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First Zoeal Stage of the Snapping Shrimp *Alpheus* Fabricius, 1798 (Caridea: Alpheidae): New Description of *Alpheus bouvieri* A. Milne-Edwards, 1878 and Literature Review

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ABSTRACT

Based on adult morphological characters, the more than 300 species of *Alpheus* were divided into seven informal species groups, but some groups are not supported by molecular data. The aim here was to describe the zoea I of *Alpheus bouvieri*, and to do a review of the larval descriptions available in the literature, analysing whether the morphological groups proposed for adults are supported by larval data. The new larvae were obtained from females sampled in Pernambuco and Rio Grande do Norte, Brazil. *Alpheus bouvieri* zoea I shares a combination of characters with most larvae in the genus, but with some diagnostic characteristics: endopod of the maxillule and maxilla with 3 and 4 setae, respectively, the base of the first maxilliped with 9 setae, endopod of the second and third maxilliped with 5 and 6 segments, respectively. In our review, 23 species were analysed from five groups: *edwardsi* (thirteen), *sulcatus* (four), *brevirostris* (three), *macrocheles* (two), and *obesomanus* (one) group; the zoea I of species from *diadema* and *crinitus* groups are unknown. Based on this review, many issues regarding mistakes in the zoea I description of *Alpheus* are pointed out, and the hypothesis that the morphological groups proposed for adults are supported by larval data has been rejected.

1 | Introduction

Alpheus Fabricius, 1798 is the most speciose genus in the infraorder Caridea Dana, 1852 (De Grave and Fransen 2011), with more than 340 valid species worldwide (DecaNet 2025) and with an estimated diversity of more than 400 species (Anker 2001a; Anker et al. 2006). The use of integrative approaches using molecular data combined with morphological and colour data has yielded the discovery and description of many new species (Mathews and Anker 2009; Anker 2012; Almeida et al. 2013, 2014; Soledade et al. 2019).

Alpheus was divided into seven informal species groups based on adult morphological characters (Coutière 1899, 1905; Anker 2001b): *brevirostris*, *crinitus*, *diadema*, *edwardsi*, *macrocheles*, *obesomanus*, and *sulcatus*. These groups were established primarily based on features of the frontal region and the first pereiopods and are still useful for the taxonomy of this rich genus, allowing the first approximate assignment for the specimens (Chace Jr. 1988). For example, when new species are described, they are usually allocated to one of these groups. On the other hand, at least three of these morphological groups (*diadema*, *edwardsi* and *sulcatus*) have been shown not to be monophyletic, based on preliminary

molecular analyses (Williams et al. 2001). Moreover, a recent phylogeny of the genus based on genomic data recovered only the *macrocheles* and *crinitus* groups as monophyletic (Hurt et al. 2021).

Studies on larval descriptions may be extremely useful to help clarify some issues of adult taxonomy (Pohle et al. 1999). Nevertheless, as in many decapod groups, the lack of larval descriptions precludes comparative studies with taxonomic purposes. Although *Alpheus* has over 300 described species, larval stages are known for only 26 species [25 cited by Sanches et al. 2024 and *Alpheus glaber* (Olivi, 1792) described by Lebour 1932]. The zoeal descriptions of *A. glaber* (by Webb 1921, as *Alpheus ruber*), *Alpheus edwardsii* (Audouin, 1826) (by Gurney 1927, as *Alpheus audouin*) and *Alpheus pacificus* Dana, 1852 (by Gohar and Al-Kholy 1957) are based on plankton samples, and it is not possible to affirm which species they belong to; for this reason, they will not be considered in the manuscript.

One of the species without known larval morphology is the amphi-Atlantic *Alpheus bouvieri* A. Milne-Edwards, 1878. This species has been recorded in the Western Atlantic, from Bermuda, Caribbean Sea to South Brazil, in the Central Atlantic (Ascension Island) and in the Eastern Atlantic, from Cape Verde to Congo (see Soledade and Almeida 2013 for review). This amphi-Atlantic distribution has been confirmed by morphological and molecular data (Anker et al. 2009). One of the explanations for species with this wide distribution is to have extended larval development, that is, many larval stages. This long duration may allow a long-distance drift in ocean currents across distant localities (Crandall et al. 2010).

This study aims to describe the morphology of the first larval stage of *A. bouvieri*, and verify the hypothesis that zoeal morphology is typical of a species of extended larval development. Additionally, the literature on larval descriptions of *Alpheus* species was reviewed with the aim of analysing whether the morphological groups proposed for adults are supported by larval data.

2 | Material and Methods

The ovigerous females were collected in northeastern Brazil in 2019. Three ovigerous females were collected manually at Praia do Paraíso, Cabo de Santo Agostinho, Pernambuco (8°21′54.89″ S 34°56′51.38″ W) and one female was collected at Praia do Madeiro, Tibau do Sul, Rio Grande do Norte (6°13′26.2″ S 35°04′14.3″ W). After collection, they were kept alive until larval hatching and then preserved in 80% ethanol, whereas larvae (zoea I) were fixed in 10% formaldehyde. All females and larvae were deposited in the Coleção de Crustáceos da Universidade Federal do Rio Grande do Sul, Brazil (DZ/UFRGS 6855, 6856, 6857, 7241).

The larvae were dissected in a Zeiss Stemi DV4 stereomicroscope and drawn/measured/analysed under an Olympus CX31 microscope with the aid of *camera lucida*. The illustrations were edited using Adobe Photoshop software. Each structure was analysed a priori in 10 larvae. In addition, measurements of carapace length (maximum length from the postorbital margin to the posterior margin of the carapace) were also performed in 10 larvae. Larval descriptions followed Clark et al. (1998) later updated by Clark and Cuesta (2015), while setae terminology is according to Garm (2004) and Landeira et al. (2009). Only complete segmentations on exopods of the antenna were considered. Plumose terminal natatory setae of maxillipeds were drawn truncated.

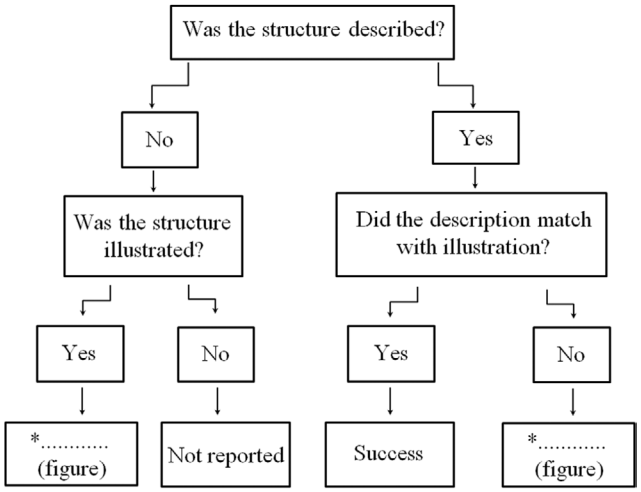

FIGURE 1 | Flowchart used to build the general comparative table. *According to figure in the original description.

Scanning Electron Microscopy (SEM) was employed to examine in detail segmentation on exopods of the antenna and maxillipeds. The zoeae were initially fixed in formaldehyde, then rinsed three times with ultrapure water, and subsequently dehydrated through a graded ethanol series. Afterward, the samples were dried using a critical point dryer (BAL-TEC CPD 030), mounted on stubs, and coated in gold (BAL-TEC SCD 050). Analyses were carried out using a Zeiss Evo MA10 scanning electron microscope at the Center for Microscopy and Microanalysis of the Federal University of Rio Grande do Sul (CMM UFRGS).

Furthermore, an extensive literature review was carried out in search of all larval descriptions available, so as to know *Alpheus* larval morphological features. The description and illustrations of the larval descriptions were analysed, and a general comparative table was generated following a flowchart (Figure 1).

3 | Results

The four parental females from *A. bouvieri* measured 4.9, 4.95, 5.1 and 5.4 mm in carapace length.

Morphological Description of *Alpheus bouvieri*

Zoea I

Carapace length: 0.44 ± 0.04 mm ($n = 10$ larvae).

Cephalothorax (Figure 2A,B): rostrum absent; pterygostomial spine present; eyes sessile.

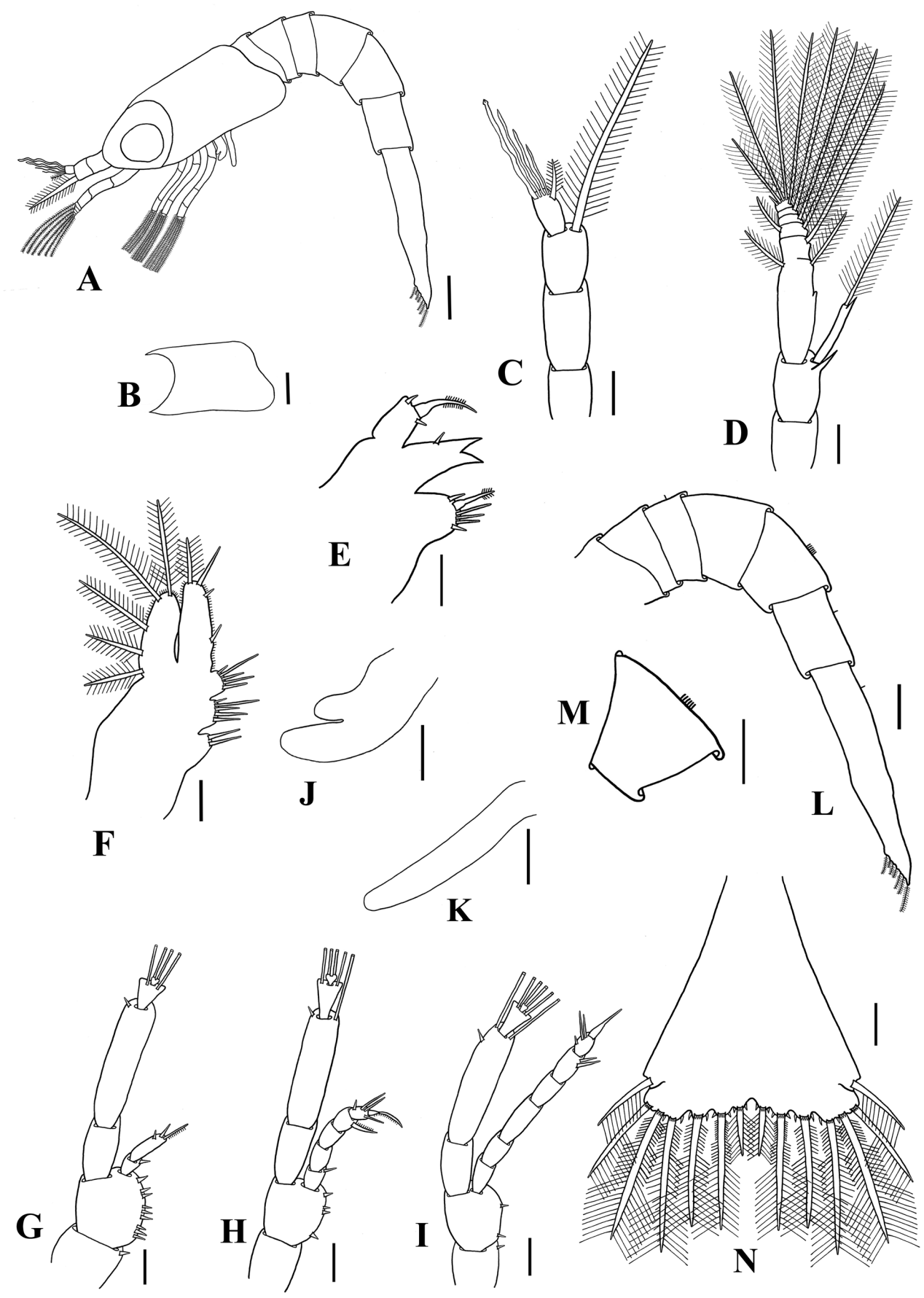

FIGURE 2 | Legend on next page.

FIGURE 2 | *Alpheus bouvieri* A. Milne-Edwards, 1878. Zoea I. (A) lateral view; (B) carapace; (C) left antennule; (D) left antenna; (E) left maxillule; (F) left maxilla; (G) left first maxilliped; (H) left second maxilliped; (I) left third maxilliped; (J) left first pereiopod; (K) left fifth pereiopod; (L) pleon, lateral view; (M) fourth segment of pleon, lateral view; (N) telson, dorsal view. Scale bars: (A, B, L, M) 0.15 mm; (C, D, G–I, N) 0.07 mm; (E, F, J, K) 0.04 mm.

Antennule (Figure 2C): peduncle 3-segmented; endopod as plumose seta; exopod with 4 terminal aesthetascs (1 spatulate and more robust) and 1 terminal plumose seta.

Antenna (Figures 2D and 3A): peduncle 2-segmented with 1 medial distal spiniform projection near endopod; endopod with 1 terminal plumose seta and 1 medial distal spiniform projection; exopod (scaphocerite) 5-segmented with 11 plumose setae (3, 2, 1, 1, 4), plus medial tubercle on proximal segment and 1 simple seta on distal segment.

Mandible: palp absent.

Maxillule (Figure 2E): coxa with 5 terminal simple setae (2 setae shorter) and 1 terminal serrulate plumose (larger in proximal region) seta; base with 2 spiniform projections and 1 lateral simple seta; endopod with 1 terminal plumoserrulate, 2 simple (1 medial distal and 1 terminal) setae; exopod absent.

Maxilla (Figure 2F): coxa with 2 medial simple setae; base bilobed, each lobe with 5 medial simple setae (1 seta shorter); endopod with 2 medial (1 proximal and 1 distal) simple setae and 2 terminal long (1 simple and 1 plumose) setae, with microtrichia; exopod (scaphognathite) with 5 plumose setae, with microtrichia.

First maxilliped (Figure 2G): coxa with 1 medial distal simple seta; base with 9 medial simple setae arranged 3+3+2+1; endopod 2-segmented with 1 medial distal simple seta, 3 [2 simple (1 lateral + 1 terminal) and 1 terminal serrulate] setae; exopod 4-segmented with 0, 0, 2, 2 terminal natatory plumose setae plus 1 lateral distal simple seta on second segment.

Second maxilliped (Figure 2H): coxa without setae; base with 4 medial simple setae arranged 1+2+1; endopod 5-segmented with 1 medial distal simple, 0, 0, 1 medial distal serrulate, 5 (1 medial simple, 3 lateral simple and 1 terminal serrulate) setae; exopod 4-segmented with 0, 1, 2, 2 terminal natatory plumose setae plus 1 lateral distal simple seta on second segment.

Third maxilliped (Figures 2I and 3B): coxa with 1 medial distal simple seta; base with 2 medial simple setae arranged 1+1; endopod 6-segmented with 0, 0, 0, 0, 2 medial distal, 4 (1 lateral proximal, 2 lateral distal, 1 terminal) simple setae; exopod 4-segmented with 0, 2, 2, 2 terminal natatory plumose setae plus 1 lateral distal simple seta on second segment.

Pereiopods (Figure 2J,K): first as biramous bud; fifth pereiopod as uniramous bud.

Pleon (Figure 2A,L): with 6 pleonites (6th pleonite fused to telson), simple setae on dorsal surface of each pleonite (Figure 2L,M); lateral spines absent; pleopods absent; anal spine absent (Figure 2N).

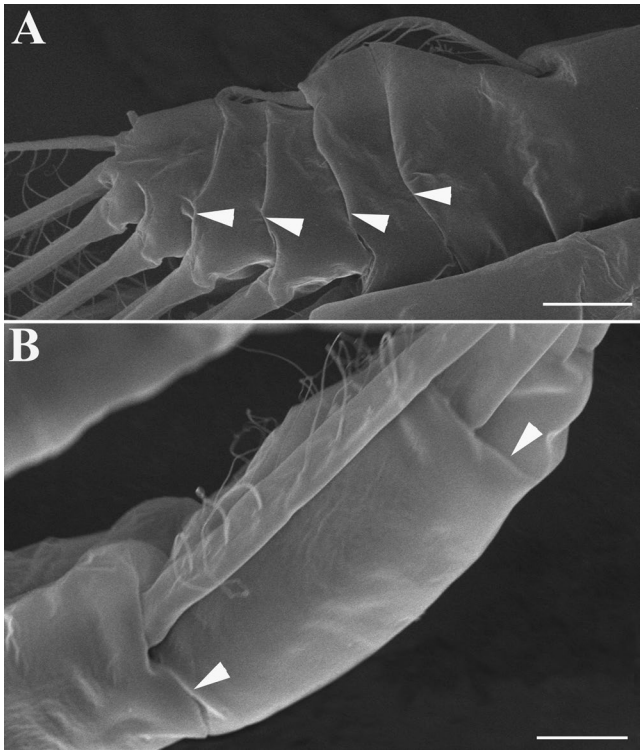

FIGURE 3 | *Alpheus bouvieri* A. Milne-Edwards, 1878. Zoea I. Scanning electron microscopy. (A) Exopod of the antenna 5-segmented; (B) exopod of the third maxilliped 3-segmented. White arrowhead indicated divisions of segmentation. Scale bars: (A) 10 μm, (B) 20 μm.

Telson (Figure 2N): triangular, with 7+7 (5 inner and 2 outer plumose laterally) setae, 4 inner setae with shorter setules on proximal region, inner pair shorter; 6 inner pairs with row of denticles on distal margin, 4 innermost pairs with marginal spines.

4 | Discussion

4.1 | Zoea of *Alpheus bouvieri*

The first larval stage of *A. bouvieri* presented characters displayed by species with an extended larval development, such as the antenna with segmented exopod (scaphocerite), pereiopods as a bud, pleopods and uropods absent, and 7 pairs of setae on the telson (Guerao and Cuesta 2014). Thus, the amphi-Atlantic distribution of *A. bouvieri* could be explained by this long larval development in the marine plankton. Although the Mid Atlantic Barrier, a 2800 km open ocean gap between the eastern Atlantic and southwestern Atlantic (Briggs 1995), can be an obstacle to the dispersal of most species, others can cross this barrier and maintain gene flow through larval dispersal (Oliveira et al. 2019).

According to Scheltema (1971), the planktonic larvae could cross the Atlantic Ocean from 36 to 109 days through the Equatorial Undercurrent. Moreover, the presence of *A. bouvieri* in some islands (Atol das Rocas, Fernando de Noronha, Ascension and Cape Verde) can support this dispersion; these islands could work as stepping stones, as suggested by Anker et al. (2016). Future phylogeographic studies with the species may prove this recent gene flow.

About comparative morphology, the zoea I of *A. bouvieri* shares features with most larvae of *Alpheus*. However, some peculiarities observed can be used as diagnostic characters for the zoea I identification of this species.

Alpheus bouvieri zoea I followed the general character set proposed in the previous literature (see the larval data in a review section below for the updated list), excepting the antennule and antenna peduncles, which were segmented in this species. In *A. bouvieri*, the antennule peduncle is 3-segmented, as well as in *A. formosus* (Table 1). This structure is 2-segmented in *A. glaber*, *A. lottini*, *A. macrocheles*, *A. malleator*, and *A. saxidomus* (Table 1). In *A. bouvieri*, the antenna peduncle is 2-segmented, as well as in *A. brasileiro*, *A. estuariensis*, *A. formosus*, *A. malleator*, and *A. saxidomus* (Table 1; see Pasinatto et al. 2020 for discussion on peduncle segmentation).

Other characteristics shared between *A. bouvieri* and other species are (Table 1): presence of four aesthetascs on the antennular exopod, 6 setae on the maxillule coxa and fifth pereiopod as an uniramous bud.

A new characteristic proposed for *A. formosus* and *A. malleator* (Pasinatto et al. 2020) was also observed in *A. bouvieri* zoea I: the presence of pleonal dorsal simple setae (observed on the 2nd to 6th pleonites); however, this character must not be used as diagnostic because we have no information regarding other species (Pasinatto et al. 2020). The presence of this character in only three species may be related to the fact that previous authors before 2020 simply did not report/describe or search for these characters, which are difficult to observe. Unfortunately, other descriptions of zoea I of *Alpheus* after 2020 (Pescinelli and Costa 2022; Pescinelli et al. 2023; Sanches et al. 2024) did not mention this character, neither present nor absent, which also makes comparison difficult.

Furthermore, the presence of a medial tubercle on the antennal exopod, which was firstly reported for *A. malleator* (Pasinatto et al. 2020) and after for *A. petronioi* (Pescinelli and Costa 2022) and *A. buckupi* (Pescinelli et al. 2023), was also observed in *A. bouvieri*. As pointed out by these authors, this character may be useful for the separation of species.

Some characteristics are unique, so far, to *A. bouvieri* zoea I and could be used to separate the zoea I of this species from other *Alpheus* species: 3 (1 plumoserrulate and 2 simple) setae on the endopod of maxillule, 4 (3 simple and 1 plumose) setae on the endopod of maxilla, 9 simple setae on the base of the first maxilliped, second maxilliped with 5-segmented endopod and third maxilliped with 6-segmented endopod.

4.2 | Review of Zoea I Descriptions of *Alpheus*

For comparative purposes, in this review, 23 species with known zoea I from extended larval development were used (Table 1). The following four larval descriptions were not part of the present review: the zoea I of *Alpheus heterochaelis* Say, 1818, and *Alpheus simus* Guérin-Méneville, 1855, have some features, such as chelate pereiopods and the presence of pleopods that characterise zoea I from abbreviated larval development (Knowlton 1973; Wehrtmann and Albornoz 2002, respectively); according to Yang and Kim (2002), the larval description of *A. rapacida* provided by Prasad and Tampi (1957) points to certain characters (broad rostrum, stalked eyes, telson with 8+8 marginal setae, and maxilliped endopod dactylus with long spine) that are typical of *Alpheus* second larval stage; *Alpheus rapax* has the zoea II described (by Al-Kholy 1960), but does not have the zoea I.

Yang and Kim (2002) also had doubt regarding *A. strenuus* zoea I description by Prasad and Tampi (1957), which considered that such larva could belong to a species of another genus due to maxillule endopod characteristics (two long setae without type definition, illustrated by Prasad and Tampi (1957) versus one long denticulate seta in other *Alpheus* zoea I species known at the time). However, in this review, variation in *Alpheus* zoeae I maxillule endopod was observed (Table 1): *A. bouvieri* with 3 setae (1 terminal plumoserrulate, 1 medial distal simple, 1 terminal simple), *A. saxidomus* with the presence of 2 long setae (no type of definition) and *A. formosus* and *A. malleator* with two setae (1 terminal plumoserrulate and 1 lateral simple). Due to this variation, *A. strenuus* was not excluded in the review.

The lack of knowledge about larval morphology in many decapod groups hinders taxonomic comparative studies (Vela and González-Gordillo 2016). According to these authors, larval descriptions are often brief or very general and deficient in details, as well as inadequate and incomplete illustrations.

For example, some studies (Lebour 1932; Gurney 1938; Prasad and Tampi 1957; Al-Kholy 1960) show very general and poorly detailed larval descriptions, as well as inaccurate illustrations, likely related to the optical equipment used at that time and the lack of standardisation in the descriptions. Thus, it is complicated to state the presence of segmentation and the type and position of setae in the structures analysed. Moreover, another problem found was that both *A. glaber* and *A. macrocheles* described by Lebour (1932) have the same description and illustrations of zoea I for both species, without specific diagnostic characters.

Given the lack of larval descriptions standardisation, many problems were faced in comparing our results with the information available in literature. Sometimes, segmentation on antennal exopod appears partially depicted, making it difficult to confirm this segmentation. Prasad and Tampi (1957, fig. 8c) illustration of *A. strenuus* zoea I antenna would be an example of that, as their unclear drawing does not allow the reader to accurately verify the number of segments.

TABLE 1 | Comparison of selected characters of the zoea I of species of *Alpheus* Fabricius, 1798.

Morphological group		*brevirostris*	*brevirostris*	*brevirostris*	*edwardsi*	*edwardsi*	*edwardsi*
Species		*A. brevicristatus* De Haan, 1844 [in De Haan, 1833–1850]	*A. digitalis* De Haan, 1844 [in De Haan, 1833–1850]	*A. glaber* (Olivi, 1792)	*A. bouvieri* A. Milne-Edwards, 1878	*A. brasileiro* Anker, 2012	*A. buckupi* Almeida, Terossi, Araújo-Silva and Mantelatto, 2013
References		Yang and Kim (1998)	Yang and Kim (2002)	Lebour (1932)	Present study	Pescinelli et al. (2017)	Pescinelli et al. (2023)
Antennule	Peduncle (segments)	unseg	unseg	2-seg	3-seg	unseg	unseg
	Exopod (aesthetascs)	3	3	3 or 4	4	4	4
	Exopod (setae)	1 ps + 1 ss	1 ps + 1 ss	1 to 2 sp 1 to 2 s (fig)*	1 ps	1 ps	1 ps
Antenna	Peduncle (segments)	unseg (fig)*	unseg (fig)*	NR	2-seg	unseg (text), 2-seg (fig)*	unseg
	Exopod (segments)	5-seg (text), 6-seg (fig)*	5-seg (text), 6-seg (fig)*	NR	8-seg	5-seg	5-seg
	Exopod (setae)	11 ps + 1 ss	11 ps + 1 ss	8 to 10 ps + 2 ss	11 ps + 1 ss	11 ps + 2 ss	11 ps + 1 ss
Maxillule	Coxa (setae)	3 pl + 1 ss	5 ps	NR	5 ss + 1 pss	4 ss + 2 sps	4 ss + 1 sps
	Basis (setae)	Absent (fig)*	1 ss	NR	1 ss	1 ss	2 ps
	Endopod (setae)	1 ds	1 ds	NR	1 pss + 2 ss	1 ds	1 ds
Maxilla	Not bilobed coxa (setae)	1 ps + 1 ss	1 ps + 1 ss	2 s (fig)*	2 ss	2 ss + 1 sps	2 ss
	Bilobed basis (setae)	7 s (3 s, 4 s)	6 s (3 s, 3 s)	NR	10 ss (5 ss, 5 ss)	6 ss (3 ss, 3 ss)	7 s (3 ss, 4ss)
	Endopod (setae)	2 ss + 1 ps	2 ss + 1 ps	2 s (fig)*	3 ss + 1 ps	2 ss + 1 ps	2 ss + 1 ps
First maxilliped	Coxa (setae)	4 sp + 1 hs (protopod)	1 ss	NR	1 ss	1 ss	1 ss
	Basis (setae)		4 sp + 3 ss	2 s (fig)*	9 ss	4 ss	5 ss
	Endopod (segments)	seg (text), unseg (fig)*	unseg (fig)*	NR	2-seg	unseg	unseg
	Endopod (setae)	3 s + 1 ss	3 s + 1 ss	3 s (fig)*	3 ss + 1 srL	3 ss + 1 sps	4 ss
	Exopod (setae)	4 nps	4 nps	4 s (fig)*	4 nps + 1 ss	4 nps	4 nps
Second maxilliped	Coxa (setae)	3 sp (protopod)	Absent	NR	Absent	Absent	Absent
	Basis (setae)		3 sp + 1 ss	2 s (fig)*	4 ss	3 ss	4 ss
	Endopod (segments)	4-seg	4-seg	NR	5-seg	4-seg	4-seg
	Endopod (setae)	5 s	6 s	3 s*	5 ss + 2 srl	5 ss + 1 sps	5 ss + 2 srr
	Exopod (setae)	5 nps	5 nps + 1 ss	6 s	5 nps + 1 ss	5 nps + 1 ss	5 nps + 1 ss

(Continues)

TABLE 1 | (Continued)

Morphological group		*brevirostris*	*brevirostris*	*brevirostris*	*edwardsi*	*edwardsi*	*edwardsi*
Third maxilliped	Coxa (setae)	1 ss (protopod)	Absent	NR	1 ss	Absent	Absent
	Basis (setae)		1 ss	2 s (fig)*	2 ss	1 ss	1 ss
	Endopod (segments)	4-seg	4-seg	NR	6-seg	4-seg	4-seg
	Endopod (setae)	5 s	6 s	1 sp	6 ss	5 ss	5 ss
	Exopod (setae)	6 nps	6 nps + 1 ss	6 s	6 nps + 1 ss	6 nps + 1 ss	6 nps + 1 ss
Pereiopods	1° pereiopod	Biramous	Biramous	Biramous	Biramous	Biramous	Biramous
	2° pereiopod	Biramous	Uniramous	Uniramous	Absent	Uniramous	Uniramous
	3° pereiopod	Absent	Absent	Absent	Absent	Absent	Absent
	4° pereiopod	Absent	Absent	Absent	Absent	Absent	Absent
	5° pereiopod	Uniramous	Uniramous	Uniramous	Uniramous	Uniramous	Uniramous
Number of known stages		4	2	9	1	3	3

Morphological group		*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*
Species		*A. carlae* Anker, 2012	*A. estuariensis* Christoffersen, 1984	*A. heeia* AH Banner and DM Banner, 1975	*A. intrinsecus* Spence Bate, 1888	*A. japonicus* Miers, 1879	*A. lobidens* De Haan, 1849 [in De Haan, 1833–1850]
References		Pantaleão et al. (2020)	Pires et al. (2008)	Yang and Kim (1999)	Pantaleão et al. (2020)	Yang and Kim (2002)	Yang et al. (2003)
Antennule	Peduncle (segments)	unseg	unseg	unseg	unseg	unseg	unseg
	Exopod (aesthetascs)	4	4	3	4	3	3
	Exopod (setae)	1 ps	1 ps	1 ps + 1 ss	1 ps	1 ps + 1 ss	1 ps + 1 ss
Antenna	Peduncle (segments)	unseg (text), 2-seg (fig)*	unseg	unseg (fig)*	unseg	unseg (fig)*	unseg (fig)*
	Exopod (segments)	4-seg (text), 5-seg (fig)*	5-seg	5-seg (text), 6-seg (fig)*	5-seg	4-seg (text), 5-seg (fig)*	6-seg
	Exopod (setae)	11 ps	11 ps + 1 ss	11 ps + 1 ss	11 ps + 1 ss	11 ps + 1 ss	11 ps + 1 ss

(Continues)

TABLE 1 | (Continued)

Morphological group		*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*
Maxillule	Coxa (setae)	3 s	5 ss + 1 sps	3 ps + 1 ss	3 ss + 2sps	3 s	4 s
	Basis (setae)	Absent (fig)*	1 ss + 1 sps	1 ss	2 ss	2 ps	2 ps
	Endopod (setae)	1 s	1 ds	1 ds	1 ds	1 ds	1 ds
Maxilla	Not bilobed coxa (setae)	2 ps	2 ss + 1 sps	2 ps	2 ss	2 ps	2 s
	Bilobed basis (setae)	2 ps	9 ss (4 ss, 5 ss)	7 s (2 s, 5 s)	8 ss (3 ss, 5 ss)	6 s (2 s, 4 ps)	8 ps (3 ps, 5 ps)
	Endopod (setae)	3 ps (fig)*	2 ss + 1 ps	2 ss + 1 ps	2 ss + 1 sps	1 ss + 2 s	1 ss + 2 s
First maxilliped	Coxa (setae)	Absent (protopod)	1 ss	4 sp (protopod)	1 ss	1 ss	1 s
	Basis (setae)		7 ss		5 ss	4 sp + 3 ss	4 sp + 3 ss
	Endopod (segments)	unseg	unseg	unseg	unseg	unseg (fig)*	? seg (text), unseg (fig)*
	Endopod (setae)	1 sp	4 ss	4 ss	2 ss + 1 srr	3 s + 1 ss	3 s + 1 ss
	Exopod (setae)	4 nps	4 nps + 1 ss	4 nps + 1 ss	4 nps + 1 ss	4 nps	4 nps
Second maxilliped	Coxa (setae)	2 ss (protopod)	Absent	3 sp (protopod)	Absent	3 sp + 2 ss (protopod)	Absent
	Basis (setae)		4 ss		4 ss		2 sp + 2 s
	Endopod (segments)	4-seg	4-seg	4-seg	4-seg	3-seg	4-seg
	Endopod (setae)	5 ss + 2 srr	5 ss + 2 srl	5 s	4 ss + 2 srr	7 s	5 s
	Exopod (setae)	6 nps	5 nps + 1 ss	5 nps	5 nps + 1 ss	5 nps	4 nps + 1 s

(Continues)

TABLE 1 | (Continued)

Morphological group		*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*
Third maxilliped	Coxa (setae)	Absent (protopod)	Absent	1 ss (protopod)	Absent	Absent	Absent
	Basis (setae)		1 ss		1 ss	1 ss	1 ss
	Endopod (segments)	4-seg	4-seg	4-seg	4-seg	2-seg	4-seg
	Endopod (setae)	3 s	5 ss	5 s	4 ss	6 s	4 s
	Exopod (setae)	6 nps	6 nps + 1 ss	6 nps	6 nps + 1 ss	6 nps	6 nps
Pereiopods	1° pereiopod	Biramous	Biramous	Biramous	Biramous	Biramous	Biramous
	2° pereiopod	Biramous (text), uniramous (fig)*	Uniramous	Biramous	Absent	Uniramous	Biramous
	3° pereiopod	Biramous (text), uniramous (fig)*	Absent	Absent	Absent	Absent	Biramous
	4° pereiopod	Biramous (text), uniramous (fig)*	Absent	Absent	Absent	Absent	Uniramous
	5° pereiopod	Biramous (text), uniramous (fig)*	Uniramous	Uniramous	Uniramous	Uniramous	Uniramous
Number of known stages		1	4	3	2	4	4

Morphological group		*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*macrocheles*	*macrocheles*
Species		*A. petronioi* Almeida, Terrosi and Mantelatto, 2014	*A. richardsoni* Yaldwyn, 1971	*A. strenuus* Dana, 1852	*A. sudara* AH Banner and DM Banner, 1966	*A. albatrossae* (AH Banner, 1953)	*A. macrocheles* (Hailstone, 1835)
References		Pescinelli and Costa (2022)	Yang and Kim (1996)	Prasad and Tampi (1957)	Yang et al. (2003)	Yang and Kim (2006)	Lebour (1932)
Antennule	Peduncle (segments)	unseg	unseg	unseg (fig)*	unseg	unseg	2-seg
	Exopod (aesthetascs)	4	3	2	3	4	3 or 4
	Exopod (setae)	1 ps	1 ps + 1 ss	Absent (fig)*	1 short ps + 1 ss	1 ps	1 or 2 spines (fig looks like seta)

(Continues)

TABLE 1 | (Continued)

Morphological group		*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*macrocheles*	*macrocheles*
Antenna	Peduncle (segments)	unseg	unseg (fig)*	unseg (fig)*	unseg (fig)*	unseg (fig)*	NR
	Exopod (segments)	5-seg	4-seg (text), 5-seg (fig)*	NR	6-seg	6-seg	NR
	Exopod (setae)	11 ps + 1 ss	11 ps + 1 ss	11 ps	11 ps + 1 ss	11 ps + 1 ss	8 to 10 ps + 2 ss
Maxillule	Coxa (setae)	3 ss + 3 sps	4 s	2 s	4 s	3 s	NR
	Basis (setae)	2 ps	1 ss	1 s	1 ss	1 ps	NR
	Endopod (setae)	1 ds + 1 ss	1 ds	2 s	1 ds	1 s	NR
Maxilla	Not bilobed coxa (setae)	3 ss	2 ss	1 s	2 s	3 s	2 s (fig)*
	Bilobed basis (setae)	9 ss (4 ss, 5 ss)	7 ss (3 ss, 4 ss)	3 s (1 s, 2 s)	7 s (3 s, 4 s)	7 s (3 s, 4 s)	NR
	Endopod (setae)	2 ss + 1 ps	2 ss + 1 ps	2 s	3 s	2 s + 1 ps	2 s (fig)*
First maxilliped	Coxa (setae)	1 ss	4 sp + 2 hs (protopod)	NR	1 s	Absent	NR
	basis (setae)	6 ss			4 sp + 2 s	4 sp + 2 s	2 s (fig)*
	Endopod (segments)	unseg	unseg	unseg (fig)*	seg (text), unseg (fig)*	unseg	NR
	Endopod (setae)	3 ss + 1 srr	3 s + 1 ss	2 s	4 s	6 s	3 s (fig)*
	Exopod (setae)	4 nps	4 nps	4 s	4 nps	4 nps	4 s (fig)*
Second maxilliped	Coxa (setae)	Absent	3 sp (protopod)	NR	Absent	Absent	NR
	Basis (setae)	5 ss			2 sp + 2 s	2 sp + 1 s	2 s (fig)*
	Endopod (segments)	4-seg	4-seg	2-seg (text), unseg (fig)*	4-seg	4-seg	NR
	Endopod (setae)	5 ss + 2 srr	4 s	3 s	6 s	5 s	3 s (fig)*
	Exopod (setae)	5 nps + 1 ss	5 nps + 1 s	5 s	4 nps + 1 s	4 nps + 1 s	6 s

(Continues)

TABLE 1 | (Continued)

Morphological group		***edwardsi***	***edwardsi***	***edwardsi***	***edwardsi***	***macrocheles***	***macrocheles***
Third maxilliped	Coxa (setae)	Absent	1 ss (protopod)	NR	Absent	Absent	NR
	Basis (setae)	1 ss			1 ss	1 ss	2 s (fig)*
	Endopod (segments)	4-seg	4-seg	unseg	3-seg	2-seg	NR
	Endopod (setae)	5 ss	5 s	2 s	5 s	4 s	1 sp
	Exopod (setae)	6 nps + 1 ss	6 nps	6 s	6 nps	6 nps	6 s
Pereiopods	1° pereiopod	Biramous	Biramous	Absent	Biramous	Biramous	Biramous
	2° pereiopod	Uniramous	Biramous	Absent	Absent	Uniramous	Uniramous
	3° pereiopod	Absent	Biramous	Absent	Absent	Uniramous	Absent
	4° pereiopod	Absent	Uniramous	Absent	Absent	Absent	Absent
	5° pereiopod	Uniramous	Uniramous	Absent	Uniramous	Uniramous	Uniramous
Number of known stages		3	3	1	3	1	9
Morphological group		***obesomanus***	***sulcatus***	***sulcatus***		***sulcatus***	***sulcatus***
Species		*A. saxidomus* Holthuis, 1980	*A. formosus* Gibbes, 1850	*A. lottini* Guérin, 1830 [in Guérin, 1829–1830]		*A. malleator* Dana, 1852	*A. packardii* Kingsley, 1880
References		Wehrtmann and Albornoz (2002)	Pasinatto et al. (2020)	Gurney (1938) (as *Alpheus ventrosus*)	Al-Kholy (1960)** (as *Alpheus ventrosus*)	Pasinatto et al. (2020)	Sanches et al. (2024)
Antennule	Peduncle (segments)	2-seg	3-seg	unseg	2-seg	2-seg	unseg
	Exopod (aesthetascs)	4	4	NR	NR	4	4
	Exopod (setae)	Absent (fig)*	1 ps	NR	2 ps	1 ps	1 ps
Antenna	Peduncle (segments)	2-seg (fig)*	2-seg	NR	NR	2-seg	unseg
	Exopod (segments)	5-seg (text), 6-seg (fig)*	8-seg	4-seg (text), 5-seg (fig)*	4-seg 5-seg***	6-seg	5-seg
	Exopod (setae)	13 ps + 1 ss	11 ps + 1 ss	10 (text), 11 ps + 1 ss (fig)*	11 ps	11 ps + 1 ss	11 ps + 1 ss

(Continues)

TABLE 1 | (Continued)

Morphological group		*obesomanus*	*sulcatus*	*sulcatus*		*sulcatus*	*sulcatus*
Maxillule	Coxa (setae)	4 s (fig)*	5 ss + 1 pss	4 s (fig)*	2 sp + 2 hs	5 ss + 1 pss	4 ss + 2 sps
	Basis (setae)	1 s (fig)*	1 ss	Absent (fig)*	2 s	1 ss	2 sp + 1 ps + 1 ss
	Endopod (setae)	2 s (fig)*	1 pss + 1 ss	1 s (fig)*	1 s	1 pss + 1 ss	1 ds
Maxilla	Not bilobed coxa (setae)	4 s (fig)*	2 ss	2 s (fig)*	2 hs	2 ss	2 sps
	Bilobed basis (setae)	8 s (4 s, 4 s) (fig)*	10 ss (5 ss, 5 ss)	5 s (2 s, 3 s) (fig)*	5 hs (2 hs, 3 hs)	10 ss (5 ss, 5 ss)	7 s (2 ss + 1 sps, 3 ss + 1 sps)
	Endopod (setae)	2 pds + 1 s (fig)*	2 ss + 1 ps	3 s (fig)*	3 s	4 ss + 1 ps	2 ss + 1 ps
First maxilliped	Coxa (setae)	Absent	1 ss	1 sp (fig)*	? sp (protopod)	1 ss	1 ss
	Basis (setae)	5 sp	7 ss	4 sp		7 ss	7 ss
	Endopod (segments)	unseg	2-seg	unseg	NR	2-seg	unseg
	Endopod (setae)	2 ss + 3 s	5 ss + 1 srl	4 s (fig)*	1 sp + ? hs	5 ss + 1 srL	3 ss + 1 srr
	Exopod (setae)	5 s	4 nps + 1 ss	NR	4 nps	4 nps + 1 ss	4 nps + 1 ss
Second maxilliped	Coxa (setae)	Absent	Absent	NR	NR	Absent	Absent
	Basis (setae)	3 sp	4 ss	NR	NR	4 ss	4 ss
	Endopod (segments)	3-seg	4-seg	unseg	NR	4-seg	4-seg
	Endopod (setae)	4 ss + 2 sp	5 ss + 2 srl	Absent	1 sp	5 ss + 2 srL	4 ss + 2 srr
	Exopod (setae)	4 s + 2 ps	5 nps + 1 ss	5 s + 1 hs	5 ps	5 nps + 1 ss	5 nps + 1 ss
Third maxilliped	Coxa (setae)	Absent	1 ss	NR	NR	1 ss	Absent
	Basis (setae)	Absent	2 ss	NR	NR	1 ss	1 ss
	Endopod (segments)	4-seg (fig)*	5-seg	unseg	unseg	4-seg	4-seg
	Endopod (setae)	4 ss	7 ss	Absent	NR	6 ss	6 ss
	Exopod (setae)	6 ps	6 nps + 1 ss	6 s	6 ps	6 nps + 2 ss	6 nps + 1 ss

(Continues)

TABLE 1 | (Continued)

Morphological group		*obesomanus*	*sulcatus*	*sulcatus*		*sulcatus*	*sulcatus*
Pereiopods	1° pereiopod	Biramous	Biramous	Biramous	Biramous	Biramous	Biramous
	2° pereiopod	Uniramous	Absent	Absent	Absent	Absent	Uniramous
	3° pereiopod	Uniramous	Absent	Absent	Absent	Absent	Absent
	4° pereiopod	Uniramous	Absent	Absent	Absent	Absent	Absent
	5° pereiopod	Uniramous	Absent	Uniramous	Uniramous	Absent	Uniramous
Number of known stages		1	1	1	4	1	3

Note: *According to figure in the original description, more details in Figure 1; **figure not available: ***the text mentioned 4 apical segments, so we considered 5 segments including the proximal one; ? number not reported.
Abbreviations: ds, denticulate seta; fig, figure; hs, hair-like seta; nps, natatory plumose seta; NR, not reported; pds, plumodenticulate seta; ps, plumose seta; pss, plumoserrulate seta; s, seta; seg, segmented; sp, spine or spiniform seta; sps, sparsely plumose seta; srl, serrulate seta; srr, serrate seta; ss, simple seta; unseg, unsegmented.

In addition, there are some disagreements about the number of segments on the antennal exopod. Some studies (Yang and Kim 1996; Wehrtmann and Albornoz 2002; Pires et al. 2008) exclude the proximal segment (usually larger) from the segment count. The proximal segment was counted in more recent descriptions (Pescinelli et al. 2017, 2023; Pasinatto et al. 2020; Pantaleão et al. 2020; Pescinelli and Costa 2022; Sanches et al. 2024; present study). In order to enable comparisons, the information on exopod segmentation used in Table 1 was based on illustrations and not on the text descriptions. Nevertheless, these considerations are denoted in the table by an asterisk (*), clearly indicating that they reflect the interpretations of the authors of the present study.

Some problems were also found in relation to maxilliped endopod and exopod segmentation. In some studies (Prasad and Tampi 1957; Yang and Kim 1999; Yang et al. 2003), the description provides information on segmentation and the illustration shows the opposite. In addition, some endopods and exopods are partially illustrated, and it is difficult to state the presence of segmentation, since this information was not reported in the description.

There is also no consistency in descriptions of position and types of setae. Some studies (Lebour 1932; Prasad and Tampi 1957; Yang et al. 2003) do not specify the type and position of the setae found in certain structures, such as antennula, antenna, maxilla and maxillipeds. Moreover, sometimes (Lebour 1932; Yang and Kim 2002; Yang et al. 2003), these setae, as well as those from the telson, appear erased or blurred, which also affects character comparison. In some cases, the descriptions reveal the presence of spines and not setae, in both the antennula and antenna exopods (Lebour 1932), as well as on the coxae and bases of the first and second maxillipeds (Yang and Kim 1996, 1998). However, in the illustrations they resemble more setae than spines. Due to inaccuracy in both descriptions and illustrations, it is difficult to know if they are really spines.

Another difficulty was found when analysing the description of *A. saxidomus* zoea I provided by Wehrtmann and Albornoz (2002). The authors describe some structures, such as mandible, maxillule, and maxilla, with embryonic cuticle and all setae semi-invaginated, respectively. In view of this, the lack of detailed observations and precision in both description and illustration makes it very difficult to know the setae classification and position. Most likely, these invaginations probably result from failures in the larvae fixation process.

Finally, non-standardised terminology of some telson structures (at the plumose setae base) also becomes an issue when trying to compare data, because each author gives a different name to the same structure. Since they are very small structures, it is not easy to spot them in the images. Yang and Kim (1996) indicate the presence of minute setules between setae 4–7. In other studies (Yang et al. 2003; Yang and Kim 2006) the same authors show the presence of a minute row of spinules at the base of the 6 setae inner pairs. Sanches et al. (2024) described one row of minute spinules in between and around the bases of the inner setae 2–7 (6 inner pairs according to the figure). Based on photos from a SEM and the nomenclature proposed by Garm (2004), Pasinatto et al. (2020) pointed out the presence of denticles at the

base of the 6 inner setae pairs and the presence of spines among the 4 inner setae pairs, which was also verified for *A. bouvieri* (present study). Because of these inaccuracies, these characters from telson were not included in the comparative tables.

4.3 | Remarks of Larval Data With Phylogenetic Issues

Species of *Alpheus* share the following larval characters: rostrum absent, pterygostomial spine present, sessile eyes, antennular endopod as a plumose seta, antenna with a terminal spine near the endopod, antennal endopod with 1 long plumose seta and 1 small inner spine, mandible without palp, maxillule without exopod, pleonites without spines and telson fused to the sixth pleonite (see Table 1 for references of all analysed descriptions). This is an updated list with additions and exclusions of some characters of the previous lists (Yang and Kim 2002; Pescinelli et al. 2017, 2023; Pantaleão et al. 2020; Pescinelli and Costa 2022; Sanches et al. 2024).

Considering the morphological groups proposed for adults, from the 23 analysed species here, thirteen belong to the *edwardsi* group; the other ten species belong to *sulcatus* (four), *brevirostris* (three), *macrocheles* (two) and *obesomanus* (one) group. The zoea I of species from *diadema* and *crinitus* groups are currently unknown. We tried to find a larval morphological pattern to separate species among the groups, as is done for adults, but no characters were found to support such separation. Such finding is corroborated by the most recent phylogenomic analyses that did not support the monophyly of five of these groups (from the groups above, only *macrocheles* and *crinitus* are considered monophyletic) (Hurt et al. 2021). About the *macrocheles* group, unfortunately, no unique larval characters of the two described species (*A. albatrossae* and *A. macrocheles*) were found, which is possibly due to the inconsistencies already mentioned in the descriptions of Lebour (1932).

Using the clades obtained in the recent phylogeny (Hurt et al. 2021) and the available larval data (Table 1), it was also not possible to find a larval morphological pattern of separation of the analysed clades (Clade III: *A. formosus* and *A. lottini*; Clade IV: *A. japonicus* and *A. strennus*; unnamed clade: *A. bouvieri* and *A. glaber*), maybe influenced by the issues in the descriptions already reported previously. Descriptions of zoea of *A. simus* and *Racilius compressus* Paulson, 1875 were not included in Clade III comparisons because they have abbreviated development (Bruce 1974; Wehrtmann and Albornoz 2002).

Additionally, other lacunae in the knowledge of *Alpheus* larval morphology is about the full development. Only two of the 23 species of *Alpheus* analysed have the complete known development, *A. glaber* and *A. macrocheles*, with nine stages described (Table 1). Such scarcity evidences that knowledge about the larval development of *Alpheus* (> 300 species) is still very incipient.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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