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Natural history update of the orange-clawed hermit crab Calcinus tibicen (Herbst, 1791) (Anomura: Diogenidae) in the Southwestern Atlantic

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Abstract

The *Calcinus tibicen* (Herbst, 1791) is one of the most widespread species of hermit crab in the Western Atlantic. However, important gaps remain in our knowledge of its ecology, distribution, and natural history in the South Atlantic. In this study, we present updated information on the geographic distribution and natural history of *C. tibicen*, including new records of its habitats, shell occupancy, and symbiotic associations. Data on its distribution, habitat use, and shell occupancy were obtained from field collections along the Brazilian coast. Additional occurrence records were compiled from literature reviews and public databases. In total, we recorded 1,306 occurrences, including 497 new records (417 in the North Atlantic and 80 in the South Atlantic). The species inhabits diverse microhabitats and is associated with several marine organisms, including anemones, corals, barnacles, mussels, sponges, zoanthids, and macroalgae. Specimens from Brazilian ecoregions primarily occupied gastropod shells, and epibionts were frequently recorded on these shells. Additionally, we present the first documented cases of *C. tibicen* associations with anemones and chitons. These findings expand our knowledge of this species' natural history and ecological interactions in the South Atlantic.

1. Introduction

The hermit crabs (family Diogenidae) are typical representatives of shallow tropical waters (Hazlett 1966a), comprising about 35 genera and more than 400 valid species (McLaughlin et al. 2010; DecaNet eds. 2025). In Brazil, this group is represented by 10 genera, such as *Calcinus* Dana, 1851 (Nucci and Melo 2015; Lemaitre and Tavares 2015; Lima et al. 2023). Even though this is a species-rich genus in the Indo-Pacific region, only three species of *Calcinus* are reported from the Western Atlantic (Campos and Lemaitre 1994; Malay and Paulay 2010; Nucci and Melo 2015), including *Calcinus tibicen* (Herbst 1791) for the Brazilian coast (Nucci and Melo 2015).

Popularly known as orange-clawed hermit crab, *C. tibicen* inhabits intertidal shallow areas up to 33 m deep and commonly found in rocky coastal areas during the low tide (Melo 1999; García and Capote 2015; Serejo et al. 2022; Boos et al. 2024). Since this species is easily collected, the orange-clawed hermit crab is one of the most exploited reef decapods in the aquarium trade (Gasparini et al. 2005; Gondim et al. 2011). In spite of the intensive commercialization, *C. tibicen* has been classified as “least concern” (LC) by the Chico Mendes Institute of Biodiversity Conservation (ICMBio). However, it should be pointed out that the commercial trade of the orange-clawed hermit crab is not formally regulated (Boos et al. 2024).

This hermit crab species is distributed along Western Atlantic with records in Bermudas, Florida, Gulf of Mexico, Cuba, Antilles, Panama, Colombia, Venezuela, and Brazil. In the Brazilian coast, the occurrence of *C. tibicen* has been documented from the state of Ceará to Santa Catarina besides the archipelagos of Abrolhos, Rocas Atoll, Fernando de Noronha, Trindade and Martim Vaz (Melo 1999; Paiva et al. 2007; García and Capote 2015; Nucci and Melo 2015; Lima et al. 2019). Nonetheless, molecular data based on

mitochondrial markers (COI and 16S) revealed a deep divergence between the populations from North and South Atlantic, dividing them into two genetic groups (Mandai et al. 2018b).

Another common feature of this species is the variation in the coloration along the cheliped and cephalothoracic shield regions, ranging from orangish, greenish, or purplish (Hazlett 1966a; Benedict 1900; Mandai et al. 2018a; Serejo et al. 2022). Yet, genetic analyses (Mandai et al. 2018a) demonstrated that this polymorphic trait is not correlated to interindividual genetic differences, but rather related to nutritional aspects and ecological factors such as camouflage or intraspecific communication.

Several aspects of the biology and ecology of *C. tibicen* have been studied over the last decades. These reports range from behavior (e.g. Hazlett and Bossert 1965; Hazlett 1966a, b, 1980, 1983b, 1987, 1989; Turra and Leite 2000), selection and utilization of shells in metabiosis – an obligatory association in which an organism, even dead specimens, provides suitable conditions for the survival of others (Van and Van 2019) – (e.g. Floeter et al. 2000; Mantelatto and Garcia 2000; Garcia and Mantelatto 2001; Turra and Leite 2001; Gilchrist 2003; Bastista-Leite et al. 2005; Lima et al. 2018; Santos et al. 2021; Silva et al. 2023), reproduction and sex maturation (e.g. Fotheringham, 1980; Mantelatto and Garcia, 1999; Fransozo et al., 2003; Amadio and Mantelatto, 2010; Ribeiro et al. 2023), spawning season (e.g. Fransozo and Mantelatto 1998), larval morphology and description (e.g. Provenzano Jr. 1962; Cházaro-Olvera et al. 2013), habitat preferences and interspecific associations (e.g. Aguirre-Aguirre et al. 2007; Quirós et al. 2012; Brown and Edmunds 2013; González-Gómez et al. 2018; Lane-Medeiros et al. 2021) and parasitic relationships (e.g. Murphy and Williams 2013; Markham 2020). Furthermore, the occurrence of this species has been documented in inventories about the local biodiversity (e. g. Souza and Serejo 2007; Almeida et al. 2010; Lenz et al. 2014; Ribeiro et al. 2019; Lima et al. 2019; Mantelatto et al. 2021; Grangeiro et al. 2024).

Nevertheless, most of studies focusing on *C. tibicen* refer to areas in North Atlantic. In South Atlantic, isolated reports are concentrated in the Southeastern, Eastern and Northeastern ecoregions, respectively. So far, the only distribution analysis in *C. tibicen*, including georeferenced information was performed by Malay and Paulay (2010). Over the last decade, sparse studies have been published, revealing the need of a historic and systematic compilation of detailed data about this species that combining precise geographic coordinates along their distribution range and natural history aspects. Therefore, the goal of the present study was to report the complete distribution of *C. tibicen* along the Western Atlantic, addressing new ecological and natural history aspects of this species in South Atlantic. Accordingly, we provide novel data about habitat, shells in metabiosis and symbiotic associations, with emphasis on the Northeastern and Eastern ecoregions of Brazil.

2. Material and methods

2.1 List of abbreviations

CAPES: Coordination for the Improvement of Higher Education Personnel; **CIASB:** Aquatic Invertebrates Collection of Southern Bahia; **Coll.:** Collectors; **GEEFAA:** Study Group in Ecology and Physiology of

Aquatic Animals; **GBIF:** Global Biodiversity Information Facility; **LABEEC:** Laboratory of Biology, Ecology and Evolution of Crustaceans; **LACRUSE:** Laboratory of Crustaceans of the Semiarid; **SISBio:** Biodiversity Authorization and Information System; **LZPA:** Laboratory of Zoology and Animal Parasitology; *UESB:* State University of Southwestern Bahia; **UESC:** State University of Santa Cruz; **UFRN:** Federal University of Rio Grande do Norte; **WORMS:** World Register of Marine Species.

2.2 Occurrence data

The information about geographic occurrence of *C. tibicen* were separated according to their mode of acquisition, following the criteria described by Alencar et al. (2017, 2023) and Muniz et al. (2026). Thus, the primary data refer to those collected in the field and analyzed in the laboratory by the authors of this manuscript. Instead, the data based on specialized literature and public databases (GBIF and SpeciesLink) were classified as secondary.

2.1.1 Primary data

The primary data were obtained after field collections carried out from March 2011 to July 2024 in the Northeastern and Eastern ecoregions of Brazil, along the coast of the states of Alagoas, Bahia, Ceará, Espírito Santo, Pernambuco, Piauí, Rio Grande do Norte, and Santa Catarina. All collections of samples were authorized by the Biodiversity Authorization and Information System – SISBIO by ICMBIO (n. 90504-5).

The hermit crabs were collected by active search for 30 min during low tide periods (<0.5 m) by two well-trained members (Santos et al., 2021). The tide periods were checked using the Tide Table provided by the Hydrographic Center of the Brazilian Navy (Brazilian Navy, 2024). In the field, the hermit crabs were collected and packaged into plastic bags, labeled based on location, cryoanesthetized, and transported to the Laboratory of Zoology and Animal Parasitology of the State University of Southwestern Bahia (LZPA-UESB).

In the laboratory, the specimens were identified based on McLaughlin (2003) and Nucci and Melo (2015), and sexed based on Amadio and Mantelatto (2009). The identification of the shells occupied by the hermit crabs in metabiosis was carried out based on the platform “Conchologists of Brazil” (conchasbrasil.org.br), and through specialized literature based on Rios (2009) and Petuch (2013). The taxonomic status was confirmed via WORMS - World Register of Marine Species platform (marinespecies.org). Subsequently, the animals were preserved in 70% ethanol and deposited in the Invertebrate Collection of the Federal University of Rio Grande do Norte (UFRN; voucher GEEFAA) and in the Aquatic Invertebrate Collection of Southern Bahia of the State University of Santa Cruz (UESC; voucher CIASB).

In addition, we also analyzed the material from the Invertebrate Collection at UFRN (GEEFAA), managed by the Laboratory of Biology, Ecology and Evolution of Crustaceans (LABEEC), with data on the species

for the states of Rio Grande do Norte and São Paulo between the years 1985 and 2023.

2.1.2 Secondary data

The secondary data were obtained in two ways: the first stage consisted of surveying the geographic occurrences of populations of *Calcinus tibicen* through a comprehensive systematic bibliographic review (SBR) of scientific documents published in the Biological Abstracts, CAB Abstracts, CSA, Google Scholar, JSTOR, ScienceDirect, Scopus, and Web of Science repositories. The search tools included predefined descriptors, including the synonyms "*Calcinus sulcatus*" and "*Calcinus formosus*", followed by command lines using the keywords and the boolean commands "AND" and "OR" in Portuguese, English, and Spanish. The second stage consisted of surveying the geographic occurrences of the species in online platforms - GBIF (https://www.gbif.org/ - accessed on December 26th, 2023) and SpeciesLink (http://splink.cria.org.br/ - accessed on December 18th, 2023), as described by Alencar et al. (2017, 2023). All occurrences based on observation were confirmed through photo documentation evaluated by a single researcher (Muniz JI).

Data from monographs, dissertations, theses, undergraduate projects, reports from NGOs and private companies, abstracts from congresses, symposia, and local, regional, national, and international events were not considered valid for this stage. In the absence of latitude and longitude information, the geographic coordinates were estimated based on the described localities, using the GeoNames geographic identification database (www.geonames.org). Subsequently, all coordinates and locations were confirmed using the Google Earth satellite mapping program (https://www.google.com.br/intl/ptBR/earth/), considering the WGS84 geographic coordinate system (Alencar et al. 2023).

All primary and secondary data were combined into a data table containing the following information, as proposed by Alencar et al. (2017, 2023): (1) data origin (GBIF, SpeciesLink, Published Literature or LABEEC); (2) data type (primary or secondary); (3) occurrence ID; (4) institution code; (5) collection; (6) accession number; (7) latitude and longitude; (8) country and/or state; (9) locality; (10) year of collection; (11) person responsible for the identification; (12) the person responsible for the recorded data; (13) use or not of GeoNames and/or Google Earth for coordinates; (14) validity of records; (15) and new register or not (supplementary material 1).

The maps of geographic distribution were generated in the software QGIS version 3.42.2 (2025), using the WGS84 coordinate system and the ocean coverage plugin “ESRI Ocean”, available in QGIS. The shapefiles of continental and national divisions were obtained from the Natural Earth platform (2022), while the divisions of Brazilian states were based on the Brazilian Institute of Geography and Statistics – IBGE (2022). The global ocean divisions were obtained from the Flanders Marine Institute (2021), based on the International Hydrographic Organization (1953). Finally, the marine ecoregions were obtained from the World Wildlife Fund website (2024), using the divisions proposed by Spalding et al. (2007).

3. Results

Infraorder Anomura MacLeay 1838

Superfamily Paguroidea Latreille 1802

Family Diogenidae Ortmann 1892

Genus *Calcinus* Dana 1851

Calcinus tibicen (Herbst 1791)

(Figs. 2d, -3d, -6egh)

Type locality. Unknown (Provenzano Jr, 1959)

Examined material. Brazil: State of Ceará. Flexeiras beach, Trairi, 3°13’01.8”S 39°16’01.7”W, 02.VIII.2023, JI Muniz and JE Lemos coll., intertidal pools (GEEFA/UFRN-3399) (Fig. 2a, b). Pedra Rachada beach, Paracuru, 3°23’55.0”S 39°00’47.3”W, 07.VIII.2023, JI Muniz and JE Lemos coll., intertidal pools (GEEFA/UFRN-3398) (Fig. 2c, d). **State of Rio Grande do Norte.** Genipabu, Extremoz, 5°41'38.2"S 35°12'12.9"W, 08.VI.2023, NFC França, MRD Alves and IDC Silva coll. (GEEFAA/UFRN-1694). Ponta Negra, Natal, between 5°48’6.3”S 35°10’49.9”W and 5°50’47.4”S 35°10’54”W, 04-11.XI.2020, CERD Alencar coll. (GEEFAA/UFRN-1364). Pirambúzios beach, Nísia Floresta, 6°00’01.3”S 35°06’39.9”W, 30.III.2010, TS Leite coll., and 31.III.2010 (GEEFAA/UFRN-0906, GEEFAA/UFRN-2504, GEEFAA/UFRN-2635). Pirangi beach, 5°58'41.8"S 35°07'12.9"W, 12.VII.2010, 13.VII.2010, TS Leite coll., and 13.XII.2007 (GEEFAA/UFRN-0903, GEEFAA/UFRN-0912, GEEFAA/UFRN-2632, GEEFAA/UFRN-2633, GEEFAA/UFRN-2639). Rocky bottom, mesolittoral, Amor beach, Tibau do Sul, 6°14’4.22”S 35°2’19.79”W, 30.IX.2012, CERD Alencar, TS Emerenciano, SASN Moraes and VLG Brito coll., and 01.X.2012, AA Cabral, CERD Alencar, TS Emerenciano, SASN Moraes and VLG Brito coll. (GEEFAA/UFRN-0047, GEEFAA/UFRN-0048, GEEFAA/UFRN-1588, GEEFAA/UFRN-1951, GEEFAA/UFRN-2121, GEEFAA/UFRN-2122, GEEFAA/UFRN-2123, GEEFAA/UFRN-2124, GEEFAA/UFRN-2125, GEEFAA/UFRN-2126, GEEFAA/UFRN-2127, GEEFAA/UFRN-2161, GEEFAA/UFRN-2162, GEEFAA/UFRN-2164, GEEFAA/UFRN-2165, GEEFAA/UFRN-2309, GEEFAA/UFRN-2634, GEEFAA/UFRN-2636, GEEFAA/UFRN-2637, GEEFAA/UFRN-2638). **State of Pernambuco.** Carneiros beach, Tamandaré, 8°42’50.7”S 35°05’00.5”W, 07.XI.2023, JI Muniz and CERD Alencar coll., exposed intertidal rocks (GEEFA/UFRN-3401) (Fig. 2e, f). Porto de Galinhas beach, Ipojuca, 8°30’20.8”S 34°59’52.9”W, 19.IV.2024, LM Omena and LF Silva coll., intertidal pools (GEEFA/UFRN-3402) (Fig. 2g, h). **State of Alagoas.** Ponta Verde beach, Maceió, 9°39'54.9"S 35°41'40.4"W, 15.X.2024, ES Santos, MFLS Feitosa and VR Santos, Coll., sandy coast (GEEFA/UFRN-3384) (Fig. 3a, b). **State of Bahia.** Forte beach, Mata de São João, 12°34’40.8”S 38°00’06.3”W, 29.IV.2023, JI Muniz and DS Soares coll., and 08.VI.2024, JI Muniz and CERD Alencar coll., intertidal pools (GEEFA/UFRN-3385/3386) (Fig. 3c, d). Tivoli beach, Mata de São João, 08.VI.2024, 12°34’57.6”S 38°00’46.3”W DS Soares and MDC Martins

coll., intertidal pools (GEEFA/UFRN-3396). Pituba beach, Salvador 13°00’39.0”S 38°27’55.0”W, 10.III.2024, PA Gulhões-Silva coll., intertidal pools (GEEFA/UFRN-3388). Concha beach, Itacaré, 14°16’25.4”S 38°59’12.2”W, 20.III.2023, JI Muniz and CERD Alencar coll., and 26.V.2024, CS Matos, AD Silva, PA Gulhões-Silva coll., intertidal pools (GEEFA/UFRN-3391) (Fig. 3e, f). Arruda beach, Itacaré 14°20’23.3”S 38°59’56.3”W, 21.III.2023, JI Muniz and CERD Alencar coll., intertidal pools (GEEFA/UFRN-3390) (Fig. 3g, h, i, j). Três Coqueiros beach, Maraú, 13°53’01.6”S 38°56’19.5”W, 03.XII.2023, JI Muniz and CERD Alencar coll., intertidal pools (GEEFA/UFRN-3395) (Fig. 4a, b). Milagres beach, Olivença, Ilhéus, 14°56’47.5”S 39°00’32.2”W, 07.X.2023, CS Matos coll., intertidal pools (GEEFA/UFRN-3393) (Fig. 4c, d). Batuba beach, Olivença, Ilhéus, 14°56’40.0”S 39°00’37.3”W, 22.VII.2024, DS Soares, FS Silva, CS Matos, AD Silva coll (GEEFA/UFRN-3392). Sirihyba beach, Olivença, Ilhéus, 14°57’30.0”S 39°00’17.5”W, 26.XI.2023, JI Muniz and CERD Alencar coll., intertidal pools (GEEFA/UFRN-3394) (Fig. 4e, f). Coroa Vermelha coral reef, Santa Cruz Cabrália, 16°19’59.5”S 39°00’05.8”W, 09.XII.2023, AD Silva, DS Soares, JI Muniz and CS Matos coll., intertidal pools (GEEFA/UFRN-3389) (Fig. 4g, h). Recife de Fora Marine Park, Porto Seguro 16°24’19.8”S 38°59’01.3”W, 10.XII.2023, JI Muniz and AD Silva coll (GEEFA/UFRN-3397). **State of Espírito Santo.** Costa Azul beach, Iriri, Anchieta, 20°49'58.9”S 40°41'33.4”W, 13.XI.2024, RG Tavares and JI Muniz coll., exposed rocky coast (GEEFA/UFRN-3400). State of São Paulo. Guarujá beach, 24°04’06”S 46°15’19.36”W, 01.XI.2011, 24°04’06”S 46°15’19.36”W, H Thomsen, CERD Alencar and PA Lima-Filho coll. (GEEFAA/UFRN-1325).

Compared material. Brazil: State of Rio Grande do Norte. In *Phragmatopoma caudata* Krøyer in Mörch 1863, Praia de Santa Rita, Extremoz, 5°41'37.2"S 35°11'45.4"W, 05.VIII.2015, MAL Rocha coll. (GEEFAA/UFRN-1243). Rocky bottom, mesolittoral, Santa Rita beach, Extremoz, 5°41’36.0”S 35°11’47.0”W, 17.IV.2011, AA Cabral coll., 26.V.2013, 30.V.2014, 28.VI.2014, 27.VII.2014, AB Moraes and DC Soares coll., and 21.I.2015 (GEEFAA/UFRN-0044, GEEFAA/UFRN-0058, GEEFAA/UFRN-1589, GEEFAA/UFRN-1592, GEEFAA/UFRN-2158, GEEFAA/UFRN-2159) (Lane-Medeiros et al., 2021). **State of São Paulo.** Araçá beach, São Sebastião, 23°48'46.9"S 45°24'31.1"W, 24.XI.1985 (GEEFAA/UFRN-2115).

Diagnosis. The shield is longer and narrower than in other species with smooth and slightly convex surface; triangular rostrum, with straight anterior margins, situated between the lateral projections. Eye stalks are slightly shorter than the shield; scales with a prominent distal spine, being occasionally bifurcated or trifurcated. Uneven, smooth and bristle-free chelipeds, being the left cheliped larger than the right one. Dactyl of the walking legs shorter than the propodus; propodus of the third pereopod with a dorsolateral groove; merus of the second pereopod laterally flattened and that of the third pereopod is laterally convex. The telson is nearly rectangular, being the left lobe slightly larger than the right one and both lack a submarginal spine; lateral and terminal margins with long bristles (Nucci and Melo 2015).

Coloration. The color pattern of chelipeds range from orangish to reddish-brown with occasional purple or green tones, while the dactyls present white tips. The walking legs exhibit white or yellow dactyls with red stripes while the distal extremities of the propodus have a light coloration. The eye stalks are reddish-orange, turning into white near the cornea. The cephalothoracic shield is generally bright red, sometimes with purple or green tones, and punctuated by small white spots. In young individuals, the

shield coloration is less conspicuous, particularly over the posterior regions (Rathbun 1900; Provenzano Jr 1959; Serejo et al. 2022; present study).

Occupied shells. Brazil: State of Ceará.*Agathistoma viridulum* (Gmelin 1791) (Fig. 1-28), *Astralium latispina* (Philippi 1844) (Fig. 1-21), *Gemophos* auritulus (Link 1807) (Fig. 1- 3), *Leucozonia* nassa (Gmelin 1791) (Fig. 1-6), *Leucozonia ocellata* (Gmelin 1791) (Fig. 1-7), *Pisania pusio* (Linnaeus 1758) (Fig. 1-8) and *Stramonita haemastoma* (Linnaeus 1767) (Fig. 1-1). **State of Pernambuco.***Agathistoma viridulum* (Gmelin 1791) (Fig. 1-28), *Columbella mercatoria* (Linnaeus 1758) (Fig. 1-25), *Cypraecassis testiculus* (Linnaeus 1758) (Fig. 1-26), *Favartia nuceus* (Mörch 1850) (Fig. 1-12), *Leucozonia nassa* (Gmelin 1791) (Fig. 1-6), *Leucozonia ocellata* (Gmelin 1791) (Fig. 1-7), *Lithopoma tectum* (Lightfoot 1786) (Fig. 1-27), *Pisania pusio* (Linnaeus 1758) (Fig. 1-8), *Stramonita haemastoma* (Linnaeus 1767) (Fig. 1-1), *Stramonita rustica* (Lamarck 1822) (Fig. 1-2) and *Vasula deltoidea* (Lamarck 1822) (Fig. 1-19). **State of Alagoas.***Agathistoma viridulum* (Gmelin 1791) (Fig. 1-28), *Astralium latispina* (Philippi 1844) (Fig. 1-21), *Leucozonia nassa* (Gmelin 1791) (Fig. 1-6), *Lithopoma tectum* (Lightfoot 1786) (Fig. 1-27), *Pisania pusio* (Linnaeus 1758) (Fig. 1-8), *Stramonita haemastoma* (Linnaeus 1767) (Fig. 1-1), *Stramonita rustica* (Lamarck 1822) (Fig. 1-2) and *Vasula deltoidea* (Lamarck 1822) (Fig. 1-19). **State of Bahia.***Agathistoma viridulum* (Gmelin 1791) (Fig. 1-28), *Alanbeuella corrugata* (Perry 1811) (Fig. 1-16), *Anachis lyrata* (Sowerby I 1832) (Fig. 1-24), *Astralium latispina* (Philippi 1844) (Fig. 1- 21), *Cerithium atratum* (Born 1778) (Fig. 1-18), *Claremontiella nodulosa* (Adams 1845) (Fig. 1-14), *Colubraria obscura* (Reeve 1844) (Fig. 1-5), *Columbella mercatoria* (Linnaeus 1758) (Fig. 1-25), *Conus archetypus Crosse 1865 (*Fig. *1-22), Coralliophila aberrans* (Adams 1850) (Fig. 1-9), *Dulcerana cubaniana* (D'Orbigny 1847) (Fig. 1-17), *Gemophos auritulus* (Link 1807) (Fig. 1-3), *Gemophos ringens* (Reeve 1846) (Fig. 1-4), *Hastula cinerea* (Born 1778) (Fig. 1-10), *Leucozonia nassa* (Gmelin 1791) (Fig. 1-6), *Leucozonia ocellata* (Gmelin 1791) (Fig. 1-7), *Lithopoma tectum* (Lightfoot 1786) (Fig. 1-27), *Monoplex pilearis* (Linnaeus 1758) (Fig. 1-15), *Phyllonotus oculatus* (Reeve 1845) (Fig. 1-5), *Pisania pusio* (Linnaeus 1758) (Fig. 1-8), *Polinices uberinus* (D'Orbigny 1842) (Fig. 1-23), *Pugilina morio* (Linnaeus 1758) (Fig. 1-13), *Stramonita haemastoma* (Linnaeus 1767) (Fig. 1-1), *Stramonita rustica* (Lamarck 1822) (Fig. 1-2), *Vasula deltoidea* (Lamarck 1822) (Fig. 1-19) and *Vasula melones* (Duclos 1832) (Fig. 1- 20). **State of Espírito Santo.***Agathistoma viridulum* (Gmelin 1791) (Fig. 1-28), *Pisania pusio* (Linnaeus 1758) (Fig. 1-8), *Leucozonia nassa* (Gmelin 1791) (Fig. 1-6).

Fig. 1 Gastropod shells and dead coral parts occupied by *Calcinus tibicen* (Herbst 1791) along the Northeastern and Eastern ecoregions in Brazil. (1) *Stramonita haemastoma* (Linnaeus 1767), (2) *Stramonita rustica* (Lamarck 1822), (3) *Gemophos auritulus* (Link 1807), (4) *Gemophos ringens* (Reeve 1846), (5) *Colubraria obscura* (Reeve 1844, (6) *Leucozonia nassa* (Gmelin 1791), (7) *Leucozonia ocellata* (Gmelin 1791), (8) *Pisania pusio* (Linnaeus 1758), (9) *Coralliophila aberrans* (Adams 1850), (10) *Hastula cinerea* (Born 1778), (11) *Phyllonotus oculatus* (Reeve 1845), (12) *Favartia nuceus* (Mörch 1850), (13) *Pugilina morio* (Linnaeus 1758), (14) *Claremontiella nodulosa* (Adams 1845), (15) *Monoplex pilearis* (Linnaeus 1758), (16) *Alanbeuella corrugata* (Perry 1811), (17) *Dulcerana cubaniana* (D'Orbigny 1847), (18) *Cerithium atratum* (Born 1778), (19) *Vasula deltoidea* (Lamarck 1822), (20) *Vasula melones* (Duclos 1832), (21) *Astralium latispina* (Philippi 1844), (22) *Conus archetypus* Crosse 1865, (23) *Polinices*

uberinus (D'Orbigny 1842), (24) *Anachis lyrate* (Sowerby I 1832), (25) *Columbella mercatoria* (Linnaeus 1758), (26) *Cypraecassis testiculus* (Linnaeus 1758), (27) *Lithopoma tectum* (Lightfoot 1786), (28) *Agathistoma viridulum* (Gmelin 1791), and (29) dead coral fragment. Scale bar = 5 mm

Habitat. Rocky shore without significant elevation and exposed rocks, intertidal pools, rocky substrate and sandy areas between tidal influence, rocky regions along the shallow mesolittoral and sublittoral zones, substrate and/or meadows covered by algae, sand and mud beds, coral reefs, hydrocorals and polychaeta galleries (Hazlett 1966a; Lira 1997; Díaz and López 2003; Vargas and Cortés 2006; Do Nascimento and Torres 2007; Quirós and Campos 2010; Brown and Edmunds 2013; García and Capote 2015; Velásquez et al. 2017; Lane-Medeiros et al. 2021; present study). **Associated species in the substrate: Anemones.***Actinia equina* (Linnaeus 1758) and *Bunodosoma cangicum* Belém and Preslercravo 1973. Corals. *Favia gravida* Verrill 1868 and *Siderastrea stellata* Verrill 1868. **Barnacles.***Chthamalus* sp. (Poli 1791). **Macroalgae.***Anadyomene stellata* (Wulfen) C. Agardh 1823, *Centroceras clavulatum* (C. Agardh) Montagne 1846, *Ceramium* sp. Roth 1797, *Chaetomorpha aerea* (Dillwyn) Kützing 1843, *Cladophora glomerata* (Linnaeus) Kützing 1843, *Cladophora vagabunda* (Linnaeus) Hoek 1963, *Codium* sp. Stackhouse 1797, *Corallina officinalis* Linnaeus 1758, *Cryptonemia seminervis* (C. Agardh) J. Agardh 1846, *Dictyota menstrualis* (Hoyt) Schnetter, Hörning and Weber-Peukert 1987, *Ernodesmis verticillata* (Kützing) Børgesen 1912, *Gelidelia acerosa* (Forsskal) Feldmann and Hamel 1934, *Gelidium pusillum* (Stackhouse) Le Jolis 1863, *Gracilaria intermedia* J. Agardh 1901, *Halimeda cuneata* Hering 1846, *Hypnea musciformis* (Wulfen) Lamouroux 1813, *Jania rubens* (Linnaeus) Lamouroux 1816, *Laurencia obtusa* (Hudson) Lamouroux 1813, *Padina pavonica* Thivy 1960, *Pterocladiella bartletti* (W.R. Taylor) Santelices 1998, *Sargassum* sp. C. Agardh 1820, *Solieira filiformis* (Kützing) Gabrielson 1985, *Spatoglossum shroederi* (C. Agardh) Kützing 1859, *Sphacelaria rigidula* Kützing 1843, *Stylonema alsidii* (Zanardini) K.M.Drew 1956, *Stypopodium zonale* (Lamouroux) Papenfuss 1940, *Ulva flexuosa* Wulfen 1803, *Ulva intestinalis* Linnaeus 1753, *Ulva lactuca* Linnaeus 1753, *Vertebrata lanosa* (Wulfen) Lamouroux 1813. **Mussels.***Brachidontes exustus* (Linnaeus 1758). **Porifera.***Cliona varians* (Duchassaing and Michelotti 1864). **Zoanthids.***Palythoa caribaeorum* Duchassaing and Michelotti 1860 and *Zoanthus sociatus* (Ellis 1768).

Distribution. Bermuda, United States of America (Florida), Bahamas, Cuba, U.S. Virgin Islands, British Virgin Islands, Puerto Rico, Dominican Republic, Haiti, Jamaica, Cayman Islands, Mexico, Belize, Honduras, Costa Rica, Panama, Antigua and Barbuda, Saint Kitts and Nevis, Saint Barthélemy, Sint Maarten, Anguilla, Saint Vincent and the Grenadines, Dominica, Guadeloupe, Grenada, Barbados, Martinique Island, Aruba, Curaçao, Bonaire, Sint Eustatius and Saba, Colombia, Trinidad and Tobago, Venezuela, and Brazil. In Brazil, the species is described for the states of Ceará, Rio Grande do Norte, Paraiba, Pernambuco, Alagoas, Sergipe, Bahia, Espirito Santo, Rio de Janeiro, São Paulo, Santa Catarina, and the oceanic islands of Abrolhos, Rocas Atoll, Fernando de Noronha, and the Trindade and Martin Vaz archipelago (Provenzano Jr 1960; Provenzano Jr 1961, 1962; Hazlett 1972; Narchi and Hebling 1972; Hazlett 1974; Bach et al. 1976; Sánchez and Campos 1978; Fotheringham 1980; Bertness 1982; Hazlett 1983a, 1983b, 1984a, 1984b; Bauer 1985; Hazlett and Baron 1989; Reyes and Néstor 1992; Brown et al. 1993; Campos and Lemaitre 1994; Campos 1995; Coelho-Santos and Coelho 1995; Rieger and Giraldi

1997; Carvalho et al. 1998; Fransozo and Mantelatto 1998; Leite et al. 1998; Iglesias and Raso 1999; Mantelatto and Garcia 1999; Melo 1999; Floeter et al. 2000; Mantelatto and Garcia 2000; Turra and Leite 2000; Garcia and Mantelatto 2001; Turra and Leite 2001; Briones-Fourzan and Lozano-Alvarez 2002; Mantelatto and Garcia 2002; Batista-Leite et al. 2003; Díaz and López 2003; Fransozo et al. 2003; Gilchrist 2003; García Raso et al. 2005; Wicksten 2005; Vargas and Cortés 2006; Aguirre-Aguirre et al. 2007; Alvarez and Alvarez 2007; Nascimento and Torres 2007; Paiva et al. 2007; Salazar et al. 2007; Souza and Serejo 2007; Amadio and Mantelatto 2009; Orensky and Williams 2009; Almeida et al. 2010; Hernández et al. 2010; Ribeiro et al. 2010; Quirós and Campos 2010; Gondim et al. 2011; Giraldes et al. 2012; Ribeiro et al. 2012; Quirós et al. 2012; Alves et al. 2013; Brown and Edmunds 2013; Cházaro-Olvera et al. 2013; Murphy and Williams 2013; Oosterhout et al. 2013; Lenz et al. 2014; García and Capote 2015; Giraldes et al. 2015; Nucci and Melo 2015; Ribeiro et al. 2016; De la Cruz-Francisco et al. 2017; Giraldes et al. 2017; Velásquez et al. 2017; González-Gómez et al. 2018; Lima et al. 2018; Mandai et al. 2018a; Mandai et al. 2018b; Vinagre et al. 2018; Vinagre et al. 2019; Lima et al. 2019; Mendonça et al. 2019; Ribeiro et al. 2019; Briones-Fourzán et al. 2020; Silva et al. 2020; Coutinho et al. 2021; Giraldes et al. 2021; Lane-Medeiros et al. 2021; Mantelatto and Garcia 2021; Santos et al. 2021; Hernández-Aguilera et al. 2022; Rodríguez et al. 2022; Moraes et al. 2022; Dubé et al. 2023; Ribeiro et al. 2023; Silva et al. 2023; present study).

Observations. The first official record of *Calcinus tibicen* in South Atlantic was carried out by Smitt (1869), dated back to 1867 in the archipelago of Abrolhos, state of Bahia, northeastern Brazil. Decades later, the species was collected by Rathbun (1900) on the coast of Alagoas (Maceió), Paraíba (Maranguape), and Pernambuco (no specific location). Both authors referred to this species using the synonym *Calcinus sulcatus* (H. Milne Edwards 1836). A year later, Moreira (1901) reported this species in Abrolhos, and a few decades later, the same author (Moreira 1920) recorded, for the first time, the occurrence of the orange-clawed hermit crab in the island of Trindade, state of Rio de Janeiro. Only 50 years later, Narchi and Hebling (1972) reported this species for the coastline of the state of Espírito Santo. In this study, the authors used the currently valid name of the species, *Calcinus tibicen* (Herbst 1791). Only in 1998, the known distribution of *C. tibicen* was expanded to the state of São Paulo in the Southeastern ecoregion (Fransozo and Mantelatto 1998). So far, the southern limit range for this species of hermit crab was established for the coast of the state of Santa Catarina (Retiro dos Padres and Sepultura beaches in Bombinhas) (Rieger and Giraldi 1997).

Fig. 2 Collection sites of *Calcinus tibicen* (Herbst 1791) along the Northeastern ecoregion of Brazil. (a) Rocky coast with natural pools and (b) active collection of specimens at the Flexeiras beach, Trairi, Ceará. (c) Sandstone reef and (d) specimen of *C. tibicen* collected at the Pedra Rachada beach, Paracuru, Ceará. (e, f) Exposed rocky coast along the Carneiros beach, Tamandaré, Pernambuco. (g) Coast along the Porto de Galinhas beach, Ipojuca, Pernambuco, (h) highlighting the sandstone reef

Fig. 3 Collection sites of *Calcinus tibicen* (Herbst 1791) along the Northeastern and Eastern ecoregions of Brazil. (a, b) Rocky coast with sandy bottom in Ponta Verde beach, Maceió, Alagoas. (c) Forte beach, Mata de São João, (d) *C. tibicen* showing a reddish coloration right after collection. (e, f) Active search

along the rocky coast in Concha beach, Itacaré, Bahia. (g) Arruda beach, Itacaré, (h) *C. tibicen* over the zoanthids *Palythoa caribaeorum* Duchassaing and Michelotti 1860 and (i) *zoanthus sociatus* (Ellis, 1768) and (j) sponges *Cliona varians* (Duchassaing and Michelotti 1864)

Fig. 4 Collection sites of *Calcinus tibicen* (Herbst 1791) along the Northeastern and Eastern ecoregions of Brazil. (a) Três Coqueiros beach, Maraú, Bahia (b) with diverse specimens of *C. tibicen* eon rocky bottom from an intertidal pool. (c) Rocky coast in Milagres beach, Olivença, Ilhéus, Bahia and (d) shells options for the occupation by *C. tibicen*. (e) Sirihyba beach, Olivença, Ilhéus, Bahia (f) showing several individuals of *C. tibicen* on rocky bottom. (g) Coroa Vermelha beach, Santa Cruz de Cabrália, Bahia, (f) *C. tibicen* camouflaged on a bleaching coral (*Siderastrea stellata* Verrill 1868)

3.1 Geographic distribution

The compilation of primary and secondary data showed a total of 1308 geographic occurrences of *Calcinus tibicen* throughout the Western Atlantic. This total encompassed 810 occurrences listed in GBIF, 396 and 44 records in the specialized literature and SpeciesLink, respectively, as well as 57 primary occurrences (Fig. 5). The results based on the systematic bibliographic review (SBR) showed a total of 121 valid occurrence data for the orange-clawed hermit crab (supplementary material 1).

According to the present survey, we reported 497 novel records for *C. tibicen*, expanding the geographic occurrence of this species in the Western Atlantic, including new sites in Antigua and Barbuda, Bahamas, Belize, Brazil, Colombia, Cuba, Curaçao, United States, Guadeloupe, Honduras, US Virgin Islands, Jamaica, Mexico, Panama, Puerto Rico, Trinidad and Tobago, and Venezuela. In addition, we reported, for the first time, localities with valid geographic coordinates for the occurrence of *C. tibicen* in Anguilla, Aruba, Bonaire, San Eustatius and Saba, Dominica, Haiti, Cayman Islands, British Virgin Islands, Martinique, Dominican Republic, Saint Barthélemy, Saint Kitts and Nevis, Saint Martin, and Saint Vincent and the Grenadines (Fig. 5).

Fig. 5 Geographic distribution of *Calcinus tibicen* (Herbst 1791). (a) Occurrence range of this species along the Western Atlantic. Details about the records of *C. tibicen* in (b) Northern Atlantic and (c) South Atlantic

The number of valid records for the distribution of *C. tibicen* was higher in the North Atlantic, totaling 964 occurrences, being 417 new records. The distribution of this species along this region ranges from the northern portion of Bermuda ecoregion (32°N), at the Bermuda island (Fort St. Catherine's Beach, 32°23'26.0"N 64°40'28.0"W), then to the Northern Gulf of Mexico, Southern Gulf of Mexico, Florida, Bahamas and Greater Antilles ecoregions and along the Western Caribbean, Southwestern Caribbean, Southern Caribbean up to the northern part (referred to as Toco) of Trinidad and Tobago in the Eastern Caribbean ecoregion (10°50'00.7"N 60°56'54.3"W). No records related to the occurrence of *C. tibicen* are available for the Guiana and Amazon ecoregions.

Along the South Atlantic, the distribution this species extends from the Northeastern ecoregion in Brazil, along the state of Ceará (Mundaú beach, Trairi, 3°10'56.1"S 39°22'02.4"W) and several Brazilian ecoregions (Fernando de Noronha and Rocas Atoll, Trindade and Martin Vaz Islands, Eastern Brazil) up to Southeastern Brazil ecoregion (Armação beach, Florianópolis, state of Santa Catarina, 27°45'00.7"S/48°30'11.6"W).

A total of 342 occurrences, including 80 new records, were reported for *C. tibicen* along the South Atlantic coast, being most records observed in the Northeastern ecoregion (129), followed by Southeastern (82), Eastern (75), Martin Vaz and Trindade (52), and Fernando de Noronha and Rocas Atoll (4) ecoregions. In addition, we included 50 and 25 novel records for the Northeastern and Eastern Brazil ecoregions, respectively. The state of São Paulo showed the highest number of occurrences of this species (60), being followed by Pernambuco (48), Bahia (43), Espírito Santo (26), and Ceará (21). No records of *C. tibicen* were observed along the coastal region in the state of Paraná. The species was also not found during our sampling efforts at the following sites: Coqueiro (2°52'55.2”S 41°38'16.5”W) and Carnaubinha (2°54'03.9”S 41°29'37.2”W) beaches in the municipality of Luís Correa, Piauí; Farol do Trapiá beach in the municipality of Camocim, Ceará (2°51’43.2”S 40°51’44.3”W); Ponta da Areia beach in the municipality of São Luís, Maranhão (2°29’16.3”S 44°18’29.0”W); and Farol Velho beach in the municipality of Salinópolis, Pará (0°35’37.7”S 47°19’24.3”W).

The habitats occupied by *C. tibicen* varied considerably along the Northeastern and Eastern ecoregions of Brazil, being more frequently associated with rocky bottoms (Fig. 2b, d,f e 4b, d,f). Furthermore, several associations were observed in their microhabitats, particularly related to corals and zoanthids (*Palythoa caribaeorum* Duchassaing and Michelotti 1860 and *Zoanthus sociatus* Ellis 1768), sponges like *Cliona varians* (Duchassaing and Michelotti 1864), barnacles (*Chthamalus* sp.), and a remarkable diversity of macroalgae. For the first time, we also reported new associations with other groups, including mussels (*Brachidontes exustus* Linnaeus 1758) and anemones (*Actinia equina* Linnaeus 1758, and *Bunodosoma cangicum* Belém and Preslercravo 1973).

3.2 Occupied shells and associated epibionts

This study represents the most comprehensive and intensive sampling effort ever reported for *C. tibicen* along the South Atlantic coast to date. In total, 1,518 orange-clawed hermit crabs and occupied shells were collected, including records of shells from 28 species being occupied by *C. tibicen* throughout the Northeastern and Eastern ecoregions of Brazil. The shells of *Stramonita rustica* were the most occupied ones (551), being followed by *Gemophos auritulus* (405), *Agathistoma viridulum* (119), *Lithopoma tectum* (85), *Leucozonia nassa* (58), *Leucozonia ocellata* (41), *Pisania pusio* (41), *Gemophos ringens* (32), *Vasula deltoidea* (35), *Cerithium atratum* (29), *Stramonita haemastoma* (29), *Vasula melones* (22), *Astralium latispina* (16), and *Monoplex pilearis* (11). The least occupied shells referred to the following species: *Columbella mercatoria* (7), *Leucozonia ponderosa* (5), *Monoplex aquatilis* (4), *Anachis lyrata* (4), *Hastula cinerea* (5), *Polinices uberinus* (4), *Alanbeuella corrugata* (4), *Coralliophila aberrans* (3), *Pugilina morio* (3), *Dulcerana cubaniana* (1), *Colubraria obscura* (1), *Conus archetypus* (1), *Claremontiella nodulosa* (1),

Favartia nuceus (1), and *Phyllonotus oculatus* (1). Among the abovementioned species, the occupation of shells from *A. lyrata*, *C. obscura*, *C. archetypus*, *D. cubaniana*, *F. nuceus*, *G. ringens*, *H. cinerea*, *P. oculatus*, *P. morio*, and *V. melones* by *C. tibicen* represent new records.

All shells exhibited dextrorotatory rotation (right-handed rotation), with females (ovigerous and non-ovigerous) occupying a higher number of shells of *C. atratum*, *H. cinerea*, *L. nassa*, *L. ocellata*, *L. tectum*, *G. auritulus*, *G. ringens*, and *P. angulata*. The males occupied the remaining shell species described earlier, accounting for the largest number of occupied shell species.

During the sampling expeditions, we described seven epibionts on the shells occupied by *C. tibicen*, particularly represented by several bryozoans (Fig. 6a, b, e) and polychaeta tubes (Fig. 6c, e) found at most of the beach sites. In particular, live polychaeta were found inhabiting a few shells at Tivoli and Pituba beaches (Fig. 6e). In addition, three bivalves were found occupying shells of *Leucozonia nassa* (Tivoli Beach, Bahia) and *Agathistoma viridulum* (Carneiros Beach, Pernambuco) (Fig. 6f). A single Polyplacophora was recorded occupying the umbilicus region in the shells of *A. viridulum* at Pituba beach in Salvador (Fig. 6c, d). An anemone was recorded occupying a shell of *Lithopoma tectum* at the Tivoli beach, Bahia (Fig. 6a, b). In Alagoas, two collected shells were covered by green and red algae at the Ponta Verde Beach (Fig. 6g, h). Calcareous algae and barnacles were recorded on shells at Porto de Galinhas beach, Pernambuco, and at Costa Azul beach in Anchieta, Espírito Santo. (Fig. 6h).

Fig. 6 Epibionts present in occupied shells by the orange-clawed hermit crab *Calcinus tibicen.* (a, b) Anemone and bryozoan colony associated with the shell of *Lithopoma tectum* (Lightfoot, 1786). (c, d) Polyplacophora found in the umbilicus of the shell of *Agathistoma viridulum* (Gmelin 1791). (e) Polychaeta tube with live specimen and bryozoan present in the siphonal canal of *Leucozonia nassa* (Gmelin 1791). (f) Bivalve found in the umbilicus of the shell of *A. viridulum*. (g) *In vivo* green and red macroalgae associated with shells of *L. tectum* occupied by *C. tibicen*. (h) *In vivo* calcareous alga growing on a shell occupied by *C. tibicen*. Scales: a, b = 1 cm; c, d = 1 mm; f = 1 mm

4. Discussion

4.1 Geographic distribution and habitat

The present results fill several gaps about the distribution range of *Calcinus tibicen* by adding new occurrence records that confirm the wide distribution of the orange-clawed hermit crab in the Western Atlantic, comprising two disjunct regions (North and South Atlantic). As pointed out by previous reports (Melo 1999; Nucci and Melo 2015), we support the evidence that this species is not present in Guiana and Amazon ecoregions. Three species of *Calcinus* are recorded along the Western Atlantic - *C. tibicen*, *C. urabaensis* Campos and Lemaitre, 1994, and *C. verrilli* (Rathbun 1901), an endemic species from Bermuda (Campos and Lemaitre 1994; Malay and Paulay 2010; Nucci and Melo 2015). Based on our inventory, *C. tibicen* stands out as the most studied, diversified and widespread species, representing the only taxon in this genus found in South Western Atlantic coast.

The only record of sampling efforts in the Guiana ecoregion refers to the expedition carried out by the “Calypso” cruise in the 1960s. During their expedition along North and South Atlantic, Forest and de Saint Laurent (1967) had no records of *C. tibicen* for Suriname, but reported the occurrence of this species only for the localities of ‘Recife’ and ‘Piedade’ (Pernambuco, Brazil) and ‘Abrolhos’ (Bahia, Brazil) in Northeastern and Eastern Brazil ecoregions. Over recent field collection efforts carried out by the authors of the present study since 2020, no records of *C. tibicen* were obtained at the northern limits of the Northeastern Brazil ecoregion (Farol do Trapiá beach in the municipality of Camocim, Ceará and Coqueiro and Carnaubinha beaches in Piauí). Similarly, no specimens of *C. tibicen* were observed in areas of the Amazon ecoregion after sampling efforts in Ponta da Areia beach (municipality of São Luís, Maranhão) and Farol Velho beach (municipality of Salinópolis, Pará).

The wide distribution of *Calcinus* species is largely influenced by oceanic conditions associated with historical events and their ecological traits and dispersal abilities (Malay and Paulay 2009). In the case of *C. tibicen*, the lack of records in the Guiana and Amazon ecoregions corroborates the idea that the estuarine region of the Amazon River and the forces imposed by both Brazilian and Equatorial currents might act as barriers to the gene flow between populations from the North and South Atlantic, as proposed by Mandai et al. (2018b). Furthermore, the presence of suitable substrates is one of the main conditions for the successful larval settlement of benthic organisms (Woodin 1991). In fact, the coastal regions in the Guianas and the state of Amapá in the Amazon region are predominantly dominated by mudflats formed by the sedimentary outflow of the Amazon River (Anthony et al. 2013). Therefore, the absence of intertidal substrates for settling the larvae of *C. tibicen* should hinder the recruitment of the species along these areas.

Accordingly, the dispersal of Paguroidea is directly related to their larval phase since, after hatching, swimming planktonic zoea larvae would migrate up to their development into glaucothoe (or megalopa) (McLaughlin et al. 2010; Harvey et al. 2014). Upon finding a suitable substratum, the specimens of *C. tibicen* undergo metamorphosis, reaching the juvenile stage (Woodin 1991). The subsequent development stages would be then driven by the availability of shells in their habitats (Kremling and Zschummel 2021; Sharma 2024). Under laboratory conditions, *C. tibicen* goes through six to eight larval stages within a period of 32 to 40 days, with optimized survival and growth rates at temperatures of 26° to 30°C and salinity levels between 31 and 35 ppt (Provenzano 1962). The extended larval period reported for *C. tibicen* ensures that this species might reach long dispersal distances (Mandai et al. 2018b) that could explain the presence of the orange-clawed hermit crab on several coastal and oceanic islands along the Western Atlantic (Fig. 5). On the other hand, Costa et al. (2011) highlighted that the presence of decapod larvae in the Amazon region is directly associated with their tolerance to salinity variations. In South Atlantic, Almeida et al. (2010) revealed that *C. tibicen* tolerates a salinity range from 35 to 41 ppt. Thus, we infer that the extreme variation in the salinity along the Amazon ecoregion caused by the Amazonas plume could also account for the lack of *C. tibicen* along this region.

In addition, the wide dispersal of the orange-clawed hermit crab should also be favored by their abilities in occupying a wide range of microhabitats. In this study, we reported specimens of *C. tibicen* inhabiting

both rocky substrates and sandy bottoms in tide pools, as well as associations with other organisms, including anemones, barnacles, corals, sponges, zoanthids, and a wide diversity of brown, green, and red algae. Nonetheless, most of the specific studies in *C. tibicen* indicate a preference of the species for rocky shores (Provenzano Jr. 1961; Narchi and Hebling 1972; Hazlett 1984b; Campos and Lemaitre 1994; Rieger and Giraldi 1997; Fransozo and Mantelatto 1998; Mantelatto and Garcia 1999; Mantelatto and Garcia 2000; Garcia and Mantelatto 2001; Mantelatto and Garcia 2002; Fransozo et al. 2003; Batista-Leite et al. 2005; Hernández-Ávila 2007; Amadio and Mantelatto 2009; Quirós et al. 2012; García and Capote 2015; De la Cruz-Francisco et al. 2017; Ribeiro et al. 2019; Silva et al. 2020; Giraldes et al. 2021; Santos et al. 2021; Moraes et al. 2022; Ribeiro et al. 2023; present study). Even though, other authors such as Brown and Edmunds (2013) reported that this species is able to live in commensal and facultative association with fire corals (*Millepora* spp.) in St. John, US Virgin Islands. Similarly, a report carried out in Mexico by González-Gómez et al. (2018) showed that *C. tibicen* inhabits different substrates, but showed a main preference for fragments of dead corals. In the present study, we recorded that *C. tibicen* was most frequently associated with zoanthids (*Palythoa caribaeorum* and *Zoanthus sociatus*), corals (*Favia gravida* and *Siderastrea stellate*), and the sponge *Cliona varians*. Less frequently, we recorded associations with anemones (*Actinia equina* and *Bunodosoma cangicum*), barnacles (*Chthamalus* sp.) and mussels (*Brachidontes exustus* Linnaeus 1758). It should be pointed out that these associations are herein reported for the first time in *C. tibicen* along the South Atlantic.

Moreover, previous reports showed a close relationship between *C. tibicen* and banks of *Thalassia testudinum* (K. D. Koenig 1805) (Aguirre-Aguirre et al. 2007), and algae like *Halimeda* sp., *Sargassum* sp., and *Ulva* sp. (Campos 1995; Carvalho et al. 1998). In the present study, we added other species of macroalgae associated on the substrata occupied by *C. tibicen* along the Northeastern and Eastern ecoregions of Brazil. Similar studies have also revealed associations of the orange-clawed hermit crab with bryozoan colonies (Alves et al. 2013), sandstone formations, calcareous algae (Coelho-Santos and Coelho 1995), rocks (Bertness 1982), and tubes of the polychaete *Phragmatopoma caudata* Mörch 1863 (Lane-Medeiros et al. 2021). Among these, only the sandstone formations were characterized by the occurrence of *C. tibicen* in the present study. Even though *C. tibicen* seems to prefer rocky shore habitats, it can inhabit different environmental substrata in association with different organisms if resources are available.

According to the present data, the distribution range of *C. tibicen* in South Atlantic begins at the Mundaú beach, municipality of Trairi, Ceará, Northeastern Brazil (Matthews-Cascon 2006; Mandai et al. 2018b) extending southwards to the Armação beach, Florianópolis, Santa Catarina, Southern Brazil (Lima et al. 2019). We observed a low number of orange-clawed hermit crabs at the distribution limits in the Northeastern and Southeastern ecoregions of Brazil. This result suggests that the northwards distribution of this species in the coast of the state of Ceará should be also influenced by the environmental conditions from the Amazon ecoregion (Mandai et al. 2018b). In the case of the southern limits in Santa Catarina, their low abundance would be related to the typical cold water of this ecoregion, often below the range tolerated by larvae of *C. tibicen* (see Provenzano 1962), demonstrating a tolerance limit of the species to low temperatures at the boundary of this ecoregion.

It should be pointed out that gaps in the geographic distribution of *C. tibicen* still remain in spite of the intensive efforts in gathering primary and secondary data carried out in this study. We believe that the distribution gaps between the states of Ceará and Rio Grande do Norte (approximately 455 km), as well as the lack of records along the coast of Paraná (25°19'S to 25°58'S) are not necessarily a true indicator of the absence of this species across these areas. As a matter of fact, few studies about the diversity of decapods (especially Anomura) are available for Rio Grande do Norte and Ceará, except for recent reports published over the last decade (e.g. Alencar et al. 2014; Ribeiro et al. 2016, 2019; Lane-Medeiros et al. 2021, Ribeiro et al. 2023; Rocha-Gomes et al. 2024). Likewise, studies focused on hermit crabs in the coast of Paraná are scarce, being limited to records of *Clibanarius symmetricus* Randall, 1840, *Clibanarius vittatus* Bosc, 1801, and *Isocheles sawayai* Forest and de Saint Laurent 1968 (Masunari and Dubiaski-Silva 1998; Masunari et al. 2008; Sampaio et al. 2009; Sampaio and Masunari 2010; Negri et al. 2014). Even though *C. tibicen* has been reported in sympatric conditions with *C. tricolor* and *C. vittatus* in other sites across the Western Atlantic (Provenzano Jr. 1960; Fotheringham 1980; Souza and Serejo 2007; Lima et al. 2019; Grangeiro et al. 2024), no reports about the occurrence of the orange-clawed hermit crab in Paraná are available so far. Thus, detailed reports about the distribution of specific taxa, as presently performed, become particularly useful to our understanding about the biogeographic patterns, habitat delimitations, and biotic and abiotic interactions of species (Alencar et al. 2023). In addition, continuous revisions of species ranges are essential to provide updated information about their distribution and sites of occurrence at broad spatial scale.

4.2 Occupied shells and association with epibionts

We revealed that *Calcinus tibicen* is able to occupy a wide variety of gastropod shells according to the availability of these resources in the environments across the Northeastern and Eastern ecoregions of Brazil. The occupied shells by the orange-clawed hermit crab previously identified along these ecoregions included the following species: *Agathistoma viridulum*, *Alanbeuella corrugata*, *Aurantilaria aurantiaca*, *Bulla striata, Cerithium atratum*, *Columbella mercatoria*, *Gemophos auritulus*, *Leocozonia nassa*, *Leucozonia ocellata*, *Lithopoma tectum*, *Macrocypraea zebra*, *Monoplex pilearis*, *Pisania pusio*, *Polinices hepaticus*, *Stramonita brasiliensis*, *Stramonita haemastoma*, *Stramonita rustica*, *Turbinella laevigata* and *Vasula deltoidea* (Batista-Leite et al. 2005; Ribeiro et al. 2016; Santos et al. 2021). In the southeastern region, *C. tibicen* has been recorded occupying shells of *Agathistoma viridulum*, *Astralium latispina*, *Cerithium atratum*, *Claremontiella nodulosa*, *Gemophos auritulus*, *Leucozonia nassa*, *Lithopoma phoebium*, *Lithopoma tectum*, *Olivancillaria deshayesiana*, *Pisania pusio*, *Polinices hepaticus*, *Stramonita brasiliensis*, and *Stramonita haemastoma* (Floeter et al. 2000; Mantelatto and Garcia 1999, 2000; Garcia and Mantelatto 2001; Turra and Leite 2001; Ribeiro et al. 2016; Lima et al. 2018). Therefore, we recorded, for the first time, specimens of *C. tibicen* using shells of *A. lyrata*, *C. obscura*, *C. archetypus*, *D. cubaniana*, *F. nuceus*, *G. ringens*, *H. cinerea*, *P. oculatus*, *P. morio*, and *V. melones* in the Northeastern and Eastern ecoregions of Brazil.

Some reports have shown that the choice of shells to be occupied by *C. tibicen* is generally related to their weight and internal volume (Floeter et al. 2000; Garcia and Mantelatto 2001; Batista-Leite et al. 2005). A study carried out by Batista-Leite et al. (2005) in the coast of Paripueira, state of Alagoas, Northeastern ecoregion, reported that shells of *L. tectum* were the most used ones by *C. tibicen*, while Ribeiro et al. (2016) indicated *A. viridulum* as the most occupied shell by hermit crabs. As for the Eastern ecoregion, Santos et al. (2021) reported a higher frequency of occupied shells from the species *G. auritulus*, *S. rustica*, and *A. viridulum*, following the pattern reported in the present study. Similarly, most of ovigerous females were found occupying shells of *G. auritulus*. The less frequent records of occupied shells by *C. tibicen* referred to *A. corrugata*, *A. lyrata*, *C. nodulosa*, *Colubraria obscura*, *C. mercatoria*, *C. archetypus*, *C. aberrans*, *D. cubaniana*, *F. nuceus*, *H. cinerea*, *L. ponderosa*, *M. aquatilis*, *P. oculatus*, *P. uberinus*, and *P. morio*. These results rather suggest the sporadic availability of these resources and should not be regarded as reliable evidence of species-specific preferences.

The diversity of shells occupied by *C. tibicen* also resulted in a significant diversity of associated epibionts (Fig. 6). A total of six distinct types of epibionts and two commensal groups were found in association with the shells occupied by *C. tibicen* in the Northeastern and Eastern ecoregions of Brazil. The calcified bryozoans and polychaeta tubes (without living individuals) were the most frequent epibionts, being recorded on all beaches collected in Ceará, Bahia, and Pernambuco. Live polychaeta were found at Forte and Pituba beaches on the coast of Bahia. In the latter, we also recorded Polyplacophora near the opening of a shell of *A. viridulum shell*. Moreover, bivalves were also found both inside and outside the occupied shells at Carneiros beach in Pernambuco and Tivoli beach in Bahia. Another highlight was the presence of an anemone occupying the upper part of an occupied shell of *L. tectum* at Tivoli beach (Fig. 6e). At Ponta Verde beach in Alagoas, green and red macroalgae were observed covering the shells occupied by *C. tibicen*. Finally, calcareous algae and barnacles were also recorded on some of the occupied shells at Porto de Galinhas beach in Pernambuco and Costa Azul beach in Anchieta, state of Espírito Santo.

In spite of the size variation of the bryozoan colonies identified in this study, they were relatively small in relation to the occupied shells, being present at different regions from practically all of the sampled shells. Similar records were reported by Ribeiro et al. (2016) who observed that bryozoans were among the most frequent epibionts found in shells occupied by *C. tibicen* at the beaches of Pedra Rachada, Paracuru (Northeastern) and Araçá, São Sebastião, São Paulo (Southeastern). These epibionts are colonial and sessile organisms (Vieira et al. 2015) commonly found encrusted on the shells of bivalves and gastropods (Taylor et al. 1989). Therefore, the shells occupied by hermit crabs are attractive to several species of bryozoans, with records of associations from the intertidal zone to deeper regions along both tropical and temperate regions (Taylor 1994). These epibionts appear to have no negative effects on hermit crabs (Sigwart 2009). Actually, they might contribute to their camouflage and protection against predators (Taylor 1994), indicating a mutualistic relationship between these organisms. However, their presence can increase the weight of the occupied shells and, in some cases, the presence of epibionts in the inner region might restrain the area available for the occupancy by the hermit crabs (Fontoura-da-Silva et al. 2011; Ribeiro et al. 2016).

The second most frequent group of epibionts were the polychaeta tubes, also recorded at all beaches and in practically all species and over different regions of the shells, including the inner region occasionally. Ribeiro et al. (2016) also reported polychaeta tubes in shells occupied by *C. tibicen*, but in lower frequencies when compared to the present study. According to Stachowit (1980), the presence of filter feeders associated with hermit crabs would be advantageous for their feeding, since the polychaeta would benefit from food debris that could be transported by the movement of their antennae. As proposed for bryozoans, the relationship between polychaeta tubes and occupied shells by the hermit crabs characterizes a mutualistic association, since it improves the camouflage and protection of these crustaceans against predators, while the number of food resources and the mobility of polychaeta would be increased. In turn, this association might lead to increased weight of shells and reduce the space inside the shells when present at inner shells parts (Creed 2000; Fontoura-da-Silva et al. 2011).

A total of three bivalve mollusks were found inhabiting the occupied shells of *Leucozonia nassa* Gmelin, 1791 (Tivoli beach, Bahia) and *Agathistoma viridulum* Gmelin, 1791 (Carneiros beach, Pernambuco) in the Northeastern Brazil. The individuals occupying *L. nassa* were found in the inner part of the shells, next to *C. tibicen* and close to the siphonal canal. In *A. viridulum*, the bivalve was present in the umbilicus region near the shell opening (Fig. 6f) at the same locality where Polyplacophora were found (Fig. 6c, d). The location and the species of shells with presence of mollusks are the same reported by Fontoura-da-Silva et al. (2011) and Ribeiro et al. (2016). According to Ribeiro et al. (2016), the presence of bivalves in shells occupied by hermit crabs would represent accidental associations. Nevertheless, other studies have recorded several cases of bivalves inhabiting shells occupied by hermit crabs (see Williams and McDermott 2004), suggesting an advantage for the locomotion of the former. In addition, Alvarez-Cerrillo et al. (2017) reported the presence of juvenile bivalves using valves of the chiton *Chiton articulatus* G. B. Sowerby I, 1832 as a probable temporary refuge in Mexico. Similarly, the bivalves found in the present study also appear to be in their juvenile stage. Therefore, the frequency of bivalves found in occupied shells could characterize a commensal relationship between these mollusks at early life stages and *C. tibicen* along the Northeastern ecoregion in Brazil. In this sense, the juvenile bivalves would benefit from the occupied shells for locomotion and as temporary refuge without apparent harmful effects on the hermit crabs, what remains to be confirmed by further studies.

Polyplacophorans or chitons are found from the intertidal zone to deep marine waters (Sigwart 2009). Along the intertidal zone, these organisms behave as sessile in relation to gastropods (Aguilar-Estrada et al. 2022). There are a few records of chitons as epibionts on occupied shells by hermit crabs in the specialized literature. Briffa and Elwood (2005) reported shells with few chitons of the species *Lepidochitona cinerea* (Linnaeus 1767) across the Irish Sea (United Kingdom) (Briffa and Elwood 2005). In Brazil, Fontoura-da-Silva et al. (2011) reported the presence of Polyplacophora as epibionts on shells of the gastropod *Agathistoma viridulum* (Gmelin 1791) on the coast of Rio de Janeiro (Flexeiras beach, Itacuruçá), the same gastropod species found in the present study. However, both reports recorded the occurrence of chitons on shells of live gastropods, Instead, the present study reported the presence of Polyplacophora associated with an occupied shell by *Calcinus tibicen* in Eastern Brazil ecoregion for the first time. The lower frequency of these chitons on gastropod shells may be related to their locomotion

abilities (Fontoura-da-Silva et al. 2011). Accordingly, the presence of these organisms on shells indicate a strategic behavior for optimizing their movement across the intertidal environment favored by the mobility provided by hermit crabs. Inasmuch as this strategy seems to provide no clear benefits to the hermit crabs, this association could be characterized as a particular type of commensalism referred to as inquilinism.

A single anemone was recorded occupying a shell of *L. tectum* at Tivoli beach. To date, the only similar record of this association was reported for *Calcinus vachoni* Forest, 1958 co-occurring with a colony of *Palythoa* aff. *mutuki* Haddon and Shackleton, 1891 on Jeju Island, South Korea (Jung and Park 2023). But, differently from the study by Jung and Park (2023), we provided the first official evidence of an anemone on a shell occupied by *C. tibicen*, representing an unprecedented record for this mutualistic association in the genus *Calcinus* Dana 1851. These cnidarians are recognized by the protection they offer through their nematocysts against the predation of the crabs. Furthermore, while the anemones enhance the camouflage of the crabs in the environment, the crustaceans serve as a mobile substrate to the anemones, thus favoring their foraging activities (Ross 1971; Stachowit 1980; Karplus 2024). On the other hand, the weight of the occupied shells is increased by the presence of these epibionts. However, it is not clear whether this association refers to a random event or a true mutualistic relationship between both organisms in the studied locality.

The green and red algae encrusted on shells occupied by *C. tibicen* in Alagoas (Ponta Verde beach) may indicate a camouflage strategy of the species in this environment. Ribeiro et al. (2016) reported algae as the most frequent ectosymbionts on shells occupied by *C. tibicen*. These authors also reported the presence of calcareous algae and barnacles in occupied shells that could be advantageous to both camouflage and feeding of hermit crabs. As for the algae, a mobile substrate could favor the dispersal of thalli and reproductive structures (Aguilar-Estrada et al. 2022), thus characterizing a mutualistic association. In the North Atlantic, Hazlett (1984b) reported that *C. tibicen* are able to choose shells that resemble the bottom environment through a passive growth process of epibionts on shells. If this is a camouflage strategy also present in *C. tibicen* remains an open question, even though the occupied shells observed in Coroa Vermelha, Bahia clearly resembled their local environment (Fig. 2h).

Even though isolated associations do not necessarily imply in the interaction between two living species (Britayev et al. 2020), our report demonstrates a possible complex network of interactions between distinct intertidal groups and *C. tibicen*. The associations between *C. tibicen* and the epibionts herein described indicate a trade-off. Among the benefits for the epibionts, the occupied shells can provide a solid substrate away from the sediment and scraping predators (Stachowit, 1980), besides improving their mobility through the environment and food intake (Karplus 2024). For hermit crabs, these interactions would provide better camouflage and protection against predators (Ross 1971; Stachowit 1980; Creed 2000; Karplus 2024). Instead, the epibionts would intensify the energy load on the hermit crab since the weight of shells are increased (Creed 2000; Fontoura-da-Silva et al. 2011).

While the behavior of *C. tibicen* has been largely adressed in the North Atlantic region (e.g. Hazlett and Bossert 1965; Hazlett 1966a, b, 1980, 1983b, 1984b, 1987, 1989), most sutides in the South Atlantic refer to hermit crab-shell relationships (e.g. Floeter et al. 2000; Mantelatto and Garcia 2000; Garcia and Mantelatto 2001; Turra and Leite 2001; Bastista-Leite et al. 2005; Lima et al. 2018; Santos et al. 2021; Silva et al. 2023). The only exception is the study carried out by Ribeiro et al. (2016) focused on epibionts associated with the shells occupied by *C. tibicen* at the beaches of Pedra Rachada, Paracuru (Ceará) and Araçá, São Sebastião (São Paulo). Thus, our results expanded the information about the interactions between the orange-clawed hermit crab and inquiline organisms or epibionts along the Northeastern and Eastern ecoregions of Brazil. The present data reinforce the importance of further behavioral studies in species from these ecoregions in order to provide a better understanding of potentially complex interaction networks.

In conclusion, this study significantly increases the knowledge about the geographic distribution and ecology of *Calcinus tibicen* in the South Atlantic, filling important gaps and confirming the occurrence of the orange-clawed hermit crab from the coast of Ceará to Santa Catarina, comprising two non-continuous ranges in the Western Atlantic. The absence of records for this species in the Guiana and Amazon ecoregions reinforces the hypothesis of ecological barriers, such as substrate, salinity, and ocean currents, that separate the populations of *C. tibicen* between the North and South Atlantic. These findings provide insights about the biogeographic pattern of this hermit crab species, besides being helpful to design further collection efforts.

Furthermore, we reported new microhabitats occupied by *C. tibicen* and previously unknown ecological interactions, including associations with several epibionts and preliminary evidence of a potential relationship with anemones. These findings expand the information about the adaptive and dispersal traits of *C. tibicen*, such as the ability in mobilizing temporary tenants, placing the orange-clawed hermit crab as an active and dynamic component of intertidal communities.

Taken together, these data highlight that both local factors (e.g. availability of shells and microhabitat structure) and macroecological barriers have shaped the distribution range and the ecological features of *C. tibicen*. The integrative approach carried out in the present study provided a novel and updated overview of this hermit crab species. At last, we emphasize the importance of further studies focusing on its biotic and abiotic interactions at different geographic scales in order to improve the understanding about the ecology and conservation status of hermit crabs in the South Atlantic.

Declarations

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Figures

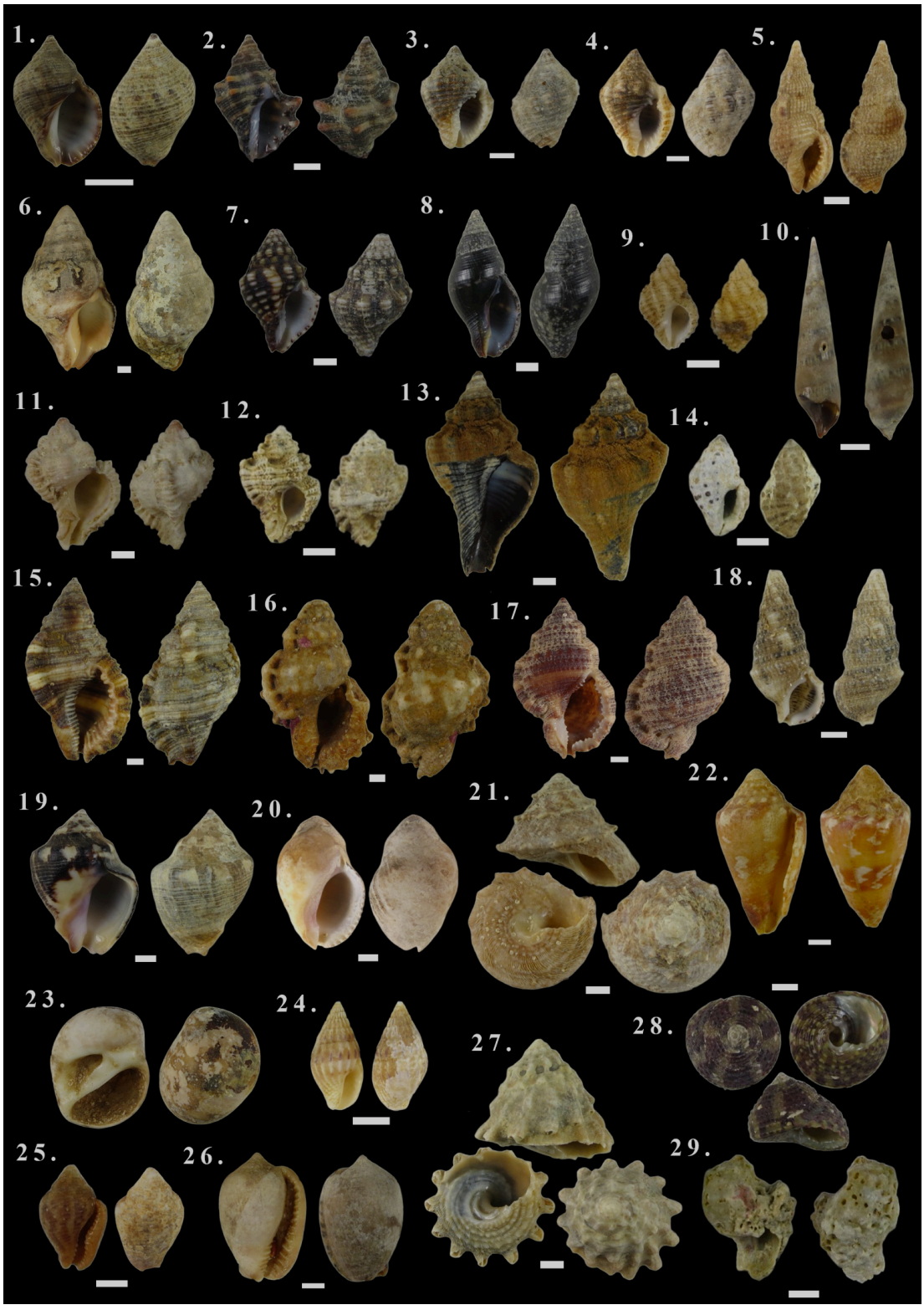


Figure 1

Gastropod shells and dead coral parts occupied by *Calcinus tibicen* (Herbst 1791) along the Northeastern and Eastern ecoregions in Brazil. (1) *Stramonita haemastoma* (Linnaeus 1767), (2) *Stramonita rustica* (Lamarck 1822), (3) *Gemophos auritulus* (Link 1807), (4) *Gemophos ringens* (Reeve 1846), (5) *Colubraria obscura* (Reeve 1844, (6) *Leucozonia nassa* (Gmelin 1791), (7) *Leucozonia ocellata* (Gmelin 1791), (8) *Pisania pusio* (Linnaeus 1758), (9) *Coralliophila aberrans* (Adams 1850), (10) *Hastula*

cinerea (Born 1778), (11) *Phyllonotus oculatus* (Reeve 1845), (12) *Favartia nuceus* (Mörch 1850), (13) *Pugilina morio* (Linnaeus 1758), (14) *Claremontiella nodulosa* (Adams 1845), (15) *Monoplex pilearis* (Linnaeus 1758), (16) *Alanbeuella corrugata* (Perry 1811), (17) *Dulcerana cubaniana* (D'Orbigny 1847), (18) *Cerithium atratum* (Born 1778), (19) *Vasula deltoidea* (Lamarck 1822), (20) *Vasula melones* (Duclos 1832), (21) *Astralium latispina* (Philippi 1844), (22) *Conus archetypus* Crosse 1865, (23) *Polinices uberinus* (D'Orbigny 1842), (24) *Anachis lyrate* (Sowerby I 1832), (25) *Columbella mercatoria* (Linnaeus 1758), (26) *Cypraecassis testiculus* (Linnaeus 1758), (27) *Lithopoma tectum* (Lightfoot 1786), (28) *Agathistoma viridulum* (Gmelin 1791), and (29) dead coral fragment. Scale bar = 5 mm



Figure 2

Collection sites of *Calcinus tibicen* (Herbst 1791) along the Northeastern ecoregion of Brazil. (a) Rocky coast with natural pools and (b) active collection of specimens at the Flexeiras beach, Trairi, Ceará. (c) Sandstone reef and (d) specimen of *C. tibicen* collected at the Pedra Rachada beach, Paracuru, Ceará. (e, f) Exposed rocky coast along the Carneiros beach, Tamandaré, Pernambuco. (g) Coast along the Porto de Galinhas beach, Ipojuca, Pernambuco, (h) highlighting the sandstone reef

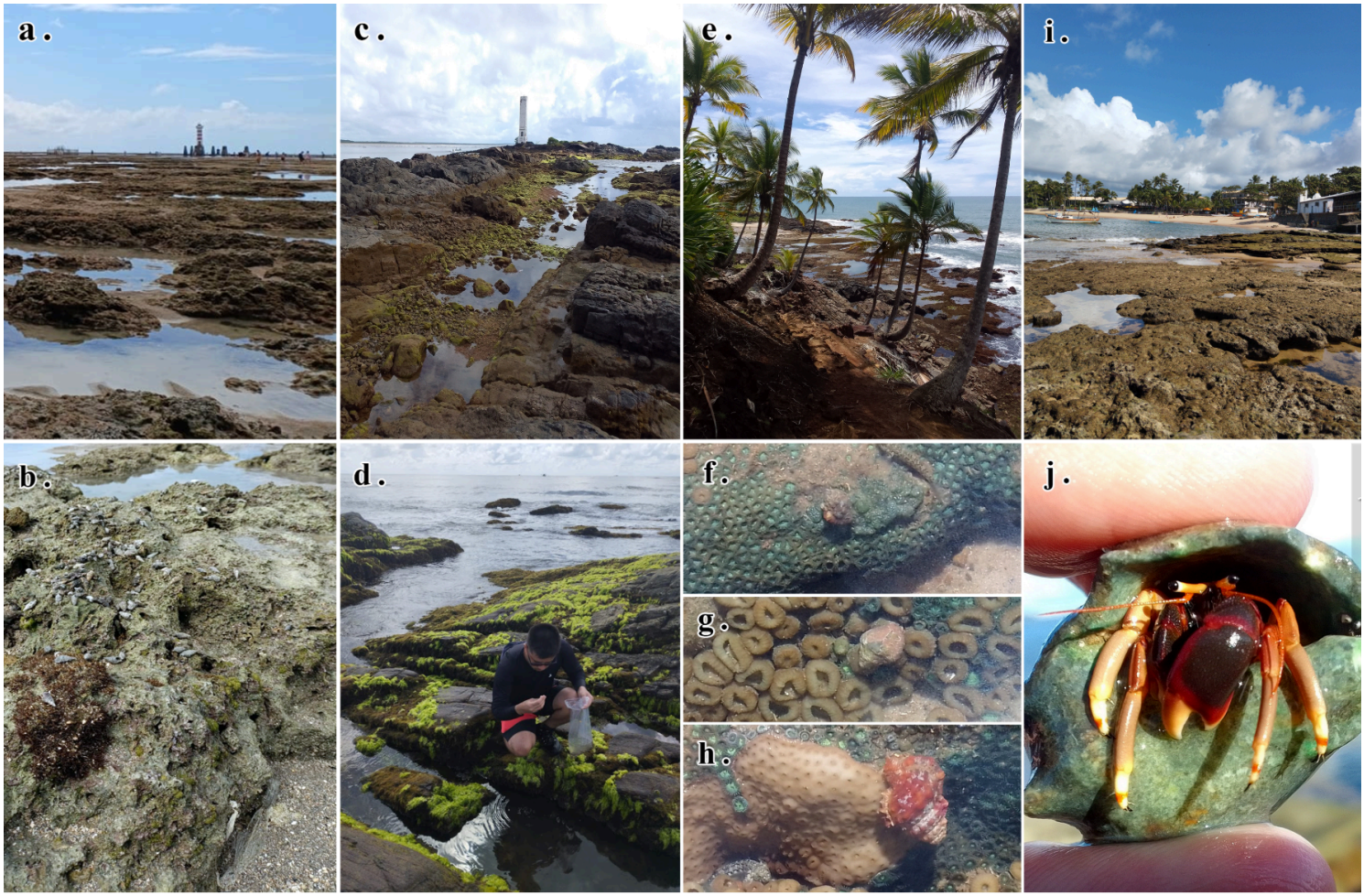


Figure 3

Collection sites of *Calcinus tibicen* (Herbst 1791) along the Northeastern and Eastern ecoregions of Brazil. (a, b) Rocky coast with sandy bottom in Ponta Verde beach, Maceió, Alagoas. (c) Forte beach, Mata de São João, (d) *C. tibicen* showing a reddish coloration right after collection. (e, f) Active search along the rocky coast in Concha beach, Itacaré, Bahia. (g) Arruda beach, Itacaré, (h) *C. tibicen* over the zoanthids *Palythoa caribaeorum* Duchassaing and Michelotti 1860 and (i) *zoanthus sociatus* (Ellis, 1768) and (j) sponges *Cliona varians* (Duchassaing and Michelotti 1864)

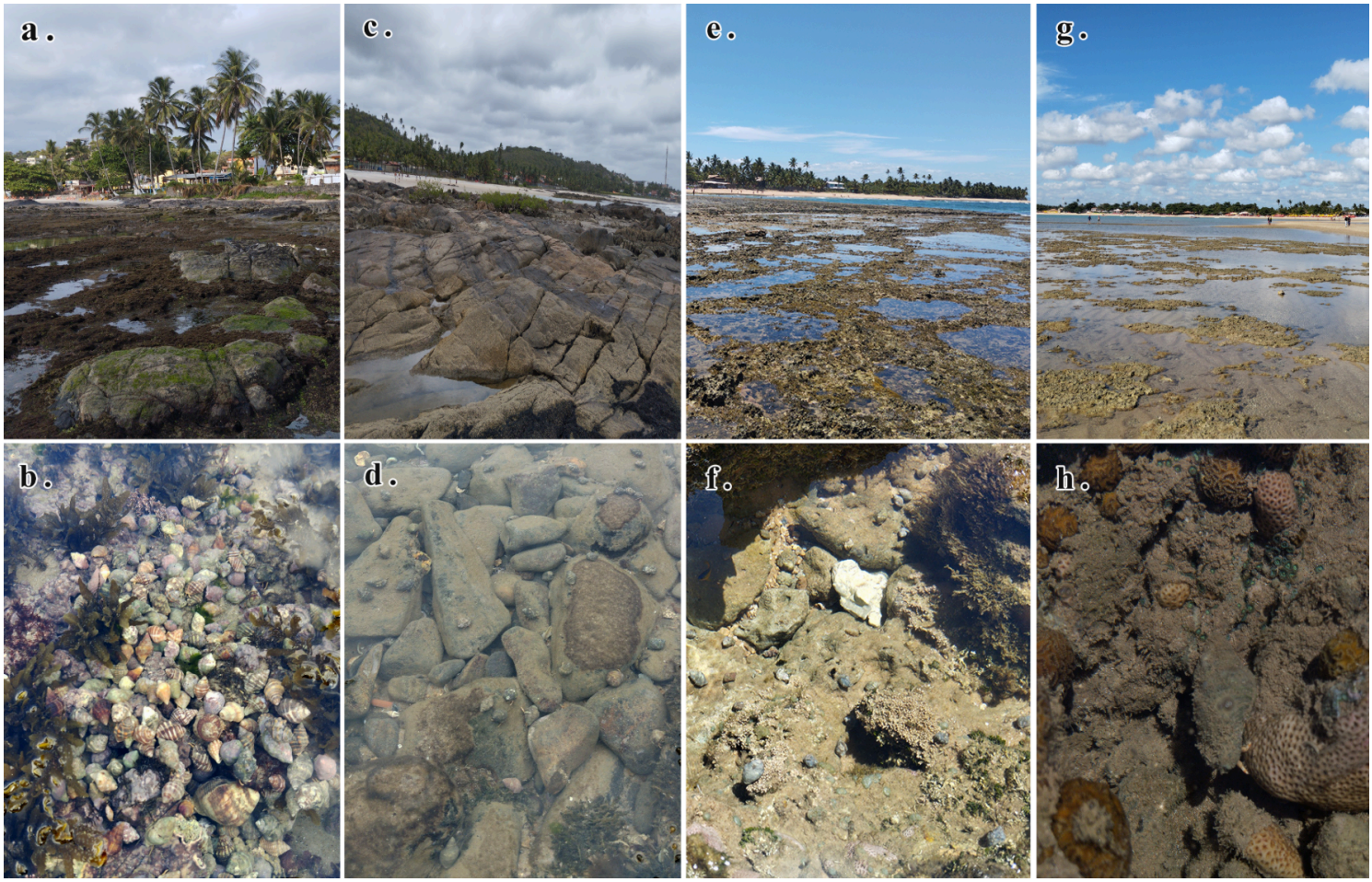


Figure 4

Collection sites of *Calcinus tibicen* (Herbst 1791) along the Northeastern and Eastern ecoregions of Brazil. (a) Três Coqueiros beach, Maraú, Bahia (b) with diverse specimens of *C. tibicen* eon rocky bottom from an intertidal pool. (c) Rocky coast in Milagres beach, Olivença, Ilhéus, Bahia and (d) shells options for the occupation by *C. tibicen*. (e) Sirihyba beach, Olivença, Ilhéus, Bahia (f) showing several individuals of *C. tibicen* on rocky bottom. (g) Coroa Vermelha beach, Santa Cruz de Cabrália, Bahia, (f) *C. tibicen* camouflaged on a bleaching coral (*Siderastrea stellata* Verrill 1868)

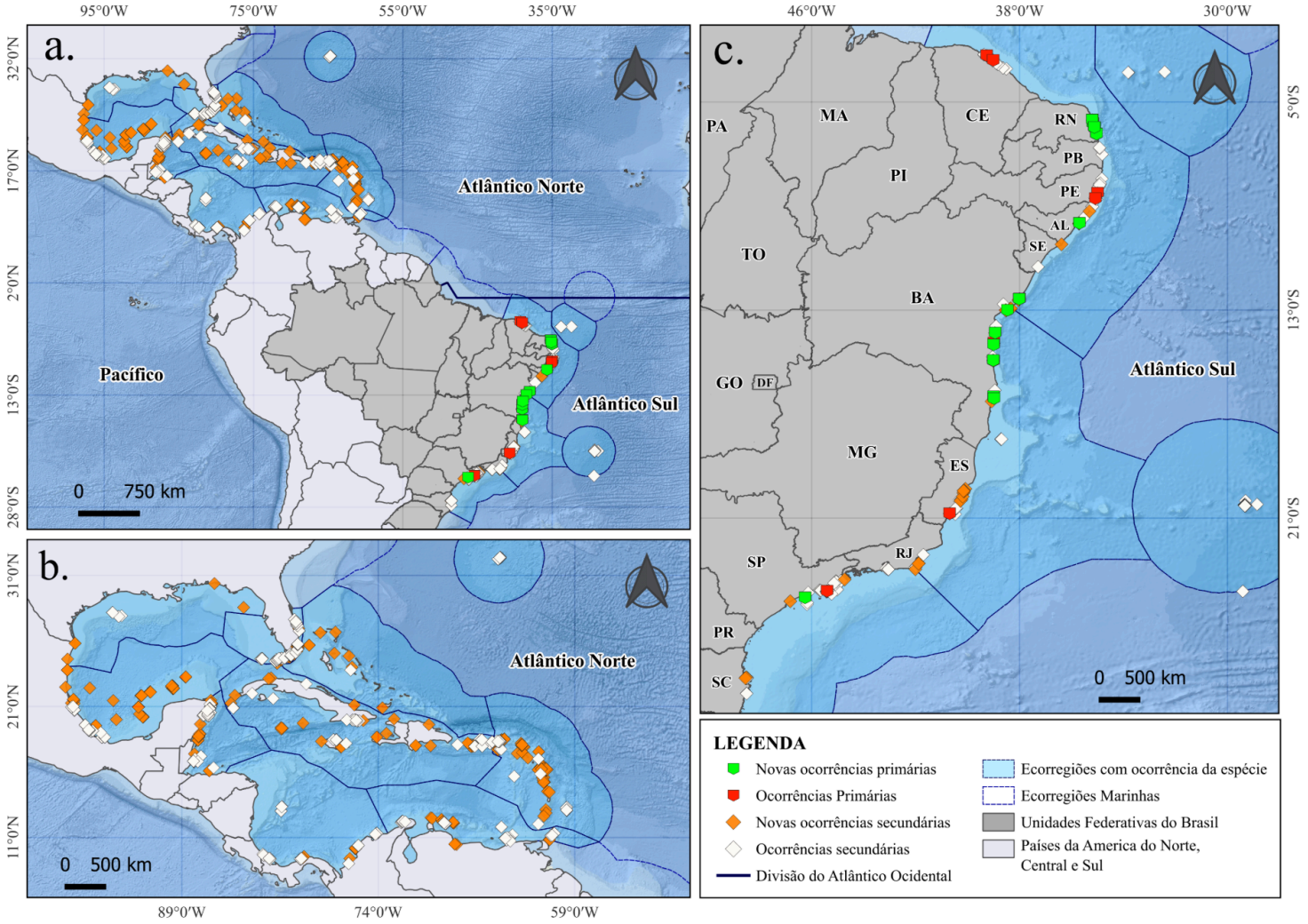


Figure 5

Geographic distribution of *Calcinus tibicen* (Herbst 1791). (a) Occurrence range of this species along the Western Atlantic. Details about the records of *C. tibicen* in (b) Northern Atlantic and (c) South Atlantic



Figure 6

Epibionts present in occupied shells by the orange-clawed hermit crab *Calcinus tibicen.* (a, b) Anemone and bryozoan colony associated with the shell of *Lithopoma tectum* (Lightfoot, 1786). (c, d) Polyplacophora found in the umbilicus of the shell of *Agathistoma viridulum* (Gmelin 1791). (e) Polychaeta tube with live specimen and bryozoan present in the siphonal canal of *Leucozonia nassa* (Gmelin 1791). (f) Bivalve found in the umbilicus of the shell of *A. viridulum*. (g) *In vivo* green and red macroalgae associated with shells of *L. tectum* occupied by *C. tibicen*. (h) *In vivo* calcareous alga growing on a shell occupied by *C. tibicen*. Scales: a, b = 1 cm; c, d = 1 mm; f = 1 mm

Supplementary Files

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- supplementarymaterial1.xlsx