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Ticks (Acari: Ixodidae) of three Timor-Leste reptiles: first country record of Amblyomma helvolum, with new interactions and an updated list of host species

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A R T I C L E   I N F O
Keywords:
Amblyomma helvolum
Carlia
Sphenomorphus
Coelognathus subradiatus
Outer Banda Arc

A B S T R A C T
We report on the presence of the ixodid tick Amblyomma helvolum on three species of reptiles from Timor-Leste. Among a total of 21 host specimens (lizards: 18 four-fingered skinks, Carla sp. ‘Meleotegi’ and two forest skinks, Sphenomorphus sp. ‘Meleotegi’; snake: one Coelognathus subradiatus) four were parasitized by ticks. Whereas nymphs were associated with the lizards, an adult male was retrieved from the snake. This report is the first of A. helvolum for Timor-Leste, the first for the skink genera Carla and Sphenomorphus, and the first for C. subradiatus. We present a comprehensive table with updated taxonomy of known associations between A. helvolum and other vertebrates.

1. Introduction
Timor-Leste, Asia’s newest country, is positioned at the south-central extreme of the Indonesian Archipelago, where it occupies the eastern half of Timor Island (Fig. 1). Timor-Leste’s territory is composed of four landmasses, including the eastern half of the island, where 12 of the country’s 13 municipalities lie, the Oecusse exclave surrounded by Indonesian West Timor, the coralligenic Jaco Island at its eastern end, all within the Outer Banda Arc, and Ataúro Island, the only portion of Timor-Leste that lies in the Inner Banda Arc. The country’s position at the southeastern extreme of the biogeographic province known as Wallacea places it at the crossroads of four interesting landmasses: Southeast Asia and the islands of the Sunda Shelf to the west, Australia to the south, Sahul Shelf islands and Melanesia to the east, and Sulawesi to the north, all of which appear to have some influence on the terrestrial fauna, including reptiles (Monk et al., 1997; O’Shea et al., 2015). An evaluation of parasite groups is therefore an important piece to the biogeographic puzzle that is the fauna of Timor.

During ten herpetofaunal surveys (Kaiser et al., 2011; O’Shea et al., 2012; Sanchez et al., 2012; Kaiser et al., 2013) HK and MOS and the members of the Tropical Research Initiative collected a variety of reptile species, some of which harbored ectoparasites, including ticks. In the following paragraphs, we detail the ixodid fauna recovered, report the first country record of Amblyomma helvolum Koch, 1844, and add some new host records for this species.

2. Materials and methods

2.1. Host survey

Lizard hosts were collected at two sites in close proximity to each other (Fig. 1) and covering an elevational range of 1150–1250 m. The first site is the Sta. Bakhita Mission in Eraúlo, Ermera Municipality (8.7811° S, 125.4438° E), where two species of four-fingered skinks (genus Carla) are sympatric (16S rRNA, CO1 mtDNA; Kaiser et al., unpubl. data). Two of the host specimens (USNM 579745, 581104), adult males collected on 5 February 2012 and 29 June 2013, respectively, are part of a north coast Timor population of Carla that reaches its highest elevations in central...
Fig. 1. Map of Timor-Leste with labelled localities where tick specimens were collected from three reptile species. The red dot indicates the collection site of four-fingered skinks (Carlia sp. “Meleotegi”) at the Santa Bakhita Mission, the yellow dot is the Meleotegi River collection site of Carlia sp. “Meleotegi” and forest skinks (Sphenomorphus sp. “Meleotegi”), and the pink dot is the locality where a freshly killed Lesser Sunda Racer (Coelognathus subradiatus) was found dead on the road. The white rectangle in the inset globe shows the position of Map A. Map A shows the Lesser Sunda Islands with two island arcs, Inner and Outer Banda Arc. The scale bar in the main map represents a distance of 100 km. Beneath the maps, habitats of the collected reptiles are illustrated with frame colors corresponding to the colors of the locality dots. Photos by Mark O’Shea.
Ermera Municipality. This is an undescribed species, hereafter referred to as *Carlia* sp. ‘Meleotegi’ (Fig. 2A). The first specimen was collected in the grounds of the mission among garden plants, whereas the second was caught along the Meleotegi River (8.7806° S, 125.4543° E), a rocky riverbed lined on both banks by agricultural plots, including coffee plantations. The second host, a member of an undescribed species of forest skink, genus *Sphenomorphus* (USNM 579765; Fig. 3A), was collected in the coffee forest on the western bank of the Meleotegi River on 5 February 2012. This specimen belongs to a high-elevation population apparently endemic to Ermera Municipality. It is not conspecific with *S. melanopogon*, a south coast low-elevation species (Shea, 2012; Justin Bernstein, pers. comm.), and this population is referred to hereafter as *Sphenomorphus* sp. ‘Meleotegi.’ The snake host (USNM 580544; Fig. 4A) is a freshly killed specimen of the Lesser Sunda Racer (*Coelognathus subradiatus*), found dead on a major north–south road near Lachubar, Manatuto Municipality (8.7765° S, 125.9653° E, elevation 870 m; Fig. 1) on 2 July 2012. Lizards were euthanized by injection with 5% procaine (Livezey, 1958) following standard animal care protocols (e.g., ASIH, 2004), fixed in 10% formalin, and stored in 70% ethanol. Animals were collected under the auspices of the Smithsonian Institution, Washington, D.C., U.S.A. with export permission from the Departamento de Protegidas e Parque Nacional, Direcção Nacional de Floresta, Secretario do Estado de Floresta no Konserwasan Natureza, Ministerio Agricultura e Pescas, Timor-Leste (permit nos. 26/DAPPN-DNF-MAP/1/2012, 22/DAPPN-DNF-MAP/VI/2012, 29/DAPPN-DNF-MAP/VI/2013) and import permission from the United States Fish and Wildlife Service (Forms 3-177, clearance nos. 2012SF1125818, 2012HN1197038, 2013SF1361984).

2.2. Photography

The live skinks and snake were photographed on sets built in a portable 19 cm x 90 cm x 90 cm Lastolite Cubelite photography dome using Canon EOS 7D camera bodies in combination with either a Canon EF-S 60 mm f2.8 USM macro lens or a Canon EF 100 mm f2.8L IS USM macro lens. Illumination was provided by Canon Macro Twin Lite MT-24EX flash units. The ticks were photographed in situ and ex situ using the same camera body with a Canon MP-E 64 mm f2.8 1-5x macro lens and a Canon Macro Twin Lite MT-24EX flash unit. This lens was pushed to 10x life size by the addition of a Canon EF 2x Extender. Figures were prepared on a Mac Pro computer running OS 10.12 Sierra and Adobe Photoshop CC 2014. Parasite images were cut out and placed on a black background using a Wacom Cintiq 13-inch HD Touch connected to an iMac Pro computer running OS 11.5 Big Sur and Adobe Photoshop 2021. The Timor-Leste map was adapted from a Shutterstock Schwa-benblitz 3D rendering, the world globe was prepared using Mountain High relief maps (http://www.mountainhighmap.com).

Fig. 2. An undescribed species of four-fingered skink, genus *Carlia*, from Timor-Leste and associated ticks. (A) An adult male *Carlia* sp. ‘Meleotegi’ with bright coloration indicating breeding readiness. (B) Engorged nymph of *Amblyomma helvolum* in a near-axillary position. (C) Another engorged nymph, showing the tick’s capitulum deeply embedded in between two ventral scales. (D) Two *A. helvolum* nymphs after detachment from their host in dorsal (right) and ventral (left) views. Photos by Mark O’Shea.
2.3. Tick identification

Each host specimen was examined for the presence of ectoparasites immediately after euthanasia. Ticks were removed from host bodies with forceps and preserved in 70% ethanol. The collected ticks were sent to the Department of Preventive Veterinary Medicine and Animal Health (VPS) of the School of Veterinary Medicine and Animal Science (FMVZ) at the University of São Paulo (USP), São Paulo, Brazil. For taxonomic

Fig. 3. An undescribed species of forest skink, genus Sphenomorphus, from Timor-Leste and an associated tick. (A) An adult Sphenomorphus sp. ‘Meleotegi’ of undetermined sex showing the characteristic lateral striping of the species. (B) Engorged nymph of Amblyomma helvolum in an axillary position. Photos by Mark O’Shea.

Fig. 4. (A) A dead Coelognathus subradiatus photographed in situ on one of the main north–south roads in Timor-Leste. It is noteworthy that this snake was not run over by a vehicle, it was instead noosed, beaten to death, and thrown into the road by a local resident. (B) An adult C. subradiatus (USNM 579240) from Timor-Leste in life. (C) Adult male Amblyomma helvolum photographed in situ while attached to the snake in (A). (D) Dorsal and ventral views in life of an adult male A. helvolum after detachment from the snake. The dorsal view (left) shows the dorsal colour and pore pattern on the strongly demarcated shield of this species. The ventral view of the same individual (right) shows anus, anal groove, genital aperture, and the laterally positioned spiracular plates. Photos by Mark O’Shea.
identification we used the reports of Anastos (1950), Robinson (1926), and Voltzit and Keirans (2002). Tick voucher specimens were deposited in the tick collection “Coleção Nacional de Carrapatos Danilo Gonçalves Saraiva” (CNC) of the FMVZ-USP, under accession numbers CNC 4205-4207.

2.4. Bibliographic review

A bibliographic search was conducted using Google Scholar to update the list of Simmons et al. (2002) of A. helvolum hosts. The search terms used were: “Amblyomma helvolum”, “amphibians”, “reptiles”, “lizards”, “snakes”, “turtles”, “birds”, and “mammals”. Old references cited by publications recovered by the primary bibliographic search were located using Biodiversity Heritage Library (https://www.biodiversitylibrary.org/), BioStor-Lite (http://biostor.org/), and Internet Archives (https://archive.org/). Scientific names of hosts were updated to current nomenclature following Uetz et al. (2021) (http://www.reptile-database.org/) for lizards and snakes, and GBIF.org (2020) Global Biodiversity Information Facility (https://www.gbif.org/) for birds and mammals.

3. Results

During the surveys that are the subject of this study, 16 specimens of Carla sp. ‘Meleotegi’, eleven of Sphenomorphus sp. ‘Meleotegi’, and eight of C. subradiatus were collected, totaling 35 host specimens. Of these, four host specimens (two Carla, one Sphenomorphus, one Coelognathus) had ticks. A total of five ticks were retrieved from the hosts. Based on morphological characteristics described in the literature, the ticks were identified as four nymphs (Fig. 2D) and one adult male (Fig. 4G, D) of A. helvolum. Nymphs were recorded from Carla sp. ‘Meleotegi,’ and Sphenomorphus sp. ‘Meleotegi,’ and the adult male from C. subradiatus (Table 1).

The adult A. helvolum male was identified by the following characteristics: scutum with eyes, without marginal groove, ornate, with yellowish patches that include large punctations in the scapular, marginal, and central areas; Coxa I with two spurs, the external twice as long as the internal, Coxae II-III with one triangular spur; basis capitulum rectangular, with small rounded cornua. The nymphs were characterized as follows: scutum with eyes and few small punctations; Coxa I with two spurs, the external longer, the internal small and situated anteriorly, coxae II-III with one triangular spur; basis capitulum triangular, without cornua.

The position of ticks on the bodies of their lizard hosts varied slightly. In Carla sp. ‘Meleotegi,’ nymphs were attached in an axillary position on either the forelimb or the hind limb (Fig. 2B), but also on the exposed surfaces of the belly (Fig. 2C). In Sphenomorphus sp. ‘Meleotegi,’ an engorged nymph was found in an axillary attachment position (Fig. 3B), whereas in C. subradiatus the adult male was attached on the dorsal surface (Fig. 4C).

Forty-four studies have reported parasitism records of A. helvolum in nine countries. Most of the records are from Indonesia (30), the Philippines (24), and Malaysia (23), followed by Thailand (16), India (13), Singapore (4), China, Laos, and Vietnam (one record each). Amblyomma helvolum was reported on 41 reptile species (15 lizards, 27 snakes, and one turtle), one bird species, and eight mammal species. Amongst the reptiles, varanids and colubrids were the most affected, accounting for 60% and 63% of the parasitism records reported in lizards and snakes, respectively (Table 2).

4. Discussion

Amblyomma helvolum is native to the Australasian and Oriental biogeographic realms, where it has been reported from China, India, Indonesia, Laos, Malaysia, the Philippines, and Vietnam (Auffenberg, 1988; Kolonin, 1995; Petney and Keirans, 1995; Ghosh et al., 2007; Chen et al., 2010; Chao et al., 2013). Australia and Papua New Guinea were included in the geographic distribution of A. helvolum by Burridge (2011), but its presence there has not been confirmed with voucher specimens (Guglielmette and Robbins, 2018).

The records of A. helvolum on two snakes in West Bengal, India, by Ghosh et al. (2018) are erroneous because of morphological discrepancies between those specimens and A. helvolum. Ghosh et al. (2018) described and illustrated the ticks retrieved from the two snakes as without eyes and Coxa I with internal and external spurs almost equal in size (eyes present, Coxa I with external spur about twice as long as the internal spur in A. helvolum; Anastos, 1950; Robinson, 1926; Voltzit and Keirans, 2002). We therefore follow Guglielmette et al. (2015) and consider the records of A. helvolum by Ghosh et al. (2017, 2021) as unconfirmed, since it seems that the authors of those reports used the same characteristics as adopted by Ghosh et al. (2018), and they are most likely of a type of tick that is not conspecific with A. helvolum. The remaining records of A. helvolum from West Bengal (India) are all from captive hosts (Table 2), and the presence of natural populations of this tick species in West Bengal remains to be confirmed.

There are three records of the introduction of A. helvolum into the United States through imported snakes from Thailand and Indonesia (USDA, 1971; Clark and Doten, 1995; Simmons et al., 2002; Keirans and Durden, 2001; Burridge and Simmons, 2003), but there is no evidence that this tick has become established there (Guglielmette et al., 2014). The tick fauna of Timor-Leste was inventoried for the first time during a parasitological survey in 1973, but A. helvolum was not found (Dias, 1988). Our finding, therefore, is the first record of A. helvolum for Timor-Leste.

Records of A. helvolum parasitizing squamates include species of the lizard families Agamidae, Scincidae, and Varanidae, and species of the snake families Boidae, Colubridae, Elapidae, Natrixidae, and Pythonidae. Among these, there are no reports to date of A. helvolum parasitizing species of the lizard genera Carla and Sphenomorphus, nor on the snake C. subradiatus. Parasitism of A. helvolum on the scincid lizards Carla sp. ‘Meleotegi’ and Sphenomorphus sp. ‘Meleotegi’, and the colubrid snake C. subradiatus are new interactions for this tick species. The herpetofauna of Timor-Leste comprises at least seven species of anurans, 42 species of lizards, 17 species of snakes, two species of turtles, and one species of crocodile (O’Shea et al., 2011, 2015). The three reptile species parasitized by A. helvolum correspond to an unexpectedly low frequency

<table>
<thead>
<tr>
<th>Host Species n</th>
<th>n</th>
<th>Amblyomma helvolum Stage n</th>
<th>Site</th>
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<tr>
<td>Carla sp. ‘Meleotegi’</td>
<td>16</td>
<td>2</td>
<td>Nymphs</td>
</tr>
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<td>Sphenomorphus sp. ‘Meleotegi’</td>
<td>11</td>
<td>1</td>
<td>Nymph</td>
</tr>
<tr>
<td>Snakes</td>
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<tr>
<td>Coelognathus subradiatus</td>
<td>8</td>
<td>1</td>
<td>Adult male</td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>4</td>
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</table>
Table 2

Checklist of the reptile hosts of *Amblyomma helvolum*. Columns include the host species, the name of the tick given in the source publication (when a current synonym of *A. helvolum* was used), the life stage reported (adult with unspecified sex, A; adult male, M; adult female, F; nymphs, N; larvae, L; no information, x), the country of record, and the source publication. Country abbreviations include China (CHN), Indonesia (IDN), India (IND), Laos (LAO), Malaysia (MYS), the Philippines (PHL), Singapore (SGP), Taiwan (TWN), Thailand (THA), Timor-Leste (TLS), and Vietnam (VNM). Species names with an asterisk (*) are those species listed as hosts of *A. helvolum* by Simmons et al. (2002).

<table>
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<th>Name</th>
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<td><em>Hydrodataurus pusillus</em> (Eschscholtz, 1829)</td>
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<tr>
<td><strong>Scincidae</strong></td>
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<tr>
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<tr>
<td><em>Dasia grisea</em> (Gray, 1845)</td>
<td>N</td>
<td>Ermera Municipality (TLS)</td>
<td>This study</td>
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<tr>
<td><em>Eutropis multifasciata</em> (Kahl, 1920)</td>
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<td><strong>Varanidae</strong></td>
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<td>Pianka et al. (2004)</td>
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<td><em>Varanus mabiang Gaulke &amp; Curio, 2001</em></td>
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<tr>
<td></td>
<td>M</td>
<td>Sakjiang Bendera Island (SGP)</td>
<td>Robinson (1926), Keirans (1984)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F,M</td>
<td>Java (IDN)</td>
<td>Anastos (1950)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>unknown locality (THA)</td>
<td>Tanakul et al. (1983)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F,M</td>
<td>West Bengal (IND)</td>
<td>Sanyal and De (1992)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>unknown locality (LAO)</td>
<td>Penney et al. (1995)</td>
<td></td>
</tr>
</tbody>
</table>

**SNAKES**

**Colubridae**

*Boiga dendrophila* (Boie, 1827) | A. quadrimaculatum | M | Java (IDN) | Neumann (1899) |
| F,M | Berhala Island, Sumatra (IDN) | Oudemans (1928) |
| M | Berhala Island, Sumatra (IDN) | Schulze (1933) |
| F | Sabah (MYS) | Mao et al. (2019) |

(continued on next page)
Table 2 (continued)

| Host Name Stage Location (Country) Source |
|----------------------------------------|-----------------------------------------|
| *Coelognathus flavolineatus* (Schlegel, 1837) F,M,N unknown locality (MYS) Audy et al. (1960) |
| *Coelognathus radiatus* (Boie, 1827) F Songkhla Province (THA) Sharif (1928) |
| A unknown locality (THA) Tangkul et al. (1983) |
| *Coelognathus subradiatus* (Schlegel, 1837) M Manantuto Municipality (TLS) This study |
| *Dendrelaphis pictus* (Gmelin, 1789) F Songkhla Province (THA) Keirans (1984) |
| *Elaphie carinata* (Günther, 1864) F Kaebisung City (TWN) Chao et al. (2013) |
| *Gonyosoma oxycephalum* (Boie, 1827) F Java (IDN) Robinson (1926), Keirans (1984) |
| *Lycodon capucinus* (Blanchard, 1856) A unknown locality (THA) Tanskul et al. (1983) |
| *Ptyas carinata* (Günther, 1858) F Mahasarakhom and Kalasin Provinces (THA) Kaenkan et al. (2020) |
| *Ptyas dipsas* (Schlegel, 1837) M Sulawesi (IDN) Robinson (1926) |
| *Ptyas fusca* (Günther, 1858) F,T,M Java (IDN) Robinson (1926), Keirans (1984) |
| *Xenochrophis trianguligerus* (Boie, 1827) F unknown locality (MYS) Audy et al. (1960) |
| Pythonidae |
| *Malayopython reticulatus* (Schneider, 1801) A. furcatus F Java (IDN) Neumann (1901) |
| *A. quadrimaculatum* F Java (IDN) Neumann (1901) |
| *A. feuerborni* M Java (IDN) Schulze (1933) |
| x unknown locality (PHL) Nakatsuji (1937) |
| *Naja naja* (Linnaeus, 1758) F Selangor (MYS) Kohls (1957) |
| F unknown locality (MYS) Audy et al. (1960) |
| F,M West Bengal (IND) Sanyal and De (1992) |
| Naja sumatrana Müller, 1887 F Sumatra (IDN) Anastos (1950) |
| M Selangor (MYS) Kohls (1957) [as *N. naja*] |
| x Johor (MYS) Kho et al. (2015) |
| Ophiophagus Hannah (Cantor, 1836) F,M,K unknown locality (IDN) Neumann (1901) |
| Natricidae |
| *Fowlea flavipunctatus* (Hallowell, 1860) F,M,Srisaket Province (THA) Kaenkan et al. (2020) |
| *Fowlea piscator* (Schneider, 1799) F Phitsanulok Province (THA) Sumrandee et al. (2014a, 2014b) |
| *Rhabdophis flaviceps* (Dumeril et al., 1854) N unknown locality (MYS) Audy et al. (1960) |
| Pythonidae incertae sedis X Sarawak (MYS) Robinson (1926), Keirans (1984) |
| TURTLES |
| *Heosemys grandis* (Gray, 1860) F,M,Srisaket Province (THA) Kaenkan et al. (2020) |
| *Geoemydidae* |
| *Bovidae* |
| *Bubalus bubalis* (Linnaeus, 1758) F,Sulawesi (IDN) Durden et al. (2008) |
| *Muridae* |
| *Chrotomys whitehead* Thomas, 1985 L Tioman Island, Pahang (MYS) Nicholson et al. (2016) |
| *Rattus everett* Günther, 1879 A unknown locality (THA) Tangkul et al. (1983) |
| *Rattus rattus* mindanensis Meorns, 1905 A unknown locality (THA) Tangkul et al. (1983) |
| *Sus scrofa* Linnaeus, 1758 F,Sulawesi (IDN) Durden et al. (2008) |
| *Bovidae* |
| *Bubalus bubalis* (Linnaeus, 1758) F,Sulawesi (IDN) Durden et al. (2008) |
| *Geemydidae* |
| *Heosemys grandis* (Gray, 1860) A,Sulawesi (IDN) Durden et al. (2008) |
| *Cervidae* |
| *Rusa marianna* (Desmarest, 1822) F,Sulawesi (IDN) Durden et al. (2008) |
| *Sus scrofa* Linnaeus, 1758 |

* Listed as *Coluber onicephalus*.
1 Listed as *Ophiophagus hannah*.
2 Guglielmone et al. (2018) stated that the diagnoses of larvae of *A. helvolum* on Muridae require confirmation.
3 Host-parasite association in captive habitats.
Reptilian hosts of the tick *A. helvolum* were most recently reviewed by Simmons et al. (2002), who listed 26 species (13 lizards, 12 snakes, and one turtle), but not always employing the correct taxonomic allocation of host species. In that study, 21 reptile species were identified as additional records (Simmons et al., 2002). Our new host records and additional records increase the number of reptile species known as hosts of *A. helvolum* to 42 (Table 2). Water monitors (*Varanus salvator*) and reticulated pythons (*Malayopython reticulatus*) are the most common reptilian hosts of *A. helvolum* in Asia (Auffenberg, 1988; King and Green, 1999; Simmons et al., 2002). The records of *A. helvolum* from the literature for the scincid lizard *Eutropis multifasciata*, the genus *Varanus*, the colubrid snake *Lycodon capucinus*, and the python *Malayopython reticulatus* suggest that these species may also be hosts for *A. helvolum* in Timor-Leste, but their potential association there requires confirmation.

CRediT authorship contribution statement

**Fabricio H. Oda:** Conceptualization, Methodology, Writing—original draft, Writing—review & editing. **Thiago F. Martins:** Conceptualization, Methodology, Data curation, Writing—original draft, Writing—review & editing. **Marcelo B. Labruna:** Methodology, Data curation, Writing—original draft, Writing—review & editing. **Mark O’Shea:** Conceptualization, Methodology, Investigation, Writing—original draft, Writing—review & editing, Supervision. **Hinrich Kaiser:** Conceptualization, Methodology, Investigation, Writing—original draft, Writing—review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that there is no conflicts of interest.

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References


