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Inventory

Entomogenous galls and their associated fauna in deciduous dry forest and woodland vegetation remnants (Caatinga) in the Northern *Depressão Sertaneja*, Brazil

Rafael Aguiar Marinho[1]*, *Valéria Cid Maia*[2] & *Maria Regina de Vasconcellos Barbosa*[3]

[1]*Universidade Federal da Paraíba, Departamento de Sistemática e Ecologia, Programa de Pós-Graduação em Ciências Biológicas, Cidade Universitária, 58051-900, João Pessoa, PB, Brasil.*
[2]*Universidade Federal do Rio de Janeiro, Departamento de Entomologia, Museu Nacional, Quinta da Boa Vista, s/n, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil.*
[3]*Universidade Federal da Paraíba, Departamento de Sistemática e Ecologia, Cidade Universitária, 58051-900, João Pessoa, PB, Brasil.*
**Corresponding author: rafa_paraibano@hotmail.com*

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Abstract: A survey and characterization of entomogenous galls and their associated fauna were carried out in six remnants of Caatinga in the Northern *Depressão Sertaneja*, in the states of Paraíba, Rio Grande do Norte and Ceará. We identified 41 gall morphotypes in 24 plant species, belonging to 12 botanical families. Fabaceae had 29.2% (n = 12) of the total number of gall morphotypes found. Leaves (61%) and stems (25%) were the most attacked organs. Most morphotypes are glabrous (75.6%), while only 24.4% exhibit trichomes. Most galls were induced by insects of the Cecidomyiidae family. The associated fauna comprised successors, cecidophages, tenants, and parasitoids. Sucessors were found in four morphotypes of galls and included spiders and four orders of insects: Hemiptera, Coleoptera, Lepidoptera, and Hymenoptera (Formicidae). The tenants were represented by *Tanaostigmoides* (Tanaostigmatidae). The parasitoids, found in 18 morphotypes (43.9%), were represented by six families of Hymenoptera. We recorded the occurrence of new types of galls in 12 species of host plants. These gall records are new references for the Northern *Depressão Sertaneja* in the studied states.
Keywords: *Caatinga; Cecidomyiidae; semi-arid; galls; morphotype; parasitoids.*

Galhas entomógenas e sua fauna associada em remanescentes de floresta seca e vegetação lenhosa decídua (Caatinga) na Depressão Sertaneja Setentrional, Brasil

Resumo: Realizou-se um levantamento e caracterização de galhas entomógenas e sua fauna associada em seis remanescentes de Caatinga presentes na Depressão Sertaneja Setentrional nos estados da Paraíba, Rio Grande do Norte e Ceará. Identificamos 41 morfotipos de galhas em 24 espécies de plantas, pertencentes a 12 famílias botânicas. Fabaceae abrigou 29,2% (n = 12) do total de morfotipos de galhas encontrados. As folhas (61%) e os caules (25%) foram os órgãos mais atacados. A maioria dos morfotipos é glabra (75,6%), enquanto apenas 24,4% exibiram tricomas. As galhas, em sua maioria, foram induzidas por insetos da família Cecidomyiidae. A fauna associada compreendeu sucessores, fungívoros, inquilinos e parasitoides. Os primeiros foram encontrados em quatro morfotipos de galhas, estando representados por aranhas e quatro ordens de insetos: Hemiptera, Coleoptera, Lepidoptera e Hymenoptera (Formicidae). Os inquilinos foram representados por *Tanaostigmoides* Ashmead, 1896 (Tanaostigmatidae). Já os parasitoides, encontrados em 18 morfotipos de galhas (43,9%), foram representados por seis famílias de Hymenoptera. Registramos a ocorrência de novos tipos de galhas em 12 espécies de plantas hospedeiras. Os registros de galhas também são novas referências para a Depressão Sertaneja Setentrional nos estados estudados.
Palavras-chave: *Caatinga; Cecidomyiidae; semiárido; galhas, morfotipo; parasitoides.*

Introduction

Some plants can undergo alterations in plant tissues, caused by parasitic insects, causing the formation of structures known as galls (Hartley 1998). Any organ of the host plant, regardless of its architecture, can have its tissue modified into a gall by a parasitic agent, which makes this association one of the most complex in the natural world (Shorthouse et al. 2005).

The emergence of galls is one of the most immediate responses of plants to the actions of gall-inducers and, therefore, it is a model capable of revealing important and quantifiable ecological patterns (Fonseca & Fleck 2007). Inside the gall, the immature forms of the insects receive protection against the effect of several abiotic factors, which vary in intensity according to the biome where they occur (Stone & Schönrogge 2003, Raman et al. 2005).

Among galling insects, the Cecidomyiidae (Diptera) present the highest radiation within the endophytic habit. They constitute a very diverse family, with ca. 6,500 described species (Gagné & Jaschhof, 2021), most of which are gall-inducing. Cecidomyiids establish complex trophic interactions with plants, symbiotic fungi, predators of larvae and parasitoids of their immature stages, making them important sources of ecological information (Stireman et al. 2010, Maia 2022).

The Cecidomyiidae appeared in the Cretaceous and intensely diversified in the Cenozoic (Gagné, 1989). Analyses of the feeding behavior in the Cecidomyiinae tribe suggest that the transition from ancestral fungus feeding to plant feeding occurred once or twice in its evolution (Dorchin et al. 2019). The colonization of plant tissues, galls, and leaf mines, dates from the Cretaceous, when fossil records of Cecidomyid bodies and insect-mediated damaged leaves were found (Srivastava et al. 2000).

Galls in the Caatinga biome began to be investigated only recently, with the first survey dating from 2011 (Santos et al. 2011). Currently there are data for the states of Ceará, Pernambuco, Alagoas, and Bahia (Carvalho-Fernandes et al. 2012, Costa et al. 2014b, Nogueira et al. 2016, Alcantara et al. 2017, Brito et al. 2018). However, the aspect that stands out about the occurrence of galls in this biome is the limited knowledge and the low number of inventories as compared to other Brazilian biomes such as the Atlantic Forest and Cerrado (Mendonça et al. 2008, Stehmann et al. 2009, Araújo et al. 2019). However, the Caatinga may have a galling fauna as relevant ecologically as have already been detected in the Cerrado (Gonçalves-Alvim & Fernandes. 2001, Araújo et al. 2013, Costa 2016) and in the Caatinga-Cerrado transition zones (Costa et al. 2014a, Nogueira et al. 2016).

The Brazilian Caatinga biome is considered one of the largest areas of the seasonally dry tropical forest and woodland biome (Pennington et al. 2001, Fernandes et al. 2020). It is composed of a mosaic of deciduous dry forests and woodland vegetation with thorns in Northeast Brazil. Veloso et al. (2002) divided the Caatinga into eight ecoregions reflecting differences in climatic seasonality, water availability (in soil and rainfall), relief, and geomorphology. According to them, the most typical Caatinga vegetation is found in the *Depressão Sertaneja*, the core region of the biome. It is divided by the Borborema Plateau in two ecoregions, the Northern and the Southern *Depressão Sertaneja*. The severe abiotic conditions, inherent to the Northern *Depressão Sertaneja*, make this Caatinga ecoregion unique for studies with galling insects, to find out variations in the occurrence of galls or even patterns of diversity.

In the present study, the Northern *Depressão Sertaneja* was selected to inventory, and characterize the occurrence of galls and their associated fauna.

Materials and Methods

1. *Study area*

The study area is the northern part of the *Depressão Sertaneja* (Figure 1). According to Veloso et al (2002), in this ecoregion, with a hot and semi-arid climate, rainfall is more scarce and concentrated than in the rest of the biome, with an annual average of 500 to 800 mm, and extremes as low as 350 mm/year. The soil is shallow, stony, of crystalline origin, with medium to high fertility, and very susceptible to erosion. Temperatures are high, with annual averages between 25 and 30 °C with only a few degrees of difference between the averages in the coldest and warmest months (Sampaio 2003). The predominant

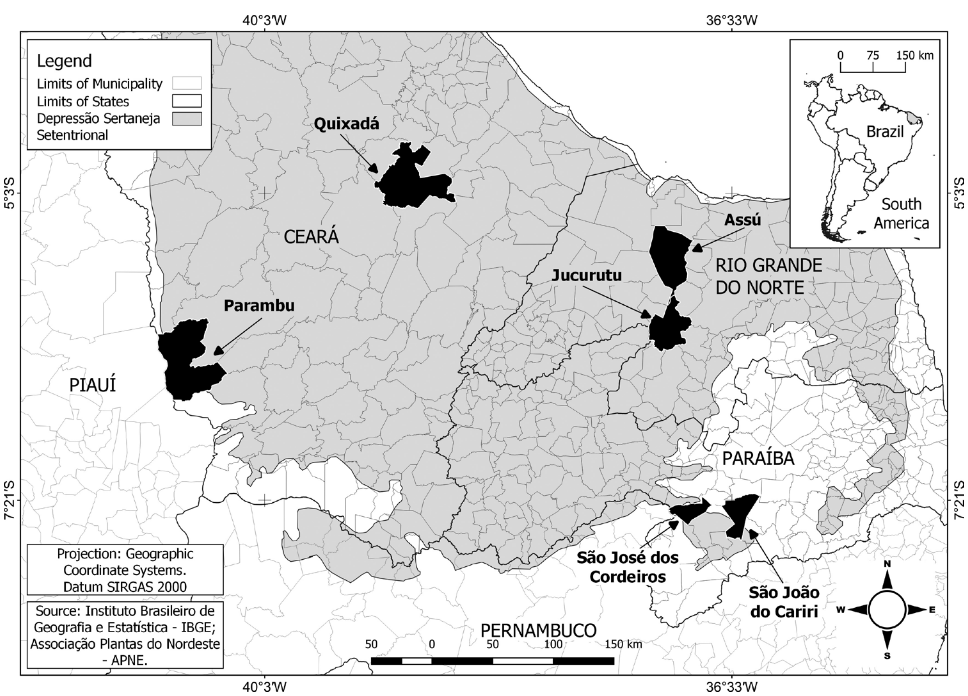

Figure 1. Location Map of the six study areas included in the Northern Depressão Sertaneja, Brazil. Map prepared by Maurício Oliveira dos Santos (2021).

vegetation physiognomy is shrub-tree, quite degraded, except in the few Conservation Units that still resist anthropic degradation.

In this region, six sites were selected: two in the state of Paraíba, both located in the Cariri Paraibano - The Experimental Station of the Federal University of Paraíba (EESJCariri), in the municipality of São João do Cariri, and the Private Natural Heritage Reserve (RPPN) Fazenda Almas (RPPN Almas), located in the municipality of São José dos Cordeiros; two in the state of Rio Grande do Norte - RPPN Stoessel de Brito (RPPN Stoessel), in the municipality of Jucurutu, and the National Forest of Açu (Flona), in the municipality of Açu; two in Ceará - the RPPN Olho d'água do Urucu, in the municipality of Parambu, and the RPPN Não me Deixes, in the municipality of Quixadá.

2. *Sampling*

The sampling of galls and host plants was conducted during two rainy seasons, from February to June 2019, and from February to May 2021, once per season at each site, totaling 9 months in the field. Due to the strong deciduousness of the vegetation during the dry season, the field work was conducted only in rainy seasons. In each area, 10 transects measuring 4 × 50 m, 100 meters apart from each other, were plotted. In each transect, for better orientation and surveying, a straight orientation line was plotted with the aid of a compass, and every 10 meters wooden stakes 1.20 m tall were inserted in the ground. Two people inspected the transects for at least one hour each seeking and collecting galls, for a total of 10 hours of minimum sampling effort per area. All trees, shrubs, and subshrubs inside the transect, with a minimum height of 1m and a maximum of 3 m, were inspected. All galls found were photographed in the field. The plants that had galls on leaves, or other visually identifiable organs, had their leaves and/or structures collected and stored in individual plastic bags with field identification. Subsequently, dried specimens of all species of plants collected were prepared and deposited at Herbarium JPB, at the Department of Systematics and Ecology of the Federal University of Paraíba (UFPB).

In the laboratory, the galls were separated by morphotype, and some samples of each morphotype were dissected under a stereomicroscope to verify the number of internal chambers, and obtain immature insect specimens, if present. These immatures were preserved in 70% ethanol and placed in labeled microtubes. The remaining samples were destined for the rearing of galling insects and possible associated fauna (parasitoids, predators, tenants, kleptoparasites, and successors). To this end, each gall morphotype was placed in labeled plastic pots lined with moistened paper (for species whose pupa matures in the gall) or containing soil from the area itself (for species whose pupa matures in the soil). The pots were inspected daily and each adult that emerged was captured using alcohol sprays with a plastic pipette. All specimens obtained from breeding in the laboratory were also preserved in 70% ethanol. The Cecidomyiidae (Diptera) were prepared and mounted on permanent microscopy slides (Gagné 1994) and identified at the Entomology Laboratory at the Rio de Janeiro National Museum (MNRJ). Gagné's keys (Gagné 1994) were used to identify the genera. For species identification, we used information from the host plant, gall morphotypes, and species descriptions. Micro-Hymenoptera were identified to the family and genus levels by Dr. Maria Antonieta Pereira de Azevedo (Collaborating Researcher, National Museum) using Gibson's key (Gibson 1997). Hymenoptera obtained only in the larval or pupal stage remained identified only to order. All insects were deposited in the Entomology collection of MNRJ.

The galls were characterized, in the laboratory, by color, shape, presence or absence of trichomes (hairy or glabrous), as well as the leaf surface on which they were found (adaxial, abaxial, both or intralaminar). To standardize the forms of the galls, we adopted the terminology of Isaias et al. (2013). Maximum specificity was considered in the separation of morphotypes so that similar galls on different plant species were classified as different morphotypes (Carneiro et al. 2009).

Results

A total of 2,796 plants, corresponding to 66 botanical species, were sampled in the six studied areas. Forty-one gall morphotypes were obtained on 24 plant species belonging to 12 botanical families (Table 1). Forty-two plant species (63,4%) did not present galls. Among the host plants, 23

Table 1. Characterization of insect galls in six areas of tropical dry forest **and woodland vegetation (Caatinga) in the Northern *Depressão Sertaneja*,** Northeastern Brazil. Legends: P = Parasitoid, S = Successor, T = Tenants, F = Fungivore; AL = RPPN Almas, FL = Flona de Açu, ND = RPPN Não me Deixes, OL = RPPN Olho do Urucu, SB = RPPN Stoessel de Brito, SC = EE São João do Cariri.

Family/ Species of host plants	Galls									
	Organ	Leaf surface	Shape	Color	Trichomes	Occurrence	Chambers	Inductor Insect	Associated fauna	Site	Figure
Anacardiaceae											
Spondias tuberosa Arruda	Stem	---	Fusiform	Gray	No	Isolated	various	Undetermined	Undetermined	AL	2-a
Bignoniaceae											
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Stem	---	Fusiform	Gray	No	Grouped	various	Undetermined	Undetermined	ND	2-b
Handroanthus serratifolius (Vahl) S. Grose	Stem	---	Globoid	Green	No	Isolated	various	Cecidomyiidae	Tanaostigmatidae (T)/ Torymidae (P) (Hymenoptera)	FL	2-c

Continue...

...Continuation

Family/ Species of host plants	Galls										
	Organ	Leaf surface	Shape	Color	Trichomes	Occurrence	Chambers	Inductor Insect	Associated fauna	Site	Figure
Boraginaceae											
Cordia glazioviana (Taub.) Gottschling & J.S.Mill.	Leaf fold	Adaxial	Lenticular	Green	No	Isolated	one	Cecidomyiidae	Undetermined	OL	2-d
Varronia leucocephala (Moric.) J.S.Mill.	Leaf fold	Abaxial	Fusiform	Green	No	Isolated	one	Cecidomyiidae	Undetermined	AL	2-e
Burseraceae											
Commiphora leptophloeos (Mart.) J.B.Gillett	Bud	---	Fusiform	Green	Yes	Grouped	one	Undetermined	Hymenoptera (P)	AL	2-f
Capparaceae											
Cynophalla flexuosa (L.) J.Presl	Leaf fold	Adaxial	Lenticular	Green	No	Grouped	One	Undetermined	Undetermined	SB	2-g
Combretaceae											
Combretum leprosum Mart.	Stem	---	Fusiform	Green	No	Isolated	various	Clinodiplosini (Cecidomyiidae)	Galeopsomyia sp (P) Pteromalidae (P) Scelionidae (P) (Hymenoptera)	AL, ND	2-h
	Leaf fold	Adaxial	Globoid	Green	No	Isolated	one	Cecidomyiidae	Undetermined	AL	2-i
	Leaf fold	Intralaminar	Lenticular	Green	No	Isolated	one	Cecidomyiidae	Undetermined	ND	2-j
Euphorbiaceae											
Croton blanchetianus Baill.	Leaf fold	Adaxial	Globoid	Green	Yes	Isolated	one	Clinodiplosini (Cecidomyiidae)	Aranae (S)/ Hemiptera (S)/ Eulophidae (P)/ Galeopsomyia sp (P)/ Torymidae (P)/ Eurytomidae (P)/Scelionidae (P) (Hymenoptera)	AL, SJ, SB, FL, ND, OL	2-k
	Leaf fold	Adaxial	Globoid	Green	No	Isolated	one	Cecidomyiidae	Undetermined	AL	2-l
Croton adenocalyx Baill.	Stem	---	Fusiform	Yellow	No	Isolated	one	Undetermined	Undetermined	ND	2-m
Croton echioides Baill.	Leaf fold	Adaxial/ abaxial	Globoid	Green	Yes	Isolated	one	Cecidomyiidae	*Stomatosema sp* (F) Eulophidae (P)/ Eupelmidae (P) (Hymenoptera)	AL, OL	2-n
	Leaf fold	Intralaminar	Lenticular	Green	Yes	Isolated	one	Cecidomyiidae	Eulophidae (P) (Hymenoptera)	AL	2-o
	Stem	---	Fusiform	Green	No	Isolated	one	Cecidomyiidae	Hymenoptera (P)	AL	2-p
Manihot carthagenensis (Jacq.) Müll. Arg.	Leaf fold	Adaxial	Globoid	Green	No	Grouped	various	Cecidomyiidae	Eulophidae (P) (Hymenoptera)	AL	2-q
	Leaf fold	Adaxial	Clavate	Green	No	Isolated	one	Cecidomyiidae	Eulophidae (P) (Hymenoptera)	AL	2-r

Continue...

...Continuation

Family/ Species of host plants	Galls										
	Organ	Leaf surface	Shape	Color	Trichomes	Occurrence	Chambers	Inductor Insect	Associated fauna	Site	Figure
Manihot dichotoma Ule	Leaf fold	Adaxial	Clavate	Green	No	Isolated	one	Cecidomyiidae	Undetermined	SB, ND	2-s
Fabaceae											
Bauhinia cheilantha (Bong.) Steud.	Leaf Fold	Adaxial	Globoid	Green	Yes	Isolated	one	Undetermined	Undetermined	AL	2-t
	Leaf Fold	Adaxial	Globoid	Green	No	Isolated	one	Undetermined	Undetermined	SB	2-u
	Leaf Fold	Adaxial	Fusiform	Green	No	Isolated	one	Cecidomyiidae	*Eurytoma sp* (P)/ Hymenoptera (P)	AL, SB	2-v
	Vein	Abaxial	Globoid	Green	Yes	Isolated	one	Undetermined	Undetermined	SB	2-w
	Leaf Fold	Intralaminar	Lenticular	Green	No	Isolated	one	Undetermined	Undetermined	SB	2-x
Cenostigma pyramidale (Tul.) Gagnon & G.P. Lewis	Leaf fold	Adaxial	Lenticular	Green	No	Isolated	one	Undetermined	Undetermined	ND	3-a
	Stem	---	Globoid	Gray	No	Isolated	various	Undetermined	Formicidae (S)/ Hymenoptera (P)	AL, SJ, ND, OL, FL, SB	3-b
	Leaf fold	Intralaminar	Lenticular	Green	Yes	Isolated	one	Undetermined	Undetermined	AL	3-c
Desmodium tortuosum (Sw.) DC.	Leaf fold	---	Marginal roll	Green	No	Grouped	one	Contarinia sp (Cecidomyiidae)	Eulophidae (P)	SB	3-d
Geoffroea spinosa Jacq.	Leaf fold	adaxial	Globoid	Green	No	Isolated	one	Undetermined	Undetermined	SB	3-e
Mimosa tenuiflora (Willd.) Poir.	Peciole	---	Fusiform	Brown	No	Isolated	one	Undetermined	Undetermined	SB	3-f
	Stem	---	Fusiform	Black	No	Isolada	one	Undetermined	Undetermined	SB	3-g
Sapindaceae											
Allophylus quercifolius (Mart.) Radlk.	Stem	---	Fusiform	Green	Yes	Isolated	one	Undetermined	Undetermined	AL	3-h
Serjania glabrata Kunth	Stem	---	Fusiform	Green	No	Isolated	one	Undetermined	Undetermined	OL	3-i
	Leaf fold	Adaxial	Lenticular	Green	No	Isolated	one	Undetermined	Undetermined	OL	3-j
Solanaceae											
Capsicum parvifolium Sendtn.	Stem	---	Fusiform	Green	No	Isolado	various	Clinodiplosis sp (Cecidomyiidae)	Eulophidae (P)	AL	3-k
Verbenaceae											
Lantana camara L.	Leaf fold	Adaxial	Globoid	Green	Yes	Isolated	one	Schismatodiplosis lantanae (Cecidomyiidae)	Eulophidae (P) Hymenoptera / Hemiptera (S)	AL, ND	3-l
	Leaf fold	Intralaminar	Lenticular	Green	No	Isolada	one	(Clinodiplosini) Cecidomyiidae	Hymenoptera (P)	AL	3-m
	Stem	---	Fusiform	Green	No	Isolated	various	Clinodiplosini (Cecidomyiidae)_	Hymenoptera (P)	AL	3-n
	Leaf fold	adaxial	Conical	Green	No	Isolada	one	Undetermined	Undetermined	AL	3-o
Vitaceae											
Cissus decidua Lombardi	Stem	---	Globoid	Gray	No	Isolated	various	Undetermined	Coleoptera (S)/ Lepidoptera (S)/ Eulophidade (P)	AL	3-q

***New record**

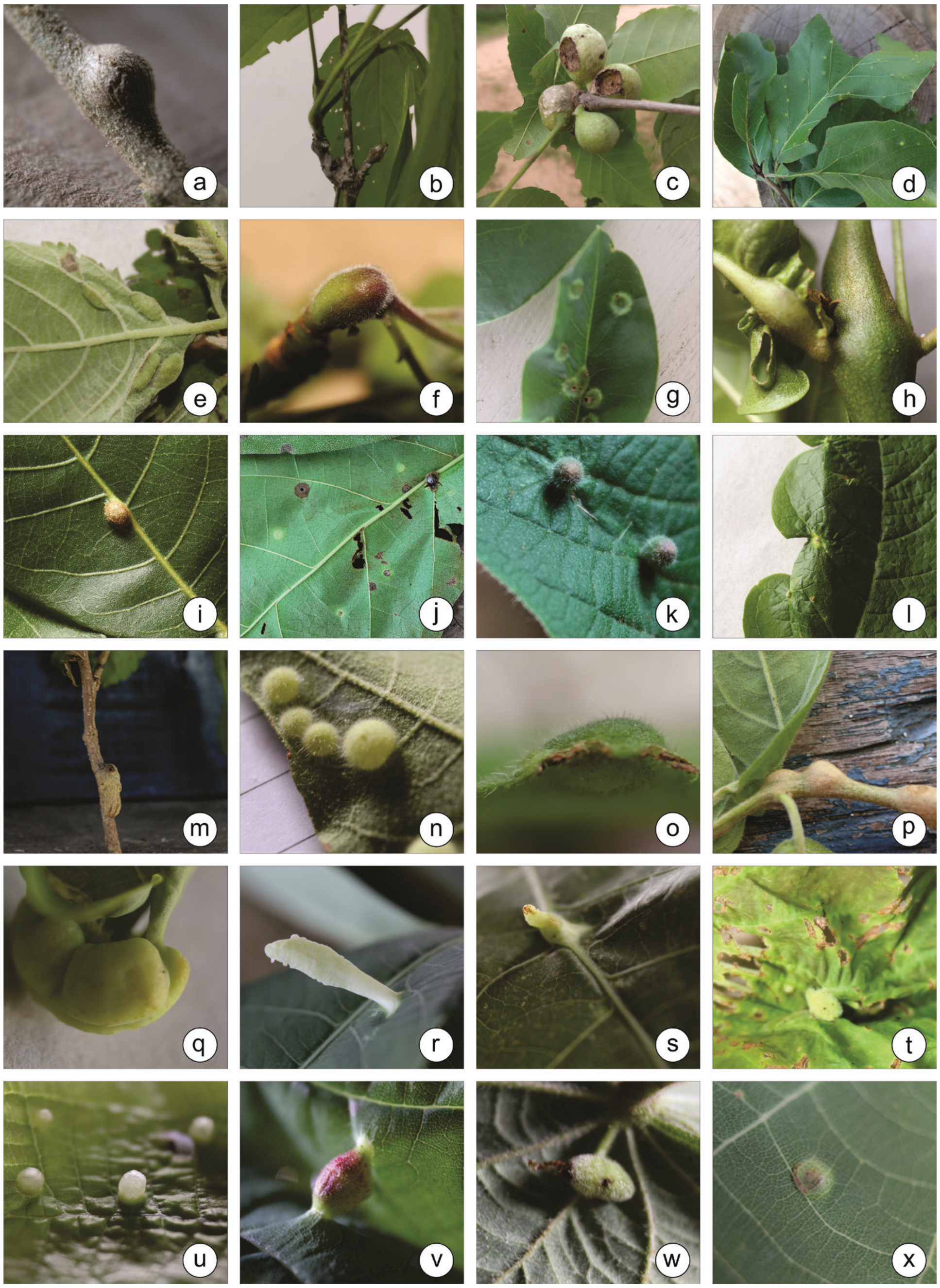

Figure 2. Galls found in six areas of Caatinga in the states of Ceará, Paraíba and Rio Grande do Norte, Brazil. a. In *Spondias tuberosa* - fusiform; b. In *Handroanthus impetiginosus* - fusiform; c. In *Handroanthus serratifolius* - globoid; d. In *Cordia glazioviana* - lenticular; e. In *Varronia leucocephala* - fusiform; f. In *Commiphora leptophloeos* - fusiform; g. In *Cynophala flexuosa* - lenticular; h-j. In *Combretum leprosum*: h. Fusiform, i. Globoid; j. lenticular; k-l. In *Croton blanchetianus*: k. globoid, l. globoid; m. In *Croton adenocalyx* - fusiform; n-p. In *Croton echioides*: n. Globoid, o. Lenticular, p. Fusiform; q-r. In *Manihot carthagenensis*, q. globoid, r. clavada; s. In *M. dichotoma* - clavate; t-x. In *Bauhinia cheilantha*: t. globoid, u. globoid, v. fusiform, w. globoid, x. lenticular. Sources: From the author (2019–2021).

are native and only *Lantana camara* L. is naturalized. Among the native species, six are endemic to the Caatinga: *Cenostigma pyramidale* (Tul.) Gagnon & G.P.Lewis; *Croton adenocalyx* Baill.; *C. blanchetianus* Baill.; *Manihot dichotoma* Ule; *Varronia leucocephala* (Moric.) J.S.Mill.; and *Spondias tuberosa* Arr. Others, endemic to Brazil but not to restricted to the Caatinga, also occur in the Cerrado, such as *Allophylus quercifolius* (Mart.) Radlk. and *Croton echioides* Baill. *Capsicum parvifolium* Sendtn. occurs in both the Caatinga and the Atlantic Forest.

The greatest richness of host plants was recorded in RPPN Almas, with 14 species distributed in 10 families. In the RPPN Olho do Urucu seven host species, belonging to five families, were identified. The EESJ Cariri presented the lowest richness, with only two species of host plants, in two botanical families (Table 1).

Fabaceae, Euphorbiaceae, and Verbenaceae had the greatest richness of host plants species, with Fabaceae harboring 29.2% (n = 12) of the total gall morphotypes found. *Bauhinia cheilantha* (Bong.) Steud.

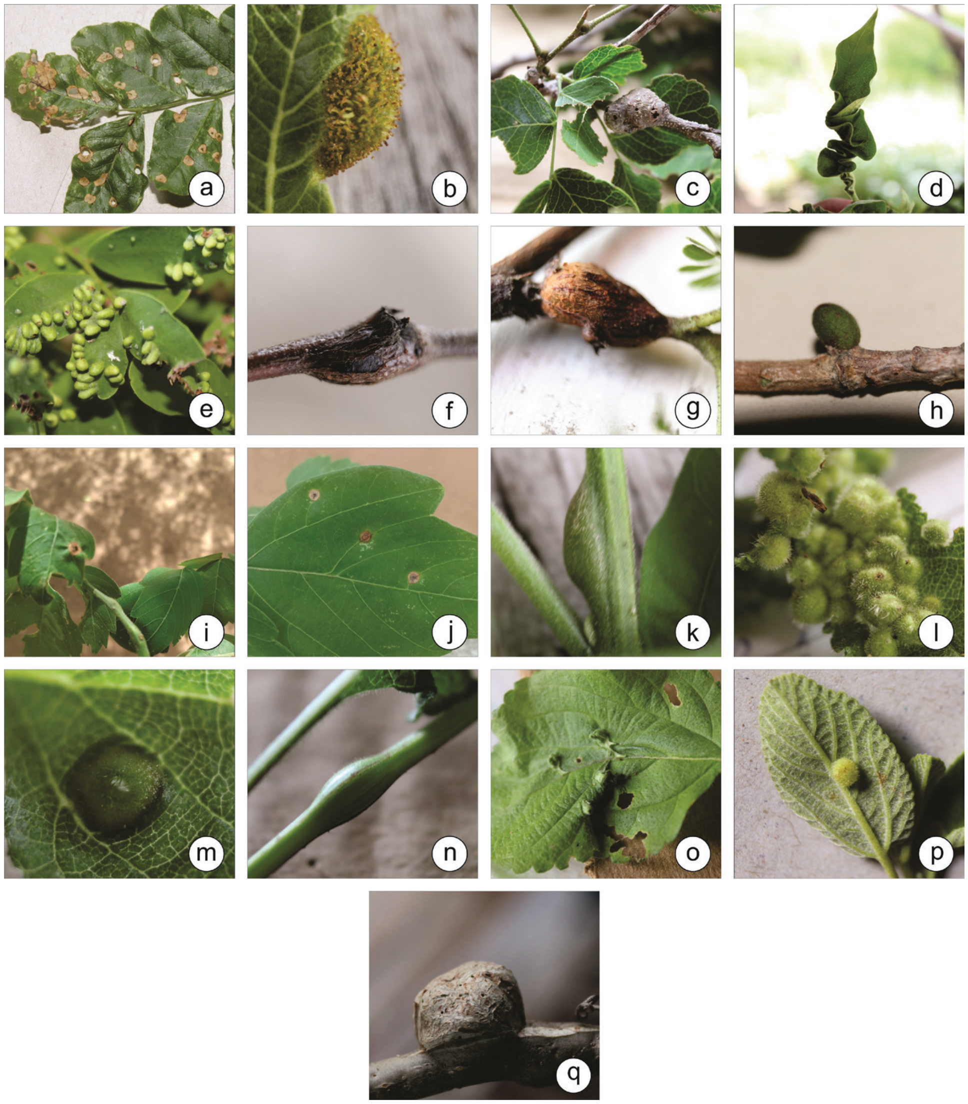

Figure 3. Galls found in six areas of Caatinga in the states of Ceará, Paraíba and Rio Grande do Norte, Brazil. a-c. In *Cenostigma pyramidale*: a. lenticular, b. Globoid, c. lenticular; d. In *Desmodium tortuosum* - marginal roll; e. In *Geoffroea spinosa* - globoid; f-g. In *Mimosa tenuiflora*; f. fusiform, g. fusiform; h. In *Allophylus quercifolius* - fusiform. i-j. In *Serjania glabrata*: i. Fusiform, j. fenticular; k. In *Capsicum parvifolium* - fusiform; l-o. In *Lantana camara*: l. globoid, m. lenticular, n. fusiform, o. conical; p. In *Lippia origanoides* - globoid; q. In *Cissus decidua* - globoid. Sources: From the author (2019–2021).

(Fabaceae) was the species with the highest gall richness, with five associated morphotypes, followed by *Lantana camara* (Verbenaceae) with four morphotypes. Therefore, these two species are indicated as super hosts. *Cenostigma pyramidale* and *Croton blanchetianus* were the only host species that occurred in all the six areas investigated. Leaves (61%) and stems (25%) were the most attacked organs.

Globoid and fusiform galls were the most frequent, each representing 34.1% of the total. Lenticular galls corresponded to 22%. Most morphotypes were glabrous (75.6%), while only 24.4% exhibited trichomes. The colors green (58.5%) and gray (9.7%) prevailed. However, we observed that the color of two morphotypes varied over time. The globoid morphotype present on the leaves of *Croton blanchetianus* varied from light green in the young stage to dark green or brown in its final stage. The clavate morphotype present on the leaves of *Manihot carthagenensis* (Jacq.) Müll.Arg., initially light green, later became red. Regarding the number of internal chambers, 32 morphotypes (78%) had a single chamber while only 9 (22%) had more than one.

Inducers of 21 morphotypes (51.21%) were identified at family level. The others were not identified, either because the galls were empty, or with parasitoids, or even with some immature whose life habits were not determined. Of four morphotypes (Figures 2h, 2k, 3m, 3n), only larvae of the tribe Clinodiplosini were obtained. Adult gallers were obtained from only three morphotypes, all belonging to Cecidomyiidae (Diptera). They were identified as: *Contarinia* sp. in *Desmodium tortuosum* (Sw.) DC. (Figure 3d); *Clinodiplosis* sp. in *Capsicum parvifolium* (Figure 3k); and *Schismatodiplosis lantanae* (Rübsaamen, 1916) in *Lantana camara* (Figure 3i). In addition to these, adults of *Stomatosema* emerged from galls on *Croton echioides* (Figure 2n), but that genus does not include galling species (Table 1) and they were considered as fungivores.

The associated fauna comprised successors, fungivores, tenants, and parasitoids. Successors, represented by spiders and four orders of insects - Hemiptera (one morphospecies), Coleoptera (one morphospecies), Lepidoptera (one morphospecies), and Hymenoptera (Formicidae - two morphospecies), were found in four morphotypes of galls. The tenants were represented by *Tanaostigmoides* Ashmead, 1896 (one morphospecies) (Tanaostigmatidae). The parasitoids, found in 18 morphotypes of galls (43.9%), were represented by six families of Hymenoptera: Eulophidae (five morphospecies), Scelionidae (one), Eupelmidae (one), Eurytomidae (one), Torymidae (one) and Pteromalidae (one).

Parasitoids were found in globoid, fusiform, lenticular, and leaf fold galls, and were more frequent in globoid (57.1%) and fusiform (42.8%) galls. Eight families of plants hosted parasitoids and, among them, Fabaceae, Euphorbiaceae, and Verbenaceae together represented 37.5% of the records. Other parasitoids were found in other gall morphotypes but, as only larvae were obtained, they could not be separated into morphospecies. The successors were found only in globoid galls, in hosts representing four botanical families, Euphorbiaceae, Fabaceae, Verbenaceae, and Vitaceae, and were more diverse in Euphorbiaceae and Vitaceae.

Parasitoids were mainly obtained from galls on leaves (55.5%) and stems (38.9%). Of the total number of leaf galls, 37.5% of them were parasitized. Likewise, 53.8% of galls on the stems were parasitized. Successors were obtained from two morphotypes of leaf galls and two morphotypes of stem galls, at frequencies below 9% of the total number of galls on these organs.

Of the total number of unilocular galls (32), 11 had parasitoids (34.4%) and two harbored successors (6.25%). Regarding the total number of multilocular galls (9), 7 galls contained parasitoids (77.8%), and 2 exhibited successors (22.2%). The occurrence of parasitoids was observed in all the six areas investigated. RPPN Almas had the highest number of parasitized galls (66.7%).

Intense occurrence of multiparasitism was observed in globoid leaf galls of *Croton blanchetianus* and *Lantana camara*, both with two wasp morphospecies. On the other hand, the presence of more than one inquiline taxon was recorded in globoid leaf galls of *Croton blanchetianus* and globoid stem galls of *Cissus decidua* Lombardi.

Since this is the first inventory of galls and their host plants carried out in areas of the *Depressão Sertaneja* in the states of Paraíba and Rio Grande do Norte, all records are new for these states. For the state of Ceará, all records are new, except the morphotypes that occur in *Croton blanchetianus* (Figure 2k and 2i) and *Combretum leprosum* Mart. (Figure 2h), already registered in a previous study (see Alcantara et al. 2017). We also registered the occurrence of new types of galls in 12 species of host plants, represented in the following illustrations: (Figures 2 - 2a, 2b, 2c, 2d, 2f, 2j, 2q) and (Figures 3 - 3d, 3e, 3h, 3j, and 3q).

Discussion

When comparing our results with the first gall inventory carried out in the Caatinga (Santos et al. 2011), we can observe differences in the richness of gall morphotypes, the composition of host plants, and the associated fauna. However, regarding the presence of parasitism in certain plant families, the results are similar. Santos et al (2011) inventoried eight areas in the state of Pernambuco, included in both the Southern *Depressão Sertaneja* and Borborema Plateau ecoregions, including Vale do Catimbau National Park and two state parks. They found 64 morphologically distinct types of insect galls in 48 species of host plants, belonging to 31 genera and 17 families. In our research, we found 41 gall morphotypes in 24 plant species, and 12 host families. The variation in morphotype richness may be partially associated with differences in floristic composition in the Northern and Southern *Depressão Sertaneja* ecoregions. In addition, Santos et al. (2011) adopted the random walk method (Fernandes & Negreiros 2006; Coelho et al. 2009, Silva et al. 2015), while we established systematically distributed transects as a way of minimizing interference of walking through more accessible or already open places.

According to Araujo et al. (2019) the total richness of gall-inducing insects differs among sampling sites of different Brazilian regions and biomes. For Fernandes and Price (1988), factors such as latitude, elevation, temperature, and humidity strongly influence the diversity and distribution of galling species in the world. Therefore, variations in morphotypes and gall-inducing insects' richness among ecoregions should be expected.

Within a single ecoregion, Carvalho-Fernandes et al. (2012) found 25 morphotypes of galls distributed in 18 host species in areas in the Southern Depressão Sertaneja, in the state of Alagoas. Their results revealed patterns like ours and those found by Santos et al. (2011). Fabaceae, the family with the greatest richness in our study, was also the richest in theirs, with eleven morphotypes. In another study in the same ecoregion, Alcântara et al. (2017) recorded only three host plants and 12 gall morphotypes. In that case, the low number of morphotypes may have been a consequence of the authors having established only three random plots of 10 m².

Our data indicated Fabaceae as the family with the most galled species, which allows us to say that it constitutes a super host taxon for galling insects (Santos-Silva, & Araújo, 2020). Carvalho-Fernandes et al. (2012) and Alcântara et al. (2017) presented a similar result to ours, indicating Fabaceae as the main host family. Fabaceae is the most species-rich family in the Caatinga, occupying the second position in the Atlantic Forest, Cerrado, and Pantanal (Brazil Flora Group 2015). This high diversity and its prominence in relation to the number of gall host species and morphotypes were also recorded in other biomes such as the Cerrado (Gonçalves-Alvim and Fernandes 2001), Pantanal (Ascendino and Maia, 2018), Atlantic Forest and Chaco (Urso-Guimarães et al. 2017). According to Gagné (1994), Fabaceae stands out as the family with the greatest richness of galls related to Cecidomyiidae in the Neotropical region. Since Fabaceae is the most species-rich family in the semi-arid region of Brazil (Queiroz et al. 2006, BFG 2015, Fernandes et al. 2020), the present study adds evidence in favor of the taxon size hypothesis, which predicts that the richness of gall morphotypes is greater in plant families with a greater number of species (Veldtman & McGeoch, 2003; Mendonça Júnior 2007).

Our data also reveals a higher colonization in Euphorbiaceae. The occurrence of galled individuals of *Croton blanchetianus* in all studied areas indicates oviposition preference on this species. *C. blanchetianus* is considered a pioneer, frequent in places that are recovering after environmental changes, with a great capacity of regrowth during the rainy season, even after being cut by man (Maia, 2004). The relationship between oviposition preference and performance of immature forms ingalling tissues can help understanding the evolution of interactions between herbivorous insects and their host plants (Thompson & Pellmyr 1991). Most plant families with non-galled species may suggest the presence of intrinsic mechanisms of herbivory resistance in them. Also, the presence of more tolerant plant species in the environment may induce changes in the target plant by galling insects, influencing the distribution and concentration of consumer species within habitats (Gaillard et al., 2010).

The prevalence in our study of gall induction on leaves confirms the worldwide pattern observed since Felt (1940) and Mani (1964), and reinforced in previous inventories carried out in the Caatinga (Santos et al, 2011; Costa et al, 2014; Brito et al, 2018). As a general pattern, the globoid and fusiform morphotypes stood out as the most frequent. According to Isaias et al (2013), gall inventories in the Neotropical region pointed to globoid galls as the predominant morphotype.

Cecidomyiidae (Diptera) were the most frequent inducers in our study, as verified in previous surveys carried out in Brazil (Julião et al. 2002; Urso-Guimarães & Scareli-Santos, 2006; Luz et al. 2012, Maia & Siqueira, 2020). Thus, our results reinforce previous results and corroborate the hypothesis of Gagné and Jaschhof (2021), which points out Cecidomyiidae as the family with the greatest diversity of galling insects in the world.

In our study area, 78% of the galls did not present trichomes on their external surface. This result can be attributed to particular characteristics of semi-arid regions, where the urgent need of the galling insect to defend itself from the action of parasitoids may have led to evolutionary pressures reinforcing the gall structure to the detriment of the presence of external trichomes. Although we did not assess this defensive role, the reported defense strategy may be applied, since a more intense attack by multiple parasitoids was verified in globoid leaf galls with trichomes. According to László et al (2014), larvae of inducers in smaller galls, with thinner walls, face the action of parasitoids more frequently, as they are closer to their ovipositors, thus becoming less secure. The presence of trichomes in the gall would have a better function in maintaining temperature and humidity, fundamental factors for the establishment and development of galls (Woodman & Fernandes 1991; Fernandes, 1994; Oliveira et al. 2006).

Almost all morphotypes in our study were one-chambered, which is also in line with previous results on gall diversity in the Caatinga (Brito et al. 2018) and other biomes in Brazil, such as the Cerrado (Gonçalves-Alvim & Fernandes, 2001) and the Atlantic Forest (Fernandes et al., 2009). Regarding color, most galls were similar in color to the organ of the attacked plant, with a predominance of green on the leaves, as already observed by several authors (Bregonci et al., 2010; Santos et al., 2011, Bergamini et al. 2017, Ascendino & Maia 2018).

As for the associated fauna, Eulophidae, Eurytomidae, Braconidae, Eupelmidae, and Pteromalidae have already been recorded as parasitoids of galling insects in Brazil (Maia & Tavares 2000, Maia & Azevedo 2009, Bergamini et al 2017). In this sense, our data reinforce that the parasitoid guild is more frequent and diverse than the tenant and successor guilds (Maia & Siqueira, 2020). However, in *Cissus decidua* Lombardi, three orders were found (Coleoptera, Lepidoptera, and Hymenoptera), forming three new associations of successors in the Caatinga. Eulophidae was the most frequent parasitoid family in our study, as previously verified by Maia and Azevedo (2009) in the restinga.

The occurrence of Micro-Hymenoptera in several galls evidences the formation of a "plant-galler-parasitoid" tritrophic system (Araujo & Maia, 2021). However, there is a need for further investigation on the status of the Micro-Hymenoptera collected, since these organisms constitute a diverse taxon, of great importance for studies of interaction with galling insects. Many galling insects, originating from hosts with less galls, could not be identified due to the intense attack of micro-Hymenoptera, which prevented the emergence of adults from the galls. This fact is recognized in the literature as one of the biggest obstacles to the success of taxonomic identification of galls (Maia et al. 2008).

According to Maia (2001), galls represent an important micro-habitat, where several trophic relationships are established. In the restinga areas of Rio de Janeiro, Maia and Azevedo (2009) found that the vast majority of microhymenopterans were parasitoids, but some of them, for example, the Tanaostigmatidae and some species of Torymidae and Eulophidae were gall tenants. According to Carvalho-Fernandes et al (2016), some species of Micro-Hymenoptera are found, as parasitoids, in galls induced by Cecidomyiidae, or even as phytophagous tenants, capable of altering the physical structure of galls. These results reinforce the need to elucidate and separate the role of parasitism and inquilinism in the plant-galler interaction observed in our results.

Price (2005) reported that many invertebrate organisms may be associated with galls. These organisms include predators, tenants, or successors, and are represented by many taxa, such as Acari, Collembola, Hymenoptera, Coleoptera, Lepidoptera, Thysanoptera, Diptera, Hemiptera, and Psocoptera (Bregonci et al., 2010).

In addition to the presence of parasitoids, many gall inducers in our work could not be identified, at the genus or species level, due to the absence of the male or female adult, as well as the stages of a complete series (larva, pupa, or pupal exuvia and adults), necessary for their identification. We point out the removal of leaves from the host plants, for gall sampling and insect rearing, as a factor that makes it difficult to obtain these individuals, since cutting off the flow of nutrients to the gall can make the development of the insect unfeasible.

Conclusions

There is a moderate occurrence of gall morphotypes in the Northern *Depressão Sertaneja* Ecoregion. Results from previous studies, which recorded the Cecidomyiidae family as the main gall-inducing group in the Caatinga, were confirmed, as well as the high rate of parasitism by Hymenoptera.

Fabaceae was confirmed as the family with the highest number of galled species, an already recognized pattern. However, we recorded new associations between host plant species, their galls, and successors, expanding the knowledge about galls in the caatinga.

The presence in the RPPNs of several plant species endemic to the Caatinga, for which new gall records were registered in our study, indicates the importance of preserving these areas for the galling insect community. The new associations registered here highlight the importance of inventories to provide information about the richness and diversity of galls in Brazil.

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Author Contributions

Rafael Aguiar Marinho: Conceptualization; Resources; Methodology, Investigation; Writing – original draft manuscript preparation; Writing – review & editing manuscript.

Valéria Cid Maia: Validation, Resources, Writing – review & editing manuscript.

Maria Regina de Vasconcellos Barbosa: Conceptualization; Validation; Methodology; Writing – review & editing manuscript.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data Availability

The datasets generated during and/or analyzed during the current study are available at: https://doi.org/10.48331/scielodata.IREBGF.

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