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KARMINE PASINATTO

MORFOLOGIA LARVAL COMPARADA (ZOEA I) DE CAMARÕES-DE-ESTALO DO GÊNERO *Alpheus* FABRICIUS, 1798 (DECAPODA: CARIDEA)

PORTO ALEGRE
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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.

Área de concentração: Biologia comparada

Orientador (a): Profa. Dra. Mariana Terossi Rodrigues Mariano

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Aprovada em ____ de _____ de _____.

BANCA EXAMINADORA

_____

Profª. Drª. Paula Beatriz de Araujo

Universidade Federal do Rio Grande do Sul

_____

Profº. Dr. Fernando Araújo Abrunhosa

Universidade Federal do Pará

_____

Dr. Guidomar Oliveira Soledade

Universidade Federal de Pernambuco

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"It is not the strongest of the species that survives,

nor the most intelligent,

but the one most responsive to change"

Charles Darwin

"Que você seja igual as ondas do mar,

que fazem de cada recuo

um impulso para ir mais adiante"

Autor desconhecido

SUMÁRIO

APRESENTAÇÃO

A presente dissertação está estruturada em “Resumo”, “Abstract” e quatro capítulos, a fim de ampliar o conhecimento sobre os primeiros estágios larvais de diversas espécies do gênero *Alpheu*s de forma comparativa.

O “Capítulo I: Introdutório” compreende uma síntese acerca de classificação, distribuição, morfologia e biologia dos camarões-de-estalo do gênero *Alpheu*s, bem como a morfologia larval de crustáceos decápodos. O “Capítulo II” aborda a descrição do primeiro estágio larval de duas espécies do gênero *Alpheu*s, com proposta de novos caracteres para o gênero. O “Capítulo III” abrange a descrição do primeiro estágio larval de uma espécie de *Alpheu*s, além de uma revisão dos caracteres larvais do gênero, com observações sobre os grupos morfológicos de adultos. Por fim, o “Capítulo IV: Conclusivo” consiste nas conclusões mais relevantes obtidas a partir deste estudo.

O “Capítulo I, II e IV” estão formatados conforme as regras da revista Zootaxa. Enquanto, o “Capítulo III” está formatado de acordo com as normas da revista Acta Zoologica.

RESUMO

Estudos sobre descrições larvais podem ser de extrema importância para auxiliar na elucidação de alguns problemas encontrados na taxonomia com os adultos, além de contribuir no entendimento da história de vida de uma espécie e possibilitar a posterior identificação das larvas no plâncton. No entanto, em muitos grupos de decápodos, a falta de descrições larvais impossibilita o estudo comparativo para fins taxonômicos. Embora os camarões-de-estalo do gênero *Alpheus* Fabricius, 1798 compreendam mais de 300 espécies descritas, a morfologia larval é conhecida para apenas 16 espécies. Na costa brasileira, somente duas das 35 espécies registradas possuem estágios larvais conhecidos. Considerando a relevância do conhecimento da morfologia larval de decápodos e dada a falta de descrições larvais de espécies de *Alpheus*, o presente estudo teve como objetivos descrever o primeiro estágio larval (zoea I) de três espécies do gênero *Alpheus* da costa brasileira, bem como realizar uma revisão dos caracteres larvais presentes na literatura, analisando se os grupos morfológicos propostos para adultos são suportados por dados larvais. Foram analisadas larvas de *Alpheus formosus* Gibbes, 1850 e *Alpheus malleator* Dana, 1852 do litoral de São Paulo, e de *Alpheus bouvieri* A. Milne-Edwards, 1878 do litoral de Pernambuco. As larvas das fêmeas parentais foram dissecadas em estereomicroscópio e desenhadas/mensuradas/analisadas em microscópio provido de câmara clara. Ademais, a microscopia eletrônica de varredura foi utilizada para analisar mais detalhadamente algumas estruturas larvais. Por fim, foi elaborada uma tabela comparativa contendo todas as descrições de zoea I de *Alpheus* disponíveis na literatura e, posteriormente, as espécies foram agrupadas de acordo com os grupos morfológicos propostos para adultos. Além de ampliar o conhecimento sobre a morfologia larval de *Alpheus*, novos caracteres foram propostos para serem analisados nas zoeas do gênero: presença de espinho anal, presença de um tubérculo no exópodo da antena e pela primeira vez reportado, presença de cerdas dorsais simples no pleon. Diante da falta de padronização nas descrições larvais, a revisão dos caracteres larvais presentes na literatura elucidou uma diagnose problemática no conhecimento da morfologia larval de *Alpheus*. Alguns caracteres são propostos para a diferenciação dos grupos morfológicos, necessitando ainda conhecimento sobre a morfologia larval de mais espécies do grupo, a fim de confirmar a robustez destes caracteres.

Palavras-chave: Alpheidae, larva, grupos morfológicos, SEM, Atlântico

ABSTRACT

Studies on larval descriptions can be extremely important to help elucidating some problems found in adults taxonomy, as well as contributing to the life history understanding of a species and enabling subsequent larvae identification in plankton. Nevertheless, in many decapod groups, the lack of larval descriptions prevents taxonomic comparative studies. Although snapping shrimps of the genus *Alpheus* Fabricius, 1798 comprises more than 300 described species, larval morphology is known for 16 species only. On the Brazilian coast, only two out of 35 registered species have known larval stages. Considering the relevance of understanding decapod larval morphology and given the lack of *Alpheus* species larval descriptions, this study aimed to describe the first larval stage (zoea I) of three *Alpheus* species from the Brazilian coast, as well as to review larval characters present in literature, in order to analyse whether morphological groups proposed for adults are supported by larval data. Larvae of *Alpheus formosus* Gibbes, 1850 and *Alpheus malleator* Dana, 1852 from São Paulo coast, and of *Alpheus bouvieri* A. Milne-Edwards, 1878 from Pernambuco coast were analyzed. Larvae of parental females were dissected under stereomicroscope and drawn/measured/analyzed under a drawing tube microscope. Moreover, scanning electron microscopy was used to analyse in more detail some larval structures. Finally, a comparative table was prepared containing all *Alpheus* zoea I descriptions available in literature and, subsequently, the species were grouped according to the morphological groups proposed for adults. In addition to expanding knowledge about *Alpheus* larval morphology, new characters were suggested to be analyzed in the zoeas of the genus: presence of anal spine, presence of a tubercle in the exopod of the antenna and reported for the first time, presence of simple dorsal setae on the pleon. Given the lack of standardization in larval descriptions, the literature review of larval characters clarified a problematic diagnosis in the larval morphology knowledge of *Alpheus*. Some characters are proposed to differentiate morphological groups, requiring further knowledge about the larval morphology of more species in the group, in order to confirm the characters robustness.

Key words: Alpheidae, larva, morphological groups, SEM, Atlantic

Capítulo I: Introdutório

INTRODUÇÃO GERAL

Alpheus Fabricius, 1798

A ordem Decapoda Latreille, 1802 abrange aproximadamente 17.600 espécies de crustáceos descritas (Martin & Davis 2001; Porter *et al*. 2005; De Grave *et al*. 2009; Fransen & De Grave 2009; Ahyong 2011). Os crustáceos decápodos (camarões, lagostas, siris, caranguejos e ermitões, entre outros) são comumente reconhecidos e estudados, devido a sua distribuição mundial, amplo registro fóssil e grande diversidade taxonômica e ecológica, além de elevado interesse econômico e comercial (Martin & Davis 2001; Bracken *et al*. 2009; De Grave *et al.* 2009; Schram 2009). Os decápodos encontram-se agrupados em duas subordens: Dendrobranchiata Spence Bate, 1888: compreende as superfamílias Penaeoidea Rafinesque, 1815 e Sergestoidea Dana, 1852; e Pleocyemata Burkenroad, 1963: representada pelas infraordens: Achelata Scholtz & Richter, 1995, Anomura MacLeay, 1838, Astacidea Latreille, 1802, Axiidea de Saint Laurent, 1979, Brachyura Latreille, 1802, Caridea Dana, 1852, Gebiidea de Saint Laurent, 1979, Glypheidea Van Straelen, 1925, Polychelida Scholtz & Richter, 1995, Stenopodidea Spence Bate, 1888, Procarididea Felgenhauer & Abele, 1983 (De Grave *et al.* 2009; Wolfe *et al*. 2019).

A infraordem Caridea Dana, 1852 engloba o maior grupo de camarões, cerca de 3.500 espécies descritas, além de ser o segundo grupo mais representativo dentro de Decapoda Pleocyemata, atrás somente dos caranguejos Brachyura (De Grave & Fransen 2011). O conhecimento da riqueza de carídeos aumenta constantemente, devido ao intenso esforço de pesquisas de viés sistemático e taxonômico no grupo, o que vem se revertendo na adição de novas espécies (De Grave *et al*. 2015). Os carídeos se distinguem morfologicamente dos demais grupos de camarões por apresentarem a pleura do segundo segmento pleonal

expandida, recobrindo lateralmente o primeiro e o terceiro segmentos pleonais, o terceiro par de pereiópodos não quelados e filobrânquias sob a carapaça (Chace 1972; McLaughlin 1980; Bliss 1990; Holthuis 1993; Bauer 2004).

Os carídeos apresentam uma grande diversidade morfológica e ecológica (Bond-Buckup & Buckup 1999; Bauer 2004), bem como utilizam cavidades, rachaduras e o interior dos organismos sésseis como abrigos (Boltaña & Thiel 2001; Anker *et al*. 2008; Pachelle *et al*. 2015). Embora a maioria das espécies seja marinha, os carídeos também se estabeleceram com sucesso em ambientes salobros e de água doce, sendo encontrados em todas as latitudes, desde as regiões tropicais até polares, em substratos não consolidados e consolidados (Bauer 2004).

Entre os carídeos marinhos, Alpheoidea Rafinesque, 1815 é a superfamília mais diversa e abundante (Bauer 2004). Os camarões da família Alpheidae Rafinesque, 1815, destacam-se entre os carídeos por serem o segundo grupo mais rico em espécies (mais de 600 espécies), distribuídas em 48 gêneros (De Grave & Fransen 2011; Anker 2020; WoRMS 2020). No Brasil, são registradas 58 espécies de alfeídeos, distribuídas em oito gêneros (Almeida & Anker 2011). Devido às novas descrições de gêneros e espécies, o número de alfeídeos está em constante alteração (De Grave & Fransen 2011). Portanto, o entendimento sobre os alfeídeos ainda está longe de ser considerado abrangente, devido às descrições recentes de novos táxons para a ciência, inclusive para a costa brasileira (Almeida *et al*. 2013, 2014; Soledade *et al*. 2014, 2019; Anker *et al*. 2016).

Os alfeídeos apresentam um corpo robusto e pesado, dotado de apêndices fortes, um rostro reduzido ou ausente, e, em muitos gêneros, os olhos são reduzidos e frequentemente cobertos pela margem anterior do cefalotórax (Bauer 2004). O corpo destes camarões apresenta facies caridoida bastante modificadas, assemelhando-se, em alguns casos, mais à morfologia corporal de uma lagosta do que a de um camarão típico (Bauer 2004; Anker *et al*. 2006). A forma corporal é uma adaptação a um estilo de vida críptico, no qual estes camarões

habitam inúmeros microhabitats, dentre os quais galerias escavadas em substrato móvel, refúgios como cavidades em substrato duro ou sob pedras, e até mesmo a vida dentro de canais de esponjas e fendas de corais, entre outros (Bauer 2004; Anker *et al*. 2006).

Os representantes desta família apresentam uma ampla distribuição geográfica, ocorrendo desde a zona entremarés até águas profundas, porém, sendo mais frequentes em habitats costeiros de águas rasas tropicais e subtropicais, constituindo um dos grupos de carídeos mais abundantes em ambiente marinho (Chace 1988; Anker *et al*. 2006). Ademais, os alfeídeos estabelecem, frequentemente, associações mutualísticas e comensais com invertebrados marinhos de diversos filos, incluindo outras espécies de crustáceos e até mesmo com peixes gobiídeos (Boltaña & Thiel 2001; Bauer 2004; Anker *et al*. 2006, 2007, 2008).

Alpheus Fabricius, 1798 é o gênero com maior riqueza de espécies descritas, pertencente à família Alpheidae, abrangendo mais de 310 espécies válidas no mundo (De Grave & Fransen 2011; Anker 2012; Almeida *et al*. 2014; Dehghani *et al*. 2019; Soledade *et al*. 2019; De Grave *et al*. 2020; Scioli & Anker 2020; WoRMS 2020) e com uma diversidade estimada em mais de 400 espécies (Anker 2001a; Anker *et al*. 2006). Para a costa brasileira foram registradas 35 espécies até o momento (Soledade & Almeida 2013; Almeida *et al*. 2014; Bracken-Grissom & Felder 2014; Anker *et al*. 2016; Soledade *et al*. 2019). No entanto, a diversidade de *Alpheus* existente em águas brasileiras, ainda, se encontra subestimada (Soledade & Almeida 2013; Almeida *et al*. 2014).

Embora a maioria dos representantes de *Alpheus* sejam marinhos, existe um único registro para ambiente de água doce, *Alpheus cyanoteles* Yeo & Ng, 1996, com ocorrência restrita para a Malásia (Yeo & Ng 1996). Estes camarões apresentam uma ampla distribuição nos ambientes marinhos e estuarinos tropicais e subtropicais, ocorrendo desde regiões entremarés podendo habitar microhabitats, como poças de maré e recifes de corais, até grandes profundidades (Chace 1988; Anker *et al*. 2006).

Tal como é comum entre alfeídeos, os camarões do gênero *Alpheus* possuem hábito críptico, vivendo no interior de galerias ou tocas contruídas em diversos substratos, como tocas escavadas em substrato lamoso e subtrato arenoso sob rochas soltas do entremarés (Nolan & Salmon 1970; Christoffersen 1984; Chace 1988). Além de viverem abrigados embaixo de rochas, cascalhos, entulhos, troncos em putrefação, os *Alpheus* possuem um amplo registro de associações com outros organismos marinhos, incluindo esponjas, anêmonas, poliquetos, briozoários, equinodermos e inclusive peixes (Boltaña & Thiel 2001; Bauer 2004; Anker *et al*. 2006, 2007, 2008; Santos *et al*. 2012).

Os camarões deste gênero, juntamente com os camarões do gênero *Synalpheus*, são popularmente conhecidos como camarões-de-estalo. Estes animais caracterizam-se, em sua maioria, devido à assimetria acentuada encontrada no primeiro par de quelípodos, com função de defesa, predação e construção de galerias (Nolan & Salmon 1970; Bauer 2004). Uma das quelas desse par de apêndices é extremamente desenvolvida comparada à outra e está relacionada ao comportamento altamente territorial e agonístico (Versluis *et al*. 2000; Rahman *et al*. 2004; Anker *et al*. 2006; Hughes *et al*. 2014). O hábito de estalar é resultante do encaixe do dedo móvel no dedo fixo do primeiro par de quelípodos, formando uma bolha de ar que ao implodir produz um som semelhante ao de um estalo (Versluis *et al*. 2000; Anker *et al*. 2006).

O estalo é utilizado para defender um abrigo ou território, proteger e disputar por parceiro sexual e atordoar e até matar presas, além de desempenhar um papel importante na comunicação intraespecífica (Versluis *et al*. 2000; Anker *et al*. 2006; Hughes *et al*. 2014). Tais estalos são capazes de serem detectados a muitos metros de distância, além de representar um dos sons mais audíveis nos habitats onde esses camarões vivem (Versluis *et al*. 2000; Anker *et al*. 2006).

Outra peculiaridade comportamental verificada em várias espécies de *Alpheus* e também em outros gêneros de Alpheidae, é a monogamia social entre macho e fêmea, os quais

compartilham o mesmo abrigo, assim como atividades relacionadas à proteção e manutenção do microhabitat e busca por alimento (Mathews 2002; Correa & Thiel 2003; Rahman *et al*. 2003). Pressupõe-se que o comportamento agonístico marcante destes camarões é um dos aspectos que pode ter colaborado para evolução da monogamia social, como a melhor estratégia de acasalamento (Hughes *et al*. 2014).

Por conta de sua grande diversificação morfológica e elevado número de espécies conhecidas, o gênero *Alpheus* foi dividido em sete grupos informais de espécies, com base em caracteres morfológicos de adultos: *brevirostris* (aproximadamente 45 espécies), *crinitus* (aproximadamente 30 espécies), *diadema* (aproximadamente 24 espécies), *edwardsi* (aproximadamente 95 espécies), *macrocheles* (aproximadamente 30 espécies), *obesomanus* (aproximadamente 11 espécies) e *sulcatus* (aproximadamente 40 espécies) (Coutière 1899, 1905; Anker 2001b). Estes grupos foram estabelecidos levando em consideração, principalmente, características da região frontal e dos primeiros quelípodos, e apesar de informais são úteis para taxonomia deste rico gênero, permitindo uma primeira atribuição aproximativa dos espécimes (Chace 1988).

Entretanto, pelo menos três dos grupos morfológicos (*diadema*, *edwardsi* e *sulcatus*) demonstraram não ser monofiléticos, baseado em análises moleculares preliminares (Williams *et al*. 2001). Ainda, além da falta de robustez para suportar alguns grupos morfológicos, há evidências moleculares em relação à existência de muitos complexos de espécies neste gênero (Williams *et al*. 2001; Anker *et al*. 2006; Mathews & Anker 2009). O número de espécies de *Alpheus* tem aumentado constantemente a partir das descrições de novas espécies, principalmente, oriundas de resoluções de alguns dos complexos de espécies do gênero (Anker 2001b, 2012; Mathews & Anker 2009; Almeida & Anker 2011; Almeida *et al*. 2013, 2014).

Morfologia larval

Todos os camarões carídeos incubam os ovos nos pleópodos encontrados na câmara de incubação, formada pela expansão das pleuras laterais nas fêmeas maduras (Bauer 2004). As fêmeas incubam os ovos no pleon por um período que varia de poucas semanas em espécies tropicais a vários meses em espécies que vivem em altas latitudes (Sastry 1983; Bauer 2004). Após o período de incubação e cuidado parental, a eclosão ocorre sob a forma de larva planctônica, na maioria dos camarões carídeos (Bauer 2004).

O desenvolvimento larval de crustáceos decápodos marinhos é caracterizado por uma sequência de formas larvais morfologicamente distintas (Anger 1987). Ademais, a morfologia funcional dos apêndices de alimentação é de extrema importância, e, entre outros, o principal critério para a classificação de formas larvais e padrões de desenvolvimento (Anger 2001).

Fase e estágios são alguns conceitos básicos de desenvolvimento morfológico encontrados nas larvas de crustáceos decápodos (Anger 2001). O termo fase refere-se a uma sequência de estágios de desenvolvimento morfologicamente equivalentes como, por exemplo, todos estágios naupliar, zoeal ou juvenil combinados (Williamson 1982). Enquanto, o termo estágio (ou estágio morfológico) é considerado e nomeado como diferentes estágios de desenvolvimento (Anger 2001), adicionando algarismos romanos para denotar estágios sucessivos dentro de uma dada fase como, por exemplo, zoea I e zoea II (Williamson 1982).

Embora exista uma grande diversidade de formas larvais, é possível distinguir três principais tipos de larvas em Decapoda: nauplius, zoea e decapodito (Anger 2001). Em camarões carídeos, o ciclo de vida consiste de zoea, decapodito, juvenil, e uma fase adulta (Guerao & Cuesta 2014). A larva eclode não apenas com dois pares de antenas e um par de mandíbulas, como nas mais primitivas larvas nauplius dos crustáceos, mas também com ambos pares de maxilas e todos três pares de maxilípodos (Bauer 2004). Esta forma planctônica é denominada zoea, porque a larva utiliza os apêndices torácicos para a natação,

enquanto, os apêndices cefálicos são responsáveis pela alimentação (Williamson 1969; Anger 2001). Após a zoea, a larva passa para a fase decapodito, que nada com os apêndices abdominais e constitui a última fase larval (Anger 2001; Bauer 2004).

As zoeas e os decapoditos de carídeos são encontrados no plâncton em água marinha, salobra, estuarina e de água doce, onde desempenham um papel fundamental na teia alimentar (Guerao & Cuesta 2014). O desenvolvimento larval pode ser abreviado ou estendido. O desenvolvimento abreviado caracteriza-se por apresentar 1 a 3 estágios de zoea e o desenvolvimento estendido de 6 a 13 estágios, e os dois tipos apresentam de 1 a 5 estágios de decapodito (Bauer 2004; Guerao & Cuesta 2014).

No desenvolvimento larval estendido, as zoeas I de carídeos são, geralmente, planctotróficas, ou seja, alimentam-se de organismos planctônicos e podem apresentar caracteres gerais como: olhos sésseis, segmentação no exópodo da antena e endópodo não segmentado, primeiros três maxilípodos natatórios, pereiópodos ausentes ou presentes como broto, pleópodos e urópodos ausentes e télson fundido ao sexto segmento do pleon, com 14 cerdas (Guerao & Cuesta 2014). No desenvolvimento abreviado, as zoeas I também apresentam olhos sésseis, primeiros três maxilípodos natatórios e urópodos ausentes, porém, são lecitotróficas, nutrem-se do próprio vitelo e apresentam ausência de segmentação no exópodo da antena e endópodo segmentado e com flagelo, pereiópodos presentes, pleópodos geralmente presentes, mas ainda não funcionais e télson fundido ao sexto segmento, com 14 ou mais cerdas (Guerao & Cuesta 2014).

Anger (2001) fornece um pequeno histórico sobre o início dos estudos com larvas. Segundo este autor, o primeiro relato morfológico conhecido de uma larva de decápodo é o de Leeuwenhoek (1699; publicado em 1807) no qual mostra, provavelmente, a prezoea do camarão *Crangon crangon* (Ingle, 1998), no mar do Norte. Após sete décadas, Linnaeus (1767) descreveu uma larva de caranguejo, como uma nova espécie *Cancer germanus*

(Linnaeus, 1767). Sendo assim, ainda segundo Anger (2001), Slabber (1778) foi provavelmente o primeiro a reconhecer corretamente e descrever uma larva de decápodo como tal. Portanto, observa-se o equívoco na terminologia e a grande dificuldade enfrentada nas primeiras descrições larvais de crustáceos decápodos. Uma padronização nas descrições larvais foi apenas proposta, mais de 200 anos depois, por Clark *et al*. (1998) e atualizado por Clark & Cuesta (2015) usando apenas Brachyura como exemplo, mas são seguidas pela maioria dos autores que descrevem larvas de decápodos.

As descrições larvais são fundamentais para compreender as estratégias de vida de uma espécie, além dos processos ecológicos nas comunidades planctônicas. Na América do Sul, a falta de descrições larvais dificulta estudos ecológicos no plâncton (Thatje & Bacardit 2000). Geralmente, a identificação das larvas de crustáceos no plâncton é uma tarefa complexa, principalmente, quando a diversidade biológica existente e a morfologia larval são desconhecidas em uma determinada região (Albornoz & Wehrtmann 1997).

Durante muito tempo, estudos taxonômicos e sistemáticos sobre crustáceos decápodos foram totalmente baseados em caracteres morfológicos de espécimes adultos. As descrições de estágios larvais de decápodos surgiram como um complemento para contribuir no conhecimento do ciclo de vida de uma espécie, na dinâmica de uma população, na ecologia do plâncton, bem como contribuir em estudos filogenéticos ou sistemáticos (González-Gordillo & Rodriguez 2000; Cuesta 2004; Vela & González-Gordillo 2016).

Entretanto, nas últimas décadas, uma importante ferramenta nos estudos taxonômicos tem sido a morfologia externa dos primeiros estágios larvais de várias espécies de crustáceos decápodos (Pohle *et al*. 1999), sendo que muitos destes caracteres morfológicos têm sido utilizados para este fim de forma comparativa (Rice & Ingle 1975; Williamson & Rice 1996; Albornoz & Wehrtmann 1997), como a morfologia do rostro, da carapaça, do pleon, do télson

e dos apêndices, e incluindo os padrões distintos de distribuição, bem como os tipos de cerdas nestas estruturas (Gurney 1937; Williamson 1957, 1982; Haynes 1985).

Apesar das larvas de Alpheidae corresponderem a uma parcela significativa do plâncton costeiro, as descrições larvais nesta família são pouco conhecidas (Knowlton 1973; Yang *et al*. 2003; Bartilotti *et al*. 2005). Ademais, assim como em outros grupos de decápodos, a falta de descrições larvais impossibilita o estudo comparativo para fins taxonômicos (Vela & González-Gordillo 2016). Embora o gênero *Alpheus* apresente mais de 300 espécies descritas, a morfologia da zoea I é conhecida para apenas 16 espécies [14 espécies na revisão recente feita por Pescinelli *et al*. 2017 (*Alpheus rapacida* de Man, 1908 foi excluída, pois a zoea descrita por Prasad & Tampi 1957 é na verdade zoea II segundo Yang & Kim 2002), mais duas espécies em Wehrtmann & Albornoz 2002]. Para a costa brasileira são registradas 35 espécies (Soledade & Almeida 2013; Almeida *et al*. 2014; Bracken-Grissom & Felder 2014; Anker *et al*. 2016; Soledade *et al*. 2019), e apenas *Alpheus estuariensis* Christoffersen, 1984 (Pires *et al.* 2008) e *Alpheus brasileiro* Anker, 2012 (Pescinelli *et al*. 2017) possuem zoea I conhecida.

O estudo da morfologia larval surge como uma ferramenta para auxiliar no processo de elucidação de complexos de espécies presentes em *Alpheus*. O conhecimento da morfologia larval destas espécies poderia auxiliar na separação das espécies inseridas nestes complexos. Considerando a relevância do conhecimento da morfologia larval de decápodos para contribuir em aspectos taxonômicos, ecológicos e filogenéticos (Pohle & Marques 2000; Mantelatto *et al*. 2014; Vela & González-Gordillo 2016) e dada a falta de descrições larvais de espécies de *Alpheus*, os estudos sobre descrições larvais podem ser de extrema importância para auxiliar na elucidação de alguns problemas encontrados na taxonomia com os adultos (Pohle *et al*. 1999), além de contribuir no entendimento da história de vida de uma espécie e possibilitar a posterior identificação das larvas no plâncton (Thatje & Bacardit 2000).

OBJETIVOS

Objetivo geral

- Analisar e descrever a morfologia larval (zoea I) de camarões-de-estalo do gênero *Alpheus* Fabricius, 1798 e comparar este estágio com outras espécies congenéricas.

Objetivos específicos

- Descrever o primeiro estágio larval de *Alpheus formosus* Gibbes, 1850, *Alpheus malleator* Dana, 1852 e *Alpheus bouvieri* A. Milne-Edwards, 1878;

- Realizar uma revisão dos caracteres larvais (zoea I) presentes na literatura, com adição de novos dados obtidos neste estudo, levando em consideração a divisão das espécies nos grupos morfológicos. A hipótese do presente estudo é que os grupos morfológicos propostos para adultos são suportados pelos dados larvais.

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Capítulo II:

First zoeal stage of the snapping shrimps *Alpheus formosus* Gibbes, 1850 and *Alpheus malleator* Dana, 1852 (Caridea: Alpheidae), with new characters to the genus

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First zoeal stage of the snapping shrimps *Alpheus formosus* Gibbes, 1850 and *Alpheus malleator* Dana, 1852 (Caridea: Alpheidae), with new characters to the genus

KARMINE PASINATTO[1,3], FERNANDO L. MANTELATTO[2] & MARIANA TEROSSI[1]

[1]*Laboratory of Carcinology, Graduate Program in Animal Biology (PPGBAN), Department of Zoology, Institute of Biosciences, Federal University of Rio Grande do Sul (UFRGS). Av. Bento Gonçalves, 9500, Agronomia, 91501-970, Porto Alegre, Rio Grande do Sul, Brazil. E-mail: kcpasinatto@gmail.com; mterossirm@gmail.com*

[2]*Laboratory of Bioecology and Crustacean Systematics (LBSC), Department of Biology, Faculty of Philosophy, Science and Letters at Ribeirão Preto (FFCLRP), University of São Paulo (USP), Av. Bandeirantes 3900, Monte Alegre, 14040-901, Ribeirão Preto, São Paulo, Brazil. E-mail: flmantel@usp.br*

[3]*Corresponding author: E-mail: kcpasinatto@gmail.com*

Abstract

The first zoeae of *Alpheus formosus* Gibbes, 1850 and *Alpheus malleator* Dana, 1852 are described and illustrated for the first time, based on laboratory-hatched larvae from parental females sampled in Vitória Island, Ubatuba, Brazil. Both species shared many characters with other species of genus *Alpheus* Fabricius, 1798, but they also have some exclusive characters as 10 setae on basis of maxilla, first maxilliped with endopod 2-segmented and exopod 4-segmented, second maxilliped with exopod 4-segmented, presence of bud only of the first pereopod, presence of anal spine and simple dorsal setae on the pleon. The zoea I of these species, nevertheless, can be separated by segmentation in the exopod of the antenna (8 in *A. formosus*, 6 in *A. malleator*); segmentation in the endopod and exopod of the third pereiopod (5 in *A. formosus* and 4 in *A. malleator*); peduncle of antennule 3-segmented in *A. formosus*

(unsegmented or 2-segmented in other species) and presence of a medial tubercle in the proximal segment in the exopod of the antenna of *A. malleator* (absent in all other species). In this study three new characters are proposed to be analyzed in zoea of the genus *Alpheus*: presence of anal spine (absent in *Alpheus saxidomus* Holthuis, 1980, but not reported in other species), presence of a tubercle in the exopod of the antenna and for the first time reported, presence of simple dorsal setae on the pleon, here analyzed under both light and scanning electron microscopy.

Keywords: larval morphology, zoea, SEM, Decapoda, Atlantic

Introduction

The family Alpheidae Rafinesque, 1815 stand out as the second most diverse group among caridean shrimps (over 650 species), distributed in 48 genera (De Grave & Fransen 2011; Anker 2020). Within this family, the genus of snapping shrimps *Alpheus* Fabricius, 1798 is the species-richest genus, with more than 310 valid species worldwide (De Grave & Fransen 2011; Anker 2012; Almeida *et al*. 2014; Dehghani *et al*. 2019; Soledade *et al*. 2019; De Grave *et al*. 2020; Scioli & Anker 2020; WoRMS 2020) and with an estimated diversity of more than 400 species (Anker 2001; Anker *et al*. 2006). On the Brazilian coast, 35 species were recorded (Soledade & Almeida 2013; Almeida *et al*. 2014; Bracken-Grissom & Felder 2014; Anker *et al*. 2016; Soledade *et al*. 2019), including *Alpheus formosus* Gibbes, 1850 and *Alpheus malleator* Dana, 1852. The former occurs in Western Atlantic – since USA (North Carolina), Bermuda, Gulf of Mexico, Caribbean Sea, and Brazil (Rocas Atoll, Fernando de Noronha, Trindade and Martin Vaz Archipelago, Abrolhos Archipelago and Ceará to Santa Catarina) (Soledade & Almeida 2013; Anker *et al.* 2016 for review), while *A. malleator* is distributed in both Western and Eastern Atlantic – Gulf of Mexico, USA (Florida), Caribbean Sea, Brazil (Fernando de Noronha, Rio de Janeiro and São Paulo) and from Cape Verde to Congo (Anker & Pachelle 2013 for review).

Although there are over 300 species described in the genus *Alpheus*, larval morphology is known for only 16 species [14 species in the recent review by Pescinelli *et al*. 2017 (*Alpheus rapacida* de Man, 1908 excluded, because the zoea described by Prasad & Tampi 1957 is actually zoea II according to Yang & Kim 2002), plus two species in Wehrtmann & Albornoz 2002] and only two of those species occurring in Brazil have zoea I described: *Alpheus estuariensis* Christoffersen, 1984 (Pires *et al*. 2008), *Alpheus brasileiro* Anker, 2012 (Pescinelli *et al*. 2017). Studies on larval morphology may be of paramount importance to help elucidating some issues found in adult taxonomy (Pohle *et al*. 1999), as well as contributing to a better understanding of species life history and enabling subsequent larvae identification in plankton (Thatje & Bacardit 2000).

Considering such importance in knowledge of larvae and given the lack of larval descriptions of species of the *Alpheus*, this study aims to describe the first zoeal stage morphology of snapping shrimps *A. formosus* and *A. malleator* obtained in laboratory conditions.

Material and Methods

The parental females of *A. formosus* and *A. malleator* were obtained on April 2013 from Vitória Island, Ubatuba, São Paulo, southeastern Brazil (23°42′02″S, 045°01′03″W) by scuba diving, as part of the multidisciplinary project Biota-FAPESP, which aimed to produce a fine-scale assessment of the marine decapod biodiversity of the State of São Paulo (see Mantelatto *et al*. 2018; Terossi *et al*. 2018 for details). After collection, one ovigerous female of each species were kept alive until larval hatching and then they were preserved in 80% ethanol, while actively swimming larvae (zoea I) were fixed in 10% formaldehyde.

Larvae were dissected under a stereomicroscope Zeiss Stemi DV4 and drawn/measured/analyzed under an Olympus CX31 microscope with the aid of *camera lucida*. The illustrations were edited using Adobe Photoshop software. Structures were analyzed in at

least 10 larvae of each species. Measurements of carapace length (maximum length from the postorbital margin to the posterior margin of the carapace) were also performed in the parental females and in 10 larvae of each species. Larval descriptions were performed according to Clark *et al.* (1998) and updated by Clark & Cuesta (2015), while setal terminology followed Garm (2004) and Landeira *et al.* (2009). Plumose terminal natatory setae of maxillipeds were drawn truncated.

Scanning Electron Microscopy (SEM) was used in order to analyse details of the dorsal setae on the pleon (type and position) and structures in the posterior margin of the telson. The zoeae were fixed in formaldehyde, washed twice with ultrapure water and dehydrated in an ascending alcohol series. Specimens were critical point dried (BAL-TEC CPD 030 Critical Point Dryer), mounted on stubs coated in gold. Samples were observed with a JEOL JSM-6060 Scanning Electron Microscope, at the Center for Microscopy and Microanalysis of the Federal University of Rio Grande do Sul - CMM UFRGS.

Voucher parental females and larvae were deposited at the Crustacean Collection of the Biology Department of FFCLRP, University of São Paulo, Brazil (CCDB/FFCLRP/USP, accession numbers: 4574 for *A. formosus* and 4573 for *A. malleator*).

Results

The parental females from *A. formosus* and *A. malleator* measured 7.83 mm and 12.17 mm in carapace length, respectively.

Morphological description of *Alpheus formosus* Gibbes, 1850

Zoea I

Carapace length: 0.42 ± 0.04 mm (n = 10 larvae)

Cephalothorax (Fig. 1A, 1B): rostrum absent; pterygostomian spine present; eyes sessile.

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

Antenna (Fig. 1D): peduncle 2-segmented with 1 medial distal spiniform projection near the endopod; endopod with 1 terminal plumose seta and 1 medial distal spiniform projection; exopod (scaphocerite) 8-segmented with 11 plumose setae (2, 1, 2, 1, 1, 1, 1, 2), distal segment with 1 simple seta.

Mandible (Fig. 1E): palp absent.

Maxillule (Fig. 1F)*:* coxa with 6 (1 medial simple, 3 terminal simple, one larger in proximal region, 1 terminal serrulate plumose, 1 lateral simple) setae; base with 2 spiniform projections and 1 lateral simple seta; endopod with 1 terminal plumoserrulate and 1 lateral simple setae; exopod absent.

Maxilla (Fig. 1G): coxa with 2 medial simple setae; base bilobed, each lobe with 5 medial simple setae (distal seta longer); endopod with 1 medial proximal simple and 2 terminal long (1 simple and 1 plumose) setae, with microtrichia; exopod (scaphognathite) with 5 plumose setae, without microtrichia.

First maxilliped (Fig. 1H): coxa with 1 medial distal simple seta; base with 7 medial simple setae arranged 2+2+2+1; endopod 2-segmented with 1 medial distal simple seta, 5 [4 simple (1 medial + 3 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 (Fig. 1I): coxa without setae; base with 4 medial simple setae arranged 1+1+1+1; endopod 4-segmented with 1 medial distal simple, 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 terminal simple seta on second segment.

Third maxilliped (Fig. 1J): coxa with 1 medial distal simple seta; base with 2 medial simple setae arranged 1+1; endopod 5-segmented with 0, 1 medial, 0, 3 (2 lateral proximal and 1 medial distal), 3 (2 medial proximal and 1 terminal) simple setae; exopod 5-segmented with 0, 0, 2, 2, 2 terminal natatory plumose setae plus 1 medial simple seta on second segment.

Pereiopod (Fig. 1K): first as a biramous bud.

Pleon (Figs. 1A, 1L, 1M, 1N, 3B, 3C): with 6 segments (6th segment fused to telson), presence of simple dorsal setae on segments; lateral spines absent; pleopods absent; anal spine present.

Telson (Figs. 1N, 3G, 3H): triangular, with 7+7 (5 inners plumose, 2 outers plumose laterally) setae, 4 inner setae with shorter setules in the proximal region, inner pair shorter; 6 inner pairs with a row of denticles in the distal margin, 4 innermost pairs with marginal spines.

Morphological description of *Alpheus malleator* Dana, 1852

Zoea I

Carapace length: 0.52 ± 0.03 mm (n = 10 larvae)

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

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

Antenna (Fig. 2D): peduncle 2-segmented with 1 medial distal spiniform projection near the endopod; endopod with 1 terminal plumose seta and 1 medial distal spiniform projection; exopod (scaphocerite) 6-segmented with 11 plumose setae (2, 1, 2, 1, 1, 4), plus a medial tubercle in the proximal segment and 1 simple seta in the distal segment.

Mandible (Fig. 2E): palp absent.

Maxillule (Fig. 2F): coxa with 6 (1 medial simple, 3 terminal simple, 1 terminal serrulate plumose, one larger in proximal region, 1 lateral simple) setae; base with 2 spiniform

projections and 1 lateral simple seta; endopod with 1 terminal plumoserrulate and 1 lateral simple setae; exopod absent.

Maxilla (Fig. 2G): coxa with 2 medial simple setae; base bilobed, each lobe with 5 medial simple setae (median seta shorter); endopod with 3 medial (1 proximal and 2 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 (Fig. 2H): coxa with 1 medial distal simple seta; base with 7 medial simple setae arranged 2+2+2+1; endopod 2-segmented with 1 medial distal simple seta, 5 [4 simple (1 medial + 1 lateral + 2 terminal) and 1 terminal serrulate] setae; exopod 4-segmented with 0, 0, 2, 2 terminal natatory plumose setae plus 1 lateral proximal simple seta on third segment.

Second maxilliped (Fig. 2I): coxa without setae; base with 4 medial simple setae arranged 1+2+1; endopod 4-segmented with 1 medial distal simple, 0, 1 medial distal serrulate seta, 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 terminal simple seta on second segment.

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

Pereiopod (Fig. 2K): first as a biramous bud.

Pleon (Figs. 2A, 2L, 2M, 2N, 3A, 3D, 3E, 3F): with 6 segments (6th segment fused to telson), presence of simple dorsal setae on segments; lateral spines absent; pleopods absent; anal spine present.

Telson (Fig. 2N): triangular, with 7+7 (5 inners plumose, 2 outers plumose laterally) setae, 4 inner setae with shorter setules in the proximal region, inner pair shorter; 6 inner pairs with a row of denticles in the distal margin, 4 innermost pairs with marginal spines.

Discussion

Our description of *A. formosus* and *A. malleator* larvae revealed that both species share typical characteristics of the most zoea I of the genus, with particularities that can be used as diagnosis to identification of both species.

According to Yang & Kim (2002) and reaffirmed by recent review of the zoea I morphology from the genus *Alpheus* proposed by Pescinelli *et al*. (2017), all zoea I share some characteristics: rostrum absent, pterygostomian spine present; eyes sessile; all pleonal segments without spines; antennule with peduncle unsegmented; endopod of antennule as a long plumose seta; antenna with peduncle unsegmented with a terminal spine near the endopod; endopod of antenna with 1 long plumose seta and 1 small inner spine; pleon without division between 6° segment and telson; telson triangular with 7+7 plumose setae. The studies of Lebour (1932) and Prasad & Tampi (1957) were disregarded in Pescinelli *et al.* (2017) review because they have poor descriptions.

Except for the peduncle of the antennule and antenna, the zoea I of *A. formosus* and *A. malleator* have the characteristics listed above. The peduncle of the antennule is 3-segmented in *A. formosus* and 2-segmented in *A. malleator* (Figs. 1C and 2C, respectively); this structure is also 2-segmented in *A. glaber* (Olivi, 1792) and *A. macrocheles* (Hailstone, 1835) described by Lebour (1932), despite this study have a poor description, the segmentation of antennule is mentioned in the description and well defined in the figure (Lebour 1932, plate II, fig. 8), with no doubt about it. Also, the zoea I of *A. saxidomus* Holthuis, 1980 described by Wehrtmann &

Albornoz (2002) have the peduncle of the antennule 2-segmented, but this study was not mentioned in the revision by Pescinelli *et al.* (2017).

The peduncle of antenna is also clearly 2-segmented in *A. formosus* and *A. malleator* (Figs. 1D and 2D, respectively). All other previous descriptions reported this peduncle as unsegmented (Wehrtmann & Albornoz 2002; Pires *et al*. 2008; Pescinelli *et al*. 2017), nevertheless, the illustrations of the peduncle of the antenna in the zoea I of three species raise doubt about a possible segmentation: *Alpheus brasileiro* (Pescinelli *et al*. 2017, Fig. 1e), *A. estuariensis* (Pires *et al*. 2008, Fig. 6) and *A. saxidomus* (Wehrtmann & Albornoz 2002, Fig. 2b). Thus, considering the 16 species that have the known zoea I until now (only extended larval development considered), the peduncle of the antennule and antenna can be unsegmented or segmented.

Some other characteristics shared by *A. formosus* and *A. malleator* and other species are: presence of four aesthetascs in the exopod of the antennule [also shared with *A. albatrossae* (Banner, 1953) (Yang & Kim 2006), *A. brasileiro* (Pescinelli *et al*. 2017), *A. estuariensis* (Pires *et al*. 2008), *A. glaber* and *A. macrocheles* (Lebour 1932, also with three aesthetascs for both species), and *A. saxidomus* (Wehrtmann & Albornoz 2002)]; 11 setae on exopod of antenna [also shared with *A. albatrossae* (Yang & Kim 2006), *A. brasileiro* (Pescinelli *et al*. 2017), *A. brevicristatus* De Haan, 1844 (Yang & Kim 1998), *A. digitalis* De Haan, 1844 (Yang & Kim 2002), *A. estuariensis* (Pires *et al*. 2008), *A. heeia* Banner & Banner, 1974 (Yang & Kim 1999), *A. japonicus* Miers, 1879 (Yang & Kim 2002), *A. lobidens* De Haan, 1849 (Yang *et al*. 2003), *A. richardsoni* Yaldwyn, 1971 (Yang & Kim 1996), *A. strenuus* Dana, 1852 (Prasad & Tampi 1957) and *A. sudara* Banner & Banner, 1966 (Yang *et al*. 2003)]; endopod of second maxilliped 4-segmented [also shared with *A. albatrossae* (Yang & Kim 2006), *A. brasileiro* (Pescinelli *et al*. 2017), *A. brevicristatus* (Yang & Kim 1998), *A. digitalis* (Yang & Kim 2002) *A. estuariensis*

(Pires *et al*. 2008), *A. heeia* (Yang & Kim 1999), *A. lobidens* (Yang *et al*. 2003), *A. richardsoni* (Yang & Kim 1996) and *A. sudara* (Yang *et al*. 2003)].

The zoea I of *A. malleator* shared the exopod of antenna 6-segmented with other 7 species [*A. albatrossae* (Yang & Kim 2006), *A. brevicristatus* (Yang & Kim 1998), *A. digitalis* (Yang & Kim 2002), *A. heeia* (Yang & Kim 1999, fig. 1E), *A. lobidens* (Yang *et al*. 2003), *A. saxidomus* (Wehrtmann & Albornoz 2002), *A. sudara* (Yang *et al*. 2003)], nevertheless, *A. formosus* is the only that presented a exopod of antenna 8-segmented.

The zoea I of *A. formosus* is the only species that was reported with endopod and exopod of third maxilliped 5-segmented. *Alpheus malleator* is the only species with exopod 4-segmented and shared the endopod 4-segmented with 8 species [*A. brevicristatus* (Yang & Kim 1998), *A. brasileiro* (Pescinelli *et al*. 2017), *A. digitalis* (Yang & Kim 2002), *A. estuariensis* (Pires *et al*. 2008), *A. heeia* (Yang & Kim 1999), *A. lobidens* (Yang *et al*. 2003), *A. richardsoni* (Yang & Kim 1996) and *A. saxidomus* (Wehrtmann & Albornoz 2002)].

Some characters are only shared, until now, by *A. formosus* and *A. malleator*: 10 setae on basis of maxilla, first maxilliped with endopod 2-segmented and exopod 4-segmented, second maxilliped with exopod 4-segmented, presence of bud only of the first pereopod, presence of anal spine and presence of dorsal simple setae on the pleon. These two last characters deserve special attention because they were almost exclusively analyzed in *A. formosus* and *A. malleator*. These characteristics were not reported previously for any known zoea I of genus *Alpheus* [except by anal spine absent reported to *A. saxidomus* (Wehrtmann & Albornoz 2002)], but they are characteristics of very difficult visualization, which should be consider with caution and cannot affirm that they are exclusive of these two species, since previous authors just not have searched for these characters. Furthermore, the presence of a medial tubercle in the proximal segment in the exopod of the antenna is a character not previously reported for any known zoea I of the genus *Alpheus*, except for *A. malleator*. Although this character is not difficult to visualize, its

presence only in *A. malleator* (present study), it may be related to the fact that previous authors simply did not see or search for this character.

The presence of dorsal simple setae on the pleon were analyzed with light microscopy (400x) and SEM. In the light microscopy (Fig. 3A), these setae were observed in the 3rd and 4th segments in *A. formosus* and 3rd to 6th segments in *A. malleator*, but under SEM, it was possible to see that they can be curved; however the position of it in the larva by using the light microscope is not precise to identify the segment of origin. The SEM used here for the first time in larvae of the *Alpheus* genus, was an essential tool for greater detail of the dorsal setae and their position in the segments. In addition, the SEM aims to clarify the structures present in the posterior margin of the télson (denticles and spines).

Only *A. brasileiro* (Pescinelli *et al.* 2017), *A. formosus* and *A. malleator* (present study) shared six setae on the coxa of the maxillule, but these three species can be separated by following characteristics: characters exclusive of *A. formosus* and *A. malleator* cited previously (*A. brasileiro* with 6 setae in the basis of maxilla, first maxilliped with endopod and exopod unsegmented, second maxilliped with exopod unsegmented, presence of first, second and fifth pereiopods), segmentation in the exopod of the antenna (5 in *A. brasileiro*, 8 in *A. formosus*, 6 in *A. malleator*); peduncle of antennule 3-segmented in *A. formosus* (unsegmented or 2-segmented in other species); presence of a medial tubercle in the exopod of the antenna of *A. malleator* (absent in all other species).

The first larval stage of *A. formosus* and *A. malleator* presented characters such as the presence of 5 setae in the exopod of the maxilla and 7 pairs of setae on the telson, inferring an extended larval development for these species (Guerao & Cuesta 2014), then the zoea I of *Alpheus heterochaelis* Say, 1818 described by Knowlton (1973), and *Alpheus simus* Guérin-Méneville, 1855 described by Wehrtmann & Albornoz (2002) were not included in the discussion, because they have characteristics of abbreviated larval development.

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Figure Captions

Figure 1. *Alpheus formosus* Gibbes, 1850. Zoea I. A. Lateral view; B. Carapace; C. Antennule; D. Antenna; E. Mandible; F. Maxillule; G. Maxilla; H. First maxilliped; I. Second maxilliped; J. Third maxilliped; K. First pereiopod; L. Third segment of pleon; M. Pleon; N. Telson. Scale bars: A, L, M. 0.15mm; B–D, H–J, N. 0.07 mm; E–G, K. 0.04 mm.

Figure 2. *Alpheus malleator* Dana, 1852. Zoea I. A. Lateral view; B. Carapace; C. Antennule; D. Antenna; E. Mandible; F. Maxillule; G. Maxilla; H. First maxilliped; I. Second maxilliped; J. Third maxilliped; K. First pereiopod; L. Fourth segment of pleon; M. Pleon; N. Telson. Scale bars: A, L, M. 0.15mm; B–D, H–K, N. 0.07 mm; E–G. 0.04 mm.

Figure 3. *Alpheus formosus* Gibbes, 1850 (B, C, G, H) and *Alpheus malleator* Dana, 1852 (A, D–F). Zoea I. Light microscopy (A), Scanning electron microscopy (B–H). A–F. Simple dorsal setae on pleon (white arrows). G–H. Denticles (black arrows) and spines (black arrowheads) in posterior margin of telson. Scale bars: A. 100 µm; B–D, F–H. 10 µm; E. 20 µm.

Figure 1

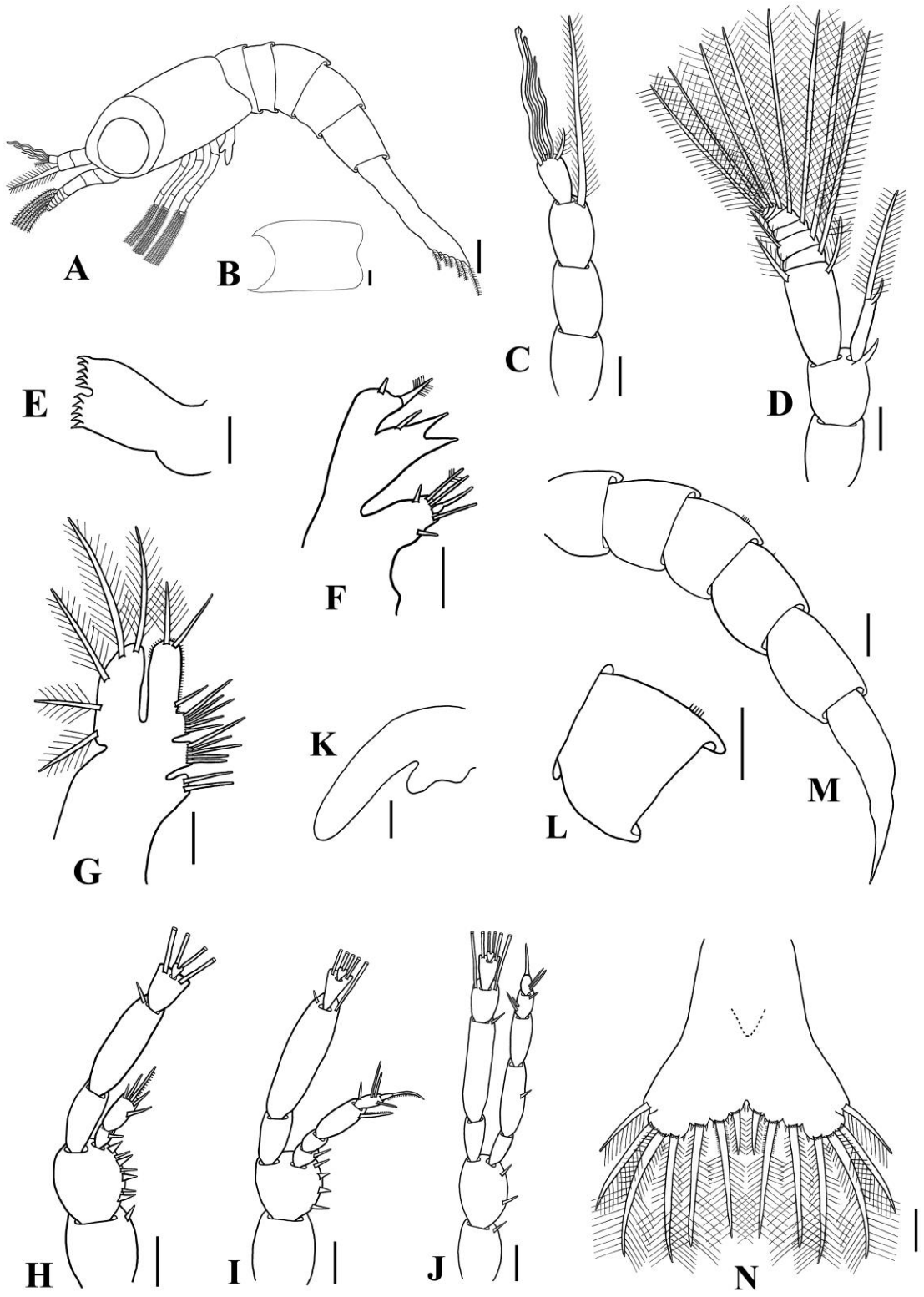


Figure 2

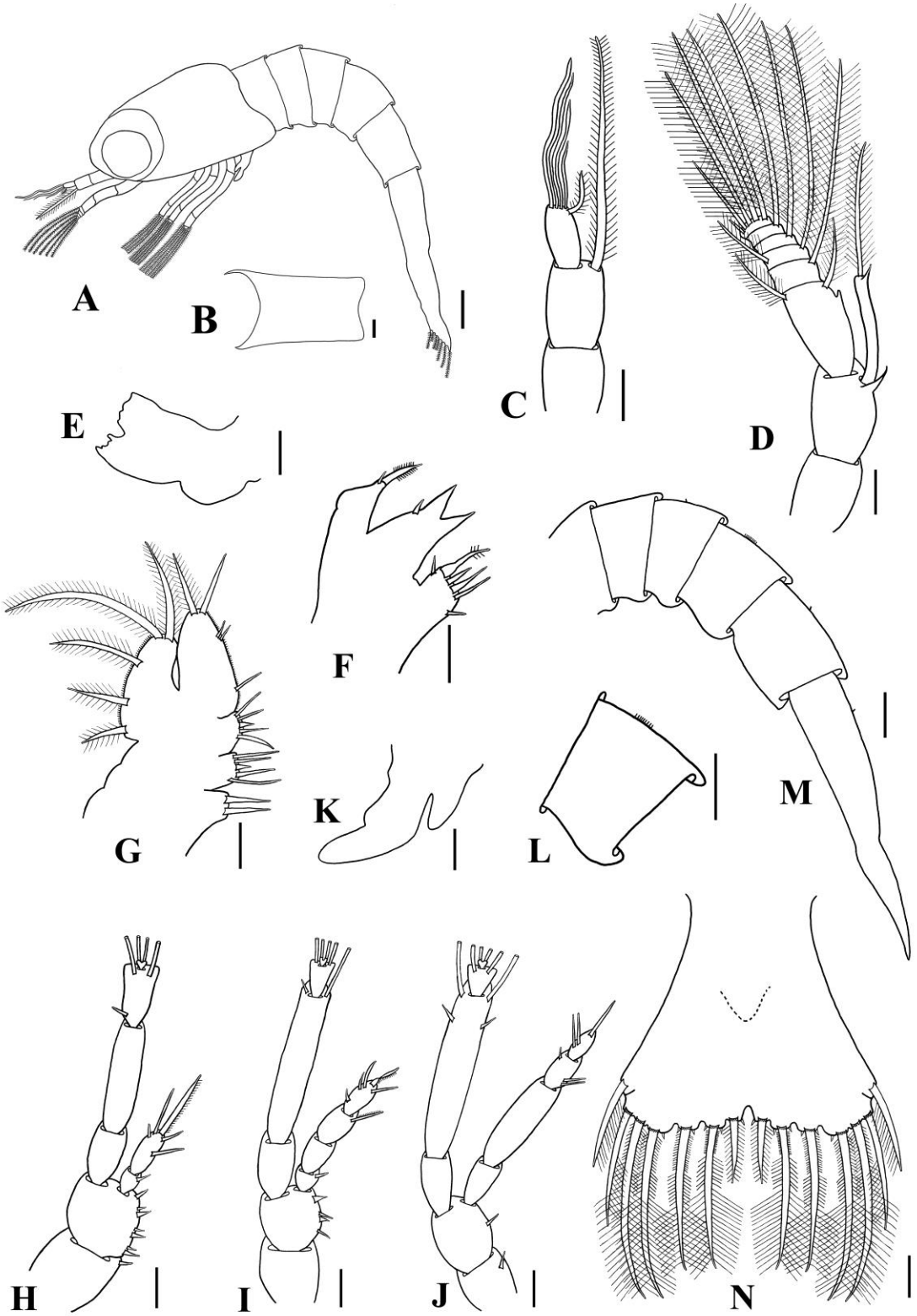
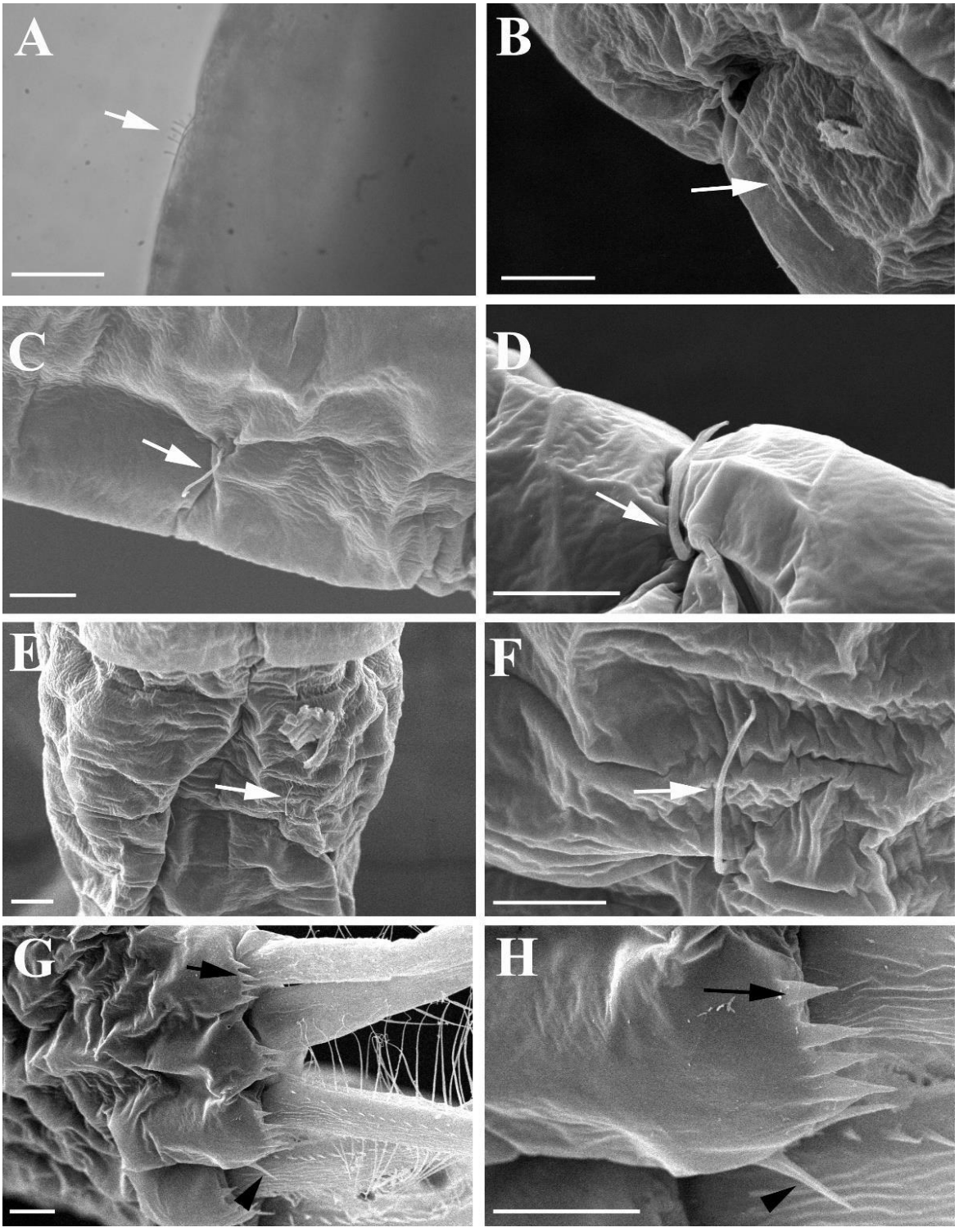


Figure 3



Capítulo III:

First zoeal stage of the snapping shrimps *Alpheus* Fabricius, 1798 (Caridea: Alpheidae): new description of *Alpheus bouvieri* A. Milne-Edwards, 1878 and review with remarks about morphological groups

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First zoeal stage of the snapping shrimps *Alpheus* Fabricius, 1798 (Caridea: Alpheidae): new description of *Alpheus bouvieri* A. Milne-Edwards, 1878 and review with remarks about morphological groups

Karmine Pasinatto[1], Alexandre O. Almeida[2] & Mariana Terossi[1]

[1]Laboratory of Carcinology, Graduate Program in Animal Biology (PPGBAN), Department of Zoology, Institute of Biosciences, Federal University of Rio Grande do Sul (UFRGS). Av. Bento Gonçalves, 9500, Agronomia, 91501-970, Porto Alegre, Rio Grande do Sul, Brazil. E-mail: kcpasinatto@gmail.com; mterossirm@gmail.com

[2]Laboratory of Crustacean Biology (LBC), Department of Zoology, Biosciences Center, Federal University of Pernambuco, Avenida Prof. Moraes Rêgo, 1235, Cidade Universitária. 50670-901 Recife, PE, Brazil. E-mail: aoalmeida.ufpe@gmail.com

Abstract

Based on adult morphological characters, the more than 300 species of *Alpheus* Fabricius, 1798 were divided into seven informal species groups, but some groups are not supported by molecular data. The aim of this study was to describe zoea I of *Alpheus bouvieri A.* Milne-Edwards, 1878, and to review the larval descriptions available in the literature, analyzing whether the morphological groups proposed for adults are supported by larval data. The larvae of *A. bouvieri* were obtained from three parental females sampled in Pernambuco, Brazil. *Alpheus bouvieri* zoea I shares a combination of characters to most larvae in the genus, but with some characteristics that could be used as diagnostics: 3 setae in the endopod of the maxillule, 4 setae in the endopod of the maxilla, 9 setae in the base of the first maxilliped, second maxilliped with 5-segmented endopod and third maxilliped with 6-segmented

endopod. In our review, 17 species were analyzed: nine belongs to *edwardsi* group; the other eight species belong to *brevirostris* (three), *macrocheles* (two), *sulcatus* (two) and *obesomanus* (one) group, the zoea I of species from *diadema* and *crinitus* groups are unknown. Many issues about zoea I of the *Alpheus* are pointed and the hypothesis that the morphological groups proposed for adults are supported by larval data has been rejected so far, since the literature data still leaves large lacunes.

Key words: zoea, larval morphology, alpheid, larval characters

Correspondence

Karmine Pasinatto. Laboratory of Carcinology, Graduate Program in Animal Biology (PPGBAN), Department of Zoology, Institute of Biosciences, Federal University of Rio Grande do Sul (UFRGS). Av. Bento Gonçalves, 9500, Agronomia, 91501-970, Porto Alegre, Rio Grande do Sul, Brazil. E-mail: kcpasinatto@gmail.com

Introduction

Alpheus Fabricius, 1798 is the most speciose genus in the infraorder Caridea Dana, 1852 (De Grave & Fransen, 2011; Almeida et al., 2014), with more than 310 valid species worldwide (De Grave & Fransen, 2011; Anker, 2012; Almeida et al., 2014; Dehghani et al., 2019; Soledade et al., 2019; De Grave et al., 2020; Scioli & Anker, 2020; WoRMS, 2020) and with an estimated diversity of more than 400 species (Anker, 2001a; Anker et al., 2006).

Based on adult morphological characters, *Alpheus* was divided into seven informal species groups (Coutière, 1899, 1905; Anker, 2001b): *brevirostris* (approximately 45 species), *crinitus* (approximately 30 species), *diadema* (approximately 24 species), *edwardsi* (approximately 95 species), *macrocheles* (approximately 30 species), *obesomanus*

(approximately 11 species) and *sulcatus* (approximately 40 species). These groups were established primarily based on features of the frontal region and the first chelipods, and are still useful for the taxonomy of this rich genus, allowing the first approximate assignment for the specimens, as well as containing important phylogenetic information (Chace, 1988), usually when new species are described they are allocated to one of these groups. Nevertheless, at least three of these morphological groups (*diadema*, *edwardsi* and *sulcatus*) have been shown not to be monophyletic, based on preliminary molecular analyzes (Williams et al., 2001).

In addition to the lack of robustness to support some morphological groups, there is molecular evidence regarding the existence of many species complex in this genus (Williams et al., 2001; Anker et al., 2006; Mathews & Anker, 2009). The literature cited shows that *Alpheus* species number has steadily increased due to new species descriptions, especially those included within a species complex (Anker, 2001b, 2012; Mathews & Anker, 2009; Almeida & Anker, 2011; Almeida et al., 2013, 2014).

Knowledge about the larval morphology of these species could help separating them within these complexes. 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 18 [14 species in the recent review by Pescinelli et al. (2017) (*Alpheus rapacida* de Man, 1908 excluded, because the zoea described by Prasad & Tampi, 1957 is actually zoea II according to Yang & Kim, 2002)], two more species in Wehrtmann & Albornoz, 2002 and other two in Pasinatto et al., in revision). One of the species without known larval morphology is *Alpheus bouvieri* A. Milne-Edwards, 1878, despite its wide distribution in Western Atlantic, from Bermuda, Caribbean Sea to Brazil, Central Atlantic (Ascension Island) and Eastern Atlantic, from Cape Verde to Congo (see Soledade & Almeida, 2013 for review).

Studies on larval descriptions may be extremely important to help elucidating some issues found in adult taxonomy (Pohle et al., 1999), as well as contributing to a better understanding of species life history and enabling subsequent larvae identification in plankton (Thatje & Bacardit, 2000).

This study aims to describe the snapping shrimp first larval stage morphology of *A. bouvieri*, as well as to review the literature in search of all available original descriptions, testing the hypothesis that the morphological groups proposed for adults are supported by larval data.

Material and Methods

Three ovigerous females of *A. bouvieri* were collected manually in March/2019 at Praia do Paraíso, Suape, Cabo de Santo Agostinho, Pernambuco, northeastern Brazil (8°21'54.89"S, 34°56'51.38"O). After collection, they were kept alive until larval hatching and then preserved in 80% ethanol, whereas larvae (zoea I) were fixed in 10% formaldehyde. Both females and larvae were included in the Department of Zoology Crustacean Collection, at Federal University of Rio Grande do Sul, Brazil (DZ/UFRGS, accession numbers: 6855, 6856, 6857).

The larvae of the three parental females were dissected in a Zeiss Stemi DV4 stereomicroscope and drawn/measured/analyzed under an Olympus CX31 microscope with the aid of *camera lucida*. The illustrations were edited using Adobe Photoshop software. Each structure was analyzed *a priori* in 10 larvae, this number increased when there were variations in the observed structures. 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) and updated by Clark & Cuesta (2015), while setae terminology according to Garm (2004) and Landeira et al. (2009).

Furthermore, an extensive literature review was carried out in search of all original descriptions available, so as to know *Alpheus* larval morphological features. The description and illustrations of the original descriptions were analyzed, and a general comparative table (Tab. S1) was built following a flowchart (Fig. 1). Subsequently, species were grouped according to the morphological groups proposed for adults.

Results

The three parental females from *A. bouvieri* measured 4.93 mm, 5.14 mm and 5.37 mm in carapace length.

Morphological description of *Alpheus bouvieri* A. Milne-Edwards, 1878

Zoea I

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

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

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

Antenna (Fig. 2D): peduncle 2-segmented with 1 medial distal spiniform projection near the endopod; endopod with 1 terminal plumose seta and 1 medial distal spiniform projection; exopod (scaphocerite) 8-segmented with 11 plumose setae (2, 1, 2, 1, 1, 1, 3), plus a medial tubercle in the proximal segment and 1 simple seta in the distal segment.

Mandible (Fig. 2E): palp absent.

Maxillule (Fig. 2F): 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 (Fig. 2G): 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 (Fig. 2H): 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 (Fig. 2I): 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 (Fig. 2J): 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 (Fig. 2K, 2L): first as a biramous bud; fifth pereiopod as a uniramous bud.

Pleon (Fig. 2A, 2M, 2N, 2O): with 6 segments (6th segment fused to telson), presence of simple dorsal setae on segments; lateral spines absent; pleopods absent; anal spine present.

Telson (Fig. 2O): triangular, with 7+7 (5 inners plumose, 2 outers plumose laterally) setae, 4 inner setae with shorter setules in the proximal region, inner pair shorter; 6 inner pairs with a row of denticles in the distal margin, 4 innermost pairs with marginal spines.

Morphological groups

Only five of the seven morphological groups proposed for adults have the morphology of the first larval stage known (Tab. 1), the zoea I of species from *diadema* and *crinitus* groups is unknown. For comparative purposes here only species with zoea I with characteristics of extended larval development was considered (more details in discussion section).

Discussion

Morphological description of *Alpheus bouvieri*

Alpheus bouvieri zoea I larvae description revealed in this study showed that the species shares a combination of characters specific to most larvae in the genus, with some peculiarities that can be used as diagnostic characters for the zoea I identification of this species.

Alpheus bouvieri zoea I followed the general character set proposed by Yang & Kim (2002) and reaffirmed by Pescinelli et al. (2017), excepting the antennule and antenna peduncles, which were segmented in this species, a feature also observed in other species (see Pasinatto et al., in revision, for more details). In *A. bouvieri*, the antennule peduncle is 3-segmented, as well as in *Alpheus formosus* Gibbes, 1850 (Pasinatto et al., in revision). This structure is 2-segmented in *Alpheus glaber* (Olivi, 1792) and *Alpheus macrocheles* (Hailstone, 1835) (Lebour, 1932), *Alpheus saxidomus* Holthuis, 1980 (Wehrtmann & Albornoz, 2002) and *Alpheus malleator* Dana, 1852 (Pasinatto et al., in revision). In *A. bouvieri*, the antenna peduncle is 2-segmented, as well as in *A. saxidomus* (Wehrtmann & Albornoz, 2002, Fig. 2b), *Alpheus estuariensis* Christoffersen, 1984 (Pires et al., 2008, Fig. 6), *Alpheus brasileiro* Anker, 2012 (Pescinelli et al., 2017, Fig. 1e), *A. malleator* and *A. formosus* (Pasinatto et al., in revision).

Some other characteristics shared by *A. bouvieri* and other species are: presence of four aesthetascs in the antennula exopod [also shared with *A. glaber* and *A. macrocheles* (Lebour,

1932, also with three aesthetascs for both species), *A. saxidomus* (Wehrtmann & Albornoz, 2002), *Alpheus albatrossae* (Banner, 1953) (Yang & Kim, 2006), *A. estuariensis* (Pires et al., 2008), *A. brasileiro* (Pescinelli et al., 2017), *A. formosus* and *A. malleator* (Pasinatto et al., in revision)]; 6 setae on the maxillule coxa [also shared with *A. brasileiro* (Pescinelli et al., 2017), *A. formosus* and *A. malleator* (Pasinatto et al., in revision)]; fifth pereiopod as a uniramous bud [also shared with *A. glaber* and *A. macrocheles* (Lebour, 1932), *Alpheus richardsoni* Yaldwyn, 1971 (Yang & Kim, 1996), *Alpheus brevicristatus* De Haan, 1844 (Yang & Kim, 1998), *Alpheus heeia* Banner & Banner, 1974 (Yang & Kim, 1999), *Alpheus japonicus* Miers, 1879 (Yang & Kim, 2002), *Alpheus digitalis* De Haan, 1844 (Yang & Kim, 2002), *A. saxidomus* (Wehrtmann & Albornoz, 2002), *Alpheus lobidens* De Haan, 1849 (Yang et al., 2003), *Alpheus sudara* Banner & Banner, 1966 (Yang et al., 2003), *A. albatrossae* (Yang & Kim, 2006) and *A. brasileiro* (Pescinelli et al., 2017)].

Alpheus bouvieri, *A. formosus* and *A. malleator* zoeas I larvae (Pasinatto et al., in revision) have some common characteristics: 10 setae at the maxila base, first maxilliped with 2-segmented endopod, first and second maxilliped exopod 4-segmented, first pereopod as a bud. *Alpheus bouvieri* shares the 4-segmented exopod of the third maxilliped and presence of a medial tubercle in the proximal segment in the exopod of the antenna with *A. malleator*; and the 8-segmented exopod of the antenna with *A. formosus*. Two new characteristics proposed by Pasinatto et al. (in revision) were also observed in *A. bouvieri* zoea I: the presence of anal spine and of dorsal simple setae on the pleon (observed in the 2nd to 6th segments), but as proposed by the authors, these characters should not be used as a diagnosis because we have no information about other species.

Furthermore, the presence of a medial tubercle in the exopod of the antenna is a character not previously reported for any known zoea I of the genus *Alpheus*, except for *Alpheus malleator* (Pasinatto et al., in revision). Although this character is not difficult to

visualize, its presence only in *Alpheus bouvieri* (present study) and *Alpheus malleator* (Pasinatto et al., in revision), may be related to the fact that previous authors simply did not see or search for this character.

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

The first larval stage of *A. bouvieri* presented characters such as the presence of 5 setae in the exopod of the maxilla and 7 pairs of setae on the telson, inferring an extended larval development (Guerao & Cuesta, 2014).

Some issues with zoea I description of the genus *Alpheus*

For comparative purposes, in this review 17 species (Tab. S1) with known zoea I were used (listed in chronological order of zoea description): *Alpheus glaber* and *A. macrocheles* (Lebour, 1932), *Alpheus strenuus* Dana, 1852 (Prasad & Tampi, 1957), *A. richardsoni*, *A. brevicristatus*, *A. heeia*, *A. digitalis*, *A. japonicus* and *A. albatrossae* (Yang & Kim, 1996, 1998, 1999, 2002, 2006, respectively), *A. saxidomus* (Wehrtmann & Albornoz, 2002), *A. lobidens* and *A. sudara* (Yang et al., 2003), *A. estuariensis* (Pires et al., 2008), *A. brasileiro* (Pescinelli et al., 2017), *A. formosus* and *A. malleator* (Pasinatto et al., in revision) and *A. bouvieri* (present study).

Alpheus heterochaelis Say, 1818 (Knowlton, 1973) and *Alpheus simus* Guérin-Méneville, 1855 (Wehrtmann & Albornoz, 2002) were excluded of this review, since they have some features, such as chelate pereopods and presence of pleopods that characterize zoea I from abbreviated larval development. According to Yang & Kim (2002), larval description of *A. rapacida* provided by Prasad & Tampi (1957) points to certain characters (broad

rostrum, stalked eyes, telson with 8+8 marginal setae, and maxilliped endopod dactyl with long spine) that are typical from *Alpheus* second larval stage. Thus, this species was not part of the present review.

Yang & Kim (2002) also had doubt about *A. strenuus* zoea I description by Prasad & 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 & Tampi (1957) *versus* one long denticulate setae in other *Alpheus* zoea I species known at the time). However, in this review it was observed that may there be variation in *Alpheus* zoeas I maxillule endopod (Tab. S1). This variation can be seen in *A. bouvieri* (present study), with 3 setae (1 terminal plumoserrulate, 1 medial distal simple, 1 terminal simple), *A. saxidomus* (Wehrtmann & Albornoz, 2002), with the presence of 2 long setae (no type definition) and *A. formosus* and *A. malleator*, with two setae (1 terminal plumoserrulate and 1 lateral simple; Pasinatto et al., in revision). Due to this variation *A. strenuus* was not excluded from the review.

The lack of knowledge about larval morphology in many decapod groups hinders taxonomic comparative studies (Vela & González-Gordillo, 2016). According to these authors, larval descriptions are often brief or very general and deficient in details, as well as with inadequate and incomplete illustrations that deviate from the standard proposed by Clark et al. (1998) and updated by Clark & Cuesta (2015).

For example, the descriptions of *A. glaber* and *A. macrocheles* (Lebour, 1932) and *A. strenuus* (Prasad & Tampi, 1957) show very confused, general and poorly detailed larval descriptions, as well as inaccurate illustrations. Thus, it is complicated to state the presence of segmentation and the type and position of setae in the structures analyzed. Therefore, it becomes difficult to morphologically compare species. Furthermore, 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 diagnose characters.

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

In addition, there are some disagreements about the number of segments in the exopod of the antenna. Some studies (Yang & Kim, 1996; Wehrtmann & Albornoz, 2002; Pires et al., 2008) exclude the proximal segment (usually larger) from the segment count. In more recent descriptions, such as *A. brasileiro* (Pescinelli et al., 2017), *A. formosus*, *A. malleator* (Pasinatto et al., in revision) and *A. bouvieri* (present study), the proximal segment was included in the count. In order to enable comparisons, the information on exopod segmentation used in the tables (Tab. S1, 1) was based on illustrations and not on the text descriptions.

Some problems were also found in relation to segmentation of endopods and exopods of the three maxillipeds. In some studies (Prasad & Tampi, 1957; Yang & 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 & 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. This lack of standardization hinders data comparisons, since each author

classifies it a different way. Moreover, in some studies (Lebour, 1932; Yang & Kim, 2002; Yang et al., 2003), these setae, as well as those from the telson, appear erased or blurred, which also affects characters 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 in the coxae and bases of the first and second maxillipeds (Yang & 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 analyzing the description of *A. saxidomus* zoea I provided by Wehrtmann & 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 result from failures in the larvae fixation process.

Finally, non-standardized terminology of some telson structures (at the plumose setae base) also become 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 & Kim (1996) indicate the presence of minute setules between setae 4-7. In other studies (Yang et al., 2003; Yang & Kim, 2006) the same authors show the presence of a minute row of spinules at the base of the 6 setae inner pairs. Pescinelli et al. (2017) 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 Scanning Electron Microscope and the nomenclature proposed by Garm (2004), Pasinatto et al. (in revision) 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.

Morphological groups

From the 17 analyzed species, nine belongs to *edwardsi* group; the other eight species belong to *brevirostris* (three), *macrocheles* (two), *sulcatus* (two) and *obesomanus* (one) group. These species share the following larval characters: rostrum absent, pterygostomian spine present, sessile eye, endopod of antennule as a plumose seta, antenna with a terminal spine near the endopod, endopod of antenna with 1 long plumose seta and 1 small inner spine, mandible without palp, maxilule without exopod, all pleonal segments without spines and pleon without division between 6° segment and telson (Tab. S1). This is an updated list (included and excluded some characters) proposed by Yang & Kim (2002) and reaffirmed by Pescinelli et al. (2017).

Some characters (tubercle in the exopod of the antenna, segmentation in the exopods of the maxillipeds, dorsal setae on the pleon, anal spine) were not included in the comparative table of groups because they were reported only recently (Pasinatto et al., in revision; present study), and we cannot affirm that do not exist in other species (Tab. S1).

In addition to the lack of standardization in the larval descriptions and the chaotic diagnosis found in the *Alpheus* zoea I morphology, the great variation found in the larval characters of the analyzed structures, may also be related to the fact that, to date, there are few species with described larval stages in each morphological group. In view of the confusion and imprecision in the description of some larval characters, it is difficult to compare them between the morphological groups of adults.

Nevetheless, despite of the low number of species with zoea I known and the inequality of these species in the groups, we can do some remarks about the morphological groups proposed for adults. Each group had until now some exclusive characters (but not present in all species):

- *brevirostris* group: antennule (1 plumose seta plus 1 simple seta in the exopod), first maxilliped (4 spine/spiniform setae plus 1 hair-like seta in the coxa and basis) and second maxilliped (3 spine/spiniform setae plus 1 seta in the basis);
- *edwardsi* group: antennule (2 aesthetascs in the exopod), antenna (exopod 5-segmented, without simple seta in the exopod), maxillule (2 setae in the coxa, 1 plumoserrulate seta plus 2 simple setae in the endopod), maxilla (1 seta in the coxa, basis not bilobed, 1 plus 2 setae or 2 setae plus 4 plumose seta or 2 plus 5 setae or 3 plus 5 plumose setae or 2 plumose setae in the basis, 3 plumose setae or 3 simple setae plus 1 plumose seta in the endopod, without microtrichia in the endopod), first maxilliped (4 spine/spiniform setae plus 2 hair-like setae in the coxa, 4 simple setae or 4 spine/spiniform setae or 4 spine/spiniform setae plus 4 setae or 4 spine/spiniform setae plus 2 hair-like setae or 9 simple setae in the basis, 1 spine/spiniform seta or 2 setae or 3 simple setae plus 1 sparsely plumose seta or 3 simple setae plus 1 serrulate seta in the endopod), second maxilliped (2 simple setae or 3 spine/spiniform setae plus 2 simple setae in the coxa, 3 spine/spiniform setae plus 2 simple setea in the basis, endopod unsegmented or with 5 segments, 4 setae or 7 setae in the endopod), third maxilliped (endopod unsegmented or with 3 or 6 segments, 2 setae or 3 setae in the endopod), pereiopods (without first pereiopod, fourth and fifth pereiopods biramous) and telson (6 plumose setae plus 1 laterally plumose setae in the posterior margin);
- *macrocheles* group: maxilla (3 setae in the coxa) and first maxilliped (6 simple setae in the endopod);
- *obesomanus* group: antenna (13 plumose setae in the exopod), maxilla (4 setae in the coxa, 4 plus 4 setae in the basis) and first maxilliped (5 simple setae in the endopod);
- *sulcatus* group: maxilla (4 simple setae plus 1 plumose seta in the endopod) and third maxilliped (5 segments and 7 simple setae in the endopod, and 6 natatoty plumose setae plus 2 simple setae in the exopod).

At the moment, it is not possible to propose exclusive and shared by all species characters that could be used to separate the groups. Therefore, the hypothesis that the morphological groups proposed for adults are supported by larval data has been rejected so far, since the literature data still leaves large lacunes. The *edwardsi* group, for example, showed the high variation, but also it was the group with more species included in the review, and it is a group already known as non-monophyletic (Anker, 2001b). But, other groups with zoea I less known maybe could be separated by larval characters, as *macrocheles* and *obesomanus* for example. It is important that all new descriptions of zoea I of *Alpheus* compare his data with these characters listed above, in order to confirm or refute them. But the data generated in this study can help in discussions about the separation of species into morphological groups in studies on the phylogenetic relationships between species of the *Alpheus* genus realized in the future.

Additionally, the other lacune in the knowledge of *Alpheus* larval morphology is about development. Although the 17 *Alpheus* species analyzed have descriptions of zoea I, only *A. glaber* and *A. macrocheles* showed the complete known development, with 9 stages described (Tab. S1). Showing that knowledge about the larval development of *Alpheus* is really scarce.

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Figure Captions

Figure 1. Flowchart used to build the general comparative table.

Figure 2. *Alpheus bouvieri* A. Milne-Edwards, 1878. Zoea I. A. Lateral view; B. Carapace; C. Antennule; D. Antenna; E. Mandible; F. Maxillule; G. Maxilla; H. First maxilliped; I. Second maxilliped; J. Third maxilliped; K. First pereiopod; L. Fifth pereipod; M. Fourth segment of pleon; N. Pleon; O. Telson. Scale bars: A, M, N. 0.15 mm; B–D, H–J, O. 0.07 mm; E–G, K, L. 0.04 mm.

Figure 1

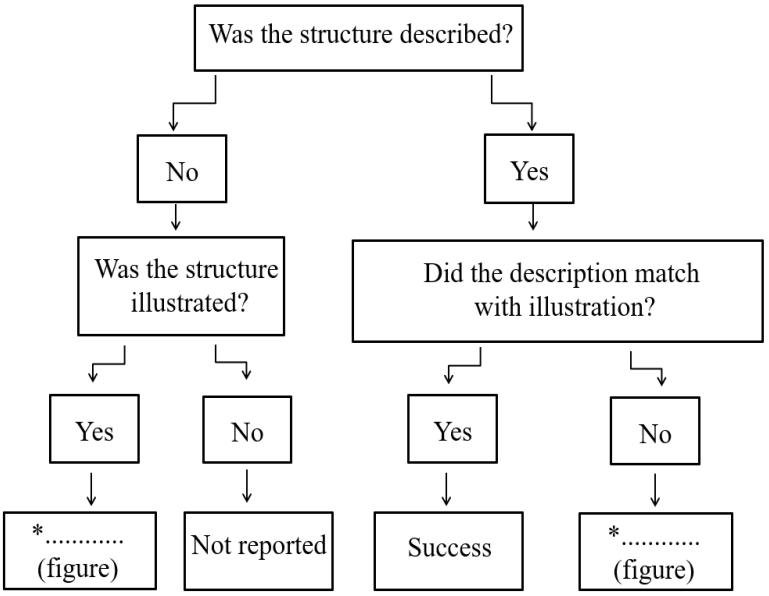
Was the structure described?
No
Yes
Was the structure illustrated?
Did the description match with illustration?
Yes
No
Yes
No
*..... (figure)
Not reported
Success
*..... (figure)

Figure 2

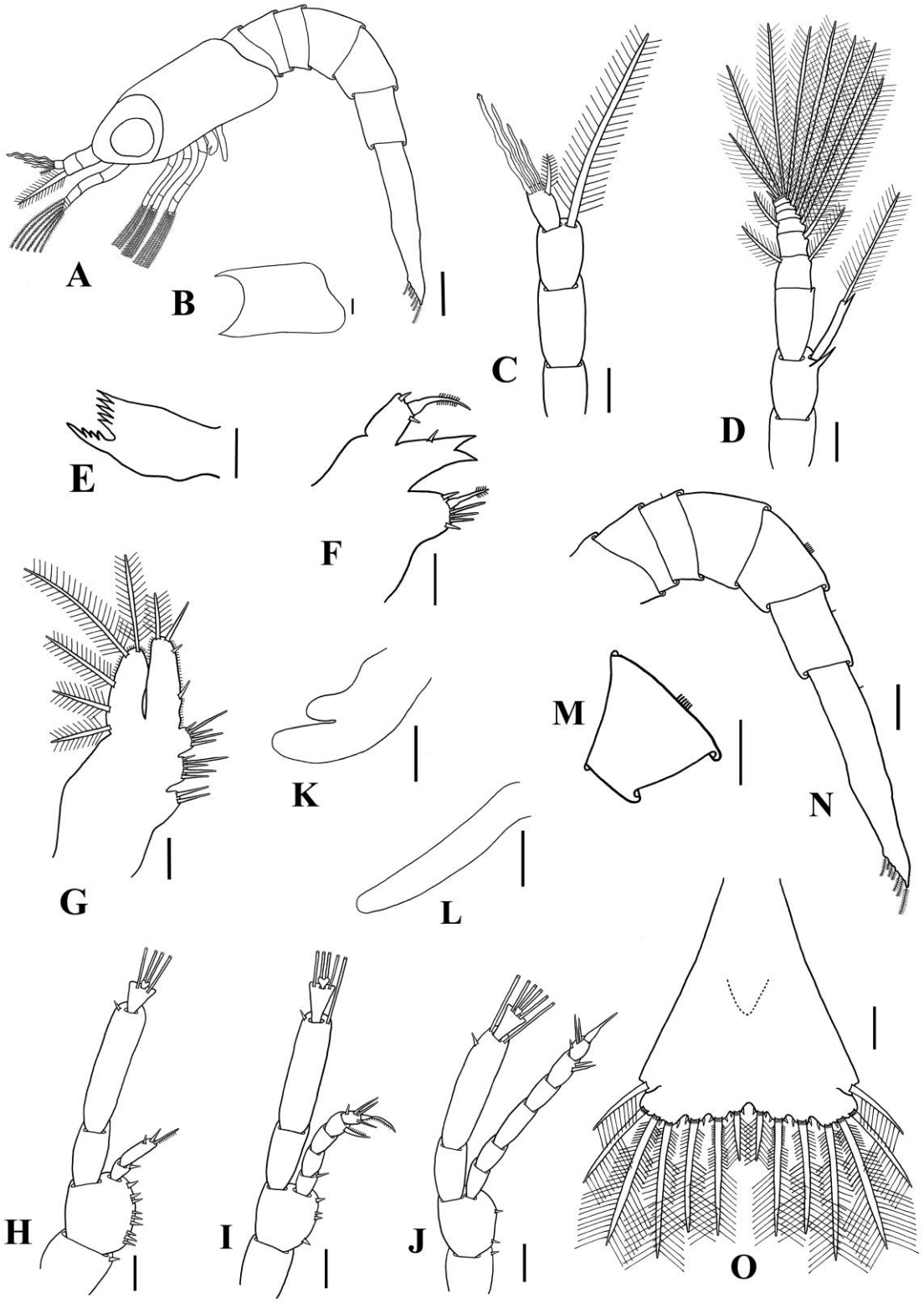

Table 1: Zoea I of species of *Alpheus* Fabricius, 1798 divided by morphological groups according to Anker (2001). Setae - ds: denticulate seta; hs: hair-like seta; lps: laterally plumose seta; nps: natatory plumose seta; pds: plumodenticulate seta; ps: plumose seta; pss: plumoserrulate seta; s: seta; sp: spine/spiniform seta; sps: sparsely plumose seta; srs: serrulate seta; ss: simple seta.

Morphological group		*brevirostris*	*edwardsi*	*macrocheles*	*obesomanus*	*sulcatus*
Species		***A. brevicristatus, A. digitalis, A. glaber***	***A. bouvieri, A. brasileiro, A. estuariensis, A. heeia, A. japonicus, A. lobidens, A. richardsoni, A. strenuus, A. sudara***	***A. albatrossae, A. macrocheles***	***A. saxidomus***	***A. formosus, A. malleator***
References		Lebour, 1932; Yang & Kim, 1998, 2002	Prasad & Tampi, 1957; Yang & Kim, 1996, 1999, 2002; Yang *et al*., 2003; Pires *et al*., 2008; Pescinelli *et al*., 2017; present study	Lebour, 1932; Yang & Kim, 2006	Wehrtmann & Albornoz, 2002	Pasinatto *et al*., in revision
Antennule	**Peduncle (segments)**	unsegmented, 2	unsegmented, 3	unsegmented, 2	2	2, 3
	Exopod (aesthetascs)	3, 4	2, 3, 4	3, 4	4	4
	Exopod (setae)	1 ps + 1 ss, 1 or 2 sp	1 ps, 1 ss, absent	1 ps, 1 or 2 sp	absent	1 ps
Antena	**Peduncle (segments)**	unsegmented	unsegmented, 2	unsegmented	2	2
	Exopod (segments)	6	5, 6, 8	6	6	6, 8
	Exopod (plumose setae)	8, 10, 11	11	8, 10, 11	13	11
	Exopod (simple setae)	1, 2	absent, 1, 2	1, 2	1	1
Maxilule	**Coxa (setae)**	4, 5	2, 3, 4, 5, 6	3	4	6
	Basis (spines)	absent, 2	absent, 2	absent, 2	2	2
	Basis (setae)	absent, 1 ss	absent, 1 ss, 2 ps	1 ps	1 s	1 ss
	Endopod (setae)	1 ds	1 s, 2 s, 1 ds, 1 pss + 2 ss	1 s	2 s	1 pss + 1 ss
Maxila	**Coxa (setae)**	2 s, 1 ps + 1 ss	1 s, 1 ss, 2 s, 2 ss, 2 ps, 1 ss + 1 sps	2 s, 3 s	4 s	2 ss
	Basis (lobes)	bilobed	bilobed, not bilobed	bilobed	bilobed	bilobed

	Basis (setae: proximal lobe + distal lobe)	3 s + 4 s, 3 s + 3 s	1s + 2 s, 2 s + 4 ps, 2 s + 5 s, 3 ss + 3 ss, 3 s + 4 s, 3 ss + 4 ss, 3 ps + 5 ps, 5 ss + 5 ss, 2 ps	3 s + 4 s	4 s + 4 s	5 ss + 5 ss
	Endopod (setae)	2 s, 2 ss + 1 ps	2 s, 3 s, 3 ps, 2 ss + 1 ps, 3 ss + 1 ps	2 s, 1 s + 1ss + 1 ps	2 pds + 1 s	2 ss + 1 ps, 4 ss + 1 ps
	Endopod (microtrichia)	present	absent, present	absent	present	present
	Exopod (scaphognathite)	5 s, 5 ps	5 ps	5 s, 5 ps	4 ps	5 ps
	Exopod (microtrichia)	absent	absent, present	absent	absent	absent, present
	Coxa (setae)	4 sp + 1 hs, 1 ss	absent, 1 s, 1 ss, 4 sp + 2hs	absent	absent	1 ss
	Basis (setae)	2ss, 4 sp + 1 hs, 4 sp + 3 ss	absent, 4 ss, 4 sp, 4 sp + 4 s, 4 sp + 2 hs, 4 sp + 3 ss, 9 ss	2 s, 4 sp + 2s	5 sp	7 ss
First maxilliped	**Endopod (segments)**	unsegmented	unsegmented, 2	unsegmented	unsegmented	2
	Endopod (total setae)	3s, 1 ss + 3 s	1 sp, 2 s, 1 ss + 3 s, 4 ss, 3 ss + 1 sps, 3 ss + 1 srs	3 ss, 6 ss	5 ss	5 ss + 1 srs
	Exopod (setae)	4 s, 4 nps	4 nps, 4 nps + 1 ss	4 s, 4 nps	4 nps + 1 s	4 nps + 1 ss
	Coxa (setae)	absent, 3 sp	absent, 2 ss, 3 sp, 3 sp + 2 ss	absent	absent	absent
	Basis (setae)	2 s, 3sp, 3 sp + 1 s	2 ss, 3 ss, 3 sp, 4 ss, 2 sp + 2 s, 3 sp + 2 ss	2 s, 2 sp + 1 s	3 sp	4 ss
Second maxilliped	**Endopod (segments)**	4	unsegmented, 3, 4, 5	4	3	4
	Endopod (total setae)	3 s, 5 s, 6 s	3 s, 4 s, 5 s, 6 s, 7 s, 5 ss + 1 sps, 5 ss + 2 srs	3 s, 5 s	6 s	5 ss + 2 srs
	Exopod (setae)	5 nps, 5 nps + 1 ss, 4 s + 2 s	4 nps + 1 s, 5 s, 5 nps, 5 nps + 1 ss, 6 nps	4 nps + 1 s, 4s + 2 s	4 s + 2 ps	5 nps + 1 ss

Third maxilliped	**Coxa (setae)**	absent, 1ss	absent, 1ss	absent	absent	1 ss
	Basis (setae)	1ss, 2s	absent, 1ss, 2ss	1ss, 2s	absent	1ss, 2ss
	Endopod (segments)	4	unsegmented, 2, 3, 4, 6	2	4	4, 5
	Endopod (total setae)	1 sp, 5 s, 6 s	2 s, 3 s, 4 s, 5 s, 5 ss, 6 s, 6 ss	1 sp, 4 s	4 ss	6 ss, 7 ss
	Exopod (setae)	6 nps, 6 nps + 1 ss, 4 s + 2 s	6 s, 6 nps, 6 nps + 1 ss, 4 nps + 2 s	4 nps + 2 s, 4 s + 2 s	4 s + 2 ps	6 nps + 1 ss, 6 nps + 2 ss
Pereiopods	**1º pereiopod**	biramous	biramous, absent	biramous	biramous	biramous
	2º pereiopod	biramous, uniramous	absent, uniramous, biramous	uniramous	uniramous	absent
	3º pereiopod	absent	absent, biramous	biramous, uniramous	uniramous	absent
	4º pereiopod	absent	absent, uniramous, biramous	absent	uniramous	absent
	5º pereiopod	uniramous	absent, uniramous, biramous	uniramous	uniramous	absent
Telson	**Posterior margin (setae)**	5 ps + 2 lps	5 ps + 2 lps, 6 ps + 1 lps	5 ps + 2 lps	5 ps + 2 lps	5 ps + 2 lps

SUPPLEMENTARY MATERIAL

Table S1 (continue): Zoea I of species of *Alpheus* Fabricius, 1798. *according to figure in the original description, more details in Figure 1, p: plumose seta, lp: laterally plumose seta.

Morphological group		***brevirostris***	***brevirostris***	***brevirostris***	***edwardsi***	***edwardsi***	***edwardsi***
Species		***A. brevicristatus***	***A. digitalis***	***A. glaber***	***A. bouvieri***	***A. brasileiro***	***A. estuariensis***
Reference		Yang & Kim 1998	Yang & Kim 2002	Lebour 1932	present study	Pescinelli *et al*. 2017	Pires *et al*. 2008
Carapace	**rostrum**	absent	absent	not reported	absent	absent	absent
	pterygostomian spine	present	present	not reported	present	present	present
	eyes	sessile	sessile	*sessile (figure)	sessile	sessile	sessile
Antennule	**peduncle (segments)**	unsegmented	unsegmented	2-segmented	3-segmented	unsegmented	unsegmented
	endopod (setae)	1 long plumose seta	1 long plumose seta	1 strong seta	1 plumose seta	1 long plumose seta	1 long plumose seta
	exopod (aesthetascs)	3	3	3 or 4	4 (1 spatulate and more robust)	4	4
	exopod (setae)	1 short plumose seta + 1 long simple seta	1 short plumose seta + 1 long simple seta	1 or 2 spine (figure looks like seta)	1 terminal plumose seta	1 terminal plumose seta	1 terminal plumose seta
	peduncle (segments)	*unsegmented (figure)	*unsegmented (figure)	not reported	2-segmented	unsegmented (text) *2-segmented (figure)	unsegmented (text) *2-segmented (figure)
Antenna	**peduncle (spine near the endopod)**	1 basal spine	1 basal spine	not reported	1 medial distal spiniform projection	1 terminal spine	*absent (figure)
	unsegmented endopod (seta)	1 long plumose seta	1 long plumose seta	not reported	1 terminal plumose seta	1 long plumose seta	1 long plumose seta
	endopod (spine)	1 small spine	1 small spine	not reported	1 medial distal spiniform projection	1 small inner spine	1 small spine

	exopod (segments)	5-segmented (text) *6-segmented (figure)	5-segmented (text) *6-segmented (figure)	not reported	8-segmented	5-segmented	4-segmented (text) *5-segmented (figure)
	exopod (plumose setae)	11	11	8 to 10 setae	11	11	11
	exopod (tubercle in the proximal segment)	not reported	not reported	not reported	present	not reported	not reported
	exopod (simple setae)	1 laterodistal spine	1 distolateral spine	2 outer spine (figure looks like seta)	1 simple seta in the distal segment	2 short simple setae (inner and outer side)	*absent (figure)
Mandible	**palp**	not reported	absent (without figure)	absent	absent	not reported	not reported
	coxa (setae)	4 (3 terminal plumose + 1 subterminal simple) setae	5 plumose setae	not reported (without figure)	6 (5 terminal simple + 1 terminal serrulate plumose) setae	6 [4 (1 proximal + 2 subterminal + 1 terminal) simple + 2 sparsely plumose) setae	3 distal setae
	basis (spines)	2 stout spines	2 stout spines	absent (without figure)	2 spiniform projections	2 stout spines (distal one with two rows of spinules)	2 stout spines
Maxillule	**basis (setae)**	*absent (figure)	1 short simple seta	not reported (without figure)	1 lateral simple seta	1 simple seta	*absent (figure)
	endopod (setae)	1 large denticulate seta	1 large denticulate seta	not reported (without figure)	3 [1 terminal plumoserrulate + 2 simple (1 medial distal and 1 terminal)] setae	1 terminal denticulate seta	1 small terminal seta
	exopod	*absent (figure)	*absent (figure)	not reported (without figure)	absent	absent	*absent (figure)
Maxilla	**coxa (setae)**	1 plumose seta + 1	1 plumose seta + 1	*2 setae (figure)	2 medial simple	2 (1 simple + 1	2 plumose setae

		simple seta	simple seta		setae	sparsely plumose) setae	
	basis (lobes)	bilobed	bilobed	*bilobed (figure)	bilobed	bilobed	not bilobed
	basis (setae)	7 (3 in proximal lobe, 4 in distal lobe) setae	6 (each lobe with 3) setae	not reported	10 (each lobe with 5) simple setae	6 (each lobe with 3) simple setae	2 plumose setae
	endopod (setae)	3 (1 basal simple + 1 terminal simple + 1 terminal plumose) setae	3 (1 simple seta at base + 1 terminal simple + 1 terminal plumose) setae	*2 setae (figure)	4 [2 medial simple + 2 terminal long (1 simple and 1 plumose)] setae	3 [2 (1 proximal + 1 terminal) simple + 1 terminal plumose) setae	*3 plumose setae (figure)
	endopod (microtrichia)	present (fine hairs)	present (fine hairs)	not reported	present	present	absent
	exopod (setae)	5 highly plumose setae	5 highly plumose setae	*5 setae (figure)	5 plumose setae (with microtrichia)	5 marginal plumose setae	5 plumose setae
	coxa (setae)	4 spines + 1 hair (protopod)	1 simple seta	not reported	1 medial distal simple seta	1 simple seta	absent
	basis (setae)		4 spiniform + 3 simple setae	*2 setae (figure)	9 simple setae arranged 3+3+2+1	4 simple setae arranged 1+1+1+1	
First maxilliped	**endopod (segments)**	segmented (text) *unsegmented (figure)	*unsegmented (figure)	not reported	2-segmented	unsegmented	unsegmented
	endopod (setae)	4 (3 terminal + 1 basal) simple setae	4 (1 simple seta basally + 3 setae terminally) setae	*3 setae (figure)	4 {1 medial distal simple, 3 [2 simple (1 lateral + 1 terminal) + 1 terminal serrulate]} setae	4 [3 (1 proximal + 1 subterminal + 1 terminal) simple + 1 terminal sparsely plumose] setae	1 long terminal spine
	exopod (segments)	not reported	not reported	not reported	4-segmented	unsegmented	*unsegmented (figure)

	exopod (setae)	4 natatory plumose setae	4 natatory plumose setae	*4 setae (figure)	5 (0, 0, 2, 2 terminal natatory plumose + 1 lateral distal simple on second segment) setae	4 long plumose natatory setae terminally	4 natatory setae
	coxa (setae)		absent	not reported	without setae	absent	
	basis (setae)	3 spines (protopod)	3 spiniform setae + 1 simple seta	*2 setae (figure)	4 medial simple setae arranged 1+2+1	3 simple setae arranged 1+1+1	2 simple setae (protopod)
	endopod (segments)	4-segmented	4-segmented	not reported	5-segmented	4-segmented	4-segmented
Second maxilliped	**endopod (setae)**	5 setae (1, 0, 1, 3)	6 setae (1, 0, 1, 4)	*3 setae (figure)	7 [1 medial distal simple, 0, 0, 1 medial distal serrulate, 5 (1 medial simple, 3 lateral simple and 1 terminal serrulate)] setae	6 [1 subterminal simple, 0, 1 terminal sparsely plumose, 4 (1 proximal and 3 subterminal simple)] setae	4 setae (1, 0, 1, 2)
	exopod (segments)	not reported	not reported	not reported	4-segmented	unsegmented	*unsegmented (figure)
	exopod (setae)	5 natatory plumose setae	6 (5 natatory plumose + 1 simple laterally) setae	6 setae *4 + 2 setae (figure)	6 (0, 1, 2, 2 terminal natatory plumose + 1 lateral distal simple on second segment) setae	6 [1 subterminal simple + 5 (1 subterminal and 4 terminal) long plumose natatory) setae	6 (2+2+2 natatory) setae
	coxa (setae)		absent	not reported	1 medial distal simple seta	absent	
Third maxilliped	**basis (setae)**	1 simple seta (protopod)	1 simple seta	*2 setae (figure)	2 medial simple setae arranged 1+1	1 simple seta	absent

	endopod (segments)	4-segmented	4-segmented	not reported	6-segmented	4-segmented	4-segmented
	endopod (setae)	5 (0, 0, 2, 3) setae	6 (0, 0, 2, 4) setae	1 long spine	6 [0, 0, 0, 0, 2 medial distal, 4 (1 lateral proximal, 2 lateral distal, 1 terminal)] simple setae	5[0, 0, 2 terminal, 3 (1 proximal + 2 on median margin)] simple setae	3 setae (0, 0, 0, 3)
	exopod (segments)	not reported	not reported	not reported	4-segmented	unsegmented	*unsegmented (figure)
	exopod (setae)	6 natatory plumose setae	7 (6 natatory plumose + 1 short simple laterally) setae	6 setae *4 + 2 setae (figure)	7 (0, 2, 2, 2 terminal natatory plumose + 1 lateral distal simple on second segment) setae	7 [1 subterminal simple + 6 (2 subterminal and 4 terminal) long plumose natatory] setae	6 (2+2+2) natatory setae
Pereiopods	**1º pereiopod**	biramous	biramous	biramous	biramous	biramous	biramous
	2º pereiopod	biramous	uniramous	uniramous	absent	uniramous	biramous
	3º pereiopod	absent	absent	absent	absent	absent	biramous
	4º pereiopod	absent	absent	absent	absent	absent	biramous
	5º pereiopod	uniramous	uniramous	uniramous	uniramous	uniramous	biramous
Pleon	**pleonites (somites)**	6 somites (last somite fused with telson)	6 somites (last somite fused with telson)	*6 somites (last somite fused with telson)	6 segments (6th segment fused to telson)	5 pleonites (text) *6-segmented (6º segment fused with telson) (figure)	6-segmented (6º segment fused with telson)
	simple dorsal setae	not reported	not reported	not reported	present	not reported (without setae and rounded)	not reported
	lateral spines	absent	absent	*absent (figure)	absent	*absent (figure)	*absent (figure)
	anal spine	not reported	not reported	not reported	present	not reported	not reported
Telson	**setae (type)**	5p + 2lp	*5p + 2lp (figure)	not reported	5p + 2lp	5p + 2lp	6p + 1lp
Number of known stages		4	2	9	1	3	4

Table S1 (continuation)

Morphological group		*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*	*edwardsi*
Species		***A. heeia***	***A. japonicus***	***A. lobidens***	***A. richardsoni***	***A. strenuus***	***A. sudara***
Reference		Yang & Kim 1999	Yang & Kim 2002	Yang *et al*. 2003	Yang & Kim 1996	Prasad & Tampi 1957	Yang *et al*. 2003
Carapace	**rostrum**	absent	absent	absent	absent	rostral spine is small (text) *absent (figure)	absent
	pterygostomian spine	present	present	present	*present (figure)	not reported	present
	eyes	sessile	sessile	sessile	sessile	*sessile (figure)	sessile
Antennule	**peduncle (segments)**	unsegmented	unsegmented	unsegmented	unsegmented	*unsegmented (figure)	unsegmented
	endopod (setae)	1 long plumose seta	1 long plumose seta	1 long plumose seta	1 long plumose seta	1 seta	1 long plumose seta
	exopod (aesthetascs)	3	3	3	3	2	3
	exopod (setae)	1 short plumose seta + 1 long simple seta	1 short plumose seta + 1 long simple seta	1 short plumose seta + 1 long simple seta	1 short plumose seta + 1 long simple seta	*absent (figure)	1 short plumose seta + 1 simple seta
	peduncle (segments)	*unsegmented (figure)	*unsegmented (figure)	*unsegmented (figure)	*unsegmented (figure)	*unsegmented (figure)	*unsegmented (figure)
Antenna	**peduncle (spine near the endopod)**	1 basal spine	1 basal spine	1 spine	1 basal spine	absent	1 spine
	unsegmented endopod (seta)	1 long plumose seta	1 long plumose seta	1 long plumose seta	1 long plumose seta	1 plumose seta	1 long plumose seta
	endopod (spine)	1 small spine	1 small spine	1 small spine	1 small spine	*absent (figure)	1 small spine
	exopod (segments)	5-segmented (text) *6-segmented (figure)	4-segmented (text) *5-segmented (figure)	6-segmented	4-segmented (text) *5-segmented (figure)	not reported	6-segmented
	exopod (plumose setae)	11	11	11	11	11	11

	exopod (tubercle in the proximal segment)	not reported	not reported	not reported	not reported	not reported	not reported
	exopod (simple setae)	1 laterodistal spine	1 distolateral spine	1 distolateral spine	1 external seta on terminal margin	*absent (figure)	1 distolateral spine
Mandible	**palp**	absent (without figure)	not reported	absent (without figure)	not reported	not reported	absent (without figure)
	coxa (setae)	4 (3 terminal plumose + 1 subterminal simple) setae	3 terminal setae	4 setae	4 (3 terminal + 1 subterminal) setae	2 setae	4 setae
	basis (spines)	2 stout spines	2 stout spines	2 stout spines	2 stout spines	*absent (figure)	2 stout spines
Maxillule	**basis (setae)**	1 short simple seta subterminally	2 plumose setae	2 subterminal plumose setae	1 short simple seta subterminally	1 seta	1 simple seta
	endopod (setae)	1 large denticulate seta	1 large denticulate seta	1 terminal denticulate seta	1 distal denticulate seta	2 setae	1 terminal denticulate seta
	exopod	*absent (figure)	*absent (figure)	*absent (figure)	*absent (figure)	*absent (figure)	*absent (figure)
	coxa (setae)	2 plumose setae	2 plumose setae	2 setae	2 simple setae	1 setae	2 setae
	basis (lobes)	bilobed	bilobed	bilobed	bilobed	bilobed	bilobed
	basis (setae)	7 (2 in proximal lobe, 5 in distal lobe) setae	6 (2 in proximal lobe, 4 in distal lobe) plumose setae	8 (3 in proximal lobe, 5 in distal lobe) plumose setae	7 (3 in proximal lobe, 4 in distal lobe) simple setae	3 (1 in proximal lobe, 2 in distal lobe) setae	7 (3 in proximal lobe, 4 in distal lobe) setae
Maxilla	**endopod (setae)**	3 (1 simple at base + 1 terminal simple + 1 terminal plumose) setae	3 (1 simple at base + 2 terminal) setae	3 (1 simple basal + 2 terminal) setae	3 (1 simple at base + 1 terminal simple + 1 terminal plumose) setae	2 setae	3 (1 basal + 2 terminal) setae
	endopod (microtrichia)	present (fine hairs)	present (fine hairs)	present (fine hairs)	present	not reported	present (fine hairs)
	exopod (setae)	5 highly plumose setae	5 highly plumose setae	5 marginal plumose setae	5 long plumose setae	5 marginal setae	5 marginal plumose setae
	coxa (setae)	4 spines (protopod)	1 simple seta	1 seta	4 spines +2 hair-	not reported	1 seta

First maxilliped	**basis (setae)**		7 (4 spiniform + 3 simple) setae	7 (4 spiniform + 3) setae segmented (text) *unsegmented (figure)	like setae (protopod)		6 (4 spiniform + 2) setae segmented (text) *unsegmented (figure)
	endopod (segments)	unsegmented	*unsegmented (figure)		unsegmented	*unsegmented (figure)	
	endopod (setae)	4 (3 simple terminally + 1 simple basally) setae	4 (1 simple at base + 3 terminal) setae	4 (1 simple basal + 3 terminal) setae	4 (3 terminal + 1 simple at base) setae	2 short terminal setae	4 (1 basal + 3 terminal) setae
	exopod (segments)	not reported	not reported	not reported	not reported	unsegmented	not reported
	exopod (setae)	5 (4 natatory plumose + 1 short simple laterally) setae	4 natatory plumose setae	4 terminal natatory setae	4 plumose natatory setae	4 long setae	4 terminal natatory setae
	coxa (setae)			absent			absent
	basis (setae)	3 spines (protopod)	5 (3 spiniform + 2 simple) setae (protopod)	4 (2 spiniform + 2) setae	3 small spines (protopod)	not reported	4 (2 spiniform + 2) setae
	endopod (segments)	4-segmented	3-segmented	4-segmented	4-segmented	2-segmented (text) *unsegmented (figure)	4-segmented
Second maxilliped	**endopod (setae)**	5 (1, 0, 1, 3) setae	7 (1, 1, 5) setae	5 (1, 0, 1, 3) setae	4 (1, 0, 1, 2) setae	3 setae	6 (1, 0, 1, 4) setae
	exopod (segments)	not reported	not reported	not reported	not reported	same kind of segmentation (text) *unsegmented (figure)	not reported
	exopod (setae)	5 natatory plumose setae	5 natatory plumose setae	5 (1 subterminal + 4 terminal natatory) setae	6 (5 plumose natatory + 1 short seta laterally) setae	5 setae	5 (1 subterminal + 4 terminal natatory) setae
Third maxilliped	**coxa (setae)**	1 simple seta (protopod)	absent	absent	1 simple seta (protopod)	not reported	absent
	basis (setae)		1 simple seta	1 simple seta			1 simple seta
	endopod	4-segmented	2-segmented	4-segmented	4-segmented	unsegmented	3-segmented

	(segments)						
	endopod (setae)	5 (0, 0, 2, 3) setae	6 (2, 4) setae	4 (0, 0, 2, 2) setae	5 (0, 0, 2, 3) setae	2 short setae	5 (0, 2, 3) setae
	exopod (segments)	not reported	not reported	not reported	not reported	unsegmented	not reported
	exopod (setae)	6 natatory plumose setae	6 natatory plumose setae	6 (2 subterminal + 4 terminal natatory) setae	6 plumose natatory setae	6 long setae	6 (2 subterminal + 4 terminal natatory) setae
	1º pereiopod	biramous	biramous	biramous	biramous	absent	biramous
	2º pereiopod	biramous	uniramous	biramous	biramous	absent	absent
Pereiopods	**3º pereiopod**	absent	absent	biramous	biramous	absent	absent
	4º pereiopod	absent	absent	uniramous	uniramous	absent	absent
	5º pereiopod	uniramous	uniramous	uniramous	uniramous	absent	uniramous
Pleon	**pleonites (somites)**	6 somites (last somite fused with telson)	6 somites (last somite fused with telson)	5 somites (text) (abdominal somite 6 not differentiated) *6 somites (last somite fused with telson) (figure)	5 somites (text) *6 somites (figure) (last somite fused with telson)	*6 somites (figure) (last somite fused with telson)	5 somites (text) (abdominal somite 6 not differentiated) *6 somites (last somite fused with telson) (figure)
	simple dorsal setae	not reported	not reported	not reported	not reported	not reported	not reported
	lateral spines	absent	absent	absent	absent	*absent (figure)	absent
	anal spine	not reported	not reported	not reported	not reported	not reported	not reported
Telson	**setae (type)**	*5p + 2lp (figure)	*5p + 2lp (figure)	5p + 2lp	5p + 2lp	6p + 1lp	5p + 2lp
Number of known stages		3	4	4	3	1	3

Table S1 (conclusion)

Morphological group		*macrocheles*	*macrocheles*	*obesomanus*	*sulcatus*	*sulcatus*
Species		***A. albatrossae***	***A. macrocheles***	***A. saxidomus***	***A. formosus***	***A. malleator***
Reference		Yang & Kim 2006	Lebour 1932	Wehrtmann & Albornoz 2002	Pasinatto *et al*., in revision	Pasinatto *et al*., in revision
Carapace	**rostrum**	absent	not reported	absent	absent	absent
	pterygostomian spine	present	not reported	present	present	present
	eyes	sessile	*sessile (figure)	sessile	sessile	sessile
Antennule	**peduncle (segments)**	unsegmented	2-segmented	2-segmented	3-segmented	2-segmented
	endopod (setae)	1 long plumose seta	1 strong seta	1 long plumose seta	as a plumose seta	as a plumose seta
	exopod (aesthetascs)	4	3 or 4	4	4	4
	exopod (setae)	1 short plumose setae	1 or 2 spines (figure looks like seta)	*absent (figure)	1 terminal plumose seta	1 terminal plumose seta
Antenna	**peduncle (segments)**	*unsegmented (figure)	not reported	*2-segmented (figure)	2-segmented	2-segmented
	peduncle (spine near the endopod)	1 spine	not reported	1 long spine	1 medial distal spiniform projection	1 medial distal spiniform projection
	unsegmented endopod (seta)	1 long terminal plumose seta	not reported	*1 seta (figure) mid-distal region with setules	1 terminal plumose seta	1 terminal plumose seta
	endopod (spine)	1 spine	not reported	1 small lateral seta	1 medial distal spiniform projection	1 medial distal spiniform projection
	exopod (segments)	6-segmented	not reported	5-segmented (text) *6-segmented (figure)	8-segmented	6-segmented
	exopod (plumose setae)	11	8 to 10	13	11	11

	exopod (tubercle in the proximal segment)	not reported	not reported	not reported	not reported	present
	exopod (simple setae)	1 distolateral spine	2 outer spine (figure looks like seta)	1 small simple seta	distal segment with 1 simple seta	1 simple seta in the distal segment
Mandible	**palp**	absent (without figure)	absent	absent	absent	absent
	coxa (setae)	3 terminal setae	not reported (without figure)	*4 setae (figure)	6 [5 (1 medial + 3 terminal + 1 lateral) simple + 1 terminal serrulate plumose) setae	6 [5 (1 medial + 3 terminal + 1 lateral) simple + 1 terminal serrulate plumose) setae
	basis (spines)	2 stout spines	absent (without figure)	*2 stout spines (figure)	2 spiniform projections	2 spiniform projections
Maxillule	**basis (setae)**	1 short terminal plumose seta	not reported (without figure)	*1 seta (figure)	1 lateral simple seta	1 lateral simple seta
	endopod (setae)	1 terminal setae	not reported (without figure)	*2 setae (figure)	2 (1 terminal plumoserrulate + 1 lateral simple) setae	2 (1 terminal plumoserrulate + 1 lateral simple) setae
	exopod	*absent (figure)	not reported (without figure)	*absent (figure)	absent	absent
	coxa (setae)	3 setae	*2 setae (figure)	*4 setae (figure)	2 medial simple setae	2 medial simple setae
	basis (lobes)	bilobed	*bilobed (figure)	bilobed	bilobed	bilobed
Maxilla	**basis (setae)**	7 (3 in proximal lobe, 4 in distal lobe) setae	not reported	8 setae *(each lobe with 4) (figure)	10 (each lobe with 5) simple setae	10 (each lobe with 5) simple setae
	endopod (setae)	3 (1 basal + 1 terminal simple + 1 terminal plumose) setae	*2 setae (figure)	3 [2 distal plumodenticulate setae + *1 seta (figure)] setae	3 [1 medial proximal simple + 2 terminal long (1 simple and 1	5 [3 medial (1 proximal and 2 distal) simple + 2 terminal long (1

					plumose)] setae	simple and 1 plumose)] setae
	endopod (microtrichia)	absent	not reported	*present (figure)	present	present
	exopod (setae)	5 plumose setae	*5 setae (figure)	5 plumose setae (text) *4 plumose setae (figure)	5 plumose setae (without microtrichia)	5 plumose setae (with microtrichia)
	coxa (setae)	absent	not reported	absent	1 medial distal simple seta	1 medial distal simple seta
	basis (setae)	6 (4 spiniform + 2) setae	*2 setae (figure)	5 spines	7 simple setae arranged 2+2+2+1	7 simple setae arranged 2+2+2+1
	endopod (segments)	unsegmented	not reported	unsegmented	2-segmented	2-segmented
First maxilliped	**endopod (setae)**	6 (1 basal + 1 subterminal + 4 terminal) setae	*3 setae (figure)	5 (3 terminal, 2 subterminal simple) setae	6 {1 medial distal simple, 5 [4 simple (1 medial + 3 terminal) + 1 terminal serrulate]} setae	6 {1 medial distal simple, 5 [4 simple (1 medial + 1 lateral + 2 terminal) +1 terminal serrulate]} setae
	exopod (segments)	not reported	not reported	not reported	4-segmented	4-segmented
	exopod (setae)	4 terminal plumose natatory setae	*4 setae (figure)	5 (1 subterminal + 4 terminal) setae	5 (0, 0, 2, 2 terminal natatory plumose + 1 lateral distal simple on second segment) setae	5 (0, 0, 2, 2 terminal natatory plumose + 1 lateral proximal simple on third segment) setae
	coxa (setae)	absent	not reported	absent	absent	absent
Second maxilliped	**basis (setae)**	3 (2 spiniform + 1) setae	*2 setae (figure)	3 spines	4 medial simple setae arranged 1+1+1+1	4 medial simple setae arranged 1+2+1

	endopod (segments)	4-segmented	not reported	3-segmented	4-segmented	4-segmented
	endopod (setae)	5 (1, 0, 1, 2+1) setae, dactylus present	*3 setae (figure)	6 (1, 0, 3 simple + 0, 1, 1 spiniform) setae	7 [1 medial distal simple, 0, 1 medial distal serrulate, 5 (1 medial simple + 3 lateral simple + 1 terminal serrulate) setae	7 [1 medial distal simple, 0,1 medial distal serrulate seta, 5 (1 medial simple + 3 lateral simple + 1 terminal serrulate) setae
	exopod (segments)	not reported	not reported	not reported	4-segmented	4-segmented
	exopod (setae)	5 (1 subterminal seta + 4 terminal plumose natatory) setae	6 setae *4 + 2 setae (figure)	6 (4 terminal + 2 subterminal plumose) setae	6 (0, 1, 2, 2 terminal natatory plumose + 1 terminal simple on second segment) setae	6 (0, 1, 2, 2 terminal natatory plumose + 1 terminal simple on second segment) setae
	coxa (setae)	absent	not reported	absent	1 medial distal simple seta	1 medial distal simple seta
	basis (setae)	1 simple seta	*2 setae (figure)		2 medial simple setae arranged 1+1	1 medial simple seta
Third maxilliped	**endopod (segments)**	2-segmented	not reported	*4-segmented (figure)	5-segmented	4-segmented
	endopod (setae)	4 (2, 2) setae, dactylus present	1 long spine	4 terminal simple setae	7 [0, 1 medial, 0, 3 (2 lateral proximal + 1 medial distal), 3 (2 medial proximal and 1 terminal)] simple setae	6 [0, 0, 3 (2 medial proximal + 1 lateral distal), 3 (2 lateral + 1 terminal)] simple setae

	exopod (segments)	not reported	not reported	not reported	5-segmented	4-segmented
	exopod (setae)	6 (2 subterminal + 4 terminal) plumose natatory setae	6 setae *4 + 2 setae (figure)	6 (2 subterminal + 4 terminal) plumose natatory setae	7 (0, 0, 2, 2, 2 terminal natatory plumose + 1 medial simple on second segment) setae	8 [0, 2, 2, 2 terminal natatory plumose + 2 (1 medial and 1 lateral) simple on second segment] setae
Pereiopods	**1º pereiopod**	biramous	biramous	biramous	biramous	biramous
	2º pereiopod	uniramous	uniramous	uniramous	absent	absent
	3º pereiopod	uniramous	absent	uniramous	absent	absent
	4º pereiopod	absent	absent	uniramous	absent	absent
	5º pereiopod	uniramous	uniramous	uniramous	absent	absent
Pleon	**pleonites (somites)**	5 somites (text) (sixth abdominal somite not differentiated) *6 somites (last somite fused with telson) (figure)	*6 somites (last somite fused with telson) (figure)	6 somites (last somite fused with telson)	6 segments (6th segment fused to telson)	6 segments (6th segment fused to telson)
	simple dorsal setae	not reported	not reported	not reported	present	present
Telson	**lateral spines**	absent	*absent (figure)	absent	absent	absent
	anal spine	not reported	not reported	absent	present	present
	setae (type)	5p + 2lp	not reported	5p + 2lp	5p + 2lp	5p + 2lp
Number of known stages		1	9	1	1	1

Capítulo IV: Conclusivo

CONSIDERAÇÕES FINAIS

Considerando a relevância do conhecimento da morfologia larval de decápodos para contribuir em aspectos taxonômicos, ecológicos e filogenéticos e dada a falta de descrições larvais de espécies de *Alpheus*, o presente estudo contribuiu para ampliar o conhecimento sobre a morfologia larval do gênero para a costa brasileira, além de ressaltar a necessidade de padronização nas descrições larvais para estudos taxonômicos de forma comparativa.

Diante da diagnose caótica encontrada na morfologia larval de *Alpheus*, este estudo revelou novos caracteres propostos para serem analisados e que podem ser úteis para diagnose das zoeas do gênero: presença de espinho anal e pela primeira vez reportado, presença de cerdas dorsais simples no pleon. No entanto, como se trata de caracteres de difícil visualização, não foi possível afirmar que o espinho anal e as cerdas dorsais simples no pleon são exclusivos das zoeas das espécies aqui descritas, uma vez que os autores das descrições anteriores não procuraram por estes caracteres. A microscopia eletrônica de varredura, usada aqui pela primeira vez em larvas do gênero *Alpheus*, foi uma ferramenta imprescindível para um detalhamento maior das cerdas dorsais e sua posição nos segmentos, além de esclarecer as estruturas presentes na margem posterior do télson (dentículos e espinhos).

O presente estudo foi o primeiro a realizar uma revisão contendo todas as descrições de zoea I de *Alpheus* disponíveis na literatura, levando em consideração os grupos morfológicos propostos para adultos. Alguns caracteres foram propostos para a diferenciação dos grupos morfológicos, porém, devido à falta de padronização nas descrições larvais e do diagnóstico problemático encontrado na morfologia da zoea I de *Alpheus*, não foi possível, até o momento, propor caracteres exclusivos e compartilhados por todas as espécies, que poderiam auxiliar na

separação destes grupos. Portanto, a hipótese de que os grupos morfológicos propostos para adultos são suportados pelos dados larvais foi rejeitada até o momento.

A alta variação encontrada no caracteres larvais das espécies dentro de cada grupo pode estar relacionada ao fato de que, até o momento, existem poucas espécies com estágios larvais descritos em cada grupo morfológico, além da não monofilia revelada em alguns dos grupos. Ademais, devido a confusão e imprecisão na descrição de alguns caracteres larvais, tornou-se uma tarefa complexa compará-los entre os grupos morfológicos de adultos. Mas os dados gerados neste estudo podem auxiliar nas discussões sobre a separação das espécies em grupos morfológicos quando forem realizados estudos sobre as relações filogenéticas entre as espécies do gênero *Alpheus*.

O desenvolvimento foi outra lacuna encontrada no entendimento da morfologia larval de *Alpheus*. Embora 17 espécies de *Alpheus* analisadas neste estudo, possuam descrições de zoea I, apenas duas espécies apresentaram o desenvolvimento completo conhecido. Sendo assim, constatou-se a necessidade de estudos de desenvolvimento larval de *Alpheus*, para compreender melhor os caracteres morfológicos larvais presentes neste táxon, além de contribuir no conhecimento do ciclo de vida do grupo.

Portanto, os dados obtidos neste estudo servirão como base para futuras análises com morfologia larval de *Alpheus*, incluindo os grupos morfológicos de adultos, além de ampliar o conhecimento das zoeas de *Alpheus* na costa brasileira.