Zoosyst. Evol. 101 (4) 2025, 1669–1689 | DOI 10.3897/zse.101.159300

PENSOFT.

für Natur MUSEUM FÜR NATURKUNDE BERLIN

Phylogenetic relationships, taxonomic contextualization and insight on the evolution of the freshwater crabs' genus *Dilocarcinus* H. Milne Edwards, 1853 (Decapoda, Trichodactylidae): a widespread species complex in the largest South American lowland river basins

Nielson Felix Caetano França[1,2], Célio Magalhães[1,3], Fernando Luis Mantelatto[1]

1 *Laboratory of Bioecology and Systematic of Crustaceans (LBSC), Department of Biology, Faculty of Philosophy, Science and Letters of Ribeirão Preto (FFCLRP), University of São Paulo, Av. Bandeirantes, 3900, 14040–901, Ribeirão Preto, São Paulo, Brazil*

2 *Laboratory of Ecology and Evolution of Crustaceans (LABEEC), Department of Botany and Zoology (DBZ), Bioscience Center (CB), Federal University of Rio Grande do Norte (UFRN), Av. Senador Salgado Filho, 3000, 59078–970, Natal, RN, Brazil*

3 *Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil*

https://zoobank.org/2368532A-765D-4058-AE7B-6F27F667C5E2

Corresponding author: Fernando Luis Mantelatto (flmantel@usp.br)

Academic editor: Magdalini Christodoulou ♦ **Received** 18 May 2025 ♦ **Accepted** 14 August 2025 ♦ **Published** 2 September 2025

Abstract

The phylogeny of the genus *Dilocarcinus* H. Milne Edwards, 1853 and the taxonomic status of *Dilocarcinus pagei* Stimpson, 1861 *lato sensu* are investigated using a molecular and morphologic integrative approach. This species is distributed over a large part of Neotropical South America in the Amazon and La Plata (Paraguay–Paraná rivers) hydrographic basins. We evaluated the genetic variability of this species along these river basins to understand the degree of the variability among its representatives, their taxonomic status, and to address the gaps in the north–south distribution that remain despite its wide area of occurrence. The morphological analysis included NanoCT–Scan images, and the molecular analysis was based on mitochondrial markers COI and 16S rRNA and included Maximum Likelihood Trees, Bayesian Inference, Genetics Distance Matrix, and Haplotype Networks. These studies revealed and supported the existence of two cryptic species: a southern one, distributed in the La Plata basin (Paraguay–Paraná basin), that kept the name *D. pagei* Stimpson, 1861, and a northern one, occurring in the Amazon basin, the name *D. cristatus* Bott, 1969 was revalidated. We discuss conjecture that *Dilocarcinus* originated in the western Amazon region between the Middle Eocene and the Lower Miocene (c. 41–19 Ma), most likely in the Oligocene (31 Ma), and later expanded to other regions in southern and eastern South America.

Key Words

Brachyura, cryptic species, DNA Barcode, genetic variability, nano-tomography, neotropical region

Introduction

The specific composition of the genus *Dilocarcinus* H. Milne Edwards, 1853 has varied considerably since it was first erected with four species. In subsequent revisions, Rathbun (1906a) included nine species under the subgenus *Trichodactylus* (*Dilocarcinus*). More than 60 years later, Pretzmann (1968), treating it at generic level, included 12 species and subspecies in *Dilocarcinus*. Bott (1969) separated *Dilocarcinus* into two subgenera, with *Dilocarcinus stricto sensu* comprising three species and one subspecies and established new genera and subgenera for some of the other species. Rodríguez (1992) did not recognize the subgenera and included 11 species in *Dilocarcinus*, but Magalhães and Türkay (2008) restricted *Dilocarcinus* to only three species, *Dilocarcinus pagei* Stimpson, 1861, *D. septemdentatus* (Herbst, 1783), and *D. truncatus* Rodriguez, 1992.

A recent taxonomic study of the genus *Dilocarcinus* based on morphological and molecular data revealed that *D. septemdentatus* (Herbst, 1783) *sensu* Magalhães and Türkay (2008) consisted of a species complex with three species (França et al. 2024). One species, *D. truncatus* Rodríguez, 1992, could not be included in that study because it is known only from a single male specimen from the Beni River in the province of Beni, in the Bolivian Amazon (Rodríguez 1992; Magalhães and Türkay 2008) and DNA could not be isolated from a sample of its tissue.

Similarly, *D. pagei* Stimpson, 1861 also has a somewhat convoluted taxonomic history. In the first review after its description by Stimpson (1861), Rathbun (1906a) treated *D. pagei* as a synonym of *Trichodactylus* (*Dilocarcinus*) *orbicularis* (Meuschen, 1781), an unavailable name according to Opinions 260–261 (ICZN 1954a, b) and which would correspond to *D. septemdentatus* (see França et al. 2024). Bott (1969) revalidated *D. pagei* and divided it into two subspecies, describing *D.* (*D.*) *pagei cristatus* Bott, 1969 from the Solimões River in the Brazilian Amazon. Soon after, Pretzmann (1978), described another subspecies, *D.* (*D.*) *pagei enriquei* Pretzmann, 1978 based on a single specimen from the southwestern Amazon basin in Peru. Lopretto (1981) synonymized *D.* (*D.*) *pagei cristatus* Bott, 1969 under the nominal form, an action that was followed by Rodríguez (1992) and Magalhães and Türkay (1996; 2008). Magalhães and Türkay (1996) provisionally recognized *D. pagei enriquei*, but later (Magalhães and Türkay 2008), those authors synonymized it under *D. pagei* because they understood that the somatic differences in the carapace and pereopods of its holotype were due to abnormal characteristics of this single specimen, since other specimens from the Peruvian Amazon did not exhibit such characteristics (that were not reflected in morphological differences of the gonopods from the other male specimens examined).

Dilocarcinus pagei l. s. has the widest distribution of a trichodactylid crab (Magalhães and Türkay 2008), that encompasses much of the neotropical region of South America where it is found along the lowlands of the Amazon basin through Colombia, Peru, Brazil, and Bolivia, as well as in the rivers of the Paraguay and lower Paraná rivers basins, in Brazil, Paraguay, and Argentina (Magalhães and Türkay 2008). The presence of this species in the upper Paraná River basin, in the Brazilian states of Paraná, São Paulo, and Minas Gerais (Magalhães et al. 2005; Azevedo-Santos and Lima-Stripari 2010) may be the result of anthropic action (Magalhães et al. 2005; Magalhães 2016).

Previous studies have revealed that other species of freshwater crabs that have a wide geographic distribution may actually be species complexes with a high degree of morphological similarity but showing distinctions in other biological aspects (Ng and Yeo 2007; Souza-Carvalho et al. 2017; França et al. 2024). In these cases, the use of molecular tools has been very useful in recognizing cryptic species and therefore helping to clarify and, in most cases, resolve a number of taxonomic problems (Daniels et al. 2003; Jesse et al. 2010; Keikhosravi and Schubart 2013; Phiri and Daniels 2014, 2016; Souza-Carvalho et al. 2017, 2025; Mantelatto et al. 2022, 2024; Peer et al. 2023; França et al. 2024).

In this study, we present the phylogeny of the genus *Dilocarcinus* obtained from an integrative study based on morphological and molecular data using two mitochondrial genes, a taxonomic revision of the species *D. pagei sensu* Magalhães and Türkay (2008) along its range of distribution to assess its genetic variability and to evaluate whether it is a species complex.

Materials and methods

Sampling

The specimens used are deposited in the crustacean collection of the following institutions: Coleção de Crustáceos do Departamento de Biologia (CCDB), Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; Coleção de Zoologia do Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Brazil; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Forschungsinsitut und Naturmuseum Senckenberg (SMF), Frankfurt a. M., Germany; Museu Paraense Emílio Goeldi (MPEG), Belém, Brazil; Museu de Zoologia, Universidade Estadual de Londrina (MZUEL), Londrina, Brazil; Museu de Zoologia, Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museum der Natur-Zoologie (ZMH), Leibniz-Institut zur Analyse des Biodiversitätswandels, Hamburg, Germany; Naturhistorisches Museum Wien (NHMW), Vienna, Austria. Additional specimens were obtained through new collections carried out in the region of the upper Paraná River basin under the collection permits (see acknowledgements) and through donations from other researchers. In addition to the morphological examination of the specimens, muscle tissue samples were obtained for molecular analysis. Tissues of the holotypes of *Dilocarcinus pagei enriquei* Pretzmann, 1968 and *Dilocarcinus truncatus* Rodríguez, 1992 were sampled but DNA extraction proved to be unfeasible.

Obtaining molecular data

Molecular analyses were performed with fragments of two mitochondrial genes, Cytochrome Oxidase I subunit (COI) and 16S rRNA (16S). Both genes have proven to be effective in a number of studies that used molecular analyses of decapod crustaceans, including phylogenetic and variability studies of different groups (Buranelli et al. 2019; Oliveira et al. 2021; Mantelatto et al. 2021) and freshwater crabs (Souza-Carvalho et al. 2017, 2025; Mantelatto et al. 2022, 2024; Peer et al. 2023; França et al. 2024).

The DNA extraction, amplification, purification, and sequencing steps followed the protocols of Schubart et al. (2000) adapted according to Mantelatto et al. (2018). DNA extraction was performed from the muscle tissue of adult male pereopods, using a protocol with Chelex® Resin (Estoup et al. 1996) and the concentration and quality of the extraction products were evaluated using a spectrophotometer of the type NanoDrop® 2000/2000 c (Thermo Scientific, Wilmington, DE, USA).

The fragments of COI and 16S were amplified by the PCR technique, using the specific primers (Table 1), with the following cycle: initial denaturation at 94 °C for 5 min, 40 cycles of denaturation at 95 °C for 45 sec, with annealing at 50 °C (COI) and 48 °C (16S) for 1 min, extension at 72° C for 1 min and a final extension step at 72 °C for 10 min. The PCR products were evaluated by electrophoresis, visualized using an L-PIX EX® photo documenter on agarose gel (1.5%) and later purified using the SureClean® Plus kit (Bioline Reagents, London, UK), according to the supplier's protocol, and, subsequently, sequenced using the ABI Big Dye® Terminator Mix on an ABI Prism 3100 Genetic Analyzer® following the manufacturer's protocols (Applied Biosystem).

The obtained strands (forward and reverse) were edited and used to create consensus sequences on Geneious Prime® (2021.2.2 Biomatters Ltd), with identification confirmed by BLAST from NCBI (http://blast.ncbi.nlm.nih.gov/Blast.cgi). Finally, the sequences were checked regarding the existence of stop codons in the Expasy platform (https://web.expasy.org/translate/). The information corresponding to the specimens used in the analyses was listed in Table 2.

Molecular analysis

Molecular analysis used the new sequences generated from our analysis, including its congeners *D. septemdentatus*, *D. spinifer* H. Milne Edwards, 1853, *D. montinavis* França, Magalhães & Mantelatto, 2024, and outgroup *Goyazana castelnaui* (H. Milne Edwards, 1853) obtained from França et al. (2024). All sequences are listed in Table 1 and available on GenBank.

The alignments used in both analyzes were obtained by the multiple alignment method, on the MAFFT online server v.7 (Katoh et al. 2019) (http://mafft.cbrc.jp/alignment/server/). Concatenated alignments, with all the sequences from both genes of *Dilocarcinus* and containing the outgroup, were used for the elaboration of the phylogram by Bayesian Inference method (BI) and by the Maximum Likelihood method (ML).

The BI analysis was performed in BEAST v.2.6.7 (Drummond and Rambaut 2007), with all parameters and input files predefined and generated in BEAUTI v.2.6.7 (Bouckaert et al. 2019). Both replacement models used were defined from MODELFINDER of IQ-TREE and MEGA 10.0.5, following the Bayesian Information Criterion (BIC). The model chosen for the COI alignments was TN93+G (G = 0.29) and for 16S it was HKY+G (G = 0.82). For this analysis, the following parameters were also considered: Birth-Death Model, sampling of a tree every 30.000 generations for 100 million generations, sampling frequency equal to 100.000, and 25% burn-in. Three runs were performed in Beast, with the same parameters, and each result was evaluated in TRACER 1.6. (Rambaut et al. 2014), referring to ESS (Estimated Sample Size) values, with all below 200 (Schneider 2017). Later, both results were combined in LOGCOMBINER v.1.8.4 and the final result was evaluated from the summary of most trees obtained in TREEANNOTATOR v2.4.4 (Drummond and Rambaut 2007). In turn, the ML analysis was performed on the IQ-TREE (http://www.iqtree.org) (Trifinopoulos et al. 2016), based on the TIM+F+G4 model, selected using the ModelFinder of the IQ-TREE (Kalyaanamoorthy et al. 2017). Branch consistency was defined in 1000 bootstrap replicates with the Ultrafast bootstrap (Hoang et al. 2018). Last, a final phylogram generated and edited in FIGTREE 1.4.4 (Rambaut 2018) and presenting the branch support values of both the analyzes was presented in Fig. 1.

A divergence time estimation analysis with concatenated partitions of COI and 16S, was also included in BEAST. In this analysis were considered all configurations of the phylogenetic analysis by BI, with the addition of information for the calibration of the molecular clock (Relaxed Log model), with the offset function of the exponential distribution, using data obtained from the fossil record of trichodactylid crabs from the Middle Eocene (dated to approximately 38–47.8 mya) (see Klaus et al. 2017).

All specimens used in the phylogenetic evaluation were subjected to species delimitation analysis, to better define and to confirm their taxonomic units. Therefore, alignments of both genes were used as input files for the Assemble Species by Automatic Partitioning (ASAP) method (Puillandre et al. 2021) and analyzed on the ASAP Web online server (https://bioinfo.mnhn.fr/abi/public/asap/). Delimitation tests were performed using both the available modes (Jukes-Cantor, Kimura, and Simple Distance). The main results of those analyses were presented in the phylogram in Fig. 1.

Table 1. List of used primers, their respective genes, and studies, where they were developed.

Gene	Primer	Sequences	References
COI	Pty1	5' CGCCTGTTTATCAAAAACAT 3'	Souza-Carvalho et al. (2025)
	Pty2	5' CCGGTCTGAACTCAGATCACGT 3'	
16S	16SL2	5' TGCCTGTTTATCAAAAACAT 3'	Schubart et al. (2002)
	1472	5' AGATAGAAACCAACCTGG 3'	Schubart et al. (2000)

Table 2. List of the specimens analyzed. Abbreviations: CCDB, Coleção de Crustáceos do Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo; FLONA, Floresta Nacional; INPA, Instituto Nacional de Pesquisas da Amazônia; MPEG, Museu Paraense Emílio Goeldi; MZUEL, Museu de Zoologia, Universidade Estadual de Londrina; MZUSP, Museu de Zoologia, Universidade de São Paulo; UFRGS, Coleção de Zoologia do Departamento de Zoologia, Universidade Federal do Rio Grande do Sul; NHMW, Naturhistorisches Museum Wien; ZMH, Museum der Natur-Zoologie, Leibniz-Institut zur Analyse des Biodiversitätswandels. Abbreviations of the Brazilian states: AM, Amazonas; AP, Amapá, MG, Minas Gerais; MS, Mato Grosso do Sul; MT, Mato Grosso; PA, Pará; PR, Paraná; SP, São Paulo; TO, Tocantins.

Specimen	Voucher	Locality	GenBank	
			COI	16S
D. pagei 004	CCDB 2727	Corumbá/MS	OP236468	–
D. pagei 006	CCDB 4603	Ribeirão Preto/SP	OP236469	OP245216
D. pagei 007	CCDB 4603	Ribeirão Preto/SP	OP236470	OP245217
D. pagei 008	CCDB 4603	Ribeirão Preto/SP	OP236471	OP245218
D. pagei 009	CCDB 2972	Porto Murtinho/MS	OP236472	OP245219
D. pagei 010	CCDB 2972	Porto Murtinho/MS	OP236473	OP245220
D. pagei 011	CCDB 2972	Porto Murtinho/MS	OP236474	OP245221
D. pagei 012	CCDB 3108	Sertãozinho/SP	OP236475	OP245222
D. pagei 013	CCDB 3108	Sertãozinho/SP	OP236476	OP245223
D. pagei 014	CCDB 3108	Sertãozinho/SP	OP236477	OP245224
D. pagei 015	CCDB 4342	Carmo do Rio Claro/MG	OP236478	OP245225
D. pagei 016	CCDB 4342	Carmo do Rio Claro/MG	OP236479	OP245226
D. pagei 017	CCDB 4342	Carmo do Rio Claro/MG	OP236480	OP245227
D. pagei 021	CCDB 6338	Castilho/SP	OP236481	OP245228
D. pagei 022	CCDB 6338	Castilho/SP	OP236482	OP245229
D. pagei 023	CCDB 6338	Castilho/SP	OP236483	OP245230
D. pagei 024	CCDB 2727	Corumbá/MS	OP236484	–
D. pagei 025	CCDB 2727	Corumbá/MS	OP236485	OP245231
D. pagei 030	CCDB 1461	Colômbia/SP	OP236486	–
D. pagei 055	INPA 1756	Carmo do Rio Claro/MG	OP236487	–
D. pagei 090	INPA 1311	Puerto Voluntad, Paraguay	OP236488	–
D. pagei 091	INPA 1311	Puerto Voluntad, Paraguay	OP236489	–
D. pagei 092	INPA 1311	Puerto Voluntad, Paraguay	OP236490	OP245232
D. pagei 093	INPA 872	Viradouro/SP	OP236491	OP245233
D. pagei 094	INPA 872	Viradouro/SP	OP236492	OP245234
D. pagei 095	UFRGS 3425	Pantanal/MS	OP236493	–
D. pagei 097	INPA 1313	Concepción, Paraguay	OP236494	–
D. pagei 098	INPA 1313	Concepción, Paraguay	OP236495	–
D. pagei 100	INPA 366	Pantanal/MT	OP236496	OP245235
D. pagei 101	INPA 366	Pantanal/MT	OP236497	OP245236
D. pagei 111	INPA 774	São José do Rio Preto/SP	OP236498	OP245237
D. pagei 112	INPA 894	Londrina/PR	OP236499	OP245238
D. pagei 117	INPA 1307	Aquidauana/MS	OP236500	OP245239
Dilocarcinus cristatus 019	CCDB 5109	Porto de Moz/PA	OP236501	OP245240
D. cristatus 020	CCDB 5109	Porto de Moz/PA	OP236502	OP245241
D. cristatus 026	CCDB 5109	Porto de Moz/PA	OP236503	OP245242
D. cristatus 066	INPA 795	Silves/AM	–	OP245244
D. cristatus 086	INPA 2491	Santarém/PA	OP236504	OP245245
D. cristatus 113	INPA 456	Ilha da Marchantaria/AM	OP236505	–
D. cristatus 153	MPEG 595	Santa Cruz do Ariri/PA	–	OP245246
D. cristatus 166	INPA 795	Silves/AM	–	OP245247
Dilocarcinus pagei enriquei (Holotype)	NHMW 4173	Pucallpa, Peru	–	–
Dilocarcinus spinifer 027	CCDB 5034	Altamira/PA	OP252629	–
D. spinifer 028	CCDB 5034	Altamira/PA	OP252630	–
D. spinifer 029	CCDB 5034	Altamira/PA	OP252631	–
Dilocarcinus septemdentatus 033	INPA 800	Carauari/AM	OP252632	OP263690
D. septemdentatus 034	INPA 800	Carauari/AM	OP252633	–
D. septemdentatus 045	INPA 805	Res. Mamirauá/AM	OP252634	OP263691
Dilocarcinus montinavis 050 (Paratype)	INPA 584	Serra do Navio/AP	OP252635	OP263692
D. montinavis 159	MPEG 1045	FLONA do Amapá/AP	OP252636	OP263693
D. montinavis 160	MPEG 1045	FLONA do Amapá/AP	–	OP263694
Dilocarcinus truncatus (Holotype)	ZMH K–3682	Beni, Bolivia	–	–
Goyazana castelnaui	CCDB 4651	Palmas/TO	MG344686	MG344657

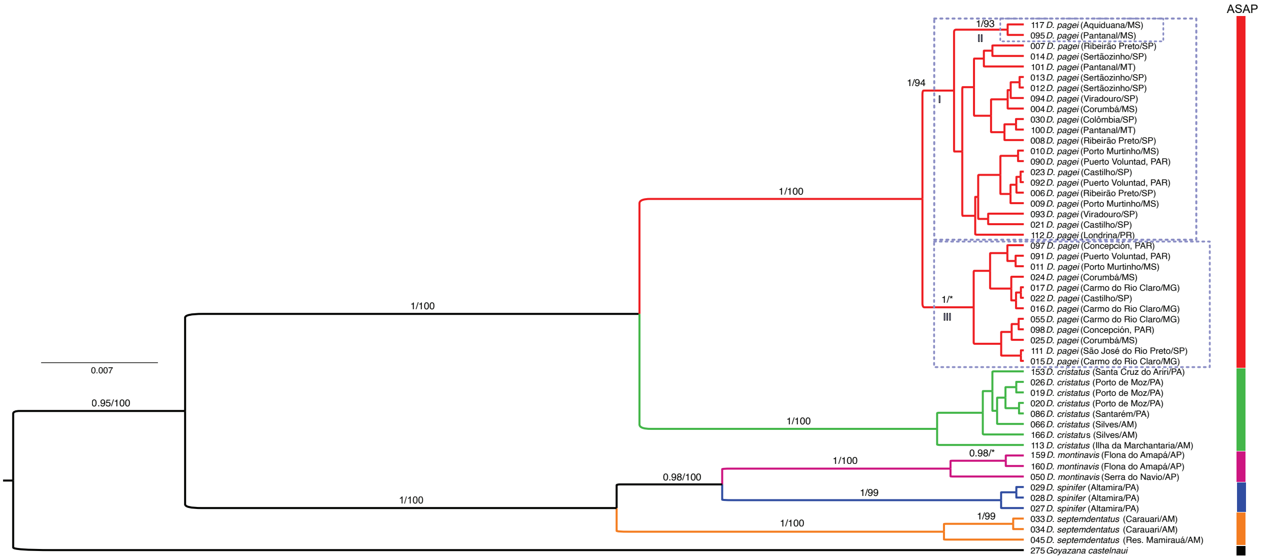

Figure 1. Phylogram generated by the Bayesian Inference and Maximum Likelihood method, with concatenated alignments of the COI and 16S genes of specimens of *Dilocarcinus* spp. (*D. truncatus* not included). The values in the branches correspond to posterior probability (left) and 1000 bootstrap replicates (right). The recovered branches, in both approaches (BI and ML) were considered with high support value (≥ 90%), showing the recovered lineages. * = bootstrap values < 90%. Dashed squares and Roman numerals = other internal groupings of *D. pagei* with high posterior probability value. ASAP = species delimitation test.

Alignments for each gene, containing only the sequences of *D. pagei*, were submitted to DNASP 6 (Rozas et al. 2017) to calculate the number of haplotypes, haplotype diversity (Hd), and preparation of the respective input files for the elaboration of the haplotype networks, built through statistical analysis of parsimony in the TCS Networks of the POPART 1.7 software (Clement et al. 2002; Leigh and Bryant 2015), for both genes. The same alignments were used for the elaboration of two genetic distance matrixes (Table 3), one for each gene, obtained from MEGA 10.0.5 (Kumar et al. 2018).

Morphological analysis

The morphological analysis was carried out based on specimens from different areas in the known distribution of *D. pagei lato sensu* Magalhães and Türkay (2008) and was conducted based on the examination of 379 specimens of *D. pagei* and 132 of *D. cristatus* (see Material examined for both species). The sex of each specimen was indicated by ♂ = male; ♀ = female, and the months are given in roman numerals. Other abbreviations used are: cw = carapace width; cl = carapace length; G1 = male first gonopod; Ma = linear age in millions of years before present; Myr = elapsed time in millions of years (according to Gradstein 2020).

For the complete morphological analysis, the original diagnosis of the species and subspecies was considered, as well as characters used by Bott (1969), Lopretto (1981), and Magalhães and Türkay (2008). This analysis was conducted by assessing somatic characters (shape and number of carapace anterolateral teeth; number of fused pleonal somites; presence or absence of transversal carina at the anterior base of the III pleonal somite; presence or absence of heterochely, type of dentition of the chelae, presence or absence of a longitudinal row of spines on the lower border of the merus), and gonopod characters. The terminology for gonopod structures was adapted from Magalhães and Türkay (2008). In addition, a search for other potentially taxonomically informative characters was also performed, but none was found relevant.

The morphological characters were evaluated using a Leica® MZ9 5 stereomicroscope with a Leica® DFC 295 camera attached, and a NanoCT-Scan, from the Center for Documentation of Biodiversity (CDB/FFCLRP/USP). The high-resolution GE Phoenix v|tome|x s 240 Nano CT equipment was used to obtain computed tomography scans of the gonopods of adult males, and 3D image volume processing and reconstruction were performed using GE PHOENIX DATOS| x 2 and volume analysis and image editing were obtained through VGSTUDIO 3.0 (Volume Graphics) (see Mantelatto et al. 2022 for more equipment details).

Results

Molecular analyses

The reconstructed phylogram obtained (Fig. 1) retrieved two well-supported clades: the first encompassing the species *D. spinifer*, *D. septemdentatus*, and *D. montinavis* and the second one composed of different populations of *D. pagei lato sensu* (according to Magalhães and Türkay 2008). The lower clade includes the three taxa associated with the *D. septemdentatus* species complex and that have already been addressed by França et al. (2024).

The upper clade is further divided into two groups that show a clear separation in their geographic distribution: the specimens grouped in the lower clade show a northern distribution, restricted to the Amazon basin, whereas those grouped in the upper clade have a southern distribution, with all occurring in localities from the Paraguay and Paraná River basins. The southern clade is additionally separated into three different lineages (see dashed squares I, II, and III in Fig. 1), but without any genetic support, according to the species delimitation test performed (ASAP – Fig.1).

The analysis of divergence time pointed to an interval among 18 and 6 Ma., in which it is estimated that cladogenesis separated the lineages representing *D. pagei s .s*. and *D. cristatus* (Fig. 2). One can also notice that the cladogenesis process of the *D. septemdentatus* species complex may have occurred first, between 22 to 8 Ma (mean 15 Ma), giving rise to the lineage today known as *D. septemdentatus*, and the clade composed of *D. montinavis* and *D. spinifer* emerged around 16 to 5.5 Ma (mean 11 Ma).

The haplotype network generated with *D. pagei sensu* Magalhães and Türkay (2008) sequences recorded 26 haplotypes (dH = 0.97) for COI (Fig. 3A) and 28 haplotypes (dH = 0.98) for 16S (Fig. 3B). The size of the circles is proportional to the haplotype frequency; haplotypes with low frequency were not presented in the networks, being concatenated by similarity. Each haplogroup corresponds to one of the lineages observed in the phylogram, with the two haplogroups delimited by dashed lines in red (*D. pagei*) and green (*D. cristatus*).

In addition to the high posterior probability values, which supported the phylogram clades (Fig. 1), the relationship between *Dilocarcinus* species was also strongly supported by genetic divergence analysis, for both genes (Table 3).

the Paraná–Paraguay basin have a lateral margin that is continuous and the lateral side and the subdistal lobe is rounded and well developed. The G1 morphology of most of the Amazonian specimens is similar to that exhibited by specimens assigned by Bott (1969) to the subspecies *D. pagei cristatus* (see Bott 1969: pl. 20, fig. 48; Magalhães and Türkay 2008: 194, fig. 9a, b), while the G1 of the majority of those from the Paraguay–Paraná river basin resembles that illustrated for *D. pagei pagei* (see Bott 1969: pl. 20, fig. 47).

All groups associated with *D. pagei l. s.* share a prominent transverse carina along the anterior margin of the third pleonal somite in both males and females, a character exclusive to these species among the trichodactylids.

Taxonomy

The results of the molecular and morphological analyses (Figs 1–5, Table 3) show that *D. pagei l. s.* comprises a species complex with two distinct groups that each have a clear geographical division. The group that is distributed in the Paraguay–Paraná river basin keeps the name *D. pagei* Stimpson, 1861, because the type locality of this species is in Paraguay. The Amazon basin group is recognized here as *D. cristatus* Bott, 1969 because the type locality of this taxon is near Manaus and is the oldest name available.

The systematics of *D. septemdentatus*, *D. spinifer*, and *D. montinavis* was presented by França et al. (2024) and the taxonomy of *D. truncatus* based on morphological characters was dealt with by Rodríguez (1992) and Magalhães and Türkay (2008). Below, we present the taxonomic treatment for the *D. pagei l. s.* species complex.

Table 3. Genetic distances of *Dilocarcinus* spp. evaluated for COI (diagonal below) and 16S (diagonal above) genes. Values in percentage (%).

		COI / 16S				
		1	2	3	4	5
1	*D. pagei*		4.0–6.5	–	6.7–9.3	8.6–12.5
2	*D. cristatus*	6.1–9.4		–	6.9–8.6	8.9–12.1
3	*D. spinifer*	11.7–13.9	12.5–15.1		–	–
4	*D. septemdentatus*	11.6–13.9	13.8–16.4	5.3–5.9		5.2–8.5
5	*D. montinavis*	11.6–13.6	12.9–16	4.1–4.4	4.9–5.3	

Morphological analysis

Dilocarcinus pagei l. s. are conservative in terms of their somatic and gonadal morphologic characters, but a slight variation in their gonopod morphology can be used to distinguish between specimens from the Amazon basin and those from the Paraná–Paraguay basin. The G1 of the examined specimens from the Amazon basin have a lateral margin with a median discontinuity and the lateral side has a rounded, weakly developed subdistal lobe, whereas the G1 of the specimens from

Order Decapoda Latreille, 1803
Family Trichodactylidae H. Milne Edwards, 1853
Genus *Dilocarcinus* H. Milne Edwards, 1853

Dilocarcinus cristatus Bott, 1969, new status

Figs 1–5C–I

Orthostoma septemdentatum — Nobili 1898: 9 [part].

Trichodactylus (*Dilocarcinus*) *orbicularis* — Rathbun, 1904: 242 (in list) [part]. — Rathbun 1906a: 58, text-fig. 119; pl. 18, figs 3, 8 [part]. — Rathbun 1906b: 504 (in list). — Rathbun, 1910: 605 (in list). — Balss 1914: 409. — Coifmann 1939: 113 (in list) [part].

Trichodactylus (*Dilocarcinus*) *septemdentatus* — Holthuis, 1959: 2018.

Dilocarcinus (*Dilocarcinus*) *pagei cristatus* Bott, 1969: 47, pl. 9, figs 17a, b, pl. 20, fig. 48. — Lopretto, 1981: 22.

Dilocarcinus (*Dilocarcinus*) *pagei enriquei* Pretzmann, 1978: 168, fig.10. — Pretzmann 1983a: 309, pl. 1, fig. 3; pl. 2, fig. 8; pl. 3, fig. 12; pl. 4, fig. 14; pl. 5, fig. 20. — Pretzmann 1983b: 324.

Dilocarcinus (*Dilocarcinus*) *pagei enricei* [sic!] — Pretzmann 1983b: 318 [Spelling error].

Dilocarcinus pagei — Rodríguez 1992: 15 (in list), 108 (in key), 125, figs 1B, 4AA, 8I, 13J, 14D, 44D–G [part]. — Magalhães 1998: 519 [part]. — Barros and Pimentel 2001: 32 (in list). — Morrone and Lopretto 2001: 52, fig. 8 (map), 53 [part]. — Magalhães 2002: 1100, tab. 1 (in list). — Magalhães 2003: 203 (in key), 204, figs 106 (map), 107 [part]. — Campos 2005: 75, fig. 17. — Magalhães and Türkay 2008: 187 (in key), 190, figs 8b, 8c, 9, 10, 11 (map) [part]. — Cumberlidge et al. 2009: suppl. material, 26 (in list) [part]. — Campos 2014: 200: figs 68A–G, 69 (map). — César and Damborenea 2015: 3, fig. 1. — Magalhães 2016: 431 (in list), 438, pl. 1 [part]. — Magalhães et al. 2018: 4 (in list), 9, 32. — Rogers et al. 2020: 946 (in key), figs 23.116B, 23.127A, 23.134B [part].

Dilocarcinus pagei pagei — Magalhães and Türkay 1996: 67 (in list), 78 (in list) [part]. — Ng et al. 2008: 187 (in list) [part].

Dilocarcinus pagei enriquei — Magalhães and Türkay 1996: 67 (in list), 78 (in list) [part]. — Ng et al. 2008: 187 (in list).

Diagnosis. G1 (Figs 4, 5C–F) ventral margin with more or less pronounced median discontinuity (“md” in Fig. 5C–F); lateral side with rounded, well-developed subdistal lobe (“sl” in Fig. 5C, E).

Description. Carapace suborbicular, markedly convex, dorsally smooth; front unarmed, deflexed, distinctly bilobed; anterolateral margin with 6–7 narrow, sharp teeth after exorbital tooth. Pleon with somites III–VI fused; third somite with distinct transverse carina along distal margin in both sexes; male telson subtriangular, anterior margin nearly as long as posterior margin of pleonal somite VI, proximal portion of telson outer margins convex, tip rounded. G1 (Figs 4, 5C–F) slender, distal half slightly curved in lateral direction; ventral margin with more or less pronounced median discontinuity, bearing proximal and median patches of setae of varying lengths; dorsal border slightly convex; marginal suture following mesial surface, slightly twisted towards lateral and dorsal surfaces close to apex after subdistal lobe; marginal suture proximal portion bearing row of short and long setae; lateral surface of apical portion with rounded subdistal lobe covered by dense patch of small spines, less dense across dorsal surface of apical portion; mesodorsal surface of apical portion covered by dense subdistal tuft of short and long setae; apex short, flat; gonopore narrow, positioned terminally.

Type locality. Solimões River, Careiro, near Manaus, Amazonas, Brazil.

Distribution. Lowlands of the Amazon basin in Colombia, Brazil (Amapá, Amazonas, Pará, Rondônia), Peru and Bolivia (Fig. 6) (Bott 1969; Rodríguez 1992; Magalhães and Türkay 2008; present study).

Material examined. ***Holotype***: **BRAZIL** • ♂ (cw 40.9 mm, cl 31.0 mm); Amazonas, Solimões River, Careiro [Paranã do Careiro, ~ 03°11'13"S, 59°51'33"W], near Manaus; E-J. Fittkaui coll.; SMF 2717.

Other material. BRAZIL — Amapá • 1 ♂; Jipiuca, Estação Ecológica Maracá; 2.ix.1995; M. Fernandes; MZUSP 12755. **— Amazonas:** • 2 ♂♂ 4 ♀♀; Solimões River, Janauacá lake, 25.viii.1978; J. Donath; INPA 139 • 3 ♂♂ 1 ♀; Solimões River, Costa do Catalão, close to Manaus; vi.1984; A.G., Santos; INPA 292 • 2 ♀♀; Jurupã River, Amanã lake; 27.viii.1979; R. Best; INPA 293 • 1 ♂; Rio Negro, Ponta do Macaco; 2.x.1982; INPA 296 • 3 ♂♂ 3 ♀♀; Solimões River, Marchantaria Island; v.1986; J. Aims; INPA 456 • 3 ♂♂; Silves, channel of Purema; 02°48'44"S, 58°8'24"W; 10.x.1998; M.N.F. Da Silva; INPA 795 • 4 ♂♂ 2 ♀♀; Tefé, Sustainable Development Reserve of Mamirauá, Zone of Jarauá; xii.1993; P. Henderson; INPA 801 • 9 ♂♂ 3 ♀♀; Tefé, Sustainable Development Reserve of Mamirauá, Volta Lake; 23.iii.1995; P. Henderson; INPA 803 • 1 ♂ 1 ♀; Purus River, Campina lake, Beruri City; 04°53'7"S, 62°54'51"W; 5.vi.2001; L. Rapp Py-Daniel; INPA 1302 • 1 ♂; Purus River, Paraná Itapuru; 04°17'1"S, 61°54'9"W; 11.vi.2001; L. Rapp Py-Daniel; INPA 1306 • 3 ♂♂ 2 ♀♀; Madeira River, Xadá lake, Paraná close to the community of São Carlos; 19.iv.2005; team PROBIO/Ictio; INPA 1454 • 1 ♀; Cambixe, Careiro Island; 25.x.1963; J. Delome; MZUSP 1790 • 4 ♂♂ 2 ♀♀; Baixio Island; x.1963; J. Delome; MZUSP 1791 • 1 ♂; Solimões River; MZUSP 3593 • 1 ♂; Humaitá; 1975; F.R. Galvani and L.C. Oliveira; MZUSP 4761 • 3 ♂♂; Tefé lake; 12.vii.1976; P. Vanzolini; MZUSP 4765 • 1 ♂; Supiá lake, Codajás, 24.x.1968; E.P.A; MZUSP 6317 • 1 ♂; Madeira River; P. Vanzolini; MZUSP 6358 **— Pará:** • 2 ♂♂ 1 ♀; Curuá–Una River, close to Altamira; x.1983; R. Huet and A.G. Santos; INPA 320 • 1 ♂; Marajó Island, Santa Cruz do Ariri, 5.v.1998; D. Embert and L. Dirksen; MPEG 595 • 1 ♂; Oriximiná; 22.v.1999, M.E. Dezincourt; MPEG 667 • 3 ♂; Santarém; 21.xi.1999; team of Laboratório de Pesquisa em Herpetologia da Amazônia; MPEG 680 • 1 ♀; same locality, 29.xii.1999; M.S. Reis; MPEG 681 • 2 ♂♂ 2 ♀♀; Amazonas River, Santarém; 02°23'21.0"S, 54°42'42.1"W; 05.vii.2011; J. Zuanon and E. Ferreira; INPA 2491 • 14 ♂♂ 8 ♀♀; Xingu River; Porto de Moz; 01°43'52.3"S, 52°15'14.8"W; 4.iii.2014; R. Robles et al.; Projeto i-Xingu; CCDB 5109 • 23 ♂; Xingu River; Porto de Moz; 01°43'55.3"S, 52°15'14.8"W; 4.iii.2014; R. Robles et al.; Projeto i-Xingu; CCDB 8560 • 1 ♂ 1 ♀; Xingu River; Porto de Moz; 01°43'52.3"S, 52°15'14.8"W; 4.iii.2014; R. Robles et al.; Projeto i-Xingu; MZUSP 1654 • 1 ♂; Marajó Island; vi.1958; P.E. Vanzolini; MZUSP 1799 • 1 ♂; same locality; 1966; N. Menezes and H. Britski; MZUSP 2142 • 5 ♂♂ 2 ♀♀; Marajó Island, Arari River,; vii.1965 N. Menezes; MZUSP 2288 • 8 ♂♂; Marajó Island, Cachoeira do Arari; vii.1966; N. Menezes and H. Britski; MZUSP 2413 • 7 ♂♂; same data as for preceding; MZUSP 2414 • 2 ♀♀; Taperinha, 1–11.ii.1968, E.P.A; MZUSP 4766 • 1 ♀; Oriximiná, Urariá lake; 7.ii.1967, H.A. Britski;

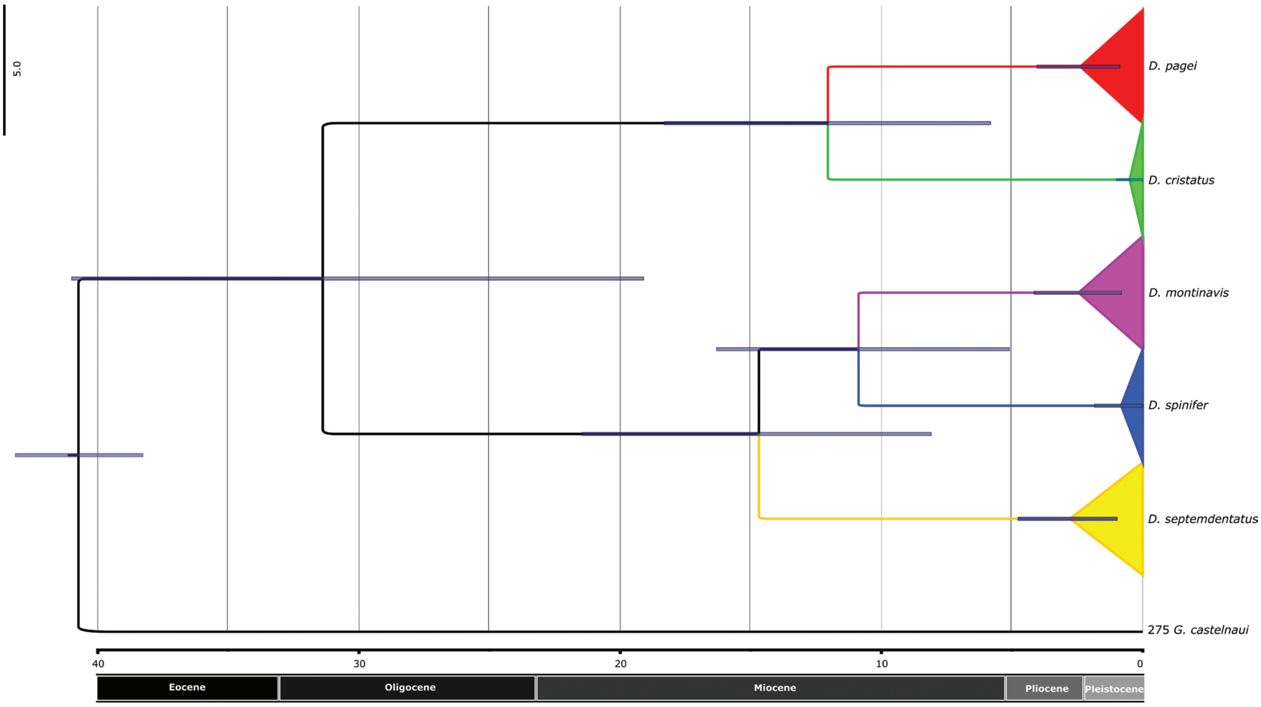

Figure 2. Phylogram with estimated divergence times generated by the Bayesian Inference method, based on concatenated alignments of the COI and 16S genes of *Dilocarcinus* species (*D. truncatus* not included). Blue bars = 95% posterior confidence intervals (HPD). Scale in millions of years (Ma).

MZUSP 4767 • 1 ♀; same locality; 14.x.1968; P.E. Vanzolini; MZUSP 4773 • 1 ♂; Fazenda Taperinha, Santarém; xi.1969; E.P.A; MZUSP 6300 • 5 ♂♂ 4 ♀♀; same locality; xi.1970; E.P.A; MZUSP 6308 • 3 ♂♂ 1 ♀; same data as for preceding; MZUSP 6311 — **Rondônia**: • 2 ♂♂ 2 ♀♀; mouth of Guaporé River, 16.vi.1984, J.C. Malta; INPA 291 • 1 ♂; Madeira River, waterfall of Guajará–Mirim River; 10°46'47"S, 65°20'37"W; 4.v.1998; Victor Py-Daniel et al.; INPA 1305 • 1 ♂; Cautário River, Costa Marques; 12°03'21.9"S, 64°22'35.3"W, 01.vi.2003, G. Villara; INPA 2490. **PERU — Loreto departament**, Provincia de Ucayali • 4 ♀♀; Rio Ucayali, Contamana; 31.v.1996; H. Ortega; INPA 799. — **Ucayali departament**, Provincia Coronel Portillo; INPA 797 • 2 ♀♀; Yarinacocha; 15.xi.1996; H. Ortega; INPA 797 • 1 ♂, cw 40.6 mm cl 31.2 mm, holotype of *Dilocarcinus* (*Dilocarcinus*) *pagei enriquei* Pretzmann, 1978 (NHMW 4173), Ucayali River, Pucallpa, vi.1970, E. M. del Solar. — **Madre de Dios departament**, Provincia de Tambopata • 2 ♂♂; Tambopata, Valencia lake; 27.vii.1995; F. Chang; INPA 798.

Remarks. Bott (1969) described *D. pagei cristatus* as a subspecies by differentiating it from the nominal form by the presence (*D. pagei pagei*) or absence (*D. pagei cristatus*) of heterochely. Lopretto (1981) found heterochely in specimens from the same population and did not recognize subspecies for this taxon, a recommendation that was followed by Rodríguez (1992) and Magalhães and Türkay (2008). The present study, based on a molecular analysis using two mitochondrial genes (COI and 16S), however, allows us to recognize *D. cristatus* for the specimens distributed in the Amazon basin. Despite the general similarity of the G1, some subtle features of this structure can be considered to morphologically differentiate the two groups: the shape of the ventral margin (that has a median discontinuity in *D. cristatus*, and is continuous in *D. pagei*) and the subdistal lobe of the ventral surface (which is slightly less developed in *D. cristatus* than in *D. pagei*). The G1 of some individuals, however, exhibits morphologies intermediate between these two character states, as observed in three specimens from the Amazon basin: INPA 1302 (Beruri, state of Amazonas, Brazil) (Fig. 5G), INPA 2491 (Santarém, state of Pará, Brazil) (Fig. 5I), and INPA 798 (Tambopata, Department of Madre de Dios, Peru) (Fig. 5H).

Pretzmann (1978) described *D.* (*D.*) *pagei enriquei* from the Peruvian Amazon based on a single individual, distinguishing it from the nominal form only by a few, somewhat variable, somatic characters of the carapace and pereiopods, which led Rodríguez (1992) to synonymize it under *D. pagei*. This action was corroborated by Magalhães and Türkay (2008), who did a comparative study of G1 and verified that its morphology did not significantly differ from that of the nominal form. We have attempted unsuccessfully to amplify DNA from a tissue sample of the holotype of *D. pagei enriquei* and, therefore, we relied on the G1 morphology to evaluate the taxonomic status of this taxon. Although the median discontinuity of the lateral margin of the G1 of the holotype of *D. pagei enriquei* (see Magalhães and Türkay 2008: 194, fig. 10) is slightly less pronounced than that exhibited in the G1 of *D. cristatus* (Fig. 4), the morphology of their G1 is otherwise very similar, and was also seen

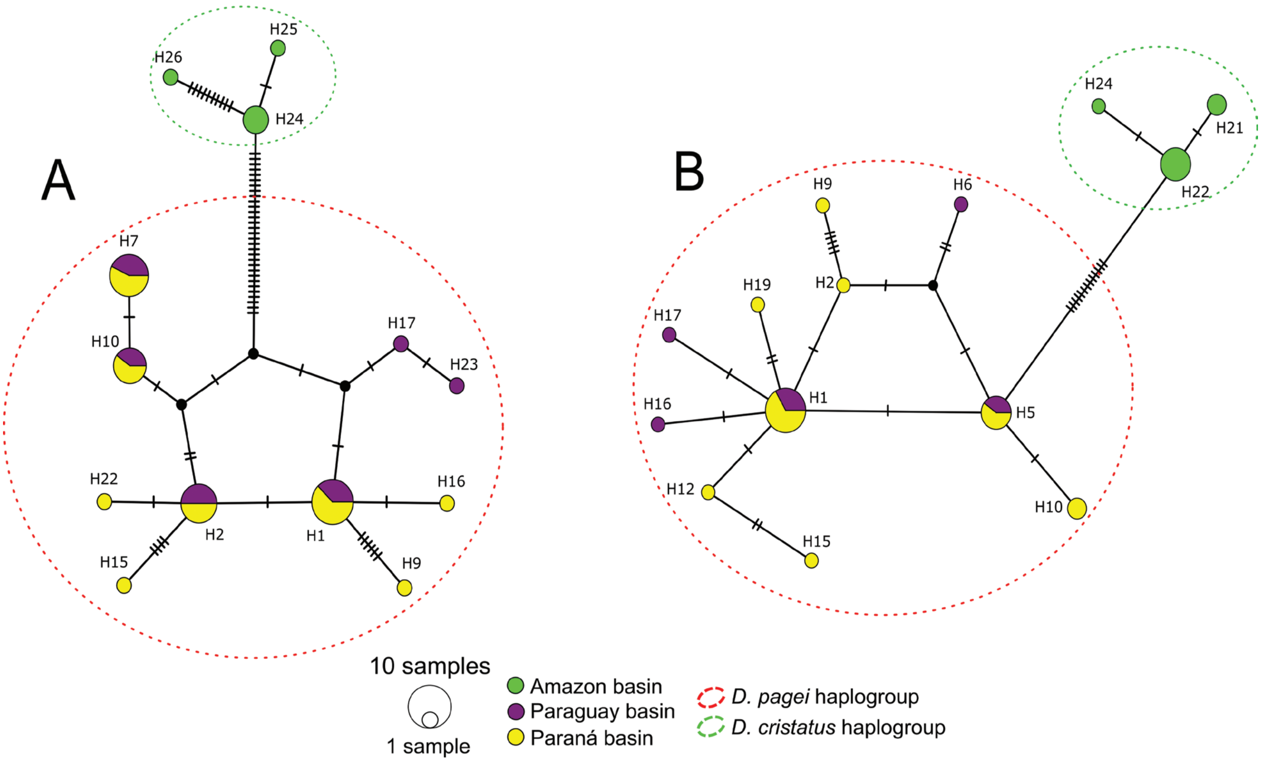

Figure 3. Haplotype networks by the parsimony of (**A**) COI and (**B**) 16S genes of *Dilocarcinus cristatus* (green dashed line) and *D. pagei* (red dashed line) specimens. Colors correspond to the arrangement of haplotypes by hydrographic basins. The size of the circles is proportional to the haplotype frequency. Haplotypes with low frequency were not presented. Haplogroups are delimited by dashed lines, and with colors corresponding to lineages.

in other Peruvian specimens (e.g., INPA 797, INPA 798, INPA 799). Thus, we prefer to maintain *D. pagei enriquei* as a synonym of *D. cristatus* considering the similarity of their G1s and their Amazonian distribution.

Dilocarcinus pagei Stimpson, 1861

Figs 1–3, 5A, B

Dilocarcinus septemdentatus – Nobili 1896: 1 [part].
Orthostoma septemdentatum — Nobili 1898: 10 [part].
Dilocarcinus pagei Stimpson, 1861: 373. — Rodríguez 1981: 48 (in list). — Rodríguez 1992: 15 (in list), 108 (in key), 125 [part]. — Morrone and Lopretto 1994: 100, fig. 19; 107 (in list). — Morrone and Lopretto 1995: 4 (in list). — Morrone and Lopretto 1996: 71 (in list). — Magalhães 1998: 519 [part]. — Magalhães 2000: 25, 56, 59 (in list), 60, 61, 120, 144, 175, 178, 180, 181, 288, 289. — Morrone and Lopretto 2001: 52, fig. 8 (map), 53 [part]. — Magalhães 2001: 70 (in list), 133 (in list), 138 (in list). — Magalhães 2003: 203 (in key), 204, figs 106 (map), 107 [part]. — Collins et al. 2004: 254 (in list). — Magalhães et al. 2005: 1934, fig. 1–5. — Magalhães and Türkay 2008: 187 (in key), 190, figs 8a, 11 (map) [part]. — Cumberlidge et al. 2009: suppl. material, 26 (in list) [part]. — Azevedo-Santos and Lima-Stripari 2010: 200, fig. 1. — Magalhães 2016: 431 (in list) [part]. — Rogers et al. 2020: 946 (in key) [part].
Dilocarcinus septemdentatus — Moreira 1901: 49 [part.].
Trichodactylus (*Dilocarcinus*) *orbicularis* — Rathbun, 1904: 242 (in list) [part]. — Rathbun 1906a: 58 [part]. — Moreira, 1912: 151, pl. 5. — Moreira, 1913: 19, pl. 7. — Colosi 1920: 13 (in list), 15. — Coifmann 1939: 113 (in list) [part]. — Ringuelet, 1948: 325. — Ringuelet, 1949: 101, pl. 9, fig. 2.
Dilocarcinus (*Dilocarcinus*) *pagei pagei* — Bott 1969: 46, pl. 9, figs 16a, b; pl. 20, fig. 47. — Lopretto 1976: 68 (in list), 84, figs 26–29. — Manning and Hobbs 1977: 159 (in list). — Lopretto 1981: 22.
Dilocarcinus (*Dilocarcinus*) *pagei cristatus* — Lopretto 1976: 68 (in list), 86, figs 14–17. — Lopretto, 1981: 22.
Dilocarcinus (*Dilocarcinus*) *pagei* — Lopretto 1981: 23, pls. 1–3. — Zwink, 1990: 103 (in list).
Dilocarcinus pagei pagei — Magalhães and Türkay 1996: 67 (in list), 78 (in list) [part]. — Lopretto, 1998: 544 (in list). — Ng et al. 2008: 187 (in list) [part].

Diagnosis. G1 with ventral margin gently continuous; lateral side with rounded subdistal lobe weakly developed (“sl” in Fig. 5A).

Description. Carapace suborbicular markedly convex, dorsally smooth; front unarmed, deflexed, distinctly bilobed; anterolateral margin with 6–7 narrow, sharp teeth after exorbital tooth. Pleon with somites III–VI fused; third somite with distinct transverse carina along distal margin in both sexes; male telson subtriangular, anterior margin nearly as long as posterior margin of pleonal somite VI, proximal portion of telson outer margins convex, tip rounded. G1 (Fig. 5A, B) slender, distal half slightly curved in lateral direction; ventral margin gently continuous, bearing proximal and median patches of setae of varying lengths; dorsal border moderately convex; marginal suture following mesial surface, slightly twisted towards lateral and

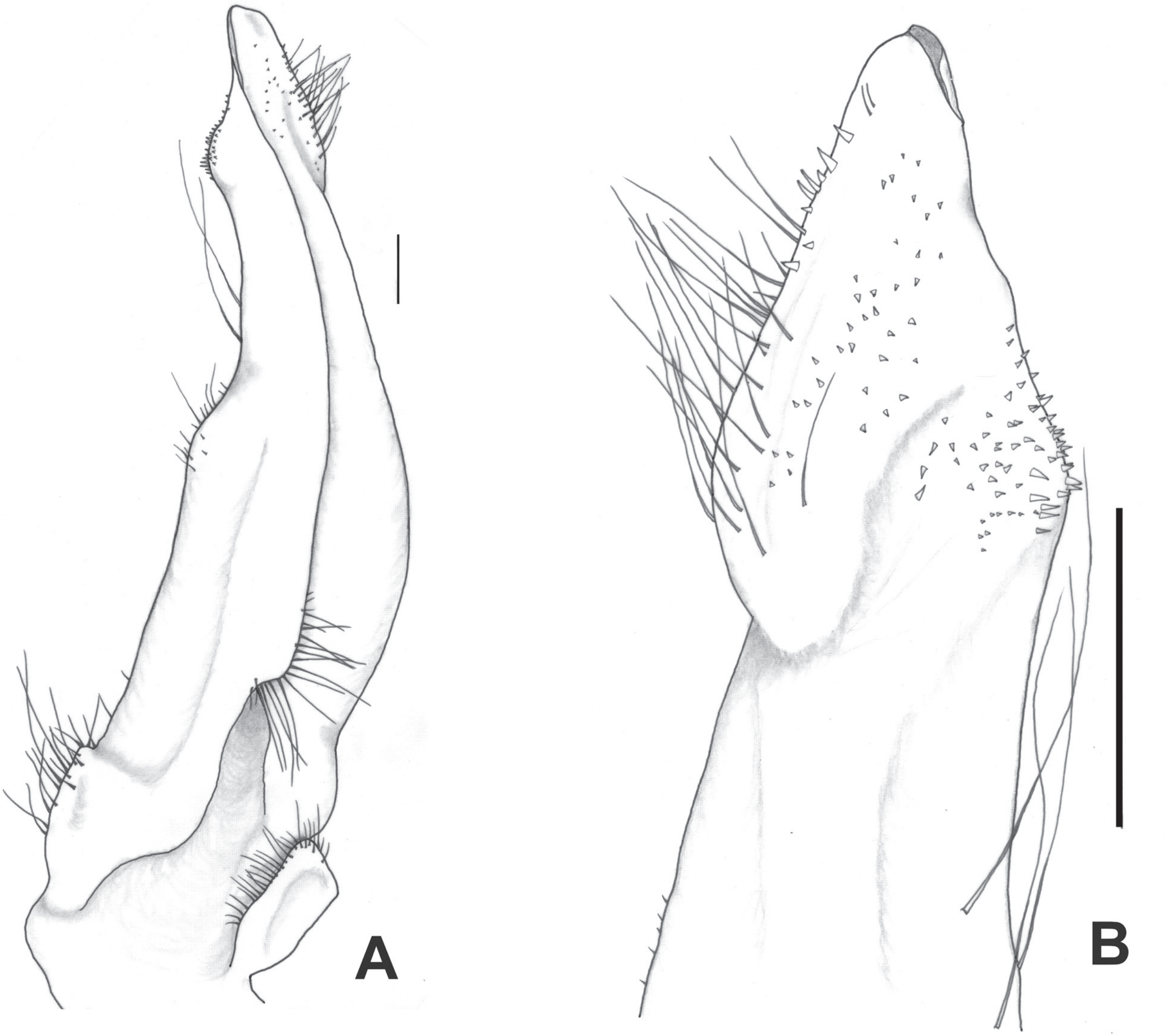

Figure 4. *Dilocarcinus cristatus* Bott, 1969, holotype, male, SMF 2717, right first gonopod. **A.** Whole organ, mesoventral view; **B.** Distal portion, mesodorsal view.

dorsal surfaces close to apex after subdistal lobe; marginal suture proximal portion bearing row of short and long setae; lateral surface of apical portion with well-developed rounded subdistal lobe, covered by dense patch of small spines, less dense across dorsal surface of apical portion; mesodorsal surface of apical portion covered by dense subdistal tuft of short and long setae; apex short, flat; gonopore narrow, positioned terminally.

Type locality. Paraguay.

Distribution. Paraguay and in both upper and lower Paraná River basins, in Brazil (Mato Grosso, Goiás, Minas Gerais, Mato Grosso do Sul, São Paulo, Paraná), Paraguay, and Argentina (Fig. 6).

Type material. ***Holotype***, 1 ♀, dry (USNM 2463), date unknown, Page [not examined].

Material examined. BRAZIL — **Mato Grosso:** • 1 ♂; Cuiabá River, Cuiabá; 6.v.1984; U. Barbosa; INPA 137 • 5 ♂♂ 1 ♀; Rodovia Transpantaneira, Poconé; 7–8.vi.1985; V.A. Araújo; INPA 366 • 1 ♀; Poconé; L. Amato; UFRGS 4431 • 1 ♀; Paranaitá; 18.i.2008; S.N.C. Hernani Filho; CCDB 2179 • 1 ♀; São Luiz de Cáceres; MZUSP 1652 • 3 ♀♀; Rodovia Transpantaneira; 13.xii.201; J. Vas; MZUSP 4771 • 1 ♀; Miranda River, Miranda; ix.1979; O. Moreira Filho; MZUSP 4774 • 3 ♀♀; Mato Grosso; 14.xii.1976; P.E. Vanzolini; MZUSP 6335 • 1 ♂ 1 ♀; Aricá River, Km 26, BR 364; 6–13.xi.1982; Equipe de Ictiologia - DCB – UFSCAR; MZUSP 7050 • 2 ♂♂ 1 ♀; Poconé, Baia do Pio; 6.vii.1985; V. Araújo; MZUSP 9502 • 1 ♀; Porto Espiridião; 25.xii.1976; P.E. Vanzolini; MZUSP 9516 • 1 ♂; Arilas River, Equipe DCB; MZUSP 9687 • 2 ♂♂ 1 ♀; confluence of Paraguay and Corumbá Rivers; 29.vi.2011; MZUSP 24547 — **Goiás:** • 2 ♂♂; Catalão; 03.vii.2021; E. Mossolin; CCDB 6822 • 1 ♂ 1 ♀; Anhanguera; 18°20'30.32"S, 48°13'02.45"W; 05.vii.2021; E. Mossolin; CCDB 6827 • 3 ♂♂; Anhanguera, Fazenda do "Dr. Paiva", 18°19'59.32"S, 49°14'06.92"W; 15.x.2021; E. Mossolin; INPA 4795 — **Minas Gerais**: • 2 ♂♂; Rio Claro, Reservatório de Furnas, region of

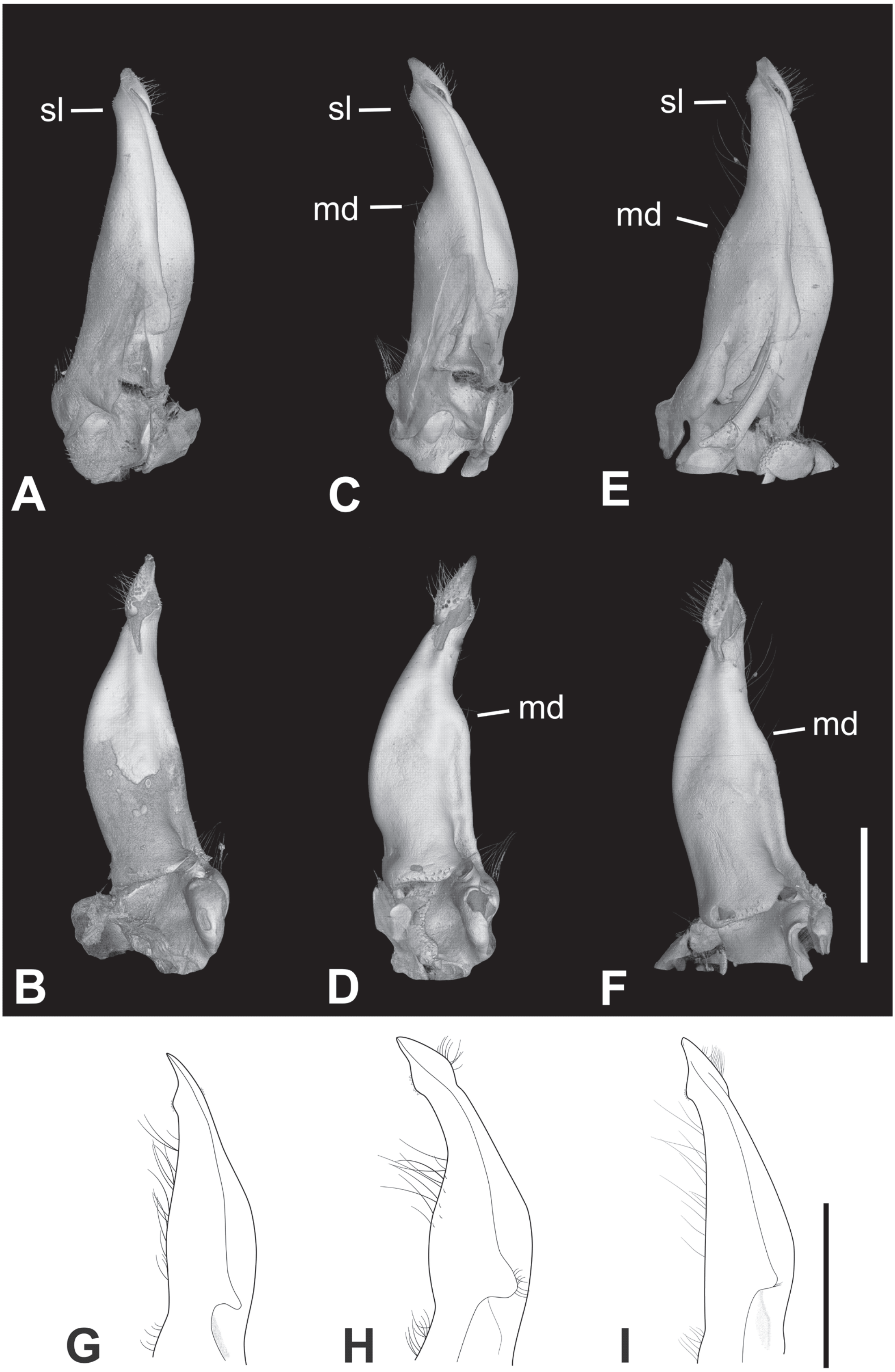

Figure 5. Computerized nano-tomography images of the right first gonopod of adult males. *Dilocarcinus pagei*. **A.** INPA 137, mesoventral view; **B.** mesodorsal view. *Dilocarcinus cristatus*, INPA 292: **C.** mesoventral view; **D.** mesodorsal view; MPEG 680: **E.** mesoventral view; **F.** mesodorsal view. Schematic outline, mesoventral view of the right first gonopod of adult males: **G.** INPA 1302; **H.** INPA 798; **I.** INPA 2491. Abbreviations: md = ventral margin median discontinuity; sl = subdistal lobe. Scale bar: 5 mm (**A–F**); 2 mm (**G–I**).

Raizama; V.M.A. Santos; INPA 1756 • 2 ♂♂; Carmo do Rio Claro; 20°57'16.7"S, 46°09'11.1"W; 27.ii.2012; F.L. Carvalho, L.P. Rezende, D.P. Andrade; CCDB 4341 • 2 ♂♂ 1 ♀; Fazenda Jacúba, Carmo do Rio Claro; 3.xi.2012; A.S. Costa; CCDB 4342 • 2 ♂♂ 1 ♀, Araguari River; 15°27'16.24"S, 48°35'33.12"W; 20.vii.2021; A.C.G. Bartoze and G. Jacobucci; INPA 4796 • 1 ♂; Conquista, Margin of Rio Grande,; 26.xii.2006; W. Santana and M. Cardoso Jr.; MZUSP 18680 — **Mato Grosso do Sul**: • 1 ♂; Aquidauana, Fazenda Taboco, Branch of Taboco River; 20°3.3'S, 55°38.8'W; 31.iii.1998; C. Magalhães; INPA 1307 • 3 ♂♂ 3 ♀♀; Corumbá; 15.x.2009; R. Biagi; CCDB 2727 • 4 ♂♂ 7 ♀♀; same locality; 12.x.2012; Guilherme; CCDB 4348 • 1 ♂; same locality; 18°59'49.0"S, 57°39'15.2"W; 16.xi.2013; F.L. Carvalho; CCDB 5013 • 1 ♂; same locality; 18°48'28.1"S, 57°30'25.9"W; 17.xi.2013; F.L. Carvalho; CCDB 5014 • 4 ♂♂ 3 ♀♀; Vermelho River, tributary of the Miranda River, Corumbá, next to Paço do Lontra; 6.ix.1998; C. Magalhães et al.; INPA 1308 • 1 ♂ 2 ♀♀; Negro River, next to rodovia Nhecolândia-BR 262, Corumbá; 19°17.1'S, 57°3.3'W; 8.ix.1998; C. Magalhães et al.; INPA 1309 • 2 ♂♂ 6 ♀♀; Porto Murtinho; 24.viii.2010; F.L. Mantelatto; CCDB 2972 • 9 ♂♂ 6 ♀♀; Miranda, Pantanal sul-matogrossense; 09.vii.2019; J.A.F. Pantaleão; CCDB 6470 • 2 ♂♂; 30 km NW de Miranda, Pantanal sul-matogrossense; 24.vii.1982; L.F.B. de Oliveira; UFRGS 3425 • 1 ♂; Paiaguás, Fazenda Milagre; 19.vii.1986; F.R. Antonelli; MZUSP 8012 • 3 ♂♂ 3 ♀♀; Miranda River, Base de Pesquisa do Pantanal da UFMS, 4.viii.1989; A.C. Marini; MZUSP 9889 • 4 ♂♂ 2 ♀♀; Lagoon next to BR–262, Miranda; 11.vi.1993; MZUSP 11534 • 6 ♂♂ 12 ♀♀; Surroundings of the city of Miranda; 5.iv.2012; MZUSP 25939 • 2 ♂♂ 2 ♀♀; Corumbá, Right margin of Paraguay River, Base Experimental da UFMS, MZUSP 25174 — **São Paulo**: • 1 ♂; Bebedouro; 21.xii.2009; R.J. Ilário; UFRGS 4565 • 8 ♂♂ 2 ♀♀; Paraná River, Castilho; 23.ix.2017; T. Magalhães; CCDB 6338 • 1 ♂; Pardo River, sub-basin of Grande River, Colômbia; 20°10'0.87"S, 48°36'8.35"W; 24.vii.2000; F.L. Mantelatto; CCDB 1461 • 2 ♂♂; Viradouro, Basin of Mogi–Guaçu River, Fazenda Três Barras; 20°54'48.9"S, 48°10'29.6"W; 11.viii.2000; W. Avelar; INPA 872 • 1 ♂ 1 ♀; Morro Agudo; 20°47'11"S, 48°01'28"W; 09.iii.2020; N. França, G. Faganello, E. Santos and L. Rogeri; CCDB 6622 • 2 ♂♂; same locality; 20°47'11"S, 48°01'28"W; 16.iii.2020; N. França, G. Faganello, E. Santos and L. Rogeri; CCDB 6623 • 1 ♂; Ribeirão Preto, lake of USP-RP; 21°10'06.31"S, 47°51'26.44"W; 01.iv.2005; E. Mossolin; CCDB 2796 • 8 ♂♂ 3 ♀♀; Ribeirão Preto, Dam of Galo Bravo; 21°07'06.72"S, 47°49'30.32"W; 3.iv.2013; E.C. Mossolin, M. Negri, T. Magalhães and R.C. Buranelli; CCDB 4603 • 5 ♂♂ 4 ♀♀; Tietê River, Campo Grande; viii.2019; A.P. Covich; CCDB 6501 • 2 ♂♂ 1 ♀; São José do Rio Preto, municipal reservoir Rio Grande Basin; 20°48'27"S, 49°21'54.9"W; 12.x.1999; M.A.A. Pinheiro and G.Y. Hottori; INPA 774 • 2 ♂♂; Viradouro. Basin of Mogi Guaçu River, Fazenda Três Barras; 20°54'48.9"S, 48°10'29.6"W; 11.viii.2000; W. Avelar; INPA 872 • 3 ♂♂ 3 ♀♀; Sertãozinho, Usina São Geraldo; 7.iii.2008; F.L. Mantelatto, E.C. Mossolin and A.S. Costa; CCDB 3108 • 1 ♀; Teodoro Sampaio; 20.ix.2019; LEPIB; MZUEL 508 • 2 ♀♀; Mogi–Guaçu River, Barrinha; 12.x.1999; M.A.A. Pinheiros and G.Y. Hattori; MZUSP 13099 • 6 ♂♂ 2 ♀♀; São José do Rio Preto; 12.x.1999; M.A.A. Pinheiros and G.Y. Hattori; MZUSP 13100 • 3 ♂♂; Colômbia; 20°10'17.0"S, 48°36'13.5"W; 24.vii.2000; W. Avelar; MZUSP 13915 • 3 ♂♂; Rio Grande, between the cities of Mira Estrela and Cardoso; 20°01'51.7"S, 50°00'59.9"W; 23.i.2003; S. Bueno, S. Rocha and E. Mossolin; MZUSP 15581 • 1 ♂ 2 ♀♀; Turvo River, between the cities of Cardoso and Riolândia; 23.i.2003; S. Bueno, S. Rocha and E. Mossolin; MZUSP 15592 • 1 ♀; Pardo River, between the cities of Guaíra and Barretos; 24.i.2003; MZUSP 15593 • 3 ♂♂ 2 ♀♀; Turvo River, between the cities of Icem and São José do Rio Preto; 20°25'07.1"S, 49°16'03"W; 23.i.2003; S. Bueno, S. Rocha and E. Mossolin; MZUSP 15595 • 6 ♂♂; Mogi–Guaçu River, Barrinha; 20°11'09"S, 48°10'35"W; 25.i.2003; S. Bueno, S. Rocha and E. Mossolin; MZUSP 15597 • 4 ♂♂ 1 ♀; Palestina, Fazenda São Pedro do Turvo; 4.xi.2005; A.M. Juares; MZUSP 16920 • 1 ♂; same locality; 4.x.2005; A.M. Juares; MZUSP 16924 • 2 ♀♀; Guapiaçu; 15.xii.2005; A.M. Juares; MZUSP 16921 • 26 ♂♂ 1 ♀; Guapiaçu, Fazenda Pepelin; 15.xii.2005; A.M. Juares; MZUSP 16922 • 8 ♂♂ 2 ♀♀; Guapiaçu; 15.xii.2005; A.M. Juares; MZUSP 17212 • 21 ♂♂ 9 ♀♀; Guapiaçu, Pesqueiro Pepelin; 10.vi.2007; A.M. Juares; MZUSP 18340 • 5 ♂♂ 6 ♀♀; Santa Albertina, Pousada Bacuri; 19°57'S, 50°45'W; 31.x.2009; P.H. Carvalho; MZUSP 20488 • 1 ♂; São José do Rio Preto, Dam of Rio Preto; 1.viii.1994; F.G. Taddei; MZUSP 26391 • 8 ♂♂ 5 ♀♀; Santa Albertina, Pousada Bacuri, Córrego Schmitt; 19°58'38.78"S, 50°46'43.01"W; 7.ix.2012, M, Cardoso Jr., R. Garcez and C.E. Lopes; MZUSP 27898 — **Paraná**: • 1 ♂ 1 ♀; Basin of Paranapanema River, em lagos, Fazenda Doralice, Londrina; 22.vi.2002; E.M. Amado; INPA 894 • 2 ♂♂; Teodoro Sampaio; 20.ix.2019; LEPIB; MZUEL 509 • 3 ♂♂ 2 ♀♀; Porto Rico, Lagoa das Garças; 22°45'27"S, 53°16'13"W; 19.ix.2010; PELD; MZUSP 24316 • 1 ♂; Cornélio Procópio, Lago São Luiz; 22.i.2019; L. Gustavo; MZUSP 42441. **PARAGUAY** • 3 ♂♂; Paraguay River, Puerto Voluntad; 6.ix.1997, C. Magalhães; INPA 1311 • 2 ♂♂ 2 ♀♀; Paraguay River, Puerto Lidia; 20°54'S, 57°55'W; 7.ix.1997; C. Magalhães et al.; INPA 1312 • 2 ♂♂; Paraguay River, carca de la desembocadura del rio Aquidabán; 23°7'S, 57°38'W; 17.ix.1997; C. Magalhães; INPA 1313 • 2 ♂♂ 2 ♀♀; Presidente Hayes; MZUSP 25923 • 2 ♀♀; Caaguazu, Road of Coronel Oviedo; 7.iii.1996; D.W. Fromm and P.A. Fromm; MZUSP 25929. **ARGENTINA — Formosa** • 1 ♂; Río Pilcomayo National Park; xi.1990; INPA 1304 — **Chaco** • 1 ♀; Chaco, Barranqueiras; 27.x.1961; P. Vanzolini; MZUSP 1793 — **Santa Fe** • 1 ♂; Paraná River, near Santa Fe; 14.xii.2012; C. Magalhães, P. Collins and D. Carvalho; INPA 2130.

Remarks. The upper clade in the phylogram of Fig. 1 groups all the specimens distributed in the Paraguay–Paraná river system, to which the name *D. pagei* is available. The holotype of *D. pagei* is a dried female specimen (see Magalhães and Türkay 2008: 191, fig. 8a) but males of the populations distributed in these southern basins have a G1 morphology like the one illustrated by Bott (1969: pl. 20, fig. 47) for a specimen from the Paraguay River (SMF 4407). The morphology of this G1 is coincident with that described above, i.e., with a continuous ventral margin and a weakly-developed subdistal lobe (Fig. 5A, B).

Discussion

Phylogenetic and morphological relationships

Two species complexes within the genus *Dilocarcinus* are evident in the phylogram resulting from the BI and ML analysis using mitochondrial COI and 16S genes (Fig. 1) because they form two highly supported clades. The lower clade, consisting of the species *D. septemdentatus*, *D. spinifer*, and *D. montinavis*, was discussed by França et al. (2024). The upper clade, composed of *D. pagei l. s.* (as in Magalhães and Türkay 2008), showed a high posterior probability value that clearly supports a branch from the Paraná–Paraguay river basin (red) and another from the Amazon basin (green) (Fig. 1). These groupings also show great genetic divergence in both genes analyzed (Table 3), and a clear separation between distinct haplogroups in both haplotype networks (Fig. 3A, B).

The results from both haplotype networks also concur with the recognition of these two groups at the species level, with the networks of both genes showing a relatively high number of evolutionary steps between the Amazon basin branch and that from the Paraná–Paraguay basin (Fig. 3A, B). Ribeiro et al. (2013) found similar results for congeneric fish species from the Amazon basin and the Pantanal (Paraná–Paraguay basin), with the occurrence of many mutational steps between the haplogroups.

The genetic divergence found between lineages from the Paraná–Paraguay basin and Amazon basin was well supported by all analyses and proved to be sufficient to determine distinct species, in accordance with the divergence observed between other groups of freshwater crabs that used the same genetic marker (Daniels et al. 2003; Jesse et al. 2010; Souza-Carvalho et al. 2017; Mantelatto et al. 2022; Peer et al. 2023; França et al. 2024). Souza-Carvalho et al. (2017), for example, obtained a genetic distance of 10.4–12.6% for COI and 6.8–8.7% for 16S between lineages of *Trichodactylus fluviatilis* Latreille, 1828, which combined with a robust phylogenetic analysis and an evaluation of a series of morphological characters, uncovered a complex of species under the name of *T. fluviatilis*.

Our results reveal the existence of two cryptic complexes species that are each well-defined geographically, morphologically, and molecularly that were hitherto considered under the name of *D. pagei* (see Fig. 1, red and green clades, respectively). This is based on three lines of evidence: the wide distribution of *D. pagei l. s.*; the great genetic variation found among its representatives from different river basins; and the subtle differences in the G1 morphology. It is proposed here to keep the name *D. pagei* for the clade from the La Plata basin (red), and to revalidate *D. cristatus* for the specimens from the Amazon basin clade (green).

Three other branches, each with a high support value, can be recognized in the *D. pagei s. s.* clade, with posterior probability equal to one (Fig. 1, dashed squares I, II, and III). However, when comparing the results of the species delimitation test (ASAP – Fig. 1) and the genetic distance matrices (Table 3), these subgroups showed little significant genetic divergence (i.e., less than 3% for both genes) when compared to other studies on Neotropical freshwater crabs (Souza-Carvalho et al. 2017; Mantelatto et al. 2022; França et al. 2024). These three subgroups in the *D. pagei s. s.* clade correspond to different lineages that do not coincide with defined geographic patterns. For example, although specimens in lineages II and III are found in both the Paraguay basin and upper Paraná basin (although this does not include representatives from the lower Paraná basin), specimens in lineage I all occur in localities in the Pantanal Matogrossense (Paraguay River basin). Magalhães et al. (2005) hypothesized that the occurrence of *D. pagei* in the upper Paraná River basin could have been caused by human action and one of the hypotheses for this could be the translocation of specimens used as bait for sports fishing from the Pantanal region to artificial fishing grounds in the upper Paraná River region. A more comprehensive phylogeographic study of these lineages would be advisable to better understand those geographic distribution patterns.

Origin and distribution

A more accurate interpretation of the zoogeography of the genus *Dilocarcinus* is hampered by the lack of a comprehensive study of the family Trichodactylidae showing both the intrafamilial relationships and the phylogenetic affinities with other groups of Brachyura, as well as the possibility of unintentional errors in the molecular clock calibration (Klaus and Prieto 2014), as already discussed by França et al. (2024). On the other hand, our understanding of the current zoogeographic patterns of the South American aquatic fauna can also be informed by the advances in the knowledge of the paleogeographic history of the region and the historical establishment of the modern drainage patterns (e.g., Hoorn et al. 1995, 2010b, 2017, 2022; Lundberg et al. 1998; Cordani et al. 2000; Cordani and Sato 1999; Wesselingh et al. 2002; Figueiredo et al. 2009; Hoorn and Wesselingh 2010; Latrubesse et al. 2010; Sacek 2014; Rodríguez-Tribaldos et al. 2017; Val et al. 2021). Paleogeographic history has proven to be particularly useful in analyzing the distributional patterns of ichthyological groups (e.g., Ribeiro 2006; Menezes et al. 2008; Albert and Reis 2011; Ribeiro et al. 2013; Roxo et al. 2014; Tagliacollo et al. 2015; Boschman et al. 2023).

Based on the study that considered only the species of the *D. septemdentatus* complex, França et al. (2024) assumed that the most parsimonious hypothesis for the origin of those lineages occurred in the western Amazon. The results of the present study also included the lineages of the *D. pagei* species complex (but without *D. truncatus*) reinforce the assumption that the western Amazon might have been where the Oligocene origin of *Dilocarcinus* and the initial diversification of the genus may have occurred (Fig. 2). This assumption is based on the current distribution of the genus, which is mostly distributed in the lowlands of the Amazon and La Plata (Paraguay–Paraná Rivers) basins, although some species are also present in the Tocantins–Araguaia Rivers basin and coastal river basins of northern South America (Fig. 6). The occurrence of *D. pagei* in the upper Paraná River drainage, as discussed by Magalhães et al. (2005), was most likely caused by human action in more recent times. Additional evidence that reinforces this conjecture is that fossil remains that are most likely trichodactylid crabs found in Peru and Brazil support a continuous presence of primary freshwater crabs in the lowlands of the western Amazonia throughout the last 40 Myr (Klaus et al. 2017; Antoine et al. 2021). Finally, western Amazonia is the hotspot of diversity for many groups and, therefore, is considered to have played a crucial role in the origin and distribution of Amazonian biodiversity due to the influence of the region's paleogeographic history in mechanisms of dispersal, allopatric speciation and extinction (Hubert and Renno 2006; Wesselingh 2006; Wesselingh and Salo 2006; Hoorn et al. 2010a, 2010b, 2022; Dagosta and De Pinna 2017; Antonelli et al. 2018; Oberdorff et al. 2019; Albert et al. 2021; Boschman et al. 2023).

Ancestral populations of the lineages that would give rise to the species complexes of *D. septemdentatus l. s.* and *D. pagei l. s.* presumably occupied the central and western portions of the Amazon region, and their separation would have occurred most likely in the Oligocene (31 Ma), from the Middle Eocene to the Lower Miocene (c. 41–19 Ma) (Fig. 2). At that time, the Amazon region had eastward- and westward-flowing fluvial systems separated by a drainage divide (the Purus Arch) that was a major biogeographic boundary which gradually migrated from the east to a more central region during the Paleogene (Hoorn et al. 2010a,b; Wesselingh et al. 2009; Wesselingh and Hoorn 2011; Val et al. 2021). The river systems draining the Amazon Craton west of the Purus Arch flowed in lowland areas to the foreland of the emerging Andes, where a south to north–oriented fluvial system dominated the region and terminated in lowland regions to the north that alternated between lacustrine and brackish conditions due to occasional marine transgressions (Hoorn et al. 1995, 2010b; Lundberg et al. 1998; Wesselingh et al. 2009; Wesselingh and Hoorn 2011; Rodríguez-Tribaldos et al. 2017).

The divergence time phylogram (Fig. 2) shows that the emergence of the *D. septemdentatus* complex lineages may have started in the Lower to Middle Miocene, as early as 22 Ma (between 22 and 8 Ma). During this period, the Purus Arch still separated the eastern and western drainages of the Amazon region but, with the intensified orogenic processes of the Andes increasing the sedimentary load and the retreat of the marine influence, a transition from a fluvial to a lacustrine landscape occurred in the western Amazon region, establishing the Pebas System (a vast aquatic ecosystem formed by anastomosing rivers, shallow lakes and marshes with episodic marine incursions through northern connection with the Caribbean Sea), which persisted between the Upper Oligocene and Lower Miocene (23–11 Ma) (Lundberg et al. 1998; Wesselingh and Salo 2006; Wesselingh et al. 2009; Hoorn et al. 2010a, 2010b, 2021, 2022; Wesselingh and Hoorn 2011; Boonstra et al. 2015; Jaramillo et al. 2017; Val et al. 2021). As commented in França et al. (2024), the diversity of habitats in the region may have favored the differentiation observed among the *Dilocarcinus* species complexes, with their cryptic lineages radiating across a large part of Western Amazonia, throughout the Lower and Middle Miocene.

The subsequent differentiation and range expansion of these species of the *Dilocarcinus* species complexes to the eastern Amazonia and coastal basins of northern South America, probably related to the establishment of the eastward course of the modern transcontinental Amazon River around the end of the Miocene, are discussed in França et al. (2024). The eastern Amazon aquatic fauna, particularly the fishes, was enriched by contact with the western Amazon in late middle Miocene after the breach of the Purus Arch established geodispersal corridors between the previously isolated western and eastern drainage systems (Albert and Carvalho 2011; Oberdorff et al. 2019; Albert et al. 2021; Boschman et al. 2023). No comparative study to evaluate this effect is available for the Amazonian freshwater crustacean fauna but the speciation process of the *D. septemdentatus* species complex (Fig. 2; França et al. 2024) suggests that the decapod fauna might have undergone a similar effect.

The ancestral lineage that gave rise to the *D. pagei* species complex was probably present in the Oligocene Subandean River system (the Proto-Amazon–Orinoco River basin) and, since this system also incorporated northwestern portions of the present-day Paraná River drainage, this lineage could have probably colonized the southern portions of the continent as well (Lundberg et al. 1998; Albert and Reis 2011; Wesselingh and Hoorn 2011). Headwater capture events between some southern tributaries of the Amazon basin and the La Plata basin could also have contributed to the southward expansion of the distribution of the *D. pagei* species complex lineage. Such events are presumed to be an explanation for the presence of many fish lineages in the Paraguay basin (Carvalho and Albert 2011; Ribeiro et al. 2013; Roxo et al. 2014; Tagliacollo et al. 2015). Tagliacollo et al. (2015) recovered three events of river capture after testing alternative landscape evolution models to represent

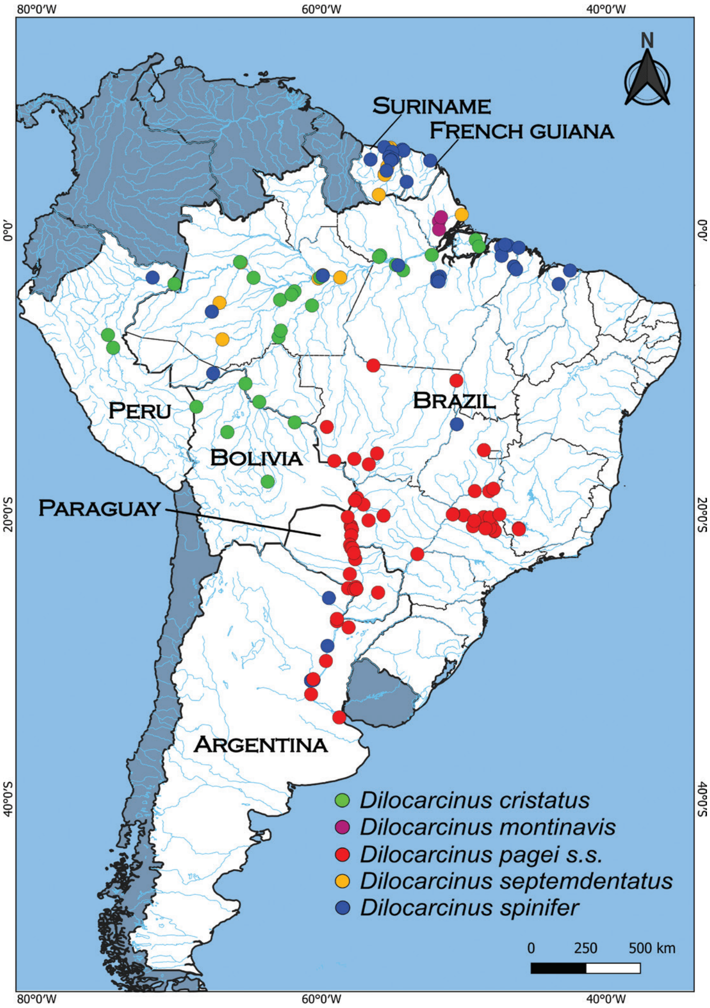

Figure 6. Map of the geographic distribution of *Dilocarcinus* species based on records of the present study and of previous studies (Magalhães and Türkay 2008; França et al. 2024).

distinct palaeogeographical river capture histories between the Western Amazon and La Plata drainages during the formation of the Central Andean (Bolivian) orocline (43.0–15.0 Ma). This may have affected the distribution of long-whiskered catfishes (Siluriformes, Pimelodidae) and it seems plausible to assume that an event that occurred between 32 and 23 Ma (Oligocene) promoted the connection of the Upper Madeira River basin (part of the Amazon basin) with the La Plata basin, and also contributed to the range expansion of the lineage that formed the *Dilocarcinus* species complexes in the La Plata basin.

According to Tagliacollo et al. (2015), a third river capture event occurred in the Early Miocene (23–15 Ma) that separated La Prata basin from the Upper Madeira River basin and this may have contributed to the cladogenesis process of the *D. pagei* species complex, which may have occurred around 12 Ma (ca. 18–6 Ma), during the Miocene (Fig. 2), with *D. pagei s. s.* being restricted to the Paraguay–Paraná basin and *D. cristatus* to the Amazon basin. In addition to headwater capture events, marine transgressions and regressions in southern South America during the Miocene (Lundberg et al. 1998; Hernández et al. 2005; Rosseti et al. 2013) may also have influenced the separation of this clade into northern (Amazon basin) and southern (La Plata basin) species. At least two marine transgression episodes are recognized in southern South America that encompassed areas of northern Argentina to southern Bolivia: the first one, known as the Paranense Sea, occurred in the Middle Miocene (15–13 Ma), and the second one occurred in the Late Miocene (10–5 Ma) (Hernández et al. 2005; Rossetti et al. 2013).

The diversity patterns of the South American primary freshwater crabs, with two families, 109 genera, and 296 species (Cumberlidge et al. 2014), are not concordant with some other freshwater taxa from the region. When compared to fishes, which comprise 69 families, 739 genera and 5,160 species (Reis et al. 2016), the freshwater crabs are surprisingly much less diverse considering that the two freshwater groups evolved under the influence of the same historical drivers that shaped the current landscapes and environments of South American river basins. The low diversity of the genus *Dilocarcinus*, comprising only six currently valid species, for a taxon with an evolutionary history of between 20 and 40 Myr in such a wide distribution area is, therefore, noteworthy. Like several other species of trichodactylid crabs (Rodríguez 1981, 1992; Magalhães 2003), all *Dilocarcinus* species are typical of lowland areas, inhabiting floodplain rivers and intermittent interfluvial wetland environments in both the Amazon valley and the Paraguay–Paraná basin (Fig. 6). The habitats currently occupied by the species must be very similar to those existing in the marshy and fluvial-lacustrine systems in the lowlands of the sedimentary basins of the Andean foreland regions occupied by the ancestral lineages of *Dilocarcinus* during the Oligocene and Miocene and that persisted in the Amazon valley and Paraguay-lower Paraná basin with the establishment of the current geomorphological conformation of these basins after the end of the Miocene (Lundberg et al. 1998; Hoorn et al. 2010a; Wesselingh and Horrn 2011; Val et al. 2021). The low species richness of *Dilocarcinus* may be a result of the relative environmental and ecological stability of the region over a long period, and these lowland regions may have served as an "evolutionary museum" (Stebbins 1974; Albert et al. 2011) for slowly-evolving freshwater crabs. These questions need to be addressed by a more in-depth investigation into the phylogeny of Neotropical primary freshwater crab groups in the future.

Conclusion

The specific composition of the genus *Dilocarcinus* has varied between three (Rodríguez 1992) and 12 taxa (Pretzmann 1968), while other studies have revealed a complex of cryptic species under the name *D. septemdentatus* (França et al. 2024). The present study found a complex with two cryptic species within *Dilocarcinus*, each with well-defined geographic distributions: a northern one restricted to the Amazon basin and a southern one distributed in the La Plata basin, supported by the molecular results and distinct morphology of G1 of each lineage. As the type locality of *D. pagei* Stimpson, 1861, occurs within the distributional range of the southern lineage, this name was kept for the La Plata basin species, whereas *D. cristatus* Bott, 1969 was revalidated for the Amazonian species because of its distribution and because the G1 of its holotype is consistent with the G1 morphology of the specimens of the northern group. The origin of the genus *Dilocarcinus* most likely occurred in the western Amazon region during the Oligocene (c. 41–19 Ma; mean 31 Ma) and expanded both into the La Plata basin (Paraguay–Paraná River basin) and into the eastern Amazon due to a series of tectonic and eustatic sea-level events related to the uplift of the Andes and marine transgressions-regressions that shaped the hydrological interconnections between the hydrographic basins along the Andean foreland region since Eocene times (Lundberg et al. 1998; Hoorn et al. 2010a; Albert and Reis 2011; Wesseling and Hoorn 2011; Val et al. 2021). The genus *Dilocarcinus* now includes six species: *D. cristatus*, *D. montinavis*, *D. pagei*, *D. septemdentatus*, *D. spinifer*, and *D. truncatus* and no subgenera are recognized. Studies like this reinforce the importance of integrative approaches that use molecular and morphological tools to address outstanding taxonomic and macroevolutionary questions, especially those involving freshwater crabs.

Acknowledgements

This study is part of LBSC's research efforts to investigate the diversity of decapod crustaceans along the Brazilian drainages and is a product of the NFCF's Doctorate thesis. This project was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (Projetos Temáticos Biota 2010/50188–8 and INTERCRUSTA 2018/13685–5; Coleções Científicas 2009/54931–0; EMU Coleções 2022/11451-2; PROTAX 2016/50376–5, 2021/08075–6 and PROTAX BIOTA 2025/07224–9) for FLM. Additional support was also provided by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), for the Research grant (PQ 302253/2019–0; 302706/2025–9 and PROTAX 445724/2024-2) for FLM. NFCF thanks Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES) for PROEX DS scholarship (Proc. 88887.369727/2019–00 – Financing code 001). Brazilian specimens were obtained under collection permits (permanent license to FLM for collection of Zoological Material No. 11777–2 MMA/IBAMA/SISBIO and SISGEN A496BF8, AEF142F and CEA7CD5). Thanks are due to the following colleagues for their support on loaning specimens and/or assistance during visits of the authors to their respective institutions: Daniel Cavalari, Flavio Bockmann (FFCLRP/USP); Jéssica Colavite, Sérgio L. S. Bueno (IB/USP); Inácia M. Vieira (IEPA); Marcio L. Oliveira, Thiago Mahlmann (INPA); Cleverson R. Santos (MPEG); Joana D'Arc de Jesus Pinto, Maria José de Souza Coelho, Marcos D. S. Tavares (MZUSP); Angelika Brandt, Andreas Alspach, Bianca Trautwein (SMF); Peter Dworschak, Martin Schwentner (NHMW) and Nancy Mercado-Salas (ZMH) (CM is especially thankful to the last two colleagues for obtaining tissue samples from the holotypes of *D. pagei enriquei* and *D. truncatus* under their respective curatorship). We are also grateful to Neil Cumberlidge, an anonymous reviewer and Magdalini Christodoulou for their useful comments and suggestions during the review process.

References

Albert JS, Carvalho TP (2011) Neogene assembly of modern faunas. In: Albert JS, Reis RE (Eds) Historical Biogeography of Neotropical Freshwater Fishes. University of California Press, Berkeley, Los Angeles, London, 119–136. https://doi.org/10.1525/california/9780520268685.003.0007

Albert JS, Reis RE (2011) Introduction to Neotropical freshwaters. In: Albert JS, Reis RE (Eds) Historical Biogeography of Neotropical Freshwater Fishes. University of California Press, Berkeley, Los Angeles, London, 21–157. https://doi.org/10.1525/california/9780520268685.003.0001

Albert JS, Petry P, Reis RE (2011) Major biogeographic and phylogenetic patterns. In: Albert JS, Reis RE (Eds) Historical Biogeography of Neotropical Freshwater Fishes. University of California Press, Berkeley, Los Angeles, London, 21–157. https://doi.org/10.1525/california/9780520268685.003.0002

Albert JS, Bernt MJ, Fronk AH, Fontenelle JP, Kuznar SL, Lovejoy NR (2021) Late Neogene mega river captures and the Great Amazonian

Biotic Interchange. Global and Planetary Change 205: 103554. https://doi.org/10.1016/j.gloplacha.2021.103554

Antoine P-O, Yans J, Castillo AA, Stutz N, Abello MA, Adnet S, Andriolli CM, Benites-Palomino A, Billet G, Boivin M, Herrera F, Jaramillo C, Mártinez C, Moreno F, Navarrete RE, Negri FR, Parra F, Pujos F, Rage J-C, Ribeiro AM, Robinet C, Roddaz M, Tejada-Lara JV, Varas-Malca R, Santos RV, Salas-Gismondi R, Marivaux L (2021) Biotic community and landscape changes around the Eocene–Oligocene transition at Shapaja, Peruvian Amazonia: Regional or global drivers? Global and Planetary Change 202: 103512. https://doi.org/10.1016/j.gloplacha.2021.103512

Antonelli A, Zizka A, Carvalho FA, Scharn R, Bacon CD, Silvestro D, Condamine FL (2018) Amazonia is the primary source of Neotropical biodiversity. Proceedings of the National Academy of Sciences of the United States of America 115(23): 6043–6049. https://doi.org/10.1073/pnas.1713819115

Azevedo-Santos VM, Lima-Stripari N (2010) Primeiro registro de *Dilocarcinus pagei* Stimpson, 1861 (Decapoda, Trichodactylidae) no estado de Minas Gerais. Biotemas 23(2): 1–4. https://doi.org/10.5007/2175-7925.2010v23n2p199

Balss H (1914) Potamonidenstudien. Zoologisch Jahrbucher (Systematic) 37: 401–410. https://doi.org/10.5962/bhl.part.1071

Barros MP, Pimentel FR (2001) A fauna de Decapoda (Crustacea) do Estado do Pará, Brasil: Lista preliminar das espécies. Boletim do Museu Paraense Emilio Goeldi, Série Zoologia 17(1): 15–41. http://repositorio.museu-goeldi.br/handle/mgoeldi/660

Boonstra M, Ramos MIF, Lammertsma EI, Antoine P-O, Hoorn C (2015) Marine connections of Amazonia: Evidence from Foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). Palaeogeography, Palaeoclimatology, Palaeoecology 417: 176–194. https://doi.org/10.1016/j.palaeo.2014.10.032

Boschman LM, Carraro L, Cassemiro FAS, Vries J, Altermatt F, Hagen O, Hoorn C, Pellissier L (2023) Freshwater fish diversity in the western Amazon basin shaped by Andean uplift since the Late Cretaceous. Nature Ecology & Evolution 7(12): 2030–2044. https://doi.org/10.1038/s41559-023-02220-8

Bott R (1969) Die Süßwasserkrabben Südamerikas und ihre Stammesgeschichte. Eine Revision der Trichodactylidae und der Pseudothelphusidae östlich der Anden (Crustacea, Decapoda). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 518: 1–94. https://www.schweizerbart.de/publications/detail/artno/190951800/Abhandlungen_d_Senckenb_Naturf_Gesell

Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fourment M, Gavryushkina A, Heled J, Jones G, Kühnert D, Maio N, Matschiner M, Mendes FK, Müller NF, Ogilvie HA, Plessis L, Popinga A, Rambaut A, Rasmussen D, Siveroni I, Suchard MA, Wu C-H, Xie D, Zhang C, Stadler T, Drummond AJ (2019) BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS Computational Biology 15(4): e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Buranelli RC, Felder DL, Mantelatto FL (2019) Genetic diversity among populations of the Western Atlantic mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Decapoda: Brachyura: Ocypodidae): evidence for panmixia and useful data for future management and conservation. Journal of Crustacean Biology 39(4): 386–395. https://doi.org/10.1093/jcbiol/ruz036

Campos MR (2005) Freshwater crabs from Colombia: A taxonomic and distributional study. Academia Colombiana de Ciencias Exactas, Fisicas y Naturales, Bogota, 363 pp. https://repositorio.accefyn.org.co/bitstream/001/108/1/ACCEFYN-2005Freshwater%20 Crabs.pdf

Campos MR (2014) Crustáceos decápodos de agua dulce de Colombia. Instituto de Ciencias Naturales, Bogotá, 692 pp. https://repositorio.unal.edu.co/handle/unal/82864

Carvalho TP, Albert JS (2011) The Amazon–Paraguay divide. In: Albert JS, Reis RE (Eds) Historical Biogeography of Neotropical Freshwater Fishes. University of California Press, Berkeley, California. 193–202. https://doi.org/10.1525/california/9780520268685.003.0011

César II, Damborenea C (2015) Catalogue of the specimens of Trichodactylidae (Crustacea, Brachyura) housed in the Museo de La Plata, Argentina. Revista del Museo de La Plata. Sección Zoología 25(184): 1–13. https://doi.org/10.24215/25456377e207

Clement M, Snell Q, Walke P, Posada D, Crandall K (2002) TCS: estimating gene genealogies. In: Parallel and Distributed Processing Symposium, International, Fort Lauderdale, California (USA), 15-19 April 2002, DBLP, 7 pp. https://doi.ieeecomputersociety.org/10.1109/IPDPS.2002.1016585

Coifmann I (1939) Potamonidi della Guiana inglese raccolti dal Prof. Nello Beccari. Archivio Zoologico Italiano 27: 93–116.

Collins PA, Williner V, Giri F (2004) Crustáceos Decápodos del litoral fluvial argentino. In: Aceñolaza FG (Ed.) Temas de la Biodiversidad Litoral Fluvial Argentino. INSUGEO, Miscelánea, San Miguel de Tucumán 12: 253–264. https://www.bfa.fcnym.unlp.edu.ar/catalogo/doc_num.php?explnum_id=2751

Colosi G (1920) Potamonidi conservati nel R. Museo zoologico di Torino. Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Universitá di Torino 35: 1–39. https://doi.org/10.5962/bhl.part.17857

Cordani UG, Sato K (1999) Crustal evolution of the South American platform, based on Nd isotopic systematics on granitoid rocks, based on Nd isotopic systematics granitoid rocks. Episodes 22(3) [for 2000]: 167–173. https://doi.org/10.18814/epiiugs/1999/v22i3/003

Cordani UG, Sato K, Teixeira W, Tassinari CCG, Basel MAS (2000) Crustal evolution of the South American platform. In: Cordani UG, Milani EJ, Thomaz-Filho A, Campos DA (Eds) Tectonic Evolution of South America. 31st International Geological Congress, Rio de Janeiro, 19–40.

Cumberlidge N, Ng PKL, Yeo DCJ, Magalhães C, Campos MR, Álvarez F, Naruse T, Daniels SR, Esser LJ, Attipoe FYK, Clotilde-Ba FL, Darwall W, Mcivor A, Ram M, Collen B (2009) Freshwater crabs and the biodiversity crisis: Importance, threats, status, and conservation challenges. Biological Conservation 142(8): 1665–1673. https://doi.org/10.1016/j.biocon.2009.02.038

Cumberlidge N, Alvarez F, Villalobos J-L (2014) Results of the global conservation assessment of the freshwatercrabs (Brachyura, Pseudothelphusidae and Trichodactylidae): The Neotropical region, with an update on diversity. In: Wehrtmann IS, Bauer RT (Eds) Proceedings of the Summer Meeting of the Crustacean Society and the Latin AmericanAssociation of Carcinology, Costa Rica, July 2013. ZooKeys 457: 133–157. https://doi.org/10.3897/zookeys.457.6598

Dagosta F, De Pinna M (2017) Biogeography of Amazonian fishes: Deconstructing river basins as biogeographic units. Neotropical Ichthyology 15(3): e170034. https://doi.org/10.1590/1982-0224-20170034

Daniels SR, Gouws RG, Stewart BA, Coke M (2003) Molecular and morphometric data demonstrate the presence of cryptic lineages among freshwater crabs (Decapoda: Potamonautidae: *Potamonautes*) from the Drakensberg Mountains, South Africa. Biological Journal of the Linnean Society. Linnean Society of London 78(1): 129–147. https://doi.org/10.1046/j.1095-8312.2003.00143.x

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7: 214. https://doi.org/10.1186/1471-2148-7-214

Estoup A, Largiadèr CR, Perrot E, Chourrout D (1996) Rapid one-tube DNA extraction for reliable PCR detection of fish polymorphic markers and transgenes. Molecular Marine Biology and Biotechnology 5: 295–298.

Figueiredo J, Hoorn C, Van der Ven P, Soares E (2009) Late Miocene onset of the Amazon River and the Amazon deep-sea fan: Evidence from the Foz do Amazonas Basin. Geology 37(7): 619–622. https://doi.org/10.1130/G25567A.1

França NFC, Magalhães C, Mantelatto FL (2024) Integrative approach revealing a species complex in the Neotropical freshwater crab *Dilocarcinus septemdentatus* (Herbst, 1783) (Decapoda: Trichodactylidae) with a description of a new species. Arthropod Systematics & Phylogeny 82: 385–405. https://doi.org/10.3897/asp.82.e115268

Gradstein F (2020) Chapter I: Introduction. In: Gradstein FM, Ogg JG, Schmitz MD, Oggi GM (Eds) Geologic Time Scale I. Elsevier BV, Amsterdam, 1: 3–20. https://doi.org/10.1016/B978-0-12-824360-2.00001-2

Herbst JFW (1783) Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Gottlieb August Lange, Berlin und Stralsund 1(4–5): 274 pp. https://www.biodiversitylibrary.org/item/131110#page/167/mode/1up

Hernández RM, Jordan TE, Dalenz Farjat A, Echavarría L, Idleman BD, Reynolds JH (2005) Age, distribution, tectonics, and eustatic controls of the Paranense and Caribbean marine transgressions in southern Bolivia and Argentina. Journal of South American Earth Sciences 19: 495–512. https://doi.org/10.1016/j.jsames.2005.06.007

Holthuis LB (1959) The Crustacea Decapoda of Suriname (Dutch Guiana). Zoologische Verhandelingen, Leiden 44: 1–296. https://repository.naturalis.nl/pub/317569

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. Molecular Biology and Evolution 35: 518–522. https://doi.org/10.1093/molbev/msx281

Hoorn C, Wesselingh FP (2010) Introduction: Amazonia, landscape and species evolution. In: Hoorn C, Wesselingh FP (Eds) Amazonia, landscape and species evolution: A look into the past. Blackwell Publishing, Oxford, 1–6. https://doi.org/10.1002/9781444306408.ch1

Hoorn C, Guerrero J, Sarmiento GA, Lorente MA (1995) Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. Geology 23(3): 237–240. https://doi.org/10.1130/0091-7613(1995)023<0237:ATAACF>2.3.CO;2

Hoorn C, Wesselingh FP, Hovikoski J, Guerrero J (2010a) The development of the Amazonian mega-wetland (Miocene; Brazil, Colombia, Peru, Bolivia). In: Hoorn C, Wesselingh FP (Eds) Amazonia: Landscape and Species Evolution, a Look into the Past. Wiley-Blackwell Publishing Ltd, Chichester, 123–142. https://doi.org/10.1002/9781444306408.ch8

Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartín I, Sanchez-Meseguer A, Anderson CL, Figueiredo JP, Jaramillo C, Riff D, Negri FR, Hooghiemstra H, Lundberg J, Stadler T, Särkinen T, Antonelli A (2010b) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330(6006): 927–931. https://doi.org/10.1126/science.1194585

Hoorn CM, Bogotá-A GR, Romero-Baez M, Lammertsma EI, Flantua SGA, Dantas EL, Dino R, do Carmo DA, Chemale Jr F (2017) The Amazon at sea: Onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin. Global and Planetary Change 153: 51–65. https://doi.org/10.1016/j.gloplacha.2017.02.005

Hoorn C, Kukla T, Bogotá-Angel G, van Soelen E, González-Arango C, Wesselingh FP, Vonhof H, Val P, Morcote-Rios G, Roddaz M, Dantas EL, Santos RV, Sinninghe Damsté JS, Kim J-H, Morley RJ (2021) Cyclic sediment deposition by orbital forcing in the Miocene wetland of western Amazonia? New insights from a multidisciplinary approach. Global and Planetary Change 210: 103717. https://doi.org/10.1016/j.gloplacha.2021.103717

Hoorn C, Boschman LM, Kukla T, Sciumbata M, Val P (2022) The Miocene wetland of western Amazonia and its role in Neotropical biogeography. Botanical Journal of the Linnean Society 199(1): 25–35. https://doi.org/10.1093/botlinnean/boab098

Hubert N, Renno J-F (2006) Historical biogeography of South American freshwater fishes. Journal of Biogeography 33(8): 1414–1436. https://doi.org/10.1111/j.1365-2699.2006.01518.x

ICZN - International Commission on Zoological Nomenclature (1954a) Opinion 260. Rejection for nomenclatorial purposes of the work by Meuschen (F.C.) issued in 1778 under the title “Museum Gronovianum”. Opinions and Declarations rendered by the International Commission on Zoological Nomenclature 5(21): 265–279. https://doi.org/10.5962/p.149926

ICZN - International Commission on Zoological Nomenclature (1954b) Opinion 261. Rejection for nomenclatorial purposes of the Index to the Zoophylacium Gronovianum of Gronovius prepared by Meuschen (F.C.) and published in 1781. Opinions and Declarations rendered by the International Commission on Zoological Nomenclature 5(22): 281–296. https://doi.org/10.5962/p.149927

Jaramillo C, Romero I, D’Apolito C, Bayona G, Duarte E, Louwye S, Escobar J, Luque J, Carrillo-Briceño JD, Zapata V, Mora A, Schouten S, Zavada M, Harrington G, Ortiz J, Wesselingh FP (2017) Miocene flooding events of western Amazonia. Science Advances 3(5): e1601693. https://doi.org/10.1126/sciadv.1601693

Jesse R, Schubart CD, Klaus S (2010) Identification of a cryptic lineage within *Potamon fluviatile* (Herbst) (Crustacea, Brachyura, Potamidae). Invertebrate Systematics 24(4): 348–356. https://doi.org/10.1071/IS10014

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates. Nature Methods 14: 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20(4): 1160–1166. https://doi.org/10.1093/bib/bbx108

Keikhosravi A, Schubart CD (2013) Revalidation and redescription of Potamon elbursi Pretzmann, 1976 (Brachyura, Potamidae) from Iran, based on morphology and genetics. Central European Journal of Biology 8: 1266–1275. https://doi.org/10.2478/s11535-013-0203-z

Klaus S, Prieto J (2014) New occurrence of Miocene freshwater crabs (Brachyura, Potamidae) in the North Alpine Foreland Basin, Germany, with a note on fossil Potamon to calibrate molecular clocks. In: Yeo DCJ, Cumberlidge N, Klaus S (Eds) Advances in freshwater decapod systematics and biology. Brill, Leiden, Crustacean Monographs 19: 161–172. https://doi.org/10.1163/9789004207615_010

Klaus S, Magalhães C, Salas-Gismondi R, Gross M, Antoine PE (2017) Palaeogene and neogene brachyurans of the Amazon basin: A revised first appearance date for primary freshwater crabs (Brachyura, Trichodactylidae). Crustaceana 90(7–10): 953–967. https://doi.org/10.1163/15685403-00003629

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Latreille PA (1828) Trichodactyle, *Trichodactylus*. In: Encyclopedie Methodique. Histoire Naturelle. Entomologie, ou Histoire Naturelle des Crustacés, des Arachnides and des Insectes 10: 705 pp. https://www.biodiversitylibrary.org/item/78665#page/713/mode/1up

Latrubesse EM, Cozzuol M, Silva-Caminha SAF, Rigsby CA, Absy ML, Jaramillo C (2010) The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. Earth-Science Reviews 99: 99–124. https://doi.org/10.1016/j. earscirev.2010.02.005

Leigh JW, Bryant D (2015) PopART: Full-feature software for haplotype network construction. Methods in Ecology and Evolution 6(9): 1110–1116. https://doi.org/10.1111/2041-210X.12410

Lopretto C (1976) Morfologia comparada de los pleopodos sexuales masculinos en los Trichodactylidae de la Argentina (Decapoda, Brachyura). Limnobios 1(3): 67–94.

Lopretto C (1981) Discusion sobre las presuntas subespecies de Dilocarcinus (D.) pagei (Crustacea, Brachyura, Trichodactylidae). Redescripcion y referencia a su polifenismo. Physis (Rio de Janeiro, Brazil) 39: 21–31.

Lopretto EC (1998) Eucarida. In: Morrone JJ and Coscarón S (Eds) Biodiversidad de Artrópodos Argentinos. Ediciones SUR, La Plata, 536–544. https://drive.google.com/file/d/1gh4JjOPe_j5C6rRe4Wy-lGOiH-QbiTE-j/view

Lundberg JG, Marshall LG, Guerrero J, Horton B, Malabarba MCSL, Wesselingh F (1998) The stage for Neotropical fish diversification: A history of tropical South American rivers. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, CAS Lucena (Eds) Phylogeny and Classification of Neotropical Fishes. EDIPUCRS, Porto Alegre, 13–48.

Magalhães C (1998) Malacostraca. Eucarida. Brachyura. Pseudothelphusidae and Trichodactylidae. In: Young PS (Ed.) Catalogue of Crustacea of Brazil. Rio de Janeiro, Museu Nacional 6: 517–523. https://decapoda.nhm.org/pdfs/29508/29508.pdf

Magalhães C (2000) Diversity and abundance of decapod crustaceans in the Rio Negro basin, Pantanal, Mato Grosso do Sul, Brazil. In: Willink PW, Chernoff B, Alonso LW, Montambault Jr, Lourival R (Eds) A biological assessment of the aquatic ecossystems of the Pantanal, Mato Grosso do Sul, Brazil. RAP Bulletin of Biological Assessment, Conservation International, Washington, D.C, 18: 56–62. https://bibdigital.epn.edu.ec/bitstream/15000/6843/1/RAP18_Pantanal_Brazil_Oct-2000.pdf

Magalhães C (2001) Diversity, distribution, and habitats of the macro-invertebrate fauna of the Rio Paraguay and Rio Apa, Paraguay, with emphasis on Decapod Crustaceans. In: Chernoff B, Willink PW, Montambault JR (Eds) A biological assessment of the aquatic ecosystems of the Río Paraguay Basin, Alto Paraguay, Paraguay. Washington DC, USA, Conservation International, 68–71. https://documentoskoha.s3.amazonaws.com/10042.pdf

Magalhães C (2002) A rapid assessment of the decapod fauna in the Rio Tahuamanu and Rio Manuripi Basins, with new records of shrimps and crabs for Bolivia (Crustacea, Decapoda, Palaemonidae, Sergestidae, Trichodactylidae). Revista brasileira de Zoologia 19(4): 1091–1103. https://doi.org/10.1590/S0101-81752002000400014

Magalhães C (2003) Brachyura: Pseudothelphusidae e Trichodactylidae In: Melo GAS (Ed.) Manual de identificação dos crustáceos decápodes de água doce do Brasil. Editora Loyola, São Paulo, 143–297. https://decapoda.nhm.org/pdfs/31205/31205.pdf

Magalhães C (2016) Avaliação dos caranguejos tricodactilídeos (Decapoda: Trichodactylidae) In: Pinheiro MAA, Boos H (Org.) Livro Vermelho dos Crustáceos do Brasil: Avaliação 2010–2014. Porto Alegre, RS: Sociedade Brasileira de Carcinologia – SBC, 420–440. https://crustacea.org.br/wp-content/uploads/2020/12/livro-vermelho-cap32-avaliacao-dos-caranguejos-tricodactilideos.pdf

Magalhães C, Türkay M (1996) Taxonomy of the Neotropical freshwater crab family Trichodactylidae I. The generic system with description of some new genera (Crustacea, Decapoda, Brachyura). Senckenbergiana biologica 75(1/2): 63–95.

Magalhães C, Türkay M (2008) Taxonomy of the Neotropical freshwater crab family Trichodactylidae, IV. The genera *Dilocarcinus* and *Poppiana* (Crustacea: Decapoda: Brachyura). Senckenbergiana biologica 88(2): 185–215.

Magalhães C, Bueno SLS, Bond-Buckup G, Valenti WC, Silva HLM, Kiyohara F, Mossolin EC, Rocha SS (2005) Exotic species of freshwater decapod crustaceans in the state of São Paulo, Brazil: Records and possible causes of their introduction. Biodiversity and Conservation 14(8): 1929–1945. https://doi.org/10.1007/s10531-004-2123-8

Magalhães C, Robles R, Souza-Carvalho EA, Carvalho FL, Malta JCO, Mantelatto FL (2018) Annotated checklist of parasitic and decapod crustaceans from the middle and lower Xingu (Amazon Basin) above and below the Belo Monte dam complex, Pará State, Brazil. Proceedings. Academy of Natural Sciences of Philadelphia 166(1): 1–34. https://doi.org/10.1635/053.166.0105

Manning RB, Hobbs HH (1977) Decapoda. In: Hulbert SH (Ed.) Biota Acuática de Sudamerica Austral. San Diego, California (San Diego State University), 157–162.

Mantelatto FL, Terossi M, Negri M, Buranelli RC, Robles R, Magalhães T, Tamburus AF, Rossi N, Miyazaki MJ (2018) DNA sequence database as a tool to identify decapod crustaceans on the São Paulo coastline. Mitochondrial DNA. Part A, DNA Mapping, Sequencing, and Analysis 29(5): 805–815. https://doi.org/10.1080/24701394.2017.1365848

Mantelatto FL, Vera-Silva AL, Do Prado BM, Pileggi LG (2021) Phylogenomic analyses reveals gene flow between populations of the freshwater shrimp *Potimirim brasiliana* (Caridea, atyidae) along its wide distribution. Anais da Academia Brasileira de Ciências 93(2): 1–14. https://doi.org/10.1590/0001-3765202120190384

Mantelatto FL, Souza-Carvalho EA, Araújo SR, Magalhães C (2022) Combined multigene and morphological analysis reveals lineage-specific diversification of the neotropical freshwater crabs of the genus *Fredius* Pretzmann, 1967 (Brachyura, Pseudothelphusidae). Systematics and Biodiversity 20(1): 1–15. https://doi.org/10.1080/14772000.2021.2008042

Mantelatto FL, Magalhães C, Souza-Carvalho EA, Pantaleão JAF, Wehrtmann IS (2024) Multi-gene phylogeny of the primary freshwater crab genus Ptychophallus Smalley, 1964 (Pseudothelphusidae: Ptychophallinae) from the Neotropical region. Zoology 164: 126169. https://doi.org/10.1016/j.zool.2024.126169

Menezes NA, Ribeiro AC, Weitzman S, Torres RA (2008) Biogeography of Glandulocaudinae (Teleostei: Characiformes: Characidae) revisited: Phylogenetic patterns, historical geology and genetic connectivity. Zootaxa 1726: 33–48. https://doi.org/10.11646/zootaxa.1726.1.3

Meuschen FC (1781) Index, continens Nomina Generica Speciorum propria, Trivialia ut et Synonyma. In: Gronovius LT, Zoophylacium Gronovianum, exhibens Animalia Quadrupeda, Amphibia, Pisces, Insecta, Vermes, Mollusca, Testacea, et Zoophyta, quae in Museo suo adservavit, examini subjecit, systematice disposuit atque descripsit. [Unnumbered index at the end of the third fascicle of the

Zoophylacium Gronovianum, 19 pp.] https://www.biodiversitylibrary.org/item/201324#page/395/mode/1up

Milne Edwards H (1853) Mémoire sur la famille des Ocypodiens. Annales des Sciences Naturelles 20(3): 163–226. https://ia801207.us.archive.org/25/items/biostor-160231/biostor-160231.pdf

Moreira C (1901) Contribuições para o conhecimento da fauna brazileira: Crustaceos do Brazil. Archivos do Museu Nacional do Rio De Janeiro 11: 1–151. https://doi.org/10.5962/bhl.title.46376

Moreira C (1912) Un crustacé nouveau du Brésil. (Decapoda, Anomura, Dromidae). Bulletin de la Société Entomologique de France 15(15): 322–324. https://doi.org/10.3406/bsef.1912.25160

Moreira C (1913) Annexo n. 5: Historia Natural, Zoologia. Crustaceos. In: Pinheiro MTC (Ed.) Commissão de Linhas Telegraphicas Estrategicas de Matto-Grosso ao Amazonas. Papelaria Macedo, Rio de Janeiro, 1–21. https://www.obrasraras.fiocruz.br/media.details.php?mediaID=260

Morrone JJ, Lopretto EC (1994) Distributional patterns of freshwater Decapoda (Crustacea: Malacostraca) in southern South America: a panbiogeographic approach. Journal of Biogeography 21(1): 97–109. https://doi.org/10.2307/2845607

Morrone JJ, Lopretto EC (1995) Parsimony analysis ofendemicity of freshwater Decapoda (Crustacea, Malacostraca)from southern South America. Neotrópica 41: 3–8.

Morrone JJ, Lopretto EC (1996) Cladistics of the family Trichodactylidae (Crustacea, Decapoda): A reappraisal. Journal of Computational Biology 1: 65–72.

Morrone JJ, Lopretto EC (2001) Trichodactylid biogeographic patterns (Crustacea, Decapoda) and the Neotropical region. Neotrópica 47: 49–55. https://www.academia.edu/1041881/Trichodactylid_biogeographic_patterns_Crustacea_Decapoda_and_the_Neotropical_region

Ng PKL, Yeo DCJ (2007) Malaysian freshwater crabs: conservation prospects and challenges. In: Chua LSL, Saw LG, Kirton LG (Eds) Proceedings of the seminar on the status of biological diversity in Malaysia and threat assessment of plant species in Malaysia. Forest Research Institute Malaysia, Kepong, 95–120. https://lkcnhm.nus.edu.sg/app/ uploads/2017/04/s17rbz.pdf

Ng PKL, Guinot D, Davie PJF (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. The Raffles Bulletin of Zoology 17: 1–286. https://lkcnhm.nus.edu.sg/app/uploads/2017/04/s17rbz.pdf

Nobili G (1896) Viaggio del Dott. A. Borelli nella Republica Argentina e nel Paraguay. XIX. Crustacei Decapodi. Bolletino die Musei di Zoologia ed Anatomia comparata della R. Università di Torino 9(222): 1–4. https://doi.org/10.5962/bhl.part.8048

Nobili G (1898) Nuove osservazioni sulla identità di *Brachycarpus neapolitanus* Cano e *Palaemon biunguiculatus* Lucas. Annuario del Museo Zoologico della R. Università di Napoli 2(21): 1–5. https://www.biodiversitylibrary.org/page/43066351#page/255/mode/1up

Oberdorff T, Dias MS, Jézéquel C, Albert JS, Arantes CC, Bigorne R, Carvajal-Valleros FM, Frederico AWR, Hidalgo JZM, Hugueny B, Leprieur F, Maldonado M, Maldonado-Ocampo M, Martens K, Ortega H, Sarmiento J, Tedesco PA, Torrente-Vilara G, Winemiller KO (2019) Unexpected fish diversity gradients in the Amazon basin. Science Advances 5(9): eaav8681. https://doi.org/10.1126/sciadv.aav8681

Oliveira CMCA, Mantelatto FL, Terossi M (2021) Systematics of the shrimp genus *Atya* (Decapoda, Atyidae) in the light of multigene-based phylogenetic and species delimitation inference. Zoologica Scripta 50(6): 780–794. https://doi.org/10.1111/zsc.12503

Peer N, Gouws G, Maliwa L, Barker N, Juby P, Perissinotto R (2023) Description of a new montane freshwater crab (Arthropoda, Malacostraca, Decapoda, Potamonautidae) from the Eastern Cape, South Africa. ZooKeys 1160: 89–108. https://doi.org/10.3897/zookeys.1160.100844

Phiri EE, Daniels SR (2014) Disentangling the divergence and cladogenesis in the freshwater crab species (Potamonautidae: *Potamonautes perlatus*) in the Cape Fold Mountains, South Africa with the description of two novel lineages. Zoological Journal of the Linnean Society 170: 310–332. https://doi.org/10.1111/zoj.12103

Phiri EE, Daniels SR (2016) Multilocus coalescent species delimitation reveals widespread cryptic differentiation among Drakensberg mountain-living freshwater crabs (Decapoda: *Potamonautes*). Invertebrate Systematics 30(1): 60–74. https://doi.org/10.1071/IS15035

Pretzmann G (1968) Die Familie Trichodactylidae (Milne-Edwards 1853) Smith 1870 (Vorläufige, Mitteilung). Entomologisches Nachrichtenblatt 15(7–8): 70–76. https://www.zobodat.at/pdf/EN_15_7_8_1968_0070-0076.pdf

Pretzmann G (1978) Neue SuBwasserkrabben aus den Anden. Sitzungsberichte der Osterreichischen Akadedmie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse 187(6–10): 163–170. https://decapoda.nhm.org/references/page.html

Pretzmann G (1983a) Ergebnisse einiger Sammelreisen in Peru und Ecuador 1976/77. 2. Teil: Neue Trichodactylidae. Annalen des Naturhistorischen Museums in Wien 84 (B): 307–311.

Pretzmann G (1983b) Die Trichodactylidae von Peru und Ecuador. Annalen des Naturhistorischen Museums in Wien 84(B): 317–330.

Puillandre N, Brouillet S, Achaz G (2021) ASAP: Assemble species by automatic partitioning. Molecular Ecology Resources 21(2): 609–620. https://doi.org/10.1111/1755-0998.13281

Rambaut A (2018) FigTree 1.4.4. http://github.com/rambaut/figtree/

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. http://beast.bio.ed.ac.uk/Tracer

Rathbun MJ (1904) Les crabes d'eau douce (Potamonidae). Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 4(6): 225–312. https://biostor.org/reference/102350

Rathbun MJ (1906a) Les crabes d'eau douce (Potamonidae). Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 4e serie, 8: 33–122. https://decapoda.nhm.org/references/referenceinfo.html?refid=28125

Rathbun MJ (1906b) Catalogue des Potamonidés des collections du Muséum d'histoire naturelle de Paris, d'après les révisions et déterminations de Mlle Mary Rathbun. Seconde et dernière partie. Bulletin du Muséum d'histoire naturelle Paris 12(7): 500–504. https://www.biodiversitylibrary.org/item/137042#page/518/mode/1up

Rathbun MJ (1910) The stalk-eyed Crustacea of Peru and the adjacent coast. Proceedings of the United States National Museum 38(1766): 531–620. https://doi.org/10.5479/si.00963801.38-1766.351

Reis RE, Albert JS, Di Dario F, Mincarone MM, Petry P, Rocha LA (2016) Fish biodiversity and conservation in South America. Journal of Fish Biology 89(1): 12–47. https://doi.org/10.1111/jfb.13016

Ribeiro AC (2006) Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: An example of faunal evolution associated with a divergent continental margin. Neotropical Ichthyology 4(2): 225–246. https://doi.org/10.1590/S1679-62252006000200009

Ribeiro AC, Jacob RM, Silva RRSR, Lima FCT, Ferreira DC, Ferreira KM, Mariguela TC, Pereira LHG, Oliveira C (2013) Distributions and phylogeographic data of rheophilic freshwater fishes provide evidences on the geographic extension of a central-Brazilian

Amazonian palaeoplateau in the area of the present day Pantanal Wetland. Neotropical Ichthyology 11(2): 319–326. https://doi.org/10.1590/S1679-62252013000200010

Ringuelet RA (1948) Una nueva *Aegla* del nordeste argentino (Decapoda, Anomura). Notas del Museo de La Plata. Zoologia 13: 203–208.

Ringuelet RA (1949) Camarones y cangrejos de la Zona de Goya (Sergestidae, Palaemonidae y Trichodactylinae). Notas del Museo de La Plata 14(119): 79–109.

Rodríguez G (1981) Decapoda. In: Hurlbert SH, Rodríguez G, Santos ND (Eds), Aquatic biota of tropical South America, 1 (Arthropoda). San Diego, California (San Diego State University), 41–51. https://decapoda.nhm.org/pdfs/31124/31124.pdf

Rodríguez G (1992) The Freshwater Crabs of America. Family Trichodactylidae and Supplement to the Family Pseudothelphusidae (Collection Faune Tropicale 31). Editions ORSTOM, Paris, 189 pp. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers20-07/36706.pdf

Rodríguez-Tribaldos V, White NJ, Roberts GG, Hoggard MJ (2017) Spatial and temporal uplift history of South America from calibrated drainage analysis. Geochemistry, Geophysics, Geosystems 18(6): 2321–2353. https://doi.org/10.1002/2017GC006909

Rogers DC, Magalhães C, Peralta M, Ribeiro FB, Bond-Buckup G, Price WW, Guerrero-Kommritz J, Mantelatto FL, Bueno A, Camacho AI, González ER, Jara CG, Pedraza M, Pedraza-Lara C, Latorre ER, Santos S (2020) Chapter 23 - Phylum Arthropoda: Crustacea: Malacostraca. In: Rogers DC, Damborenea C, Thorp J (Eds) Thorp and Covich's Freshwater Invertebrates (Fourth Edition). Academic Press, 809–986. https://doi.org/10.1016/B978-0-12-804225-0.00023-X

Rossetti DF, Bezerra FHR, Dominguez JML (2013) Late Oligocene-Miocene transgressions along the equatorial and eastern margins of Brazil. Earth-Science Reviews 123: 87–112. https://doi.org/10.1016/j.earscirev.2013.04.005

Roxo FF, Albert JS, Silva GSC, Zawadzki CH, Foresti F, Oliveira C (2014) Molecular phylogeny and biogeographic history of the armored Neotropical catfish subfamilies Hypoptopomatinae, Neoplecostominae and Otothyrinae (Siluriformes, Loricariidae). PLoS ONE 9(8): e105564. https://doi.org/10.1371/journal.pone.0105564

Rozas J, Ferrer-Mata A, Sánchez-DelBarrio JC, Guirao-Rico S, Librado P, Ramos-Onsins SE, Sánchez-Gracia A (2017) DnaSP v6: DNA Sequence polymorphism analysis and large datasets. Molecular Biology and Evolution 34(12): 3299–3302. https://doi.org/10.1093/molbev/msx248

Sacek V (2014) Drainage reversal of the Amazon River due to the coupling of surface and lithospheric processes. Earth and Planetary Science Letters 401: 301–312. https://doi.org/10.1016/j.epsl.2014.06.022

Schneider H (2017) Métodos de análise filogenética. Chiado Editora, São Paulo, 4: 354 pp.

Schubart CD, Neigel JE, Felder DL (2000) Use of the mitochondrial 16S rRNA gene for phylogenetic and population studies of Crustacea. In: Vaupel Klein JC, Schram FR (Eds) The Biodiversity Crisis and Crustacea: Proceedings of the Fourth International Crustacean Congress, Amsterdam, Netherlands, 20–24 July 1998, volume 2. Rotterdam: Balkema AA, 12: 817–830.

Schubart CD, Cuesta JA, Felder DL (2002) Glyptograpsidae, a new brachyuran family from Central America: Larval and adult morphology, and a molecular phylogeny of the Grapsoidea. Journal of Crustacean Biology 22(1): 28–44. https://doi.org/10.1163/20021975-99990206

Souza-Carvalho EA, Magalhães C, Mantelatto FL (2017) Molecular phylogeny of the *Trichodactylus fluviatilis* Latreille, 1828 (Brachyura: Trichodactylidae) species complex. Journal of Crustacean Biology 37(2): 187–194. https://doi.org/10.1093/jcbiol/rux005

Souza-Carvalho EA, Magalhães C, Carvalho FL, Mantelatto FL (2025) Systematics of Neotropical freshwater crabs Trichodactylinae based on multi-genes and morphological data: New tribe and new combinations. Arthropod Systematics & Phylogeny 83: 315–329. https://doi.org/10.3897/asp.83.e153079

Stebbins GL (1974) Flowering plants: evolution above the species level. Cambridge, MA, Harvard University Press, 480 pp. https://doi.org/10.4159/harvard.9780674864856

Stimpson WM (1861) Notes on certain decapods Crustacea. Proceedings. Academy of Natural Sciences of Philadelphia 13: 372–375. https://www.biodiversitylibrary.org/page/1683173#page/7/mode/1up

Tagliacollo VA, Roxo FF, Duke-Sykvester S, Oliveira C, Albert JS (2015) Biogeographical signature of river capture events in Amazonian lowlands. Journal of Biogeography 42(12): 2349–2362. https://doi.org/10.1111/jbi.12594

Trifinopoulos J, Nguyen L-T, Haeseler A, Minh BQ (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44(W1): W232–W235. https://doi.org/10.1093/nar/gkw256

Val P, Figueiredo J, Melo G, Flantua SGA, Quesada CA, Fan Y, Albert JS, Guayasamin JM, Hoorn C (2021) Chapter 1: Geological History and Geodiversity of the Amazon. In: Nobre C, Encalada A, Anderson E, Roca Alcazar FH, Bustamante M, Mena C, Peña-Claros M, Poveda G, Rodriguez JP, Saleska S, Trumbore S, Val AL, Villa Nova L, Abramovay R, Alencar A, Rodríguez Alzza C, Armenteras D, Artaxo P, Athayde S, Barretto Filho HT, Barlow J, Berenguer E, Bortolotto F, Costa FA, Costa MH, Cuvi N, Fearnside PM, Ferreira J, Flores BM, Frieri S, Gatti LV, Guayasamin JM, Hecht S, Hirota M, Hoorn C, Josse C, Lapola DM, Larrea C, Larrea-Alcazar DM, Lehm Ardaya Z, Malhi Y, Marengo JA, Melack J, Moraes R M, Moutinho P, Murmis MR, Neves EG, Paez B, Painter L, Ramos A, Rosero-Peña MC, Schmink M, Sist P, ter Steege H, Val P, van der Voort H, Varese M, Zapata-Ríos G (Eds) Amazon Assessment Report 2021. United Nations Sustainable Development Solutions Network, New York, USA, 2–33. https://doi.org/10.55161/POFE6241

Wesselingh FP (2006) Miocene long-lived lake Pebas as a stage of mollusk radiations, with implications for landscape evolution in western Amazonia. Scripta Geologica 133: 1–17. https://repository.naturalis.nl/pub/209724

Wesselingh FP, Hoorn C (2011) Geological development of Amazon and Orinoco basins. In: Albert JS, Reis RE (Eds) Historical Biogeography of Neotropical Freshwater Fishes. University of California Press, Berkeley, Los Angeles, London, 59–67. https://doi.org/10.1525/california/9780520268685.003.0003

Wesselingh FP, Salo JA (2006) Miocene perspective on the evolution of the Amazonian biota. Scripta Geologica 133: 439–458. https://repository.naturalis.nl/pub/209738

Wesselingh FP, Räsänen ME, Iron G, Vonhof HB, Kaandorp R, Renema W, Romero-Pittman L, Gingras M (2002) Lake Pebas: A palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. Cainozoic Research 1(1–2): 35–68. https://natuurtijdschriften.nl/pub/541674/CR2002001001004.pdf

Wesselingh FP, Hoorn C, Kroonenberg SB, Antonelli A, Lundberg JG, Vonhof HB, Hooghiemstra H (2009) Chapter 26: On the Origin of Amazonian Landscapes and Biodiversity: A Synthesis. In: Hoorn C, Wesselingh FP (Eds) Amazonia: Landscape and Species Evolution. Blackwell Publishing Ltd, Oxford, England, 421–432. https://doi.org/10.1002/9781444306408.ch26