Ticks and Tick-borne Diseases 14 (2023) 102219

Contents lists available at ScienceDirect

Ticks and Tick-borne Diseases

journal homepage: www.elsevier.com/locate/ttbdis

Original article

# Morphological anomalies in hard ticks (Acari: Ixodidae) from Brazil

Hermes R. Luz[a,*], Marcelo B. Labruna[b], Richard C. Pacheco[c], Sergio L. Gianizella[d], Pablo H. Nunes[e], Matias P.J. Szabó[f], Monize Gerardi[b,f], Rodrigo H.F. Teixeira[g,h,i], Silvio C. da Silva[j], Louise B. Kmetiuk[k], Isabella P. Pesenato[b], Arlei Marcili[l], João L.H. Faccini[m], Thiago F. Martins[b,j]

[a] *Post-Graduation Program in Health and Environment, Biodiversity and Conservation, Northeast Biotechnology Network (RENORBIO) from the Center of Biological and Health Sciences, Federal University of Maranhão, São Luís, MA, Brazil*

[b] *Department of Preventive Veterinary Medicine and Animal Health, Faculty of Veterinary Medicine and Animal Science, University of São Paulo, São Paulo, Brazil*

[c] *Post-Graduation Program in Veterinary Sciences, Faculty of Veterinary Medicine, Federal University of Mato Grosso, Cuiabá, MT, Brazil*

[d] *Laboratory of Zoology, Department of Biology, Institute of Biological Sciences, Federal University of Amazonas, Manaus, AM, Brazil*

[e] *Latin American Institute of Life and Nature Sciences, Federal University of Latin American Integration, Foz do Iguaçu, PR, Brazil*

[f] *Faculty of Veterinary Medicine, Federal University of Uberlândia, Uberlândia, MG, Brazil*

[g] *Municipal Zoological Park "Quinzinho de Barros", Sorocaba, SP, Brazil*

[h] *University of Sorocaba (UNISO), Sorocaba, SP, Brazil*

[i] *Post-Graduation Program in Wild Animals, Faculty of Veterinary Medicine and Animal Science (FMVZ) of the São Paulo State University "Júlio de Mesquita Filho" (UNESP), Botucatu, SP, Brazil*

[j] *Pasteur Institute, São Paulo State Department of Health, São Paulo, SP, Brazil*

[k] *Carlos Chagas Institute, Oswaldo Cruz Foundation, Curitiba, PR, Brazil*

[l] *Post-Graduation in Medicine and Animal Welfare, Doctorate in Single Health, Santo Amaro University, São Paulo, SP, Brazil*

[m] *Post-Graduation Program in Health Sciences from the Center of Biological and Health Sciences, Federal University of Maranhão, São Luís, MA, Brazil*

A R T I C L E I N F O

*Keywords:*
Amblyomma
Rhipicephalus
Gynandromorphism
Neotropical region

A B S T R A C T

Tick abnormalities have been unusual in nature, and they can be divided into local and general. In the present study, external morphological anomalies were described in 31 individual adult ticks of 15 different species of Ixodidae, which were collected on wild hosts (20 ticks), domestic hosts (7 ticks), and in the environment (4 ticks) in 11 states of Brazil from 1998 to 2022. Among the 31 tick specimens, 14 (45%) were categorized as local anomalies, and 17 (55%) as general anomalies. The ticks were taxonomically identified into 14 species of *Amblyomma*, and one species of *Rhipicephalus*. Local anomalies included malformations of scutum/alloscutum, ectromely, leg atrophy, and a third ectopic spiracular plate. General anomalies included opisthosoma duplication, no expansion of dorsal alloscutum in engorged females, and gynandromorphism; the latter is described for 13 tick specimens. Morphological anomalies in *Amblyomma aureolatum, Amblyomma brasiliense, Amblyomma humerale* and *Amblyomma longirostre* are reported for the first time. Although the results herein expand the list of anomalous tick species in the Neotropics, future studies should be conducted to clarify the origin of these anomalies.

## 1. Introduction

Tick morphological anomalies have been reported in different species (Guglielmone et al., 2000; Estrada-Peña, 2001; Labruna et al., 2002; Kar et al., 2015; Chitimia-Dobler et al., 2017; Domínguez and Bermúdez, 2020) since the end of the 19th century (Neumann, 1899). Recently, a case of exoskeleton anomaly was reported in a tick fossil from the late Cretaceous (Chitimia-Dobler et al., 2023). Overall, tick morphological anomalies have been reported at low frequencies among field-collected ticks (Estrada-Peña, 2001; Labruna et al., 2002; Domínguez and Bermúdez, 2020; Shuaib et al., 2020), possibly due to the deleterious effect on feeding and survival of ticks (Estrada-Peña, 2001), especially those more severe (e.g., missing or fusion of structures).

Tick anomalies have several phenotypic patterns and are broadly organized as local or general anomalies. Structural deformities of the capitulum (basis, hypostome, and palps), idiosoma (scutum or

* Corresponding author.
*E-mail address:* hermes.luz@ufma.br (H.R. Luz).

https://doi.org/10.1016/j.ttbdis.2023.102219
Received 17 April 2023; Received in revised form 13 June 2023; Accepted 16 June 2023
Available online 1 July 2023
1877-959X/

alloscutum), missing leg(s) (ectromely) or leg segment(s) and fusion of appendages are examples of local anomalies, while asymmetry of idiosome, duplication, nanism, gigantism and gynandromorphism are some examples of general anomalies (Campana-Rouget, 1959; Latif et al., 1988; Estrada-Peña, 2001; Molaei and Little, 2018; Balinandi et al., 2019; Buczek et al., 2019; Domínguez and Bermúdez, 2020; Shuaib et al., 2020).

Gynandromorphism refer to individuals possessing male and female phenotypic characteristics. According to the classification of Campana-Rouget (1959), there are five gynandromorph types in ticks: (i) bipartite protogynander, where the external sex-linked features are equally represented; (ii) deuterogynander, where one sex is reduced to a quadrant; (iii) metagynander, where one sex is reduced to a small segment; (iv) gynander intriqué, which may be any of the previous three, with 'islands' of male or female chitin embedded in areas of the opposite sex; and (v) mosaics, where there is no definite line separating the male from the female features, but the zones are intimately mixed without indication of symmetry.

Several factors may induce morphological abnormalities in ticks, and some studies point to somatic or germline mutations, exposure to synthetic products (e.g., tick control with acaricides), microbiota (e.g., viruses, bacteria and protozoa), abiotic factors (e.g., humidity, temperature, solar radiation), anthropic (e.g., pollution, chemicals) and host resistance as the main causes (Campana-Rouget, 1959; Latif et al., 1988; Zharkov et al., 2000; Estrada-Peña, 2001; Alekseev et al., 2007; Alekseev and Dubinina, 2008; Nowak-Chmura, 2012; Keskin et al., 2016; Chitimia-Dobler and Pfeffer, 2017; Buczek et al., 2019). Therefore, it is possible that the effect of these factors in experimental conditions could induce anomalies in ticks, although exposure of ticks under experimental conditions are needed to prove their teratogenic activity.

In the Neotropical region, anomalies in ticks have been described over the past 100 years, and currently reported in ~25 species (Pereira and Castro, 1945; Guglielmone et al., 2000; Labruna et al., 2000; 2002, 2009; Martins et al., 2017; Rivera-Páez et al., 2017; Muñoz-Leal et al., 2018; Dominguez et al., 2020; Domínguez and Bermúdez, 2020). Only six species of ticks have been reported with some type of anomaly in Brazil, despite its tick richness comprising 76 species (Fonseca, 1935; Labruna et al., 2000, 2002, 2009; Serra-Freire et al., 2012; Luz et al., 2013; Martins et al., 2017; Muñoz-Leal et al., 2018; Dantas-Torres et al., 2019). Thus, this study aimed to report different morphological anomalies in ticks from Brazil.

## 2. Materials and methods

In the present study, morphological anomalies were described in ticks collected from domestic or wild hosts and environment in all Brazilian regions, from 1998 to 2022. Ticks were identified to species level using the morphological characters according to Dantas-Torres et al. (2019). The anomalies were classified into two categories: local anomalies (scutum, aloscutum, festoons, anus, spiracular plates and legs) and general anomalies (duplication, gynandromorphism) following Campana-Rouget (1959).

External morphology of all specimens was examined, and anomalous individuals were photographed using a SteREO Discovery V12 stereomicroscope (Carl Zeiss, Munich, Germany). In addition, some anomalies were studied in detail through scanning electron microscopy, according to Corwin et al. (1979).

Ticks from this study have been deposited in the tick collections "Coleção Nacional de Carrapatos Danilo Gonçalves Saraiva" (CNC), University of São Paulo, São Paulo, SP, Brazil, or "Coleção Zoológica Paulo Bürhnheim" (UFAM), Federal University, Manaus, AM, Brazil (accession numbers provided in Tables 1 and 2). Some of the tick specimens were already available in the tick collection before starting the present study, although their morphological anomalies were never reported (except in one case, *Amblyomma parkeri,* see Discussion). Other specimens were collected and deposited in the course of the present study.

## 3. Results

External morphological anomalies were described in 31 individual adult ticks of the family Ixodidae, which were collected on wild hosts (20 ticks; 65%), domestic hosts (7 ticks; 22%), or in the environment (4 ticks; 13%), from 11 different states of Brazil from 1998 to 2022. Among

**Table 1**
Data of the ticks from Brazil presenting morphological local anomalies, according to host, geographical location, year of collection, tick collection code, and the presented figures in the manuscript (when available).

| Tick species | Host | Municipality, state* | Year | Code | Tick stage and type of local anomaly | Figures |
|---|---|---|---|---|---|---|
| *Amblyomma dubitatum* | Environment | Angra dos Reis, RJ | 2021 | CNC-4267 | ♀, malformation of scutum, lacking a posterolateral area | 1 |
| *A. dubitatum* | *Hydrochoerus hydrochaeris* | São Miguel Arcanjo, SP | 2021 | CNC-4479 | ♀, malformation of scutum, lacking a posterolateral area | - |
| *Amblyomma sculptum* | *Priodontes maximus* | Aquidauana, MS | 2020 | CNC-4505 | ♀, malformation of scutum, lacking part of one lateral area | 2 |
| *Amblyomma aureolatum* | *Alouatta guariba clamitans* | São Paulo, SP | 2014 | CNC-1094 | ♀, malformation of alloscutum | 3 |
| *A. sculptum* | *Tapirus terrestris* | Aquidauana, MS | 2012 | CNC-2268 | ♀, malformation of alloscutum | 4 |
| *A. sculptum* | *Bos taurus* | São Carlos, SP | 2018 | CNC-4294 | ♀, malformation of alloscutum | 5 |
| *A. sculptum* | *T. terrestris* | Itu, SP | 2000 | CNC-4245 | ♂, lacking central festoons | 6 |
| *Amblyomma tigrinum* | *Chrysocyon brachyurus* | Mineiros, GO | 2005 | CNC-1661 | ♂, lacking central festoons | 7 |
| *A. sculptum* | *Cerdocyon thous* | Chapada dos Guimarães, MT | 2001 | CNC-674 | ♀, three spiracular plates | 8 |
| *Amblyomma dissimile* | *Bothrops mattogrossensis* | Corumbá, MS | 2007 | CNC-4288 | ♂, ectromely (six legs) | 9 |
| *A. sculptum* | Environment | Araçariguama, SP | 1998 | CNC-127 | ♂, ectromely (seven legs) | – |
| *Rhipicephalus sanguineus* s. l. | *Canis familiaris* | Campo Grande, MS | 2013 | CNC-3022 | ♂, ectromely (seven legs) | 10 |
| *Amblyomma coelebs* | *Sapajus macrocephalus* | Santa Isabel do Rio Negro, AM | 2012 | CNC-2165 | ♀, atrophy of right leg I | 11 |
| *Amblyomma humerale* | *Chelonoidis carbonaria* | Santa Inês, MA | 2021 | CNC-4485 | ♂, atrophy of left leg IV | 12 |

* Brazilian states: AM- Amazonas, GO- Goiás, MA- Maranhão, MS- Mato Grosso do Sul, MT- Mato Grosso, PA- Pará, RJ- Rio de Janeiro, SP- São Paulo.

**Table 2**
Data of the ticks from Brazil presenting morphological general anomalies, according to host, geographical location, year of collection, tick collection code, and the presented figures in the manuscript.

| Tick species | Host | Municipality, state* | Year | Code | Type of general anomaly | Figure |
|---|---|---|---|---|---|---|
| *Amblyomma aureolatum* | *Canis lupus familiaris* | Mogi das Cruzes, SP | 2001 | CNC-542 | ♂, opisthosoma duplication; two anuses | 13 |
| *Amblyomma geayi* | *Bradypus variegatus* | Belém, PA | 2010 | CNC-4291 | ♂, opisthosoma duplication; two anuses, three spiracular plates | 14 |
| *Amblyomma tigrinum* | *Chrysocyon brachyurus* | Mineiros, GO | 2004 | CNC-1697 | ♀, no expansion of dorsal alloscutum | 15 |
| *Amblyomma sculptum* | *Myrmecophaga tridactyla* | Cuiabá, MT | 2021 | CNC-4519 | ♀, no expansion of opisthosoma | 16 |
| *Amblyomma brasiliense* | *Sus scrofa* ¤ | Ponta Grossa, PR | 2017 | CNC-4286 | Gynandromorphism (protogynander intriqué) | 17 |
| *Amblyomma dissimile* | *Boa constrictor* | Manaus, AM | 2014 | CZPB-IX00921 | Gynandromorphism (protogynander intriqué) | 18 |
| *A. dissimile* | *B. constrictor* | Manaus, AM | 2015 | CZPB-IX00714 | Gynandromorphism (protogynander intrique) | 19 |
| *A. dissimile* | *B. constrictor* | Cuiabá, MT | 2014 | CNC-4290 | Gynandromorphism (protogynander intriqué) | 20 |
| *A. dissimile* | *B. constrictor* | Cuiabá, MT | 2019 | CNC-4289 | Gynandromorphism (protogynander intriqué) | 21 |
| *Amblyomma longirostre* | *Turdus rufiventris* | Itatiaia, RJ | 2016 | CNC-4295 | Gynandromorphism (protogynander intriqué) # | 22 |
| *Amblyomma parkeri* | *Coendou prehensilis* | Biritiba-Mirim, SP | 2004 | CNC-4296 | Gynandromorphism (protogynander intriqué) | 23 |
| *Amblyomma parvum* | *C. lupus familiaris* | Araguapaz, GO | 2011 | CNC-4293 | Gynandromorphism (protogynander intriqué) | 24 |
| *A. brasiliense* | Environment | Ribeirão Grande, SP | 2004 | CNC-4287 | Gynandromorphism (deuterogynander intriqué) | 25 |
| *A. aureolatum* | *C. lupus familiaris* | Viamão, RS | 2008 | CNC-2738 | Gynandromorphism (metagynander) | 26 |
| *Amblyomma cajennense* s.s. | *Tapirus terrestris* | Querência, MT | 2022 | CNC-4518 | Gynandromorphism (metagynander) | 27 |
| *Amblyomma oblongoguttatum* | *C. lupus familiaris* | Monte Negro, RO | 2001 | CNC-4292 | Gynandromorphism (metagynander) | 28 |
| *A. brasiliense* | Environment | Miracatu, SP | 2020 | CNC-4285 | Gynandromorphism (metagynander intriqué) | 29 |

* Brazilian states: AM- Amazonas, GO- Goiás, MT- Mato Grosso, PR- Paraná, RJ- Rio de Janeiro, RO- Rondônia, RS- Rio Grande do Sul, SP- São Paulo.
¤ Free-range wild boar.
# This adult specimen was collected from the wild bird host as an engorged nymph, which molted to the adult gynander in the laboratory.
t specimen was collected from the wild bird host as an engorged nymph, which molted to the adult gynander in the laboratory.

the 31 tick specimens, 14 (45%) were categorized as local anomalies (Table 1), and 17 (55%) as general anomalies (Table 2). The ticks were taxonomically identified into 14 species of *Amblyomma,* and one species of *Rhipicephalus* (Figs. 1-29).

Regarding the local anomalies (Table 1), three ticks had malformation of scutum, lacking one of the posterolateral areas (*Amblyomma dubitatum* ♀, Fig. 1; *A. dubitatum* ♀, not illustrated) or lacking part of the right lateral area (*Amblyomma sculptum* ♀, Fig. 2). Six ticks had malformation of alloscutum, characterized by a constriction in the mid-postero area (*Amblyomma aureolatum* ♀, Fig. 3), constriction of one of the lateral areas with displacement of the anus in partial engorged females (*A. sculptum* ♀, Fig. 4; *A. sculptum* ♀, Fig. 5), lacking central festoons (*A. sculptum* ♂, Fig. 6; *Amblyomma tigrinum* ♂, Fig. 7), or presence of a third spiracular plate on the dorsal lateral area (*A. sculptum* ♀, Fig. 8). Three ticks had ectromely, which was characterized by missing two legs (*Amblyomma dissimile* ♂, Fig. 9) or one leg (*Rhipicephalus sanguineus* sensu lato ♂, Fig. 10; *A. sculptum* ♂, not illustrated). Two specimens presented leg atrophy; in one of them, the entire right leg I was compatible with the nymphal stage, except for coxa I, which had nymphal external spur and female internal spur (*Amblyomma coelebs* ♀, Fig. 11); the second specimen had its left leg IV reduced to a nymphal coxa IV (*Amblyomma humerale* ♂, Fig. 12).

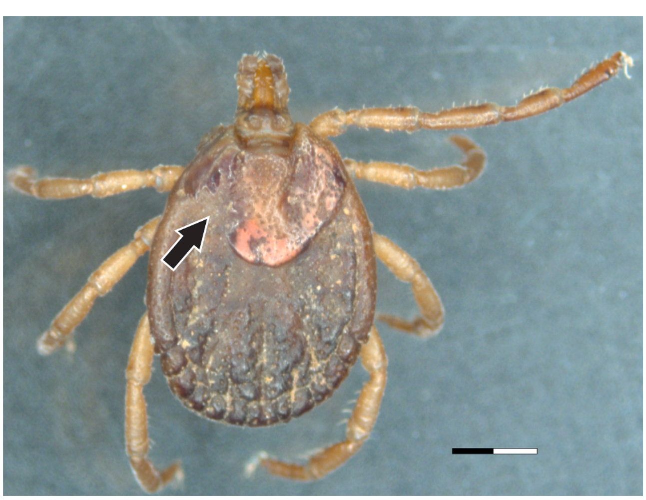

**Fig. 1.** Dorsal view of *Amblyomma dubitatum* female with malformation of scutum, lacking the left posterolateral area (arrow). Bar: 1 mm.

Regarding the general anomalies (Table 2), two ticks had opisthosoma duplication with the presence of two anuses (*A. aureolatum* ♂, Fig. 13; *Amblyomma geayi* ♂, Fig. 14); the latter tick also had a third spiracular plate located at the mid-postero margin. One engorged female showed a lack of expansion of the dorsal surface of the alloscutum (*A. tigrinum*, Fig. 15), while another engorged female showed lack of expansion restricted to the opisthosoma (*A. sculptum*, Fig. 16). Other 13 specimens showed different types of gynandromorphism, as follows: eight specimens classified as protogynanders intriqué (one *Amblyomma brasiliense*, Fig. 17; four *A. dissimile*, Figs. 18-21 one *Amblyomma longirostre*, Fig. 22; one *A. parkeri*, Fig. 23; one *Amblyomma parvum*, Fig. 24), one deuterogynander intriqué (*A. brasiliense*, Fig. 25), three metagynanders (*A. aureolatum*, Fig. 26; *Amblyomma cajennense* sensu stricto, Fig. 27; *Amblyomma oblongoguttatum*, Fig. 28), and one metagynander intriqué (*A. brasiliense*, Fig. 29).

## 4. Discussion

The present study reports morphological anomalies in 31 specimens of hard ticks (Ixodidae), which were classified in 15 different species. Except for a single *R. sanguineus* specimen, all other 30 abnormal ticks belonged to the genus *Amblyomma.* Previous reports of morphological abnormalities in Neotropical ticks also encompassed much more *Amblyomma* specimens than all other tick genera together (Guglielmone et al., 2000; Dominguez et al., 2020; Domínguez et al., 2021). Actually, *Amblyomma* is the most diverse tick genus in the Neotropics, including Brazil, where the current tick fauna of 76 species includes 33 *Amblyomma* spp. (Krawczak et al., 2015; Dantas-Torres et al., 2019; Martins et al., 2019). To the authors knowledge, this is the first report of morphological anomalies in *A. aureolatum, A. brasiliense, A. humerale* and *A. longirostre*.

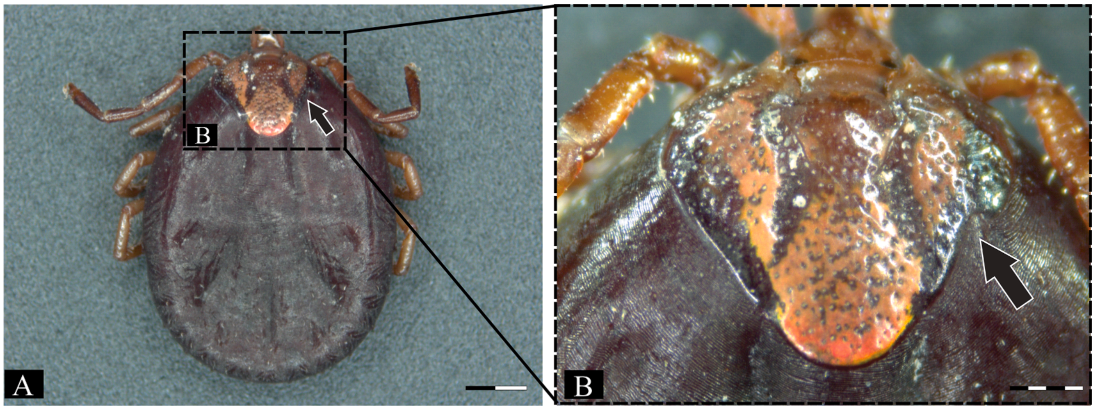


**Fig. 2.** Dorsal view (A) of *Amblyomma sculptum* female with malformation of scutum, lacking the right posterolateral area (arrows). (B) Higher magnification of the scutum. Bars: 1 mm in A, and 2 mm in B.

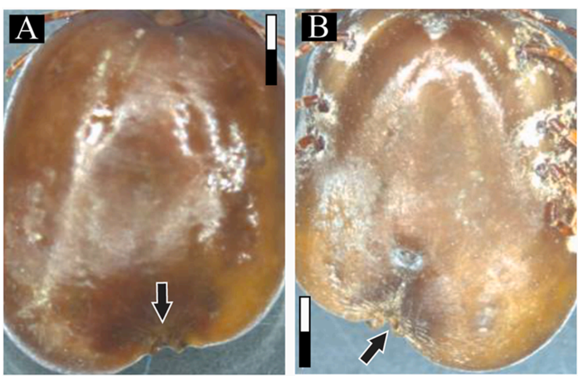


**Fig. 3.** *Amblyomma aureolatum* female with malformation of alloscutum (arrows), dorsal view (A), ventral view (B). Bars: 1 mm.

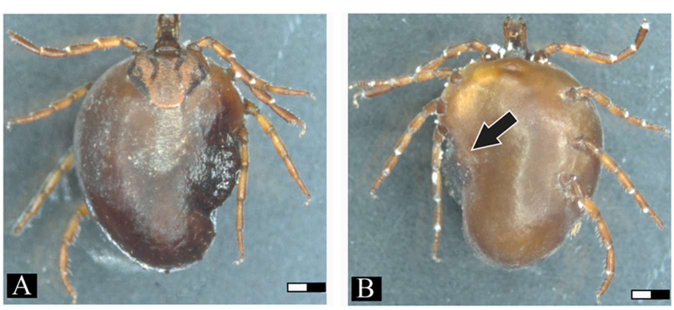


**Fig. 4.** *Amblyomma sculptum* partially engorged female showing malformation of alloscutum characterized by constriction of one lateral area with lateral displacement of the anus (arrow); dorsal (A) and ventral (B) views. Bars: 1 mm.

Morphological abnormalities have been reported in Ixodidae (hard ticks) and Argasidae (soft ticks) families worldwide (Campana-Rouget, 1959; Guglielmone et al., 2000; Zharkov et al., 2000; Alekseev et al., 2007; Kar et al., 2015; Keskin et al., 2016; Chitimia-Dobler and Pfeffer, 2017; Molaei and Little, 2018; Azzi et al., 2019; Balinandi et al., 2019; Domínguez and Bermúdez, 2020; Shuaib et al., 2020; Domínguez et al., 2022). This phenomenon has been frequently reported in hard ticks (*Amblyomma, Dermacentor, Haemaphysalis, Hyalomma, Ixodes* and *Rhipicephalus*), with rare records in soft ticks (*Argas* and *Ornithodoros*) (Guglielmone et al., 2000; Labruna et al., 2000, 2002; Balinandi et al., 2019; Buczek et al., 2019). In the present study, abnormalities were also only reported in hard ticks, even though hundreds of soft tick specimens of the CNC tick collection have been examined (data not shown).

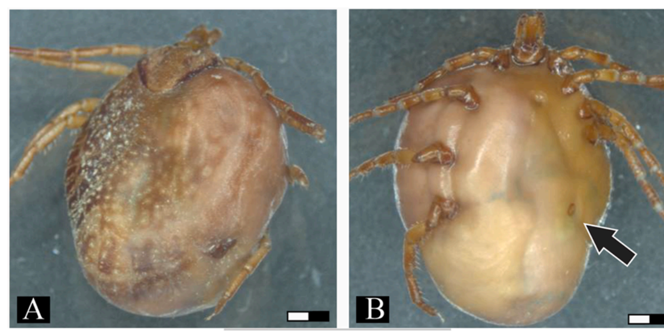


**Fig. 5.** *Amblyomma sculptum* partially engorged female showing malformation of alloscutum characterized by constriction of one lateral area with lateral displacement of the anus (arrow); dorsal (A) and ventral (B) views. Bars: 1 mm.

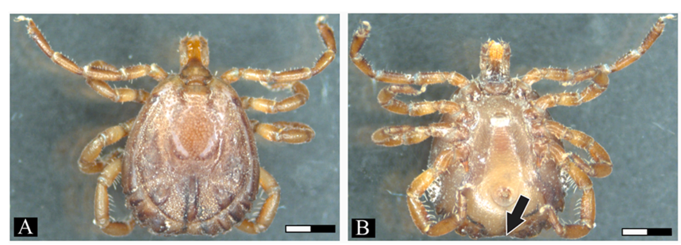


**Fig. 6.** *Amblyomma sculptum* male with malformation of alloscutum, dorsal view (A) and ventral view (B) lacking central festoons (arrow). Bars: 1 mm.

Authors speculate that may be a consequence of a biased hard ticks survey, more sampled than soft ticks. It is also possible that hard ticks have been generally more exposed to mutagenic factors such environmental pollution and synthetic products (e.g., insecticide or acaricides) than soft ticks, which are nidicolous, and post-larval stages are usually fast feeding. Thus, soft ticks may be likely less exposed to adverse environmental conditions. Such adverse conditions mean mutagenic factors, precursors for somatic or germinal mutations, which may give rise to morphologically anomalous ticks (Estrada-Peña, 2001; Keskin et al., 2016; Buczek et al., 2019; Shuaib et al., 2020). In fact, some of the hard ticks reported here refer to species of concern to animal and public health and therefore, a more frequent chemical control target (Guglielmone et al., 2006; Szabó et al., 2006; Parola et al., 2013).

*Amblyomma sculptum* was the most encountered species with local anomalies herein (six specimens), followed by *A. dubitatum* (two specimens); the remaining six species with local anomalies were each represented by a single specimen. Regarding general anomalies, *A. dissimile*

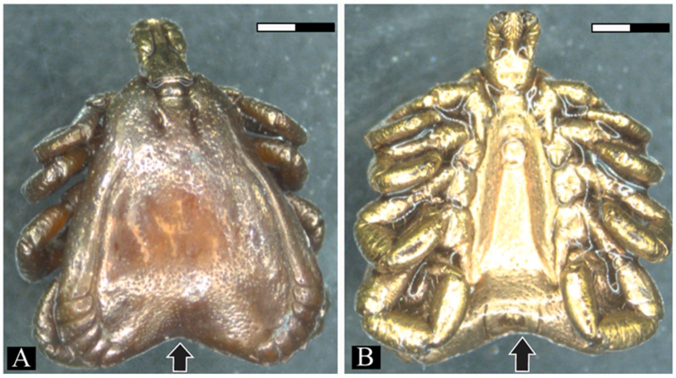


**Fig. 7.** *Amblyomma tigrinum* male with malformation of alloscutum, dorsal view (A) and ventral view (B) lacking central festoons (arrows). Specimen shows gold metallization because it was previous prepared for scanning electron microscopy, which couldnot be accomplished. Bars: 1 mm.

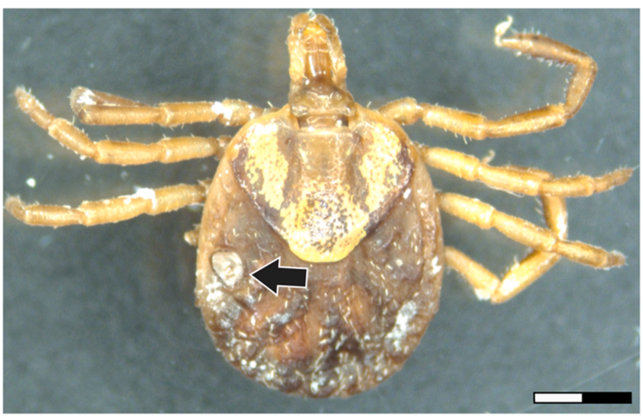

**Fig. 8.** *Amblyomma sculptum* female with malformation of alloscutum, showing the presence of a third spiracular plate on the dorsal left lateral area (arrow). Bar: 0.5 mm.

**Fig. 9.** Ventral view of *Amblyomma dissimile* male lacking right legs III and IV, ectromely (arrows). Bar: 0.5 mm.

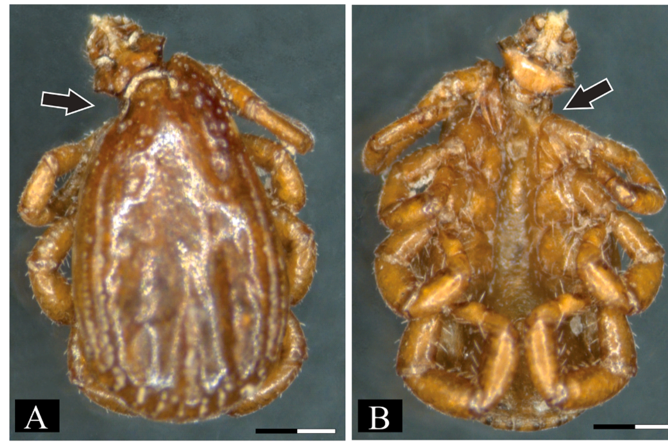


**Fig. 10.** *Rhipicephalus sanguineus* sensu lato male. Dorsal view (A) showing body asymmetry (arrow) as a consequence of ectromely (lacking left leg I, arrow), as shown in ventral view (B). Bars: 0.5 mm.

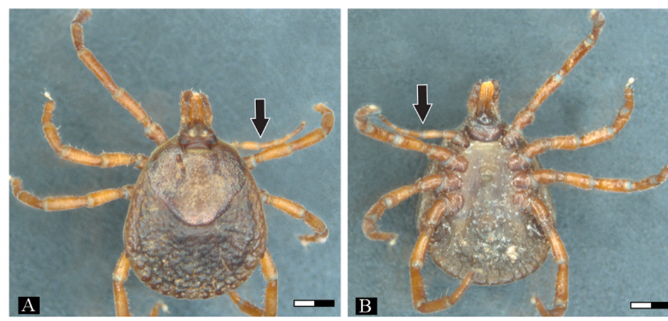


**Fig. 11.** *Amblyomma coelebs* female presenting atrophy of right leg I (arrows). (A) dorsal view, (B) ventral view. Right coxa I with nymphal external spur and female internal spur. Bars: 1 mm.

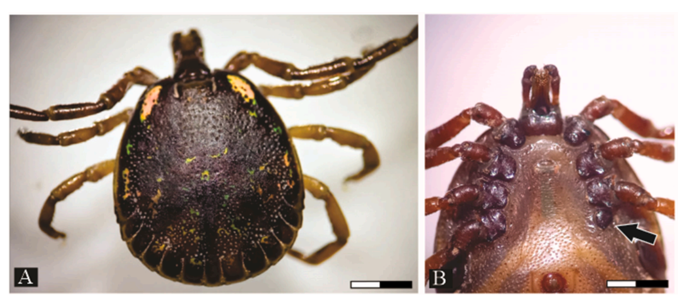


**Fig. 12.** *Amblyomma humerale* male presenting atrophy of left leg IV, reduced to a nymphal coxa IV (arrow). (A) dorsal view, (B) ventral view. Bars: 2 mm.

was the most encountered species (four specimens), followed by *A. brasiliense* (three specimens) and *A. aureolatum* (two specimens); the remaining eight species with general anomalies were each represented by a single specimen.

*Amblyomma sculptum* is one of the six species that form the *A. cajennense* sensu lato (s.l.) species complex (Nava et al., 2014). Among the morphological anomalies previously reported for *A. cajennense* s.l. (Brumpt, 1934; Fonseca, 1935; Guglielmone et al., 2000; Labruna et al., 2002), at least two can bee assinged to *A. sculptum* based on the geographical localities where ticks were collected (Fonseca, 1935; Labruna et al., 2002). Interestingly, the present *A. sculptum* specimens had several local anomalies (malformation of scutum or alloscutum, ectromely), and at least one general anomaly (no expansion of postero-dorsal alloscutum). We cannot disregard a sample bias towards *A. sculptum,* which has public health concern in Brazil (Szabó et al., 2013). Besides the partial lack of expansion of dorsal alloscutum of an *A. sculptum* engorged female, a complete lack of expansion of the dorsal alloscutum of an *A. tigrinum* engorged female was reported herein. To the authors knowledge, this type of general anomaly has not been reported in *Amblyomma* ticks.

Gynandromorphism was the predominant type of general anomaly

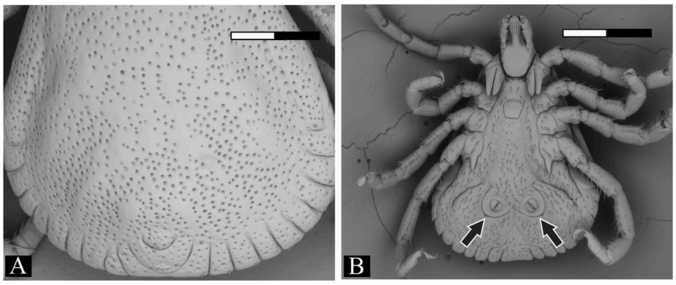


**Fig. 13.** *Amblyomma aureolatum* male with opisthosoma duplication, dorsal view (A), ventral view (B) with the presence of two anuses (arrows). Bars: 1 mm in A, 2 mm in B.

reported in the present study, observed in 13 specimens of the species *A. dissimile* (*n* = 4), *A. brasiliense* (*n* = 3), *A. aureolatum* (*n* = 1), *A. cajennense* (*n* = 1), *A. longirostre* (*n* = 1), *A. oblongoguttatum* (*n* = 1), *A. parkeri* (*n* = 1) and *A. parvum* (*n* = 1) (Table 2). Gynandromorphism in *A. dissimile* was reported in Venezuela (Brumpt, 1934) and in Panamá (Domínguez and Bermúdez, 2020). This is the first record of gynandromorphism in *A. parvum,* which has been previously reported with local (lack of structure) and general (asymmetry and constriction) anomalies in Argentina (Guglielmone et al., 2000). For *A. oblongoguttatum*, both local and general anomalies (gynandromorphism) were reported in northern Brazil (Labruna et al., 2000; Azzi et al., 2019). General anomalies (asymmetry of idiosoma and nanism) have been previously reported in *A. oblongoguttatum* from Central America, where this tick species has been called as *A.* cf. *oblongoguttatum* (Lopes et al., 2016; Domínguez and Bermúdez, 2020; Domínguez et al., 2020; 2021).

The gynander of *A. parkeri* of the present study was previously reported (without illustration) by Labruna et al. (2009), who classified it as a bipartite protogynander. We re-examined this specimen and have re-classified it as protogynander intriqué. The reason for that is because there is a narrow invagination of female alloscutum on the male side, delimitating the female scutum on the male side (Fig. 23C). In addition, the basis capituli has a pair of porose areas (Fig. 23D). Due to these features, this specimen cannot be considered as a perfect bipartite protogynander, which is characterized by external sex-linked features equally represented on each body size, divided by an imaginary longitudinal line from the central anterior margin of the hypostome to the central posterior margin of the sixth festoon (Campana-Rouget, 1959).

In the present study, 27 out of 31 anomalous ticks were collected parasitizing domestic or wild animals, indicating that their morphological anomalies did not prevent them from seeking and settling on a host. Finally, as stated by Nowak-Chmura (2012), morphological anomalies may affect diagnostic structures of the ticks (e.g., legs, scutum), leading to misidentification.

## 5. Conclusion

External morphological anomalies were described in 31 individual adult ticks of 15 different species of the genera *Amblyomma* and *Rhipicephalus*, mostly collected from domestic or wild animals. Morphological abnormalities were reported for the first time in *A. aureolatum, A. brasiliense, A. humerale* and *A. longirostre*. Local anomalies comprised

**Fig. 15.** *Amblyomma tigrinum* engorged female showing no expansion of the dorsal surface of the alloscutum. Specimen shows gold metallization because it was previously prepared for scanning electron microscopy, which could not be accomplished. Bar: 1 mm. Bar: 1 mm.

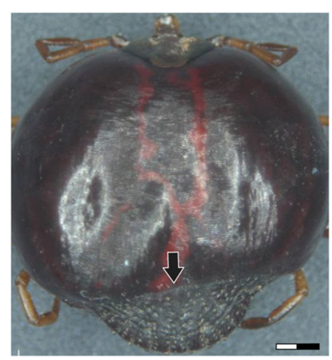

**Fig. 16.** *Amblyomma sculptum* engorged female showing no expansion of the opisthosoma (arrow). Bar: 1 mm.

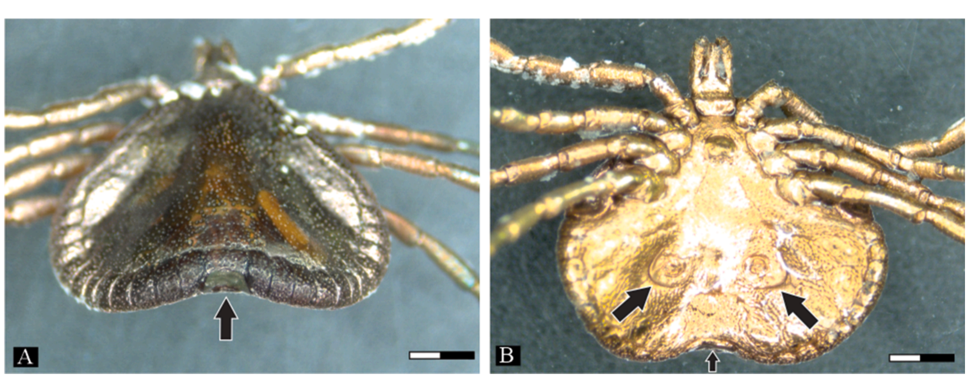


**Fig. 14.** *Amblyomma geayi* male with opisthosoma duplication, dorsal view (A) showing a third spiracular plate at the mid-postero area (arrow), ventral view (B) with the presence of two anuses (arrows). Specimen shows gold metallization because it was previous prepared for scanning electron microscopy, which could not be accomplished. Bars: 0.5 mm.

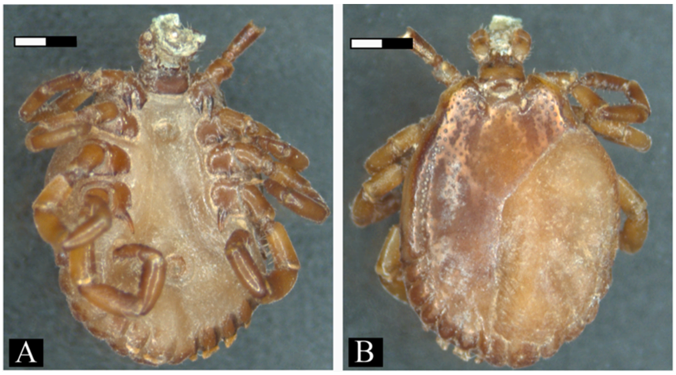

**Fig. 17.** Gynandromorphism (protogynander intriqué) in *Amblyomma brasiliense*, with a male capitulum and a dorsal (A) idiosoma that is male on the left and female on the right; few female features (few right festoons and the right spiracular plate) ventrally (B). Bars: 1 mm.

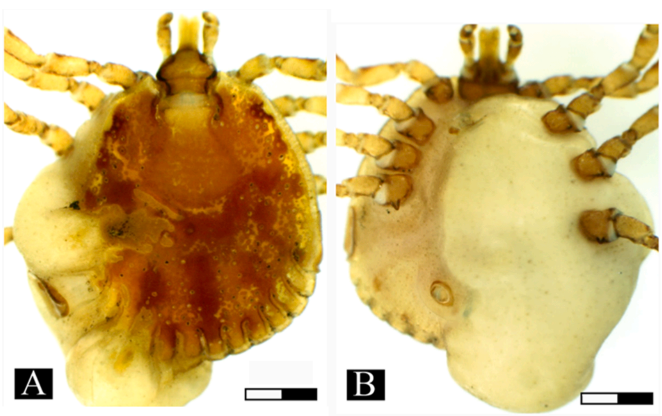

**Fig. 18.** Gynandromorphism in *Amblyomma dissimile.* Protogynander intriqué, with capitulum and idiosoma represented by male features on the right side and female features on the left side; while male scutum 'invades' the female side dorsally (A), the two halves are perfectly separated ventrally (B), including the genital opening. Bars: 2 mm.

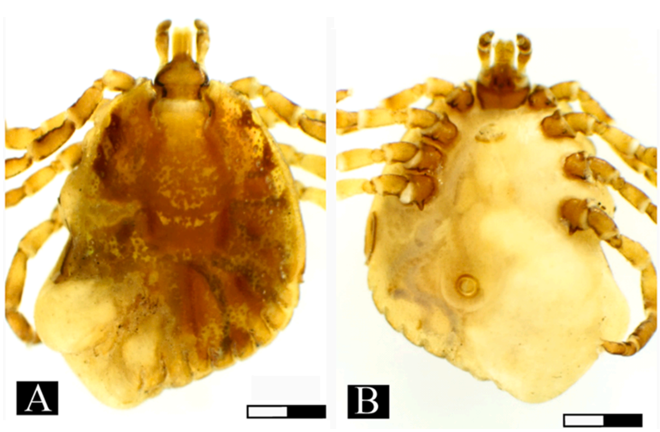

**Fig. 19.** Gynandromorphism in *Amblyomma dissimile.* Protogynander intriqué, with capitulum and idiosoma represented by male features on the right side and female features on the left side; while male scutum 'invades' the female side dorsally (A), the two halves are perfectly separated ventrally (B), including the genital opening. Bars: 2 mm.

malformation of scutum or alloscutum, ectromely, and leg atrophy. General anomalies comprised opisthosoma duplication or no expansion, and different types of gynandromorphism.

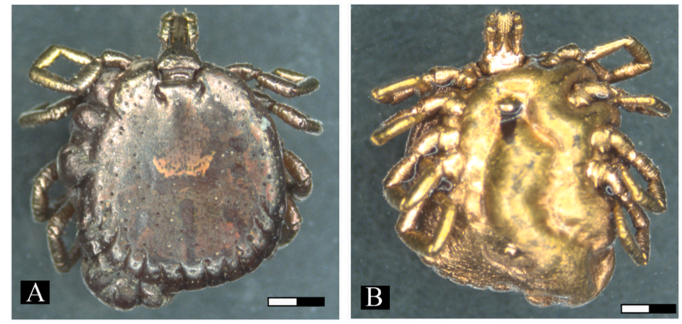

**Fig. 20.** Gynandromorphism in *Amblyomma dissimile.* Protogynander intriqué, with dorsal male idiosoma and capitulum (A); ventrally (B), the idiosoma is male on the right side and female on the left side; this division is also seen in the genital opening. Specimen shows gold metallization because it was previously prepared for scanning electron microscopy, which could not be accomplished. Bars: 0.5 mm.

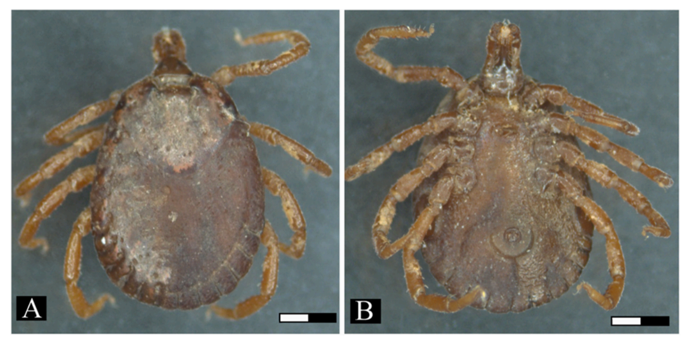

**Fig. 21.** Gynandromorphism in *Amblyomma dissimile.* Protogynander intriqué with female capitulum and dorsal idiosoma with female features on the right side (A), whereas the left side is composed mostly of male features; ventrally (B), the idiosoma is male on the left side and female on the right side; this division is also seen in the genital opening.

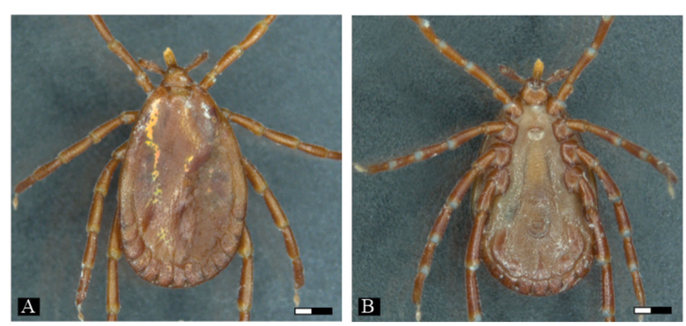

**Fig. 22.** Gynandromorphism (protogynander intriqué) in *Amblyomma longirostre.* Dorsally (A), the two sexes are equally represented, male capitulum and idiosoma on the left side, female capitulum and idiosoma on the right side. Ventrally (B) composed by male features, including the hypostome, genital opening, spiracular plates, and ventral plates on the posterior part of the idiosoma. Bars: 1 mm.

## CRediT authorship contribution statement

**Hermes R. Luz:** Conceptualization, Funding acquisition, Investigation, Resources, Writing – original draft, Writing – review & editing. **Marcelo B. Labruna:** Conceptualization, Funding acquisition, Investigation, Resources, Writing – original draft, Writing – review & editing. **Richard C. Pacheco:** Investigation, Resources, Writing – review & editing. **Sergio L. Gianizella:** Investigation, Resources, Writing – review

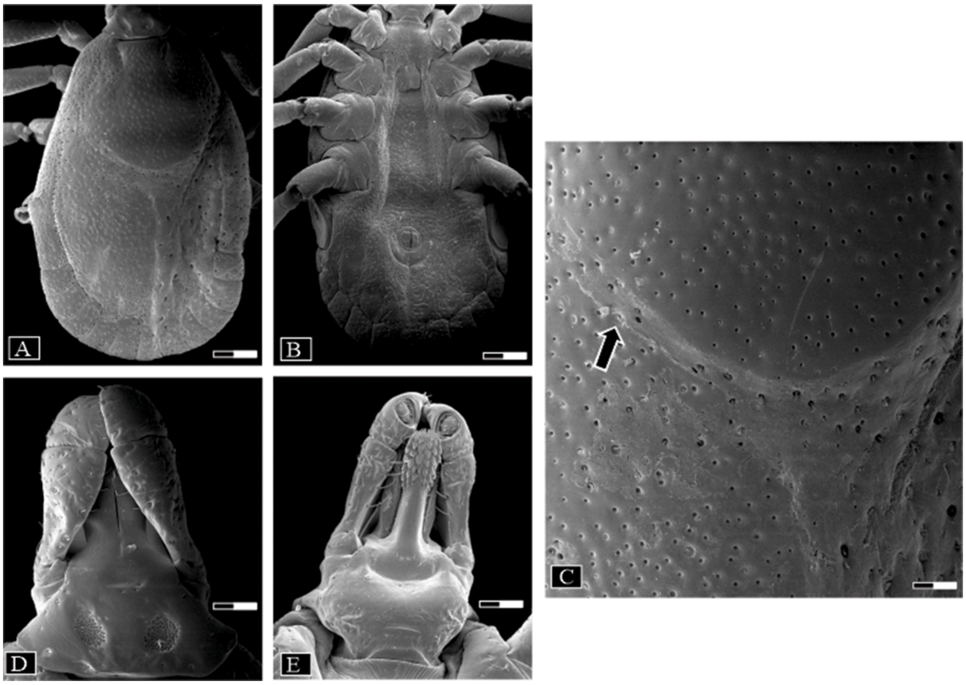

**Fig. 23.** Gynandromorphism (protogynander intriqué) in *Amblyomma parkeri.* The idiosoma is represented by male features on the left side and female features on the right side, dorsally (A) and ventrally (B); however, there is a narrow invagination of female alloscutum on the male side (arrow), delimitating the female scutum on the male side (C). The Gnathosoma has a male palp on the left side and a female palp on the right side, but the basis capituli has a pair of porose areas (D, E). Bars: 0.5 mm in A, 1 mm in B, and 2 mm in C, D, E.

**Fig. 24.** Gynandromorphism (protogynander intriqué) in *Amblyomma parvum.* The two sexes are equally represented in dorsal (A) and ventral (B) views of the idiosoma (male on left, female on right); however, the capitulum is entirely male. Bars: 0.5 mm.

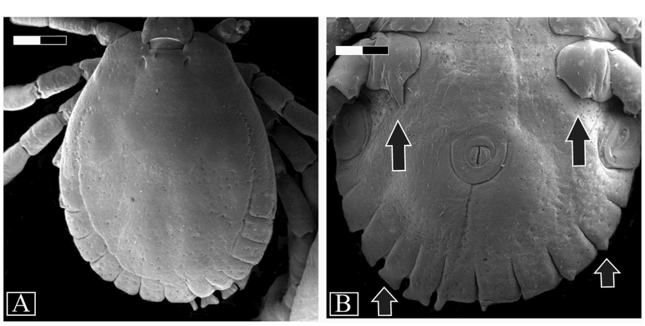

**Fig. 25.** Gynandromorphism (deuterogynander intriqué) in *Amblyomma brasiliense*, with female features restricted to the posterior left quadrant, dorsally (A) and ventrally (B), with few female parts on the alloscutum of the posterior right quadrant (arrows) and a female genital opening (not illustrated). Bars: 0.5 mm.

**Fig. 26.** *Amblyomma aureolatum* gynandromorph, small portion of male scutum and two male festoons on the right posterolateral area (metagynander). Bar: 1 mm.

& editing. **Pablo H. Nunes:** Investigation, Resources, Writing – review & editing. **Matias P.J. Szabó:** Investigation, Resources, Writing – review & editing. **Monize Gerardi:** Investigation, Resources, Writing – review & editing. **Rodrigo H.F. Teixeira:** Investigation, Resources, Writing – review & editing. **Silvio C. da Silva:** Investigation, Resources, Writing – review & editing. **Louise B. Kmetiuk:** Investigation, Resources, Writing – review & editing. **Isabella P. Pesenato:** Investigation, Resources, Writing – review & editing. **Arlei Marcili:** Investigation, Resources, Writing – review & editing. **João L.H. Faccini:** Investigation, Resources, Writing – review & editing. **Thiago F. Martins:** Conceptualization, Funding acquisition, Investigation, Resources, Writing – original draft, Writing – review & editing.

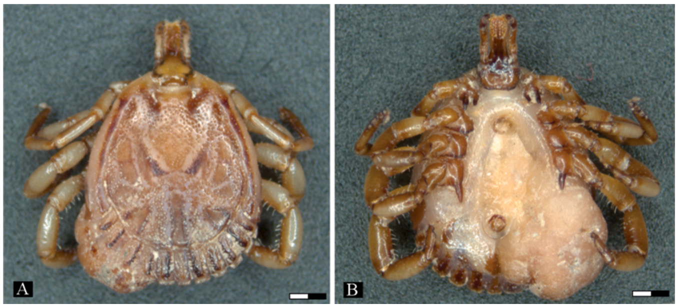

**Fig. 27.** Gynandromorphism (metagynander) in *Amblyomma cajennense* sensu stricto. Dorsally (A) of male features. Ventrally (B), female features restricted to a postero-left region of the idiosoma, which can also be noted as an expanded cuticle from the dorsal view. Bars: 1 mm.

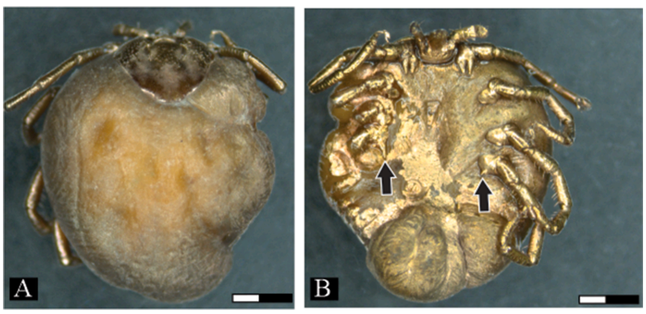

**Fig. 28.** Gynandromorphism (metagynander) in *Amblyomma oblongoguttatum.* Dorsally (A) of female features. Ventrally (B), male features restricted to right festoons and right coxa IV with long external spur (arrows). Specimen shows gold metallization because it was previously prepared for scanning electron microscopy, which could not be accomplished. Bars: 0.5 mm.

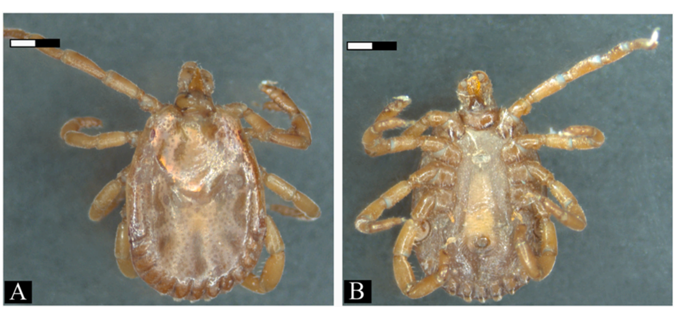

**Fig. 29.** Gynandromorphism (metagynander intriqué) in *Amblyomma brasiliense*, with female features restricted to left capitulum dorsally (A) and ventrally (B), with partial delimitation of female suctum dorsally. Bars: 1 mm.

### Declaration of Competing Interest

The authors declare no conflict of interest

### Data availability

Data will be made available on request.

### Acknowledgements

Authors are kindly thankful to CAPES/DPG - "Amazônia-Legal" (Support Program for Postgraduate Studies in the Legal Amazon), number- 088.990.417-09 for H.R.L. research supporting. The researcher T.F.M. is supported by "Fundação de Amparo à Pesquisa do Estado de São Paulo" (FAPESP Process N°. 2019/03167-0, 2020/05987-1).

We also thank all researchers that contributed to data collection: Arnaud J. L. Desbiez, Associate Researcher, The Royal Zoological Society of Scotland (RZSS), Giant Armadillo Conservation Project (Pantanal), "Instituto de Pesquisas Ecológicas" (IPÊ); Emília Patrícia Medici, International Union for Conservation of Nature, Species Survival Commission, Tapir Specialist Group, Lowland Tapir Conservation Initiative, Institute for Ecological Research, School of Environmental Conservation and Sustainability; Mariana M. Furtado, "Instituto Onça-Pintada".

### References

Alekseev, A., Dubinina, H., Jääskeläinen, A., Vapalahti, O., Vaheri, A., 2007. First report on tick-borne pathogens and exoskeleton anomalies in *Ixodes persulcatus* Schulze (Acari : ixodidae) collected in Kokkola Coastal Region, Finland. Int. J. Acarol. 33, 253–258. https://doi.org/10.1080/01647950708684530.

Alekseev, A.N., Dubinina, H.V., 2008. Enhancement of risk of tick-borne infection: environmental and parasitological aspects of the problem. J. Med. Entomol. 45, 812–815. https://doi.org/10.1603/0022-2585(2008)45-812:eoroti-2.0.co;2.

Azzi, C., Aprígio, C., Souza, R., Borsoi, A., Bitencourth, K., Ferreira, A., Amorim, M., Oliveira, S., Gazeta, G., 2019. Morphological abnormality in larvae of *Amblyomma oblongoguttatum* (Acari: ixodidae). Vet. News. 25, 1–10. https://doi.org/10.14393/VTN-v25n1-2019.1.

Balinandi, S., Mugisha, L., Bbira, J., Kabasa, W., Nakayiki, T., Bakkes, D.K., Lutwama, J. J., Chitimia-Dobler, L., Malmberg, M., 2019. General and local morphological anomalies in *Amblyomma lepidum* (Acari: ixodidae) and *Rhipicephalus decoloratus* infesting cattle in Uganda. J. Med. Entomol. 56, 873–877. https://doi.org/10.1093/jme/tjy221.

Brumpt, P.E., 1934. Le gynandromorphisme chez les ixodinés. Un curieux cas obtenu dans un élevage d'*Amblyomma dissimile*. Ann. Parasitol. Hum. Comparée. 12, 98–104. https://doi.org/10.1051/PARASITE/1934122098.

Buczek, A., Bartosik, K., Buczek, A.M., Buczek, W., Kulina, D., 2019. Abnormal development of *Hyalomma marginatum* ticks (Acari: ixodidae) induced by plant cytotoxic substances. Toxins (Basel) 11, 445. https://doi.org/10.3390/toxins11080445.

Campana-Rouget, Y., 1959. [Teratology of ticks]. Ann. Parasitol. Hum. Comp. 34, 354–431.

Chitimia-Dobler, L., Bestehorn, M., Bröker, M., Borde, J., Molcanyi, T., Andersen, N.S., Pfeffer, M., Dobler, G., 2017. Morphological anomalies in *Ixodes ricinus* and *Ixodes inopinatus* collected from tick-borne encephalitis natural foci in Central Europe. Exp. Appl. Acarol. 72, 379–397. https://doi.org/10.1007/s10493-017-0163-5.

Chitimia-Dobler, L., Pfeffer, M., 2017. Gynandromorphism and local morphological abnormalities in *Dermacentor reticulatus* (Acari: ixodidae). Syst. Appl. Acarol. 22, 449–455. https://doi.org/10.11158/saa.22.4.1.

Chitimia-Dobler, L., Dunlop, J.A., Pfeffer, T., Würzinger, F., Handschuh, S., Mans, B.J., 2023. Hard ticks in Burmese amber with Australasian affinities. Parasitology 150, 157–171. https://doi.org/10.1017/S0031182022001585.

Corwin, D., Clifford, C.M., Keirans, J.E., 1979. An improved method for cleaning and preparing ticks for examination with the scanning electron microscope. J. Med. Entomol. 16, 352–353.

Dantas-Torres, F., Fernandes Martins, T., Muñoz-Leal, S., Onofrio, V.C., Barros-Battesti, D.M., 2019. Ticks (Ixodida: argasidae, Ixodidae) of Brazil: updated species checklist and taxonomic keys. Ticks Tick Borne Dis 10, 101252. https://doi.org/10.1016/j.ttbdis.2019.06.012.

Domínguez, A.L., Bermúdez, C.S., 2020. Firsts records of abnormalities and gynandromorphism in hard ticks (Ixodida: ixodidae) from Panama. Syst. Appl. Acarol. 25, 1199–1208. https://doi.org/10.11158/SAA.25.7.4.

Domínguez, A., .L.., Arana-Espinoza, J., Bermúdez, C., .S.., 2022. Abnormal morphology in *Amblyomma coelebs* and *Amblyomma* cf. *oblongoguttatum* (Acari: ixodidae) collected on free-roaming Central American Tapir (*Tapirus bairdii*) from Nicaragua. Acarol. Stud. 4, 46–50. https://doi.org/10.47121/acarolstud.990448.

Domínguez, L., Perez, E., Castillero, S.B., 2020. First report of abnormal morphology in the tick *Dermacentor dissimilis* (Acari: ixodidae) and evidence of molt nymph-adult on hosts from Nicaragua. Acarol. Stud. 2, 46–50.

Domínguez, L.G., Montenegro, V.M., Bermúdez, S.E., 2021. Morphologic abnormalities in *Amblyomma mixtum, Amblyomma naponense, Amblyomma* cf. *oblongoguttatum* and *Amblyomma tapirellum* (Acari: ixodidae) of Costa Rica. Syst. Appl. Acarol. 26, 509–518. https://doi.org/10.11158/saa.26.3.1.

Estrada-Peña, A., 2001. Abnormal development of *Rhipicephalus sanguineus* (Ixodidae). Exp. Appl. Acarol. 25, 757–761. https://doi.org/10.1023/A:1016310214918.

Fonseca, F., 1935. Notas de Acareologia. XXI. Gymnandromorphismo em *Amblyomma cajennense* (Fabr., 1787). Mem. Inst. Butantan. 10, 39–41.

Guglielmone, A.A., Beati, L., Barros-Battesti, D.M., Labruna, M.B., Nava, S., Venzal, J.M., Mangold, A.J., Szabó, M.P.J., Martins, J.R., González-Acuña, D., Estrada-Peña, A., 2006. Ticks (Ixodidae) on humans in South America. Exp. Appl. Acarol. 40, 83–100. https://doi.org/10.1007/s10493-006-9027-0.

Guglielmone, A.A., Castella, J., Mangold, A.J., Estrada-Peña, A., Vinabal, A.E., 2000. Phenotypic anomalies in a collection of Neotropical ticks (Ixodidae). Acarologia 40, 127–132.

Kar, S., Akyildiz, G., Yilmazer, N., Shaibi, T., Gargili, A., Vatansever, Z., 2015. External morphological anomalies in ixodid ticks from Thrace. Turkey. Exp. Appl. Acarol. 67, 457–466. https://doi.org/10.1007/s10493-015-9948-6.

Keskin, A., Simsek, E., Bursali, A., Keskin, A., 2016. Morphological abnormalities in ticks (Acari: ixodidae) feeding on humans in Central Black Sea region. Turkey. Zoomorphology 135, 167–172. https://doi.org/10.1007/s00435-016-0306-y.

Krawczak, F.S., Martins, T.F., Oliveira, C.S., Binder, L.C., Costa, F.B., Nunes, P.H., Gregori, F., Labruna, M.B., 2015. *Amblyomma yucumense* n. sp. (Acari: ixodidae), a parasite of wild mammals in southern Brazil. J. Med. Entomol. 52, 28–37. https://doi.org/10.1093/jme/tju007.

Labruna, M.B., Homem, V.S.F., Heinemann, M.B., Ferreira Neto, J.S., 2000. A case of Gynandromorphism in *Amblyomma oblongoguttatum* (Acari: ixodidae). J. Med. Entomol. 37, 777–779. https://doi.org/10.1603/0022-2585-37.5.777.

Labruna, M.B., Onofrio, V.C., Beati, L., Arzua, M., Bertola, P.B., Ribeiro, A.F., Barros-Battesti, D.M., 2009. Redescription of the female, description of the male, and several new records of *Amblyomma parkeri* (Acari: ixodidae), a South American tick species. Exp. Appl. Acarol. 49, 243–260. https://doi.org/10.1007/S10493-009-9257-Z.

Labruna, M.B., Ribeiro, A.F., Cruz, M.V., Camargo, L.M.A., Camargo, E.P., 2002. Gynandromorphism in *Amblyomma cajennense* and *Rhipicephalus sanguineus* (Acari: ixodidae). J. Parasitol. 88, 810–811. https://doi.org/10.1645/0022-3395(2002)088-0810:GIACAR-2.0.CO;2.

Latif, A.A., Dhadialla, T.S., Newson, R.M., 1988. Abnormal development of *Amblyomma variegatum* (Acarina: ixodidae). J. Med. Entomol. 25, 142–143. https://doi.org/10.1093/jmedent/25.2.142.

Lopes, M.G., May Junior, J., Foster, R.J., Harmsen, B.J., Sanchez, E., Martins, T.F., Quigley, H., Marcili, A., Labruna, M.B., 2016. Ticks and rickettsiae from wildlife in Belize, Central America. Parasit. Vectors. 9, 62. https://doi.org/10.1186/s13071-016-1348-1.

Luz, H., Faccini, J.L., Landulfo, G., Sampaio, J., Neto, S., Famadas, K., Onofrio, V., Barros Battesti, D., 2013. New host records of *Ixodes luciae* (Acari: ixodidae) in the State of Pará. Brazil. Rev. Bras. Parasitol. Vet. 22, 152–154. https://doi.org/10.1590/S1984-29612013000100028.

Martins, T.F., Igayara-Souza, C.A., Sanches, T.C., Melo, M.A., Bolochio, C.E., Nagahama, A.A., Hidasi, H.W., Junior, G.N.P., Acosta, I.C.L., Muñoz-Leal, S., Labruna, M.B., 2017. Diversidade de carrapatos (Acari: ixodidae) em animais silvestres recebidos pelo zoológico municipal de Guarulhos. Ars Vet. 33, 20–25. https://doi.org/10.15361/2175-0106.2017V33N1P20-25.

Martins, T.F., Luz, H.R., Muñoz-Leal, S., Ramirez, D.G., Milanelo, L., Marques, S., Sanches, T.C., Onofrio, V.C., da, C.L., Acosta, I., Benatti, H.R., Maturano, R., de Oliveira, P.B., Albuquerque, G.R., Marcili, A., Flausino, W., Silveira, L.F., McIntosh, D., Faccini, J.L.H., Labruna, M.B., 2019. A new species of *Amblyomma* (Acari: ixodidae) associated with monkeys and passerines of the Atlantic rainforest biome, Southeastern Brazil. Ticks Tick. Borne. Dis. 10, 101259 https://doi.org/10.1016/j.ttbdis.2019.07.003.

Molaei, G., Little, E.A.H., 2018. A nine-legged tick: report of a morphological anomaly in the blacklegged tick, *Ixodes scapularis* (Acari: ixodidae) from the northeastern United States. Ticks Tick. Borne. Dis. 9, 778–780. https://doi.org/10.1016/j.ttbdis.2018.03.003.

Muñoz-Leal, S., Martins, T.F., Luna, L.R., Rodriguez, A., Labruna, M.B., 2018. A new collection of *Amblyomma parvitarsum* (Acari: ixodidae) in Peru, with description of a gynandromorph and report of *Rickettsia* detection. J. Med. Entomol. 55, 464–467. https://doi.org/10.1093/jme/tjx194.

Nava, S., Beati, L., Labruna, M.B., Cáceres, A.G., Mangold, A.J., Guglielmone, A.A., 2014. Reassessment of the taxonomic status of *Amblyomma cajennense* (Fabricius, 1787) with the description of three new species, *Amblyomma tonelliae* n. sp., *Amblyomma interandinum* n. sp. And *Amblyomma patinoi* n. sp., and reinstatement of *Amblyomma mixtum* Koch, 1844, and *Amblyomma sculptum* Berlese, 1888 (Ixodida: ixodidae). Ticks Tick Borne Dis. 5, 252–276. https://doi.org/10.1016/j.ttbdis.2013.11.004.

Neumann, L.G., 1899. Révision De La Famille Des Ixodidés (3e Mémoire), 12. Mémoires de la Société Zoologique de France, pp. 107–294.

Nowak-Chmura, M., 2012. Teratological changes in tick morphology in ticks feeding on exotic reptiles. J. Nat. Hist. 46, 911–921. https://doi.org/10.1080/00222933.2011.651635.

Parola, P., Paddock, C.D., Socolovschi, C., Labruna, M.B., Mediannikov, O., Kernif, T., Abdad, M.Y., Stenos, J., Bitam, I., Fournier, P.-E., Raoult, D., 2013. Update on tick-borne rickettsioses around the world: a geographic approach. Clin. Microbiol. Rev. 26, 657–702. https://doi.org/10.1128/CMR.00032-13.

Pereira, C., Castro, M.P., 1945. Sobre um ginandromorfo de *Rhipicephalus sanguineus* Latr., 1804. Arq. Inst. Biol. 10, 187–192.

Rivera-Páez, F.A., Labruna, M.B., Martins, T.F., Rodrigues-Sampieri, B., Camargo-Mathias, M.I., 2017. A case of gynandromorphism in *Amblyomma mixtum* (Acari, Ixodidae). Rev. Colomb. Entomol. 43, 268–270. https://doi.org/10.25100/socolen.v43i2.5956.

Serra-Freire, N.M., Batalla, L.A., Julca-Lozano, R., 2012. Mutagenic occurrence in male of *Amblyomma* (*Cernyomma*) *extraoculatum* (Linnaeus, 1766) from forest environment in Peru - Case report. Rev. Bras. Med. Vet. 34, 31–34.

Shuaib, Y.A., Isaa, M.H., Ezz-Eldin, M.I.-E., Abdalla, M.A., Bakhiet, A.O., Chitimia-Dobler, L., 2020. Morphological abnormalities in ticks (Acari: ixodidae) collected from domestic animal species in Sudan. Exp. Appl. Acarol. 82, 161–169. https://doi.org/10.1007/s10493-020-00534-x.

Szabó, M.P.J., Labruna, M.B., Castagnolli, K.C., Garcia, M.V., Pinter, A., Veronez, V.A., Magalhães, G.M., Castro, M.B., Vogliotti, A., 2006. Ticks (Acari: ixodidae) parasitizing humans in an Atlantic rainforest reserve of Southeastern Brazil with notes on host suitability. Exp. Appl. Acarol. 39, 339–346. https://doi.org/10.1007/s10493-006-9013-6.

Szabó, M.P.J., Pinter, A., Labruna, M.B., 2013. Ecology, biology and distribution of spotted-fever tick vectors in Brazil. Front. Cell. Infect. Microbiol. 3, 27. https://doi.org/10.3389/fcimb.2013.00027.

Zharkov, S.D., Dubinina, H.V., Alekseev, A.N., Jensen, P.M., 2000. Anthropogenic pressure and changes in *Ixodes* tick populations in the Baltic region of Russia and Denmark. Acarina 8, 137–141.