F- G); 0.1 mm (A - E , H- P).*
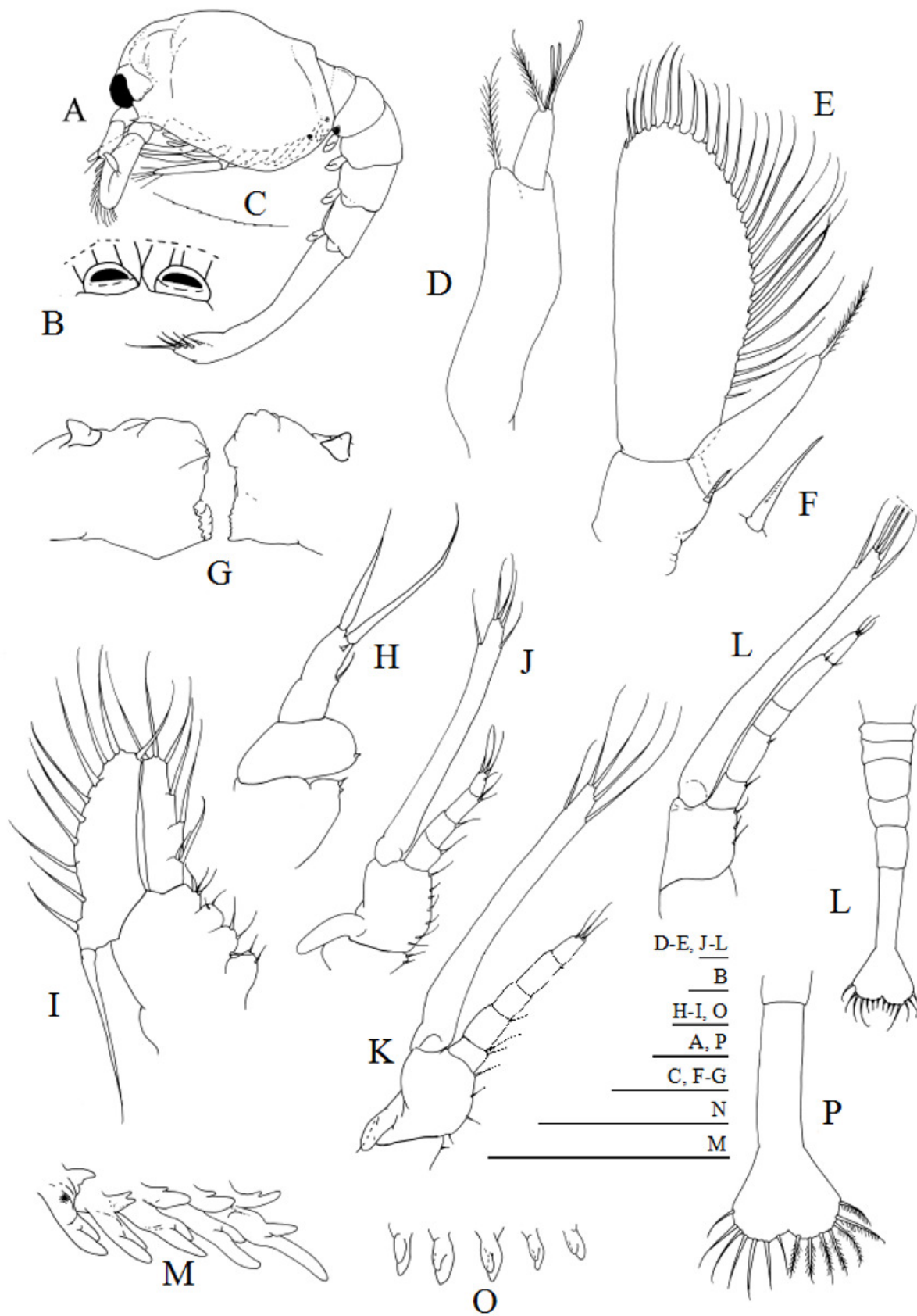
Figure 3

Second zoea.

Systellaspis debilis . Second zoea: (A) total animal, lateral view . (B) detail of carapace anterior ventral margin . (C) antennule . (D) antenna . (E) mandibles . (F) maxillule . (G) detail of maxillule coxal endite . (H) detail of maxillule basial endite . (I) maxilla . (J) first maxilliped . (K) second maxilliped . (L) third maxilliped . (M) first to fifth pereo pods . (N) pleopods . (O) telson. Scale bars: 0.05 mm (G- H); 0.1 mm (A- F, I- L, O); 1 mm (M- N).

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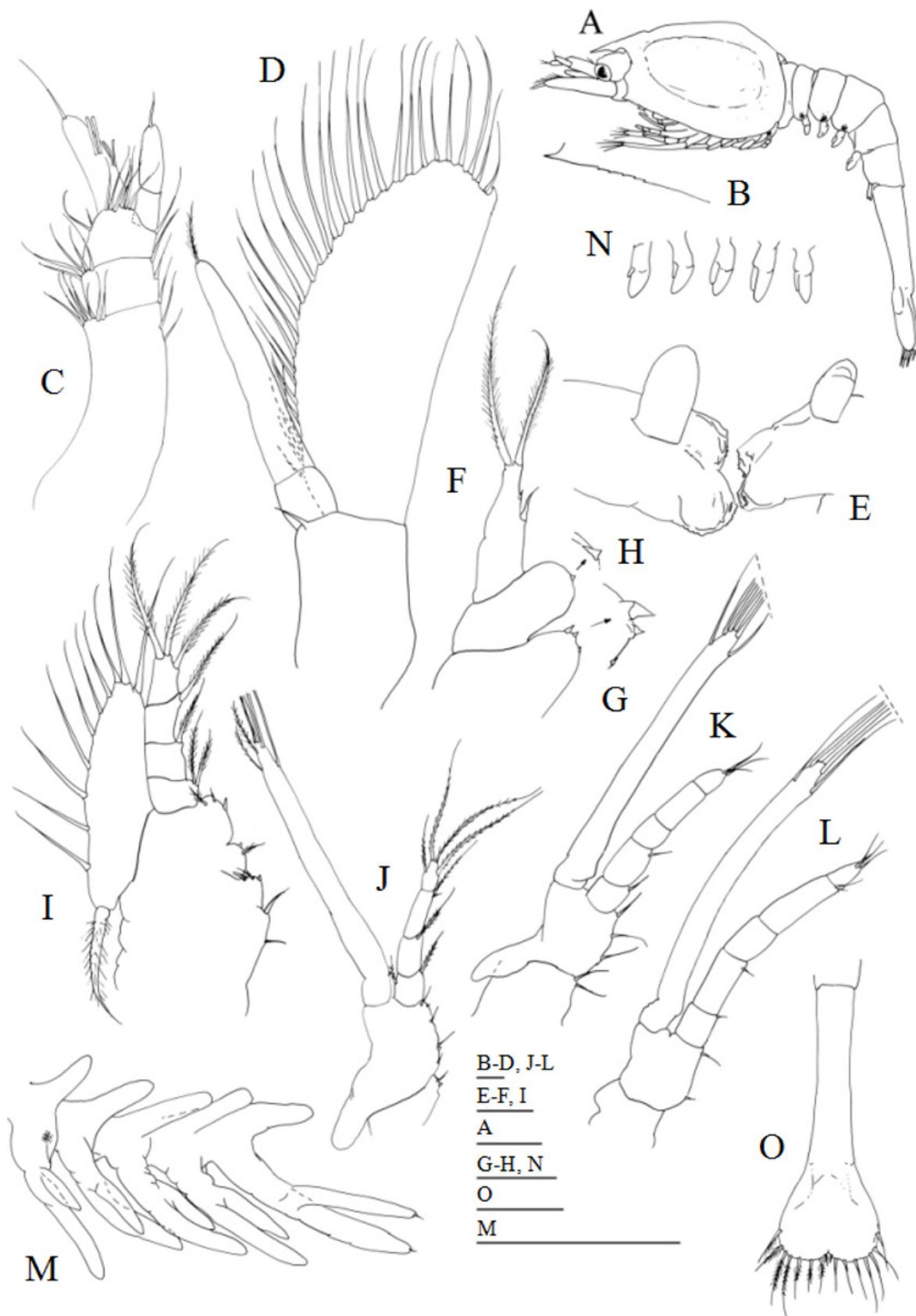
Figure 4

Third zoea.

Systellaspis debilis . Third zoea: (A) total animal, lateral view . (B) detail of carapace anterior ventral margin . (C) antennule . (D) antenna . (E) mandibles . (F) maxillule . (G) detail of maxillule coxal endite . (H) detail of maxillule basial endite . (I) maxilla . (J) first maxilliped . (K) second maxilliped . (L) third maxilliped . (M) first to fifth pereo pods . (N) pleopods . (O) detail of first pleopod exopod posterior margin . (P) detail of second pleopod exopod posterior margin . (Q) detail of third pleopod exopod posterior margin . (R) detail of fourth pleopod exopod posterior margin . (S) detail of fifth pleopod exopod posterior margin . (T) telson and uropods . (U) detail of uropods . (V) detail of uropods endopod posterior margin. Scale bars: 0.05 mm (G- H, O- S, V); 0.1 mm (A- F, I- N, T- U).
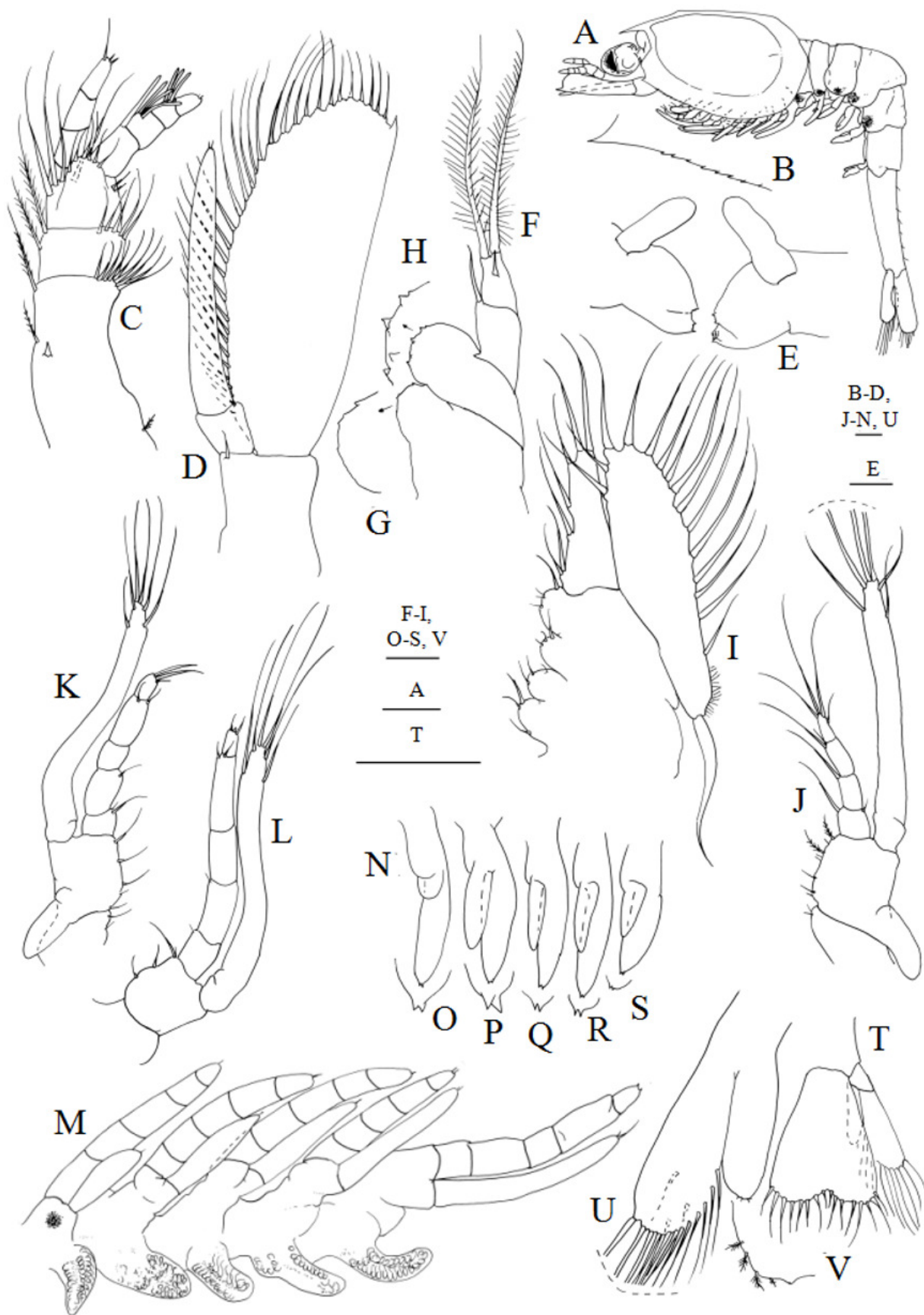
Figure 5

Fourth zoea.

Systellaspis debilis . Fourth zoea: (A) total animal, lateral view . (B) detail of rostrum . (C) antennule . (D) antenna . (E) mandibles . (F) maxillule . (G) maxilla . (H) first maxilliped . (I) second maxilliped . (J) detail of propodus posterior end and dactylus of third maxilliped . (K) first pereo pod . (L) second pereo pod . (M) third pereo pod . (N) fourth pereo pod . (O) fifth pereo pod . (P) detail of fourth pleomere posteromedial margin . (Q) detail of fifth pleomere posterior margin . (R) detail of sixth pleomere posterior margin . (S) pleopods . (T) telson and uropods. Scale bars: 0.1 mm (A, C- O); 1 mm (B, P- R, S- T).

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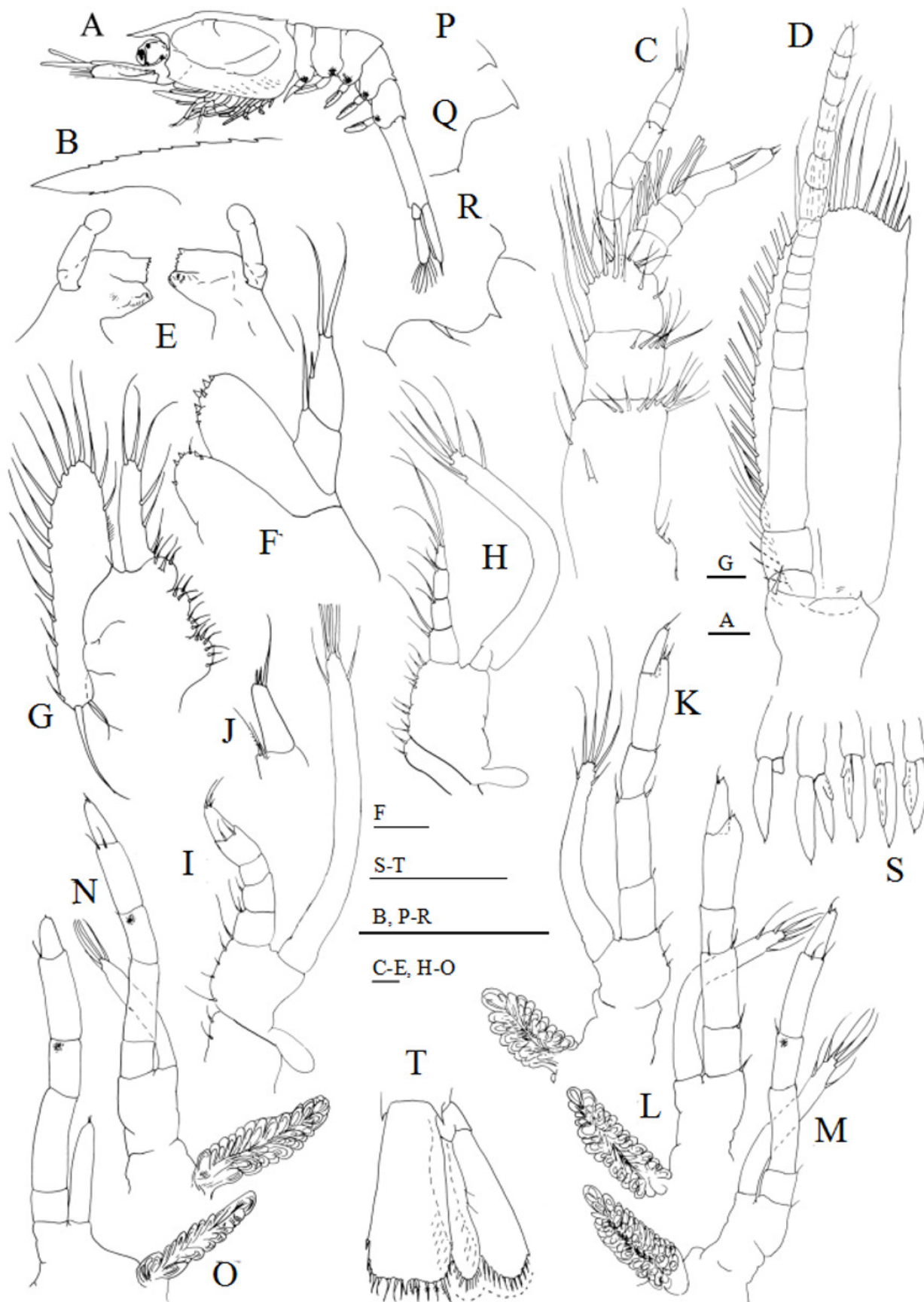
Figure 6

Decapodid.

Systellaspis debilis . Decapodid: (A) total animal, lateral view . (B) detail of rostrum . (C) detail of carapace anterior ventral margin . (D) detail of third pleomere posteromedial margin . (E) detail of fourth pleomere posteromedial margin . (F) detail of fifth pleomere posterior margin . (G) detail of sixth pleomere posterior margin . (H) antennule . (I) antenna . (J) mandibles . (K) maxillule . (L) maxilla . (M) first maxilliped . (N) second maxilliped . (O) third maxilliped . (P) detail of propodus and dactylus of third maxilliped. Scale bars: 0.1 mm (A, D- P); 1 mm (B- C).

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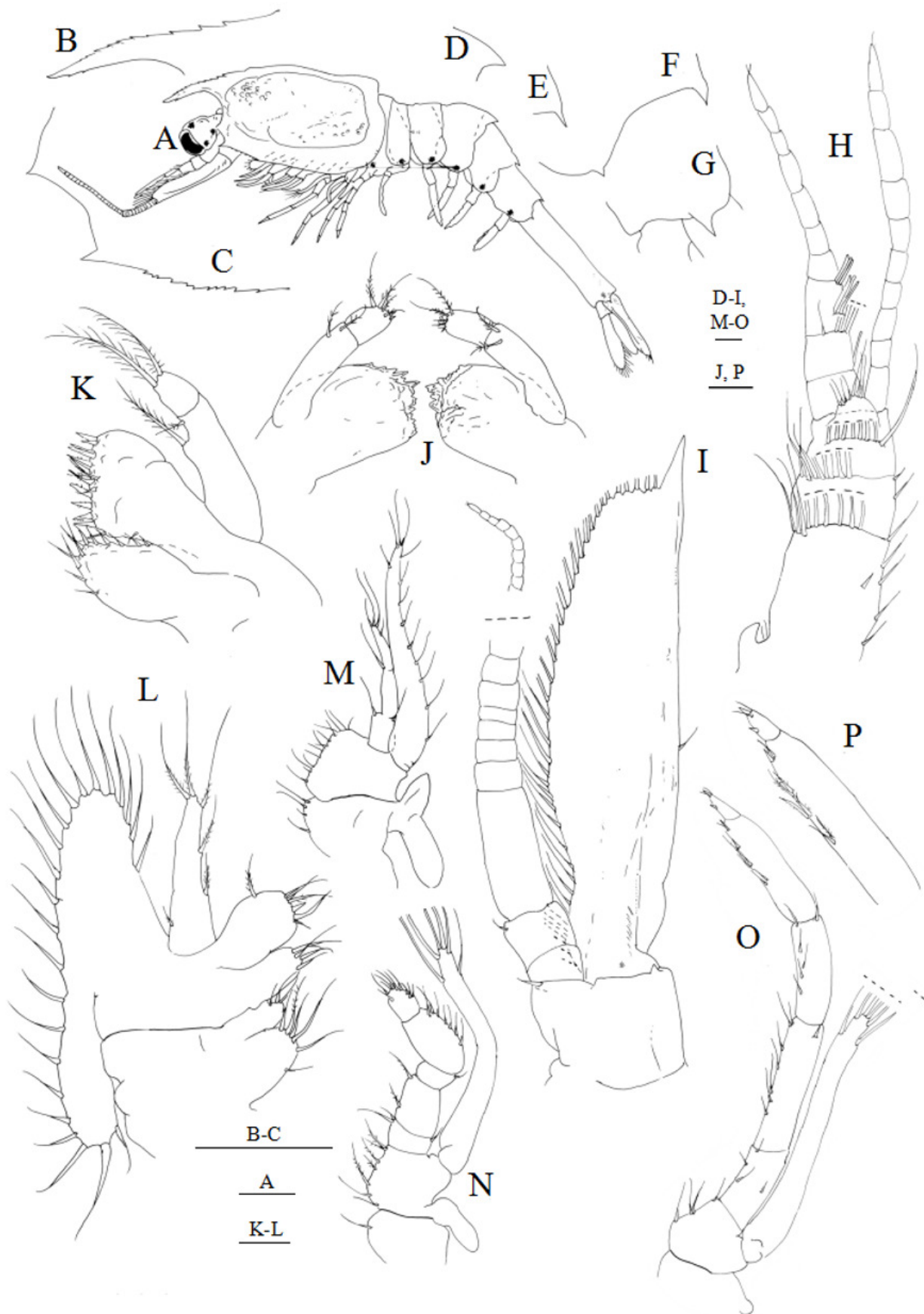
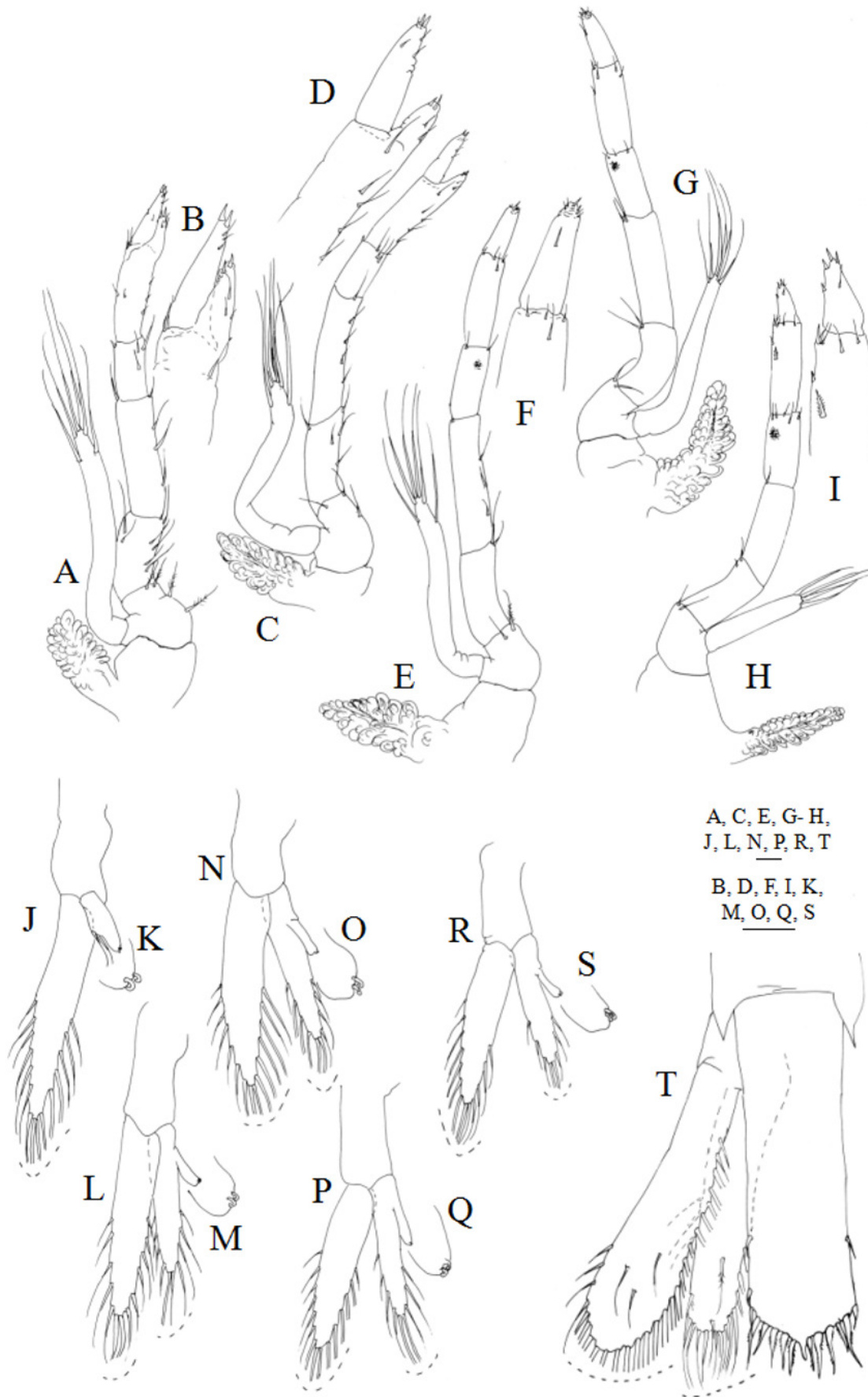


Figure 7

Decapodid.

Systellaspis debilis . Decapodid: (A) first pereo pod . (B) detail of propodus and dactylus of first pereo pod . (C) second pereo pod . (D) detail of propodus and dactylus of second pereo pod . (E) first pereo pod . (F) detail of propodus and dactylus of third pereo pod . (G) fourth pereo pod . (H) fifth pereo pod . (I) detail of propodus and dactylus of fifth pereo pod . (J) first pleopod . (K) first pleopod *appendix interna* posterior margin, detail of cincinulli . (L) second pleopod . (M) second pleopod *appendix interna* posterior margin, detail of cincinulli . (N) third pleopod . (O) third pleopod *appendix interna* posterior margin, detail of cincinulli . (P) fourth pleopod . (Q) fourth pleopod *appendix interna* posterior margin, detail of cincinulli . (R) fifth pleopod . (S) fifth pleopod *appendix interna* posterior margin, detail of cincinulli . (T) telson and uropods. Scale bars: 0.05 mm (K, M, O, Q, S); 0.1 mm (A- J, L, N, P, R, T).

Sampled females used in present study.

Sampled females used in present study, per date of collection ; number of eggs ; stage of the eggs - defined as early stage (1) , with intense colour and no other pigmentation visible , middle stage (2), with a more pale colour and an embryo having a slight eye pigmentation , and , late stag e (3), almost without colour and with an embryo with the eye pigmentation well visible and developed (adapted from *Company & Sardà, 1997*) ; size (length, corresponding to the major axis distance x width, corresponding to the minor axis distance , in mm) and volume of the eggs ; number of hatchings ; and date of hatching.

1 **Table 1**

Female	Date of collection	Nr of eggs	Stage of the eggs	Size of the eggs (in mm)	Volume of the eggs (in mm⁻³)	Nr of hatchings	Date of hatching
1	15/08/10	12	1	3.4- 3.6 x 1.9- 2.1	6.43- 8.31	0	-
2	15/08/10	8	3	3.6 x 2.1	8.31	5	20/08/10
3	15/08/10	9	3	3.5- 3.6 x 2.1	8.08- 8.31	2	7 to 8/09/10
4	15/08/10	7	1	3.6- 3.8 x 2.0	7.54- 7.96	0	-
5	15/08/10	10	2	3.5 x 2.0	7.33	4	21/09/10
6	28/06/11	9	3	3.7 x 2.0	7.75	8	1/07/11
7	28/06/11	7	2	3. 5- 3.9 x 2.0	7.33- 8.17	6	25/07/11
8	28/06/11	3	2	3. 6- 3.9 x 2.0	7.54- 8.17	0	-
9	28/06/11	2	2	3. 5- 3.9 x 2.1	8.08-9.01	0	-
10	29/06/11	11	2	3.6 x 2.1	8.31	1	29/07/11
11	21/06/11	12	3	3.7 x 2.0	7.75	9	4 to 6/07/11
12	28/06/11	10	2	3.5- 4.0 x 2.0	7.33- 8.38	8	25/07/11
13	21/06/11	12	3	3.6- 3.9 x 2.0	7.54- 8.17	10	8 to 9/07/11
		Total: 112	-	*Average:* 3.65± 0.09 x 2.0± 0.05	*Average:* 7.90± 0.53	*Total:* 53	-