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Article

Early larval development of the rock shrimps *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864) (Dendrobranchiata) with remarks of larval morphology of Sicyoniidae Ortmann, 1898

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Abstract: The aim of this study was to describe and illustrate the early larval stages, *i.e.*, the complete naupliar development and the first protozoea (PZI) of *Sicyonia dorsalis* and *S. typica* obtained under laboratory conditions. We also provide remarks from a comparative analysis of the morphology of these stages among representatives of the genus and furnish morphological characteristics to distinguish them from another penaeoidean in the plankton. Our results indicate that the naupliar development of *Sicyonia* is composed of five stages (NI to NV). No differences were found in the morphology of the naupliar and PZI stages of the two studied species, even though they are considered phylogenetically distant into the genus. We suspect that morphological differences arise later during ontogenetic development. The comparisons with larval descriptions of congeners revealed that naupliar stages and PZI were very similar, nevertheless, some morphological differences were observed. As illustrated here, there is a clear need of new descriptions of the studied group and generalizations and conclusions of larval morphology patterns at this point need to be made with caution, because data of a still insufficient number of species is available.
***Keywords*:** *Decapoda; larval morphology; metanauplius; nauplius; Penaeoidea; protozoea.*

Desenvolvimento larval inicial dos camarões-pedra *Sicyonia dorsalis* Kingsley, 1878 e *S. typica* (Boeck, 1864) (Dendrobranchiata) com observações sobre a morfologia larval de Sicyoniidae Ortmann, 1898

Resumo: O objetivo deste estudo foi descrever e ilustrar os estágios larvais iniciais, ou seja, o desenvolvimento naupliar completo e a primeira protozoea (PZI) de *Sicyonia dorsalis* e *S. typica* obtidos em laboratório. Também fornecemos observações a partir de uma análise comparativa da morfologia desses estágios entre representantes do gênero e as características morfológicas para distingui-los de outros Penaeoidea no plâncton. Nossos resultados indicam que o desenvolvimento naupliar de *Sicyonia* é composto por cinco estágios (NI a NV). Não foram encontradas diferenças na morfologia dos estágios naupliares e PZI das duas espécies estudadas, apesar de serem consideradas filogeneticamente distantes dentro do gênero. Nossa hipótese é que as diferenças morfológicas surgem mais tarde durante o desenvolvimento ontogenético. As comparações com as descrições larvais de congêneres revelaram que os estágios naupliares e PZI são muito semelhantes, no entanto, algumas diferenças morfológicas foram observadas. Conforme ilustrado aqui, há uma clara necessidade de novas descrições do grupo estudado e generalizações e conclusões de padrões na morfologia larval neste momento precisam ser feitas com cautela, pois dados de um número ainda insuficiente de espécies estão disponíveis.
***Palavras-chave*:** *Decapoda; morfologia larval; metanáuplio; náuplio; Penaeoidea; protozoea.*

Introduction

The monotypic family Sicyoniidae Ortmann, 1898 is one of five families included among the Penaeoidea Rafinesque, 1815, with 52 described species distributed worldwide in tropical and subtropical areas of the Atlantic, Pacific, and Indian oceans (Pérez Farfante & Kensley 1997, De Grave & Fransen 2011). From the nine species already registered in the Atlantic coast of Americas, six occur in Brazilian waters: *Sicyonia dorsa*lis Kingsley, 1878, *Sicyonia typica* (Boeck, 1864), *Sicyonia laevigata* Stimpson, 1871, *Sicyonia parri* (Burkenroad, 1934), *Sicyonia burkenroadi* Cobb, 1971, and *Sicyonia olgae* Pérez Farfante, 1980 (D'Incao 1995, Pérez Farfante & Kensley 1997, De Grave & Fransen 2011). Among these, *S. dorsalis*, *S. laevigata*, *S. parri,* and *S. typica* occur in the southeastern subtropical region of Brazil (Costa et al. 2000, Mantelatto et al. 2022).

Sicyonia dorsalis and *S. typica* have being found in shallow coastal regions, from North Carolina (USA) to Rio Grande do Sul (Brazil) (D'Incao 1995, Mantelatto et al. 2022). Even though rock shrimp species are currently not commercially exploited in Brazil, they are part of the by-catch of penaeid shrimp fisheries of high economic interest (Keunecke et al. 2007, Costa et al. 2016). *Sicyonia dorsalis* and *S. typica* are the most abundant sicyoniid species in the bycatch of the trawling of commercial species such as the seabob shrimp *Xiphopenaeus* spp. Smith, 1869 and the pink shrimp *Farfantepenaeus* spp. Burukovsky, 1997, respectively (Costa et al. 2005, Costa & Simões 2016). As explained by Carreton et al. (2020), a key aspect of fisheries science is the study of species connectivity, and planktonic larvae directly influence this mechanism by its dispersal capability. In this context, correct identification of dendrobranchiate larvae by means of larval keys (*e.g.*, Calazans 1993, Carreton et al. 2020) is particularly useful for fisheries science because it can furnish information on the spawning areas as initial stages occur from a few hours to a few days after hatching (Martin et al. 2014).

Sicyonia dorsalis has already been studied in relation to copulation and insemination system (Bauer 1992, 1996a, b), and population dynamics (Castilho et al. 2008a, b). Published information on the biology of *S. typica* is not available, except for mentions in ecological studies on the benthic community (Fransozo et al. 2002, Costa et al. 2000, 2003, Castilho et al. 2008c, Pantaleão et al. 2016, among others). In a study of integrative analysis of sperm ultrastructure and molecular phylogeny, Camargo et al. (2015) showed that these two species are not closely related within the genus.

After a review of the larval descriptions of *Sicyonia* we noted that less than 10% of the species had at least some larval stage described. Information on larval morphology of *Sicyonia* is currently limited to five species: *S. sculpta* H. Milne Edwards, 1830 by Monticelli & Lo Bianco (1900); *S. carinata* (Brünnich, 1768) by Heldt (1938); *S. stimpsoni* Bouvier, 1905 as *Eusicyonia stimpsoni* (Bouvier) by Pearson (1939); *S. wheeleri* Gurney, 1943 by Gurney (1942) and Gurney (1943); and *S. brevirostris* Stimpson, 1871 by Cook & Murphy (1965). In addition to these five species, a protozoea III and the decapodid of *Sicyonia* sp. were described by Paulinose (1982). The larval descriptions of *S. stimpsoni* by Pearson (1939) and *Sicyonia* sp. by Paulinose (1982) were carried out from plankton samples.

The knowledge of larval morphology is important to solve phylogenetic issues, besides allowing the elaboration of identification keys for the study of larval ecology (Iorio et al. 1990, González-Gordillo & Rodriguez 2000, Vela & González-Gordillo 2016). One of the best ways to safely describe penaeid larvae is to obtain them in the laboratory, starting with the eggs of adults identified with security (Jackson et al. 1989). Thus, the aim of this study was to describe and illustrate for the first time the early larval stages of *S. dorsalis* and *S. typica* obtained under laboratory conditions. We also provide remarks from a comparative analysis of the morphology of these stages among representatives of the genus.

Material and Methods

One female of *Sicyonia dorsalis* and two of *S. typica* with developed ovaries were captured at Ubatuba, state of São Paulo, Brazil (23°26′13″S;45°04′4″W) in October 2012 and July 2013, respectively. Collections were made at 10 m depth, using a shrimp-fishing boat equipped with two otter-trawl nets with 5 m door openings, mesh size 20 mm and 18 mm in the cod end.

The females were transported alive to Laboratory of Biology of Marine and Freshwater Shrimps (LABCAM) and maintained in individuals 2-liter containers with seawater from the sampling site until spawning, when females were removed from the containers. No food was offered to the females during this period. After spawning, the carapace length (posterior margin of the ocular orbit to the posterior margin of the carapace = CL mm) of females was measured with a digital caliper of 0.01 mm accuracy and they were conserved with ethyl alcohol 98%. The hatched larvae were mass-reared with no food offer, under continuously moderate aeration and constant 25°C and salinity 33 in small beakers of 500 ml. Twenty individuals with active natatory behavior were removed every 3 h and conserved in a mixture (1:1) of ethyl alcohol (80%) and glycerin. The initial number of larvae per batch was not quantified. Experiments were stopped after the first protozoeal stage because all larvae died during this stage.

Dissections, drawings, and measurements were made under a Zeiss Stemi 2000C trinocular stereomicroscope, and a Leica DM750 microscope equipped with a *camera lucida*. Morphological description and measurement of each larval stage were based on the observation of at least 10 individuals. Larvae were measured as follows: total length (TL) of nauplius, from the apical to caudal margins, excluding furcal spines; total length (TL) of protozoea, from the apical margin of carapace to the apex of telson, excluding furcal spines; carapace length (CL) of protozoea, the distance between the postorbital margin and the median posterior border of the carapace (Ronquillo & Saisho 1997, Ronquillo et al. 2006). All measurements were made with an ocular micrometer. GraphPad Prism 8.0.2 (GraphPad Software, Inc., San Diego, CA, USA) was used for size data (TL) analysis. Data were evaluated by Shapiro–Wilk normality test. Considering a 2-way layout, interaction means were compared using analysis of variance (ANOVA) followed by Sidak's post hoc test. Data were shown as the mean ± SD and results were considered statistically significant when $p < 0.05$.

Nomenclature of larval stages and body parts followed Dall et al. (1990), Leong et al. (1992) and Ronquillo et al. (2006). Because there is no standardization for larval descriptions of Penaeoidea until now, sequence of larval descriptions followed the standards proposed for brachyuran larval descriptions (Clark et al. 1998, Clark & Cuesta 2015) complemented by standards of larval descriptions of penaeoideans (Ronquillo & Saisho 1997, Carreton et al. 2020) and caridean shrimps

(Pantaleão et al. 2020). Setal terminology is based on that used by Garm (2004).

Parental females and respective larvae (from each obtained stage) were deposited as voucher specimens at the Crustacean Collection of the Biology Department of Faculty of Philosophy, Sciences and Letters at Ribeirão Preto (FFCLRP), University of São Paulo (USP), Brazil (CCDB/FFCLRP/USP) under access numbers: CCDB 6676 and CCDB 6677, for *S. dorsalis* and *S. typica*, respectively. Tissue samples were taken from the parental females for molecular analysis of partial fragments of the ribosomal rRNA, 16S rRNA gene to confirm identification (GenBank Accession number OM971000 and OM970999 for *S. dorsalis* and *S. typica*, respectively).

A comparative analysis of selected characters of the naupliar stages and first protozoeal stage of *Sicyonia* species was performed using original descriptions and illustrations of each species. Larval stages from some studies were not included (naupliar, protozoeal or both) in the comparisons for different reasons, such as being very brief, *i.e.*, without sufficient morphological details to allow comparisons (Monticelli & Lo Bianco 1901, Gurney 1943) and/or obtained from plankton samples without assurance of the identification (Pearson 1939, Paulinose 1982).

Results

The parental females of *S. dorsalis* had a CL of 11.71 mm, and *S. typica* of 13.20 mm and 21.32 mm. Spawnings were observed between 10:00 and 12:00 p.m., and about 90% of larvae emerged 12 h after spawning time. The larvae passed through 5 naupliar stages (NI to NV) before reaching first protozoeal stage (PZI) in a minimum of about two days (48h) from hatching (Table 1). The naupliar and PZI stages of *S. dorsalis* and *S. typica* were completely described in detail. Size (TL) of larvae differed among each larval stage but did not differ between species in each larval stage (two-way ANOVA, $p < 0.05$) (Figure 1). As the external morphology did not differ between species, illustrations were made for both species together.

Larval description

Order DECAPODA Latreille, 1802
Suborder DENDROBRANCHIATA Spence Bate, 1888
Family SICYONIIDAE Ortmann, 1898
Genus *SICYONIA* H. Milne Edwards, 1830
Sicyonia dorsalis Kingsley, 1878 and *Sicyonia typica* (Boeck, 1864) [Figures 2–3(A–H)]

Table 1. Chronology of larval development of *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864) from Ubatuba, state of São Paulo, Brazil, at 25 ºC and 33 of salinity.

Cumulative time (hours)	Stage
00	First nauplius (NI)
06	Second nauplius (NII)
13	Third nauplius (NIII)
21	Fourth nauplius (NIV)
37	Fifth nauplius (NV)
47	First protozoea (PZI)

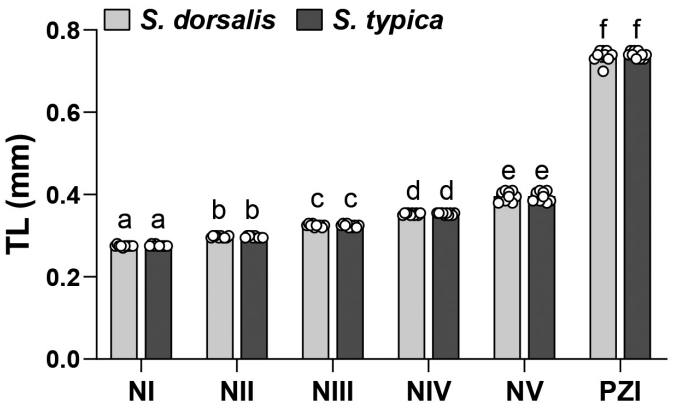

Figure 1. Total length (TL) of *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864) naupliar and first protozoeal (PZI) stages. The TL was measured in ten larvae of each developmental stage of both species and compared using two-way ANOVA followed by Sidak post hoc test. Different letters represent significant differences ($p < 0.05$) among stages. NI. Fist nauplius; NII. Second nauplius; NIII. Third nauplius; NIV. Fourth nauplius; NV. Fifth nauplius; PZI. First protozoea.

FIRST NAUPLIUS (NI) (Figure 2)

Dimensions: *Sicyonia dorsalis* TL: 0.275 ± 0.002 mm; *S. typica* TL: 0.276 ± 0.002 mm (10 larvae from each species).

Body: ovoid and unsegmented, with pairs of antennules, antennae and mandibles; labrum projects ventrally from enlarged cephalic region; median ocellus located near anterior end; furcal spine formula 1 + 1 + 1.

Antennule: uniramous; with 2 short ventrolateral, 1 dorsolateral, and 2 terminal simple setae plus a small terminal spine.

Antenna: endopod with 2 small ventrolateral and 2 terminal simple setae plus a small terminal spine; exopod with 5 ventrolateral simple setae plus a small terminal spine.

Mandible: endopod and exopod with 1 subterminal and 2 terminal simple setae.

SECOND NAUPLIUS (NII) (Figure 2)

Dimensions: *Sicyonia dorsalis* TL: 0.298 ± 0.003 mm; *S. typica* TL: 0.297 ± 0.003 mm (10 larvae from each species).

Body: similar to previous stage, except for the absence of the median protuberance on the posterior rounded region; furcal spine formula 1 + 1.

Antennule: uniramous; with 3 small ventrolateral simple, 1 dorsolateral simple and 3 (2 simple and 1 plumose) terminal setae; minute distal spinules on outer margin, as illustrated.

Antenna: endopod with 2 small ventrolateral simple and 2 terminal plumose setae plus a small terminal spine; exopod with 5 ventrolateral plumose setae plus a small terminal spine.

Mandible: as in previous stage, but all setae are plumose.

THIRD NAUPLIUS (NIII) (Figure 2)

Dimensions: *Sicyonia dorsalis* TL: 0.325 ± 0.003 mm; *S. typica* TL: 0.325 ± 0.004 mm (10 larvae from each species).

Body: similar to previous stage; a depression separates two developing furcal processes; furcal spine formula 3 + 3.

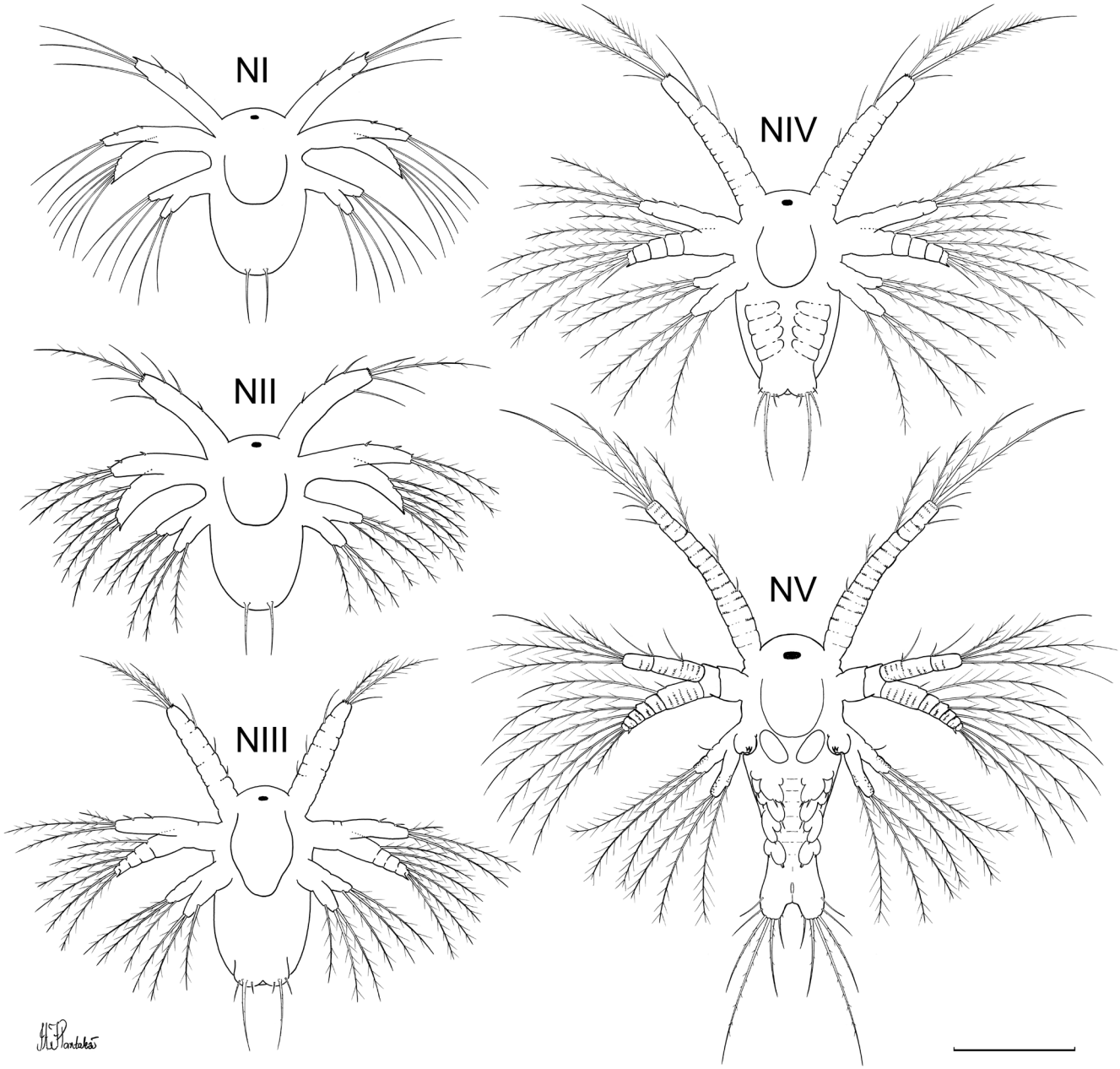

Figure 2. *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864), naupliar stages, ventral view. NI. Fist nauplius; NII. Second nauplius; NIII. Third nauplius; NIV. Fourth nauplius; NV. Fifth nauplius. (Scale bar = 0.2 mm).

Antennule: uniramous with annular indentions; 3 small ventrolateral simple and 3 (1 simple and 2 plumose) terminal setae; minute distal spinules on outer margin, as illustrated.

Antenna: endopod with 2 small ventrolateral simple and 3 terminal plumose setae; exopod with 4 ringlets with transversal incomplete separations, 6 plumose setae on the inner side (1, 1, 1, 3), plus a small terminal spine.

Mandible: unchanged.

FOURTH NAUPLIUS (NIV) (Figure 2)

Dimensions: *Sicyonia dorsalis* TL: 0.353 ± 0.003 mm (10 larvae); *S. typica* TL: 0.354 ± 0.002 mm (10 larvae from each species).

Body: similar to previous stage except for the elongation of the abdominal region, with outline of developing limbs (maxillule, maxilla and first and second maxillipeds) evident following mandible; furcal spine formula 5 + 5.

Antennule: unchanged, except by the number of annular indentions.

Antenna: endopod unchanged; exopod with 5 ringlets with 6 plumose setae on the inner side (1, 1, 1, 1, 2), plus a simple seta on the inner side and a small terminal spine on the fifth ringlet.

Mandible: unchanged.

FIFTH NAUPLIUS (NV) (Figure 2)

Dimensions: *Sicyonia dorsalis* TL: 0.397 ± 0.012 mm (10 larvae); *S. typica* TL: 0.396 ± 0.011 mm (10 larvae from each species).

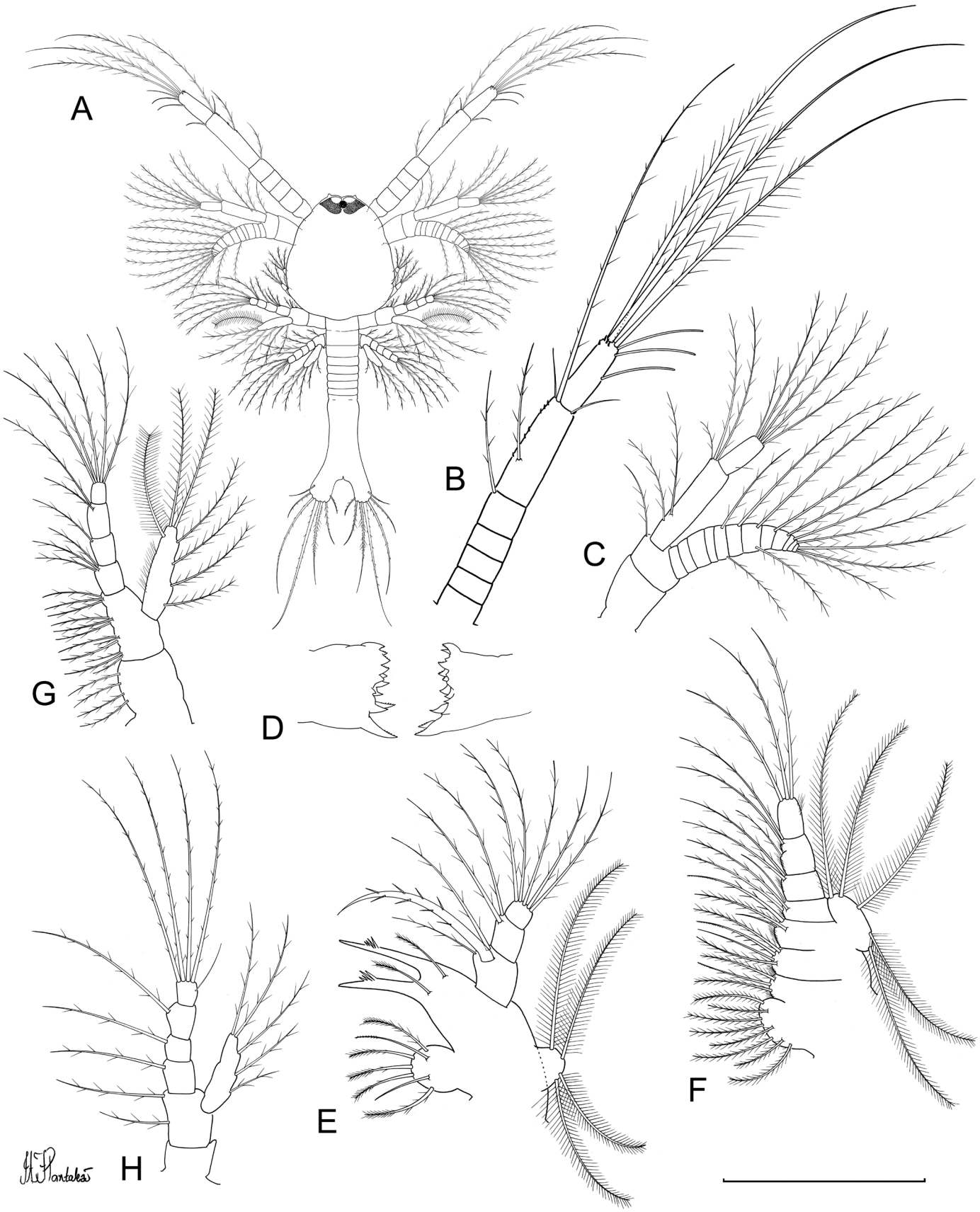

Figure 3. *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864), first protozoea (PZI). I. A. Dorsal view; B. Antennule; C. Antenna; D. Mandibules; E. Maxillule; F. Maxilla; G. First maxilliped; H. Second Maxilliped. (Scale bar: A = 0.5 mm; D, E, F = 0.05 mm; B, C, G, H = 0.1 mm).

Body: abdominal region has become slender; furcal spine formula 6–7 + 6–7.

Antennule: inner and outer margins with rows of minute spinules on the annular indentions as illustrated; 3 (1 small simple and 2 plumose) ventrolateral, 1 dorsolateral simple and 5 (2 simple and 3 plumose) terminal setae.

Antenna: coxa and basis without setae; endopod 2-segmented with 4 simple setae arranged 2 + 2 and 4 terminal plumose setae, respectively; exopod with 6 ringlets with 8 plumose setae on the inner side (1, 1, 1, 1, 1, 3), plus a marginal simple seta on the inner side of first ringlet and a small terminal spine on the outer side of fifth ringlet; rows of minute spinules on inner and outer margin of endopod and exopod, as illustrated.

Mandible: basal nodule (gnathobase) with initial serration; endopod with 1 ventrolateral simple and 3 terminal plumose setae; exopod with 3 terminal plumose setae; rows of minute spinules on inner and outer margin of endopod and exopod, as illustrated.

Maxillule, *Maxilla, First maxilliped* and *Second maxilliped*: present as biramous non-articulated buds; primordial setae present at tips of endopods and exopods.

FIRST PROTOZOEA (Figures 3A–H)

Dimensions: *Sicyonia dorsalis* CL 0.340 ± 0.009 mm, TL 0.737 ± 0.015 mm; *S. typica* CL 0.341 ± 0.009 mm, TL 0.740 ± 0.008 mm (10 larvae from each species).

Carapace (Figure 3A): almost rounded, longer than wider, reaching the level of the second maxilliped, without rostrum; frontal organs visible at the anterior part; naupliar eye present flanked by compound eyes visible through the carapace; 7 thoracic somites visible.

Antennule (Figures 3A, B): consisting of 3 articles; proximal article subdivided in 5 ringlets with 0, 0, 0, 0, 1 sparsely plumose seta; second article with 4 (1 marginal and 1 terminal sparsely plumose and 2 terminal simple) setae; distal article with 3 (1 marginal and 2 terminal) aesthetascs and 3 terminal plumose setae; minute spinules on outer margin of second and third articles, as illustrated.

Antenna (Figures 3A, C): shorter than antennule; peduncle 2-segmented, proximal segment without setae, distal segment with 1 terminal sparsely plumose seta; endopod 2-segmented with 5 (2 proximal and 3 terminal) sparsely plumose and 6 (1 proximal simple and 5 terminal sparsely plumose) setae, respectively; exopod with 12 ringlets with 12 sparsely plumose setae, 10 on the inner side (0, 0, 0, 0, 1, 1, 1, 1, 1, 1, 1, 3) and 2 on the outer side (0, 0, 0, 0, 1, 0, 1, 0, 0, 0, 0, 0).

Mandible (Figure 3D): incisor and molar processes well developed; palp absent.

Maxillule (Figure 3E): coxal endite with 7 (1 simple, 1 denticulate and 5 plumose) setae; basial endite with 2 cuspidate processes and 2 plumose setae; endopod 3-segmented, with 3 (1 cuspidate and 2 sparsely plumose), 2 sparsely plumose and 5 sparsely plumose setae, respectively; exopod margin with 4 long plumose setae.

Maxilla (Figure 3F): coxal endite bilobed, with 8 plumose and 3 (2 plumose and 1 sparsely plumodenticulate) setae on proximal and distal lobes, respectively; basial endite bilobed, with 4 (1 sparsely plumose, 1 sparsely plumodenticulate and 2 plumose) and 3 (1 simple, 1 sparsely plumodenticulate and 1 plumose) setae on proximal and distal lobes, respectively; endopod 4-segmented, with 3 (1 simple and 2 sparsely plumose), 2 sparsely plumose, 3 sparsely plumose and 3 sparsely plumose setae, respectively; exopod (scaphognathite) margin with 5 long plumose setae; microtrichia on margins of coxal endite, basial endite and endopod, as illustrated.

First maxilliped (Figures 3A, G): coxa with 4 sparsely plumose setae arranged 1 + 1 + 1 + 1; basis with 12 sparsely plumose setae arranged 3 + 3 + 3 + 3; endopod 4-segmented with 3, 1, 2, 5 sparsely plumose setae, respectively; exopod with 6 (4 marginal and 2 distal) sparsely plumose setae and 1 subterminal plumose seta; microtrichia on inner margin of exopod.

Second maxilliped (Figure 3A, H): coxa without setae, with a terminal process on outer margin; basis with 2 sparsely plumose setae arranged 1 + 1; endopod 4-segmented, with 1, 1, 1 sparsely plumose, and 5 (1 subterminal simple and 4 sparsely plumose) setae, respectively; exopod with 5 (3 marginal and 2 distal) sparsely plumose setae.

Third maxilliped: absent.

Pereiopods: absent.

Pleon (Figure 3A): pleomeres not completely differentiated, fused with the telson and unarmed.

Pleopods: absent.

Uropods: absent.

Telson (Figure 3A): broadly bifurcate, each branch with 7 plumose setae with distinct number of setules as illustrated.

Discussion

In the present study, no differences were found in the morphology and size of the naupliar and first protozoeal stages of two species of *Sicyonia* that occur on the southeast coast of Brazil, even though these species are considered phylogenetically distant into the genus (see Camargo et al. 2015). Thus, it is possible that morphological differences arise later during ontogenetic development, and that some differences in relation to other congeners (Tables 2 and 3) are result of misidentification in previous studies, as discussed below.

In the published larval descriptions of *Sicyonia* there are reports of different numbers of naupliar stages. In descriptions based on plankton samples, Pearson (1939) observed five. Studying naupliar development in the laboratory, Heldt (1938) described eight stages for *S. carinata* while Cook & Murphy (1965) observed five stages, similar to our results and probably the common number of stages of naupliar development of *Sicyonia*. Another divergent result was observed by Gurney (1943) who distinguished only three stages for *S. wheeleri* in the laboratory.

Interestingly, Gurney (1943) mentioned that he was convinced that the naupliar stages are not so numerous in *S. wheeleri* as eight in *S. carinata* (Heldt 1938); but he believed that there may be more than he had seen (three stages). Gurney (1943) also mentioned that it was probable that the first stage (NI) may have been missed, and that he was able to state with certainty that there was no moult, or at least no observable change, between 9 a.m. and 6 p.m. on the day of hatching. Thus, Gurney (1943) probably missed some stages, and for this reason, together with the lack of many morphological details, we have not included descriptions of *S. wheeleri* in our comparative table of naupliar development (Table 2). The loss of some naupliar

Table 2. Comparison of selected morphological characters of naupliar stages of the genus *Sicyonia.* Abbreviations: ps = plumose seta; seg. = segmented; sp = spine; ss = simple seta.

Source			**Heldt (1938)**	**Cook & Murphy (1965)**	**Present study**	**Present study**
Species			*Sicyonia carinata*	*Sicyonia brevirostris*	*Sicyonia dorsalis*	*Sicyonia typica*
Locality			Tunisia	Gulf of Mexico	Brazil	Brazil
First nauplius (NI)	TL (mm)		0.26	0.3 (0.28 – 0.32)	0.275 ± 0.002	0.276 ± 0.002
	Antenulle		5ss + 1sp	5ss + 1sp	5ss + 1sp	5ss + 1sp
	Antenna	Endopod	4ss + 1sp	4ss	4ss + 1sp	4ss + 1sp
		Exopod	5ss + 1sp	5ss	5ss + 1sp	5ss + 1sp
	Mandible	Endopod	3ss	3ss	3ss	3ss
		Exopod	3ss	3ss	3ss	3ss
	Buds of other limbs		absent	absent	absent	absent
	Furcal formula		1 + 1	1 + 1	1 + 1	1+1
Second nauplius (NII)	TL (mm)		–	0.31 (0.29 – 0.34)	0.298 ± 0.003	0.297 ± 0.003
	Antenulle		6 setae	6 setae	6ss + 1ps	6ss + 1ps
	Antenna	Endopod	4 setae + 1sp	4 setae	2ss + 2ps + 1sp	2ss + 2ps + 1sp
		Exopod	5 setae + 1sp	6 setae	5ps + 1sp	5ps + 1sp
	Mandible	Endopod	3 setae	3 setae	3ps	3ps
		Exopod	3 setae	3 setae	3ps	3ps
	Buds of other limbs		absent	absent	absent	absent
	Furcal formula		1 + 1	1 + 1	1 + 1	1 + 1
Third nauplius (NIII)	TL (mm)		0.32	0.35 (0.32 – 0.37)	0.325 ± 0.003	0.325 ± 0.004
	Antenulle		6 setae	6 setae	4ss + 2ps	4ss + 2ps
	Antenna	Endopod	5 setae	5 setae	2ss + 3ps	2ss + 3ps
		Exopod	6 setae + 1sp	7 setae	6ps + 1sp	6ps + 1sp
	Mandible	Endopod	3ps	3 setae	3ps	3ps
		Exopod	3ps	3 setae	3ps	3ps
	Buds of other limbs		outline	outline	absent	absent
	Furcal formula		2 + 2	3 + 3	3 + 3	3 + 3
Fourth nauplius (NIV)	TL (mm)		0.33 – 0.34	0.37 (0.33 – 0.40)	0.353 ± 0.003	0.354 ± 0.002
	Antenulle		6 setae	7 setae	4ss + 2ps	4ss + 2ps
	Antenna	Endopod	5 setae	5 setae	2ss + 3ps	2ss + 3ps
		Exopod	6 setae + 2sp	8 setae	4-seg., 6ps + 1ss + 1sp	4-seg., 6ps + 1ss + 1sp
	Mandible	Endopod	3ps	3 setae	3ps	3ps
		Exopod	3ps	3 setae	3ps	3ps
	Buds of other limbs		outline	outline	outline	outline
	Furcal formula		4 + 4	5 + 5	5 + 5	5 + 5
Fifth nauplius (NV)	TL (mm)		0.38 – 0.40	0.44 (0.38 – 0.46)	0.397 ± 0.012	0.396 ± 0.011
	Antenulle		9 setae	10 setae	4ss + 5ps	4ss + 5ps
	Antenna	Endopod	8 setae	8 setae	4ss + 4ps	4ss + 4ps
		Exopod	9 setae	9 setae	5-seg., 1ss + 8ps + 1sp	5-seg., 1ss + 8ps + 1sp
	Mandible	Endopod	3ps	3 setae	**1ss** + 3ps	**1ss** + 3ps
		Exopod	3ps	3 setae	3ps	3ps
	Buds of other limbs		present	present	present	present
	Furcal formula		7 + 7	7 + 7	6 – 7 + 6 – 7	6 – 7 + 6 – 7

stages during cultivation of larvae in the laboratory is probably common during the study of larval development of penaeoids as the morphological changes between naupliar stages are very subtle making it difficult to differentiate them with observations of live animals under a stereomicroscope. In this way, constant and rigorous monitoring during cultivation is essential.

Regarding naupliar development, it was possible to compare the morphology of the studied species with available descriptions of *S. brevirostris* (Cook & Murphy 1965) and *S. carinata* (Heldt 1938) (Table 2). The morphology of naupliar stages was very similar. Even so, it was detected some differences in all stages. In the NI, *S. brevirostris* is the single species that lacks a spine at the apex of both endopod and exopod of the antenna; this spine was also not described for *S. brevirostris* on the endopod of NII. For the NII, the species studied here presented an extra seta (total of seven) on the antennule, when compared with *S. brevirostris* and *S. carinata*. The NIII of *S. carinata* was the single species with furcal formula 2 + 2, while the others had 3 + 3; furcal formula of NIV was also different between *S. carinata* (4 + 4) and the others (5 + 5). The NIV of *S. brevirostris* was the single species with seven setae on the antennule, while others had six. The NV of *S. brevirostris* also had one more seta (ten) in the antennule than other species (nine); additionally, a spine on the exopod of antenna and a simple seta on the endopod of mandible were found only in *S. dorsalis* and *S. typica*. In relation to size, we observed a gradual increase in the TL of larvae during naupliar development, and a faster growth (almost doubling the size) in the passage to PZI. These results were very similar to the observed for *S. brevirostris* and *S. carinata* (see Tables 1 and 2, and references therein) and seems to be a pattern for the early larval development of sycioniids.

As aforementioned, Heldt (1938) obtained eight naupliar stages of *S. carinata* under laboratory conditions at approximately 20ºC. To perform morphological comparisons, we matched the stages obtained in the present study with those of *S. carinata*. In general, the NI, NII and NIII described by Heldt (1938) are very similar with the same stages obtained here. After that, Heldt's NIV and NV showed no differences and probably correspond to the NIV of the other species, while the NVI, NVII and NVIII seem to have gradually acquired the characteristics corresponding to the NV (or metanauplius) of congeners. Among other species and stages, Heldt (1938) described the naupliar development and PZI of *Penaeus kerathurus* (Forskål, 1775) as *Penaeus trisulcatus* (Leach, 1814 [in Leach, 1813–1815]) and explained that the larvae of *S. carinata* were practically identical. However, in the study of Heldt (1938) there is an illustration of *S. carinata* (Figure 56, 2) with a naupliar stage in which furcal formula is 3 + 3, and this formula was not mentioned for any of the eight described stages. Therefore, it is possible that some observed differences from Table 2 (such as the 2 + 2 furcal formula of NIII of *S. carinata*) are a result of undescribed details rather than actual morphological differences.

The morphology of the first protozoa was also similar, but it is possible to point out characteristics that distinguish the species described so far (Table 3). Both species studied here and *S. carinata* have eight setae in the antennule, while for *S. wheeleri* and *S. brevirostris* the exact number was not mentioned, and the three aesthetascs were described only in the present study; *S. breviostris* and *S. carinata* had one and two less setae on the endopod of antenna, respectively, when compared with the species studied here; endopod of maxillule of *S. brevirotris* and *S. carinata* had one less seta on the proximal lobe (formula of 2,2,5, while 3,2,5 for *S. dorsalis* and *S. typica*); coxal endite of maxilla with 7 + 4 and 9 + 3 setae in *S. brevirostris* and *S. carinata*, respectively, instead of 4 + 3, for *S. dorsalis* and *S. typica*; basial endite of maxilla with 3 + 3 setae in *S. brevirostris* and *S. carinata*, instead of 4 + 3, for *S. dorsalis* and *S. typica*; proximal segment of endopod of maxilla with one less seta in the proximal segment of *S. brevirostris* (formula of 2,2,3,3, while 3,2,3,3 for *S. carinata, S. dorsalis* and *S. typica*); basis of first maxilliped with 9–11 setae, while *S. carinata, S. dorsalis* and *S. typica* had 12 setae, and endopod with one less seta in the proximal segment of *S. brevirostris* (formula of 2,1,2,5 instead of 3, 1,2,5 for *S. carinata*, *S. dorsalis* and *S. typica*); exopod of the second maxilliped with five setae in *S. dorsalis* and *S. typica*, and with six setae in *S. breviostris* and *S. wheeleri*; and finally, the third maxilliped is absent in both species described here, but it appears as biramous buds in all other species.

Regarding all described stages here (NI to NV and PZI), other morphological differences were found during our descriptions in relation to congeners. We found small terminal spinules at the antennule of NII, NIII and NIV, and along practically the entire length of the limbs (antennule, antenna, and mandible) of the NV, which were not described for other *Sicyonia* species (Gurney 1943, Heldt 1938, Cook & Murphy 1965). It would be premature to conclude if these differences are exclusive of the studied species, as well as to affirm if they are real differences or effect of misidentification, considering the low number of available descriptions that fit modern standards. The descriptions of *S. brevirostris* and *S. wheeleri* are somewhat brief and did not include several details, as the types of setae that were practically not mentioned by Cook and Murphy (1965) and very few limbs or regions of the body were described for *S. wheeleri* (Gurney 1943).

A conspicuous terminal spine in the antennule of first nauplius (NI) is probably present in all studied sicyoniids to date (see Table 2 and references therein). We hypothesize that this morphological character, together with the aforementioned spinules (antennule of NII, NIII, NIV and all limbs of NV) could represent informative characteristics to differentiate the genus in the plankton. Considering previous descriptions of penaeoideans that occur in Brazilian coast, these characteristics were not observed in any of them. These larval descriptions include: *Litopenaeus schmitti* (Burkenroad, 1936) (Garcia-Pinto & Ewald 1974), *Pleoticus muelleri* (Spence Bate, 1888) (Iorio et al. 1990), *Artemesia longinaris* Spence Bate, 1888 (Boschi & Scelzo 1977), *Rimapenaeus constrictus* (Stimpson, 1871) (Pearson 1939, from plankton), and *Xiphopenaeus* sp. (Heller, 1862) (Renfro & Cook 1962). Further advancements in descriptions and redescriptions will be required to confirm if the pointed characteristics are generalities of *Sicyonia* and could be used in identification keys for sympatric penaeoidean species, as well as for the phylogenetic contextualization, also because we used larvae from one and two females for *S. dorsalis* and *S. typica*, respectively, and possible intraspecific natural variations could not be detected.

After morphological descriptions of PZI of *S. dorsalis* and *S. carinata* we tested the efficacy of the key to the larvae of the dendrobranchiate genera from Southern Brazilian coast proposed

Table 3. Comparison of selected morphological characters of first protozoea (PZI) of the genus *Sicyonia.* Abbreviations: ae = aesthetascs; cp = cuspidate process; ds = denticulate seta; ps = plumose seta; seg. = segmented; sp = spine; ss = simple seta; sps = sparsely plumose seta; rl = ringlet; NA = not available in descriptions.

Source		Heldt (1938)	Gurney (1943)	Cook & Murphy (1965)	Present study	Present study
Species		*Sicyonia carinata*	*Sicyonia wheeleri*	*Sicyonia brevirostris*	*Sicyonia dorsalis*	*Sicyonia typica*
Locality		Tunisia	Bermuda	Gulf of Mexico	Brazil	Brazil
CL (mm)		0.30	NA	0.33 (0.30 – 0.36)	0.34 ± 0.009	0.34 ± 0.008
TL (mm)		0.76 – 0.86	0.7 – 0.75	0.81(0.70 – 0.89)	0.74 ± 0.015	0.74 ± 0.008
Antenulle	Proximal article	5-seg., 1seta	5-seg., 1 seta	1 seta	5-seg., 1sps	5-seg., 1sps
	Second article	7 setae	NA	3 setae	2ss + 2sps	2ss + 2sps
	Distal article		NA	6 setae	3ae + 3ps	3ae + 3ps
Antenna	Peduncle distal article	NA	NA	1 seta	1sps	1sps
	Endopod	2-seg., 9 setae	NA	2-seg., 10 setae	2seg., 1ss + 10ps	2seg., 1ss + 10ps
	Exopod	9rl, 12 setae	12 setae	7–9rl, 12 setae	12rl, 12sps	12rl, 12sps
Maxillule	Coxal endite	7 setae	NA	7 setae	1ss + 1ds + 5ps	1ss + 1ds + 5ps
	Basial endite	4 setae	NA	2cp + 2 setae	2cp + 2ps	2cp + 2ps
	Endopod (setation)	3-seg., 2,2,5	NA	3-seg., 2,2,5	3-seg., 3,2,5	3-seg., 3,2,5
	Exopod	4ps	NA	4 setae	4ps	4ps
Maxilla	Coxal endite (setation)	bilobed, 9 + 3	NA	bilobed, 7 + 4	bilobed, 8 + 3	bilobed, 8 + 3
	Basial endite (setation)	bilobed, 3 + 3	NA	bilobed, 3 + 3	bilobed, 4 + 3	bilobed, 4 + 3
	Endopod (setation)	4-seg., 3,2,3,3	NA	4-seg., 2,2,3,3	4-seg., 3,2,3,3	4-seg., 3,2,3,3
	Exopod	5ps	NA	5 setae	5ps	5ps
Fist maxilliped	Coxa	4ps	NA	4 setae	4sps (1 + 1 + 1 + 1)	4sps (1 + 1 + 1 + 1)
	Basis	12 setae	NA	9–11 setae	12sps (3 + 3+ 3 + 3)	12sps (3 + 3 + 3 + 3)
	Endopod (setation)	4-seg., 3,1,2,5	4-seg.	4-seg., 2,1,2,5	4-seg., 3,1,2,5	4-seg., 3,1,2,5
	Exopod	7 setae	7 setae	7 setae	6sps + 1ps	6sps + 1ps
Second maxilliped	Coxa	NA	NA	without setae	without setae	without setae
	Basis	NA	NA	2 setae (1 + 1)	2sps (1 + 1)	2sps (1 + 1)
	Endopod (setation)	4-seg.	4-seg.	4-seg., 1,1,1,5	4-seg., 1,1,1,5	4-seg., 1,1,1,5
	Exopod	NA	6 setae	6 setae	5sps	5sps
Third maxilliped		biramous bud	biramous bud	biramous bud	absent	absent
Furcal formula		7 + 7	7 + 7	7 + 7	7 + 7	7 + 7

by Calazans (1993). The characteristics that lead to PZI stage are: eyes not mobile, covered by carapace; unsegmented abdomen; and pereiopods absent. Regarding the PZI of *Sicyonia*, the following characteristics were used: spine absent on anterior portion of carapace; frontal organs present; antennule and antenna of different lengths; antennule about twice as long as antenna; and formula of antennal protopod (distal article) and endopod (proximal and marginal setae) is 1 + 2 + 3 [see Figure 2C of Calazans (1993) for details]. Therefore, we can conclude that the characteristics used in the previous key for the PZI of the genus proved to be efficient, and adjustments are not necessary.

As evidenced in the present study, there is a clear need of new larval descriptions of sicyoniids. As pointed out by Martin et al. (2014) and illustrated by the descriptions of two species conducted here, the penaeoidean protozoeal stages are very difficult to be distinguished at species level. In this sense, sampling of plankton and the use of

refined techniques such as DNA-barcode will be useful to enable morphological descriptions of the entire larval development, when capturing reproductive females becomes difficult or even obtaining the complete cycle in the laboratory. With an increase in penaeoidean larval descriptions from Brazilian coast we will be able to contribute to the identification of plankton samples, helping to recognize spawning sites, which will allow us to improve the decisions for the conservation of such species, especially regarding fishing.

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Fernando Luis Mantelatto: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to critical revision, adding intellectual content; mentored work, funding acquisition.

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Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Data Availability

Supporting data are available at <https://doi.org/10.48331/scielodata.EXB8J5>.

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