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Multigene Phylogenetics Reveal the Relationships of the Mysterious Genus *Alarconia* Glassell, 1938 (Brachyura, Pinnotheridae): Elevation of Alarconiini Števčić, 2005 to the Subfamily Level and Redescription of the Atlantic Species *Alarconia guinotae* Coelho, 1996

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Alarconia is currently composed of only two poorly studied species. The genus and its type species, *A. seaholmi*, were originally described based on a single male specimen collected from Acapulco, on the Pacific coast of Mexico. Decades later, specimens belonging to the genus collected in the southwestern Atlantic, in Brazil, led to the description of the second species, *A. guinotae*. Recently, a series of phylogenetic studies have elucidated the taxonomy of Pinnotheridae, leading to the current classification with three subfamilies. However, the genus *Alarconia* was not addressed in these studies and its phylogenetic relationships, and consequently its taxonomy, remained poorly understood. Herein, we have used sequence fragments of three genes, the mitochondrial 16S rRNA and 12S rRNA and the nuclear H3, to elucidate the phylogenetic relationships of the genus *Alarconia* using specimens of *A. guinotae.* Additionally, we have used morphological data to further discuss the relationship between the two species of *Alarconia* and their phylogenetic relationships to other pinnotherids. The genus *Alarconia* was recovered as the sister group of all other pinnotherid subfamilies, thus leading to the elevation of the tribe Alarconiini to the subfamily level, with the name Alarconiinae stat. nov., for which we have proposed a rediagnosis. Additionally, we have redescribed the poorly studied Brazilian species, *A. guinotae*, further discussing its morphology and relationship to the type species. Lastly, a key to the currently known families and subfamilies of Pinnotheroidea is provided.

Keywords. Alarconiinae stat. nov., Brazil, Molecular phylogenetics, Pinnotheroidea, Taxonomy

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BACKGROUND

Alarconia Glassell, 1938 and its type species, *Alarconia seaholmi* Glassell, 1938, were described based on a single male specimen collected from Acapulco, Guerrero, Mexico (Glassell 1938). Glassell (1938) provided a description and some remarks on this genus' relationship to *Pinnixa* White, 1846, stating that they are allied by the general shape of the carapace and the relative sizes and shapes of the ambulatory pereopods. Additionally, the author also stated that *Alarconia* can be distinguished from *Pinnixa* by the third maxilliped (Mxp3) ischium and merus not being fused, but rather articulated, and by the proportionally longer ischium in the former (Glassell 1938).

Glassell (1938) stated that *Alarconia* resembles two genera at the time included in Asthenognathinae Stimpson, 1858 (Varunidae H. Milne Edwards, 1853): *Tritodynamia* Ortmann, 1894, and *Asthenognathus* Stimpson, 1858. Similarities between the Mxp3 of *Alarconia* and *Tritodynamia* were detected, but the former has smaller eyes, a less smooth carapace, and the second pair of ambulatory pereopods is not the largest (Glassell 1938). *Tritodynamia* is now included in the monotypic subfamily Tritodynamiinae Števčić, 2005 within Macrophthalmidae Dana, 1851 (WoRMS 2026), although its position within this family is questionable and the genus might belong to Varunidae (Tsang et al. 2022). The ambulatory pereopods of *Alarconia* and *Asthenognathus* are similar, however, these genera differ in the disposition of the segments of the Mxp3 palp (Glassell 1938). *Asthenognathus* was considered part of Pinnotheroidea De Haan, 1833 (Dai and Yang 1991), but was later transferred to Varunidae (Ng et al. 2008) after morphological re-examination, which was then further confirmed by the use of molecular data (Palacios-Theil et al. 2009). Recently, the genus *Asthenognathus* was divided, with two genera being described and classified in a new subfamily, Schubartinae Muñoz, García-Raso & Cuesta, 2025 (Muñoz et al. 2025). Members of Asthenognathinae and Schubartinae, like pinnotherids, engage in symbiotic relationships with other marine invertebrates (Muñoz et al. 2025), and superficially resemble *Alarconia.* Furthermore, Glassell (1938) also indicates a relationship between the therein described genus and *Lambdophallus* Alcock, 1900 (Hexapodidae Miers, 1866), given that they both possess male first gonopods (G1) that are not distally confined by the pleon.

The type species, *Alarconia seaholmi*, remained as the only species in the genus until Coelho (1996) described *Alarconia guinotae* Coelho, 1996 from the Brazilian coast, which was the

first record of the genus in the Atlantic Ocean. *A. guinotae* can be distinguished from *A. seaholmi* by the presence of only two sulci on the branchial region of the carapace and by the G1 being completely covered by the pleon (Coelho 1996). Coelho (1996) discussed that *Alarconia* shares similarities with some species of *Pinnixa*, like *Pinnixa valerii* Rathbun, 1931, *Pinnixa richardsoni* Glassell, 1936 and *Pinnixa minuta* Rathbun, 1901. Coelho (1996), however, mentions that Lemaitre and Alvarez Léon (1992) and Hendrickx (1995) examined specimens of *P. valerii* and *P. richardsoni* and retained them in *Pinnixa*.

Števčić (2005) described the tribe Alarconiini Števčić, 2005 to accommodate *Alarconia*, under the subfamily Pinnothereliinae Alcock, 1900. However, with large-scale phylogenetic studies of the superfamily Pinnotheroidea De Haan, 1833, it was revealed that *Pinnotherelia* A. Milne-Edwards and Lucas, 1843, the type genus of Pinnothereliinae, is not a pinnotherid, but rather a varunid (Palacios Theil et al. 2016; Poore and Ahyong 2023). Thus, most members of Pinnothereliinae were then reassigned to Pinnixinae Števčić, 2005 (Palcios Theil et al. 2016). Furthermore, Palacios Theil et al. (2016), in a phylogenetic study using molecular data, recovered *P. valerii*, along with some other species assigned to *Pinnixa* at the time, in a separate clade, describing the new genus *Pinnixulala* Palacios Theil, Cuesta and Felder, 2016 and the new subfamily Pinnixulalinae Palacios Theil, Cuesta and Felder, 2016 to accommodate them. Although the analyses conducted by Palacios Theil et al. (2016) were robust, samples of the genus *Alarconia* were not included. With the allocation of *P. valerii*, a supposed close relative of *Alarconia* (according to Coelho, 1996), to a new genus and subfamily, questions were raised regarding the classification of *Alarconia* (Palacios Theil et al. 2016).

Thus, the present study has reconstructed a molecular phylogenetic hypothesis to elucidate the phylogenetic relationships of the genus *Alarconia* to other genera and subfamilies of Pinnotheridae. Also, given the lack of detail in the description of *A. guinotae*, the present study has also redescribed this taxon and provided further morphological characters that can be used in the diagnosis of the genus and species. With our results, we provide a redescription of the monotypic subfamily, Alarconiinae Števčić, 2005 stat. nov.

MATERIALS AND METHODS

Obtaining specimens and morphological analyses

Material belonging to *Alarconia guinotae*, including paratypes, was obtained from the following collections: Coleção de Crustáceos do Departamento de Biologia (CCDB), Faculdade de

Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP), Universidade de São Paulo (USP), Ribeirão Preto, São Paulo, Brazil; Coleção Carcinológica do Museu de Oceanografia Prof. Petrônio Alves Coelho (MOUFPE), Universidade Federal de Pernambuco (UFPE), Recife, Pernambuco, Brazil; Coleção Biológica (ColBio), Instituto Oceanográfico (IO) , Universidade de São Paulo (USP), São Paulo, São Paulo, Brazil. Despite several attempts to obtain photographs of the holotype and only known specimen of the type species, *A. seaholmi* (San Diego Society of Natural History, catalog number 1159), we were only able to analyze this taxon through the illustrations and description provided by Glassell (1938).

The specimens' morphology was analyzed using a Leica© M205 C stereomicroscope equipped with a Leica© DFC295 digital camera and with the computer software Leica Application Suite v. 3.8.0, which was used to photograph the individuals.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from muscle tissue of the pereopods of the individuals. The target genes were the mitochondrial 16S rRNA, 12S rRNA and the nuclear H3, which have been previously used in phylogenetic studies of pinnotherids (Palacios Theil et al. 2016; Palacios Theil and Felder 2020a b). Several 16S rRNA sequences available in GenBank also contained the adjacent tRNA-Leu and NADH dehydrogenase subunit 1 sequences. Analyses were run both including and excluding these extra genes. When used, these portions were included as gaps for the sequences in which these portions were unavailable.

For sequence fragment amplification, Polymerase Chain Reactions (PCRs) reactions were carried out based on the methods proposed by Mantelatto et al. (2007 2009 2018) and Ocampo et al. (2013) using the following cycle: initial denaturing for 5 minutes at 95°C, followed by 40 cycles of denaturing for 1 minute at 94°C, primer annealing for 1 minute at 52–55°C (depending on the primer) and extension for 2 minutes at 72°C, followed by a final extension for 10 minutes at 72°C. The following primers were used: for 16S rRNA, 16SL2/16S-pH2 (Schubart et al. 2002; Palacios-Theil et al. 2009) and 16S-pL1/16S-pH2 (Palacios-Theil et al. 2009); for 12S rRNA, 12SF/12S1R (Buhay et al. 2007); for H3, H3af/H3ar (Colgan et al. 1998) (Table 1).

Table 1. Primers used in the present study

Gene	Primer	Primer sequence	Primer pair	References	Base-pairs obtained
16S rRNA	16SL2	5'-TGCCTGTTTATCAAAAACAT-3'	16S-pH2	Schubart et al. 2002	570
	16S-pH2	5'-CCT GGC TCA CGC CGG TCT GAA-3'	16SL2 / 16S-pL1	Palacios-Theil et al. 2009	570 / 380
	16S-pL1	5'-AAC TTT TAA GTG AAA AGG CTT-3'	16S-pH2	Palacios-Theil et al. 2009	380
12S rRNA	12Sf	5'-GAA ACC AGG ATT AGA TAC CC-3'	12S1R	Buhay et al. 2007	395
	12S1R	5'-AGC GAC GGG CGA TAT GTA C-3'	12Sf	Buhay et al. 2007	395
H3	H3af	5'-ATG GCT CGT ACC AAG CAG ACV GC-3'	H3ar	Colgan et al. 1998	400
	H3ar	5'-ATA TCC TTR GGC ATR ATR GTG AC-3'	H3af	Colgan et al. 1998	400

Positive PCR results were sent for Sanger sequencing at the private company BPI Biotecnologia Pesquisa e Inovação, in Botucatu, São Paulo, Brazil. The sequences were then edited on BioEdit v.7.2.5 (Hall 1999) and Geneious Prime v.2021.2 (Kearse et al. 2012), where forward and reverse strands were used to generate the consensus sequences which were used in the phylogenetic analyses.

Phylogenetic analyses

Available sequences of pinnotheroid genera were obtained from the GenBank platform in order to contextualize *Alarconia* within the group. The consensus sequences, along with others obtained from GenBank (Table 2) were aligned in MAFFT v.7 (Katoh et al. 2017). These alignments were used to construct two phylogenetic hypotheses, one using Maximum Likelihood (ML) (Huelsenbeck and Crandall 1997), and another using Bayesian Inference (BI) (Huelsenbeck and Ronquist 2001).

The ML hypothesis was constructed with a concatenated alignment of all three genes on the online platform W-IQ-TREE (Trifinopoulos et al. 2016), using the substitution models proposed by the program for each gene, which were GTR+F+I+G4 for 16S rRNA and 12SrRNA and TNe+I+G4 for H3. Branch support was analyzed based on 1000 pseudoreplicate ultrafast bootstrap values; values over 70 were considered high enough to be further discussed.

The BI tree was constructed using the concatenated alignment of all three genes; however, the different substitution models were applied by using partitions for each gene directly on the NEXUS script. The analysis was carried out using MrBayes v.3.2.7 (Ronquist et al. 2012). The closest substitution models to those proposed by W-IQ-TREE available in MrBayes were chosen, being GTR+G+I for 16S rRNA and 12S rRNA and HKY+G+I for H3. The MCMC chain length was 20 million generations with sampling every 2000. All ESS values were checked and were superior to 200, the PSRF values were all contained between 1 and 1.01, and the ASDSF was 0.002.

Node support was assessed using posterior probability (pp), for which values above 0.9 were considered for further discussion. Both the ML and BI trees were visualized and edited in FigTree v.1.4.4 (Rambaut 2018). A single tree is presented below (Fig. 1) with support values of both analyses.

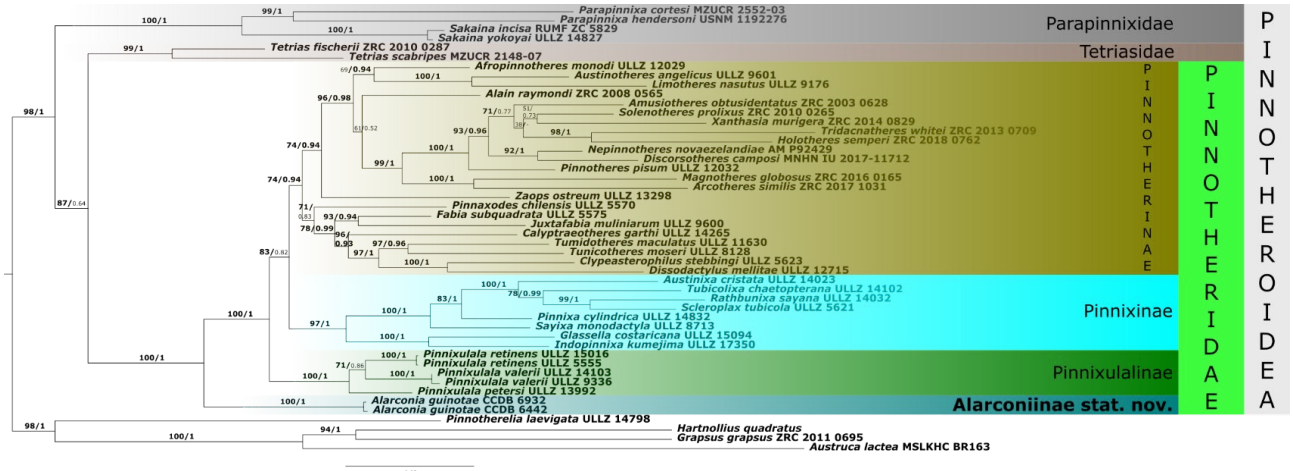

Fig. 1. Phylogenetic hypothesis of Pinnotheroidea De Haan, 1833 inferred from a concatenated alignment of 16S rRNA, 12S rRNA and H3 sequences using Maximum Likelihood (ML) and Bayesian Inference (BI). Bootstrap and Posterior Probability values are respectively shown at the branches, values considered for further discussion are in bold. Species names are followed by the catalog number of specimens in their respective collections.

Table 2. Specimens of Pinnotheroidea De Haan, 1833 and outgroup taxa used in the phylogenetic analyses. Sequences in bold were generated herein

Species	Locality	Catalog number	GenBank acession numbers		
			16S rRNA	12S rRNA	H3
FAMILY PINNOTHERIDAE DE HAAN, 1833					
Subfamily Alarconiinae Števčić, 2005					
Alarconia guinotae Coelho, 1996	Ubatuba, São Paulo, Brazil	CCDB 6442	**PV607934**	**PV607935**	**PV611711**
	Cedro, Ubatuba, São Paulo, Brazil	CCDB 6932	**PV607933**	**PV607936**	**PV611710**
Subfamily Pinnixinae Števčić, 2005					
Austinixa cristata (Rathbun, 1900)	Gulf Shores, Alabama, USA	ULLZ 14023	KU679679	KU679483	KU679761
Glassella costaricana (Wicksten, 1982)	San Juanillo, Guanacaste, Costa Rica	ULLZ 15094	KU679659	KU679520	KU679795
Indopinnixa kumejima Naruse and Maenoso, 2012	Iguma Bay, Hahajima, Japan	ULLZ 17350	MN341021	MN341017	MN341030
Pinnixa cylindrica (Say, 1818)	off Perdido Key Beach, Florida, USA	ULLZ 14832	KU679694	KU679554	KU679830
Rathbunixa sayana (Stimpson, 1860)	Fort Pierce, FL, USA	ULLZ 14032	KU679717	KU679572	KU679848
Sayixa monodactyla (Say, 1818)	Fort Pierce, FL, USA	ULLZ 8713	MN341023	MN341014	MN341027
Scleroplax tubicola (Holmes, 1894)	Baranof Island, Alaska, USA	ULLZ 5621	EU934973	KU679577	KU679853
Tubicolixa chaetopterana (Stimpson, 1860)	Isla Margarita, Venezuela	ULLZ 14102	KU679710	KU679548	KU679824
Subfamily Pinnixulalinae Palacios Theil, Cuesta and Felder, 2016					
Pinnixulala petersi (Bott, 1955)	off Panama, Pacific	ULLZ 13992	KU679640	KU679566	KU679842
Pinnixulala retinens (Rathbun, 1918)	Fort Pierce, FL, USA	ULLZ 5555	KU679638	KU679568	KU679844
	Barra del Tordo, Mexico	ULLZ 15016	KU679639	KU679570	KU679846
Pinnixulala valerii (Rathbun, 1931)	Estero Coriento, Nicaragua	ULLZ 9336	EU934993	KU679578	KU679854
	Panama canal entrance, Pacific	ULLZ 14103	KU679637	KU679579	KU679855
Subfamily Pinnotherinae De Haan, 1833					-
Afropinnotheres monodi Manning, 1993	Ria Formosa, Portugal	ULLZ 12029	KU679625	KU679462	KU679740
Alain raymondi Ahyong and Ng, 2008	Philippines	ZRC 2008-0565	KU679636	KU679463	KU679741
Amusiotheres obtusidentatus (Dai in Dai, Feng, Song and Chen, 1980)	Pattani, Thailand	ZRC 2003-0628	KU679723	KU679517	KU679792
Arcotheres similis (Bürger, 1895)	not informed in literature	ZRC 2017-1031	OR034148	OR034170	OR030776
Austinotheres angelicus (Lockington, 1877)	San Felipe, Mexico	ULLZ 9601	EU935002	KU679500	KU679778
Calyptraeotheres garthi (Fenucci, 1975)	Golfo San Matías, Argentina	ULLZ 14265	KU679652	KU679501	KU679779
Clypeasterophilus stebbingi (Rathbun, 1918)	Ilha Anchieta, Ubatuba, Brazil	ULLZ 5623	KU679647	KU679509	KU679785
Discorsotheres camposi Ahyong, 2018	not informed in literature	MNHN-IU 2017-11712	OR034151	OR034173	OR030779

Dissodactylus mellitae (Rathbun, 1900)	St. Joseph Peninsula, Florida, USA	ULLZ 12715	KU679651	KU679514	KU679790
Fabia subquadrata Dana, 1851	Bodega Bay, California, USA	ULLZ 5575	EU935000	KU679518	KU679793
Holotheres semperi (Bürger, 1895)	not informed in literature	ZRC 2018-0762	OP798072	OP798083	OP765686
Juxtafabia muliniarum (Rathbun, 1918)	San Felipe, Mexico	ULLZ 9600	EU934990	KU679522	KU679797
Limotheres nasutus Holthuis, 1975	off South Carolina, USA	ULLZ 9176	EU934996	KU679527	KU679802
Magnotheres globosus (Hombron and Jacquinot, 1846)	not informed in literature	ZRC 2016-0165	OR034154	OR034175	OR030781
Nepinnotheres novaezelandiae (Filhol, 1885)	Oriental Bay, Wellington, New Zealand	AM P92429	KU679727	KU679528	KU679803
Pinnaxodes chilensis (H. Milne Edwards, 1837)	Cocholgue, Chile	ULLZ 5570	EU934998	KU679534	KU679809
Pinnotheres pisum (Linnaeus, 1767)	Algeciras, Spain	ULLZ 12032	KU679724	KU679586	KU679862
Solenotheres prolixus Ng and Ngo 2010	Vinh Chan, Vietnam	ZRC 2010-0265	KU679726	KU679591	KU679867
Tridacnatheres whitei (De Man, 1887)	not informed in literature	ZRC 2013-0709	OR030788	OR034181	OR034163
Tumidotheres maculatus (Say, 1818)	New Harbor Island, Louisiana, USA	ULLZ 11630	KU679633	KU679600	KU679876
Tunicotheres moseri (Rathbun, 1918)	Tampa Bay, Florida, USA	ULLZ 8128	KU679731	KU679608	KU679884
Xanthasia murigera White, 1846	not informed in literature	ZRC 2014-0829	OP798077	OP798090	OP765689
Zaops ostreum (Say, 1817)	Bocas del Toro, Panama	ULLZ 13298	KU679654	KU679619	KU679895
FAMILY PARAPINNIXIDAE ŠTEVČIĆ, 2005					
Parapinnixa cortesi Thoma, Heard and Vargas, 2005	Isla del Coco, Costa Rica	MZUCR 2552-03	KU679739	KU679531	KU679806
Parapinnixa hendersoni Rathbun, 1918	Islas del Rosario, Colombia	USNM 1192276	KU679738	KU679533	KU679808
Sakaina incisa Sakai, 1969	not informed in literature	RUMF-ZC 5829	OP798080	OP798092	OP765692
Sakaina yokoyai (Glassell, 1933)	Sea of Japan, Russia	ULLZ 14827	KU679736	KU679589	KU679865
FAMILY TETRIASIDAE TSANG and NARUSE, 2023					
Tetrias fischerii (A. Milne Edwards, 1867)	Balicasaq Island, Black Forest, Philippines	ZRC 2010-0287	KU679734	KU679592	KU679868
Tetrias scabripes Rathbun, 1898	Bahía de Junquillal, Golfo de Sta. Elena, Guanacaste, Costa Rica	MZUCR 2148-07	KU679735	KU679593	KU679869
Outgroup taxa					
Austruca lactea (De Haan, 1835)	not informed in literature	MSLKHC-BR163	KJ132647	KJ132504	KJ133203
Hartnollius quadratus (de Saussure, 1853)	not informed in literature	w/o catalog number	ON379427	ON379383	ON379765
Grapsus grapsus (Linnaeus, 1758)	Bahamas	ZRC 2011-0695	KM510103	KM510071	KM510134
Pinnotherelia laevigata H. Milne Edwards and Lucas, 1844	Cascabeles, Chile	ULLZ 14798	KU679733	KU679585	KU679861

RESULTS

Molecular data obtained

We generated sequences of two specimens of *Alarconia guinotae* for each gene (Table 2). The final concatenated alignments used for the phylogenetic analyses consisted of 1,690 base pairs (bp) (including tRNA-Leu and NADH dehydrogenase subunit 1) and 1310 bp (excluding tRNA-Leu and NADH dehydrogenase subunit 1). Alignments for individual genes were 865 bp for 16S rRNA, tRNA-Leu and NADH dehydrogenase subunit 1,567 bp for 16S rRNA only, 416 bp for 12S rRNA and 328 bp for H3. Tree topologies of analyses including and excluding the tRNA-Leu and NADH dehydrogenase subunit 1 were identical, however, overall slightly better support was observed in the analyses including these sequences and are thus presented herein.

Phylogenetic hypotheses

Both ML and BI phylogenetic analyses generated congruent topologies (Fig. 1). Pinnotheroidea was recovered as a monophyletic group with very high support (98) and maximum support (1) for the ML and BI trees respectively. Within Pinnotheroidea, Parapinnixidae Števčić, 2005 was recovered as a monophyletic group with maximum support in both (100 in ML, 1 in BI) and is the sister group of the remaining Pinnotheroidea, which form a clade with high support (87) for the ML, but low support for the BI analysis. Within this subclade, Tetriasidae Tsang and Naruse, 2023 was recovered as monophyletic with very high support (99 in ML) and maximum support (1 in BI) and is the sister group of Pinnotheridae, which was also recovered as monophyletic with maximum support (100 in ML, 1 in BI) in both. Within Pinnotheridae, specimens belonging to *Alarconia* were recovered in a clade with maximum support (100 in ML, 1 in BI) in both analyses, and are the sister group of the remaining pinnotherids, which in turn form a clade with maximum support (100 in ML, 1 in BI).

Within the subclade encompassing the remaining Pinnotheridae, Pinnixulalinae is recovered as monophyletic and with maximum support (100 in ML, 1 in BI) and is the sister group of the clade composed of Pinnixinae and Pinnotherinae, which was also recovered with high support (83) in ML, but low support in BI. Pinnixinae is recovered as monophyletic with very high support (97), whereas Pinnotherinae is recovered as monophyletic with relatively high support in ML (74) and maximum support in BI (1). Overall, this phylogenetic hypothesis is consistent with the current

pinnotherid classification and indicates that *Alarconia* belongs in a separate subfamily within Pinnotheridae.

Taxonomy

Superfamily Pinnotheroidea De Haan, 1833

Family Pinnotheridae De Haan, 1833

Subfamily Alarconiinae Števčić, 2005 stat. nov.

(Figs. 2–9)

Diagnosis: Carapace irregularly subhexagonal, wider than long, widest posterior to mid-length; relatively well-calcified, granulated, regions well-defined. Buccal cavern large, semicircular; Mxp3 ischium and merus elongate, slender, functionally fused with a deep, well-marked suture (mobility uncertain in *A. seaholmi*), merus slightly longer than ischium; palpus only slightly longer than merus; dactylus articulated subproximally on inner face of propodus. Chelipeds relatively small; propodus inferior proximal margin inflated. Ambulatory pereopod relative sizes P4 > P3 > P2 > P5, long, setose, with several tubercles and spines; carpi and propodi clearly flattened; P2 and P3 relatively long, robust; P4 visibly the most robust; P5 shortest. Male pleon slender; pleonites 3–5 or 4 and 5 fused; telson small, subtriangular. G1 elongated, about as long as or longer than pleon. Female pleon wide, rounded, pleonites free; telson narrower than pleon, subtriangular.

Type genus: *Alarconia* Glassell, 1938.

Remarks: Alarconiinae stat. nov. shares several morphological similarities with other pinnotheroid groups, including the carapace, cheliped, ambulatory pereopod and pleon morphology. Alarconiinae stat. nov. can be distinguished from members of Pinnotherinae by the carapace, which is conspicuously wider than long and well-calcified, and by the relative sizes and the presence of spines on the ambulatory pereopods, with the P4 being the longest and most robust, and the P5 the shortest, compared to a carapace that is about as wide as long and poorly sclerotized, and ambulatory pereopods unarmed and not visibly more robust than one another (see Palacios Theil et al. 2016; Tsang and Naruse 2023). Alarconiinae stat. nov. shares many similarities with Pinnixulalinae and Pinnixinae, including the relative sizes and robustness of the ambulatory pereopods and the carapace proportions (see Palacios Theil et al. 2016). However, Alarconiinae stat. nov. can be distinguished from Pinnixinae by having a more well-sclerotized carapace with the widest point posterior to mid-length, Mxp3 ischium and merus long, with the ischium being slightly shorter than merus, and by the P2 and P3 being relatively longer and more robust than those of members of Pinnixinae. Morphologically, the subfamily Pinnixulalinae is the most similar to Alarconiinae stat. nov., given that they share characteristics such as the presence of a more well-

sclerotized carapace with well demarked regions, the overall cheliped morphology and the presence of spines on the ambulatory pereopods (see Palacios Theil et al. 2016). However, Alarconiinae stat. nov. can be distinguished from Pinnixulalinae by the shape of the carapace, which is widest posterior to mid-length in the former, with an irregular hexagonal shape, and by the more elongated ischium and merus of the Mxp3, which are also separated by a deep, well-defined suture, as opposed to an oval-shaped carapace with the widest point at about mid-length and shorter and more robust ischium and merus on the Mxp3 which are clearly fused and with or without a weak suture in Pinnixulalinae (see Palacios Theil et al. 2016).

Alarconiinae stat. nov. also shares superficial similarities with Tetriasidae, such as the presence of grooves that define carapace regions, but can be distinguished by the overall morphology of the Mxp3, with Tetriasidae having a proportionally wider ischium and merus, separated by a superficial suture, and the dactylus being inserted distolaterally on the propodus (Tsang and Naruse 2023), contrasting with the slender and elongated ischium and merus in Alarconiinae stat. nov., which are separated by a deep and well-delimited suture, and the dactylus being inserted proximolaterally on the propodus. Alarconiinae stat. nov. can be distinguished from Parapinnixidae by the presence of grooves that delimit carapace regions, which are absent in the latter, the abovementioned morphology of the Mxp3, which is very distinct from the very wide and fused ischiomerus in Parapinnixidae, with the dactylus being inserted distally on the propodus, and the male pleon, which is chalice-shaped in the latter and overall slender in Alarconiinae stat. nov. (see Tsang and Naruse 2023). The presence of the deep and well-defined suture between the ischium and merus of the Mpx3 is an important character in distinguishing Alarconiinae stat. nov. from other groups of pinnotheroids, as it is unique to this group. The presence of a weak and superficial suture between the ischium and merus of the Mxp3 was previously used to transfer *Pinnaxodes mutuensis* Sakai, 1939 to the genus *Holothuriophilus* Nauck, 1880, (Takeda and Principe Masahito 2000). However, Ng and Manning (2003) later argued that this suture was not visible in the Fig.s provided by Takeda and Principe Masahito (2000), and that, although the weak suture was indeed present, the Mxp3 of *P. mutuensis* was similar to that of the other species of *Pinnaxodes* Heller, 1865 from which it had been separated. Ng and Manning (2003) further argue that this suture is also present in *P. chilensis* (H. Milne Edwards, 1837), although very faint. Furthermore, Balbino et al. (2025) state that the ischium and merus of the Mxp3 of the therein described genus *Brasilixa* Balbino, Tamburus & Mantelatto, 2025 are articulated, however, after further analysis of the holotype, it was determined that only a well-marked suture is present, and that the mobility observed between these two articles is likely due to the preservation state of the specimen, with the exoskeleton having become soft and malleable. Thus, given this context, the

presence of a well-defined and deep suture in *Alarconia* sets it apart from other members of Pinnotheroidea as a whole.

Genus *Alarconia* Glassell, 1938

(Figs. 2–9)

Diagnosis: Carapace irregularly subhexagonal, wider than long, widest posterior to mid-length; relatively well-calcified, granulated, regions well-defined. Front narrow, nearly transverse, with a median groove. Eyes short, completely filling orbits. Buccal cavern large, semicircular; Mxp3 ischium and merus elongate, slender, functionally fused with a deep, well-marked suture (mobility uncertain in *A. seaholmi*), merus slightly longer than ischium; palpus only slightly longer than merus; dactylus articulated subproximally on inner face of propodus. Chelipeds relatively small; propodus inferior proximal margin inflated. Pereopod relative sizes P4 > P3 > P2 > P5, long, setose, with several tubercles and spines; carpi and propodi flattened; P2 and P3 relatively long, and robust; P4 the most robust; P5 shortest. Male pleon slender; pleonites 3–5 or 4 and-5 fused; telson small, subtriangular. G1 elongated, about as long as or longer than pleon. Female pleon wide, rounded, pleonites free; telson narrower than pleon, subtriangular.

Type species: *Alarconia seaholmi* Glassell, 1938.

Other included species: *Alarconia guinotae* Coelho, 1996.

Distribution: Known from Acapulco, Guerrero, Mexico (*A. seaholmi*) and from Brazil (Pará, Alagoas, São Paulo and Paraná) (*A. guinotae*) (Glassell 1938; Coelho 1996; Bezerra et al. 2006).

Remarks: *Alarconia* is currently the only genus in Alarconiinae stat. nov. and can be distinguished from other pinnotherid genera using morphological characters used to distinguish the subfamily, including the overall morphology of the carapace, Mxp3 and ambulatory pereopods.

Glassell (1938) described *Alarconia* and its type species, *A. seaholmi*, based on a single male specimen collected from Acapulco (Guerrero, Mexico), providing diagnostic characters such as the firm integument and well-defined regions of the carapace, relative lengths of the ischium and merus of the Mxp3, cheliped and ambulatory pereopod morphology. Later, Coelho (1996) described *A. guinotae*, given that this species possesses the diagnostic characters of the genus. Coelho (1996) also mentioned that the grooves in the branchial region are different between the two species. However, given that most other morphological characters appear to be clearly delimited and unique to this group, both species are maintained in *Alarconia*.

Coelho (1996) also mentioned that other similar taxa might need taxonomic reappraisal, including *Pinnixa valerii*, *P. minuta* and *P. richardsoni*, hinting at the possibility that some of them might belong to *Alarconia*. However, Palacios Theil et al. (2016) then included *P. valerii* in a new

genus, *Pinnixulala*, which was transferred to its own monotypic subfamily, Pinnixulalinae. We conclude that *Pinnixulala* and *Alarconia* are not closely related and belong in separate subfamilies. Their morphological similarities are probably due to either convergence or retention of plesiomorphic characteristics (see DISCUSSION). Regarding *P. minuta*, Rathbun (1918) provided Fig.s of various structures, including the Mxp3, which does not resemble that of *Alarconia*, and is more similar to those of juvenile stages of species of *Glassella* (Felder and Palacios Theil 2020). Glassell (1936), when describing *P. richardsoni*, noted similarities between this species and *P. valerii*, even mentioning that such characteristics set them apart from other members of *Pinnixa*. However, *P. richardsoni* differs from *Pinnixulala valerii* by the smooth chelipeds and carpus, arched outer margin of Mxp3 and some pleonal somites being fused (Glassell 1936). The only Fig. provided by Glassell (1936: fig. 4) shows the Mxp3 with a very long ischiomerus, however, it is fused with no suture. Thus, these species likely do not belong to the genus *Alarconia*.

***Alarconia seaholmi* Glassell, 1938**

(Fig. 2)

Alarconia seaholmi—Glassell 1938: 448; Schmitt et al. 1973: 101; Hendrickx 1995: 141; Ng et al. 2008: 247.

Diagnosis: Carapace wider than long, irregularly hexagonal in shape, well-sclerotized; branchial region with tuberculated ridge, three deep sulci on lateral regions of carapace, extending from branchial ridge to cardiac region, median and posterior sulci converging towards lateral margin of carapace; cardiac region with ridge extending across median half of carapace, delimited on both sides by a large spine; Mxp3 ischium and merus with well-defined suture (mobility uncertain), both elongated; ischium slightly shorter than merus; dactylus articulated proximo-laterally on inner face of propodus. Chelipeds relatively small; propodus large, flattened laterally, inferior proximal margin extended, rounded, covered in tubercles. Ambulatory pereopods relatively robust; P2 and P3 relatively long; P4 longest, most robust, P5 shortest, slenderest. Male pleon slender, pleonites 4 and 5 fused; telson subtriangular, less wide than last pleonite. G1 long, slender, longer than pleon, not completely concealed by pleon, lateral and mesial margins sinuous, distal portion with large triangular projection, apex abruptly curved (based on Glassell 1938; Coelho 1996).

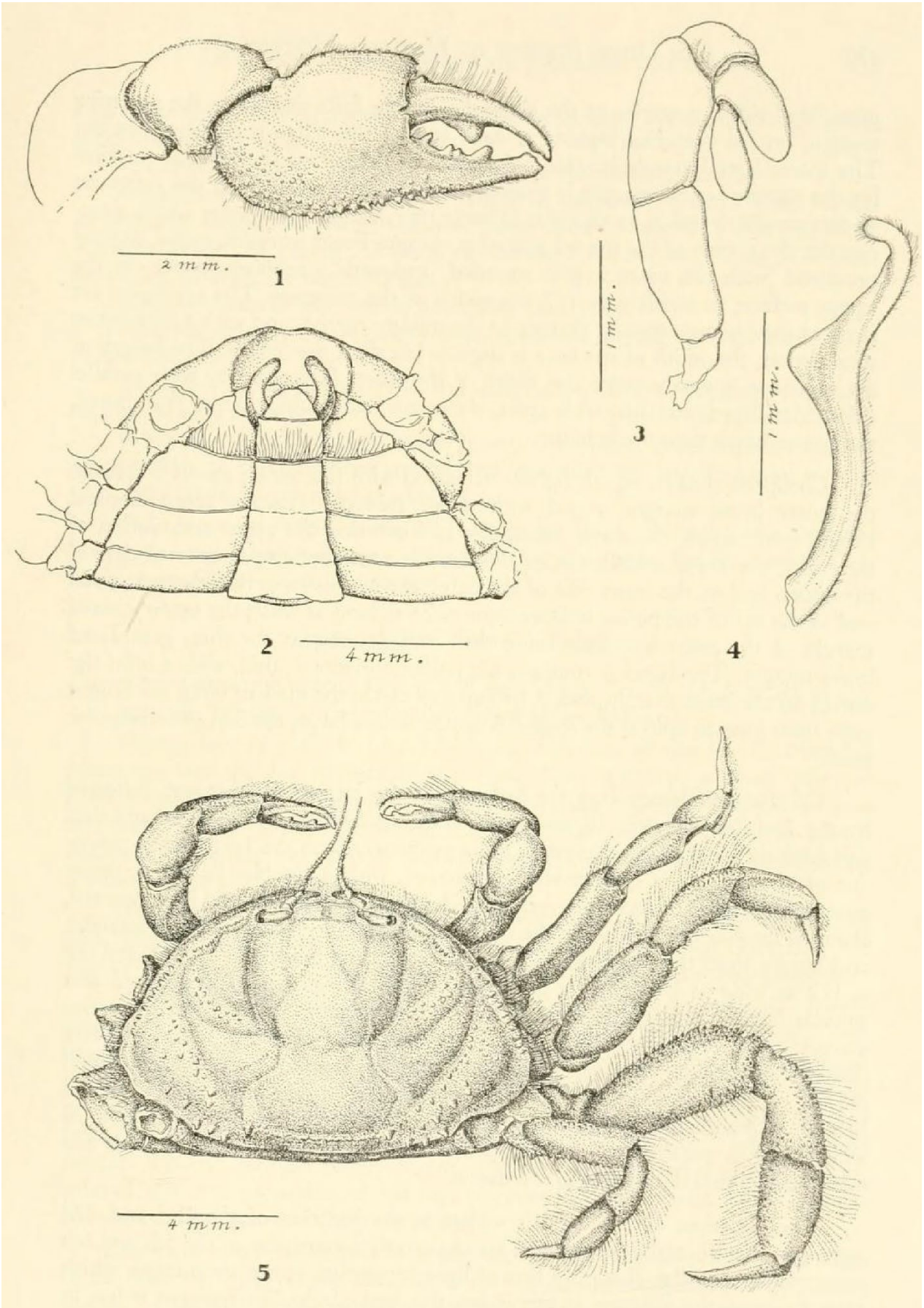

Fig. 2. *Alarconia seaholmi* Glassell, 1938. Male holotype (SDNHM 1159), Acapulco, Guerrero, Mexico (1–5). 1, external face of right cheliped; 2, ventral view of thoracic sternites and pleon; 3, external surface of right third maxilliped; 4, sternal (?) face of male first gonopod; 5, dorsal view of

entire specimen. Scale bars included in image. (Plate 36 from Glassell, 1938 ©San Diego Natural History Museum).

Type locality: Acapulco, Guerrero, Mexico.

Distribution: Known only from the type locality, in the Eastern Pacific in Acapulco, Guerrero, Mexico (Glassell 1938, Coelho 1996).

Habitat and host: The only known specimen was collected from 6-10 fathoms (~11 to 18.3m) in depth (Glassell 1938). The host of this species is unknown (see Discussion).

Remarks: We did not have access to the holotype of *A. seaholmi* (San Diego Society of Natural History, catalog number 1159) despite our effort to obtain photographs of the specimen, but the descriptions and Fig.s provided by Glassell (1938) (reproduced herein as Fig. 2) are clear and informative, providing the necessary information for the present comparison, which further corroborated that both species belong to the same genus. Since only the male holotype of the type species is known and no other specimens have been collected since (Hendrickx 1995; Coelho 1996), female structures, such as the vulva and pleon remain unknown. Thus, if more specimens are collected or identified, especially females, it is of extreme importance that a redescription is made to further add to the knowledge of this elusive genus and species.

Glassell (1938) described the ischium and merus of the Mxp3 in *A. seaholmi* as articulated, which differs from what we have observed in *A. guinotae*, in which the ischium and merus are clearly fused, although a very deep and well-delimited suture is present between them. However, in the illustration of the Mxp3 of *A. seaholmi* provided by Glassell (1938) (reproduced herein as fig. 2–3), the suture looks identical to what we have observed for *A. guinotae*. Thus, the mobility of this suture might be limited, rendering the ischium and merus functionally fused, like in the Brazilian taxon. This is further supported by comparisons of the Mxp3 morphology to other brachyuran families in which the articles are not fused. This remains uncertain until further examination of the male holotype of *A. seaholmi*.

Alarconia guinotae Coelho, 1996

(Figs. 3–9)

Pinnixa sp. G.—Coelho et al. 1980: 131; Barreto et al. 1991/93: 303; Barreto et al. 1993: 651.

Alarconia guinotae—Coelho 1996: 175, 176; Melo et al. 2003: 432; Bezerra et al. 2006: 1043; Ng et al. 2008: 247.

Type material examined: Paratypes: Brazil, Pará, offshore, near Algodoal, ~0°26'S 47°35'W, 21/XI/1968, 6 males, 7 females (3 ovigerous), depth of 25m, coll. R/V Almirante Saldanha (MOUFPE 15147).

Other material examined: Brazil, São Paulo: Ubatuba, Praia do Cedro, 13/XI/2021, 1 male, coll. Zara, F.J. et al. (CCDB 6932); Ubatuba, Praia do Flamengo, 27/IV/2023, 1 male, depth of 7.7m, coll. not informed (ColBio 1); Ubatuba, IV/2019, 1 female, depth of 5m, coll. Rosa, D. (CCDB 6442).

Diagnosis: Carapace wider than long, irregularly hexagonal in shape, well-sclerotized; branchial region with tuberculated ridge, two deep sulci on lateral regions of carapace, extending from branchial ridge to cardiac region; cardiac region with bilobed ridge, dented medially, extending across median half of carapace, delimited on both sides by sulcus followed by large spine; intestinal region with low elevation extending across most of carapace width, delimited on both sides by large spine. Mxp3 ischium and merus not articulated, partially fused, with well-defined suture, both elongated; ischium slightly shorter than merus; dactylus articulated proximo-laterally on inner face of propodus. Chelipeds relatively small; propodus large, flattened laterally, covered in small tubercles, inferior proximal margin extended, rounded. Ambulatory pereopods relatively robust; P2 and P3 relatively long; P4 longest, most robust, P5 shortest, slenderest. Female gonopore with horizontally oval slightly projected vulva. Male pleon slender, pleonites 3-5 fused; telson subtriangular, about as wide as last pleonite. G1 long, slender, as long as pleon, completely concealed by pleon, apex trifid, outer face of apex with small, elongated leaf-shaped projection, inner face with rounded inferior projection and broad slightly rounded subtrapezoidal projection. G2 minute, stout, broader proximally, tapering towards distal end, base with a sulcus extending to apex, distal half curved inwards, apex stout, blunt, with a small blunt projection on lower portion. Female pleon with mostly rounded outline, covering part of thoracic sternites; telson subtriangular, not consistent with outline of pleon.

Redescription: Carapace (Fig. 3A) irregularly subhexagonal, widest point posterior to mid-length; well-sclerotized, rigid, covered in small tubercles, with regions clearly defined by sulci and depressions; front (Fig. 3B) narrow, about $1/6^{th}$ as wide as carapace, truncated when viewed dorsally, trilobed when viewed anteriorly, with shallow median sulcus; carapace behind front with 2 elevated lobes about as wide as front; orbits relatively small, with elevated margins; pterygostomial region (Fig. 4A) with elevated tuberculated crest just above membranous line; hepatic region with elevated tuberculated ridge, extending from orbits to hepatic depression, sloping down towards lateral margin of carapace; branchial region with angled elevated tuberculated ridge, extending from lateral angle of carapace to hepatic depression, carapace dropping abruptly laterally to ridge, 2 shallow sulci, anterior perpendicular and posterior oblique to branchial ridge, extending from branchial ridge to cardiac region, regions adjacent to sulci heavily tuberculated, innermost posterior branchial region with large tubercles; cardiac region well delimited by relatively deep sulcus, 2 oblique shallow sulci extending from gastric sulcus to about mid-length of gastric region, tubercles

present more densely anteriorly; cardiac region (Figs. 3C, 4B, C) well delimited by sulcus, elevated bilobed ridge extending entirely across region, delimited on sides by sulcus, with adjacent large spine; intestinal region with curved elevation, much less conspicuous than cardiac ridge, extending across most of carapace width , with large spines on each side, followed by variable number of smaller spines.

Antennules (Fig. 3D) small, tucked under front; basal article stout, large; second article elongated, slightly flattened laterally; third article subequal to second in length, elongated, tapering slightly towards distal end, slightly flattened laterally; inner ramus small, less than half of length of third article, spearhead shaped; outer ramus four-segmented, small, setose. Antennae (Fig. 3E) short, about as long as front and one of the orbits combined, 10 segmented; first and second articles stout, subcylindrical, first slightly longer than second; third article elongated, longest, subcylindrical; fourth through tenth articles shorter, tapering slightly towards distal end, with sparse spiniform setae.

Mandible (Fig. 4D) basipodite rigid, calcified, proximal region elongated, widening distally, excavated, distal region enlarged, inflated, subtriangular, excavated, fitting palpus; palpus fragile, membranous, composed of 2 articles; basal article elongated, with straight margins, setose distally; distal article flattened, elongated, longer than first, very setose proximolaterally on outer face and distally, distal margin rounded. First maxilla (Fig. 4E) small, membranous; large basal endite present, with margins curving upwards, inwards, very setose throughout; elongated endite present just above basal endite, with very slender, crooked base, tapering distally, distal end inflated, subtrapezoidal, with margins curving inwards, setose; basipodite small, less than half as long as height of inflated distal end of endite, with rounded margins; endopodite reduced, smaller than basipodite, slightly curved inwards. Second maxilla (Fig. 4F) large, fragile, membranous; whip-like endite present basally, setose; large bilobed bean-shaped endite present just above basal endite, lower lobe with rounded margins throughout, upper lobe outer margin rounded, distal margin straight, both lobes setose; endopod composed of single fused part, as long as endites, elongated, tapering towards distal end, pointed outwards; exopod very large, flattened, forming scaphognathite, upper margin rounded, outer margin almost straight, angle between upper and outer margin pointed, inner margin slightly convex.

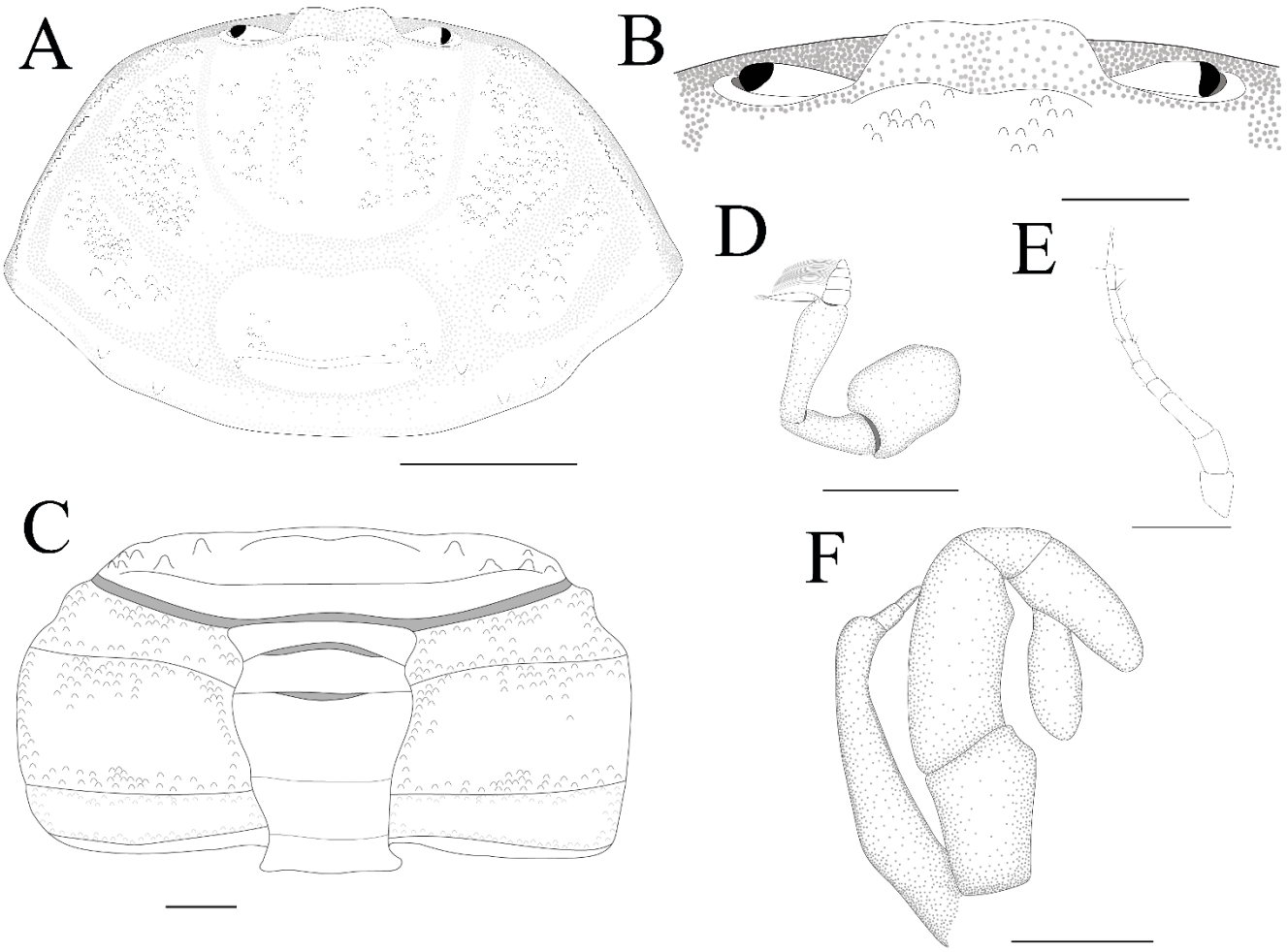

Fig. 3. *Alarconia guinotae* Coelho, 1996. Male paratype (MOFUPE 15147), offshore near Algodoal, Pará, Brazil (A–C). Male (ColBio 1), Praia do Flamengo, Ubatuba, São Paulo, Brazil (D, E). Female (CCDB 6442), Ubatuba, São Paulo, Brazil (F). A, dorsal view of carapace; B, dorsal view of front; C, posterior view of cardiac ridge; D, right antennule; E, right antenna; F, external face of right third maxilliped (setae omitted). Scale bars: A = 3 mm; B, C, F = 1 mm; D, E = 0.5 mm.

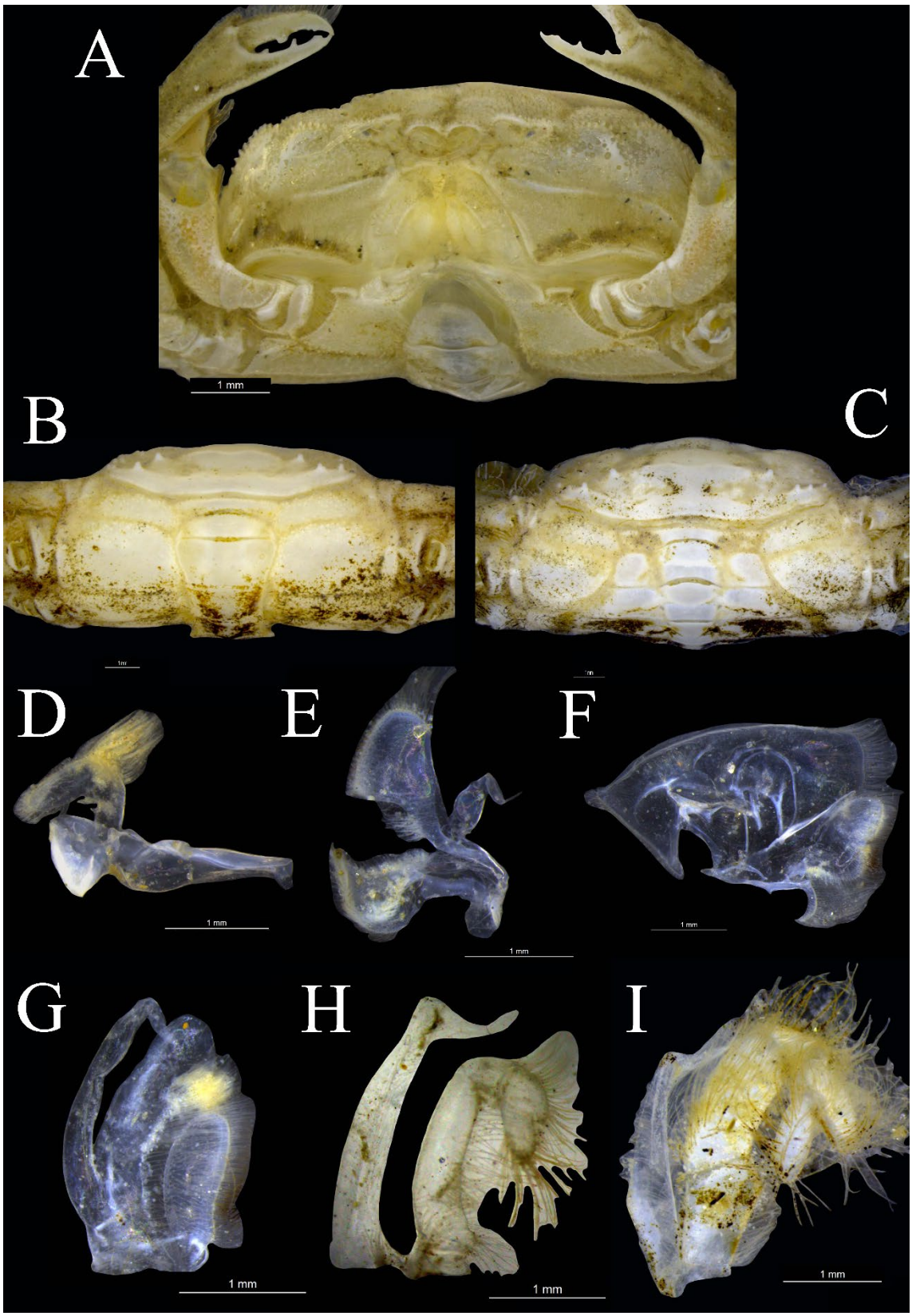

Fig. 4. *Alarconia guinotae* Coelho, 1996. Male (ColBio 1), Praia do Flamengo, Ubatuba, São Paulo, Brazil (A). Male paratype (MOUFPE 15147), offshore near Algodoal, Pará, Brazil (B). Female paratype (MOUFPE 15147), offshore near Algodoal, Pará, Brazil (C). Female (CCDB 6442), Ubatuba, São Paulo, Brazil (D–I). A, frontal view of pterygostomial region; B, posterior view of cardiac ridge; C, posterior view of cardiac ridge; D, left mandible; E, right first maxilla; F, right second maxilla; G, external face of right first maxilliped; H, external face of right second maxilliped; I, external face of right third maxilliped. Scale bars: A–I = 1mm, included in image.

First maxilliped (Mxp1) (Fig. 4G) small, membranous; small endite present basally, bean shaped, setose; a second bean-shaped endite present just above basal endite, large, longer than half of endopod, setose; endopod elongated, curved, setose, distal portion subquadrilateral, with distolateral tuft of setae; exopod elongated; basal segment curved, only slightly longer than endopod, second article small, elongated, curved, flagellum absent. Second maxilliped (Mxp2) (Fig. 4H) larger than first, membranous, more rigid than first; endopod slender, elongated; ischium and merus fused; ischiomerus elongated, slender, much longer than palp, ischium slightly oblique in relation to merus; palp relatively small; carpus tapering towards distal end; propodus small in relation to other articles, spatuliform, very setose; dactylus slightly longer than propodus, elongate, setose, with straight lateral margins and rounded distal margin, articulated proximolaterally on inner face of propodus; exopod elongated, basal article mostly tapering towards distal end, distalmost portion expanded, forming subtriangular region; second article minute, tapering towards distal end, third article as long as second, widest near mid-length, flagellum absent. Third maxilliped (Mxp3) (Figs. 3F, 4I) large, well calcified, rigid, setose overall; endopod ischium and merus fused forming ischiomerus, with deep suture clearly delimiting both articles on outer face; ischium relatively slender, long, slightly shorter than merus; merus elongated, slender, subrectangular; palpus long, longer than half of the length of ischiomerus; carpus subtrapezoidal, tapering slightly towards distal end, shorter than propodus and dactylus; propodus elongate, setose, with straight lateral margins and rounded distal margin, outer margin slightly more angled; dactylus slightly shorter than propodus, elongated, setose, with rounded margins throughout, widest at around 2/3^{rds} of length, articulated proximolaterally on inner face of propodus; exopod elongated; basal article slightly shorter than ischiomerus, widest at about 1/3rd of length, after which it mostly tapers towards distal end, distalmost portion slightly inflated, curved; flagellum present, short.

Chelipeds (Figs. 5A, 6A, B) relatively small, weak, setose, not sexually dimorphic, inner margins fit with carapace anterior outline; merus somewhat short, only slightly longer than carpus, very setose, with rugose texture, with subtriangular transversal cut, narrower proximally, widening towards distal end; carpus small, slightly shorter than palm, with rugose texture, subtrapezoidal when viewed anteriorly, widening slightly towards distal end, distal margin densely covered in short setae, small subtriangular projection present distolaterally near articulation with upper margin of palm; palm flattened laterally, outer face with several small tubercles appearing rugose, tubercles concentrated proximally, lower margin setose, expanded proximally forming angle of almost 90°, a row of small densely packed tubercles starting proximally extending to about mid-length of fixed finger, upper margin with proximal blunt projection, aligned with that of carpus, upper margin distally expanded, forming a subtrapezoidal crest, inner face with tuberculated ridge at about height

of articulation with dactylus, long upwards facing plumose setae present along ridge; fixed finger long, about 3/4ths of length of palm, slender, tapering towards distal end, lower margin almost straight, lightly setose, with a row of tightly packed tubercles extending to mid-length of fixed finger, cutting edge lightly setose, with medium-sized, blunt, narrow proximal tooth, similar tooth just past mid-length of inner face, followed by another similar tooth, wide bifid elevation close to distal end, followed by sudden drop leading to curved tip of finger; dactylus long, about as long as fixed finger, slender, tapering towards distal end, upper margin slightly convex, cutting edge lightly setose, with large, wide tooth at about mid-length, very small elevation near distal end, tip curved, lateral faces setose, inner face with long upwards facing plumose setae, outer face with irregular row of small setae.

Ambulatory pereopods (Fig. 5B–E) large, very setose, tuberculated, relative sizes P4 > P3 > P2 > P5. P2 (Fig. 5B) strong, setose; merus long, slightly inflated, upper margin with many small tubercles giving it rugose appearance except for distalmost portion, several long plumose setae present superiorly, opposable margin with small tuberculated ridge on posterior face; carpus long, more than half of length of merus, almost subtriangular when viewed anteriorly, lightly setose, somewhat flattened antero-posteriorly, lateral margins mostly convex, upper margin expanded into crest, covered in tubercles, opposable margin with smooth setose ridge; propodus flattened antero-posteriorly, short, about half of length of carpus, lightly setose superiorly, inferiorly and on posterior margin, upper margin convex with tuberculated crest, opposable margin very convex with smooth setose ridge; dactylus flattened laterally, perpendicular to flattening axis of carpus and propodus, lanceolate, slightly longer than propodus, setose on lateral margins, more so on posterior margin, tip corneous and curved inwards. P3 (Fig. 5C) longer but not stronger than P2, strong, setose, articles overall similar to P2; merus long, proportionally longer than that of P2, propodus proportionally longer, slightly longer than half of length of carpus. P4 (Fig. 5D) longest, stoutest, inflated, armed, lightly setose; merus inflated, with rounded and setose upper margin, lower margin almost straight, upper margin with many small tubercles, appearing rugose, outer face upper proximal portion with tuberculated ridge, mesial portion with ridge with tubercles of varied sizes, ranging from proximal third to distal end of merus, merus sloping down towards opposable margin below ridge, opposable margin with 2 rows of relatively large spines, parallel proximally, diverging towards articulation with carpus, anterior ridge with less prominent tubercles distally, posterior ridge with prominent tubercles throughout, distal portion of merus on outer face densely packed with small tubercles, inner face of merus smooth; carpus relatively long, about half of length of merus, setose, outer face granulated, rugose, inner face smooth, upper margin projected into small tuberculated crest, posterior margin with densely packed small setae; propodus subtrapezoidal, wider proximally, tapering towards distal end, slightly longer than carpus, setose, densely tuberculated on outer face,

lower portion of outer face with large tubercles, upper margin with very low tuberculated crest lined by dense small setae, opposable margin setose, with a row of larger tubercles extending from proximal to distal end; dactylus somewhat flattened, although thicker, more robust than those of P2 and P3, lanceolate, lined by setae on both sides, with corneous tip curved inwards. P5 (Fig. 5E) shortest, stout, weakest among pereopods, densely setose; merus subrectangular when viewed from above, densely setose especially on upper and lower margin, granulated on outer face, inner face smooth; carpus subtrapezoidal when viewed from above, about half as long as merus, with setose upper margin, outer face granulated, upper margin with a tuberculated ridge, not elevated into crest; propodus subtrapezoidal, wider proximally, tapering towards distal end, upper margin setose, with tuberculated ridge lined by dense small setae, outer face tuberculated, opposable margin with larger tubercles, inner face smooth; dactylus somewhat flattened, thicker, more robust than those of other ambulatory pereopods, lanceolate, tip corneous, curved outwards.

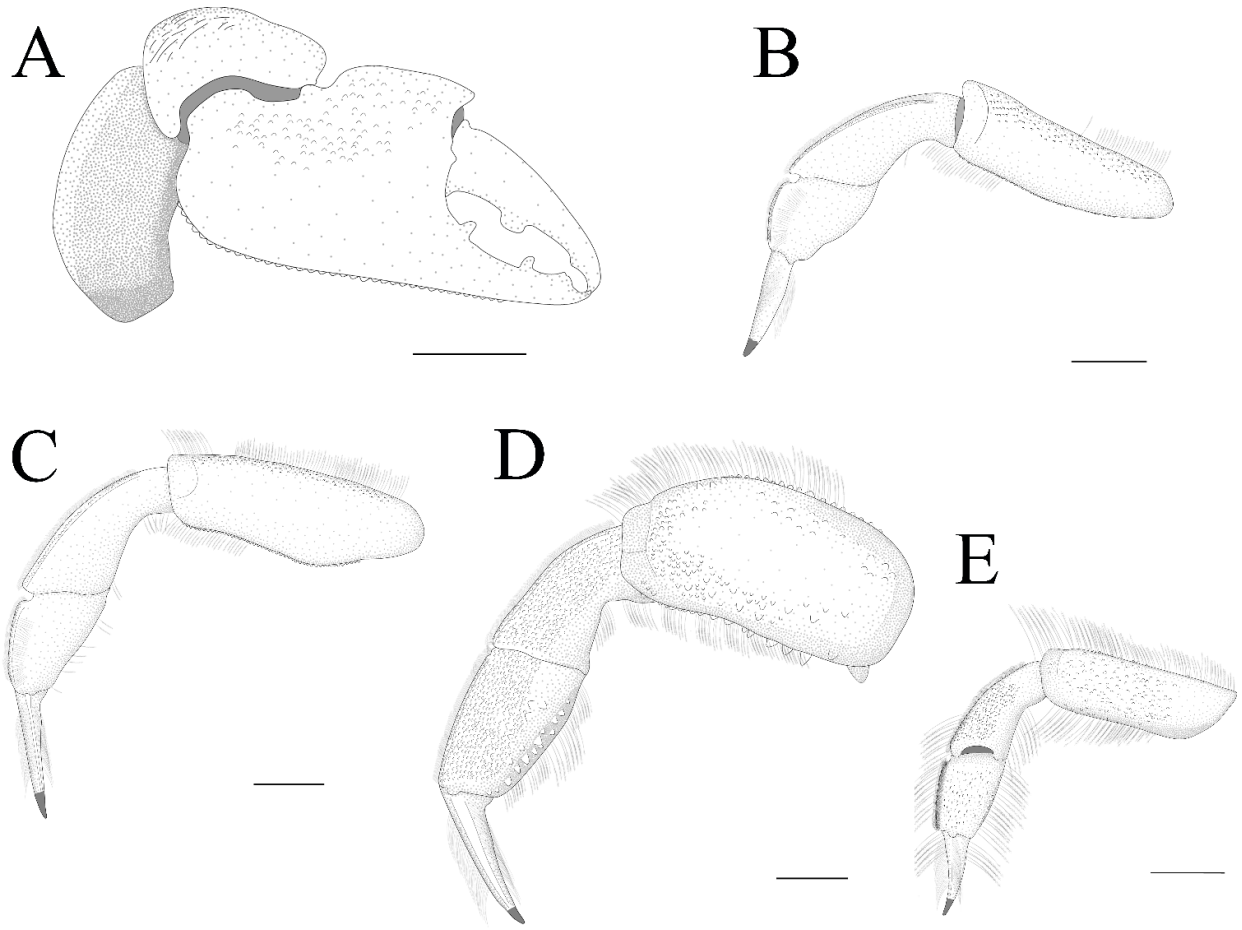

Fig. 5. *Alarconia guinotae* Coelho, 1996. Male paratype (MOUFPE 15147), offshore near Algodoal, Pará, Brazil (A–E). A, external face of right cheliped (setae omitted); B, dorsal view of left second pereopod; C, dorsal view of left third pereopod; D, dorsal view of left fourth pereopod; E, dorsal view of left fifth pereopod. Scale bars: A–E = 1 mm.

Male thoracic sternites (Figs. 6C, 7A) large, mostly rugose; sternites 1 and 2 (bearing Mxp1 and Mxp2) fused into a small longitudinally narrow structure, smooth; sternites 3 and 4 (bearing Mxp3 and cheliped) fused into a wide plate, with a lateral suture visible anterolaterally and a large transverse sulcus dividing the fused sternites mesially, granulated, with several tubercles present throughout, plate irregular in shape; sternites 5-8 (bearing ambulatory pereopods) free, subrectangular, tuberculated proximally, distally and along articulations with other sternites, smooth medially; all sternites smooth within pleonal cavity. Female thoracic sternites large, mostly rugose outside of pleonal cavity; sternites 1 and 2 similar to those of male; sternites 3 and 4 also similar to those of male, lightly rugose outside of pleonal cavity, smooth otherwise, dropping abruptly inside of pleonal cavity; sternites 5-8 free, subtrapezoidal; 5 and 6 mostly covered by pleon, rugose outside of pleonal cavity, otherwise smooth, dropping abruptly inside of pleonal cavity; sternite 6 bearing female gonopore; sternites 7 and 8 mostly outside of pleonal cavity, rugosity similar to that of male. Female gonopore (Fig. 6D) large, conspicuous, vulva slightly projected, oval; operculum membranous, covering gonopore.

Male pleon (Figs. 7B, 8A) long, slender, extending to buccal cavity, lined by very small setae; first pleonite small, short, widest, subtrapezoidal, tapering towards distal end, with a small row of tubercles along proximal margin, distal margin concave; second pleonite slightly longer than first, subtrapezoidal, slenderer proximally, widening towards distal end, proximal margin convex, distal margin straight; third through fifth pleonites fused with visible sutures, third pleonite subtrapezoidal, wide, widest proximally, tapering towards distal end, long, about twice as long as second pleonite; fourth pleonite subtrapezoidal, as wide as distal end of third proximally, tapering towards distal end, as long as third; fifth pleonite subquadrate, margins straight, as long as fourth; sixth pleonite free, subquadrate, margins straight, as long as fifth. Telson small, slender, subtriangular lined by small setae. G1 (Figs. 7C, 8B–D) long, as long as pleon, concealed by pleon, extending almost to Mxp3 origin, slender, lined by setae, almost straight proximally, curved inwards at about last quarter of its length; apex small, without setae, trifid, outer face of apex with small, elongated leaf-shaped projection, inner face with rounded inferior projection and broad slightly rounded subtrapezoidal projection. G2 (Fig. 7D) minute, stout, broader proximally, tapering towards distal end, base with sulcus extending to apex, distal half curved inwards, apex stout, blunt, with small blunt projection on lower portion.

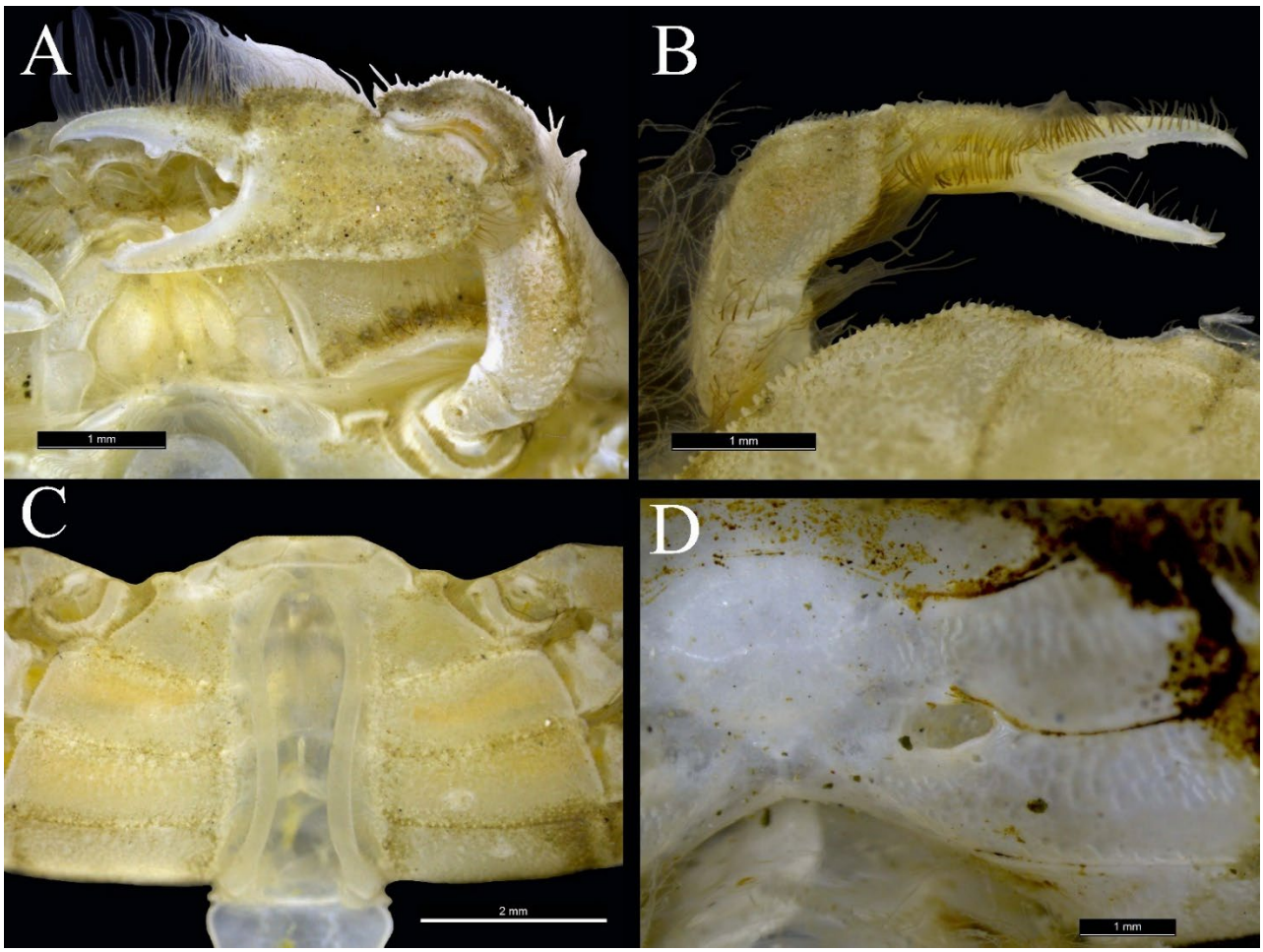

Fig. 6. *Alarconia guinotae* Coelho, 1996. Male (ColBio 1), Praia do Flamengo, Ubatuba, São Paulo, Brazil (A–C). Female (CCDB 6442), Ubatuba, São Paulo, Brazil (D). A, frontal view of external face left cheliped; B, dorsal view of internal face of left cheliped; C, ventral view of male thoracic sternites; D, left female gonopore. Scale bars: A, B, D = 1 mm; C = 2 mm; included in image.

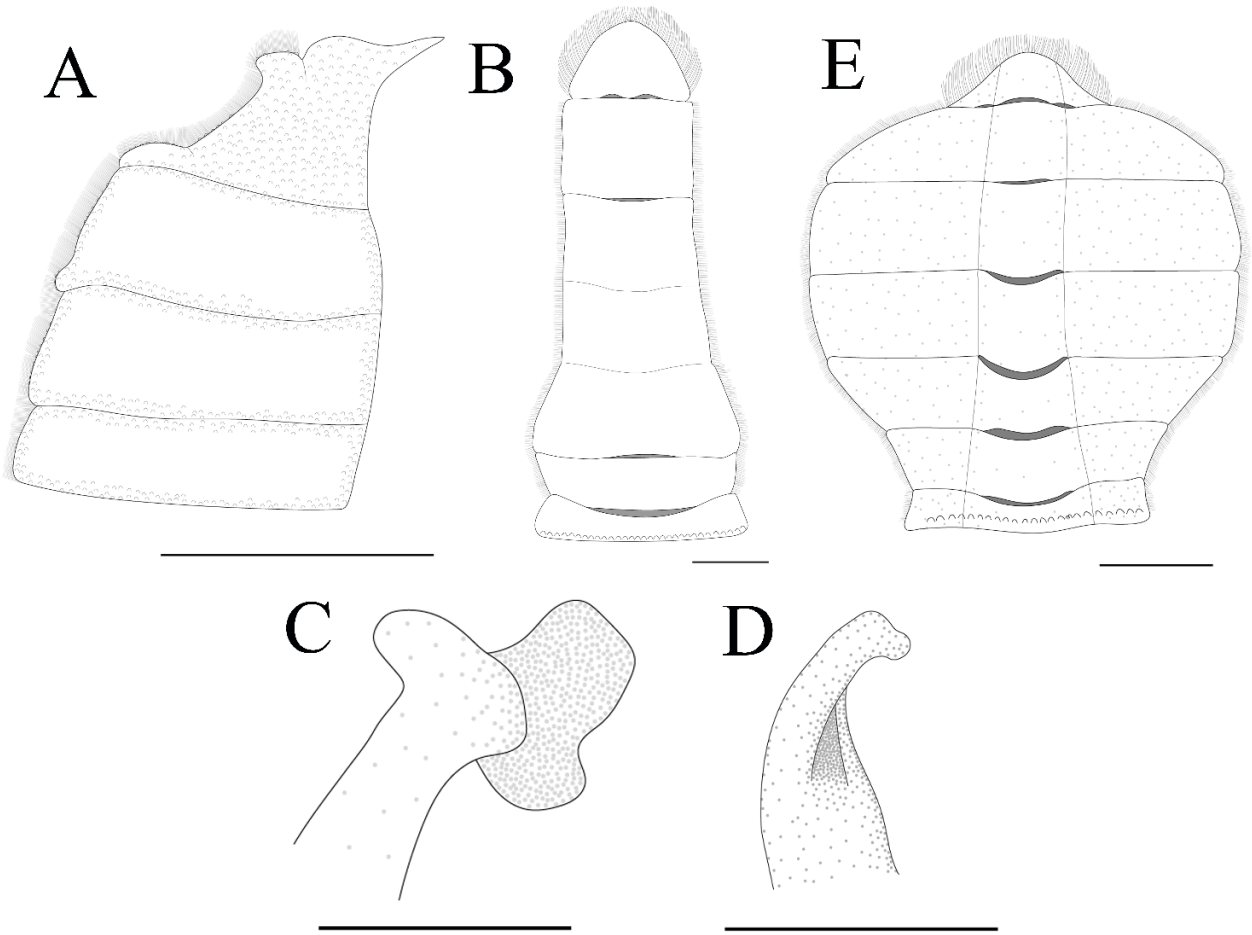

Fig. 7. *Alarconia guinotae* Coelho, 1996. Male (ColBio 1), Praia do Flamengo, Ubatuba, São Paulo, Brazil (A). Male paratype (MOUFPE 15147), offshore near Algodoal, Pará, Brazil (B, D). Female paratype, same information as male paratype (C). Male (CCDB 6932), Praia do Cedro, Ubatuba, São Paulo, Brazil (E). A, ventral view of right male thoracic sternites; B, ventral view of male pleon; C, ventral view of female pleon; D, pleonal face of apex of right male first gonopod; E, pleonal face of right male second gonopod. Scale bars: A, C = 2 mm; B = 1 mm; D, E = 0.5 mm.

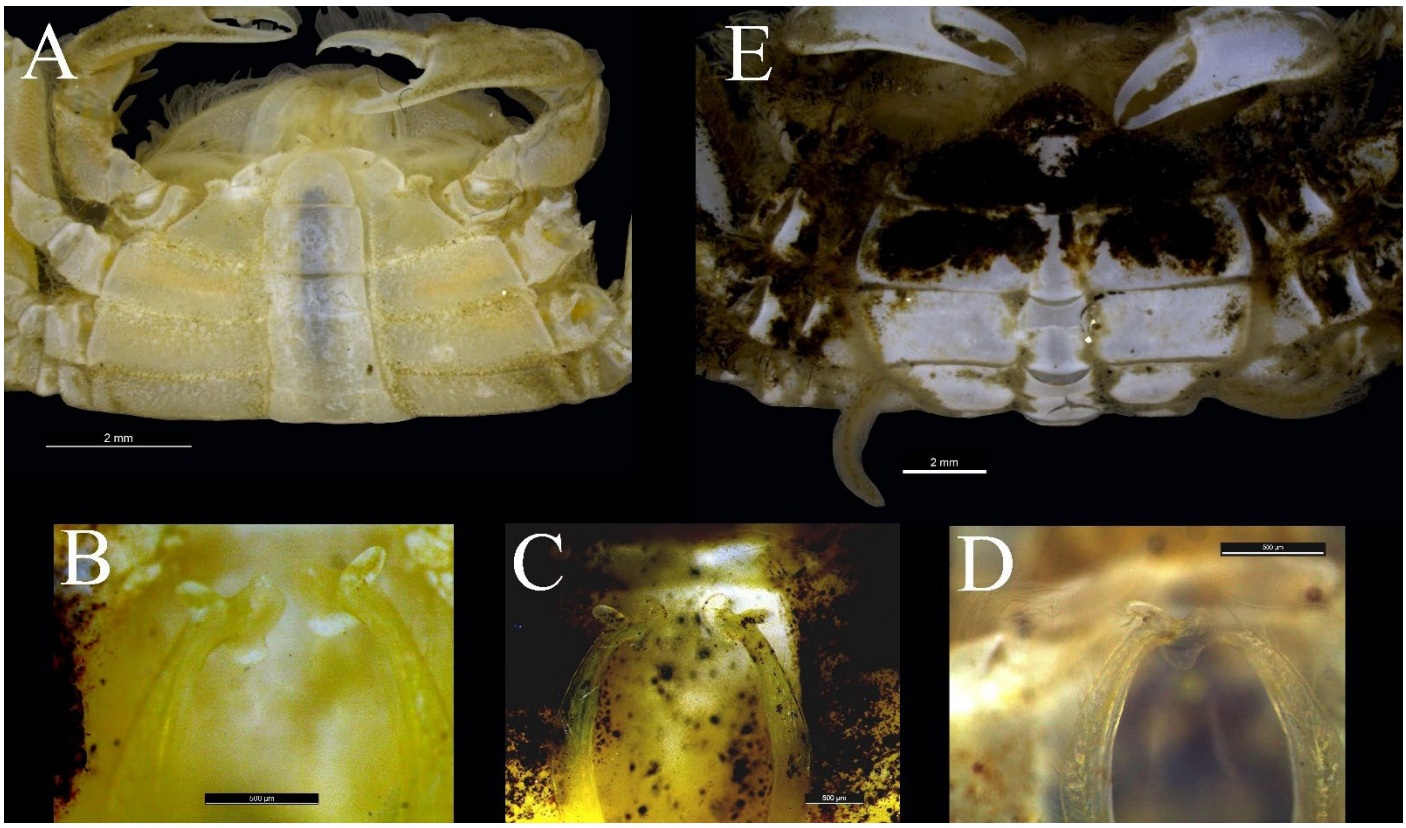

Fig. 8. *Alarconia guinotae* Coelho, 1996. Male (ColBio 1), Praia do Flamengo, Ubatuba, São Paulo, Brazil (A, E). Female paratype (MOUFPE 15147), offshore near Algodoal, Pará, Brazil (B). Male paratype (MOUFPE 15147), offshore near Algodoal, Pará, Brazil (C). Male (CCDB 6932), Praia do Cedro, Ubatuba, São Paulo, Brazil (D). A, ventral view of male pleon; B, ventral view of female pleon; C, D, E, pleonal view of first male gonopods. Scale bars: A, B = 2 mm; C, D, E = 0.5 mm; included in image.

Female pleon (Figs. 7E, 8E) wide, vertically suboval in shape, lined by setae, central portion of pleonites elevated; first pleonite short, thinnest, subtrapezoidal, widest proximally, tapering distally, row of small tubercles along proximal margin; second pleonite subtrapezoidal, twice as long as first, about as wide as first, proximally as wide as distal portion of first, widening distally becoming as wide as proximal portion of first; third pleonite subtrapezoidal, as long as second, wider than first and second, thinner proximally, widening towards distal end; fourth pleonite longer and wider than third, almost subrectangular, proximal margin slightly thinner than distal margin, articulation between fourth and fifth pleonites the widest point of pleon; fifth pleonite subtrapezoidal, wide, as long as fourth, wider proximally, tapering towards distal end; sixth pleonite subtrapezoidal, as long as fourth, as wide as distal end of fourth proximally, tapering towards distal end, lateral margins strongly angled, rounded. Telson small, not continuous with margins of pleon, subtriangular, lined by setae.

Type locality: Offshore (~0°26'S 47°35'W), near Algodoal, Pará, Brazil.

Distribution: Known from the Southwestern Atlantic in Brazil, including the states of Pará, Alagoas, São Paulo and Paraná (Coelho 1996; Bezerra et al. 2006).

Habitat and host: Found on sandy bottoms from the intertidal zone up to 25 m in depth (Coelho 1996). The host of this species is still unknown (see DISCUSSION).

Remarks: *Alarconia guinotae* was described by Coelho (1996) and was the first record of the genus for Brazil and the Atlantic. Coelho (1996) proposed the following diagnostic characters: Carapace slightly wider than long, cardiac ridge consisted of a series of closely spaced tubercles (Coelho 1996). However, in the discussion, Coelho (1996) also mentions that the texture of the branchial region, including the presence of two sulci, and the G1 not being exposed are also useful in distinguishing this species from *A. seaholmi*. The description of *A. guinotae* is brief, and the illustrations do not show important details of the morphology, which led us to construct a redescription. With the information provided by Coelho (1996) and further analysis of specimens, we have also observed a series of other characteristics that distinguish *A. guinotae* from the type species, *A. seaholmi*, as mentioned above. Although similar and clearly belonging to the same genus, these two species are distinct morphologically and do not co-occur, thus making them easily distinguishable.

No molecular data was obtained for *A. seaholmi*, since only one specimen is known, the male holotype, for which we did not have tissue samples. However, given the shared morphological characters that set these two species apart from the rest of the pinnotherids, it is clear that they are closely related.

DISCUSSION

Phylogeny of Pinnotheroidea

The phylogenetic trees constructed in the present study mostly resemble others in literature (see Palacios Theil et al. 2016; Tsang and Naruse 2023; Chow et al. 2023). The three families included within Pinnotheroidea are all recovered as monophyletic groups, all with very high to maximum support, in our ML and BI analyses. Herein and in previous studies (see Palacios Theil et al. 2016; Tsang and Naruse 2023), Parapinnixidae is the sister group of all other pinnotheroids, and Tetriasidae is more closely related to Pinnotheridae. Possible morphological support for this relationship can be found in the overall morphology of the Mxp3, in which the dactylus usually articulates either proximolaterally, subdistally (in Pinnotheridae) or distolaterally (Tetriasidae) on the propodus, which is distinct from most other Brachyura, whereas in Parapinnixidae the dactylus articulates distally on the propodus, like in most other crabs. Thus, this different articulation of the Mxp3 propodus and dactylus could be a synapomorphy of the clade (Pinnotheridae + Tetriasidae). However, Chow et al. (2023), using a more robust set of molecular data including eight genes,

recovered a different tree topology, with Parapinnixidae and Tetriasidae being sister taxa. This leads to different interpretations of these morphological similarities, with a likely convergence between tetriasids and pinnotherids. Within Pinnotheridae, the phylogenetic relationships recovered herein were also congruent with some previous studies (*e.g.*, Palacios Theil et al. 2016; Chow et al. 2023), with Pinnixulalinae as the sister group of a clade consisting of Pinnixinae and Pinnotherinae, with all three being monophyletic. In our study, Alarconiinae stat. nov. is positioned as the sister group of the remaining pinnotherids.

Distribution of *Alarconia seaholmi* and *A. guinotae*

Alarconia guinotae has been found throughout the Brazilian coast, in the states of Pará, Alagoas, São Paulo and Paraná (Coelho 1996). However, apart from São Paulo and Paraná, which are adjacent, these localities are separated by over 1000 km of coastline. This raises suspicions regarding this disjunct distribution. It is very likely that this taxon occurs in these areas but has not yet been sampled from such localities. Given this context, it seems that this genus is rare or at least hard to collect. Thus, little is known about this species' ecology, including its host (see below).

Furthermore, the distribution of the two species on opposite sides of the American continent, with *A. guinotae* in the western Atlantic and *A. seaholmi* in the eastern Pacific, might suggest that vicariant events led to the separation of these two species after the complete closure of the isthmus of Panama, as is the case for many groups of animals (*e.g.*, Thacker 2017; Lima et al. 2020).

Evolution of Pinnotheroidea and host association in *Alarconia*

Large-scale pinnotheroid phylogenetic systematics have been the target of many studies (*e.g.*, Palacios-Theil et al. 2009; Palacios Theil et al. 2016; Tsang and Naruse 2023; Chow et al. 2023) and are becoming better understood. Herein, our phylogenetic hypotheses recover a similar tree topology to those of these studies, further evidencing the existence of three families within Pinnotheroidea (Parapinnixidae, Tetriasidae and Pinnotheridae) and four subfamilies within Pinnotheridae (Alarconiinae stat. nov., Pinnixulalinae, Pinnixinae and Pinnotherinae). Thus, given this context, some inferences can be made regarding the evolution of this group and the host association of *Alarconia*.

Hultgren et al. (2022) concluded that the width of the carapace in pinnotherids is strongly associated with the type of host, with crabs with a wider carapace being associated with burrowing or tube-dwelling hosts, such as annelids and other malacostracans (stomatopods or decapods), whereas those that have rounder carapaces are commensal with echinoderms, mollusks and

tunicates. Additionally, Chow et al. (2023) also concluded that most inquiline species of pinnotheroids (mostly members of Pinnixinae, Pinnixulalinae, Parapinnixidae and Tetriasidae) have at least a slightly wider carapace, whereas pinnotherines (mostly associated with mollusks and echinoderms) have rounder ones. Thus, given this situation, it is very likely that *Alarconia* is associated with a burrowing or tube-dwelling animal, likely an annelid or malacostracan. It is also possible that host association and overall carapace morphology are related to the phylogenetic history of the group, with the inquiline commensal lifestyle and relatively wide carapace being plesiomorphies that were retained by Parapinnixidae, Tetriasidae, Pinnixulalinae and Pinnixinae (Chow et al. 2023), and likely Alarconiinae stat. nov. Other brachyuran groups that engage in symbiotic relationships with burrowing animals, such as Aphanodactylidae Ahyong & Ng, 2009 and Asthenognathinae, also appear to possess a proportionally wider carapace (see Ahyong and Ng 2009; Muñoz et al. 2025), although this has not been formally tested. However, if corroborated by future studies, this might further support the hypothesis that a wider carapace is related to an inquiline lifestyle in commensal crabs, with similar evolutionary pressures convergently leading to this characteristic in at least the three abovementioned groups.

Other morphological characteristics in pinnotheroids that appear to be related to the symbiotic lifestyle are the Mxp3 and ambulatory pereopods, as highlighted by Chow et al. (2023). The Mxp3 structure of pinnixines, pinnixulalines and alarconiines (as observed herein) is similar, with the articles of the palp forming a basket-like structure, forming a net of setae which enables suspension feeding, which could be used by inquiline taxa to exploit the water current generated by the hosts for feeding (Chow et al. 2023). The enlargement of one pair of ambulatory pereopods, as observed in Pinnixinae, Pinnixulalinae, and Alarconiinae stat. nov. is considered an adaptative characteristic of an inquiline lifestyle, facilitating locomotion (Zmarzly 1992) or the gripping of the walls of tubes and burrows (de Gier and Becker 2020). This is furtherly evidenced by the presence of tubercles or spines in the flexor margins of the ambulatory pereopods of some pinnixines and pinnixulalines (Chow et al. 2023), which is also observed in Alarconiinae stat. nov.

Chow et al. (2023) studied the evolution of host association in Pinnotheroidea and concluded that the symbiotic lifestyle appeared once in the clade and first evolved in the form of inquilinism, with the ancestral species living inside either burrows or tubes. The authors also mention that the last common ancestor of Pinnotheridae was likely associated with burrow-dwelling hosts, which was retained in Pinnixinae and Pinnixulalinae. Discovering the host of *Alarconia* would be very important in supporting this hypothesis, given that it is the sister group of all other pinnotherids. If *Alarconia* is associated with burrowing animals, it is likely that the last common ancestor of Pinnotheridae was associated with a burrow-dwelling host. However, if it is associated

with tube-dwelling animals, it is likely that the ancestor of Pinnotheridae was also associated with tube-dwelling hosts, given that Parapinnixidae and Tetriasidae also share this lifestyle.

Furthermore, it is possible that the similarities of Alarconiinae stat. nov. and Pinnixulalinae are shared plesiomorphies. Our phylogenetic analyses indicate that the presence of a merely well-calcified carapace and heavily armed ambulatory pereopods with large spines might be plesiomorphic within Pinnotheridae, since these characteristics are present in Alarconiinae stat. nov. and in Pinnixulalinae, the latter which, in our analyses, is the siter group of (Pinnixinae + Pinnotherinae). It is also possible that these and other characteristics are convergences between these two groups, which could be further elucidated by the discovery of the hosts of Alarconiinae stat. nov.

Additionally, the overall morphology of the mouthparts of pinnotherids, as described herein for *Alarconia* (Figs. 3F, 4D–I), although rarely described and illustrated (except for the Mxp3), may possess important neglected anatomical characteristics useful in understanding the phylogeny and evolution of the group (de Gier and Becker 2020). Lastly, female gonopores and other reproductive structures, as well as internal anatomy, might be useful in large scale comparative studies of Pinnotheroidea. Since many characteristics that are used in pinnotherid taxonomy can sometimes prove to be quite variable within species (see Ng and Ahyong 2022), exploring such neglected traits might be useful in future taxonomic studies.

Fig. 9. *Alarconia guinotae* Coelho, 1996, whole animals. A, male paratype (MOUFPE 15147); B, female paratype (MOUFPE 15147); C, male (ColBio 1); D, male (CCDB 6932). Scale bars: A–D = 2 mm; included in image.

CONCLUSIONS

With our multigene phylogenetic hypotheses, we conclude that *Alarconia* is the sister group of all other pinnotherids. We also elevate Alarconiinae stat. nov. to the subfamily level. The morphological data presented here provide diagnostic characters that distinguish Alarconiinae stat. nov. from other pinnotheroid groups and support the redescription of *A. guinotae*. Furthermore, it is likely that members of the genus have a wider distribution than is currently known, given that this taxon is rare or hard to collect. Lastly, some morphological and ecological similarities shared by Alarconiinae stat. nov. and other subfamilies may reflect either retained ancestral conditions or convergent evolution.

Key to the families and subfamilies of Pinnotheroidea De Haan, 1833

1a. Ambulatory pereopods increasing in size from P2 to P3 or P4; P3 or P4 longest ……..……..…..……..... 2
1b. Ambulatory pereopods decreasing in size from P2 to P5, with P2 being longest, most robust ……..…… Parapinnixidae Števčić, 2005
2a. Mxp3 dactylus, when present, inserted subdistally or proximolaterally on lateral margin of propodus ……...… Pinnotheridae De Haan, 1833 ……. 3
2b. Mxp3 dactylus always present, inserted laterally on distal corner of propodus ……..……. Tetriasidae Tsang and Naruse, 2023
3a. Carapace well-sclerotized, with well-defined regions. Ambulatory pereopods always with spines or tubercles 4
3b. Carapace more flexible and less sclerotized, generally with poorly defined regions. Ambulatory pereopods generally without large spines 5
4a. Carapace with the widest point at about mid-length. Mxp3 with ischium and merus, fused, forming an ischiomerus, with or without a weak suture between them, ischiomerus wide, robust ..... Pinnixulalinae Palacios Theil, Cuesta and Felder, 2016
4b. Carapace irregularly subhexagonal, widest point posterior to mid-length. Mxp3 with ischium and merus functionally fused, but with a clearly delimited suture, ischium and merus slender ……..... Alarconiinae Števčić, 2005 stat. nov.
5a. Carapace approximately as wide as long. P4 not distinctly more robust than other ambulatory pereopods ……..... Pinnotherinae De Haan, 1833
5b. Carapace clearly wider than long. P4 distinctly more robust and elongated than other ambulatory pereopods ..... Pinnixinae Števčić, 2005

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Competing interests: FCB and FLM declare that they have no conflict of interest.

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