



Systematics of Neotropical freshwater crabs Trichodactylinae based on multi-genes and morphological data: new tribe and new combinations

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<https://zoobank.org/#AC85D852-ADB6-43DE-81D9-B6811F552D83>

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Received 15 March 2025

Accepted 07 May 2025

Published 18 July 2025

Academic Editor Vinicius S. Ferreira

Citation: 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>

Abstract

The generic system of the Neotropical crabs of the subfamily Trichodactylinae H. Milne Edwards, 1853 has remained quite stable over the last 30 years, but the recognition or not of the genus *Mikrotrichodactylus* Pretzmann, 1968 has been a matter of debate: erected as a subgenus, it was treated with generic status in Rodríguez' classificatory system but some subsequent works considered it a junior synonym of *Trichodactylus* Latreille, 1828. Based on this scenario, an integrative analysis based on molecular (using two mitochondrial, 16S rRNA and COI, and one nuclear, Histone 3, genes) and morphological (using diagnostic characters traditionally used on the identification of the family) data was performed in order to clarify the phylogenetic position of the genera within Trichodactylinae. The inferred phylogeny recovered three great lineages within Trichodactylinae with high support values in both Bayesian Inference and Maximum Likelihood phylogenetic analyses, corroborated the non-monophyletic status of *Trichodactylus*, and confirmed the full generic status of *Mikrotrichodactylus*. A taxonomic rearrangement of Trichodactylinae is proposed but the positioning of “*Trichodactylus*” *quinquedentatus* Rathbun, 1893 remains doubtful and was treated herein as a taxon inquirendum et incertae sedis. This taxon seems to be closer related to *Rodriguezia* Bott, 1969, and *Avotrichodactylus* Pretzmann, 1968; however, more data are needed before additional taxonomic adjustments concerning its positioning within the subfamily is proposed. In the current proposal, *Trichodactylus* is composed by four species, *Mikrotrichodactylus* by six species, *Avotrichodactylus* and *Rodriguezia* by three each, in addition to “*Trichodactylus*” *quinquedentatus*.

Keywords

Mikrotrichodactylus, Molecular systematics, Paraphyletic group, Phylogeny, Taxonomy, *Trichodactylus*

1. Introduction

Trichodactylidae H. Milne Edwards, 1853 is one of the three families of primary freshwater crabs from the Neotropics (Álvarez et al. 2020). It is widely distributed

from southern Mexico to Argentina, with most species being found in the hydrographic basins of the Atlantic drainage, and only two species occurring in the Pacific

ic versant in Panama (Rodríguez 1992; Magalhães and Türkay 1996b; Magalhães et al. 2013; Cumberlidge et al. 2014; Magalhães and Ng, 2019). Although its phylogenetic affinities with other families of true freshwater crabs, or even among the Brachyura, are not yet well established (Sternberg et al. 1999; Cumberlidge and Ng 2009; Klaus et al. 2011; Tsang et al. 2014; Wolfe et al. 2024), the taxonomy of the family has been stable since the revisions by Rodríguez (1992) and Magalhães and Türkay (1996a, 1996b, 1996c, 2008a, 2008b, 2012). The classification systems proposed in their revisions coincide in the subdivision of the family into two subfamilies: Trichodactylinae H. Milne Edwards, 1853 and Dilocarcininae Pretzmann, 1978b, differing only slightly in the tribal and generic arrangements.

In a phylogenetic study based on morphological characters, Rodríguez (1992) indicated that the subfamilies Dilocarcininae and Trichodactylinae are distinct lineages, with Trichodactylinae comprising four genera: *Trichodactylus* Latreille, 1828, *Mikrotrichodactylus* Pretzmann, 1968, *Rodriguezia* Bott, 1969, and *Avotrichodactylus* Pretzmann, 1968. Magalhães and Türkay (1996a), however, did not recognize *Mikrotrichodactylus* because their proposal was based mainly on the characters of the male first gonopod and considered that the peculiarities of the gonopod shape exhibited by the species previously included by Rodríguez (1992) in this group did not justify a separate genus.

The phylogenetic analyses by Rodríguez (1992), which was later reappraised by Morrone and Lopretto (1996) and Sternberg (1997), provided evidence that *Trichodactylus* might be paraphyletic. Even so, Magalhães and Türkay's (1996a) proposal was the one more widely followed in subsequent treatments of the family (e.g., Campos 2005, 2014; Collins 2005; Ng et al. 2008; César and Damborenea 2015). A detailed study of the axial skeleton of 17 species belonging to 10 representative genera of the Trichodactylidae subfamilies carried out by Pedraza et al. (2015) corroborated the subfamilial division proposed in the two classification systems (Rodríguez 1992; Magalhães and Türkay 1996a) but several features allowed the recognition of two subgroups within the subfamily Trichodactylinae, one of which comprised by larger species (up to 50 mm carapace width, such as *Trichodactylus fluviatilis* Latreille, 1828; *T. petropolitanus* Göldi, 1886; and *T. dentatus* H. Milne Edwards, 1853) and the other by smaller species (up to 30 mm carapace width); the latter subgroup included, in addition to *Avotrichodactylus constrictus* Pretzmann, 1968, *T. borellianus* Nobili, 1896, and *T. panoplus* (Martens, 1869), the latter two species belonging to *Mikrotrichodactylus* in Rodríguez' (1992) classification proposal. Although the distinctive features of the axial skeleton between these two subgroups could mean confirming *Mikrotrichodactylus* as a valid genus, Pedraza et al. (2015) cautiously recommended that this should be done after more comprehensive studies.

Given the uncertainties regarding which species should be appropriately placed in *Trichodactylus* and allies, we conducted the most comprehensive molecular approach,

linked with the morphological support, to date for the subfamily Trichodactylinae with the aim of assessing its phylogenetic relationships and establishing the validity of its constituent genera.

2. Material and methods

2.1. Taxon sampling

Specimens used in this study were obtained from field collections and from loans, donations from, and visits to, crustacean collections of the following institutions: Coleção de Crustáceos do Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil (CCDB); Coleção de Invertebrados Aquáticos do Sul da Bahia, Universidade Federal do Sul da Bahia and Universidade Estadual de Santa Cruz, Ilhéus, Brazil (CIASB); Colección Nacional de Crustáceos, Universidad Nacional Autónoma de México, Mexico City, Mexico (CNCR); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu de História Natural Capão da Imbuia, Curitiba, Brazil (MHNCI); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP); Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (PUCRS); Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil (UFRGS); Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum (previously Raffles Museum), National University of Singapore, Singapore.

In the field, the freshwater crabs were hand collected using sieves, dip nets, and/or traps in various environments such as rivers, streams, brooks, waterfalls, and creeks. After collection, the specimens were properly labeled and initially placed in containers with ice; subsequently, the specimens were temporarily stored in 96% ethanol. In the laboratory, the collected specimens were identified and preserved in 80% ethanol and incorporated into the CCDB. Brazilian specimens were obtained under collection permits (nos. 41779-5 and 11777-2 MMA/IBAMA/SISBIO and SISGEN AE942E3, A496BF8, AEF142F, CEA7CD5).

2.2. Molecular analysis

The genomic DNA was extracted from the muscle tissue of the pereopods or chelipeds of fresh or 80% ethanol-preserved adult male specimens (whenever possible; when no specimen of this category was available, adult females were used). The voucher specimens used in the molecular analyses were deposited in the CCDB/FFCLRP/USP or in the original scientific collection (Table S1).

DNA extraction was performed using a saline (Miller et al. 1988) and tissue kit following the manufacturers'

Table 1. List of used primers and respective genes in this study, and the source.

Gene	Primer	Primer sequence	Reference
16S rRNA	br	5'-CCG GTC TGA ACT CAG ATC AC-3'	Palumbi and Benzie (1991)
	ar	5'-CGC CTG TTT ATC AAA AAC AT-3'	
COI	LCO1490	5'-CGCCTGTTTATCAAAAACAT-3'	Folmer et al. (1994)
	HCO2198	5'-TAAACTTCAGGGTGACCAAAAATCA-3'	
	TriI	5'-TCTAGGAGCATGAGCAGGGATAG-3'	Present study
	TriII	5'-5'-GGTATAAAAACAGGGTCTCCTCCTC-3'	
H3	H3af	5'-ATGGCTCGTACCAAGCAGACVGC-3'	Colgan et al. (1998)
	H3ar	5'-ATGGCTCGTACCAAGCAGACVGC-3'	

protocol and the ethanol precipitation methods followed Schubart et al. (2000), Mantelatto et al. (2007, 2022, 2024), Souza-Carvalho et al. (2017) and Álvarez et al. (2020), including appropriate modifications (adjustments in the concentration of DNA sample and temperature of annealing) for the specific material. The DNA concentration of the samples was evaluated using a NanoDrop® 2000/2000 c spectrophotometer (Thermo Scientific, Wilmington, DE, USA). The adequate samples proceed to the polymerase chain reaction (PCR) technique amplification.

Molecular analyzes were performed based on three markers: two mitochondrial genes Cytochrome Oxidase subunit I (COI) and 16S Ribosomal RNA (16SrRNA), and one nuclear gene, histone 3 (H3). These markers have proven their effectiveness in studies with different groups of decapod crustaceans, including primary crabs (Souza-Carvalho et al. 2017; Álvarez et al. 2020; Mantelatto et al. 2022, 2024; França et al. 2024).

The regions of genes interest were amplified using universal primers, and a new primer was developed for the genus using the Primer-Blast software [(available at: <http://www.ncbi.nlm.nih.gov/tools/primer-blast>; see Ye et al. 2012 for more details)] (Table 1).

PCR products were obtained in a reaction with a final volume of 25 µl for primers and the PCR profiles for each of the markers and performed on an Applied Biosystems Veriti 96 Well Thermal Cycler®. The PCR began with an initial denaturation period of 5 minutes at 95°C, followed by 40 thermal cycles [45 seconds of denaturation at 95°C, 45 seconds for annealing with variable temperature (44–48°C for the 16S gene; 48–50°C for COI and 48–54°C for H3), and 1 minute at 72°C], and a final extension cycle at 72°C for 10 minutes. The PCR products were visualized on agarose gel (1.5%), purified by precipitation with SureClean® kit (Bioline Reagents, London, UK) and sequenced using the ABI Big Dye® Terminator Mix in an ABI Prism 3100 Genetic Analyzer®, from the Department of Technology of the Faculty of Agricultural and Veterinary Sciences of Jaboticabal, São Paulo State University “Júlio de Mesquita Filho” (FCAV-UNESP), Jaboticabal, São Paulo, Brazil.

All nucleotide sequences obtained were confirmed by sequencing both strands (sense and antisense). Editing was performed using BioEdit 7.0.5 software (Hall 2005), and subsequent alignment was conducted on the online platform MAFFT (Multiple Alignment Program for Ami-

no Acid or Nucleotide Sequences) version 7 (Kuraku et al. 2013; Katoh et al. 2017). Additional adjustments were made manually. The consensus sequences obtained were submitted to the BLAST system (“Basic Local Alignment Search Tool”) (Altschul et al. 1990) through the National Center for Biotechnology Information (NCBI) (USA) for comparison with the NCBI database assembly (<http://blast.ncbi.nlm.nih.gov/blast.cgi>) to confirm their respective identities.

2.3. Morphological analysis

In total, 764 specimens were analyzed and a comparison of the external morphology with other genera in the family was conducted. In addition to the specimens of the lots listed in Table S1, specimens related in Table S2 were also examined for morphological characters. Taxonomic determinations were made according to current specific concepts and based on original descriptions and other relevant literature, especially the main taxonomic revisions on the family (Latreille, 1828; H. Milne Edwards, 1853; A. Milne-Edwards, 1869; Martens, 1869; Göldi, 1886; Rathbun, 1893; Nobili, 1896; Rathbun, 1905; Moreira, 1912; Bott, 1969; Rodríguez, 1992; Magalhães and Türkay, 1996a, 1996b, 1996c, 2008a, 2008b, 2012; Magalhães, 2003). The abbreviations used in the morphological descriptions are as follow: carapace width (CW); gonopods 1 and 2 (G1, G2); pereopods (P1–P5); thoracic interosternites (ie) (see Secretan, 1998; Guinot et al., 2013; Pedraza et al., 2015 for definition of the axial skeleton morphologic elements).

2.4. Outgroup selection

Outgroup taxa were selected from the two tribes of Dilocarcininae: *Sylviocarcinus pictus* (H. Milne Edwards, 1853), *S. devillei* H. Milne Edwards, 1853, *Valdivia serrata* White, 1847b, and *Zilchiopsis collastinensis* Pretzmann, 1968 [Valdiviini], and *Goyazana castelnaui* (H. Milne Edwards, 1853), *Dilocarcinus pagei* Stimpson, 1861, *Fredilocarcinus apyratii* Magalhães and Türkay, 2008, and *Moreiroparcinus laevifrons* (Moreira, 1901) [Dilocarcinini] since this subfamily was found to be the sister-group of Trichodactylinae in Rodríguez’ (1992) phylogenetic analysis.

Table 2. Evolutionary models selected by jModelTest for each gene.

Model	16S rRNA	COI	H3
	HKY+G	HKY+I+G	K80+I+G
Gamma distribution	0.2400	0.6590	0.7040
Proportion of invariant sites	—	0.5140	0.5540
Transition / Tranversion rate	35.560	52.365	11.465
Frequency of A	0.3616	0.3832	—
Frequency of C	0.1407	0.0871	—
Frequency of G	0.0513	0.1735	—
Frequency of T	0.4464	0.3561	—

2.5. Phylogenetic analyses

In total, 87 new sequences were generated in the present study, and 187 nucleotide sequences were included in the phylogenetic analyses, comprising 72 sequences for the COI gene, 80 for the 16S rRNA gene, and 35 for the H3 gene. Additionally, 2 sequences for the 16S rRNA and H3 genes were extracted from GenBank.

The quality of the data regarding the level of saturation was verified using Xia's saturation test (Xia et al. 2003), implemented in DAMBE (version 5), which did not reveal significant saturation for any of the genes analyzed ($P < 0.05$). The substitution models for each gene were selected using jModelTest (version 2.1.4) (Guindon and Gascuel 2003; Darriba et al. 2012) based on the Bayesian Information Criterion (BIC) (Table 2). The selected models and the generated parameters for each were implemented in the Bayesian inference.

Alignments were constructed for each gene (COI, 16S rRNA, and H3). Phylogenies were inferred using Bayesian Inference and Maximum Likelihood analyses. Additionally, the genes were concatenated using the Sequence Matrix software (version 1.7.8) (Vaidya et al. 2011), constructing a data matrix with 1497 sites.

The Maximum Likelihood (ML) analysis was performed using RAxML (7.2.7) (Stamatakis 2006) implemented on CIPRES ("Cyberinfrastructure for Phylogenetic Research") (<http://www.phylo.org>). The consistency of the topologies was evaluated by the bootstrap method (Felsenstein 1985), with the number of pseudo-replicates defined by RAxML, and only confidence values $> 50\%$ were reported.

The Bayesian Inference (BI) analyses were performed using the MrBayes software v. 3.2.4 (Huelsenbeck and Ronquist 2001), with each gene assigned to a distinct partition, totaling three partitions. The Metropolis-Hastings Markov chain Monte Carlo (MCMC) algorithm was employed to empirically determine the posterior probability distribution of trees, branch lengths, and substitution parameters. The models indicated by the Bayesian Information Criterion (BIC) available in jModelTest (Table 2) were used as prior distributions for each dataset gene.

Bayesian inference analyses were conducted with 10 million generations in two simulations, each with one cold and four heated parallel chains. Parameter values were saved once every 1,000 rounds. The analyses were concluded upon reaching stationarity, indicated by an av-

erage standard deviation of split frequencies below 0.01. The first quarter of parameters and trees were discarded as burn-in (25%) (see Ronquist et al. 2009).

Consensus trees between the Maximum Likelihood and Bayesian Inference methods were generated using the Mesquite package, applying the 50% majority-rule criterion.

3. Results

3.1. Phylogenetic analysis

The concatenated ML and IB phylogram (Fig. 1) recovered the subfamily Trichodactylinae as monophyletic group and composed of two major lineages with high support values (100) in both analyses, which indicates that the current composition of the genus *Trichodactylus* does not represent a monophyletic group. These results were also found when each gene was analyzed separately (Figs S1–S3). The "*Trichodactylus*" stricto sensu lineage is formed exclusively by species of *Trichodactylus* whose distribution is restricted to coastal basins from northeastern, southeastern, and southern Brazil. This lineage includes *T. fluviatilis*, the type species of the genus, *T. dentatus*, *T. petropolitanus*, *T. crassus* A. Milne-Edwards, 1869, and undetermined species currently under study. These are all large-sized species (up to 50 mm CW). This lineage exhibits significant genetic structuring and high support values within its internal lineages (Fig. 1). The observed structuring highlights considerable species richness within this lineage, with terminal clades exhibiting restricted geographical distribution.

The other lineage, here referred to as the "non-*Trichodactylus*" lineage, has a wide distribution in other regions of South America and Mesoamerica and includes *Mikrotrichodactylus borellianus*, *M. panoplus*, *M. ehrhardti* Bott, 1969, *M. faxoni* Rathbun, 1905, *M. kensleyi* Rodríguez, 1992, *M. parvus* Moreira, 1912, *Avotrichodactylus constrictus* (Pearse, 1911), *A. oaxensis* Rodríguez, 1992, *Rodriguezia adani* Alvarez & Villalobos, 2018, and "*T.*" *quinquedentatus* Rathbun, 1893, all small-sized species (up to 30 mm CW).

The "non-*Trichodactylus*" lineage contains two well-defined and highly supported internal groups. The first group encompasses species from northern (Amazon

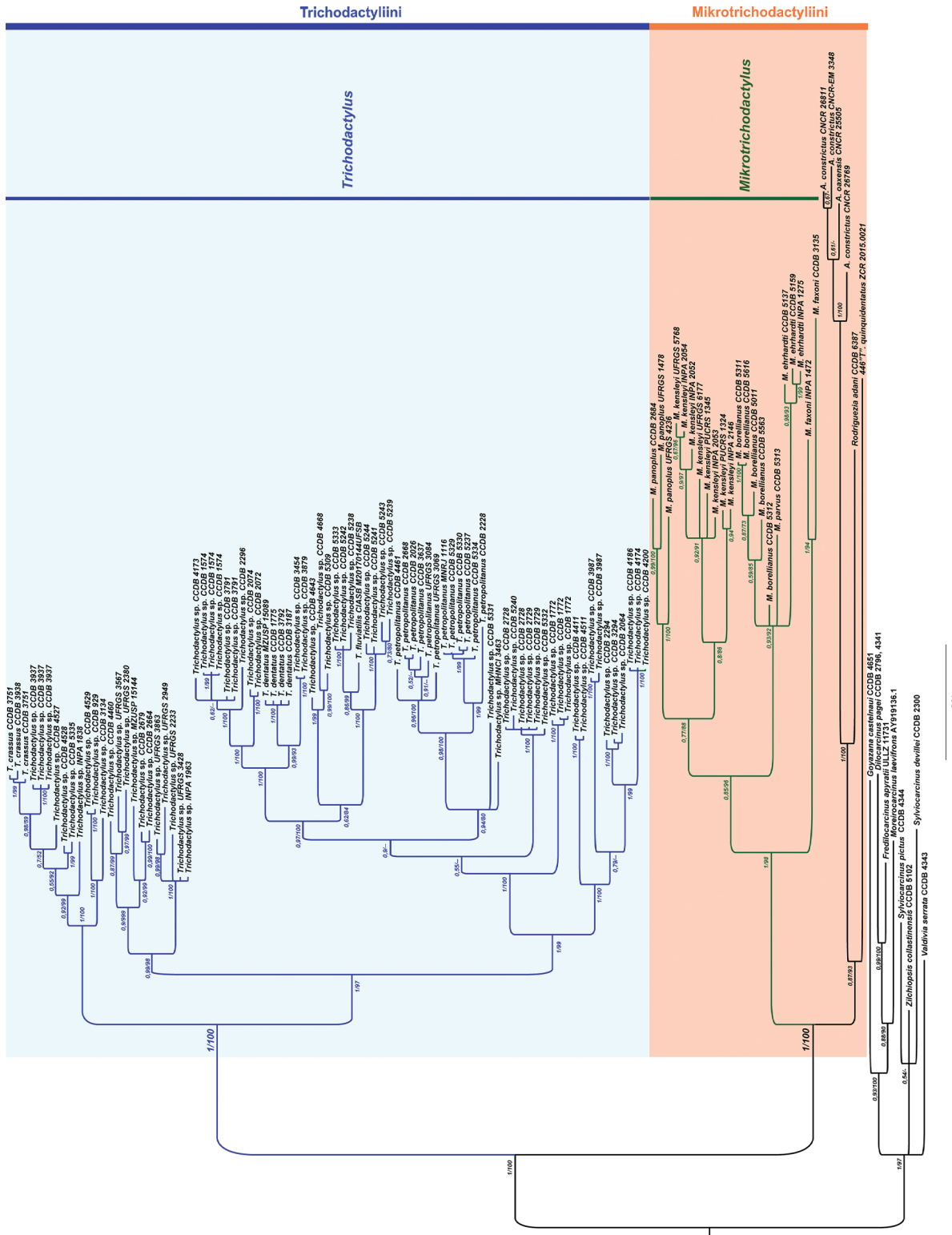


Figure 1. Phylogenetic tree inferred by Maximum Likelihood and Bayesian analysis for Trichodactylinae species based on concatenated analysis of COI, 16S rRNA, and H3 genes.

basin) and southern South America (Paraguay/Paraná River basin and some coastal river basins of southern Brazil and Uruguay) and includes those originally allocated in *Mikrotrichodactylus* (*M. borellianus* and *M. panoplus*) by Pretzmann (1968) and Rodríguez (1992), as well as *M. ehrhardti*, *M. faxoni*, *M. kensleyi*, and *M. parvus*. The second group includes species from north-western South America (Magdalena, Sinu, and upper Orinoco river basins) and Mesoamerica: “*T. quinquedentatus*”, *M. constrictus*, *A. oaxensis*, and *R. adani*.

3.2. Systematic account

The Trichodactylinae species from the Paraná/Paraguay, the southern South America coastal river basins, and the Amazon basin, formed a monophyletic group distinct from “*Trichodactylus*” stricto sensu. They are closer to the *Avotrichodactylus* and *Rodriguezia* genera, both from southern Mexico. Therefore, *Mikrotrichodactylus* Pretzmann, 1968b is hereby confirmed as a valid genus to accommodate the “non-*Trichodactylus*” lineage men-

tioned above and encompassing six species previously allocated in *Trichodactylus* by Magalhães and Türkay (1996a): *T. borellianus*, *T. ehrhardti*, *T. faxoni*, *T. kensleyi*, *T. panoplus*, and *T. parvus*.

The two highly supported monophyletic groups recovered in the analysis (Fig. 1), however, allow us to propose that the subfamily Trichodactylinae be divided into two tribes: one, Trichodactylini stricto sensu, encompasses the genus *Trichodactylus* and all large-sized species (up to 50 mm CW) distributed along the coastal strip from the northeast to the south of Brazil; the other, Mikrotrichodactylini trib. nov., includes the South American and Mesoamerican small-sized species (up to 30 mm CW) belonging to the genera *Mikrotrichodactylus*, *Avotrichodactylus*, *Rodriguezia*, and a taxon inquerendum et incertae sedis for “*Trichodactylus*” *quinquedentatus* (see Remarks below).

Family Trichodactylidae H. Milne Edwards, 1853

Subfamily Trichodactylinae H. Milne Edwards, 1853

Tribe Trichodactylini Pretzmann, 1978b

Trichodactylini Pretzmann, 1978b: 169. — Pretzmann, 1983b: 318.

Type genus. *Trichodactylus* Latreille, 1828, designated by Pretzmann (1978b).

Diagnosis. Carapace: lateral margin devoid of teeth or with vestigial, reduced or developed teeth (usually up to 3 on anterolateral margin; posterolateral margin rarely with 1–2 vestigial teeth); lower orbital margin: inner corner with blunt projection sometimes absent. Efferent branchial channel: aperture with yugal lateral lobe absent. Third maxilliped, meri: distal external spine triangular, acute. Axial skeleton, interosternites: ie4/ie5, ie5/ie6, ie6/ie7 extended mesially, reaching sternum midline as conspicuously elevated phragma; ie7/ie8 interrupted mesially, not extended to sternum midline (see Magalhães and Türkay, 1996a: fig. 7; Pedraza et al., 2015: figs. 3A, 5A); ie7/ie8 separated from junction plate mesially (see Pedraza et al., 2015: figs. 4A, 6A). Pleon: pleonal somites free. Telson (male): subtriangular; anterior margin as broad as posterior margin of pleonal somite VI. G1: simple, straight; positioned longitudinally in sternopleonal cavity; distal half subcylindrical, with lateral and mesial surfaces straight or slightly convex; distal opening wide, V-shaped, directed ventrally, apex usually regularly convex or slightly angled. G2: longer than G1. Large-sized species (up to 50 mm CW).

Genus *Trichodactylus* Latreille, 1828

Trichodactylus Latreille, 1828: 705. — Latreille 1829: 43. — Latreille 1831: 343. — H. Milne Edwards 1837: 10 (in key), 16. — H. Milne

Edwards 1839 [1836–1844]: 60. — Eydoux and Souleyet 1842: 237. — White 1847a: 31. — Nicolet 1849: 151. — Dana 1851: 130. — Dana 1852a: 293, 294. — Dana 1852b: 124. — H. Milne Edwards 1853: 214. — Lucas 1857: 8. — Heller 1865: 35. — Martens 1868: 18 (in list). — A. Milne-Edwards 1869: 170. — Wood-Mason 1871: 191 (in list). — Ortmann 1893: 491. — Ortmann 1897: 325 [part]. — Young 1900: 227 [part]. — Moreira 1901: 45 [part]. — Ortmann 1902: 310 [part]. — Calman 1909: 315. — Colosi 1919: 42. — Colosi 1920: 10, 11 (in key) [part]. — Coifmann 1939: 111 [part]. — Garth 1957: 39. — Pretzmann 1968: 70 [part]. — Rodríguez 1992: 42 [part]. — Morrone and Lopretto 1996: 71 [part]. — Magalhães and Türkay 1996a: 67 (in list), 71 (in key), 73 [part]. — Sternberg 1997: 56 (in tab.), 57, 58 (in fig.) [part]. — Magalhães 1998: 520 [part]. — Magalhães 2003: 199 (in key), 246 [part]. — Ng et al. 2008: 188 (in list) [part]. — De Grave et al. 2009: 42 (in list) [part]. — Brito-Fonseca et al. 2018: 908. — Sternberg and Cumberlidge 2001: 28 (in tab.), 32 (in fig.). — Rogers et al. 2020: 942 (in key) [part]. — Jacobucci et al. 2023: 413.

Cancer (*Trichodactylus*) — Herklots 1861a: 13. — Herklots, 1861b: 126.

Trichodactylus (*Trichodactylus*) — Rathbun 1906a: 34 [part]. — Rathbun 1906b: 503. — Bott 1969: 14 [part].

Trichodactylus (*Valdivia*) — Rathbun 1906a: 43 [part]. — Coifmann 1939: 111 [part].

Type species. *Trichodactylus fluviatilis* Latreille, 1828, by monotypy.

Diagnosis. Same as for the tribe.

Distribution. Atlantic drainage in coastal river basins of the northeastern, southeastern and southern Brazil, from the state of Sergipe to northeastern part of the state of Rio Grande do Sul, as well as in the Upper Paraná River basin in the states of São Paulo and Paraná.

Composition. *Trichodactylus fluviatilis* Latreille, 1828; *Trichodactylus dentatus* H. Milne Edwards, 1853; *Trichodactylus crassus* A. Milne-Edwards, 1869; *Trichodactylus petropolitanus* Göldi, 1886. See below under the section Genus inquiredum et incertae sedis for remarks on the status of “*Trichodactylus*” *quinquedentatus* Rathbun, 1893.

Remarks. In addition to these four species currently recognized as valid in the genus *Trichodactylus*, Souza-Carvalho et al. (2017) found that *T. fluviatilis* could be considered a complex of species with at least four distinct lineages. The taxonomic study of this complex is currently ongoing.

Tribe Mikrotrichodactylini trib. nov.

<https://zoobank.org/80705D91-C5A5-4693-A417-15E37C-C755FD>

Type genus. *Mikrotrichodactylus* Pretzmann, 1968, by present designation.

Diagnosis. Carapace: lateral margin devoid of teeth or usually with up to 5 vestigial, small or developed teeth (some species with 1–2 vestigial or developed teeth on posterolateral margin); lower orbital margin: inner corner with distinct sharp or blunt projection. Third maxilliped, meri: distal external spine reduced. Axial skeleton, interosternites: ie4/ie5, ie5/ie6, ie6/ie7 extended mesially, reaching sternum midline as inconspicuous phragma, being ie6/ie7 noticeable low (vestigial in *A. constrictus*); ie7/ie8 fused to junction plate mesially (see Pedraza et al., 2015: figs. 4B, 6B). Pleon: pleonal somites free (except in *Avotrichodactylus*, with pleonal somites III–V fused). Telson (male): subtriangular or campaniform; anterior margin as broad as or slightly shorter than posterior margin of pleonal somite VI. G1: simple, straight or more or less bent (in *Avotrichodactylus*); positioned more or less diagonally in sternopleonal cavity; distal half subcylindrical, with or without distinct lobes on lateral and/or mesial surfaces, or tapering (in *Avotrichodactylus*); distal opening wide, its apex symmetrical, regularly convex, asymmetrical, with mesodorsally directed projection, or very narrow (in *Avotrichodactylus*). G2: longer or shorter (in *Avotrichodactylus* and *Rodriguezia*) than G1. Small-sized species (up to 30 mm CW).

Genus *Mikrotrichodactylus* Pretzmann, 1968

Dilocarcinus — Ortmann 1893: 491 [part].

Trichodactylus — Nobili 1896: 2. — Ortmann 1902: 310 [part]. — Colosi 1920: 10, 11 (in key) [part]. — Lopretto 1976: 68 (in list) [part]. — Pretzmann 1978b: 165. — Holthuis 1986: 614 (in list) [part]. — Bisbal 1987: 121. — Rodríguez 1992: 42 [part]. — Morrone and Lopretto 1996: 71 [part]. — Magalhães and Türkay 1996a: 67 (in list), 71 (in key), 73 [part]. — Sternberg 1997: 55 (in tab.), 57, 58 (in fig.). — Magalhães 1998: 520 [part]. — Magalhães 2003: 199 (in key), 246 [part]. — Campos 2005: 13, 24 [part]. — Ng et al. 2008: 188 [part]. — De Grave et al. 2009: 42 (in list) [part]. — Campos 2014: 251 [part]. — César and Damborenea 2015: 4 [part]. — Rogers et al. 2020: 942 (in key) [part].

Trichodactylus (*Valdivia*) — Rathbun 1906a: 43 [part]. — Rathbun 1906b: 503 [part]. — Coifmann 1939: 111 [part].

Trichodactylus (*Trichodactylus*) — Coifmann 1939: 111 [part]. — Pretzmann 1968: 70 [part]. — Bott 1969: 14 [part]. — Lopretto 1976: 68 (in list) [part]. — Pretzmann 1983a: 307. — Pretzmann 1983b: 320.

Trichodactylus (*Mikrotrichodactylus*) Pretzmann, 1968: 71.

Mikrotrichodactylus — Rodríguez 1992: 55.

Type species. *Mikrotrichodactylus borellianus* Nobili, 1896, by original designation.

Diagnosis. Carapace: lateral margin devoid of teeth or usually with up to 5 teeth of variable development (vestigial, small or well-developed teeth) in antero- and/or postero-lateral margins. Efferent branchial channel: aperture with yugal lateral lobe present. P2–P5: dactyli and propodi covered by felt-like pubescence; Pleon: pleonal somites free; male pleon usually very wide. Telson (male): anterior margin as broad as or slightly shorter than posterior mar-

gin of pleonal somite VI. G1: simple, straight, positioned more or less diagonally in the sternopleonal cavity; distal half subcylindrical, with or without distinct lobes on lateral and/or mesial surfaces; distal opening wide, V-shaped, fusiform or subtrapezoidal, directed mesially, apex regularly convex, slightly concave or produced mesodorsally. G2: longer than G1. Small-sized species (up to 30 mm CW).

Distribution. Atlantic drainage in northern, center and southern South America (in the Amazon basin, the Paraguay-lower Parana River system, as well as in some coastal river basins of southern Brazil and Uruguay).

Composition. *Mikrotrichodactylus borellianus* (Nobili, 1896); *Mikrotrichodactylus panoplus* (Martens, 1869); *Mikrotrichodactylus faxoni* (Rathbun, 1906a), **comb. nov.**; *Mikrotrichodactylus parvus* (Moreira, 1912), **comb. nov.**; *Mikrotrichodactylus ehrhardti* (Bott, 1969), **comb. nov.**; *Mikrotrichodactylus kensleyi* (Rodríguez, 1992), **comb. nov.**

Remarks. *Mikrotrichodactylus* was erected by Pretzmann (1968) as a subgenus of *Trichodactylus* to accommodate *M. borellianus* and *M. panoplus*. Rodríguez (1992) raised it to generic status and kept these same species in the genus. Magalhães and Türkay (1996a) did not follow the decisions of Pretzmann (1968) and Rodríguez (1992) and treated *Trichodactylus* and *Mikrotrichodactylus* as synonyms in their classificatory system. As the present study corroborated the validity of *Mikrotrichodactylus*, and since different authors have followed either Rodríguez' (1992) or Magalhães and Türkay's (1996a) proposals, we prefer not to treat *M. borellianus*, and *M. panoplus* as new combinations herein.

Genus *Avotrichodactylus* Pretzmann, 1978a

Trichodactylus (*Trichodactylus*) — Coifmann 1939: 111 [part].

Trichodactylus (*Avotrichodactylus*) Pretzmann, 1968: 71.

Trichodactylus (*Rodriguezia*) — Bott 1969: 25 [part].

Avotrichodactylus — Pretzmann 1978a: 54. — Pretzmann 1980: 661.

— Rodríguez 1992: 63. — Villalobos-Hiriart et al. 1993: 284. — Álvarez et al. 1996: 129. — Magalhães and Türkay 1996a: 67 (in list), 71 (in key), 72. — Sternberg 1997: 57, 58 (text, in fig.). — Álvarez and Villalobos 1997: 416. — Álvarez et al. 2005: 191. — Suárez 2005: 155. — Ng et al. 2008: 188 (in list). — De Grave et al. 2009: 42. — Álvarez et al. 2011: 275. — Magalhães and Türkay 2012: 28. — Rogers et al. 2020: 942 (in key).

Trichodactylus — Guinot 1988: 19 [part]. — Morrone and Lopretto 1996: 71 [part].

Type species. *Trichodactylus constrictus* Pearse, 1911, by monotypy.

Diagnosis. Carapace: anterolateral margin with up to 3 teeth of variable development (vestigial, small or well-developed teeth). Efferent branchial channel: aperture with yugal lateral lobe absent. Pleon: pleonal somites III–V fused. Telson (male): campaniform; anterior margin slightly shorter than posterior margin of pleonal

somite VI. G1: simple, strongly or slightly bent; distal half subcylindrical, distinctly tapering, without lobes on lateral and/or mesial surfaces; distal opening narrow, subcircular, situated terminally. G2: shorter than G1, apex tapering. Small-sized species (up to 30 mm CW).

Distribution. Atlantic drainage in southern Mexico.

Composition. *Avotrichodactylus constrictus* (Pearse, 1911); *Avotrichodactylus bidens* (Bott, 1969); *Avotrichodactylus oaxensis* Rodríguez, 1992.

Genus *Rodriguezia* Bott, 1969

Trichodactylus (*Trichodactylus*) — Pretzmann 1968: 70 [part.].

Trichodactylus (*Rodriguezia*) Bott, 1969: 25 [part.].

Trichodactylus — Holthuis 1986: 614 (in list) [part.]. — Guinot 1988: 19 [part.]. — Morrone and Lopretto 1996: 71 [part.].

Rodriguezia — Rodríguez 1992: 62. — Sternberg 1997: 55 (in tab.), 58 (in fig.) [part.]. — Villalobos-Hiriart et al. 1993: 284. — Álvarez et al. 1996: 129. — Magalhães and Türkay 1996a: 67 (in list), 71 (in key), 72. — Ng et al. 2008: 188 (in list). — De Grave et al. 2009: 42. — Álvarez et al. 2011: 276. — Magalhães and Türkay 2012: 34. — Alvarez and Villalobos 2018: 138. — Rogers et al. 2020: 942 (in key).

Type species. *Trichodactylus villalobosi* Rodríguez & Manrique, 1967, by original designation.

Diagnosis. Carapace: lateral margin devoid of teeth. Efferent branchial channel: aperture with yugal lateral lobe absent. Pleon: pleonal somites free. Telson (male): subtriangular; anterior margin nearly as broad as posterior margin of pleonal somite VI. G1: simple, nearly straight; distal half subcylindrical, with weakly developed lobes on ventrolateral surface; distal opening wide, subcircular, apex symmetrical, situated terminally. G2: shorter than G1; apex lanceolate or subtriangular. Small-sized species (up to 30 mm CW).

Distribution. Atlantic drainage in southern Mexico.

Composition. *Rodriguezia villalobosi* (Rodríguez & Manrique, 1967); *Rodriguezia mensabak* (Cottarelli & Argano, 1977); *Rodriguezia adani* Alvarez & Villalobos, 2018.

Remarks. *Rodriguezia* was previously described as a subgenus of *Trichodactylus* by Bott (1969) and later elevated to generic status by Rodríguez (1992). This genus is found only in the Atlantic drainage of southern Mexico and comprises three species as listed above. *Rodriguezia villalobosi* and *R. mensabak* are known only from their holotypes. *Rodriguezia adani* and *R. mensabak* are stygobitic species and exhibit morphological adaptations associated with cave life, such as the absence of eyes, a reduced ocular peduncle, and elongated, slender legs (Cottarelli and Argano, 1977; Alvarez and Villalobos, 2018).

Taxon inquirendum et incertae sedis

"Trichodactylus" quinquedentatus Rathbun, 1893

Remarks. To render *Trichodactylus* a monophyletic genus, the status of "*T.*" *quinquedentatus* still needs to be resolved. The positioning of the only specimen of "*T.*" *quinquedentatus* available for this study as a sister group of the southern Mexico genera would suggest that this species could be considered as belonging to a new genus to be described. We, however, have chosen not to do so and treated it as a taxon inquirendum et incertae sedis for the time being because we had only one specimen from Panama (the same one studied by Magalhães and Ng 2019). The species has a wide distribution in Central and South America, occurring from Honduras to north-western Colombia (Magalhães and Ng 2019). The peculiar geographic distribution of the specimens currently attributed to "*T.*" *quinquedentatus*, with the Panamanian population occurring in the Pacific versant, while all others are from Atlantic river drainages, as well as the Colombian populations exhibiting a transbasinal distribution (Sinu, Magdalena, and upper Orinoco river basins), recommends caution in taking such decision since the resolution of the taxonomic status of this group would require a more comprehensive morphological and molecular study to determine with more certainty its real generic positioning.

4. Discussion

The phylogenetic relationships inferred from molecular data of all described and several still undescribed species of *Trichodactylus* (sensu Magalhães and Türkay 1996a) showed the paraphyletic status of the genus, which implied in the taxonomic adjustments proposed above. With the confirmation of *Mikrotrichodactylus* as a valid genus and considering the genus to which "*T.*" *quinquedentatus* is allocated as a taxon inquirendum et incertae sedis, all genera of Trichodactylinae are rendered monophyletic, based on the currently available data.

The paraphyletic status of *Trichodactylus* was already explicit in the morphology-based phylogenies proposed by Rodríguez (1992), Morrone and Lopretto (1996), and Sternberg (1997). Rodríguez (1992) based his study on somatic characters mainly, as he found it difficult to trace the homologies in the G1 characters and used only two from those of the G1. The tree resulting from his analysis showed *Rodriguezia* nested among *Trichodactylus fluvialtilis* and *T. petropolitanus*, and *M. kensleyi* forming a sister group with "*T.*" *quinquedentatus*. The other species, *M. ehrhardti*, *M. faxoni* and *M. parvus*, were not included in Rodríguez's (1992) study.

Magalhães and Türkay (1996a) did not recognize *Mikrotrichodactylus* because the diagonal folding of G1

was also found in other small *Trichodactylus* species from the Amazon basin, which, however, did not present a mesially inclined apex (they were referring to *T. ehrhardti* and *T. faxoni*).

Morrone and Lopretto (1996) alleged methodological problems in Rodríguez's (1992) analysis, which would have resulted in a classification inconsistent with the obtained cladogram. They revised it, using the same data matrix as Rodríguez (1992) but analyzed it with a different methodological approach. In order to propose a classification that reflected the phylogenetic affinities within the family, Morrone and Lopretto (1996) synonymized *Avotrichodactylus*, *Rodriguezia*, and *Mikrotrichodactylus* under *Trichodactylus*, considering it the sister taxon of the remaining Trichodactylidae.

Sternberg (1997) questioned the approach and conclusions of Morrone and Lopretto (1996) and critically revised their analysis based on a rereading of the data of Rodríguez (1992), in which he incorporated new characters presented by Magalhães and Türkay (1996a, 1996b, 1996c) and based the character state polarization in a broader context within the Section Heterotremata. This reworking of the relationships among trichodactylids corroborated the monophyly of Trichodactylinae, with *Rodriguezia* as the sister group of the clade *Trichodactylus* + *Mikrotrichodactylus*, and *Avotrichodactylus* as the most basal group within the subfamily (Sternberg 1997: 58, fig. 1). Sternberg (1997) found four synapomorphies to support the validity of the genus: carapace lateral teeth found beyond middle (1 or 2 vestigial teeth can also be found beyond middle in some undescribed species of *Trichodactylus* studied by Souza-Carvalho et al. 2017); aperture of efferent channel with lateral yugal lobe present; pleonal somite VIII with episternite laterally expanded; G1 diagonally folded in the sternopleonal cavity. Of these four synapomorphies, only the presence of the yugal lobe seems to be exclusively found in all *Mikrotrichodactylus* species; in *Trichodactylus*, *Avotrichodactylus*, and *Rodriguezia* the yugal lobe is absent. Some undescribed species of *Trichodactylus* studied by Souza-Carvalho et al. (2017) can bear one or two vestigial lateral teeth found beyond middle of the carapace, and the diagonal positioning of G1 is also present in *Avotrichodactylus*, *Rodriguezia*, and "*T.*" *quinquedentatus*, which seems to be an apomorphy for the tribe Mikrotrichodactylini.

Sternberg (1997) carried out his analysis only up to the generic level and considered the species-level classification scheme proposed by Rodríguez (1992), as modified by Magalhães and Türkay (1996a), the most conservative and informative framework for the family. Therefore, when compared with the present study based on molecular data, in Sternberg's (1997) re-analysis, the genus *Trichodactylus* would remain paraphyletic by including *T. kensleyi*, *T. ehrhardti*, *T. maytai* Pretzmann, 1978b (= *T. faxoni*), and "*T.*" *quinquedentatus*.

Pedraza et al. (2015), studying the comparative morphology of the axial skeleton of several species of the family, found morphological differences that can divide Trichodactylinae into two subgroups: A, comprising *Trichodactylus dentatus*, *T. fluviatilis*, and *T.*

petropolitanus; and B, comprising *T. borellianus*, *T. panoplus*, and *A. constrictus*. In the species of the former subgroup, Pedraza et al. (2015) described that the laminae of the intersternites are more developed, more longitudinally curved, and the endosternite 7/8 is mesially separated from the junction plate. In contrast, species of the subgroup B have the intersternite 7/8 mesially fused to the junction plate. Additionally, Pedraza et al. (2015) referred to the character found by Rodríguez (1992) regarding the partial coverage of the penial groove by the episternite 7, which, when combined with the other characters found in their study, could justify the revalidation of *Mikrotrichodactylus*. Pedraza et al. (2015) did not include *M. faxoni*, comb. nov., *M. parvus*, comb. nov., *M. ehrhardti*, comb. nov., and *M. kensleyi* in their study and the axial skeleton characters of these species still need to be properly verified. However, the phylogeny inferred from molecular data in this study, combined with the morphological characters (e.g., the diagonally positioned G1 and the presence of the yugal lobe on the efferent branchial channel aperture, as well as their small size) found in previous works (Rodríguez 1996; Magalhães and Türkay 1996a; Sternberg 1997; Almeida et al. 2008; Pedraza et al. 2015; Souza-Carvalho et al. 2017), bring us strong evidences to support the confirmation of *Mikrotrichodactylus* as a valid genus, crucial for resolving the taxonomic inconsistencies of the group.

Mikrotrichodactylus can be additionally distinguished from *Trichodactylus* by the shape of the merus of the third maxilliped (in *Mikrotrichodactylus*, *Avotrichodactylus*, *Rodriguezia*, and "*T.*" *quinquedentatus* the mesial margin is straight whereas it is convex in *Trichodactylus*), the apex of G1 with asymmetrical distal margin directed mesially (symmetrical in *Trichodactylus*), and the male telson usually campaniform, with proximal margin narrower than the distal margin of the sixth pleonal somite (in *Trichodactylus*, the telson is subtriangular, with its proximal margin as broad as the distal margin of the sixth pleonal somite). However, in *A. borellianus* and *A. parvus* comb. nov., which are phylogenetically closer to each other compared to other *Mikrotrichodactylus* species, the male telson is subtriangular, being the only species of the genus to exhibit such character state, which is likely a regression to a plesiomorphic state. A subtriangular male telson is also present in other genera of Trichodactylinae (*Trichodactylus* and *Rodriguezia*), as well as in the genera of Dilocarcininae and Valdiviinae (except for *Rotundovaldivia* Pretzmann, 1968), making this character state probably a plesiomorphic characteristic.

In the phylogenetic reconstruction based on multigene (Fig. 1), "*Trichodactylus*" *quinquedentatus* was recovered among the Mikrotrichodactylini trib. nov. clade as a sister group of the clade grouping *Avotrichodactylus* and *Rodriguezia*. Although the basic plan of the G1 of "*T.*" *quinquedentatus* has more similarities with that of *Trichodactylus* (see Magalhães and Ng 2019: 70, fig. 7) differences can be highlighted in the distal opening of the G1 (distal margin of apex nearly straight or slightly asymmetric vs rounded or angled in *Trichodactylus*);

in the male telson (campaniform vs subtriangular in *Trichodactylus*); in the third maxilliped merus (distal external spine reduced vs triangular, acute in *Trichodactylus*); and in the carapace lateral teeth (five low, sharp teeth vs smooth or, usually, one to three vestigial to acute teeth on the antero-lateral margin, rarely one to two vestigial teeth on the postero-lateral margin in *Trichodactylus* spp.). As explained above, due to sampling limitations, “*T.*” *quinquedentatus* is treated here as a taxon inquirendum and incertae sedis and its proper phylogenetic positioning among the Trichodactylinae will still require further studies.

Beyond the supraspecific taxonomic questions addressed herein, several species-level taxonomic issues remain unresolved and require further study. The uncertainty regarding which clades truly belong to *Trichodactylus fluviatilis* and allies, the validity of its synonyms must be clarified through a comprehensive morphological, molecular, and historical analysis, incorporating a sufficient number of samples, before describing any potential new species.

5. Declarations

Author contributions. Conceptualization, E.A.S.-C., C.M. and F.L.M.; methodology, E.A.S.-C., F.L.C., C.M. and F.L.M.; perform the molecular analysis, E.A.S.-C., F.L.C.; investigation, morphological and molecular analysis, E.A.S.-C., F.L.C., C.M. and F.L.M.; data curation, E.A.S.-C., C.M. and F.L.M.; preparing, writing, review and editing, E.A.S.-C., F.L.C., 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.

6. Acknowledgements

We are grateful for support and scientific grants provided to FLM by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (2002/08178-9; Scientific Collections 2009/54931-0 and EMU Coleções 2022/11451-2; Temáticos Biota 2010/50188-8 and INTERCRUSTA 2018/13685-5), the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (research grants 472746/2004-9, 471794/2006-6, 473050/2007-2, and 471011/2011-8; 491490/2004-6, 490122/2006-0, 490353/2007-0, 3013359/2007-5; 302748/2010-5; 302253/2019-0). EAS-C was supported by a Doctoral fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). We are grateful to the INPA (Instituto Nacional de Pesquisas da Amazônia), Department of Biology and Post Graduation Program in Comparative Biology of the FFCLRP/USP, ICMBio and Projeto Piabanha for partial financial and logistic support, and to many colleagues and friends (Alexandre Almeida, Fernando Álvarez, José Luis Villalobos, Fernando Zara, Irene Cardoso, Paula Araújo, Paula Martin-Lefèvre, Peter Dworschak, Rafael Lemaitre, Rafael Robles, Sandro Santos, Sérgio Rocha, Sérgio Bueno) for helping in field collections, for making available some essential fresh specimens, and for lending us material from their collections. Special thanks are due to Charles Oliver for all support during the sandwich

PhD of EAS-C to the Museum für Naturkunde in Berlin, and to Fernando Álvarez for donating a sample of *Rodriguezia adani* from the lot CNCR 33914 to the CCDB in 2019.

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Supplementary Material 1

Figures S1–S3

Authors: Souza-Carvalho EA, Magalhães C, Carvalho FL, Mantelatto FL (2025)

Data type: .pdf

Explanation notes: **Figure S1.** Maximum likelihood tree of Trichodactylinae based on cytochrome c oxidase subunit 1 gene sequences. — **Figure S2.** Maximum likelihood tree of Trichodactylinae based on 16S rRNA gene sequences. — **Figure S3.** Maximum likelihood tree of Trichodactylinae based on histone H3 gene sequences.

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Link: <https://doi.org/10.3897/asp.83.e153079.suppl1>

Supplementary Material 2

Tables S1, S2

Authors: Souza-Carvalho EA, Magalhães C, Carvalho FL, Mantelatto FL (2025)

Data type: .zip

Explanation notes: **Table S1.** Crab species of the family Trichodactylidae used in genetic analyses. CCDB: Crustacean Collection of the Department of Biology, Faculty of Philosophy, Sciences, and Letters of Ribeirão Preto, University of São Paulo; CIASB/UFSB-UESC: Aquatic Invertebrates Collection of Southern Bahia, Federal University of Southern Bahia and State University of Santa Cruz, Ilhéus, Bahia; INPA: Crustacean Collection of the National Institute of Amazonian Research; MHNCI: Capão da Imbuia Natural History Museum; MZUSP: Zoology Museum, University of São Paulo; PUCRS: Pontifical Catholic University of Rio Grande do Sul; UFRGS: Crustacean Collection of the Federal University of Rio Grande do Sul; ZRC: Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore. Abbreviations of Brazilian states: AL, Alagoas; AM, Amazonas; BA, Bahia; ES, Espírito Santo; MG, Minas Gerais; MS, Mato Grosso do Sul; MT, Mato Grosso; PR, Paraná; SC, Santa Catarina; SE, Sergipe; SP, São Paulo; RJ, Rio de Janeiro; RS, Rio Grande do Sul; TO, Tocantins. — **Table S2.** Additional specimens of Trichodactylidae used in the morphological analysis. Abbreviations of Brazilian states: AM, Amazonas; GO, Goiás; MT, Mato Grosso; PA, Pará; RO, Rondônia; SC, Santa Catarina; TO, Tocantins.

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