THE LARVAL DEVELOPMENT OF PALAEMONID SHRIMPS FROM THE AMAZON REGION REARED IN THE LABORATORY. VII. ABBREVIATED DEVELOPMENT OF *Pseudopalaemon amazonensis* RAMOS-PORTO, 1979 (CRUSTACEA: DECAPODA: CARIDEA).

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ABSTRACT — Larval development of the freshwater shrimp *Pseudopalaemon amazonensis* Ramos-Porto was studied in the laboratory based on the offspring of ovigerous females collected in a small „terra-firme" forest stream near Manaus, Brazil. Ovigerous females with a mean total length of 36.5 ± 1.9 mm carried 13-19 eliptical, yolk-rich eggs measuring 2.55 ± 0.16 x 1.64 ± 0.11 mm. The larval period consisted of 3 benthic stages and the larvae accomplished metamorphosis after 7-8 days without feeding. The newly-hatched larva had sessile eyes and all appendages, except for the uropods; chelipeds were present as uniramous buds, but walking legs were fully developed and functional. Descriptions and illustrations of the 3 larval and first juvenile stages are presented.

Key words: Palaemonidae, *Pseudopalaemon amazonensis*, larval development, Amazon, freshwater shrimp.

Desenvolvimento Larval de Camarões Palaemonídeos da Região Amazônica Obtido em Laboratório. VII. Desenvolvimento Abreviado de *Pseudopalaemon amazonensis* Ramos-Porto, 1979 (Crustacea: Decapoda: Caridea).

RESUMO — Foi estudado o desenvolvimento larval do camarão dulcícola *Pseudopalaemon amazonensis* Ramos-Porto criado em laboratório, a partir das larvas eclodidas de fêmeas ovadas coletadas em um pequeno igarapé de terra-firme das proximidades de Manaus, Brasil. Fêmeas ovadas de comprimento total médio de 36,5 ± 1,9 mm carregavam 13-19 ovos elípticos e ricos em vitelo, medindo 2,55 ± 0,16 x 1,64 ± 0,11 mm. O período larval consistiu de 3 estágios larvais bentônicos e as larvas alcançaram a metamorfose após 7-8 dias, sem ingestão de alimento. A larva recém-eclodida apresentou olhos sésseis e todos os apêndices, à exceção dos urópodos; quelíopodos estavam presentem na forma de botões unirremes, mas as pernas locomotoras estavam totalmente desenvolvidas e funcionais. São apresentadas as descrições e ilustrações dos 3 estágios larvais e do 1º estágio de juvenil.

Palavras chaves: Palaemonidae, *Pseudopalaemon amazonensis*, desenvolvimento larval, Amazônia, camarão de água doce.

INTRODUCTION

Four of the five known species of the genus *Pseudopalaemon* Sollaud are found in the Amazon river basin (Kensley & Walker, 1982). One of these, *Pseudopalaemon amazonensis* Ramos-Porto, 1979, commonly occurs in the Central Amazonian region, either in the „terra-firme" forest streams or in the periodically inundated forest ("igapó") of larger rivers. Walker & Ferreira (1985), studing the ecology of shrimps from the Tarumã-Mirim River, found that *P. amazonensis* reproduces during the rising water period in the "igapó", while ovigerous females occur during the whole year in the forest streams.

Most of the Amazonian palaemonid shrimps have abbreviated or direct larval development (Magalhães & Walker, 1988). A complete description of the larval development has already been provided for *Macrobrachium amazonicum*

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(Heller) (see Magalhães, 1985), *M. nattereri* (Heller) (see Magalhães, 1989), *Euryrhynchus* spp. (see Magalhães, 1988a), *Palaemonetes ivonicus* Holthuis (see Magalhães, 1986), *P. mercedae* Pereira (see Magalhães, 1988b) and *Pseudopalaemon chryseus* Kensley & Walker (see Magalhães, 1986/87). For the genus *Pseudopalaemon*, there is a brief account on the larvae of *P. bouvieri* Sollaud in Sollaud's (1923) classic paper on the larval development of the Palaemoninae. The purpose of this paper is to provide morphological descriptions and illustrations of the three larval and first juvenile stages of *Pseudopalaemon amazonensis*, as well as offer new data on some life history characteristics.

MATERIAL AND METHODS

Ovigerous females of *Pseudopalaemon amazonensis* were collected in Preto da Eva River and in the Igarapé Candirú, a "terra-firme" forest stream near Manaus, from March to June 1993. The females were transported to the laboratory in plastics bags filled with water from the environment and with aquatic plants for shelter. Six to ten specimens were kept together in a 68x30x40 cm aquarium and were fed chopped fish and artificial food. Newly-hatched larvae were individually transferred to 80 ml transparent plastic vials for rearing. The water was partially changed once a day. Larvae hatched and were reared in room temperature (temperature of the water in the aquarium: 26°C). Food was not offered before metamorphosis. For dissecting and preparing specimens for illustrations a larva was put in 10% alcohol during approximately 15 minutes. Morphological descriptions were based on at least five specimens dissected under a low power binocular microscope and figured with the aid of a drawing tube mounted in a high power binocular microscope. For greater clarity, plumose setae are shown as simple naked setae in the drawings in dorsal view and where plumes are represented, they can be denser and longer than is indicated.

Fresh eggs with advanced embryos were removed from five females for measurements. Total length (TL) of the larvae was measured from the tip of the rostrum to the posterior margin of the telson, excluding setae. Six spent females used in this study were preserved and deposited in the Invertebrate Collection (Crustacea) of the Instituto Nacional de Pesquisas da Amazônia (INPA 643), as well as some specimens of each larval and first juvenile stages (INPA 644).

RESULTS

It usually takes two to three days for a female to release all of the clutch. Hatching was never observed during daytime. Five ovigerous females with a mean total length of 36.5 ± 1.90 mm carried 13 to 19 eliptical, yolk-rich eggs measuring 2.55 ± 0.16 x 1.64 ± 0.11 mm (n = 31).

The species goes through three benthic larval stages without feeding. The duration of the larval period was seven (62% of the 26 observed cases) or eight (38%) days. The first, second and third larval stages lasted, respectively, two, two, and three to four days.

Description of the larval and first juvenile stages:

Body

Larva I (TL 5.97 ± 0.13 mm, n = 6, 5.80 to 6.21 mm) (Figs. 1, 2): Rostrum unarmed and straight, reaching about one-third of the antennular peduncle. Carapace with 1 spine on the anterolateral border. Eyes sessile. Abdomen 6-segmented, smooth.

Larva II (TL 6.44 ± 0.06 mm, n = 3, 6.37 to 6.52 mm) (Figs. 16, 17): Rostrum almost reaching distal margin of the first segment of the antennular peduncle, bearing 3-4 dorsal teeth; distal end slightly curved downwards. Carapace with 2 teeth on the anterolateral border. Eyes stalked. Abdomen with 2 setae on the posterodorsal border of the 5th somite.

Larva III (TL 6.66 ± 0.12 mm, n = 4, 6.60 to 6.85 mm) (Figs. 24, 25): Rostrum with 4-5 dorsal teeth; ventral border smooth. Carapace, eyes and abdomen similar to the preceding stage.

Juvenile I (TL 7.29 ± 0.31 mm, n = 12, 6.93 to 7.89 mm) (Figs. 32, 33): Rostrum straight, slightly surpassing distal margin of the second segment of the antennular peduncle; dorsal border with 4-6 teeth, ventral border with a minute tooth. Carapace with the 2 teeth placed subterminally on the anterolateral border.

Antennule

Larva I (Fig. 3): Peduncle unsegmented, but joints visible under the cuticle. Distally with 2 flagella: inner flagellum tapering and bearing longitudinal rows of plumes; outer flagellum with 2 naked setae, 1 plumose seta and a longer apical aesthete.

Larva II (Fig. 18): Peduncle 3-segmented with several, short and long plumose setae as illustrated. Proximal segment with a small ventral spine, a developing stylocerite and a distal spine on the lateral corner. Inner flagellum 5-segmented, first segmentation indistinct; outer flagellum subdivided, basal part unsegmented, inner ramus shorter and bearing 2 apical slender aesthetes, outer ramus 3-segmented, but segmentations undistinct. Both flagella showing small setae, but minute aesthetes present only on the inner one.

Larva III (Fig. 26): Stylocerite a little more proeminent. Distal flagella longer than in the preceding stage; inner flagellum 6-segmented, all segmentations clearly marked; outer flagellum with inner ramus bearing 2 spatulate aesthetes.

Juvenile I (Fig. 34): Peduncle with a developing statocyst and a sharp stylocerite. Distal flagella longer than in larva III; outer flagellum with the basal joint distinct, the ramification beginning in the second joint, outer ramus 5-segmented and longer than the inner flagellum.

Antenna

Larva I (Fig. 4): Protopod with a sharp ventral spine on the distal border. Scaphocerite with entire inner and distal margins fringed with 28-30 plumose setae and a spine on the distolateral corner. Endopod as a long, multi-articulated flagellum about 5 times as long as the scaphocerite.

Larvae II, III and Juvenile I: Similar to that of the preceding stage, except for the bisegmented protopod and the antenal flagellum longer, about 7.5 times as long as the scaphocerite.

Mandibles

Larvae I (Fig. 5), II and III (Fig. 27): Rudimentary. Incisor process with

1-2 small teeth, molar process obtuse; cleft between the processes increasing from first to third larval stages.

Juvenile I (Fig. 35): Fully developed, strong. Incisor process bearing 3 sharp teeth; molar process stouter, with rounded teeth and several denticles.

Maxillula

Larvae I (Fig. 6), II and III: Rudimentary. Coxal and basal endites bearing a few distal and subdistal protuberances. Endopod bilobed, lower lobe smooth or with a spine or with a small plumose seta; upper lobe rounded and smooth.

Juvenile I (Fig. 36): Fully developed and functional. Coxal endite with 8 naked and weakly plumose setae terminally and subterminaly. Basal endite bearing 11 spinose setae terminally and subterminally, and 2 plumose setae proximally on the inner margin. Endopod strongly bilobed, with a curved spine on the lower lobe.

Maxilla

Larvae I (Fig. 7), II and III: Protopod bilobed, both endites devoid of setae. Endopod usually smooth, a plumose seta ocasionally present terminally on the third stage. Scaphognathite large, fringed with 26-27 plumose setae, and bearing 1 small naked seta either dorsally or ventrally on the anterior part.

Juvenile I (Fig. 37): Protopod with lower and upper endites bearing, respectively, 3 and 4 naked and weakly plumose setae. Endopod with 1 small plumose setae proximally.

Maxilliped 1

Larvae I (Fig. 8), II and III: Protopod with 1 small epipod, bilobed on the third stage; inner margin slightly bilobed, bearing 2-3 plumose setae distally and some marginal protuberances. Endopod with 3-5 plumose setae. Exopod longer than endopod, showing 3 terminal plumose setae; proximal outer border slightly bulged on the third larval stage.

Juvenile I (Fig. 38): Fully developed. Protopod with coxal endite bearing 1 naked and 2 plumose setae, and basal endite with several naked and weakly plumose setae terminally and subterminally. Endopod showing 1 subterminal plumose seta. Exopodal lobe more bulged, bearing 2-4 plumose setae.

Maxilliped 2

Larva I (Fig. 9) and II (Fig. 19): Protopod naked. Endopod 5-segmented, segmentation sometimes not clear, mainly the one between penultimate and last segments; penultimate segment bearing 1 plumose seta, last segment with some protuberances and 1 weakly plumose seta, sometimes reduced or absent. Exopod longer than the endopod, with 3 terminal plumose setae and 1 subterminal naked seta.

Larva III (Fig. 28): Endopod without any seta on the last two segments.

Juvenile I (Fig. 39): Fully developed. Coxa with 1 plumose and 1-2 naked seta on the inner side and 1 large epipod on the outer margin. Endopod 5-segmented, strongly incurved, last 2 segments widened; penultimate segment with 3-5 naked and weakly plumose setae on the outer margin and 2 on the distal margin; last segment bearing many naked and weakly plumose setae

terminally and subterminally.

Maxilliped 3

Larvae I (Fig. 10), II and III: Coxa naked, basis with 2 naked setae on inner margin. Endopod 5-segmented, with 0-1/0-1/1-2/3-5/2 naked and weakly plumose setae from proximal to distal segment; distal segment also bearing 1 apical weakly plumose spine. Exopod reaching about penultimate segment of the endopod, showing 3 terminal plumose setae.

Juvenile I (Fig. 40): Coxa 1 naked, basis with 1 short weakly plumose seta and 1 longer naked seta, all on inner margin. Endopod 3-segmented, bearing several naked and weakly plumose setae situated mainly along the inner margin of the segments. Exopod shorter than in larval stages, not surpassing the first segment of the endopod.

Pereiopods 1 and 2

Larva I (Figs. 11, 12): Well developed, chelate, uniramous buds, that of the second longer than the first; segmentation only between basis and ischium distinct.

Larva II (Fig. 20, 21): More developed than the preceding stage, with a few small naked setae present; segmentation between ischium and merus not yet distinct.

Larva III (Fig. 29, 30): All articles clearly distinct.

Juvenile I (Fig. 41, 42): Fully developed and functional. Short, naked and/or weakly plumose, setae present along all the segments; a tuft present at the tip of the fixed and movable fingers. Pereiopod 1 bearing a oblique row of 4-5 weakly plumose setae on the inner side of the carpus and 1 plumose spiniform seta on the inner proximal side of the palm.

Pereiopods 3, 4 and 5

Larvae I (Figs. 13), II, III and Juvenile I: Morphologically all similar, uniramous and fully developed. Coxa naked, basis with 2 naked setae on inner margin. Endopod 5-segmented, dactylus with 1 short terminal spine; several short naked and/or weakly plumose setae scattered on the segments, mainly in the propodus.

Pleopods 1 to 5

Larva I (Fig. 14a-e): Well developed. Exopod and endopod with marginal plumose setae, except the endopod of pleopods 1 and 5, the latter bearing rudiments of marginal setae. Appendices internae already present, showing minute hooks.

Larvae II (Fig. 22a-e), III and Juvenile I: Endopod of pleopod 5 with marginal plumose setae; exopod of pleopods 2-5 bearing 1 subterminal naked seta.

Uropod

Larvae I (Fig. 15) and II (Fig. 23): Buds visible through the telsonal cuticle.

Larva III (Fig. 31): Protopod with the outer distal corner rounded. Exopod developed, with 1 distolateral spine, 23-24 plumose setae along the inner and distal margins, 2 short weakly plumose setae present on the outer proximal margin and 2 subterminally on the distal margin. Endopod rudimentary, bearing only 5 short weakly plumose setae along the outer margin.

Juvenile I (Fig. 43): Protopod with the outer distal corner spiniform.

Exopod with an increased number of marginal and superficial setae. Endopod developed, with 14 plumose setae along most of the inner and distal margins, and several short weakly plumose setae dorsally and along the outer margin.

Telson

Larvae I (Fig. 15) and II (Fig. 23): Fan-like; posterior margin strongly convex, bearing 26-27 plumose setae.

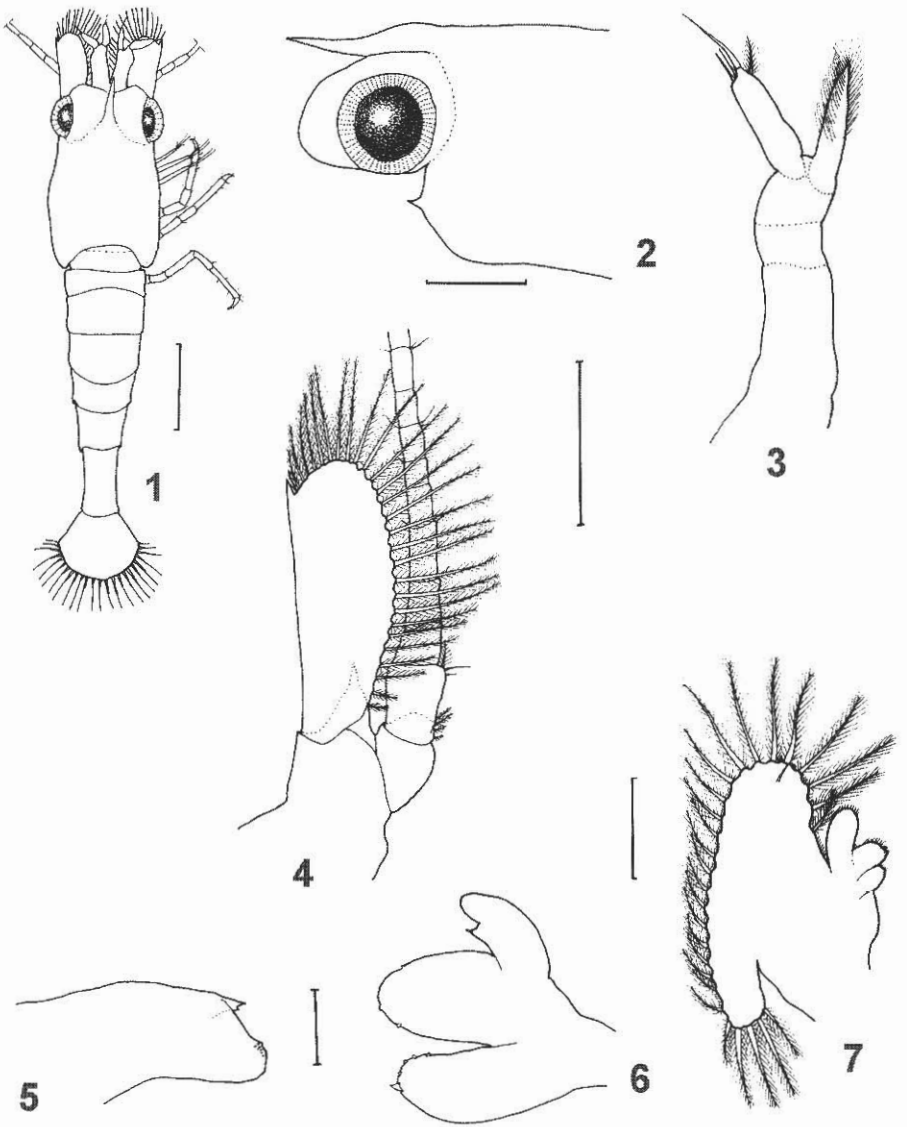
Larva III (Fig. 31): Narrower and longer than in the preceding stage; posterior part slightly wider, bearing 1 pair of small spines on the distolateral corners and 22-25 plumose setae along the posterior margin.

Juvenile I (Fig. 43): Longer than in the preceding stage; posterior part gently narrowing as far as the first pair of lateral spines, than becoming distinctly narrower; 2 pairs of small spines placed subterminally on the distolateral margin; posterior margin irregular, slightly convex, bearing 1 pair of strong spines on the lateral corner and 10-17 irregular setae (size and shape variable) in between.

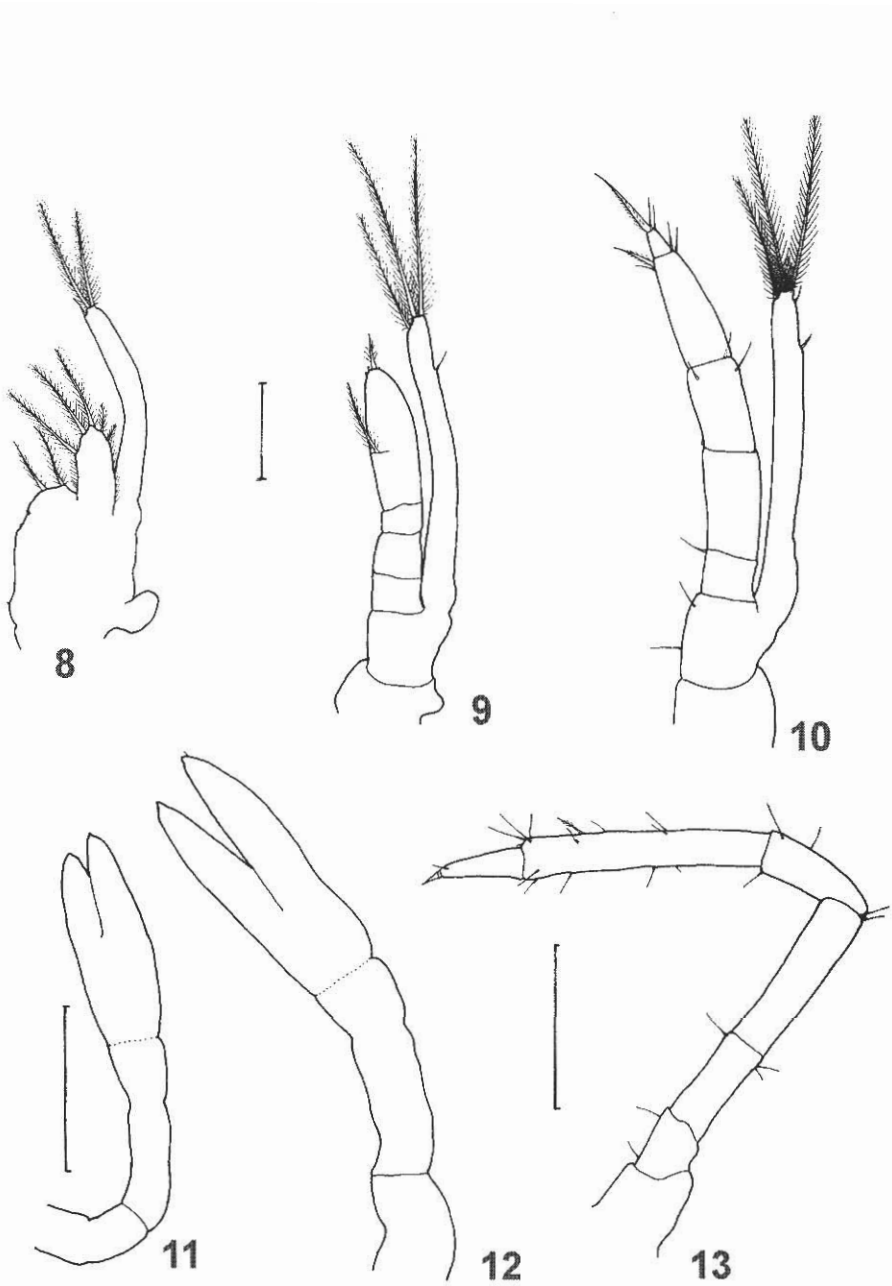
DISCUSSION

The larval development of *Pseudopalaemon amazonensis* is very similar to that of *P. chryseus*. Both have three brief stages and larvae showing very advanced morphological features. On hatching, both species already have fully developed and functional walking legs; the chelipeds, although not functional, are present as well developed buds. Neither species have even a trace of exopods in the pereiopods, and the pleopods can bear marginal plumose setae and appendices internae. Other structures, such as antennules, antennae, mouth parts, maxillipeds, uropods and telson, are usually alike and exhibit only minor differences. The noteworthy morphological features distinguishing these two species are: a) Rostrum: in *P. chryseus*, it is clearly curved downwards in the first larval stage and shows one ventral tooth from the second stage on while in *P. amazonensis*, it is straight in the first stage and a ventral tooth appears only in the juvenile phase; b) Spines of the anterolateral margin of the carapace: *P. chryseus* has two spines on the first stage, *P. amazonensis* has just one; c) Setae of the pleopods: the pleopods of *P. amazonensis* are almost fully setaceous and functional on hatching, while only a few setae are present in the pleopods of *P. chryseus*; d) Telson: in the first juvenile of *P. amazonensis*, it is distinctly narrowed after the first pair of lateral spines, has an irregular posterior margin in which the median setae are usually shorter than, or at most as long as, the strong distolateral pair of spines while in the same stage, *P. chryseus* shows a slight narrowing of the telson, its posterior margin having a regular convex shape and median setae always longer than the short distolateral pair of spines.

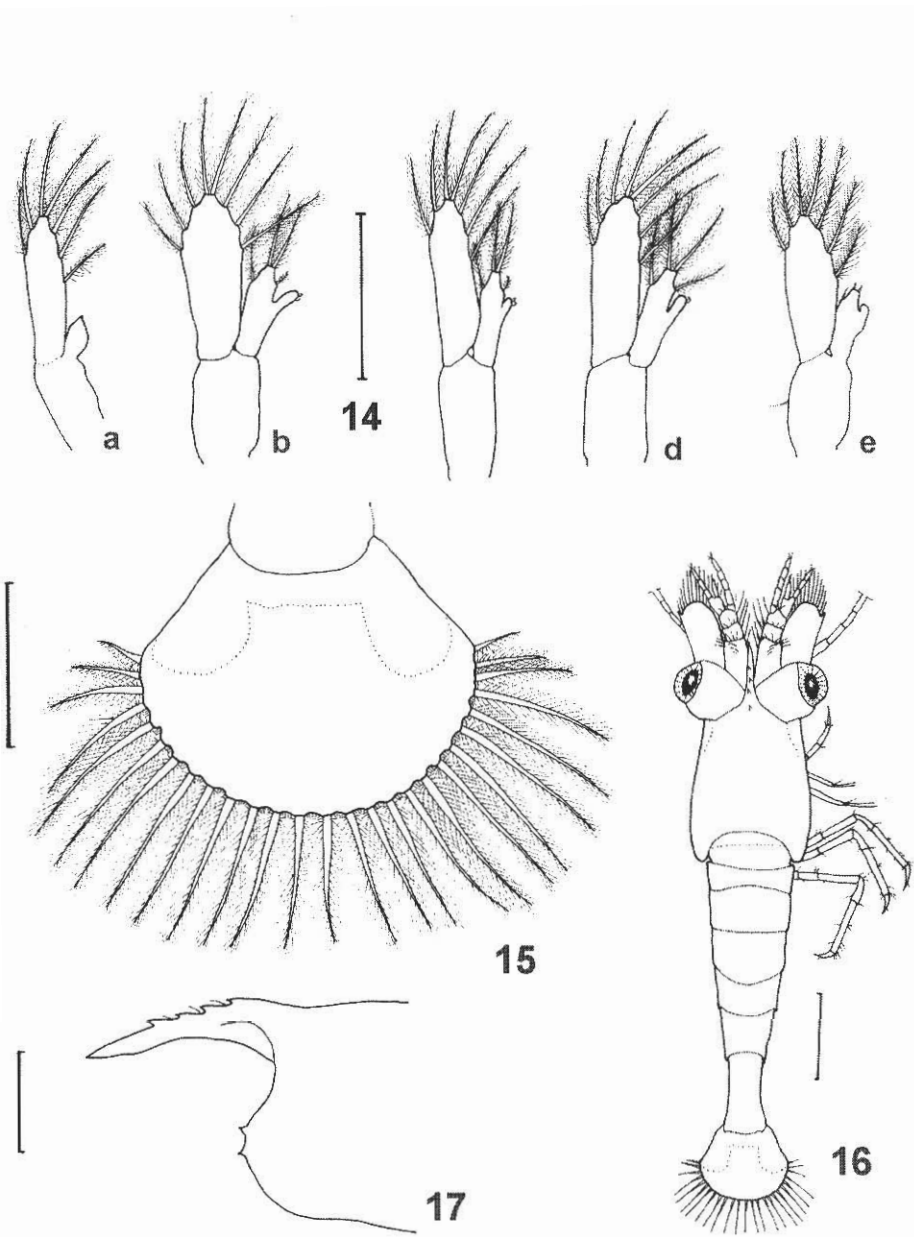
The main differences between *Pseudopalaemon amazonensis* and *P. bouvieri* seem to be in the pereiopods and in the setation of the telson. The study of late embryos of the later species by Sollaud (1923) suggests that its larvae still carry exopods, even if rudimentary, on the chelipeds. Also, the walking legs are not functional, and



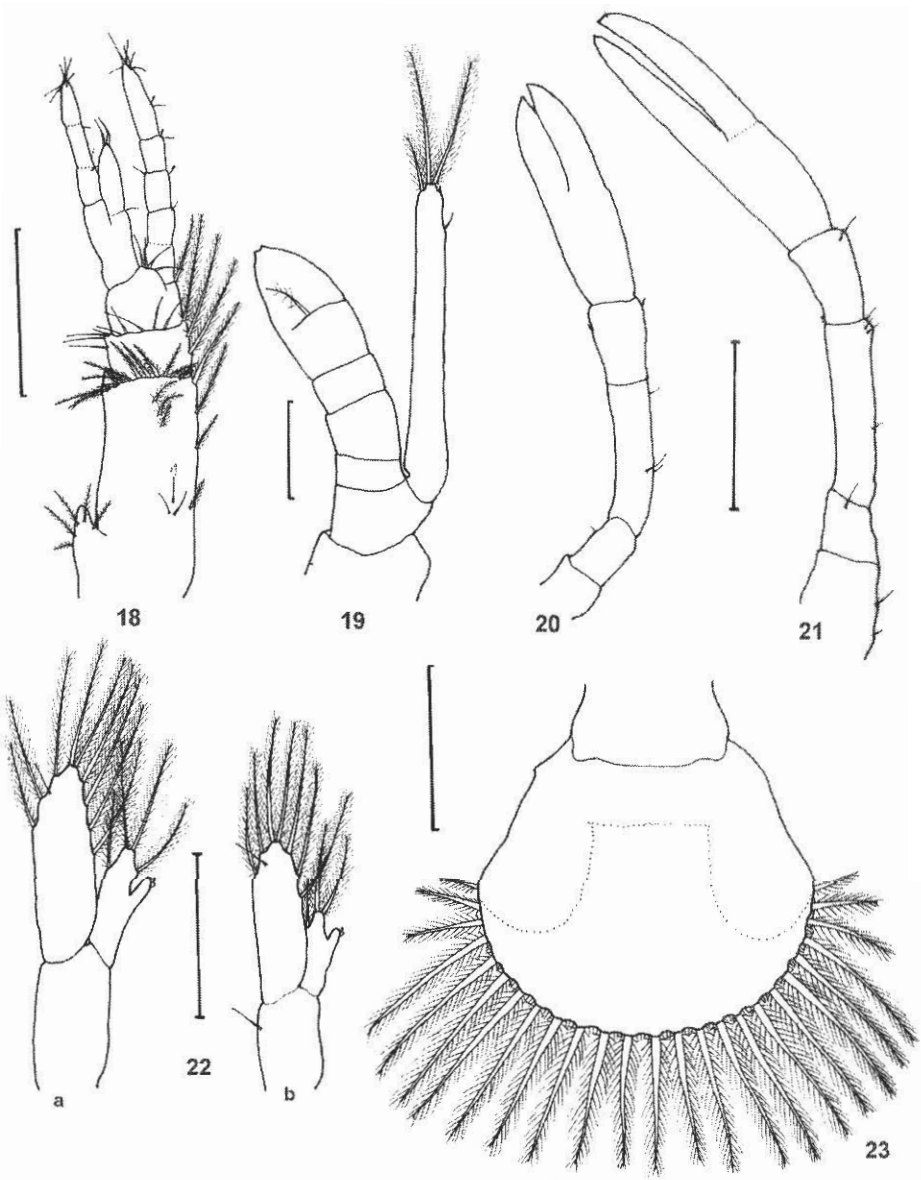
Figs. 1-7. *Pseudopalaemon amazonensis*, Larva I. 1, Dorsal view (left pereiopods removed); 2, Anterolateral margin of the carapace; 3, Antennule; 4, Antenna; 5, Mandible; 6, Maxillula, 7, Maxilla. (Scale bars: figs. 1-2 = 1 mm; figs. 3-4 = 0.5 mm; figs. 5-6 = 0.1 mm; fig. 7 = 0.2 mm)



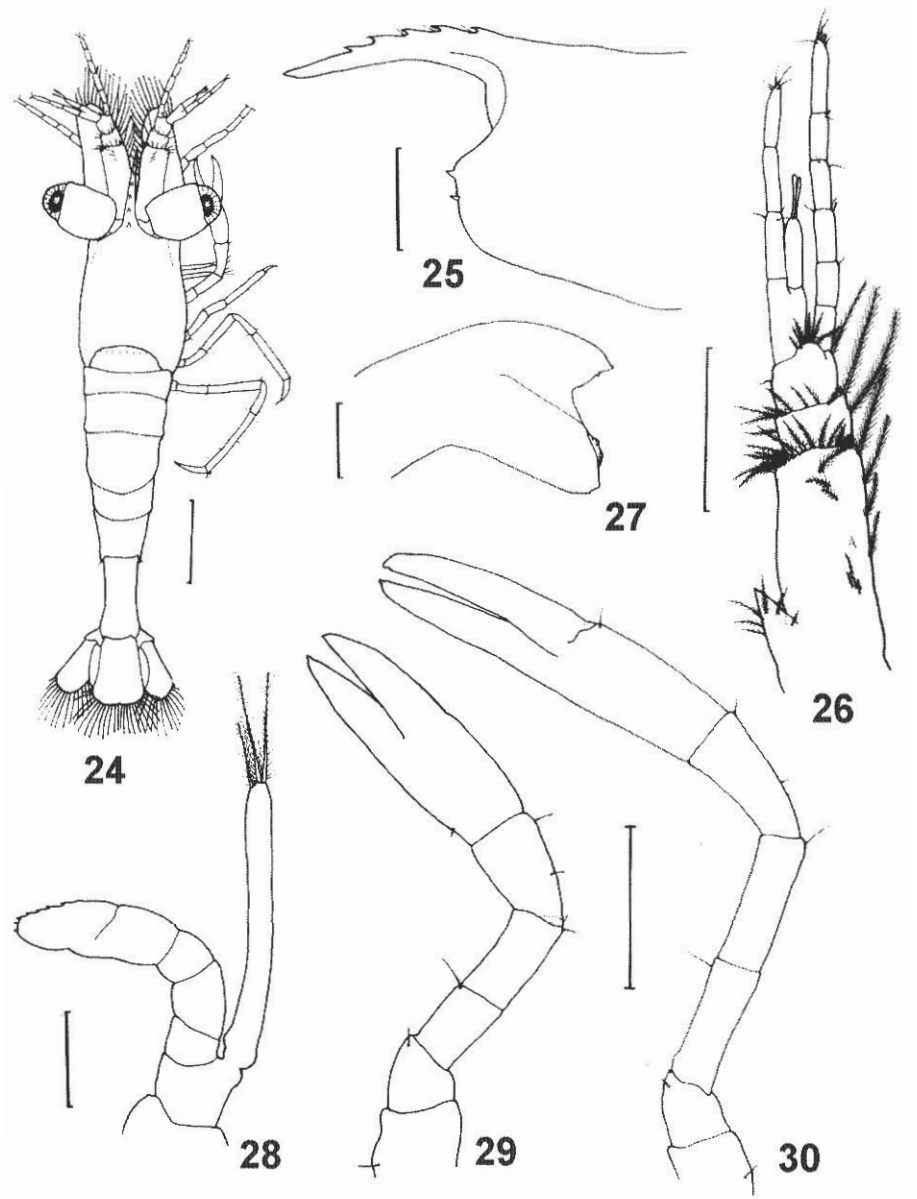
Figs. 8-13. *Pseudopalaemon amazonensis*, Larva I. 8, Maxilliped 1; 9, Maxilliped 2; 10, Maxilliped 3; 11, Pereiopod 1; 12, Pereiopod 2; 13, Pereiopod 3. (Scale bars: figs. 8-10 = 0.2 mm; figs. 11-13 = 0.5 mm).



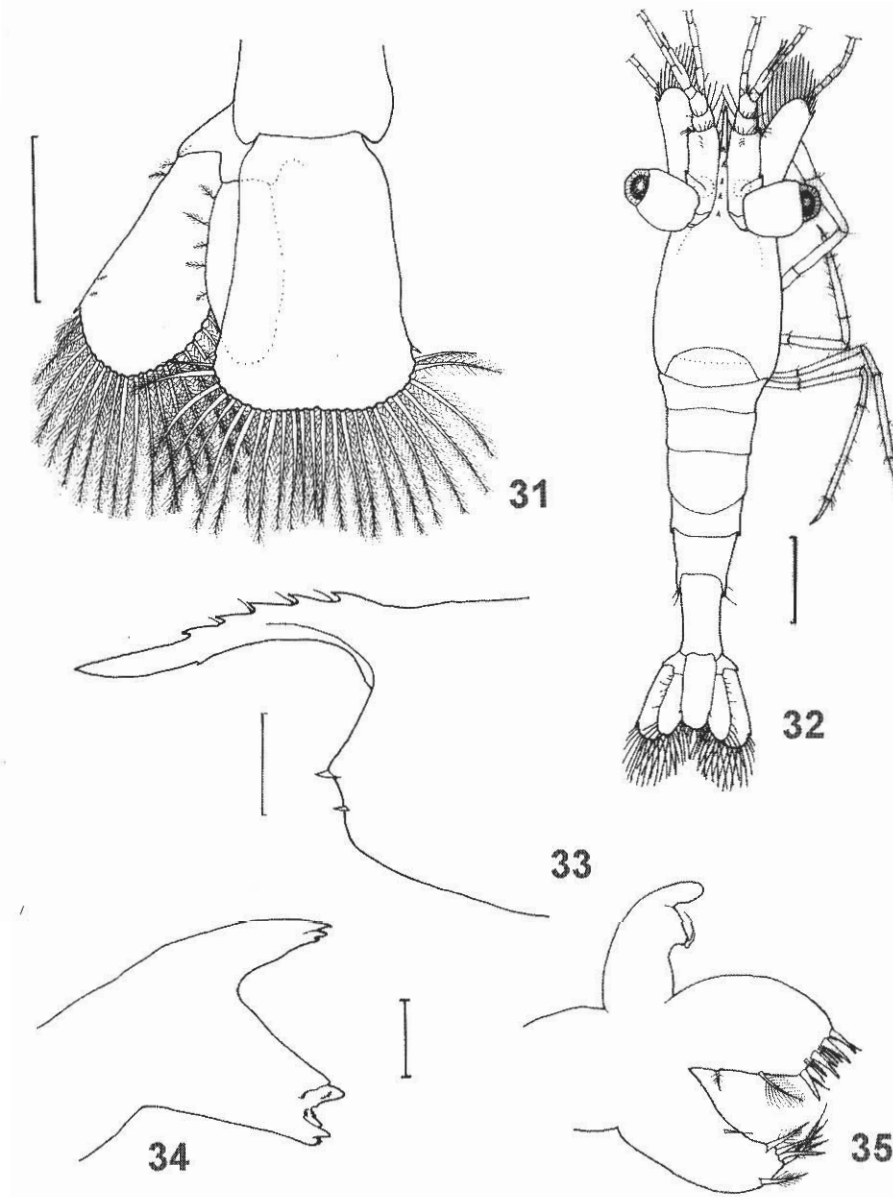
Figs. 14-17. *Pseudopalaemon amazonensis*, Larva I. 14a-e, Pleopods 1-5; 15, Telson. Figs. 16-23. Larva II. 16, Dorsal view (left pereiopods removed); 17, Anterolateral margin of the carapace. (Scale bars: figs. 14-15 = 0.5 mm; figs. 16-17 = 1 mm).



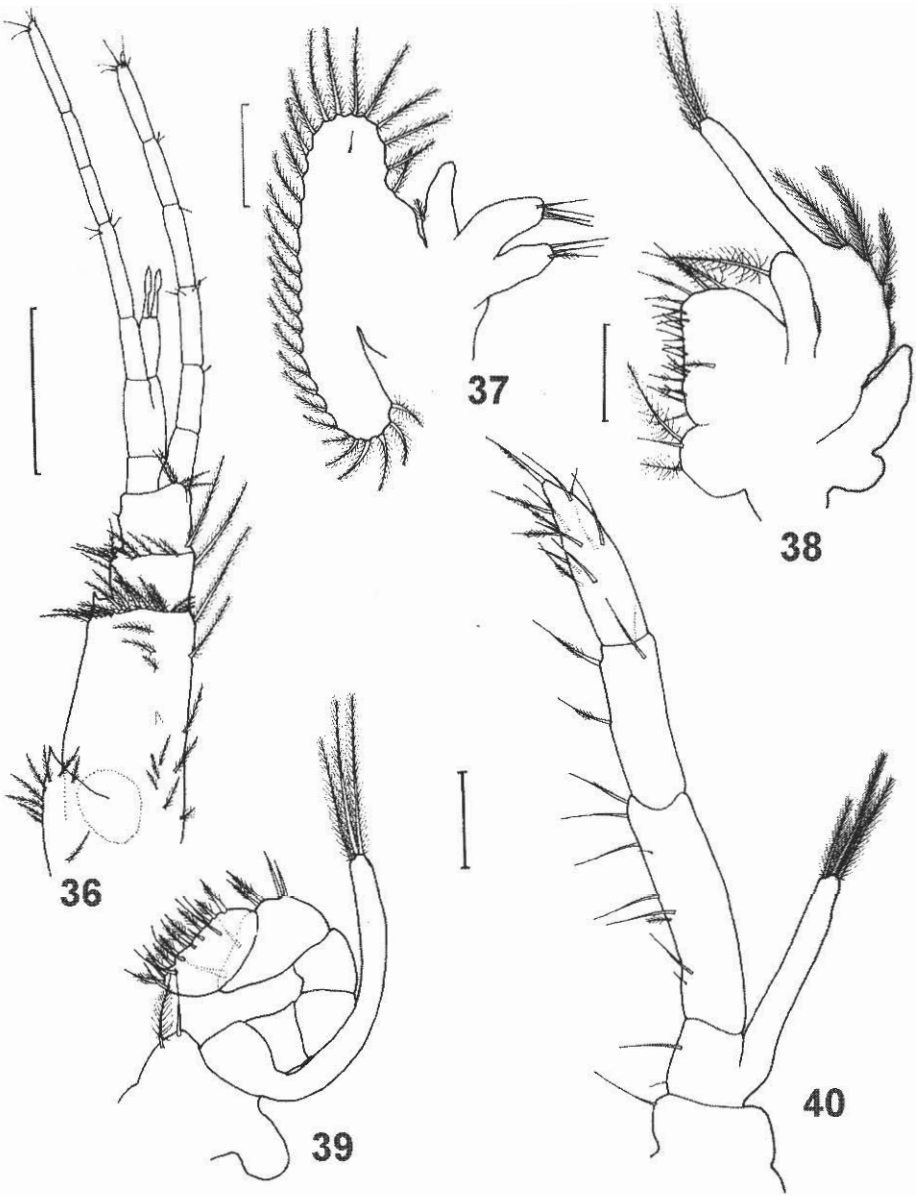
Figs. 18-23. *Pseudopalaemon amazonensis*, Larva II. 18, Antennule; 19, Maxilliped 2; 20, Pereiopod 1; 21, Pereiopod 2; 22a-b, Pleopods 3 and 5; 23, Telson. (Scale bars: figs. 18,20-23 = 0.5 mm; fig. 19 = 0.2 mm).



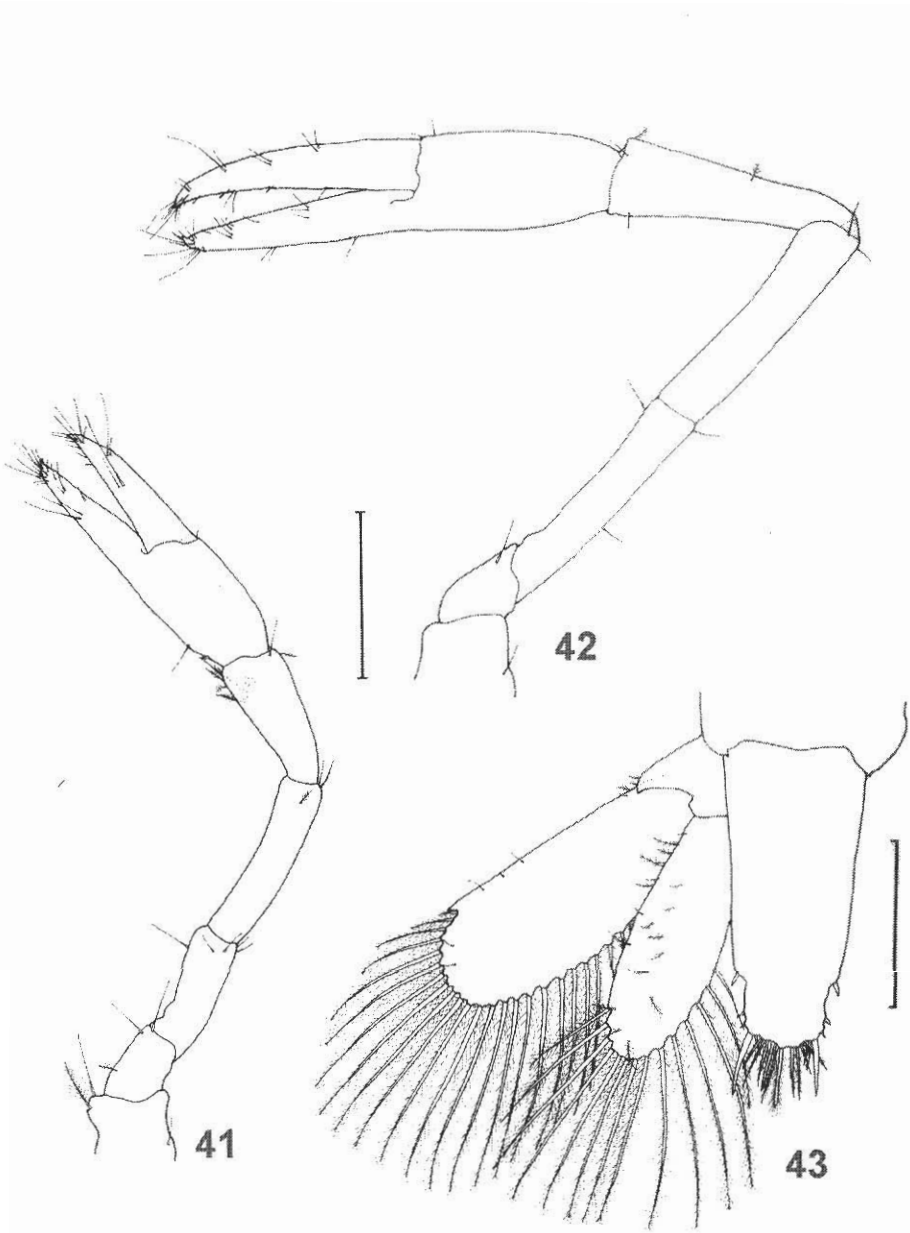
Figs. 24-30. *Pseudopalaemon amazonensis*, Larva III. 24, Dorsal view (left pereiopods removed); 25, Anterolateral margin of the carapace; 26, Antennule; 27, Mandible; 28, Maxilliped 2; 29, Pereiopod 1; 30, Pereiopod 2. (Scale bars: figs. 24-25 = 1 mm; figs. 26,29-30 = 0.5 mm; fig. 27 = 0.1 mm; fig. 28 = 0.2 mm).



Figs. 31-35. *Pseudopalaemon amazonensis*, Larva III. 31, Telson. Juvenile I. 32, Dorsal view (left pereiopods removed); 33, Anterolateral margin of the carapace; 34, Mandible; 35, Maxillula. (Scale bars: fig. 31 = 0.5 mm; figs. 32-33 = 1 mm; figs. 34-35 = 0.1 mm).



Figs. 36-40. *Pseudopalaemon amazonensis*, Juvenile I. 36, Antennule; 37, Maxilla; 38, Maxilliped 1; 39, Maxilliped 2; 40, Maxilliped 3. (Scale bars: fig. 36 = 0.5 mm; fig. 37-40 = 0.2 mm).



Figs. 41-43. *Pseudopalaemon amazonensis*, Juvenile I. 41, Pereiopod 1; 42, Pereiopod 2; 43, Left uropod and telson. (Scale bars: figs. 41-43 = 0.5 mm).

the posterior margin of the telson has seven pairs of setae.

Gore (1985) pointed out that abbreviated development can be considered as being direct, in which the young hatch with a more or less adult form, or advanced, *i.e.*, the young hatch as a developed zoeae which will undergo additional ecdyses until metamorphosis is accomplished. With the exception of *Macrobrachium amazonicum*, that has an extended development going through 10-11 stages of a free-swimming zoea (Magalhães, 1985), abbreviated development is a common feature in the Central Amazonian palaemonid shrimps (Magalhães & Walker, 1988). However, within this group many differences can be noticed. There are species which present only a single instar before metamorphosis and can be considered as having direct development; examples are *Euryrhynchus* spp. and *Palaemonetes mercedae* (see Magalhães, 1988a; Magalhães, 1988b). There are also species with advanced development, having three brief larval stages before molting to juvenile, as is the case of *Palaemonetes ivonicus*, *Pseudopalaemon chryseus*, *Macrobrachium nattereri* (see Magalhães 1986; 1986/87; 1989) and the present species.

Even within the group with advanced development variations are frequently found. Depending on the species, the newly-hatched larvae can present structures in a more or less advanced state of development. The main characteristics of the first larval stage of the Amazonian palaemonids with advanced development are summarized in Table 1. When compared with the other Amazonian species with advanced development, *Pseudopalemon amazonensis* shows a more complete state of development at eclosion, with some structures bearing an adult-like form even earlier than those in *P. chryseus*.

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Table 1. Developmental characteristics of the first larval stage of Amazonian palaemonids with known advanced larval development.

Structures	*Palaemonetes ivonicus* [1]	*Macrobrachium nattereri* [2]	*Pseudopalaemon chryseus* [3]	*Pseudopalaemon amazonensis*
Carapace				
Anterolateral border	*2 spines*	*no spines*	*2 spines*	*1 spine*
Antenna				
Flagellum	*4.6-5.3 x scale length, multi-articulated*	*2 x scale length, unsegmented*	*6 x scale length, multi-articulated*	*5 x scale length, multi-articulated*
Setation of scale	*21 - 25*	*11*	*26 - 30*	*28 - 30*
Pereiopods				
Chelipeds	*biramous buds*	*uniramous buds*	*uniramous buds developed, functional*	*uniramous buds developed, functional*
Walking legs	*uniramous buds*	*uniramous buds*		
Pleopods	*rudimentary buds, glabrous*	*rudimentary buds, glabrous*	*well-developed buds, few setae on endopods 2-4, appendices internae present*	*well-developed, with plumose setae and appendices internae*
Telson setation	*8 + 7 (at most)*	*7 + 7*	*21 - 24*	*26 - 27*

1- Magalhães (1986); 2- Magalhães (1989); Magalhães (1986/87)

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