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Larval development of *Notolopas brasiliensis* Miers, 1886 (Brachyura: Majoidea: Pisidae) described from laboratory reared material and a reappraisal of the characters of Pisidae

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ABSTRACT

The complete larval stages of Notolopas brasiliensis *are described from laboratory reared material, with emphasis on the external morphological features of Majoidea, and compare the morphology of* N. brasiliensis *with other genera of Pisidae. Larval development of* N. brasiliensis *consists of two zoeal stages and one megalopa. The duration mean of each zoeal stage was 4.2 ± 1.0 days for Zoea I and 3.8 ± 0.7 days for Zoea II, the megalopa instar appearing 8.1 ± 0.4 days after hatching. The characters previously used to define larval forms of Pisidae are either symplesiomorphic or potentially highly homoplastic. As well, was observed that there are no common sets of larval characters that would define Pisidae nowadays. However, was showed that only a combination of characters could differentiate* Notolopas *from other pisid genera.*

Keywords: Larval characters, *Notolopas,* spider crabs, Majidae, Pisidae.

INTRODUCTION

The understanding of evolutionary relationships amongst crustaceans is largely based on adult morphology, and larvae remain a much neglected source of characters that may help solve relationships among taxa. In few particular cases, larval characters have been shown to be useful in phylogenetic inferences (Clark & Webber, 1991; Baisre, 1994; Marques & Pohle, 1995, 1998, 2003; Pohle & Marques, 1998, 2000; Maas & Waloszek, 2001). However, we are still at the stage of providing well detailed descriptions of larval forms that would allow us to make phylogenetic inferences based on those characters for many higher taxa within Brachyura.

The Majoidea (*sensu* Martin & Davis, 2001) is one of the most diverse groups within Brachyura, with ap-

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proximately 900 species worldwide (Provenzano & Brownell, 1977). In the Southwest Atlantic this group is represented by approximately 80 species in 45 genera arranged into eight families, in which the family Pisidae is represented by 11 genera with 14 species (Melo, 1996).

The spider crab *Notolopas brasiliensis* Miers, 1886 is known to inhabit sandy, muddy or gravel bottoms from the intertidal region to depths of 30 m on the coasts of the western Atlantic of Colombia, Venezuela and Brazil. In Brazilian waters, this species is distributed from Amapá to São Paulo States (Melo, 1996). The purpose of this study is to describe the complete larval stages of *Notolopas brasiliensis,* reared under laboratory conditions, with emphasis on the external morphological features of Majoidea, and compare the morphology of *N. brasiliensis* with other genera of Pisidae.

MATERIALS AND METHODS

Two ovigerous specimens of *Notolopas brasiliensis* were collected in March 1998 in Ubatuba, São Paulo, Brazil (23°26'18"S, 45°02'30"W) by trawling in depths of 10 m. The specimens were held in an aquarium until hatching, which occurred at night for both females. After hatching, 50 of the most active, positively phototactic larvae from each female were reared individually in 70 ml acrylic jars containing 30 ml of filtered seawater. The remaining larvae were kept in mass culture as extra specimens to be used for morphological description.

Newly hatched larvae were fed *ad libitum* with *Artemia* nauplii. Sea water was changed, and specimens were inspected and fed daily. All acrylic jars were washed in fresh water and air-dried before re-use with fresh seawater in the following day. Mean daily water temperature in the tank was 24° ± 1°C. Average salinity was 32. A 14L:10D photoperiod was maintained.

Whenever possible, a minimum of five specimens of each stage, from each females, were dissected for morphological description, and intra-specific observation. For slide preparations polyvinyl lactophenol mounting medium was used with Acid Fuchsin and/or chlorazol black stains.

The description of setae follows Pohle & Telford (1981), but here includes only analysis by light microscopy (LM), using an Olympus BH-2 microscope with Nomarski Differential Interference Contrast and drawing tube. Some of the setae designated as plumose herein may be plumodenticulate setae due to the lower resolution limits of LM as compared to scanning electron microscopy (SEM). Description guidelines of Clark *et al.* (1998) were generally followed.

Specimens of larval stages and a spent female crabs have been deposited at the NEBECC Decapod Larval Collection, Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos, Department of Zoology – IB, Universidade Estadual Paulista, Botucatu, State of São Paulo, Brazil, accession numbers NEBECCLC # 00066 and 0078. Slides used in the description have been deposited at the Museu de Zoologia da Universidade de São Paulo, São Paulo, State of São Paulo, Brazil under register number MZUSP 17086.

RESULTS

Larval development and description – Larval development of *Notolopas brasiliensis* consists of two zoeal stages and one megalopa. The duration mean of each zoeal stage was 4.2 ± 1.0 days for Zoea I and 3.8 ± 0.7 days for Zoea II, the megalopa instar appearing 8.1 ± 0.4 days after hatching. Only morphological changes are described for the second zoeal stage.

Description

Notolopas brasiliensis Miers, 1886
First zoea (Figure 1)

Carapace (Figure 1A) – Dorsal spine curved, and short straight rostral spine not extending beyond antennule; lateral spines absent. On ventral margin with densely plumose "anterior seta" posterior to scaphognathite notch, followed by 5 additional sparsely plumose setae. Eyes sessile. Frontal area between dorsal and rostral spine forming a distinct swelling with strong muscle bands and bearing small protuberance with dorsal organ (*sensu* Martin & Laverack, 1992). Additional small knob with dorsal organ posterior to dorsal spine. One pair of simple or sparsely plumose setae present posterior to the dorsal spine.

Antennule (Figure 1B) – Unsegmented, smooth, conical. Terminally bearing two long aesthetascs, 2 shorter aesthetascs, and 2 short setae.

Antenna (Figure 1C) – Biramous, protopod long and pointed, bearing 2 rows of spinules, increasing in size distally; endopod bud present; unsegmented exopod with long spinulated distal process and pair of serrulate setae about 1/3 from tip.

Mandible (Figure 1D) – Medial toothed molar process and enlarged lateral incisor process bearing marginal teeth. Palp absent.

Maxillule (Figure 1E) – Epipod seta absent. Coxal endite bearing 7 setae, 5 terminal graded plumodenticulate and subterminally 2 plumodenticulate setae. Basial endite with 3 terminal plumodenticulate cuspidate setae and 4 subterminal plumodenticulate setae. Two-segmented endopod with proximal segment bearing plumodenticulate seta, distal segment bearing plumodenticulate seta medially and 2 pairs of plumodenticulate setae apically. Exopod seta absent. Microtrichia not observed.

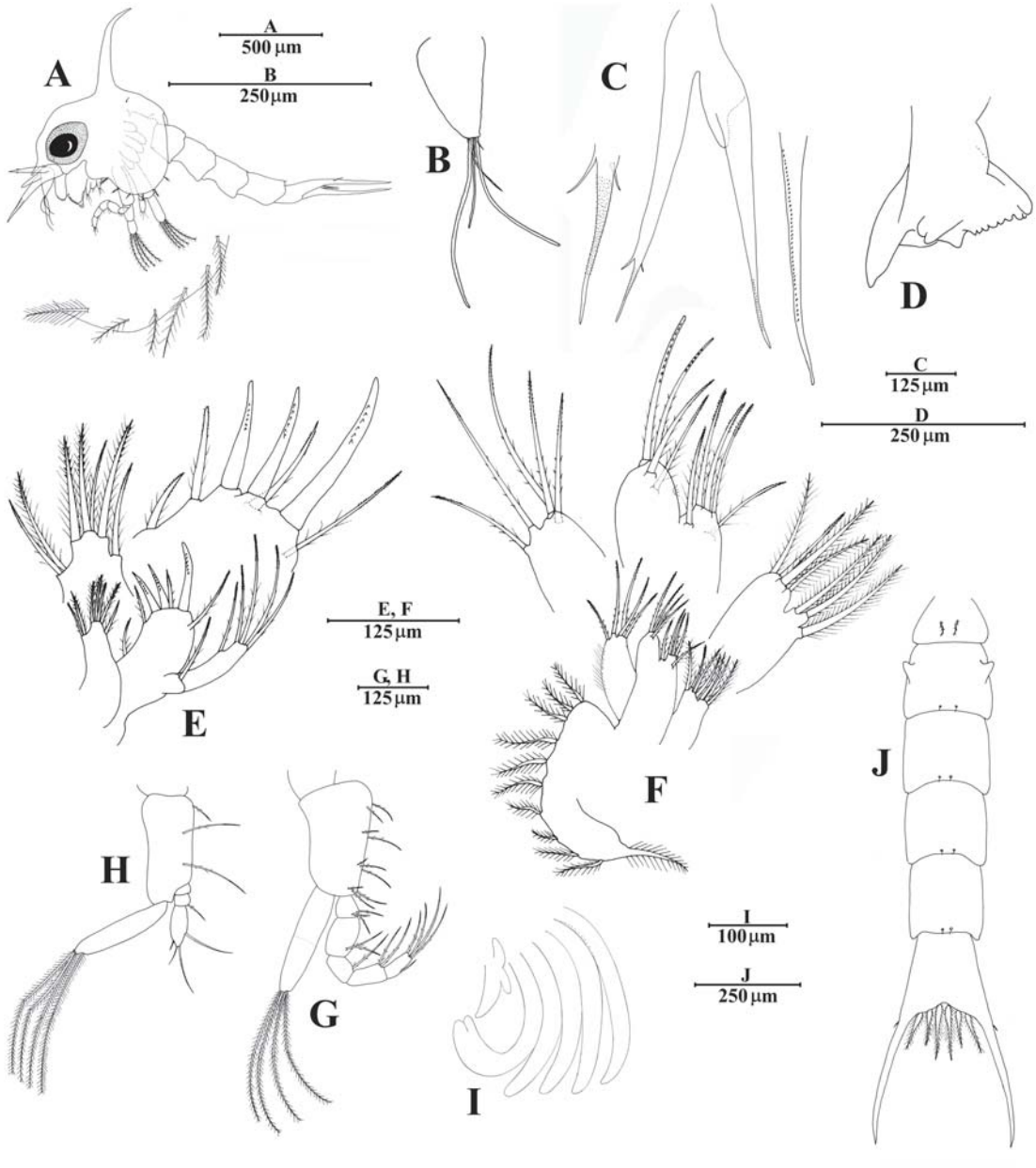

FIGURE 1. First zoea of *Notolopas brasiliensis* Miers, 1886. **A,** lateral view; **B,** antennule; **C,** antenna; **D,** mandible; **E,** maxillule; **F,** maxilla; **G,** maxilliped 2; **H,** maxilliped 1; **I,** developing maxilliped 3 and pereiopods; **J,** dorsal view of abdomen and telson.

Maxilla (Figure 1F) – Coxal endite bilobed, proximal lobe with 3 plumose setae, distal lobe with 4 setae, 3 plumose and 1 plumodenticulate; microtrichia not observed on the proximal and distal lobe. Basial endite bilobed, proximal lobe with 5 plumodenticulate setae, distal lobe bearing 4 plumodenticulate setae and microtrichia on proximal margin. Unsegmented, not bilobed endopod distally with 4 terminal and 1 subterminal plumodenticulate setae; microtrichia on lateral margin. Scaphognathite marginally with 11 densely plumose setae, including distal process.

Maxilliped 1 (Figure 1G) – Coxa without setae. Basis with 10 plumodenticulate setae arranged 2,2,3,3. Endopod 5-segmented with 3,2,1,2,4+1 plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 2 (Figure 1H) – Coxa without setae. Basis with 3 plumodenticulate setae. Endopod 3-segmented, with 0,1,4 (2 subterminal, 2 trerminal) plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 3 (Figure 1I) – Birramous, present as small endo-, exo- and epipod buds.

Pereiopods (Figure 1I) – Present as small buds, chelipod bilobed.

Abdomen (Figure 1J) – Five somites. Somite 1 with a pair of middorsal plumodenticulate setae, somites 2-5 each with pair of posterodorsal shorter sparsely plumose or simple setae. Somite 2 with pair of dorsolateral processes. Pleopods absent.

Telson (Figure 1J) – Bifurcated, distinct median notch, 3 pairs of serrulate setae on inner margin; each furcal shaft proximally bearing minute lateral spine, furcal shafts and spines covered with rows of spinules to just below tips.

Second zoea (Figure 2)

Carapace (Figure 2A) – Eyes stalked. Three additional pairs of simple or sparsely plumose setae, two pairs just above eyes, another at base of dorsal spine. Lateral margin anteriorly to posteriorly now with 2 densely plumose and 6 plumose or plumodenticulate setae.

Antennule (Figure 2B) – With 3 long and 4 short aesthetascs and a short seta; endopod bud absent.

Antenna (Figure 2C) – Endopod bud enlarged to middle of protopod.

Mandible (Figure 2D) – With palp bud.

Maxillule (Figure 2E) – Coxa with extra subterminal plumodenticulate seta; basis with 2 additional cuspidate setae, and 1-2 additional subterminal plumodenticulate setae; exopod pappose seta present.

Maxilla (Figure 2F) – Coxal endite with proximal lobe bearing 3-4 plumose seta. Basial endite with 5 proximal and 5-6 distal plumodenticulate setae. Scaphognathite with 15-20 marginal plumose setae.

Maxilliped 1 (Figure 2G) – Coxa with plumodenticulate seta. Exopod with 6 plumose natatory setae.

Maxilliped 2 (Figure 2A) – Exopod with 6 plumose natatory setae.

Maxilliped 3 (Figure 2H) – Endo-, exo- and epipod buds developing.

Pereiopods (Figure 2H) – Longer, chela distinct.

Abdomen (Figure 2I) – Separated sixth somite. Somite 1 with 3 middorsal plumodenticulate setae. Additional pair of middorsal simple setae on somite 2. Somites 2-5 with pair of unsegmented biramous pleopods, endopods distinct. Uropods absent.

Megalopa (Figures 3 and 4)

Carapace (Figure 3A) – Longer than wide, narrowing anteriorly, with small rostrum deflected slightly ventrally; lateral and dorsolateral ridge extending from eyes to the beginning of branchial area, two additional pairs of dorsal protuberances near border of gastric area. Two small protuberances on the urogastric region, and a pair of tubercles on the metabranquial region. Surface with mostly simple setae as shown.

Antennule (Figure 3B) – Three-segmented peduncle with two simple setae on middle and single seta on distal segment; unsegmented endopod with one subterminal plumodenticulate and 2 terminal simple setae; three-segmented exopod with naked proximal segment,

single plumodenticulate seta and 7 aesthetascs on middle segment, and distal segment with 4 aesthetascs with aesthetasc-like apical seta.

Antenna (Figure 3C) – Segments 1-7, progressing proximally to distally, each with 0,2,2,0,0,4,4 simple setae, respectively; 3 terminal setae longer. First segment with exopod process.

Mandible (Figure 3D) – Scoop-shaped process with cutting edge and unsegmented palp bearing 5 apical plumodenticulate setae.

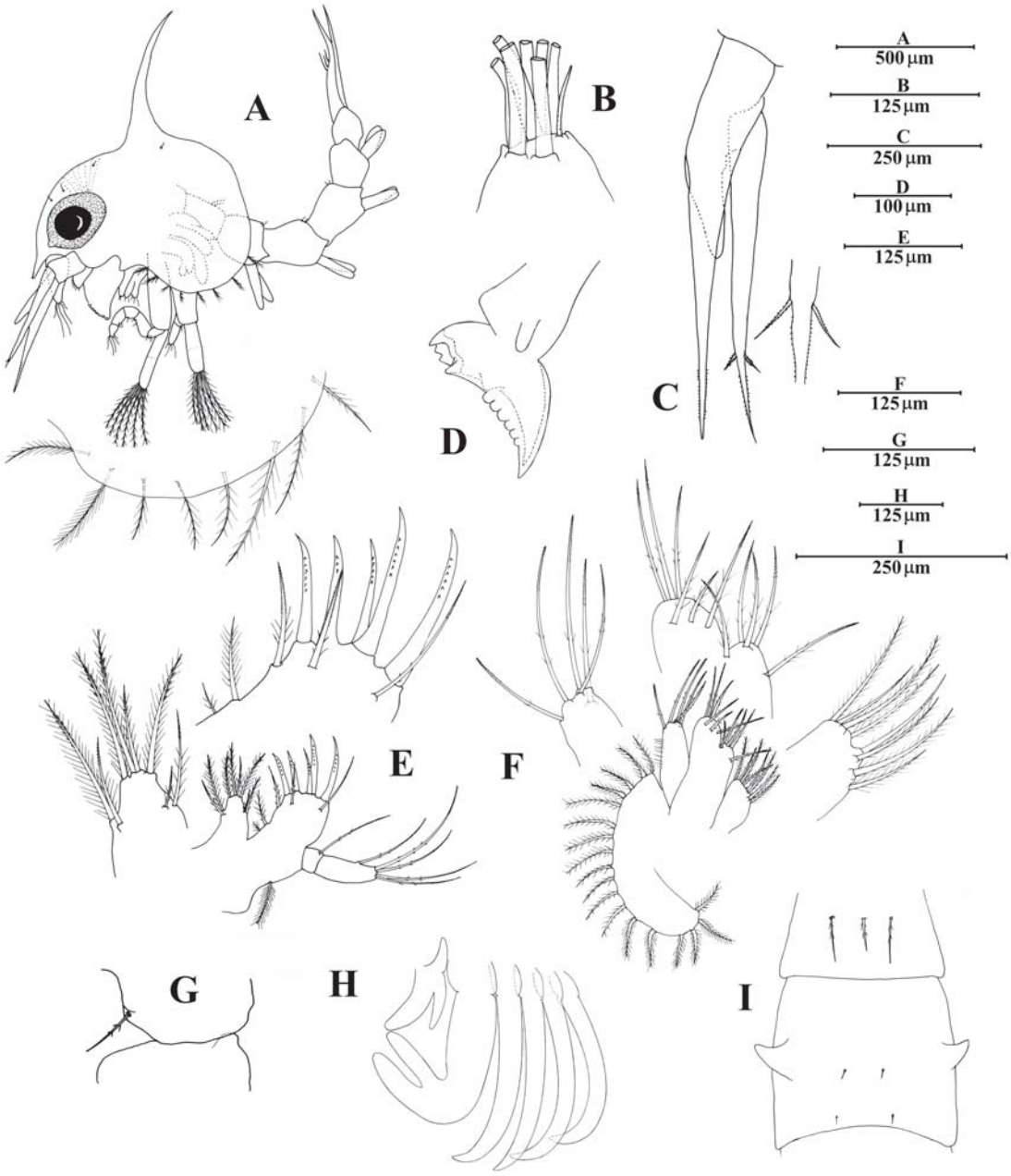

FIGURE 2. Second zoea of *Notolopas brasiliensis* Miers, 1886. **A,** lateral view; **B,** detail of the antennule; **C,** antenna; **D,** mandible; **E,** maxillule; **F,** maxilla; **G,** detail of the coxal endite of the first maxilliped; **H,** developing maxilliped 3and pereiopods; **I,** dorsal view of abdominal somites 1-2.

Maxillule (Figure 3E) – Coxal endite with about 10 subterminal and terminal plumodenticulate setae. Basial endite with 18 mostly plumodenticulate setae distal to endopod. Unsegmented endopod naked.

Maxilla (Figure 3F) – Coxal endite proximal and distal lobes with 4 (3 plumose, 1 plumodenticulate) and 3 (2 plumose, 1 plumodenticulate) setae, respectively; basial endite proximal and distal lobes with 5+5 plumodenticulate setae, respectively. Endopod bearing 0-1 plumodenticulate seta terminally. Scaphognathite with 29 marginal plumose setae; blade with 3 simple setae.

Maxilliped 1 (Figure 4A) – Epipod with 3 plumodenticulate setae. Coxal endite with about 4-6 plumodenticulate setae, basial endite bearing about 9-11 plumodenticulate setae; endopod absent; exopod with optional pappose or plumose seta distally on proximal segment and 4 plumose setae on distal segment.

Maxilliped 2 (Figure 4B) – Coxa and basis not clearly differentiated; endopod with indistinct basal segment, subsequent four segments proximally to distally with 0, 1, 3 and 6 plumodenticulate setae respectively; exopod with naked proximal segment and 4 plumose setae on

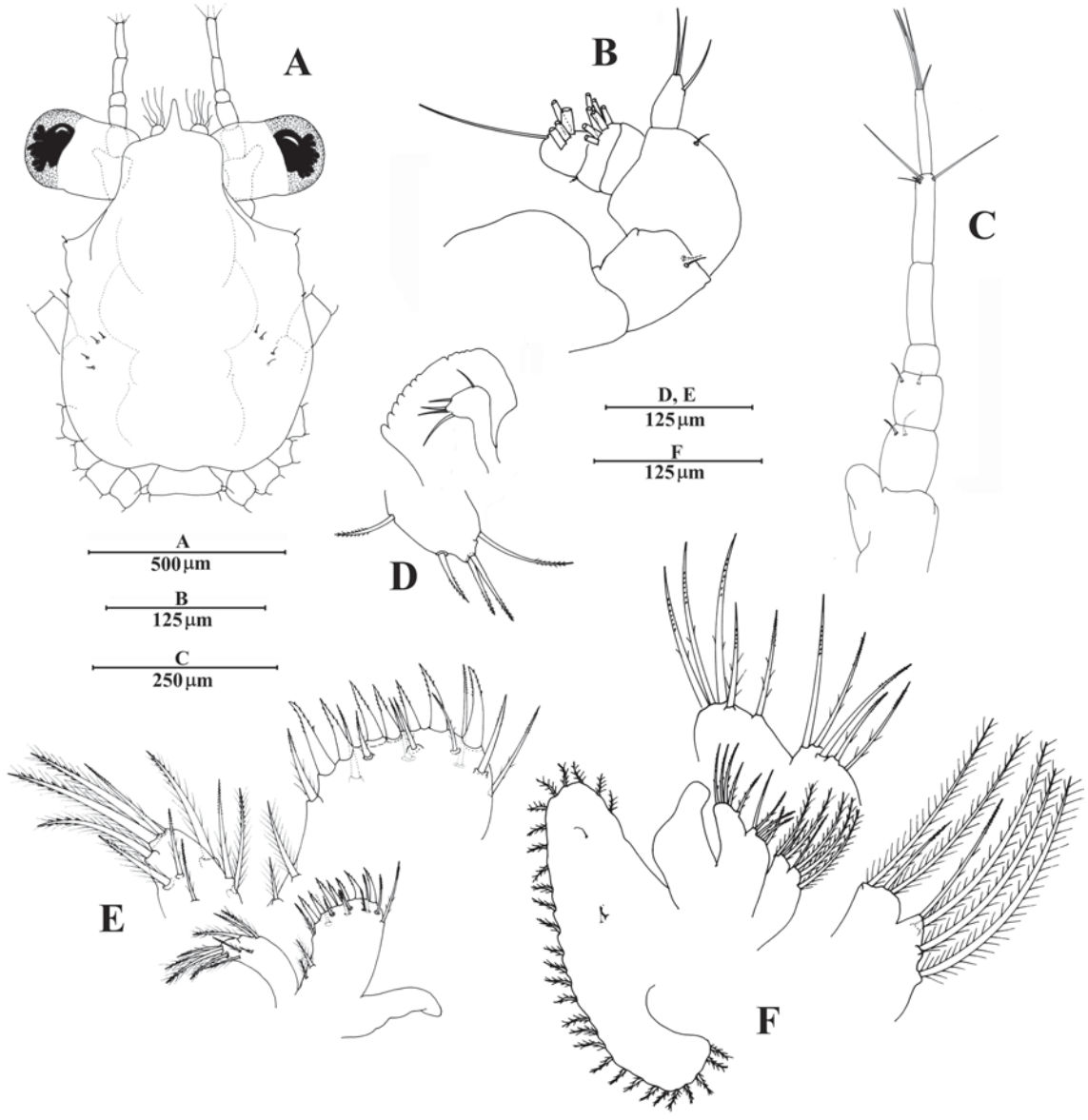

FIGURE 3. Megalopa of *Notolopas brasiliensis* Miers, 1886. **A,** dorsal view, **B,** antennule; **C,** antenna; **D,** mandible; **E,** maxillule; **F,** maxilla.

distal segment; epipodite not present on examined specimens.

Maxilliped 3 (Figure 4C) – Epipod with 3 plumodenticulate setae distally. Coxa with 5-7, basis not differentiated with 2 plumodenticulate setae; endopod proximally to distally with 8, 8, 5, 5 and 4 mostly plumodenticulate setae; ischium with crista dentata; bisegmented exopod with naked proximal segment and 4 setae apically on distal segment.

Pereiopods (Figure 4D) – Covered with mostly simple setae; coxa of pereiopods 1-4 with single ventral simple seta, coxa of pereiopod 1 with short projection fitting into sternal notch; coxa of pereiopods 2 and 3 with single spine, vestigial spine on coxa of pereiopod 4,

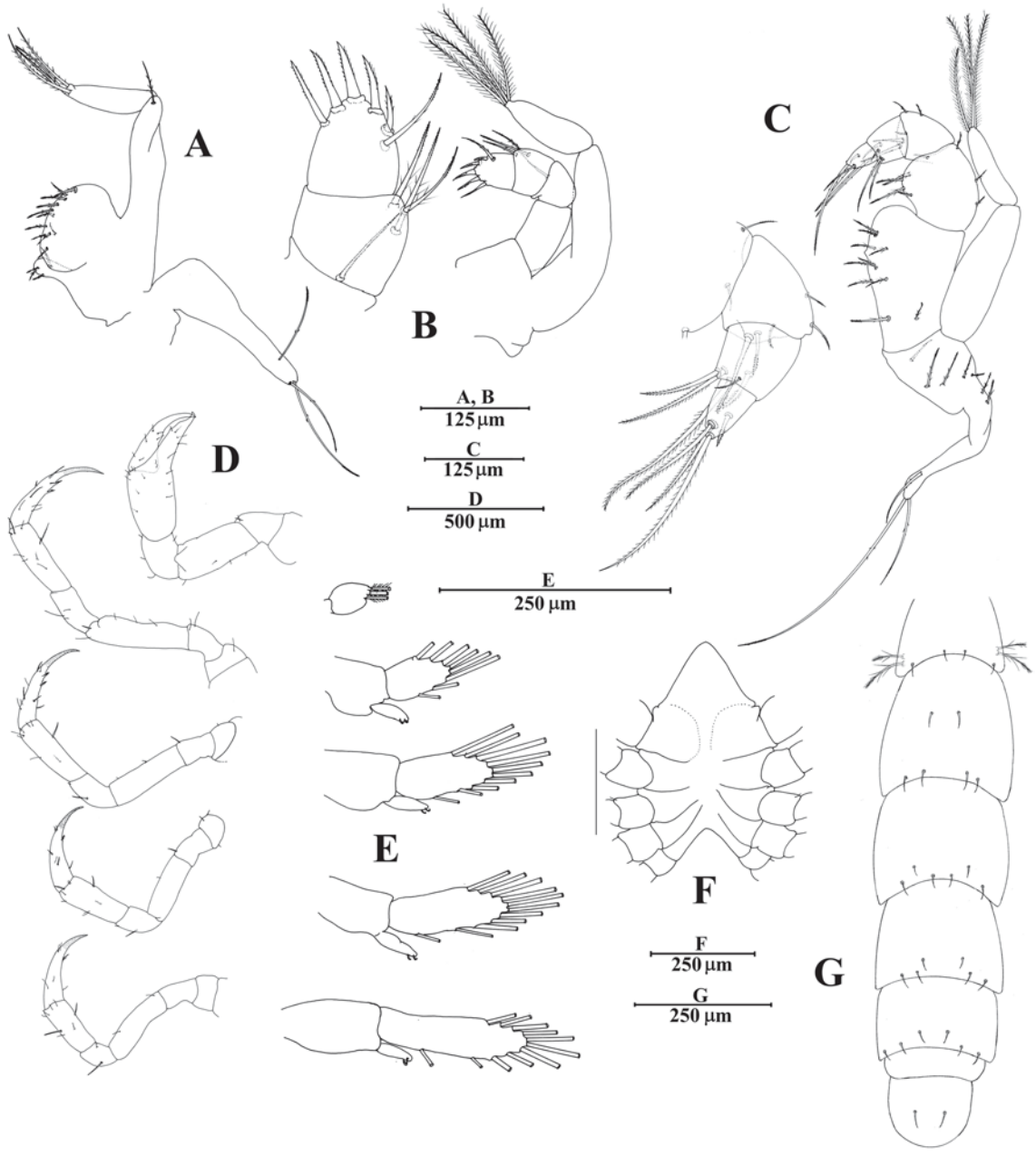

FIGURE 4. Megalopa of *Notolopas brasiliensis* Miers, 1886. **A,** maxilliped 1; **B,** maxilliped 2; **C,** maxilliped 3; **D,** cheliped and pereiopods; **E,** pleopods; **F,** sternum; **G,** dorsal view of abdomen and telson.

ischium of pereiopod 2 with additional spine; dactyl of pereiopods 1-4 with spinules as shown and 1-2 serrate setae on inner margin.

Sternum (Figure 4F) – Small lateral notch present on sternite 4.

Abdomen (Figure 4G, E) – Posterolateral margins of all somites rounded, dorsally and laterally ornamented with mostly simple setae, somites 1-5 proximally to distally with 4, 6, 6, 6, 6 setae, sixth somite naked. Somite 1 with two additional pairs of distinct plumose or plumodenticulate setae ventrolaterally. Exopod of pleopods 1-5 on somites 2-6 with 11,11,10,8 and 3 plumose setae, respectively; endopod of pleopods 1-4 with 2 cincinnuli each, pleopod 5, i.e. uropod, lacking endopod.

Telson (Figure 4G) – Rounded posteriorly, bearing a pair of dorsal setae. Some specimens bear variously reduced setae on the posterior margin.

DISCUSSION

This study reports for the first time larval stages from *Notolopas*. Previous accounts of the larval features within Pisidae have addressed the larval stages of 30 species within 15 genera (Table 1). However, some authors have argued that there are no larval characters that would define this family (e.g., Pohle & Marques, 2000; Marques & Pohle, 2003).

Ingle (1979) discussed character sets for families within Majoidea, and hence postulated some larval features that would characterize pisid larvae. His character set for this family included: absence of carapace lateral spines, rostral and dorsal spines of moderate length, one spine on the telson fork, dorsolateral processes on the 2nd abdominal somite, rarely on the 3rd; posterolateral processes on the 3rd-5th abdominal somite often short; basis of the 2nd maxilliped with not more than 3 setae; antennal exopod with subterminal setae. However, as we have accumulated larval descriptions over the years, these characters became inadequate to represent pisid species with known larval development.

A detailed exam of the characters used by Ingle (1979) to define larval forms of Pisidae shows that most of these characters are either symplesiomorphic or potentially highly homoplastic ones based on previous phylogenetic studies on larval morphology (Clark & Webber, 1991; Marques & Pohle, 1998, 2003; Pohle & Marques, 1998, 2000). For instance, the absence of lateral spines on the carapace is also observed in larval forms within Mithracidae, Epialtidae, Inachidae, Inachoididae and some members of Majidae. The presence of dorsolateral process on the 2nd abdominal somite can be found in some species of Mithracidae, all Majidae, Epialtidae, Inachidae, Inachoididae. The presence of 3 setae on the basis of the 2nd maxilliped is shared with species within Majidae, Mithracidae, and most Epialtidae, Inachidae and Inachoididae. Finally, presence of subterminal setae on the exopod of the antenna can also be observed in members of Majidae, Mithracidae, Epialtidae and most Inachoididae (Marques & Pohle, 1998, 2003; Pohle & Marques, 1998, 2000; Santana *et al.,* 2004). Thus, we suggest, as previous works (e.g., Santana *et al.,* 2004), that these characters should not be used to define the larval forms within Pisidae. In addition, as have been asserted for many families within Majoidea (Pohle & Marques, 2000; Marques & Pohle, 2003), there is no unique larval characters and/or combinations of them that would distinguish larval stages of Pisidae from other members of Majoidea.

In contrast to other families of Majoidea in which larvae are difficult to differentiate because of the great consistency of larval morphology within it (e.g., Mithracidae) – especially in zoeal stages (Santana *et al.,* 2003), larvae of Pisidae are difficult to identify because of the great heterogeneity of its larval forms (Santana *et al.* 2004) showing characters resembling other families. The corollary is the difficulty to find common sets of characters that would define the group as mentioned above. Be that as it may, Santana *et al.* (2004) compared larval morphology within Pisidae and pointed out some characters that could suggest Pisidae as a phenetically coherent group, with the exception of few genera. However, as stated by Santana *et al.* (2004), those characters could be overall similarities, i.e., simplesiomorphies and/or homoplasies within Majoidea. The larval morphology of *Notolopas brasiliensis* is in agreement with the zoeal characters proposed by Santana *et al.* (2004) that characterize Pisidae. In the first zoeal stage, the setation of the coxal and basial endites of the maxillule (excluding *Pisoides*), and the endopod of the first maxilliped (excluding *Doclea*) could be mentioned (Table 2). The character that could distinguish the second zoeal stage is: the presence of the exopod seta on the maxillule (excluding *Pisoides*) (Table 3). The megalopa presents no consistent morphological character among genera (Table 4).

Among Pisidae, *Notolopas* has no single zoeal character that could distinguish the genus from other members of the family (Tables 2, 3, 4). However, a combination of characters can differentiate *Notolopas* from other pisids. For instance, the arrangement of the setation on

TABLE 1: Species of the Pisidae with known larval descriptions, indicating source and stages described. * not included in comparison.

Species	Authors	Stages described
Anamathia rissoana	Guerao & Abelló, 1996;	PZ, Z1;
Apiomithrax violaceus	Santana *et al.,* 2004;	Z1, Z2, M;
Doclea gracilipes	Chhapgar, 1956;	M, C1;
	Krishnan & Kannupandi, 1988;	Z1, Z2, M;
D. hybrida	Sankolli & Shenoy, 1975;	Z1, Z2, M;
D. ovis	Mohan & Kannupandi, 1985;	Z1, Z2, M;
D. muricata	Krishnan & Kannupandi, 1987;	Z1, Z2, M;
Eurynolambrus australis	Webber & Wear, 1981;	Z1, Z2, M;
Eurynome aspera	Kinahan, 1858;	PZ;
	Kinahan, 1860;	Z1;
	Gurney, 1924;	PZ, Z1;
	Lebour, 1928;	Z1, Z2, M;
	Bourdillon-Casanova, 1960;	M;
	Salman, 1982;	Z1, Z2, M;
	Wear & Fielder, 1985;	Z2, M;
E. spinosa	Salman, 1982;	Z1;
	Hong, 1998;	Z1, Z2, M;
*Herbstia condyliata**	Cano, 1893;	Z2, M;
	Bourdillon-Casanova, 1960;	Z1;
*Hyastenus diacanthus**	Kurata, 1969;	Z1, M;
*H. elongatus**	Terada, 1983;	Z1, Z2;
	Ko, 1997;	Z1;
Libidoclaea granaria	Fagetti, 1969;	Z1, Z2, M;
Libinia dubia	Sandifer & van Engel, 1971;	Z1, Z2, M;
L. emarginata	Johns & Lang, 1977;	Z1, Z2, M;
*L. erinacea**	Yang, 1967;	Z1, Z2, M;
L. ferreirae	de Bakker *et al.,* 1990;	Z1, Z2, M;
*L. setosa**	Rathbun, 1923;	M;
L. spinosa	Boschi & Scelzo, 1968;	Z1, Z2, M;
	Clark *et al.,* 1998a;	Z1, Z2, M, C1;
*Lissa chiragra**	Cano, 1893 (Lissa sp.);	Z1, Z2, M;
	Boraschi, 1921;	Z1;
	Bourdillon-Casanova, 1960;	Z1;
	Heegaard, 1963;	Z1;
	Guerao *et al.,* 2003;	Z1, Z2, M, C1
*Naxioides histrix**	Kurata, 1969;	Z1;
*N. serpulifera**	Rathbun, 1914 (direct develop.);	C1, C2;
Pisa armata	Heegaard, 1963;	Z1;
	Ingle & Clark, 1980;	Z1, Z2, M, C1;
*P. corallina**	Gourret, 1884;	Z1;
*P. nodipes**	Heegaard, 1963;	Z1;
P. tetraodon	Heegaard, 1963;	Z1;
	Rodriguez, 1997;	Z1, Z2, M, C1;
Pisoides edwardsi	Fagetti, 1969a;	Z1, Z2, M;
*P. ortmanni**	Kurata, 1969;	Z1, M;
	Terada, 1983;	Z1, Z2;
Rochinia carpenteri	Ingle, 1979;	Z1, Z2, M;
Scyra compressipes	Kim & Hong, 1999;	Z1, Z2, M;

Modified from Santana *et al.* (2004)

the endopod of the maxillule with one seta on the proximal segment and 5 setae on the distal segment (similar to *Apiomithrax, Libidoclea,* and *Libinia*) in addition to the setation of the coxal endite of the maxilla (similar in *Doclea,* and *Eurynolambrus*) can be used to differentiate the first zoeal stage of *Notolopas* from the other pisids (Table 2). For the second zoeal stage, the number of aesthetascs and seta on the antennule (resembling *Doclea,* and *Eurynome*), the setation on the endopod of the maxillule (congruent with the pattern found in *Apiomithrax, Libidoclea,* and *Libinia*), and the setation on the endopod of the second maxilliped (simi-

TABLE 2. Comparison of larval characters of the first zoeal stage for Pisidae genera.

Zoea 1	*Notolopas*	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*
carapace	RS: short;	RS: long;	RS: short or absent;	RS: intermediate;	RS: intermediate;	RS: long;
	LS absent;	(RS > DS);	LS absent;	LS absent;	LS absent;	(RS < DS);
	6 s ventral margin	LS present;	5-8 s ventral margin	7 s ventral margin	4 s ventral margin	LS absent;
		5-6 s ventral margin				6 s ventral margin
antennule	4 aes, 2 s	4 aes, 2 s	4 aes, 0-2 s	4 aes, 2 s	4 aes, 1-2 s	3 aes, 2 s
antenna	exo < pro	exo > pro	exo < pro	exo < pro	exo < pro;	exo = pro
maxillule	cox: 7;	cox: 7;	cox: 7;	cox: 7;	cox: 7;	cox: 7;
	bas: 7;	bas: 7;	bas: 7;	bas: 7;	bas: 7;	bas: 7*;
	end: 1, 5	end: 1, 5	end: 0-1, 6-7	end: 1, 6	end: 1,6	end: 1,5
maxilla	cox: 3, 4;	cox: 4, 4;	cox: 3-5, 3-5;	cox: 3, 4;	cox: 5, 4;	cox: 4, 5;
	bas: 5, 4;	bas: 5, 4;	bas: 2-5, 3-4;	bas: 5, 4;	bas: 4-5, 4;	bas: 4, 5;
	end: 5;	end: 3-4;	end: 4-5;	end: 5;	end: 5;	end: 3, 3;
	sca: 11	sca: 10	sca: 11-16	sca: 13	sca: 9-10	sca: 15
mxpd 1	cox: 0;	cox: 1;	cox: 0*;	cox: 1;	coxa 0-1;	cox: 0*;
	bas: 2, 2, 3, 3;	bas: 2, 2, 2, 3;	bas: 2, 1-2, 2, 3;	bas: 2, 2, 2, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 3, 3;
	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3-4, 2, 1-2, 2-3, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5
mxpd 2	bas: 3;	bas: 3;	bas: 2-4;	bas: 3;	bas: 3;	bas: 3;
	end: 0, 1, 4	end: 0, 1, 4	end: 0, 1, 3-4	end: 0, 1, 6	end: 1, 1-2, 5	end: 0, 1, 5
abdomen	S1: 2;	S1: 2;	S1: 2-3;	S1: 2;	S1: 2;	
	S2-5: 2;	S2-5: 2;	S2-5: 0 or 2;	S2-5: 2;	S2-5: 2;	
	dlp: S2	dlp: S2-3	dlp: S2	dlp: S2	dlp: S2	dlp: S2
telson	furca: 1 sp;	furca: 2 sp;	furca: 0 sp;	furca: 3 sp;	furca: 2-4 sp;	furca: 1 sp;
	spi present;	spi present;	spi absent;	spi present;	spi present;	spi present;
	6 s	6 s	6 s	6 s	6 s	6 s
Zoea 1	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*	
carapace	RS: short;	RS: short;	RS: short;	RS: long	RS: intermediate;	
	LS absent;	LS absent;	LS absent;	(RS < DS);	LS absent;	
	6-8 s ventral margin	6-7 s ventral margin	6-7 s ventral margin	LS present;	6 s ventral margin	
				4* s ventral margin		
antennule	2-4 aes, 1-2 s	4-6 aes, 0 or 2 s	4 aes, 2 s	2 aes, 1 s	5 aes, 1* s	
antenna	exo < pro*	exo = pro	exo > pro	exo > pro	exo < pro	
maxillule	cox: 7;	cox: 7;	cox: 8;	cox: 7;	cox: 7;	
	bas: 7;	bas: 7;	bas: 7;	bas: 7;	bas:is 7;	
	end: 1,5	end: 1,6	end: 1,6	end: 1,6	end: 1,4	
maxilla	cox: 4, 4;	cox: 5-6, 4;	cox: 5, 4;	cox: 5, 4;	cox: 4, 4;	
	bas: 4, 4-5;	bas: 4-5, 4;	bas: 4, 4;	bas: 5, 4;	bas: 5, 4;	
	end: 4-5;	end: 5;	end: 5;	end: 6;	end: 4;	
	sca: 10-11	sca: 11-13	sca: 13	sca: 12	sca: 9-10	
mxpd 1	cox: 0-1;	cox: 0*;	cox: 0*;	cox: 0*;	cox: 0*;	
	bas: 2, 2*, 3, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 2, 3;	
	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	
mxpd 2	bas: 3;	bas: 3;	bas: 3;	bas: 3;	bas: 3;	
	end: 0, 1, 4-5	end: 0-1, 1-2, 5or3	end: 1, 1, 4	end: 0, 1, 5	end: 0, 1, 4	
abdomen	S1: 2;	S1: 2;	S1: 2;	S1: 2;	S1: 2;	
	S2-5: 2;	S2-5: 2;	S2-5: 2;	S2-5: 2;	S2-5: 2;	
	dlp: S2	dlp: S2	dlp: S2	dlp: S2	dlp: S2	
telson	furca: 1 sp;	furca: 1 sp;	furca: 1 sp;	furca: 1 sp;	furca: 1 sp;	
	spi present;	spi present;	spi present;	spi present;	spi present;	
	6 s	6 s	6 s	6 s	6 s	

RS: rostral spine; DS: dorsal spine; LS: lateral spine; dlp: dorsolateral process; cox: coxa or coxal endite; bas: basis or basial endite; end: endopod; exo: exopod; sca: scaphognathite; epi: epipod; pro: protopod; ped: peduncle; S: somite; s: setae; aes: aesthetasc; sp: spine; spi: spinules, * observation from figure, n/a: not available.

lar to *Apiomithrax, Libinia,* and *Pisa*) can separate *Notolopas* from other pisids (Table 3). Conversely, the megalopa posses some unique larval characters, which could be useful to diagnose the species within pisids. For instance, the number of aesthetascs of the exopod of the antennule, the setation of the coxal endite and scaphognatite of the maxilla, the number of setae on the endopod of the third maxilliped, and the abdominal setation are only found in megalopa of *Notolopas* (Table 4).

TABLE 3. Comparisons of larval characters of second zoeal stage for Pisidae genera; see table 2 for definition of abbreviations.

Zoea 2	*Notolopas*	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*
carapace	RS: short;	RS: long;	RS: short or absent;	RS: intermediate;	RS: intermediate;	RS: long;
	LS absent;	(RS > DS);	LS absent;	LS absent;	LS absent;	(RS < DS);
	8 s ventral margin	LS present;	6-10 s ventral margin	8 s ventral margin	4-6 s ventral margin	LS absent;
		7-8 s ventral margin				7 s ventral margin
antennule	7 aes, 1 s	8 aes, 2 s	5-8 aes, 0-2 s	8 aes	5-7 aes, 1 s	7 aes
antenna	exo < pro	exo > pro	exo < pro	exo < pro	exo < pro	exo < pro*
maxillule	cox: 8;	cox: 8;	cox: 6-8;	cox: 7;	cox: 7;	cox: 7;
	bas: 9-10;	bas: 10;	bas: 8-10;	bas: 9;	bas: 9*;	bas: 10*;
	end: 1, 5;	end: 1, 5;	end: 0-1, 6-7;	end: 1, 6;	end: 1, 6;	end: 1, 5;
	exo: 1	exo: 1	exo: 0-1	exo: 1	exo: 1	exo: 1
maxilla	cox: 3-4, 4;	cox: 4, 4;	cox: 4-6, 3-5;	cox: 3, 4;	cox: 5,4;	cox: 4, 5;
	bas: 5, 5-6;	bas: 4-5, 5;	bas: 4-5, 3-4;	bas: 5, 5;	bas: 5,5;	bas: 5, 5*;
	end: 5;	end: 3-4;	end: 4-5;	end: 5;	end: 5;	end: 5;
	sca: 15-20	sca: 20	sca: 25-30	sca: 23-25	sca: 16-19	sca: 29
mxpd 1	cox: 1;	cox: 1;	cox: 0-1;	cox: 1,	cox: 0-1;	cox: 0*;
	bas: 2, 2, 3, 3;	bas: 2, 2, 2, 3;	bas: 1-2, 2, 2-3, 3;	bas: 2, 2, 2, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 3, 3;
	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 2-4, 2, 1-2, 2-3, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5
mxpd 2	bas: 3;	bas: 3;	bas: 2-6;	bas: 3;	bas: 3;	bas: 3;
	end: 0, 1, 4	end: 0, 1, 4	end: 0, 1, 3-5	end: 0, 1, 6	end: 1, 1-2, 5	end: 0, 1, 5
abdomen	S1: 3;	S1: 5;	S1: 3;	S1: 2;	S1: 3;	S1: 2;
	S2: 4;	S2-3: 4;	S2-5: 0 or 2 (5 or 6 S);	S2-5: 2;	S2-5: 2;	
	S3-5: 2;	S4-5: 2;				
	dlp: S2	dlp: S2-S3	dlp: S2	dlp: S2	dlp: S2	
telson	furca: 1 sp;	furca: 2 sp;	furca: 0 sp;	furca: 3 sp;	furca: 2-4 sp*;	furca: 1 sp;
	spi present;	spi present;	spi absent;	spi present;	spinules present;	spinules present;
	6 s	8 s	6 s	8 s	8 s	6 s

Zoea 2	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
carapace	RS: short;	RS: short;	RS: short;	RS: long;	RS: intermediate;
	LS absent;	LS absent;	LS absent;	(RS < DS);	LS absent;
	7-10 s ventral margin	7 s ventral margin	11 s ventral margin	LS present	6 s ventral margin
antennule	6 or 8 aes, 1-2 s	6 or 8 aes, 0 or 2 s	6 aes	5 aes, 1 s	8 aes, 2 s
antenna	exo < pro*	exo = pro	exo > pro	exo > pro	exo = pro
maxillule	cox: 7-8;	cox: 7-8;	cox: 7F 8T;	cox: 6-7;	cox: 7;
	bas: 9-10;	bas: 8-9;	bas: 9;	bas: 10;	bas: 10;
	end: 1, 5;	end: 1, 6;	end: 1, 6;	end: 1, 6;	end: 1, 4;
	exo: 1	exo: 1	exo: 0*	exo: 1	exo: 1
maxilla	cox: 4, 3-4;	cox: 5, 4;	cox: 4T 5F, 4*;	cox: 5, 4;	cox: 4, 4;
	bas: 5, 4-5;	bas: 5, 4-5;	bas: 5, 4;	bas: 5, 8;	bas: 5, 5;
	end: 5;	end: 5;	end: 5;	end: 7;	end: 4;
	sca: 16 or 20	sca: 20-23	sca: 21	sca: 21-23	sca: 16
mxpd 1	cox: 0-1;	cox: 0;	cox: 0*;	cox: 0*;	cox: 0*;
	bas: 2, 2, 3, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 3, 3;	bas: 2, 2, 2, 3;
	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5	end: 3, 2, 1, 2, 5
mxpd 2	bas: 3;	bas: 3;	bas: 3;	bas: 3;	bas: 3;
	end: 0, 1, 4-5	end: 0-1, 1-2, 3or5	end: 1, 1, 4	end: 0, 1, 5	end: 0, 1, 4
abdomen	S1: 3;	S1: 2;	S1: 4;	S1-2: 2;	S1: 2*;
	S2-3: 4;	S2: 4;	S2: 4;	S3-4: 4;	S2-3: 4;
	S4-5: 2*;	S3-5: 2;	S3-5: 2;	S5: 2or4;	S3-5: 2;
	dlp: S2	dlp: S2	dlp: S2	dlp: S2	dlp: S2
telson	furca: 1 sp;	furca: 1 sp;	furca: 1 sp;	furca: 1 sp;	furca: 1 sp;
	spinules present;	spi present;	spi present;	spi present;	spi present;
	6 s	6 s	6 s	6 s	6 s

Phylogenetic studies considering larval characters within majoids have failed to demonstrate the monophyly of most of the families including Pisidae (Clark & Webber, 1991; Marques & Pohle, 1998, 2003; Pohle & Marques, 2000). Hence, the most recent phylogenetic analysis using larval characters for Majoidea (Marques & Pohle, 2003) was unable to resolve the sister-group relationships within Pisidae. Thus, we are still waiting for larval characters that upon phylogenetic analysis would provide a set of synapomorphies that could be used to diagnose the family.

TABLE 4. Comparisons of larval characters of the megalopa stage for Pisidae genera; see table 2 for definition of abbreviations.

Megalopa	*Notolopas*	*Apiomithrax*	*Doclea*	*Eurynolambrus*	*Eurynome*	*Libidoclaea*
carapace	RS: short; DS: absent; 7-8 s posterior margin	RS: long; DS: present; 7-8 s posterior margin	RS: short or 2 horned; DS: absent; 0* s posterior margin	RS: absent; DS: absent; 5* s posterior margin	RS: short; DS: absent; 0 s posterior margin	RS: short; DS: absent; 0 s posterior margin
antennule	ped: 0,2,1; end: 3; exo: 7+1s,5 ae;	ped: 1,2,1; end: 3; exo: 10+1s,5 ae;	ped: 0 or 4,0,1-2; end: 2-3; exo: 0 or 5,3-4,2-3,0-1ae+ 1s;	ped: 0,1,1; end: 3; exo: 10+1,4,1ae;	ped: 0-1,2,0or2; end: 3-4; exo: 4or6,3 ae;	ped: 0,1,1*; end: 3; exo: 8+1*,4+1* ae;
antenna	seg 1-7: 0,2,2,0,0,4,4;	seg 1-7: 1,2,3,0,0,4,3;	seg 1-7: 0,0or2,1or3,0,0-1,2-3,1or4;	seg 1-7: 0,1,1,3,0,4,3*;	seg 1-7: 2,1-2,2-3,0-1,0,3,3-4;	seg 1-7: 0,2,3,0,0,4,4;
mandible	palp 5 s	palp 5-6 s	palp 4-5 s	palp 4 s	palp 6 s	palp 5 s
maxillule	cox: 10; bas: 18; end: 0; epi: 0;	cox: 10-11+1; bas: 19; end: 2; epi: 1;	cox: 7or 9-10; bas: 12 or17; end: 2-3 or 5; epi: 0;	cox: 8; bas: 11; end: 2; epi: 1;	cox: 9-10; bas: 15-16; end: 1-2; epi: 0;	cox: 11*; bas: 18; end: 1; epi: 0*;
maxilla	cox: 4, 3; bas: 5, 5; end: 0-1; sca: 20, 3;	cox: 5, 3; bas: 5-6, 6-7; end: 0; sca: 37-40, 3;	cox: 5-7, 2or4or6-7; bas: 3or5or7, 4-5or7; end: 0; sca: 36-45, 0or6??;	cox: 5, 5; bas: 6, 6; end: 0; sca: 36-37, 4;	cox: 6, 3; bas: 3-5, 5; end: 0; sca: 30-34, 0or3*;	cox: 7, 3; bas: 6, 6; end: 0; sca: 51, 0*;
mxpd 1	cox: 4-6; bas: 9-11; end: 0; exo: 0-1, 4; epi: 3;	cox: 6-8; bas: 12-14; end: 0-1; exo: 1, 4; epi: 7;	cox: 4-5 or 8; bas: 7 or 12-13; end: 1-2 or 4; exo: 0-2, 4; epi: 4-6;	cox bas: 16; end: 0; exo: 1, 4; epi: 6;	cox: 5-7; bas: 9-11; end: 1; exo: 0*-1, 4; epi: 0*or 2-4;	cox: 7*; bas: 12*; end: 0*; exo: 1, 4*; epi: 14*;
mxpd 2	end: 0,1,3,6; exo: 0, 4;	end: 0,1,2-3,5-6; exo: 0, 4;	end: 0,0or2,0or 3-4,4-5or7; exo: 0, 5-6;	end: 0,1,3,5; exo: 0, 4;	end: 0,1,3,5-6; exo: 0, 4;	end: 0,1,4,6*; exo: 0, 4*;
mxpd 3	cox: 7-9; end: 10,8,5,5,4; exo: 4; epi: 3;	cox: 6-7; end: 13,9-11,4-5,7,4; exo: 4-5; epi: 7;	cox: 3-4?; end: 0or9or12,5-6or 8-9,2or4-5,2-3or5-6,3-5; exo: 4; epi: 4or8??;	cox: 9; end: 13,6,4,7,5; exo: 2, 4; epi: 13*;	cox: 5-6 or 11; end: 12-14,5,1-2,4-5,5; exo: 1, 4-5; epi: 5*-6;	cox: 8*; end: 12,9,5,5,4*; exo: 0, 5*; epi: 11*;
abdomen	S1-6: 6,6,6,6,6,0;	S1-6: 6,6,8,8,8,2;	n/a	S1-6: 6,10,8,8,8,2;	S1-6: 6*-0,4or6,4or 6,4or6,4or6,0;	S1-6: 4,2,2,2,0,0*;

Megalopa	*Libinia*	*Pisa*	*Pisoides*	*Rochinia*	*Scyra*
carapace	RS:short or long (L.spinosa); DS: present (L. spinosa); 6-7* or 15* s posterior margin	RS: short; DS: absent; 0* s posterior margin	RS: intermediate; DS: absent; 5 s posterior margin	RS: long; DS: present; 0* s posterior margin	RS: short; DS: absent; 0* s posterior margin
antennule	ped: 0,1-2,1-2; end: 3; exo: 5-6or10+0-1,3-4or6+1* ae;	ped: 0,1,1; end: 3; exo: 6or8+1,4+0-1ae;	ped: 0,2,1; end: 3; exo: 10+1,4+1ae;	ped: 0,2,0; end: 3; exo: 6+1,4,3,1+1ae;	ped: 1,1,1; end: 2; exo: 6,5+1 ae;
antenna	seg 1-7: 0-1,1-2,1-3,0,0,3-4,3-4*;	seg 1-7: 0,2,3,0,0,4,4;	seg 1-7: 0,2,3,0,0,3,4*;	seg 1-7: 0,2,2,0,0,3,3;	seg 1-7: 0,2,3,0,0,3,4;
mandible	palp 5 s	palp 5 s	palp 4 s	palp 5 s	palp 5 s
maxillule	cox: 10-11; bas: 16-18; end: 0-4*; epi: 0;	cox: 9-10; bas: 17; end: 2-3; epi: 0*;	cox: 10; bas: 17; end: 0,2; epi: 0*;	cox: 10; bas: 11-12*; end: 4; epi: 0*;	cox: 10; bas: 15; end: 2; epi: 0;
maxilla	cox: 5-6, 3; bas: 6-7, 5-7; end: 0-2; sca: 31-36, 2;	cox: 7, 3; bas: 4-5, 6; end: 0; sca: 30-32, 0*or3;	cox: 5, 2; bas: 5, 6; end: 0; sca: 42, 0*;	cox: 9, 3-4; bas: 6, 6; end: 0; sca: 40*, 0*;	cox: 6, 2; bas: 6, 7; end: 0; sca: 31-32, 2;
mxpd 1	cox: 5-7; bas: 8-12; end: 0-3; exo: 1, 4-6; epi: 3-5 or 7;	cox: 7-8; bas: 11or16; end: 0or4; exo: 1, 4-5; epi: 5-6;	cox: 7*; bas: 8*; end: 0*; exo: 1, 4*; epi: 6*;	cox: 6; bas: 10; end: 0; exo: 1, 4; epi: 6;	cox: 7; bas: 11; end: 0; exo: 0, 4; epi: 0*;
mxpd 2	end: 0,1,3,6; exo: 0, 4-6;	end: 0,1,3,6; exo: 0, 4-5;	cox: 5* end: 0,1,4,6*; exo: 0, 4*; epi: 6*	end: 0,1,4,7; exo: 0, 4;	end: 0,1,3,6; exo: 0, 4;
mxpd 3	cox: 6or8*-10; end: 9-13,7-9,4-6,5-6,4; exo: 0, 5-6 epi: 7-9*;	cox: 6-7; end: 11-12,8-9,5-6,6,4; exo: 0, 5; epi: 9-10;	cox: 3*; end: 8,4,4,4,4*; exo: 0*; epi: 6*;	cox: 8*; end: 13-15,6-7,5,5,4; exo: 0,6-7; epi: 5;	cox: 5; end: 13,8,5,6,4; exo: 0,4; epi: 0*;
abdomen	S1-6: 6or8,6,6or8,4or6or8,6or8,0or2*;	S1-6: 6or8,8,6,6,6or 8,0or2*;	S1-6: 4*,2,2,2,2,2*;	S1-6: 8*,6,4,4,6,2*;	S1-6: 6,8,8,8,8,2*;

RESUMO

O completo desenvolvimento larval de Notolopas brasiliensis *é descrito, a partir de material criado em laboratório, com ênfase na morfologia externa de Majoidea e comparado aos demais gêneros de Pisidae. O desenvolvimento larval de* N. brasiliensis *consiste em dois estágios de zoea e um de megalopa. A duração media de cada estágio foi de 4.2 ± 1.0 dias para a Zoea I e 3.8 ± 0.7 dias para a Zoea II, a megalopa aparece entre 8.1 ± 0.4 dias após a eclosão. Os caracteres previamente utilizados para definir as formas larvais de Pisidae ou são simplesiomórficos ou altamente homoplásticos. Foi observado que não existe um conjunto de caracteres capazes de definir Pisidae até o presente.Contudo foi mostrado que uma combinação de caracteres pode ser utilizada para diferenciar* Notolopas *dos demais gêneros da família.*

PALAVRAS-CHAVE: Larval characters, *Notolopas,* spider crabs, Majidae, Pisidae.

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