



Integrative approach revealing a species complex in the Neotropical freshwater crab *Dilocarcinus septemdentatus* (Herbst, 1783) (Decapoda: Trichodactylidae) with a description of a new species

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<https://zoobank.org/421FD567-CC36-4DA6-BF2C-DCA07A226DE6>

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Received 5 November 2023

Accepted 17 January 2024

Published 15 May 2024

Academic Editors Martin Schwentner, Klaus-Dieter Klass

Citation: 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>

Abstract

The taxonomic status of the freshwater crab *Dilocarcinus septemdentatus* (Herbst, 1783) is still not well established. Currently, the main issue involves synonymization with *D. spinifer* H. Milne Edwards, 1853, based on a variation of the angulation of the gonopod apex. These species are distributed along rivers and lakes in northern South America, with disjunct occurrences in central-west Brazil and Argentina. Due to these inconsistencies, an integrative approach was performed to elucidate these questions, with morphological (including NanoCT-Scan) and molecular analysis (Maximum Likelihood Trees, Bayesian Inference, Genetics Distance Matrix, and Haplotype Network), based on mitochondrial markers COI and 16S rRNA. Both analysis revealed and supported the existence of a species complex under the name of *D. septemdentatus*. Based on the results obtained, we propose the revalidation of *D. spinifer*, the description of a new species, and the redescription of *D. septemdentatus* s. str., with a neotype designation for this species. The hypothesis that this species complex originated in the Pebas System, an extensive mega wetland system that existed along the lowlands of Western Amazonia from late Oligocene to late Miocene (c. 23–11 mya) is discussed.

Keywords

CT-scan, DNA barcode, Haplotype diversity, Molecular systematics, Taxonomy

1. Introduction

The primary freshwater crab genus *Dilocarcinus* H. Milne Edwards, 1853 has a somewhat complex taxonomic history. In the first comprehensive revision of the group, Rathbun (1906) considered it as a subgenus of *Trichodactylus* Latreille, 1828, including nine species. In

Pretzmann's (1968) and Bott's (1969) revisions, it was treated at the generic level; the former author included 12 species and subspecies, whereas the latter author split the genus into two subgenera, with *Dilocarcinus* s. str. counting three species. Rodríguez's (1992) system dis-

regarded the subgenera and was more inclusive in terms of constituent species, with 11 species belonging to the genus. Magalhães and Türkay (1996a, b, 2008), based on existing differences in the male first gonopod and abdominal segmentation, separated the afore mentioned species into four genera, being *Dilocarcinus* composed by three species only: *D. septemdentatus* (Herbst, 1783), *D. pagei* Stimpson, 1861, and *D. truncatus* Rodríguez, 1992.

In their specific treatment of the genus, Magalhães and Türkay (2008) proposed that *D. spinifer* H. Milne Edwards, 1853, the type species of *Dilocarcinus*, be considered a junior synonym of *D. septemdentatus*. This synonymization was made based on the variation in the arrangement of the apex of their first male gonopod, a diagnostic character for those species, which was then considered somewhat inconsistent. *Dilocarcinus septemdentatus* sensu Magalhães and Türkay (2008) is widely distributed in northern South America, encompassing the Amazon basin, coastal river basins of Suriname, French Guiana, and northern and northeastern Brazil (states of Acre, Amapá, Amazonas, Pará, Maranhão, and Goiás) and eastern Peru (Magalhães and Türkay 2008; Santos and Vieira 2017; Andrade et al. 2018), with disjunct occurrences in the Araguaia basin in Brazil (Magalhães and Türkay 2008) as well as in the middle Paraná River basin in Argentina (Collins et al. 2009).

Such a wide area of occurrence, with the existence of isolated spots (central-west region of Brazil, state of Goiás, and Argentina, near Santa Fé), raises the hypothesis that this species corresponds, in fact, to more than one cryptic species under the same nomination. The occurrence of complexes of two or more cryptic species has been increasingly reported for freshwater crabs using molecular tools (Daniels et al. 2003; Jesse et al. 2010; Keik-hosravi and Schubart 2013; Phiri and Daniels 2014, 2016; Souza-Carvalho et al. 2017; Mantelatto et al. 2022). In some of these studies, the use of molecular techniques has provided excellent contributions to clarify the diversity, assuming an important role in the elucidation of taxonomic problems when the morphology alone was not enough to make clear conclusion of this field. In the present study, we aimed to evaluate the real taxonomic status of *D. septemdentatus* sensu Magalhães and Türkay (2008) from the perspective of molecular systematics integrated with morphological analysis.

2. Material and methods

2.1. Sampling

All specimens used in the present study were evaluated through visits to, or loans from, the crustacean collections 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; Forschungsinstitut und Naturmuseum Senckenberg (SMF), Frankfurt

am Main, Germany; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá (IEPA), Macapá, Brazil; Museo Regionale di Scienze Naturali di Torino, Sezione di Zoologia (formerly Museo di Zoologia del Dipartimento di Biologia Animale dell'Università di Torino) (MZUT), Turin, Italy; Museu Paraense Emílio Goeldi (MPEG), Belém, 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; Museum für Naturkunde (ZMB), Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; Muséum national d'Histoire naturelle (MNHN), Paris, France; National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C., United States of America; Natural History Museum (NHM), London, England; Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie) (RMNH), Leiden, The Netherlands; Universidade Federal do Maranhão (CCUFMA), São Luiz, Brazil; and Zoologische Staatssammlung (ZSM), München, Germany.

Other abbreviations used: **cl** = carapace length; **cw** = carapace width; **G1**, **G2** = male first and second gonopods; **P2–5** = second to fifth pereopods. Measurements are in millimeters and are given in parentheses (cw, cl) after specimen counts when available; '?' is used when the measurement could not be obtained. Tissue samples were also obtained, under appropriate permits, from the specimens available in the referred collections, except for the CCUFMA material, in which the specimens were fixed in formalin and despite our efforts did not allow for DNA sequencing.

2.2. Morphological analysis

Morphological analysis was performed on specimens of *D. septemdentatus* from different geographic distribution as listed in the material examined section. When indicating the number and sex (♂ = male; ♀ = female) of the specimens examined, one symbol corresponds to a single individual of the respective sex, while two symbols correspond to two or more individuals of the respective sex.

The morphological examination was conducted by assessing somatic (shape and number of carapace anterolateral teeth; the number of fused abdominal somites) and gonopods (shape and angulation of the apex) characters. In addition to this preliminary assessment, a search for other potentially taxonomically informative characters was also performed, but none was found relevant. The terminology for gonopod structures was adapted from Magalhães and Türkay (2008). The diagnoses of *D. septemdentatus* and *D. spinifer* proposed by Magalhães and Türkay (2008) were considered for the morphological evaluation, as well as complementary information available in the literature and compiled in Magalhães and Türkay (2008). The morphological examination was

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. (pers. communication)
	Pty2	5' CCGGTCTGAACTCAGATCACGT 3'	
16S	16SL2	5' TGCCTGTTTATCAAAAACAT 3'	Schubart et al. (2002)
	1472	5' AGATAGAAACCAACCTGG 3'	Schubart et al. (2000)
	16SL15	5' GACGATAAGACCTATAAAGCTT 3'	Schubart et al. (2001)

Table 2. Information on specimens of *Dilocarcinus* species used in molecular analyses. CCDB: Coleção de Crustáceos do Departamento de Biologia da FFCLRP/USP; INPA: Instituto Nacional de Pesquisas da Amazônia; MPEG: Museu Paraense Emílio Goeldi. AM = Amazonas; PA = Pará; SP = São Paulo; TO = Tocantins.

Specimen	Voucher	Locality	GenBank Access	
			COI	16S
<i>Dilocarcinus spinifer</i> 027	CCDB 5034	Altamira/PA	OP252629	—
<i>Dilocarcinus spinifer</i> 028	CCDB 5034	Altamira/PA	OP252630	—
<i>Dilocarcinus spinifer</i> 029	CCDB 5034	Altamira/PA	OP252631	—
<i>Dilocarcinus septemdentatus</i> 033	INPA 800	Carauari/AM	OP252632	OP263690
<i>Dilocarcinus septemdentatus</i> 034	INPA 800	Carauari/AM	OP252633	—
<i>Dilocarcinus septemdentatus</i> 045	INPA 805	Res. Mamirauá/AM	OP252634	OP263691
<i>Dilocarcinus montinavis</i> sp. n. 050	INPA 0584	Serra do Navio/AP	OP252635	OP263692
<i>Dilocarcinus montinavis</i> sp. n. 159	MPEG 1045	Flona do Amapá/AP	OP252636	OP263693
<i>Dilocarcinus montinavis</i> sp. n. 160	MPEG 1045	Flona do Amapá/AP	—	OP263694
<i>Dilocarcinus pagei</i> 021	CCDB 6338	Castilho/SP	OP236481	OP245228
Goyazana castelnaui	CCDB 4651	Palmas/TO	MG344686	MG344657

made using a Leica® MZ9 5 stereomicroscope with a Leica® DFC 295 camera attached, and a Nanotomography CT-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 equipment details).

2.3. Obtaining molecular data

Both molecular analyzes were performed based on mitochondrial genes: Cytochrome Oxidase subunit I (COI) and 16S Ribosomal RNA (16S). These markers have proven their effectiveness in studies with decapod crustaceans, both phylogenetic and variability in different taxon levels, including primary crabs (Negri et al. 2014; Laurenzano et al. 2012; Silva et al. 2012; Souza-Carvalho et al. 2017; Buranelli et al. 2019; Álvarez et al. 2020; Mantelatto et al. 2022).

The steps of DNA extraction, amplification, purification, and sequencing followed the protocols of Schubart et al. (2000), adapted according to Robles et al. (2007), as presented in Mantelatto et al. (2018). DNA extraction was performed from pereopod muscle tissue, according to the following steps: the tissue was initially incubated in a dry bath at 55°C for about 12 h in a solution of 200 µL

of Chelex resin (5%) with 10 µL of proteinase K (PK), this time may vary until the tissue is completely digested; with complete digestion, the temperature of the bath was raised to 95°C for 3 min, for PK inactivation; then, the samples were transferred to a freezer for 10 min and subsequently centrifuged at 14,000 rpm, 18°C for 3 min; finally, the supernatant was transferred to a new tube, from which the contraction and DNA quality of the samples is evaluated, using a NanoDrop® 2000/2000 c spectrophotometer (Thermo Scientific, Wilmington, DE, USA) and, once adequate, the samples proceed to the PCR amplification step.

Approximately 600 base pairs (bp) corresponding to the COI gene and 500 corresponding to 16S were amplified using the primers listed in Table 1, with the following cycle configurations: initial denaturation at 94°C for 5 min, 40 denaturation cycles 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 using agarose gel electrophoresis (1.5%), visualized on an L-PIX EX® photodocumenter, purified using the SureClean® Plus kit (according to the supplier's protocol), and sequenced using the ABI Big Dye® Terminator Mix in an ABI Prism 3100 Genetic Analyzer®, from the FCAV Technology Department of UNESP in Jaboticabal, São Paulo, Brazil.

The strands obtained (forward and reverse) were evaluated, edited, and used to create consensus sequences, using GENEIOUS PRIME® (2021.2.2 Biomatters Ltd). Sequence identification was confirmed using the Gen-

Bank BLAST tool (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>). Information regarding the sequences used are listed in Table 2. After the end of the entire process, the new sequences were submitted to GenBank.

2.4. Molecular analyses

Fourteen sequences were used and obtained from individuals previously identified as *D. septemdentatus* (8 from COI and 6 from 16S), and four sequences from *D. pagei* and *Goyazana castelnaui* (H. Milne Edwards, 1853) (one from each gene). The *G. castelnaui* sequences were chosen as an outgroup for the phylogenetic analyses due to the close relationship between this species and those of the genus *Dilocarcinus* (see Magalhães and Türkay 1996a). Tissues from several other individuals/lots were also processed, but despite our efforts sequencing of these samples was unsuccessful, possibly due to previous formalin and/or dry preservation.

All alignments were performed on the MAFFT v.7 online servers (Katoh et al. 2019) (<http://mafft.cbrc.jp/alignment/server>). An alignment for each gene, containing only sequences from the target species, was submitted to DNASP 6 (Rozas et al. 2017) to calculate the number of haplotypes, and haplotype diversity (dH) and create the POPART 1.7 input files, for the elaboration of haplotype networks. Both networks were built by the parsimony method in POPART 1.7's TCS Networks (Clement et al. 2002; Leigh and Bryant 2015). These same alignments were also used to generate the two genetic distance matrices (for COI and 16S), using MEGA 10.0.5 (Kumar et al. 2018).

Concatenated alignments were used, with sequences from both genes of *D. septemdentatus*, from *D. pagei* (sister group), and from *G. castelnaui* (outgroup), for the reconstruction of phylograms, one by the Maximum Likelihood (ML) method and another by Bayesian Inference (IB). ML analysis was performed on the IQ-TREE (<http://www.iqtree.org>) (Trifinopoulos et al. 2016), based on the TN93+G model, selected through the ModelFinder of the IQ-TREE (Kalyaanamoorthy et al. 2017). Branch consistency was defined in 1000 bootstrap replicates with Ultrafast bootstrap (Hoang et al. 2018) also from IQ-TREE. In turn, the BI analysis was performed in BEAST v.2.6.7 (Bouckaert et al. 2019), with predefined parameters and input files in BEAUTI v.2.6.7 (Bouckaert et al. 2019), with both the pre-selected models from the ModelFinder of IQ-TREE and MEGA 10.0.5, following the BIC. The model chosen for COI alignments was TN93+G (G = 0.20) and for 16S it was TN93. To carry out the BI analysis, the following parameters were considered: Birth-Death model, sampling of a tree every 15.000 generations, for 30 million generations, sampling frequency equal to 100.000, and burn-in of 25%. Three repetitions were performed in BEAST, with the same parameters, with each result evaluated in TRACER 1.6. (Rambaut et al. 2014), referring to ESS values (values above 200) (Schneider 2017). After that, both results were combined in LOGCOMBINER v.1.8.4 (Drummond and Rambaut

2007) and the result was evaluated from the summary of most trees obtained in TREEANNOTATOR v2.4.4 (Drummond and Rambaut 2007). After this process, a final tree was generated and viewed/edited in Figtree 1.4.4 (Rambaut 2018).

After comparing the results of both approaches, only the phylogram of the tree by IB was presented, with the bootstrap value (right) and posterior probability (left) (> 95%), considering that all clades were recovered by both analyzes.

Finally, a divergence time estimation analysis with concatenated partitions, referring to COI and 16S, was also included in BEAST v.2.6.7. For this purpose, all configurations of the phylogenetic analysis by IB were considered, with the addition of information for the calibration of the molecular clock (Relaxed Log model), obtained from the fossil record of trichodactylid crabs from the Middle Eocene (dated to approximately 38–47.8 mya) (see Klaus et al. 2017), using the offset function of the exponential distribution.

3. Results

3.1. Morphological analysis

The morphological analysis included specimens identified a priori as *D. septemdentatus* sensu Magalhães and Türkay (2008), as listed in the material examined sections.

The main variation observed in *D. septemdentatus* sensu Magalhães and Türkay (2008) was in the shape and curvature of the G1 distal portion (Fig. 1A–C), in which three distinct forms were found: (a) G1 with the distal strongly curved laterally, with an apex approximately as long as the moderately developed subdistal lobe (Fig. 1A); (b) G1 with a slightly bent laterally to nearly straight distal portion, apex obliquely inclined towards the lateral side and slightly longer than the inconspicuous or weakly developed subdistal lobe (Fig. 1B); and (c) G1 bearing a distinctly sinuous distal portion, with an accentuated curvature towards the lateral side and an inconspicuous apex distinctly shorter than the strongly developed subdistal lobe bearing a dense field of spines (Fig. 1C).

It was also interesting to note a correlation found between the shape of the apex of G1 and the shape of the carapace front among the specimens examined. Specimens with bent distal portion of the G1 (forms a and c) usually show a sinuous frontal margin of the carapace, with a distinct median concavity (Fig. 1D) whereas those with G1 distal portion straight or slightly inclined laterally (form b) tend to bear a nearly straight frontal margin (Fig. 1E).

3.2. Molecular analyses

The results evidenced that the specimens considered under the name *D. septemdentatus* sensu Magalhães and

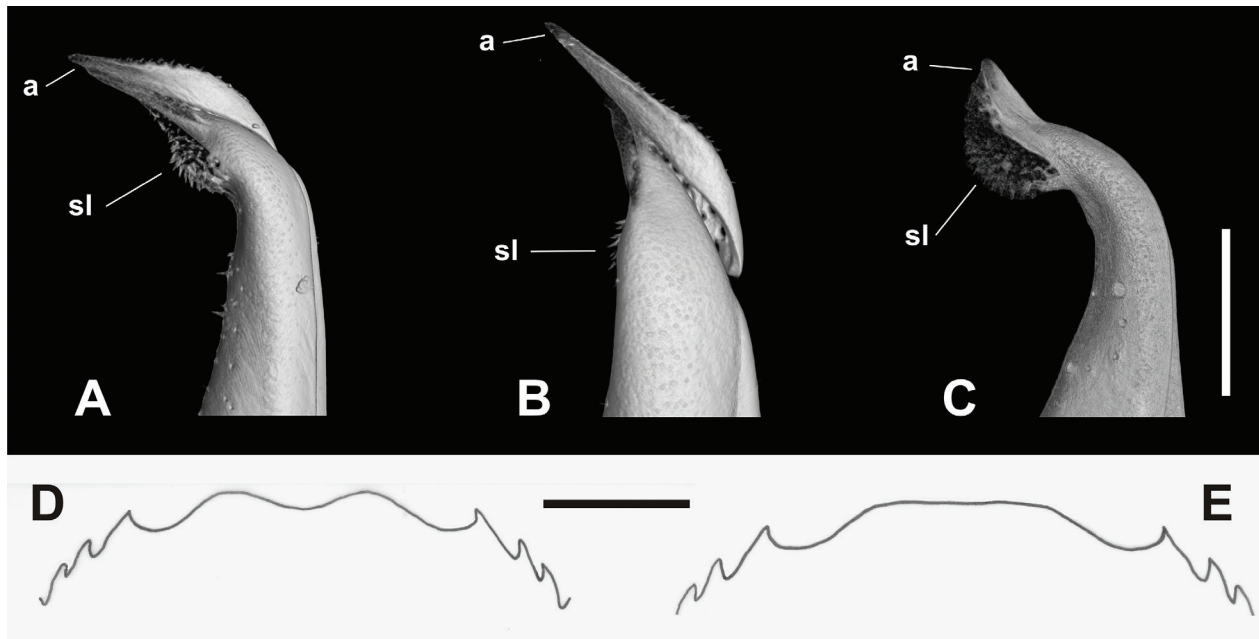


Figure 1. Computerized nano-tomography of the distal portion of the male right first gonopod of *Dilocarcinus septemdentatus*, INPA 1470 (A), *D. spinifer*, MPEG 697 (B), and *D. montinavis* sp. n., paratype, INPA 584 (C), photographed in ventromesial view. Outline of the frontal margin of *D. septemdentatus* (D) and *D. spinifer* (E). — Abbreviations: a = apex; sl = subdistal lobe. Scale bars: 1 mm (A–C), 5 mm (D, E).

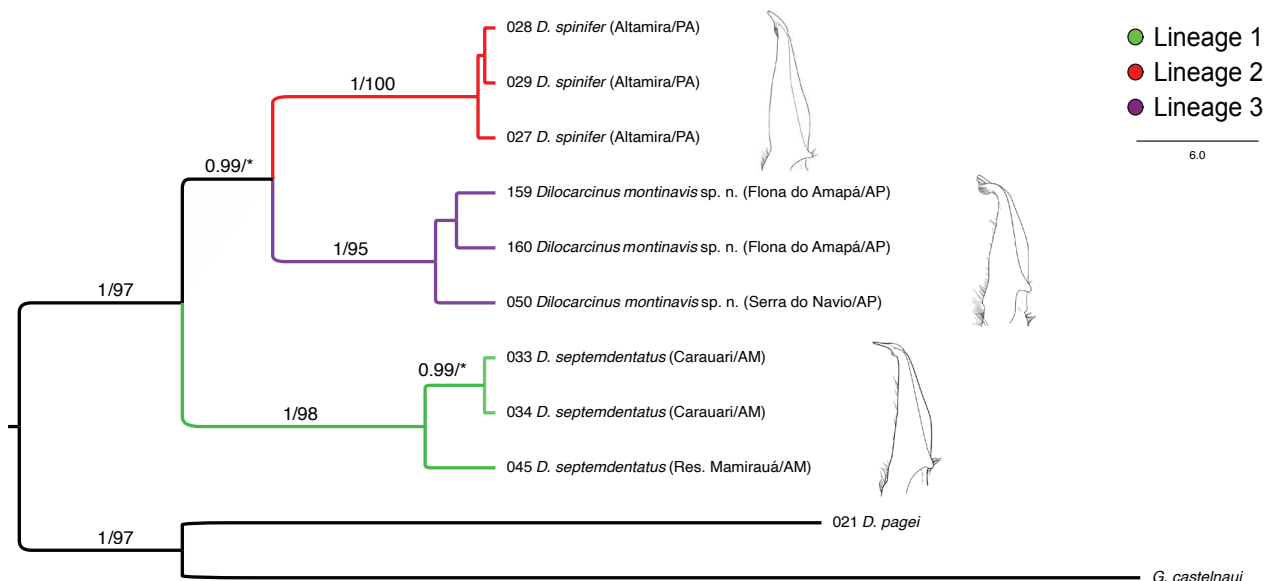


Figure 2. Phylogram generated by the Bayesian Inference method, based on concatenated alignments of the COI and 16S genes of specimens belonging to the *Dilocarcinus septemdentatus* sensu Magalhães and Türkay (2008) species complex. The values in the branches correspond to posterior probability (left) and 1000 bootstrap replicates (right). We considered the recovered branches, in both approaches (ML and IB) and with high support value ($\geq 95\%$), showing the recovered lineages. * = bootstrap values $< 95\%$. L1, L2, and L3 = strains 1, 2, and 3, respectively.

Türkay (2008) were grouped into three distinct lineages, as shown in the concatenated phylogram (IB and ML, Fig. 2). In addition to the high values of posterior probability and bootstrap that support the branches of the lineages, these lineages are also strongly supported by the analysis of genetic divergence for both genes (Table 3). When the specimens grouped in each lineage were correlated with the morphology of their G1 distal portion, they were taxonomically determined as follows: Lineage 1 = *D.*

septemdentatus – G1 distal portion strongly bent laterally (form a, Fig. 1A); Lineage 2 = *D. spinifer* – G1 distal portion nearly straight (form b, Fig. 1B); and Lineage 3 = a new species, named here as *Dilocarcinus montinavis* sp. n. – G1 distal portion distinctly sinuous (form c, Fig. 1C) (see section 3.3.).

The analysis of estimated divergence time pointed to an interval between 19 and 13 mya, in which it is estimated that the process of separation of L1 from L2 and

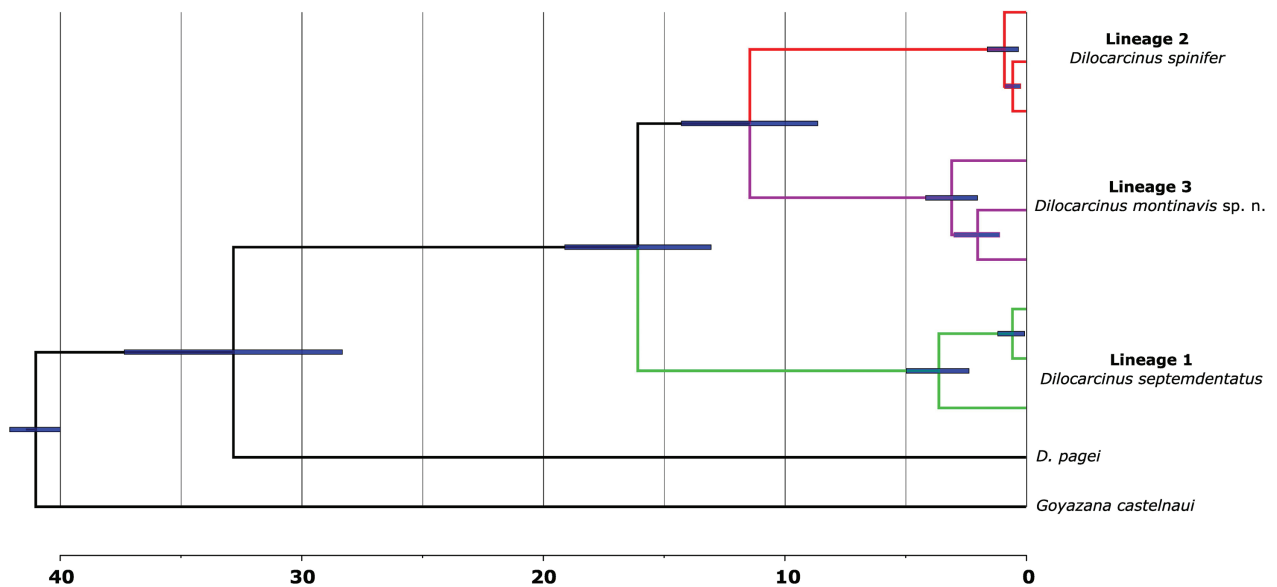


Figure 3. Phylogram with estimated divergence time generated by the Bayesian Inference method, based on concatenated alignments of the COI and 16S genes of specimens belonging to the *Dilocarcinus septemdentatus* sensu Magalhães and Türkay (2008) species complex, to *Dilocarcinus pagei*, and to *Goyazana castelnaui*. Blue bars correspond to 95% posterior confidence intervals (HPD). Scale in millions of years (Ma).

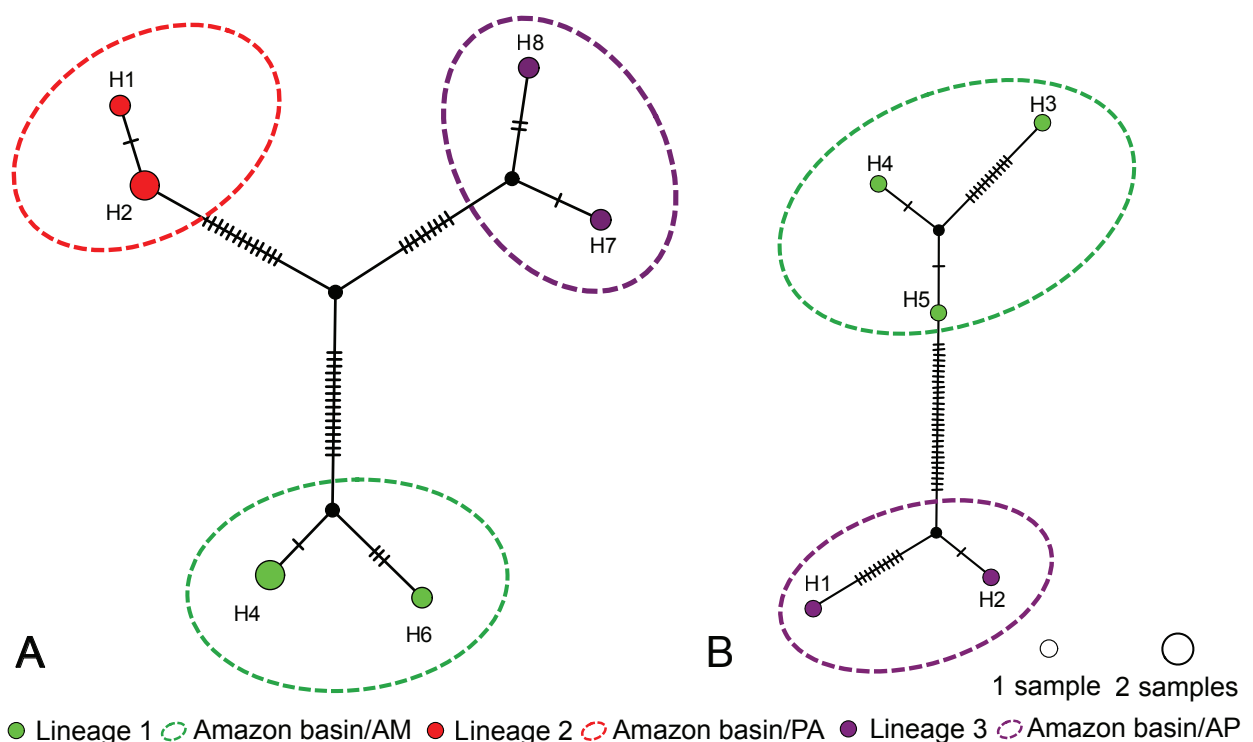


Figure 4. Parsimony haplotype network of COI (A) and 16S (B) gene fragments from populations of the *Dilocarcinus septemdentatus* sensu Magalhães and Türkay (2008) species complex. H = haplotype. The size of the circles is proportional to the haplotype frequency. The haplotypes with the colors red, blue, and black correspond, respectively, to Lineages 1, 2, and 3. Likewise, the red, green, and purple ellipses correspond, respectively, to samples collected in the states of Pará, Amazonas, and Amapá (Amazon Basin), Brazil.

L3 occurred. In turn, it is estimated that the separation between *D. spinifer* (L2) and *Dilocarcinus montinavis* n. sp. (L3) occurred in the interval from 14 to 8 Ma. Fig. 3 below shows the divergence time phylogram.

The haplotype network generated with *D. septemdentatus* sensu Magalhães and Türkay (2008) sequences recorded

8 haplotypes ($dH = 1$) for COI (Fig. 4A) and 5 haplotypes ($dH = 1$) for 16S (Fig. 4B). The size of the circles is proportional to the haplotype frequency and haplotypes with low frequency were not presented in the networks, being concatenated by similarity. Thus, haplotype 2 (H2) gathered H2 and H3, while H4 gathered H4 and H5.

Table 3. Intra- and interlineage genetic distances of *Dilocarcinus septemdentatus*, *D. spinifer*, and *Dilocarcinus montinavis* sp. n. for COI and 16S genes. Values in percentage (%).

COI		
	Lineage 1 (<i>D. septemdentatus</i>)	Lineage 3 (<i>D. montinavis</i> sp. n.)
Lineage 1 (<i>D. septemdentatus</i>)	0–0.68	
Lineage 2 (<i>D. spinifer</i>)	5.29–5.90	
Lineage 3 (<i>D. montinavis</i> sp. n.)	4.09–5.31	0–0.51
16S		
	Lineage 1 (<i>D. septemdentatus</i>)	
Lineage 1 (<i>D. septemdentatus</i>)	0–1.70	
Lineage 3 (<i>D. montinavis</i> sp. n.)	4.29–6.73	

3.3. Taxonomy

Based on the obtained results, it is proposed herein the resurrection of *Dilocarcinus spinifer* as a valid species, besides proposing the description of a new species for the genus based on morphological and molecular data, as well as adjustments in the diagnosis and description of the studied species.

Order Decapoda Latreille, 1803

Infraorder Brachyura Latreille, 1803

Family Trichodactylidae H. Milne Edwards, 1853

Genus *Dilocarcinus* H. Milne Edwards, 1853

Type species. *Dilocarcinus spinifer* H. Milne Edwards, 1853 [subsequent designation by Pretzmann 1968]

3.3.1. *Dilocarcinus septemdentatus* (Herbst, 1783)

Figures 1A, C, 2 (L1), 5A–E

Cancer n. 957 — Gronovius 1764: 222.
Cancer Orbicularis — Meuschen 1778: 84 (n. 788) [unavailable name, Opinion 260 (ICZN 1954a)].
Cancer Orbicularis — Meuschen 1781: unnumbered page (n. 957) [Unavailable name, Opinion 261 (ICZN 1954b)].
Cancer septemdentatus Herbst, 1783: 155.
Arica septemdentata — White 1847: 31 [nomen nudum].
Dilocarcinus septemdentatus — Gerstaecker 1856: 148. — Göldi 1885: 662. — Göldi 1886: 28, pl. 2 figs 3–17. — Nobili 1896: 1 [part]. — Moreira 1901: 44, 49, 109 [part]. — Pretzmann 1968: 75 (in list). — Rodríguez 1981: 48 (in list). — Rodríguez 1992: 128. — Magalhães and Türkay 1996a: 67 (in list) [part], 69 (in list) [part], 78 (in list) [part], 79, figs 23, 24. — Magalhães 1998: 519 (in list) [part]. — Barros and Pimentel 2001: 32 (in list). — Magalhães 2003: 203 (in key), 206, figs 108 (map), 109a, b, e. — Collins et al. 2004: 254 (in list). — Ng et al. 2008: 187 (in list). — Magalhães and Türkay

2008: 187, figs 3, 5, 6 [part]. — Vieira 2008: 68, 69, table 5.1 (in list). — Collins et al. 2009: 50, fig. 1a. — Collins et al. 2011: 191, Appendix (in list). — ICMBio 2014: 178. — Magalhães 2016: 431 (in list) [part].
Orthostoma septemdentatum — Ortmann 1897: 326 (in key), 327 [part].
Dilocarcinus (Dilocarcinus) septemdentatus — Bott 1969: 44, pl. 8, fig. 14a, b, pl. 20, fig. 45.

Diagnosis. G1 with distal portion strongly curved laterally; subdistal lobe moderately to well developed; apex directed laterally, approximately as long as the subdistal lobe.

Description (amended from Magalhães and Türkay 2008). Carapace (Fig. 5A) smooth, strongly convex longitudinally; frontal margin unarmed, distinctly bilobed; anterolateral margins with 6–7 acute teeth behind exorbital tooth. Pleonal somites (Fig. 5B) III–VI fused; somite III smooth, without transversal carina along anterior margin. G1 (Fig. 5C–E) with distal portion strongly bent laterally; lateral border (“lb” in Fig. 5) gently sinuous, with few minute setae medially and dense patch of long setae along basal portion; marginal suture (“ms” in Fig. 5) running along mesial surface, twisted towards lateral side near apex (“a” in Figs 1, 5); lateroventral side with distinct, moderately to well-developed rounded subdistal lobe (“sl” in Figs 1, 5C); field of short spines (“fs” in Fig. 5) continuous, located subterminally on lateroventral side, denser along and extending distally to dorsal surface; subapical bristles, when present, in small number; apex strongly bent laterally, flat, narrow, approximately as long as subdistal lobe; distal aperture (“do” in Fig. 5) very narrow, slit-like, directed laterally.

Type material. **Neotype** (designated herein): Male (cw 47.9, cl 37.6), MZUSP 44534, Brazil, Pará, municipality of Peixe-Boi, braços do rio Peixe-Boi, 01°11'31"S 47°18'44"W, 34 m altitude, III.1994, E. Matos.

Type locality. Brazil, state of Pará, municipality of Peixe-Boi, Peixe-Boi River.

Material examined (herein confirmed as *Dilocarcinus septemdentatus*). SURINAME — • 1 ♂, NHM 1959.3.20.6, 1838, I.T. Sandersen. — **Paramaribo District:** • 2 ♂ (cw 48.2, cl 37.8; cw 48.7,

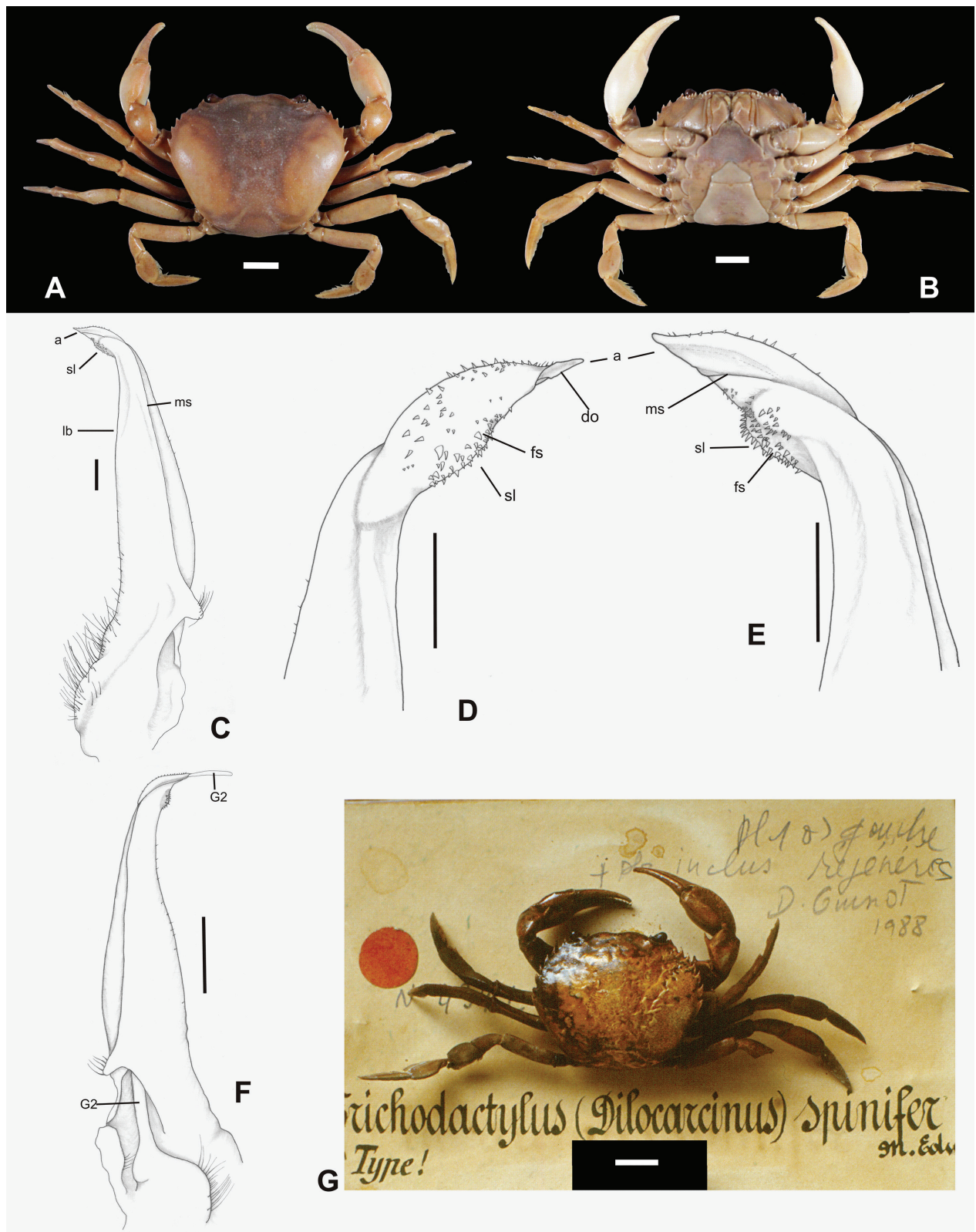


Figure 5. *Dilocarcinus septemdentatus*, neotype male (cw 47.9, cl 37.6), MZUSP 44534. Habitus: dorsal view (A), ventral view (B). Right G1: ventromesial view (C); detail of distal portion, dorsal view (D); detail of distal portion, ventral view (E). *Dilocarcinus spinifer*, lectotype male (cw 38.8, cl 31.8), MNHN 4391: left G1 (regenerated) with G2 in place, ventromesial view (F); dry specimen, habitus, dorsal view, in preservation box (G). — Abbreviations: a = apex; do = distal opening; fs = field of spines; lb = lateral border; ms = marginal suture; sl = subdistal lobe. Scale bars = 1 mm. Photo credits: A, B by J. Colavite; G by C. Magalhães.

cl 39.9), ZMB 12981, near Paramaribo, C. Heller. — **Saramacca District:** • 1 ♂, RMNH D 20711, near Granmankanare, Saramacca River, 7.iv.1964, M. Boeseman. — **Brokopondo District:** • 2 ♂, NHM

1959.3.20.7-8, near Donderberg [= Donder Bari Berg, 05°09'50"N 55°15'07"W], about 91.5 Km S. of Paramaribo, 4.xi.1938, I.T. Sanderson. — **Sipaliwini District:** • 2 ♂ (cw 37.2, cl 30.8) 1 ♀ (cw 25.8,

cl 22.5), RMNH D 20710, Suriname River, Kasi-kriki near Pokigron, 20.iii.1964, M. Boeseman • 1 ♂ (cw 35.5, cl 28.8), RMNH D 21790, Ligorio, 03°54'22"N 55°33'59"W, 16.vi.1965, G.F. Mees • 1 ♂ (cw 32.6, cl 27.6), RMNH ZMA.Crust.D.102298, near Ligorio, 27.i.1967, H. Nijssen. BRAZIL — **Amapá**: • 1 ♂ (cw 50.5, cl 39.5), IEPA 255, furo do Araguari, arquipélago do Bailique, Macapá, 9.iv.2000, I.M. Vieira, O.A. Alencar, O.M. Costa, J. Cardoso and A.C. Souza — **Pará**: • 1 ♂ (cw 36.1, cl 29.8), RMNH D 12187, Apisiké [tributary creek of upper West Paru River], 20.iv.1952, D.C. Geijkes • 1 ♂ (cw 51.3, cl 39.7), SMF 2718, Quatipuru, campo Santarém, 06.iv.1963, E.-J. Fittkau • 1 ♂ (cw 44.8, cl 35.3), MZUSP 11694, municipality of Peixe-Boi, braços do rio Peixe-Boi, 01°11'31"S 47°18'44"W, 34 m altitude, iii.1994, E. Matos col. — **Amazonas**: • 2 ♂♂ (cw 41.2, cl 30.7; cw 49.1, cl 36.9), INPA 805, rio Solimões, Tefé, Reserva de Desenvolvimento Sustentável de Mamirauá, 26.iv.1994, P. Henderson • 2 ♂♂ (cw 20.5, cl 16.2; cw 44.5, cl 33.3) 1 ♀ (cw 13.4, cl 10.4), INPA 802, rio Solimões, Tefé, Reserva de Desenvolvimento Sustentável de Mamirauá, xii.1993; 1 ♂ (cw 46.7, cl 36.1), INPA 796, Iranduba, rio Solimões, ponta do Catalão, lago do Pirapora, 03°11'S 59°55'W, ix.1999, L. Rapp Py-Daniel et al. • 1 ♂ (cw 42.2, cl 31.9), INPA 1255, Iranduba, rio Solimões, ponta do Catalão, lago do Pirapora, braço do paranã do Ximborena, 03°11'S 59°55'W, 24.v.2000, L. Rapp Py-Daniel et al. • 1 ♂ (cw 44.9, cl 35.1), SMF 29878, Iranduba, rio Solimões, ponta do Catalão, lago do Pirapora, 03°09'07"S 59°54'50"W, 13.vii.2000, L. Rapp Py-Daniel et al. • 1 ♂ (cw 47.2, cl 36.7), INPA 1301, rio Amazonas, lago Coró-Coró, 03°13'50.5"S 58°41'28.7"W, 7.vii.2000, A. Varela • 1 ♂ (cw 47.7, cl 36.9) 1 ♀ (cw 31.7, cl 25.6), INPA 151, lago Janauacá, rio Solimões, 8.viii.1985, G.M. Soares • 1 ♀ (cw 12.9, cl 9.9), NHMW 6632, lago Janauacá, v.1971, U. Irmeler • 1 ♂ (cw 41.5, cl 31.0) 1 ♀ (cw 43.2, cl 34.8), INPA 1470, Carauari, Reserva Extrativista (Resex) Médio-Juruá, comunidade Nova Esperança, 05°05'31"S 67°10'03"W, 27.vi.–16.vii.2005, F. Xavier Filho and A.L. Henriques • 14 ♂♂ (cw 11.1, cl 9.4 – cw 44.2, cl 37.0) 7 ♀♀ (cw 19.4, cl 16.1 – cw 34.1, cl 27.4), INPA 800, rio Juruá, lago do Rato/Caroçal, Carauari, 05°43'02.4"S 67°42'12.8"W, 6.iv.2000, J. Zuanon • 1 ♀ (MZUSP 4770), Pauini, 07°40'S 66°58'W, 19.xii.1974, P. Vanzolini.

Additional material examined (see Remarks below; herein considered as not belonging to *Dilocarcinus septemdentatus*). *Dilocarcinus pagei* Stimpson, 1861: • 7 ♀♀ (cw 36.5, cl 30.7 – 45.7:38.9), ZSM 1089-4, Brazil, Pará, ilha do Marajó, L. Müller; • 1 ♂ (cw 51.2, cl 40.3 mm), 2 ♂♂ (cw 34.2, cl 27.6; cw 50.9, cl 41.3) 4 ♀♀ (cw 43.3, cl 35.0 – cw 46.7, cl 36.6), MZUT Cr 291, Brazil, Mato Grosso, Carandazinhol [= Carandazinhol], 1899, Dr. A. Borelli • 1 ♀, dry, NHM 1955.2.21.24 (ex-MZUT), idem; RMNH D-11126, Bolivia, Beni, rio Yacuma, near Espiritu, 13–28.iv.1954, W. Forster and O. Schindler • 2 ♂♂ 2 ♀♀ (MZUT Cr 293), Paraguay, Concepción, Colonia Risso, 1893, Dr. A. Borelli • 5 ♂♂ (cw 16.7, cl 12.7 – cw ?, cl ?), 8 ♀♀ (cw 12.5, cl 10.4 – cw ?, cl ?) [in bad condition], MZUT Cr 289, Argentina, Chaco, Resistencia, 1893, Dr. A. Borelli. — *Poppiana argentiniana* (Rathbun, 1905): • 3 ♂♂ (cw ?, cl ? – cw 28.5, cl 23.5), MZUT Cr 289, Argentina, Chaco, Resistencia, 1893, Dr. A. Borelli.

Distribution. Northern South America, in the central and lower Amazon basin as well as in coastal river basins in Suriname and Brazil (Fig. 6A) (Magalhães and Türkay 2008; present paper).

Remarks. Herbst's (1783) specimen used to describe *D. septemdentatus* could not be found in the ZMB's hold-

ings despite the efforts of Sakai (1999) and Magalhães and Türkay (2008). One of us (C.M.) made a last attempt to locate the specimen on a visit to the ZMB on 4th October 2023, but this search was equally unsuccessful. Thus, considering that: (a) the name-bearing type specimen can be considered not extant; (b) the three species of *Dilocarcinus* studied herein are sympatric (and can be even syntopic); and (c) the original description of *D. septemdentatus* was based on somatic characters of a single female specimen, with insufficient morphological resolution, it seems essential to designate a neotype in order to define the present taxon objectively (ICZN 1999: Art. 75).

Herbst (1783) did not specify the exact provenance of his specimen; he just mentioned it was from American coastal waters. Bott (1969) restricted the type locality to the lower Amazon (Brazil, state of Pará, surroundings of Belém) but without further explanation. The neotype specimen (MZUSP 44534) was therefore chosen from specimens collected about 150 km northeast of Belém, in a coastal river basin from the state of Pará, northern Brazil.

Nobili (1896: 1; 1898: 9) examined specimens collected by Dr. Borelli from Colonia Risso (rio Apa, upper rio Paraguay) and Resistencia (province Chaco, Argentina) preserved in the "R. Museo Zoologico di Torino" (currently Museo Regionale di Scienze Naturali di Torino, Sezione di Zoologia) and assigned them, respectively, to *Dilocarcinus septemdentatus* and *Orthostoma septemdentatum*. Colosi (1920: 15), in addition to this material, also examined specimens from Carandazinhol (state of Mato Grosso, Brazil) and treated them as *Trichodactylus (Dilocarcinus) orbicularis*. These lots have been reexamined by one of us (C.M.) in November 1988 on a visit to the MZUT and the specimens were found to be *Dilocarcinus pagei* Stimpson, 1861 and *Poppiana argentiniana* (Rathbun, 1905) (see above). Rathbun (1906: 58) and Balss (1914: 409) listed *D. septemdentatus* as a junior synonym of *Trichodactylus (Dilocarcinus) orbicularis* but the specimens they have dealt with actually belong to *D. pagei*. The specimen from Bolivia (rio Yacuma) treated by Holthuis (1959: 218) as *Trichodactylus (Dilocarcinus) septemdentatus* is also *D. pagei* (C.M., pers. observation).

3.3.2. *Dilocarcinus spinifer* H. Milne Edwards, 1853

Figures 1B, E, 2 (L2), 5F, G

Dilocarcinus spinifer H. Milne Edwards, 1853: 215 — H. Milne Edwards 1854: 178, pl. 14 fig. 3, 3a–e; A. Milne-Edwards 1869: 176, 178 (in key). — Young 1900: 231 (in key), 234. — Moreira 1901: 44 (in list), 49, 109 (in list). — Rodríguez 1981: 48 (in list). — Rodríguez 1992: 128, fig. 45. — Holthuis 1994: 9. — Pereira and Berrestein 2006: 58, tab. 4.1 (in list).

Dilocarcinus castelnaui — H. Milne Edwards 1853: 216 [part, 1 ♂, MNHN 3866]. — H. Milne Edwards 1854: 182 [part, 1 ♂, MNHN 3866]. — Smith 1870: 36 [part] (in list).

Orthostoma spiniferum Ortmann, 1897: 326 (in key), 327.

Trichodactylus (Dilocarcinus) spinifer — Rathbun 1904: 242 (in list). — Rathbun 1906: 60 [part], pl. 18 fig. 1, text-fig. 121. — Holthuis 1959: 216, text-figs 50c, 52.

Dilocarcinus (Dilocarcinus) spinifer — Bott 1969: 45, pl. 8, figs 15a, b; pl. 20, fig. 46.

Dilocarcinus septemdentatus — Magalhães and Türkay 1996a: 67, table 1 (in list) [part], 69, table 2 (in list) [part], 78 (in list) [part], fig. 17. — Magalhães and Türkay 1996b: 139. — Magalhães 2003: 206, figs 108 (map) [part], 109c, d. — Magalhães and Türkay 2008: 187 [part], figs 1, 2, 4a, b, 6 [part, not figs 3, 5]. — Collins et al. 2009: 51, fig. 1A, A'. — Magalhães et al. 2018: 4, table 1 (in list), 9 (in list), 32, fig. 12 (map). — Andrade et al. 2018: 3, figs 1A (map), 2C. — Magalhães 2016: 431 (in list) [part]. — Santos and Vieira 2017: 3, figs 1–9.

Diagnosis. G1 (Fig. 5F) with distal portion straight or slightly inclined laterally; subdistal lobe inconspicuous or weakly developed; apex slightly longer than the distal lobe.

Description. Carapace (Fig. 5G) smooth, strongly convex longitudinally; frontal margin unarmed, slightly bilobed to nearly straight; anterolateral margins with 6–7 acute teeth behind exorbital tooth. Pleonal somites III–VI fused and smooth. G1 (Fig. 5F) with distal portion straight or slightly inclined laterally; lateral border slightly sinuous, with few short setae medially and dense patch of long setae along basal portion; marginal suture running along mesial surface, twisted towards lateral side very close to apex; lateroventral side with weakly developed rounded subdistal lobe; field of short spines continuous, located subterminally on lateroventral side, denser along lateral surface of subdistal lobe, extending distally to dorsal surface; subapical bristles, when present, in small number; apex directed laterally, slightly longer than subdistal lobe; distal aperture very narrow, slit-like, directed laterally.

Type material. **Lectotype** (designated herein): 1 ♂ (cw 38.8, cl 31.8), dry, MNHN 4391, French Guiana, Cayenne, Saint-Armand coll. — **Paralectotype**: 1 ♂ (cw 31.1, cl 27.5), dry, MNHN 3867, French Guiana, Cayenne, Saint-Armand col.

Type locality. Cayenne, French Guiana.

Material examined. SURINAME: • 1 ♂, INPA 354 • 1 ♂, NHM 1959.3.20.6, 1838, I.T. Sanderson • 1 ♂ (cw 37.5, cl 31.0), RMNH D 5332, 7.vi.1944, D.C. Geijkes • 1 ♂ (cw 22.6, cl 20.2), RMNH D 3231, Suriname River, 21–28.ix.1938, D.C. Geijkes. — **Paramaribo District**: • 2 ♂ (cw 48.2, cl 37.8; 48.7:39.9), ZMB 12981, near Paramaribo, C. Heller. — **Saramacca District**: • 1 ♂ (cw 43.9, cl 33.9), INPA 353, Saramacca, Toni Holo, iv.1959, D.C. Geijkes. — **Marowijne District**: • 1 ♂ (cw 36.4, cl 29.9), RMNH D 12359, 14.6 Km N.V. Moengatapoe, 11.x.1948, Suriname Exped. 1948–49 • 2 ♂♂ (cw 23.6, cl 20.3; cw 35.7, cl 29.9) 2 ♀♀ (cw 16.0, cl 14.5; cw 19.2, cl 17.0), RMNH D 12123, 8.4 Km N.V. Moengatapoe, 6.x.1948, Suriname Exped. 1948–49. — **Brokopondo District**: • 2 ♂♂, NHM 1959.3.20.7–8, near Donderberg, about 91.5 km of Paramaribo, 04.xi.1938, I.T. Sanderson • 4 ♂♂ (cw 31.0, cl 26.5 – 43.6:36.0) 2 ♀♀ (cw 31.5, cl 27.7; cw

35.7, cl 30.5), RMNH D 21247, creek tributary of Suriname River near Brokopondo, 13.iv.1965, G.F. Mees • 1 ♂ (cw 25.7, cl 22.1), RMNH D 21530, Suriname riviertussen, N.V. Kabel, 2.vi.1964, M. Boeseman • 2 ♂ (cw ?, cl ?; cw 29.4, cl 24.9), RMNH D 3237, Kabelstation, Makambikreek, 27.ix.1938, D.C. Geijkes. — **Sipaliwini District**: • 3 ♂ (cw 38.7, cl 32.8 – cw 41.1, cl 34.2), 1 ♀ (cw 30.2, cl 26.8), RMNH D 27200, creek trib. of Fallawatra river, upper Nickerie river, 2.ii.1971, M. Boeseman • 1 ♂ (cw 45.7, cl 38.0), SMF 4887, Sipaliwini, Awara creek, trib. of Suriname river, 1.5 Km S. from Botopasi, 18.iii.1967, H. Nijssen • 1 ♀ (cw 22.9, cl 20.4), MZUSP 1885, Anapaiké village [= Kawemhaven, 03°24'42"N 54°01'16"W], 24.xi.1963, B. Malkin. FRENCH GUIANA: • 2 ♂ (cw 38.7, cl 32.7; cw 40.3, cl 32.8), NHML 1890.10.7.106.7, Cayenne, K.R. Jelski. BRAZIL: • 1 ♂ (cw 46.3, cl 35.6 mm), USNM 32009, Amazon River region, Pará to Manaus, J.B. Steere • 2 ♂♂ (cw 16.6, cl 14.1; cw 34.0, cl 27.9), NHMW 6661, unknown locality, date and collector. — **Amazonas**: • 1 ♀ (cw 27.8, cl 21.8), NHMW 6642, rio Negro, J. Natterer • 1 ♂ (35.7:27.8), INPA 2563, Iranduba, rio Solimões, ponta do Catalão, lago do Pirapora, braço do paranã do Ximborena, 03°11'S 59°55'W, 24.v.2000, L. Rapp Py-Daniel et al. • 2 ♂♂ (cw 33.1, cl 26.5; 37.5:29.5) 2 ♀♀ (cw 29.7, cl 24.1; cw 35.1, cl 27.9), SMF 29879, rio Juruá, lago do Rato/Caroçal, Carauari, 05°43'02.4"S 67°42'12.8"W, 6.iv.2000, J. Zuanon. — **Pará**: • 1 ♂ 1 ♀, INPA 1509, Tracuateua, 10.ix.2004, S. Alves • 1 ♂ 2 ♀♀, MPEG 937, Peixe Boi, balneário Urubuquara, 01°10'20.5"S 47°18'56.7"W, 11.iii.2010, D. Guimarães and I.M. Silva • 1 ♂, CCDB 7593, igarapé unnamed, tributary of rio Livramento, municipality of Nova Timboteua, 01.ii.2019, M.A. Almeida, F.A. Bockmann, A.L.H. Esguícero, J. Muriel-Cunha, D.F. Regasso, E.L. Reis, P.P. Rizzato, V. Slobodian and O.G. Victório • 1 ♂ (cw 53.0, cl 40.0), MPEG 697, fazenda EMA, município de Viseu, 15.vi.2000, J.O. Dias • 1 ♂ 1 ♀, CCDB 7592, igarapé Borges, tributary of rio Piripindeu, rio Irituia basin, rio Guamá drainage, municipality of Irituia, 02.ii.2019, M.A. Almeida, F.A. Bockmann, A.L.H. Esguícero, J. Muriel-Cunha, D.F. Regasso, E.L. Reis, P.P. Rizzato, V. Slobodian and O.G. Victório • 1 ♂ (cw 41.7, cl 33.8), MZUSP 1806, rio Gurupi, iv.1963, B. Malkin • 2 ♂♂ (cw 34.7, cl 28.6; cw 48.8, cl 37.0), MZUSP 2317, rio Gurupi, aldeia Coraci, 12 Km W. from Canindé, 16–26.iv.1963, B. Malkin • 1 ♂ (cw 27.3, cl 23.3) 1 ♀ (cw 26.5, cl 22.0), INPA 513, idem • 1 ♂, CCDB 7118, rio Xingu, Vitória do Xingu, 03°14'42.9"S 51°44'50.8"W, 01.iv.2012, D. Bastos; 1 ♂, INPA 2504, rio Xingu, 03°19'30.7"S, 51°52'18.2"W 5.iv.2012, D. Bastos • 4 ♂♂, INPA 2505, rio Xingu, 03°28'07.7"S 51°52'40.4"W, 4.x.2012, D. Bastos • 1 ♂, CCDB 7117, rio Xingu, Vitória do Xingu, 03°30'30"S 51°53'05.8"W, 03.iv.2012, D. Bastos et al. • 3 ♂♂, CCDB 5034, rio Bacajai, Altamira, 03°36'13"S 51°46'03.5"W, 10.iii.2014, R. Robles et al. — **Maranhão**: • 11 ♂♂ (cw 21.0, cl 17.9 – cw 49.3, cl 38.7) 3 ♀♀ (cw 22.2, cl 18.7 – cw 28.6, cl 22.9), MZUSP 1807, aldeia Araçu, igarapé Gurupi-Una, afluente do rio Gurupi, 50 Km E from Canindé [≈ 02°34'S 46°31'W], 1–15.v.1963, B. Malkin • 1 ♂ 1 ♀, CCUFMA 15, rio Repouso, Chapadinha, 24.iii.2015, J.L.S. Nunes. — **Acre**: • 1 ♂, CCDB 7116, igarapé Quinoá, rio Branco, 2016–2018, F. Correa. PERU: 1 ♂ (cw 38.4, cl ?), MZUSP 9248, Departamento de Loreto, rio Ampiyacu, 15–25.iv.1966, B. Malkin. — **Goiaás**: • 1 ♂, dry (damaged) (MNHN 3866), Salinas [≈ 13°38'S 50°30'W], Ht Amazone, F. de Castelnau and E. Deville.

Previous records. BRAZIL, Maranhão: municipality of Paulino Neves, riacho São José, 02°49'26.2"S 42°32'38.3"W (Andrade et al. 2018). Pará: municipality of Primavera, igarapé Rio Preto (00°59'59.2"S 47°06'53.7"W) (Santos and Vieira 2017). ARGENTINA,

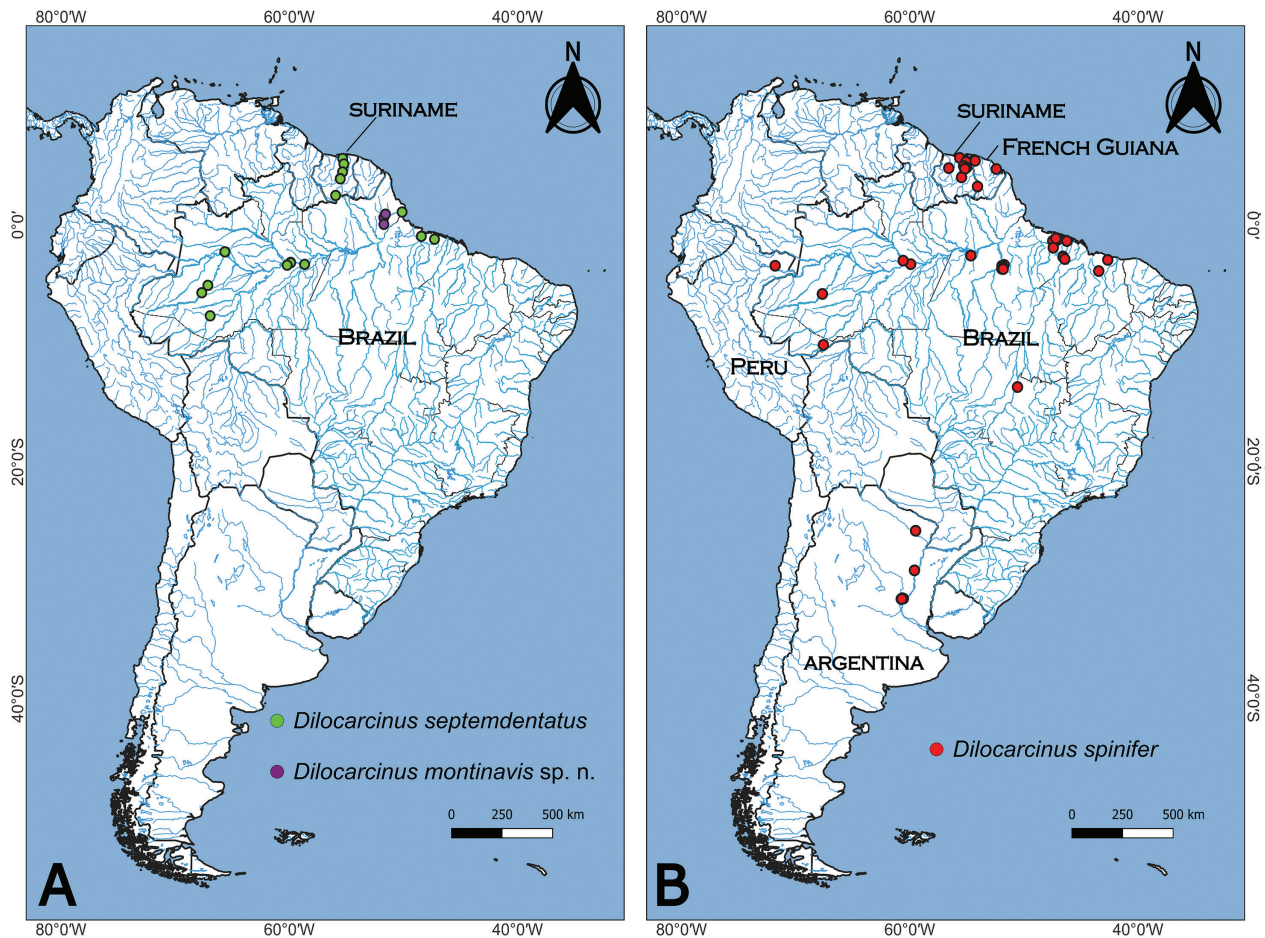


Figure 6. Map of the geographic distribution of *Dilocarcinus septemdentatus* and *D. montinavis* sp. n. (A) and *D. spinifer* (B).

Santa Fe: Salado River, Santo Tomé (31°39'S 60°45'W); San Javier River (29°13'S 59°35'W); Colastiné River, Colastiné Sur (31°37'S 60°34'W); Setúbal lagoon, Rincón (31°35'S 60°39'W); Los Amores stream (28°51'S 59°29'W); Parque del Sur lake, Santa Fe city (31°39'S 60°42'W) (Collins et al. 2009).

Distribution. Northern and southern South America, occurring in coastal river basins from Suriname, French Guiana, and Brazil (states of Pará and Maranhão), the Amazon River basin in Brazil and Peru, the Araguaia-Tocantins Rivers basin, and the middle Paraná River basin in northern Argentina (Fig. 6B) (Magalhães and Türkay 2008; Collins et al. 2009; present paper).

Remarks. Both male syntypes of *D. spinifer* are dried specimens that are glued by the abdomen to the base of the box in which they are preserved. The left G1 of the larger specimen (MNHN 4391) was regenerated in 1988 (according to handwritten note by Danièle Guinot in the box with the specimen – see Fig. 5G), being currently preserved in a vial with 70% alcohol, which allowed us to illustrate it (Fig. 5F). Because of this, it was chosen herein as lectotype.

The three species studied here exhibit a sympatric and sometimes even syntopic geographic distribution (Fig. 6). Based on the current records, *D. spinifer* seems to have the widest distribution. It extends further east

and south than that of *D. septemdentatus* (Fig. 6A), as evidenced by the occurrences reported by Andrade et al. (2018) from the state of Maranhão and by Collins et al. (2009) from northern Argentina (both records as *D. septemdentatus*), respectively. The identity of the specimens from Maranhão was confirmed as *D. spinifer* after examining Andrade's et al. (2018) material (N.F.C.F., pers. observation). The disjunct distribution of *D. spinifer* in the middle Paraná River basin is somewhat unexpected. Unfortunately, the specimens recorded from the area (Collins et al. 2009) could not be reexamined. Those listed as being deposited in the Macrocrustaceans Laboratory of the Instituto Nacional de Limnología (ML-INALI) in Argentina were lost during a flood of the Paraná River that destroyed the ML-INALI facilities (P.A. Collins, pers. communication to C.M.). The specimens deposited at the Florentino Ameghino Natural Museum (FANM), a municipality museum used mainly for environmental education purposes, could not be found by one of us (C.M.) during a visit made in December 2012. However, judging by the illustration in Collins et al. (2009: 51, fig. 1A), the G1 exhibits a morphology that appears to be very much similar to that of *D. spinifer*.

The specimen figured by Rathbun (1906: 61, text-fig. 121, pl. 18 fig. 1) was the male from the lot USNM 32009, which contains two small labels indicating “Photographed” and “Abd. fig.” (C.M., pers. observation).

3.3.3. *Dilocarcinus montinavis* sp. n.

<https://zoobank.org/4CD40FFB-BB0C-4886-9D24-86CC5B18EBEA>

Figures 1C, 2 (L3), 7

Dilocarcinus septemdentatus — Magalhães and Türkay 2008: 187 [part, only USU 510, 514, INPA 584].

Diagnosis. G1 with distal portion distinctly sinuous, strongly curved laterally; subdistal lobe (“sl” in Figs 1, 7) well developed, rounded, bearing dense field of short spines; apex (form a in Figs 1, 7) directed apically, very short, less than 1/3 length of subdistal lobe.

Description of the holotype. Carapace (Fig. 7A) smooth, distinctly convex longitudinally, slightly curved transversally; post-frontal lobes as very low protuberances, barely distinguishable; carapacial regions ill discernible; H-shaped central groove (delimited by the posterior and lateral borders of the gastric and lateral borders of the cardiac regions) very shallow; meso, urogastric and branchial regions not elevated compared to other regions; post-gastric pits present, very faint. Frontal margin (Fig. 7A, C, D) smooth, unarmed, distinctly bilobed, slightly directed downwards, fringed by minute papillae only seen under magnification. Exorbital tooth with sharp tooth; anterolateral borders bearing 6 regularly spaced acute teeth, posterolateral borders unarmed, marked by conspicuous ridge. Suborbital borders (Fig. 7C, D) with 8 slender spines increasing size towards inner corner, one at inner corner distinctly curved, largest and strongest. Eyes (Fig. 7C) well developed. Anterolateral corner of the buccal cavity (Fig. 7C, D) bearing 4 strong sharp spines. Suborbital region (Fig. 7C, D) somewhat pilose, pilosity denser towards inner side. Epistome (Fig. 7C) barely visible in dorsal view, its median portion smooth, glabrous; opening of efferent channels wide, upper arch distinctly curved, mid-gutter with 2 distinct points separated by narrow concavity. Grooves dividing subhepatic and pterygostomial regions (Fig. 7D) somewhat deep, distinctly pilose. Pterygostomial regions with scattered hairs, smooth and glabrous towards buccal frame.

Third maxilliped (Fig. 7D) with subtrapezoidal merus, its outer margin slightly convex, about 2.3× longer than inner one, bearing distinct blunt tooth-like projection at distal corner; ischium outer margin slightly concave. Exopodite about 0.8 times as long as endopodite, bearing well-developed flagellum recurved inwards and downwards.

Chelipeds (Fig. 7A, B) slender, slightly heterochelous, right chela a little stronger than left one. Merus outer border with subdistal acute spine, inner corner of distal lower border blunt, outer corner of distal lower border with small spine; distal upper border distinctly arched, with row of minute hairs. Carpus upper border with strong acute spine, outer surface smooth, glabrous. Palm smooth, mostly glabrous, with minute hairs scattered along inner, outer surfaces, with small distal, blunt spine on upper border; lower border rounded, smooth. Fingers

slender, no distinct gap between them, bearing triangular blunt teeth usually slightly larger in middle section of cutting edge; tips not crossing. P2–4 (Fig. 7A, B) smooth, lower margin of dactylus and half distal portion of propodus with longitudinal row of hairs; P5 lower margin of both dactylus and propodus bearing longitudinal row of hairs [P3 left detached from body of holotype].

Median line of sternum as deep sulcus extending from somites V–VIII, interrupted by transversal link at somites VI/VII; furrow corresponding to endosternite IV/V reaching midline, following ones ending about halfway between beginning of sternopleonal cavity and midline.

Pleon (Fig. 7B) broader proximally at somites III, IV; somites III–VI fused; lateral borders somewhat concave; lateral borders of somite VI roughly continuous with those of telson. Telson (Fig. 7B) about 2.3× broader than long; lateral borders bearing slight concavity subterminally; tip rounded.

G1 (Figs 1C, 7E, F) slender, straight for about 4/5 of its length; broader proximally, with several short, long setae along proximal portion of mesial, lateral surfaces; irregular row of short setae extending distally along median portion of lateral border. Lateral border slightly sinuous proximal- and medially, with strong concavity subdistally and well-developed, rounded subdistal lobe. Distal portion narrower, distinctly sinuous, strongly curved laterally (slightly curved in subadult specimen). Marginal suture (“ms” in Fig. 7) running along mesial surface, twisted towards lateral side very close to apex (“a” in Figs 1, 7); its proximal portion with narrow, rounded protrusion bearing few long setae. Field of short spines continuous, located subterminally on lateroventral side, denser along subdistal lobe (“sl” in Figs 1, 7), extending distally to dorsal surface. Subapical bristles, when present, in small number. Apex flat, narrow, very short, less than 1/3 length of subdistal lobe; distal aperture very narrow, slit-like, directed apically.

G2 (Fig. 7G) as very slender flagellum, slightly sinuous, just 1.1× longer than G1, with slight median constriction; tip flat, rounded.

Type material. Holotype: 1 ♂ (cw 39.5, cl 32.7), MZUSP 17440, Brazil, Amapá, Serra do Navio region, rio Amapari, município de Porto Grande, vila de Cupixi [≈ 00°38'N 51°45'W], comunidade do Vila Nova, 5.v.1994, M.D.S. Tavares coll. (Projeto Diversitas Neotropica n° 335). — **Paratypes:** 1 ♂ (cw 36.6, cl 31.2) 2 ♀♀ (cw 35.1, cl 30.4; 21.0:18.8), MZUSP 42728, same data as holotype • 1 ♂ (cw 38.9, cl 30.7), INPA 584, same data as holotype • 1 ♂ (cw 35.5, cl 29.5), MZUSP 44033, Brazil, Amapá, Serra do Navio region, rio Amapari, 6.v.1994, M.D.S. Tavares coll. (Projeto Diversitas Neotropica n° 405).

Additional material examined. 1 ♂ 1 ♀, MPEG 1045, Brazil, Amapá, Floresta Nacional (FLONA) do Amapá [≈ 00°55'N 51°35'W], 27.x.2009, C.R. Santos and J.E.M. Wanzeler.

Type locality. Serra do Navio region, rio Amapari, Cupixi, state of Amapá, Brazil.

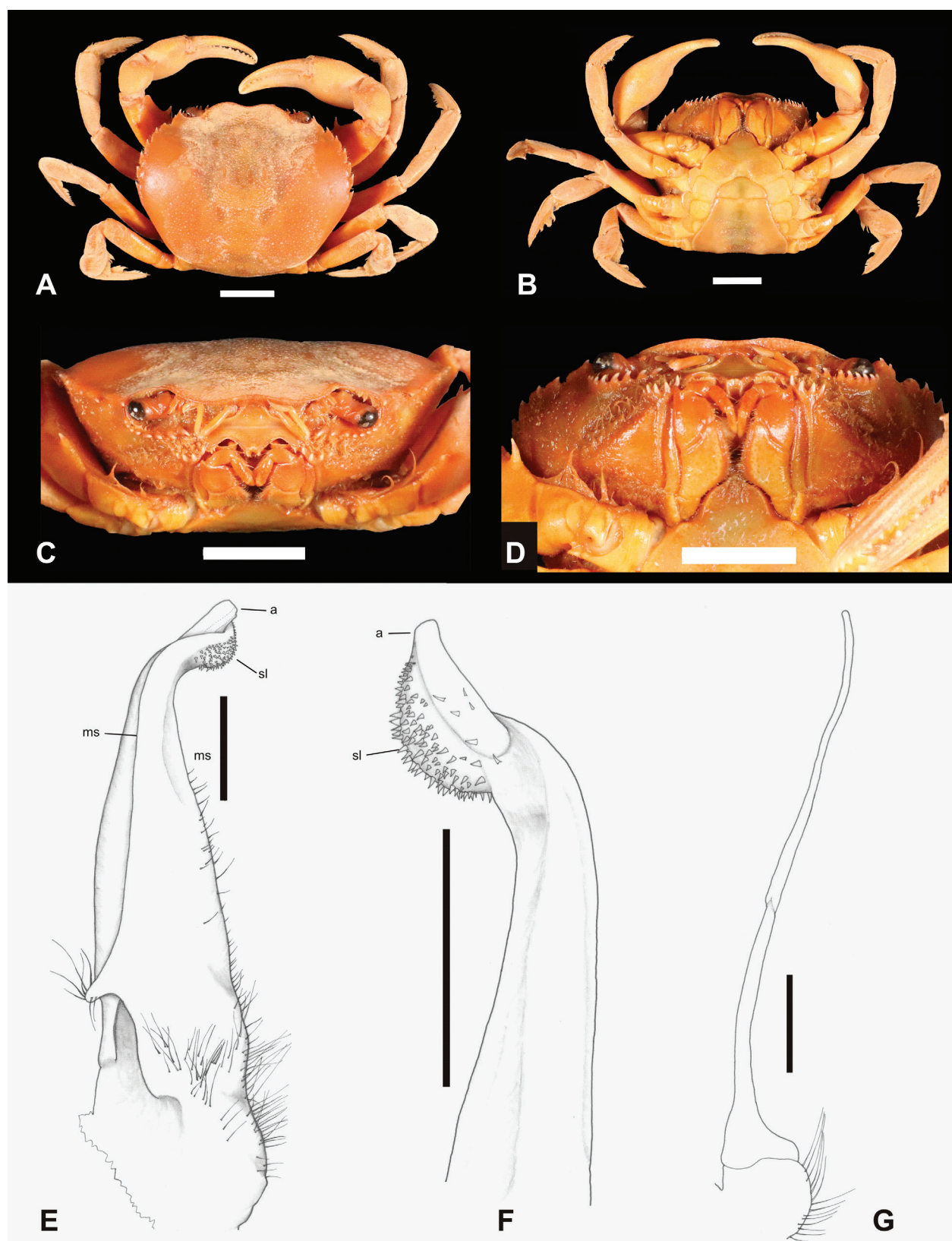


Figure 7. *Dilocarcinus montinavis* sp. n., holotype male (cw 39.5, cl 32.7), MZUSP 17440. Habitus, dorsal view (A), ventral view (B), frontal view (C), buccal frame and pterygostomial region (D); left G1, ventromesial view (E); left G1, detail of distal portion, ventrodorsal view (F); left G2, ventrolateral view (G). — Abbreviations: a = apex; ms = marginal suture, sl = subdistal lobe. Scale bars = 1 mm. Photo credits: J. Colavite, S. Bueno.

Etymology. The specific epithet refers to the region where the type locality of the species is situated, Serra do Navio (Serra = mountain range; Navio = ship). It is composed by

the root (*mont*) of the Latin word *montes* (nominative plural, meaning “mountains”), the connecting vowel *i*, and the word *navis* (genitive singular, meaning “of the ship”).

Distribution. The currently known distribution is limited to the state of Amapá, rio Araguari basin, Brazil (Fig. 6A).

Remarks. Magalhães and Türkay (2008) considered that the peculiar morphology of the distal portion of the gonopod exhibited by the few male specimens from Amapá examined in their study would be within the variation range they observed in the G1 of *D. septemdentatus* (C.M., pers. observation). This characteristic was also verified in a subadult male from the FLO-NA of Amapá (MPEG 1054), although the lateral curvature of the G1 distal portion is much less pronounced than that observed in fully adult specimens. This peculiar morphology of the distal portion of the G1 of these specimens and the results of the molecular analyzes (Fig. 2), which showed a significant genetic divergence (Table 3), support the decision of considering them a new species for the genus *Dilocarcinus*. The geographical distribution of this new species, based on currently available data, seems to be restricted to the state of Amapá, Brazil.

The type series of the present species was listed by Magalhães and Türkay (2008: 187 – as *D. septemdentatus*) as deposited in the then carcinological collection of Universidade Santa Úrsula (Rio de Janeiro, Brazil). This collection was later transferred to MZUSP and the lots were catalogued as follows: USU 514 (2 ♂ 2 ♀♀) = MZUSP 17440 (1 ♂) and MZUSP 42728 (1 ♂ 2 ♀♀); USU 510 (1 ♂) = MZUSP 44033.

Although *Dilocarcinus montinavis* sp. n. (Lineage 3) was retrieved as a sister species of *D. spinifer* (Lineage 2) in the concatenated tree using ML and IB analyzes (Fig. 2), morphologically it shows a closer resemblance with *D. septemdentatus*, as indicated by the morphology of their G1 distal portion (characterized by the strong curvature towards the lateral side) and that of the frontal margin (clearly bilobed versus near straight in *D. spinifer*).

The very short apex of the G1 of *Dilocarcinus montinavis* sp. n. is also found in the G1 of *Dilocarcinus truncatus* Rodríguez, 1992. Both species can be morphologically distinguished from each other by the orientation of the G1 distal portion, which is sinuous and distinctly curved laterally in the former (Fig. 7E, F) and nearly straight in the latter (see Rodríguez 1992: 112, fig. 39). *Dilocarcinus truncatus* was based on a single male specimen from the Beni River (province of Beni, Bolivia). Unfortunately, without the inclusion of molecular tools, the phylogenetic affinities between this species and those studied herein could not be properly evaluated.

4. Discussion

4.1. Phylogenetic and morphological affinities

The existence of cryptic species under the name of *D. septemdentatus* sensu Magalhães and Türkay (2008) is indicated by the three highly supported, well-established

clades (Fig. 2), the haplotype network with the formation of distinct haplogroups, separated by a series of mutational steps (Fig. 4), and the genetic divergence matrix (see Table 3). For COI gene, a genetic distance > 5% between *D. septemdentatus* and *D. spinifer*, and a distance > 4% both between *D. septemdentatus* and *Dilocarcinus montinavis* sp. n., and between *D. spinifer* and *Dilocarcinus montinavis* sp. n. For 16S, a variation of 4.3–6.7% was observed between *D. septemdentatus* and *Dilocarcinus montinavis* sp. n. Genetic divergence, combined with morphological characters, also proved to be sufficient for defining other different freshwater crab lineages under *Trichodactylus fluviatilis* Latreille, 1828 (Trichodactylidae) (Souza-Carvalho et al. 2017), and within some lineages of *Fredius* Pretzmann, 1967 (Pseudothelphusidae) (Mantelatto et al. 2022).

Each lineage recovered in the present phylogenetic analyzes can be related to a particular morphology of the G1 (Fig. 2). Since the specimens grouped in Lineage 2 exhibit G1 with morphology similar to that of the syntype of *D. spinifer* (MNHN 4391), this name was revalidated to designate the species characterized by G1 with distal portion nearly straight or just slightly bent laterally. The Lineage 1 kept the name *D. septemdentatus* s.str., characterized by those specimens with the distal portion of G1 strongly curved laterally, considering that such morphology of the G1 had already been associated to this name by previous authors (Bott 1969; Magalhães and Türkay 2008). Specimens included in Lineage 3, whose G1 bears a distinct shape (sinuous distal portion with a pronounced lateral curvature, and very short apex) was treated herein as a new taxonomic entity and named *D. montinavis* sp. n.

The variation in the curvature of the G1 distal portion (Figs 1A–C, 5C–F, 7E–F) was the more informative taxonomic character to distinguish the species associated to the *D. septemdentatus* sensu Magalhães and Türkay (2008) complex. Bott (1969) and Rodríguez (1992) had already considered that the inclination of the G1 distal portion would be sufficient to differentiate between *D. septemdentatus* and *D. spinifer*. Magalhães and Türkay (2008), after evaluating many individuals, found intermediate stages of this character in some specimens from the same region, thus proposing the synonymization of both. It is important, however, to emphasize that this curvature of the distal portion of G1 may be the result of the ontogenetic development, being consolidated only in adult individuals. The lot INPA 800, for instance, composed of 14 males of varying sizes, shows a clear variability in this character from juvenile to fully adult specimens. Future studies with an ontogenetic focus on G1 characters may help to elucidate this issue.

4.2. Origin and distribution

Although several studies in the last two decades have refined paleoclimatic and paleoenvironmental reconstructions of Cenozoic South America (Hoorn 1993; Lundberg et al. 1998; Wesselingh et al. 2002; Albert et al. 2006; Figueiredo et al. 2009; Hoorn and Wesselingh 2010;

Latrubesse et al. 2010; Hoorn et al. 1995, 2010b, 2017, 2022; Albert and Reis 2011; Sacek 2014; Rodríguez-Tribaldos et al. 2017), which greatly contributed to the understanding of the processes that led to the great biotic diversification in the continent (Ribas et al. 2011; Antonelli et al. 2018; Albert et al. 2018, 2021; Roberto et al. 2020; Cassemiro et al. 2023), the evaluation of the current patterns of geographic distribution of the *D. septemdentatus* species complex may be compromised by some aspects that hamper a clearer association between the speciation process within this group and the geomorphological history of the region. The main constraint may be the fact that the origins and the phylogenetic affinities of Trichodactylidae among the Brachyura are unclear (Rodríguez 1986, 1992; Sternberg 1998; Sternberg and Cumberlidge 2001; Cumberlidge and Ng 2009; Schubart and Reuschel 2009; Klaus et al. 2014; Tsang et al. 2014) as a comprehensive phylogenetic study that proposes a more consistent macroevolutionary scenario for the family is still missing.

However, considering the wide geographic distribution of the genus *Dilocarcinus* along the lowland areas of the Amazon, Paraguay-Paraná and northern South America coastal river basins (Magalhães and Türkay 2008; Fig. 6), a Western Amazonia origin for the *Dilocarcinus* lineages (noting that *D. truncatus* is not included in the analysis) during the late Eocene (Fig. 3) is herein assumed as being the most parsimonious hypothesis, since the region has been considered a primary source of Neotropical lineages for several groups (Hubert and Renno 2006; Wesselingh 2006; Wesselingh and Salo 2006; Antonelli et al. 2018; Albert et al. 2021; Hoorn et al. 2022).

Taking these constraints into account, as well as possible non-intentional errors in the molecular clock calibration process (Klaus and Prieto 2014), the divergence time estimation analysis suggests that the separation between *D. septemdentatus* and the clade of *D. spinifer* and *Dilocarcinus montinavis* sp. n. took place approximately between 19 and 13 mya (Fig. 3). At that time, the Purus arch at around 62° longitude divided most of northern South America into two separated drainage systems with the respective rivers flowing eastward and westward, and the lowlands of the western Amazonia were occupied by the Pebas System, a vast aquatic environment that lasted from late Oligocene to late Miocene (c. 23–11 mya) characterized by shallow lakes and swamps eventually submitted to episodic marine incursions from its northwestern connection with the Caribbean through the Llanos basin (Lundberg et al. 1998; Wesselingh and Salo 2006; Hoorn et al. 2010a, b, 2021, 2022; Wesselingh and Hoorn 2011; Boonstra et al. 2015; Jaramillo et al. 2017). The Pebas System is believed to have had an important role as a cradle of speciation for aquatic and amphibious groups, a barrier for dispersal and gene flow (mainly for terrestrial ones), and a permeable biogeographic system, in which the diversity of the environments was a driver for speciation by the constant back and forth between gene flow and isolation (Hoorn et al. 2010a, b, 2022). This extensive lowland, lacustrine environment must have favored subtle differentiation between populations of the *D. septemdentatus* complex ancestral stock leading to cryp-

tic lineages that radiated throughout the Western Amazonia during early to middle Miocene (19–12 mya) and later reaching eastern and southern regions of the continent.

The radiation of the *D. septemdentatus* complex towards the eastern Amazonia and coastal river basins of northern South America must have occurred from the late Miocene onwards coevally with the gradual evolution of the Western Amazonia from a megawetland to a fluviodeltaic system following the combined effect of late Miocene global sea-level lowstand and ongoing Andean orogeny coupled with surface processes (sedimentation and erosion) on the Western Amazonia that culminated in the overcoming of the Purus arch and the reorganization of the drainage system into the present-day eastward-flowing Amazon River during the late Miocene and early Pliocene (c. 10.5–4.5 mya) (Lundberg et al. 1998; Figueiredo et al. 2009, 2010; Hoorn et al. 2010b, 2017; Wesselingh and Hoorn 2011; Sacek 2014; Rodríguez-Tribaldos et al. 2017; Albert et al. 2018, 2021). The separation between *D. spinifer* and *D. montinavis* sp. n. c. 14–8 mya (Fig. 3) might be related to the onset of the transcontinental Amazon River during the late Miocene. The dispersion of representatives of this species complex towards lower Amazon region and coastal basins of northern South America must have been facilitated by sea-level fluctuation during the Pleistocene.

A possible hypothesis to explain the current occurrence of *D. spinifer* in the middle Paraná River basin (Collins et al. 2009) could most likely be the radiation from the Western Amazonia due to the capture of the headwaters of upper Paraguay by Western Amazonia drainages during middle Miocene (11.8–10.0 mya) (Lundberg et al. 1998; Carvalho and Albert 2011). The geologic history of the watersheds between upper Paraguay River and adjacent basins is complex and the boundaries between the Paraguay and Amazon basins underwent several hydrogeological changes since the middle Eocene due to Andean orogeny and headwaters capture events (Lundberg et al. 1998; Carvalho and Albert 2011). The hydrological interconnections between these regions, particularly between the Paraguay and upper Madeira basins (which are still in place in modern times) and the Paraguay and the Tocantins-Xingu, served as dispersal routes for many fish groups (Hubert and Renno 2006; Albert and Carvalho 2011; Carvalho and Albert 2011) and might also have been used for this group of freshwater crabs to disperse towards the Paraguay-Paraná basin.

Confirmation of these hypotheses, or another more consistent one to better explain the origin and distribution of this species complex, however, can only be achieved when the aforementioned constraints, in particular the inclusion of other species of the genus in the analysis, can be overcome.

5. Conclusion

The morphology-based studies on the systematics of the trichodactylid genus *Dilocarcinus* included either

eight (Rodríguez 1992) or three species (Magalhães and Türkay 2008), depending on the characters used to delimit the genus. The present unprecedented study of *D. septemdentatus* sensu Magalhães and Türkay (2008) using an integrative approach through molecular systematics and morphological analysis based on specimens from a wide area along the Amazon basin and north of the South America coastal river basins revealed a complex consisting of three cryptic species. Each of these species was associated with a distinct morphological character of the G1 and available names were assigned to the taxa: *D. spinifer*, the type species of the genus, was revalidated and a lectotype was chosen; a neotype was designated for *D. septemdentatus*; and *D. montinavis* sp. n. was described as a new entity. The origin of this complex of mainly lowland species could presumptively be associated with the Pebas System, an extensive megawetland system that existed along the lowlands of Western Amazonia from late Oligocene to late Miocene (c. 23–11 mya). The use of this integrative approach based on molecular and morphological data proved to be very useful and should be recommended for the elucidation of taxonomic questions still pending, whether in this genus or in other groups of freshwater crabs. Furthermore, a clearer definition of the taxonomic situation of the group is relevant to provide support for conservation status assessments of the aquatic fauna.

6. Declarations

Author contributions. Conceptualization, C.M. and F.L.M.; methodology, N.F.C.F., C.M. and F.L.M.; perform the molecular analysis, N.F.C.F.; investigation, morphological and molecular analysis, N.F.C.F., C.M. and F.L.M.; data curation, N.F.C.F., C.M. and F.L.M.; preparing, writing, review and editing, N.F.C.F., C.M. and F.L.M.; supervision, C.M. and F.L.M.; project administration, F.L.M.; resources and funding acquisition, F.L.M. All authors have read and agreed to the published version of the manuscript.

Competing interests. The authors declare no competing interests.

7. 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; PROTAX 2016/50376-5 and 2021/08075-6) for FLM. Additional support was also provided by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), for the Research grant (PQ 302253/2019-0) 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 AE942E3, CEA7CD5, AEF142F). Thanks are due to the following colleagues for their sup-

port 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); Jorge Nunes, Kelly Andrade (UFMA); Paul Clark, Ray Ingle (NHM); Danièle Guinot, Paula Martin-Lefevre (MNHN); M. Zunino (MZUT); Angelika Brandt, Torben Riehl, Andreas Alspach, Bianca Trautwein, Michael Türkay, (SMF); Martin Schwentner (NHMW); Charles Franzen (RMNH); Antje Schwiering, Kristina von Rintelen, (ZMB); Nancy Mercado-Salas (ZMH); Ludwig Tiefenbacher (ZSM); Rafael Robles (UAC), Brian Kensley, Karen Reed, Rafael Lemaître (USNM). Thanks are also due to Eric Moreno Juarez, Marta Campos and Klaus Klass for useful comments and suggestions during the review process.

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Zeitschrift/Journal: [Arthropod Systematics and Phylogeny](#)

Jahr/Year: 2024

Band/Volume: [82](#)

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Artikel/Article: [Integrative approach revealing a species complex in the Neotropical freshwater crab *Dilocarcinus septemdentatus* \(Herbst, 1783\) \(Decapoda: Trichodactylidae\) with a description of a new species 385-405](#)