Richness and composition of gall-inducing arthropods at Coiba National Park, Panama

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Abstract: Interest in studying galls and their arthropods inducers has been growing rapidly in the last two decades. However, the Neotropical region is probably the least studied region for gall-inducing arthropods. A study of the richness and composition of gall-inducing arthropods was carried out at Coiba National Park in the Republic of Panama. Field data come from samples obtained between August 1997 and September 1999, with three (two-week long) more intensive samplings. Seventeen sites, representing the main land habitats of Coiba National Park were surveyed. 4942 galls of 50 insect and 9 mite species inducing galls on 50 vascular plants from 30 botanical families were colleted. 62.7% of the galls were induced by gall midges (Diptera, Cecidomyiidae), 15.3% by mites, Eriophyidae, 8.5% by Homoptera, Psyllidae, 6.8% by Coccidae and 5.1% by Phlaeothripidae (Tysanoptera). The host plant families with the most galls were Myrtaceae with seven, Bignoniaceae with five and Euphorbiaceae, Fabaceae and Melastomataceae with four. Leaf galls accounted for about 93% of collected galls. Most leaf galls were pit/blister galls followed by covering and pouch galls. Gall richness per collecting site was between 1 and 19 species. Coiba's gall diversity is discussed in relation to data available from other tropical sites from continental Panama and the Neotropical region. Our results support the idea that it may be premature to conclude that species richness of gall inducers declines near the equator. Rev. Biol. Trop. 56 (3): 1269-1286. Epub 2008 September 30.

Key words: Coiba, gall-inducing insects, gall richness, host plant, insect/plant interaction, Panama.

Many groups of insects and mites, estimated in a range from 21 000 to 211 000 species, with an average of 132 930 species (Espírito-Santo and Fernandes 2007), are capable of inducing galls on plants, which are structures that involve active differentiation and growth of plant tissues providing shelter, nutrition and protection for the gall-inducing organism (Meyer 1987, Nieves-Aldrey 1998, Stone and Schönrogge 2003).

Galls and gall-inducing arthropods have been the object of research for the last three centuries by dozens of naturalists and scientists worldwide (Mani 1992, see Raman *et al.* 2005 for a recent synthesis). Earlier information was compiled in a classic work by Houard (1908-1913, 1922, 1933, 1940). The most important groups of gall-inducing insects are Diptera (Cecidomyiidae), Homoptera (Cicadoidea, Psylloidea, Aphidoidea and Coccoidea), Thysanoptera and the hymenopteran families Tenthredinidae and Cynipidae. Mites inducing galls belong mostly to the family Eriophyidae. These galling-insect groups have different distribution patterns, and their distribution may be correlated with the breaking up and movement of continents (Gagné 1984). Geographic and climatic factors could also have determined the

distribution patterns of gall-inducing arthropods (Schlinger 1974). The most important family of gall insects is Cecidomyiidae (Diptera), predominant in almost all zoogeographic regions, both tropical and temperate. Cynipidae and Tenthredinidae are mainly holarctic, gall-inducing thrips (Thysanoptera) are restricted mostly to Western Asia and gall-inducing psyllids and coccids are predominant in tropical regions (Felt 1940, Gagné 1984).

Interest in studying galls and their arthropod inducers has been growing rapidly in the last two decades (Raman *et al*. 2005). However, the Neotropical region continuous to be a poorly studied region for gall-inducing arthropods in general (Espírito-Santo and Fernandes 2007). The most important references are the classic work by Houard (1933), the book by Gagné (1994) on gall midges (Cecidomyiidae) and local studies in Brazil (Maia 2001, 2005, Gonçalves-Alvin and Fernandes 2001, Maia and Fernandes 2004, Costa De Oliveira and Maia 2005, Urso-Guiamares and Scareli-Santos 2006); Costa Rica (Hanson and Goméz-Laurito 2005); Mexico (Cuevas-Reyes *et al*. 2004a, 2004b) and Panama (Medianero *et al* 2001). Future research in the Neotropical region will likely change the biogeographical patterns assumed until now for gall inducing insects (Espírito-Santo and Fernandes 2007).

The aim of this study is to estimate the richness and composition of gall inducing arthropod species in an unexplored insular tropical habitat off the Pacific coast of Panama, and compare them with data available from continental Panama.

MATERIALS AND METHODS

Study area: The research was performed at Coiba National Park (World Heritage Site), as a part of the Joint Hispanic-Panamanian Program for National Parks. Coiba National Park is located in the Panamanian Pacific Ocean (7º39´-7º18´ N & 81º53´-81º35´W), 22 Km from the mainland, and encompasses an area of 270 125 ha, of which 53 528 ha are insular and 216 543 are marine. The insular area is composed of Coiba (50 314 ha), the largest island in tropical Pacific America, eight other minor islands and 30 islets. The maximum altitude in the Park is 420 m on Coiba Island. Annual rainfall is 3 483 mm. The yearly average humidity is 80% and the mean temperature is 25 ºC. The area is characterized by an intense dry season, from December to April and a rainy season from May to November. The natural vegetation is well conserved, with about 80% forest coverage. An untouched tropical moist and wet forest occupies 60% of the park (Castroviejo 1997). The island of Coiba became separate from the mainland about 12 000 to 18 000 years ago and houses many endemic species of animals and plants. The rough forested terrain has served to make the island inhospitable and preserved, but even more so the presence of a prison, consisting of some twenty camps scattered along the coastline, that was in operation from 1918 to 2004 (Castroviejo 1997, Fontal and Nieves-Aldrey 2004).

Field and laboratory work: Field data were obtained from several samples between August 1997 and September 1999 with three more intensive samples (two-week long) in August 1997, July 1998 and August 1999. The sampling method consisted of transects during not less than one hour (see Price *et al*. 1998). Along the selected collecting sites all plants were searched for galls. Seventeen sites representing the main terrestrial habitats in Coiba National Park were surveyed (Table 1, Fig. 1). Plants with galls were collected and photographed. Specimens of galled plants were dried and put into a herbarium collection, where plants were identified later. Samples of the galls were also stored in 70% ethanol to allow further dissection and identification. Data of altitude and geographic position was taken in the field (Table 1).

The galls were dissected in the laboratory for adult and larval identification to family level. Gall-inducing species were separated by the external morphology of the galls, the larvae and the host plant. It is assumed in a study like this that gall morphotype is unique

TABLE 1
List of sampling sites data at Coiba Nacional Park

Nº	Sampling sites	UTM	ALT(m)
1	Campamento Las Salinas	17NMU1922	0-50
2	Campamento Playa Blanca	17NMU2615	0
3	Campamento Playa Blanca-Campamento Barco Quebrado	17NMU2615	0
4	Campamento Playa Hermosa and Río Playa Hermosa	17NMNO532	0
5	Cerro de la Equis	17NMU1841	100-200
6	Cerro de la Torre	17NMU0731	400
7	Estación Biológica	17NMU196429	40
8	Estación Biológica – Río Santa Cruz	17NMU1942-1642	
9	Isla Jicarón	17NMJ1205	0
10	Isla Ranchería	17NMU2244	0-100
11	Playa Hermosa-Santa Clara (La Falla)	17NMU0328	100
12	Playa Rosario	17NMU1644	0
13	Punta Esquina	17NMU2533	0
14	Río Escondido	17NMU1341	0-10
15	Río Manila	17NMU1413	0
16	Río Negro	17NMU1720	100
17	Sendero Yuma	17NMU2039	0

Numbers represented on map of Figure 1.

for each gall-inducing species (Mani 1964, Ananthakrishnan 1984). Yet a very conservative methodology was employed (see Hanson and Goméz-Laurito 2005); galls found in petioles, in leaf blades, as well as in the nerve of a given leaf, and those without differentiation in plant species of the same genus were considered as of the same gall-inducing species.

Data analysis: Gall-inducing arthropod species richness (S) was calculated based on the number of different galls found and the alpha diversity index (α) was estimated (Fisher 1943):

$$S = \alpha \text{Log e } (I + N/\alpha).$$

S is the number of species in a sample, *N* is the number of individuals in a sample and α is the diversity index. This index is not influenced by the two limitations of other known indeces because it is independent of sample size and it does not give more weight to species abundance (Wolda 1983).

To verify sampling efficiency we constructed species accumulation curves with the estimator Chao 1, Bootstrap and Jacknife 1 (100 random). The species accumulation curve is based on individual-based assessment protocol (see Gotelli and Colwell 2001). We used the software EstimatesS® 8 (Colwell 2006).

RESULTS

Taxonomic and faunistic considerations: A total 4 942 galls of 59 species, 50 insects and 9 mites, associated with 50 species of plants from 37 genera and 30 families were collected at Coiba National Park. It was not possible to identify the genus of nine host plant species

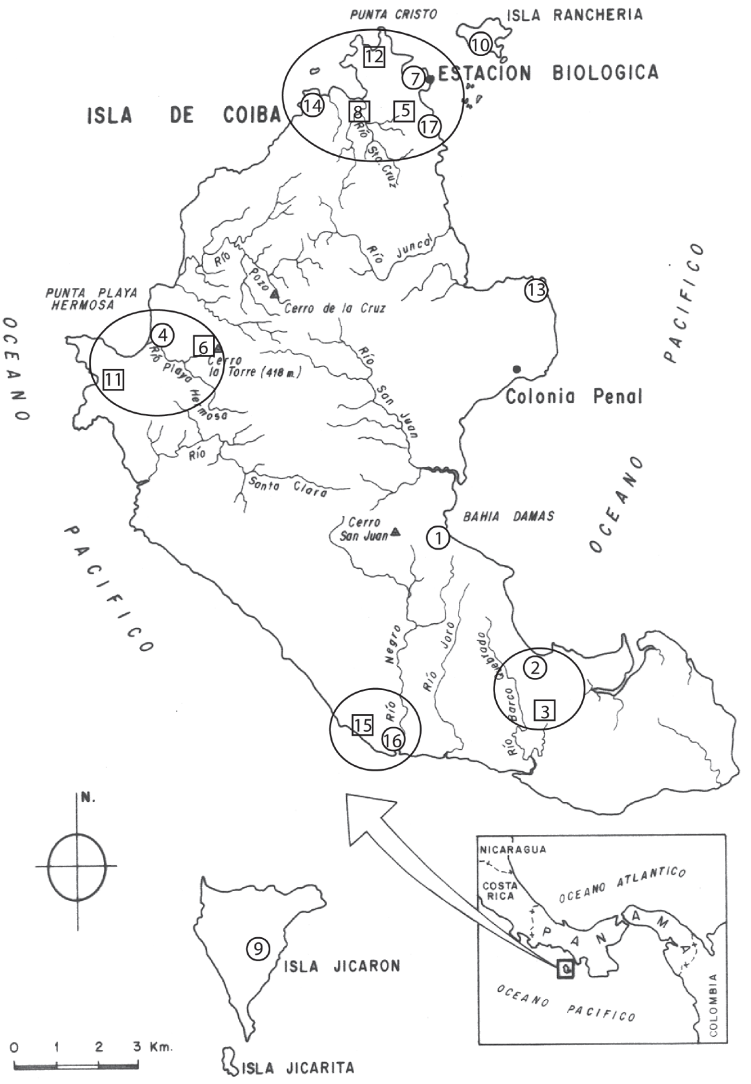

Fig. 1. Map of Coiba National Park, showing sampling sites. The four groupings correspond to the four different plant communities at Coiba Island.

mostly Myrtaceae. 62.7% of the galls were induced by species of the family Cecidomyiidae, 15.3% by Eriophyidae, 8.5% by Psyllidae, 6.8% by Coccidae, 5.1% by Phlaeothripidae; one species corresponding to 1.7% could not be determined. 93. 1% of the galls were found on leaves, 3.4% on stems and 5.2% on buds (Table 2). The plant families hosting the most gall-inducing species were Myrtaceae with seven, Bignoniaceae with five and Euphorbiaceae, Fabaceae and Melastomataceae with four (Table 3). The plant species with the greatest diversity of galls was *Calophyllum longifolium* (Clusiaceae) with three, seven species were found with two galls (*Amphitecna latifolia, Mansoa sp., Acalypha diversifolia, Casearia commersoniana, Lacistema aggregatum, Cassipourea elliptica* and *Pouteria foveolata*) whilst only one

TABLE 2
Number of gall-inducing species per insect family and their affected host plant organ

Gall inducing family	Leaf gall	Stem gall	Bud gall	Total
Cecidomyiidae	36	1		37
Eriophyidae	7	1	2	9
Psyllidae	5			5
Coccidae	4			4
Phlaeothripidae	2		1	3
Indeterminate	1			1

TABLE 3
Plant family and gall inducing arthropods numbers

Plant family	No. of species with galls	Total No. of galls	Mites	Midges	Psyllids	Coccids	Thrips
Annonaceae	1	1		1			
Asteraceae	1	1					1
Bignoniaceae	3	5		4		1	
Bombacaceae	1	1		1			
Burseraceae	2	2			2		
Celastraceae	1	1		1			
Chrysobalanaceae	2	2		2			
Clusiaceae	1	3	1	2			
Combretaceae	1	1		1			
Euphorbiaceae	3	4	2	2			
Flacourtiaceae	1	2		2			
Lacistemataceae	1	2		2			
Lauraceae	1	1			1		
Leguminosae	4	4		3	1		
Melastomataceae	4	4	4				
Moraceae	2	2		1	1		
Myristicaceae	1	1		1			
Myrsinaceae	1	1		1			
Myrtaceae	7	7	1	3		1	2
Nyctaginaceae	1	1		1			
Ochnaceae	1	1					
Pellicieraceae	1	1				1	
Rhamnaceae	1	1		1			
Rhizophoraceae	1	2		1		1	
Rubiaceae	2	2		2			
Sapindaceae	1	1		1			
Sapotaceae	1	2		2			
Sterculiaceae	1	1		1			
Verbenaceae	1	1	1				
Vitaceae	1	1		1			

gall-inducing species was found infesting two species of *Ficus*. Alpha diversity was 9.4 but, species accumulation curves did not become asymptotic suggesting than there are more gall-inducing species at Coiba National Park than those collected in this study. Gall-inducing species number increases with individual sample (Fig. 2). Gall richness per collecting site was between 1 and 19 species. 71% of all species were found at only one site, 22% in two, 5% in three, 2% in four, while no species was present in more than four sites. The gall inducing arthropod community studied shows a high complementarity among collecting sites.

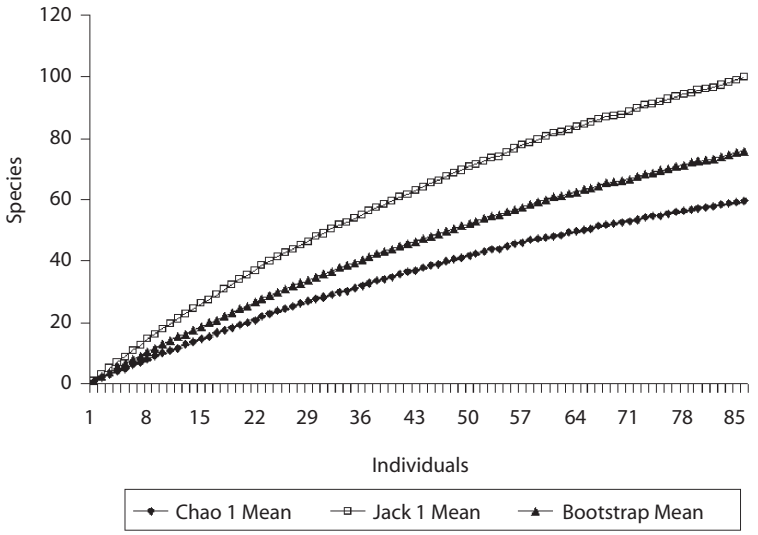

Fig. 2. Species accumulation curves with estimator Chao 1, Bootstrap and Jacknife 1 (100 random).

List of gall-inducing taxa and host plant species at Coiba National Park (G = Gall).

ANNONACEAE

Gen. Ind.

G59. (Fig. 4H). Family gall-inducer: Cecidomyiidae.

Leaf gall, ovoid with hairs on upper side.

BIGNONIACEAE

Amphitecna latifolia (Mill.) A.H. Gentry

G1 (Fig. 3A). Family gall-inducer: Cecidomyiidae

Leaf gall, spindle shaped, on mid or secondary veins, distinct on both sides of leaf.

Manglar De Sta. Cruz. 31-VIII-97. J. L. Nieves *leg*.

G2. Family gall-inducer: Coccidae

Leaf gall; blister more distinct on low surface.

Manglar de Sta. Cruz. 31-VIII-97. J. L. Nieves *leg*.

Cydista aequinoctialis (L) Miers.

G3 (Fig. 3B). Family gall-inducer: Cecidomyiidae

Leaf gall; spindle shaped, on petiole, mid and secondary veins.
I. Jicarón. 3-X-97. A. Ibáñez *leg*
I. Ranchería. 7-IX-97. A. Ibáñez *leg*
Beach estación Biológica. 30-VIII-97. J. L. Nieves *leg*
Cerro Equis. 26-VIII-97. J. L. Nieves *leg*.

Mansoa sp.

G4. Family gall-inducer: Cecidomyiidae
Leaf gall, a blister distinct on both sides of leaf.
Sendero Yuma. IX-97. A. Ibáñez *leg.*
G4a. Family Gall Inducer: Cecidomyiidae
Leaf gall, a spindle shaped swelling on mid vein.
Sendero Yuma. IX-97. A. Ibáñez *leg*.

BOMBACACEAE

Quararibea asterolepis Pittier

G5. Family gall-inducer: Cecidomyiidae
Leaf gall, a small blister distinct on both sides of leaf.
I. Jicarón. 3-X-97. A. Ibáñez *leg*.

BURSERACEAE

Tetragastris panamensis (Engl.) Kuntze

G6. Family gall-inducer: Psyllidae
Leaf gall, small circular blister more distinct on upper side; on lower side appear as a pit or depression.
Cerro Equis XI-97. A. Ibáñez *leg.*

Protium confusum (Rose) Pittier

G7. (Fig. 3C). Family gall-inducer: Psyllidae
Leaf gall, circular, small, distinct on upper side; a pit on low part.
I. Ranchería. 7-IX-97. A. Ibáñez *leg*
Cerro de la Torre. 12-VI-98. A. Ibáñez *leg*.

CELASTRACEAE

Maytenus schippii Lundell

G9. Family gall-inducer: Cecidomyiidae
Leaf gall, a median size blister of leaf blade distinct on both sides of leaf.
Río Santa Clara. 29-XI-97. A. Ibáñez *leg*.

CHRYSOBALANACEAE

Licania hypoleuca Benth.

G10. Family gall-inducer: Cecidomyiidae
Leaf gall, subspherical, small.
Playa Rosario. 22-VII-98. J. L. Nieves *leg*.

Licania platypus (Hemsl.) Fritsch

G11. Family gall-inducer: Cecidomyiidae
Leaf gall, on blades subspherical, small and abundant.
I. Canal De Afuera. 6-XI-97. A. Ibáñez *leg*.

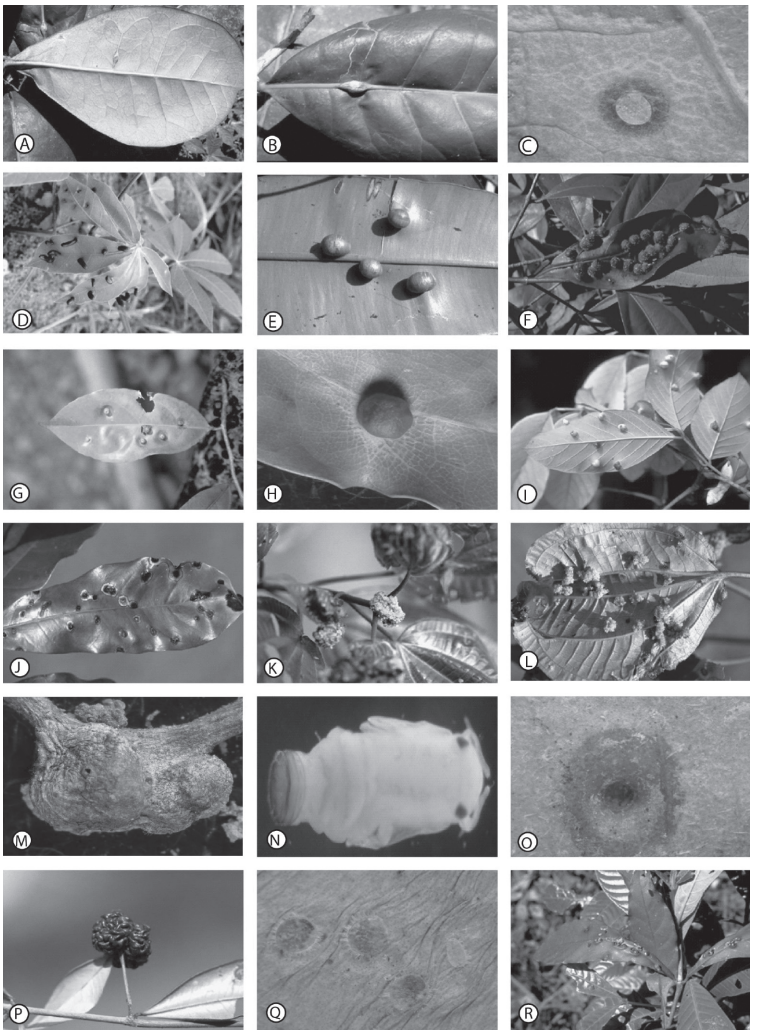

Fig. 3. Pictures of galls from Coiba: (A) gall midge on *Amphitecna latifolia,* (B) gall midge on *Cydista aequinoctialis,* (C) psyllid on *Protium confusum,* (D) gall midge on *Manihot esculenta,* (E) gall midge on *Calophyllum longifolium,* (F - G) gall midge on *Lacistema aggregatum,* (H) psyllid on *Cinnamomum triplinerve,* (I) gall midge on *Lonchocarpus sp*., (J) gall midge on *Pouteria foveolata,* (K) mite gall on *Miconia lacera,* (L), mite on *Miconia nervosa*, (M) gall midge on *Casearia commersoniana,* (N) psyllid on *Sorocea sp*., (O) coccoid gall on Myrtaceae, (P) thrip gall on Myrtaceae, (Q) coccoid gall on *Pelliciera rhizophorae,* (R) gall midge on *Psychotria horizontalis.*

CLUSIACEAE

Calophyllum longifolium Willd.

G20 (Fig. 3E). Family gall-inducer: Cecidomyiidae
Leaf gall, on blades, bean shaped, big more obvious on underside.
Playa Blanca-Cativales. 26-VIII-97. J .L. Nieves *leg*
Cerro De La Equis. 21-III-98. A. Ibáñez *leg.*
G21. Family gall-inducer: Eriophyidae
Gall leaf, on blades, tiny pocks in eyelet shape, on both sides of midrib.
Cerro De La Torre. 18-VII-98. J. L. Nieves *leg.*
G22. Family gall-inducer: Cecidomyiidae
Gall leaf, small pustule on blades.
Cerro De La Equis. 26-VIII-97. J. L. Nieves *leg*.

COMBRETACEAE

Terminalia amazonia (J.F. Gmel.) Exell

G12. Family gall-inducer: Cecidomyiidae
Leaf gall, ovoid irregular distinct on both sides of leaf.
Cerro de la Torre. 22-VII-98. J. L. Nieves *leg*.

COMPOSITAE (ASTERACEAE)

Gen. sp. Indet.

G13. Family gall-inducer: Phlaeotripidae
Gall a folded at tip of the leaf blades.
Sendero de Santa Cruz. 26-VIII-99. A. Ibáñez *leg.*

EUPHORBIACEAE

Acalypha diversifolia Jacq.

G14. Family gall-inducer: Eriophyidae
Bud gall, large, subspherical.
Rio Negro. 9-XII-97. A. Ibáñez *leg*
I. Jicarón. 9-XII-97. A. Ibáñez *leg.*
G15. Family gall-inducer: Eriophyidae
Leaf gall, a small pouch more obvious on upper side.
Rio Negro. XII-97. A. Ibáñez *leg*
Cerca De Sta. Cruz. XII-97. A. Ibáñez *leg.*

Croton schiedeanus Schltdl.

G16. (Fig. 4A).Family gall-inducer: Cecidomyiidae
Leaf gall, small blister on blades, more obvious in underside.
Manila, cerca de la parcela. 19-VI-98. A. Ibáñez *leg.*

Manihot esculenta Crantz

G17 (Fig. 3D). Family gall-inducer: Cecidomyiidae
Leaf gall, spindle shaped on blades, colour red, more obvious on upper side.
Playa Blanca. VIII-97. J. L. Nieves *leg*.

FABACEAE

Inga multijuga Benth.

G25. Family gall-inducer: Cecidomyiidae
Leaf gall, tiny pustule, more obvious on upper side.
Cerro De La Equis. 12-VI-98. A. Ibáñez *leg*.

Inga sp.

G26. Family gall-inducer: Cecidomyiidae
Leaf gall, small blister.
Camino de las Salinas. 27-VIII-99. A. Ibáñez *leg*.

Lonchocarpus sp.

G27 (Fig. 3I). Family gall-inducer: Psyllidae
Leaf gall, ovoid, on both sides of blades, medial size.
Punta Esquina. 25-VIII-97. J. L. Nieves *leg*.

Prioria copaifera Griseb.

G28. (Fig. 4G). Family gall-inducer: Cecidomyiidae
Leaf gall, spherical small, abundant, scar on underside.
Playa Blanca-Cativales. 26-VIII-97. J.L.Nieves *leg*.

FLACOURTIACEAE

Casearia commersoniana Cambess.

G18. (Fig. 3M). Family gall-inducer: Cecidomyiidae
Gall on stems, swelling irregular, mainly on one side.
Río Negro. 9-XII-97. A. Ibáñez *leg*.
G19. Family gall-inducer: Cecidomyiidae
Gall on leaf, small pouch on mid vein, more obvious on upper side.
Río Negro. 9-XII-97. A. Ibáñez *leg*.

LACISTEMATACEAE

Lacistema aggregatum (Bergius) Rusby

G23 (Fig. 3F). Family gall-inducer: Cecidomyiidae
Leaf gall, spherical in groups, hairy, medial size.
Cerro De La Equis. 25-VIII-97. J. L. Nieves *leg*
G23a (Fig. 3G)
Family gall-inducer: Cecidomyiidae
Leaf gall, pit gall, cilíndrical distint on low blade of leaf.
Playa Hermosa (Falla). 20-VII-98. J. L. Nieves *leg*.

LAURACEAE

Cinnamomum triplinerve (Ruiz & Pav.) Kosterm

G24 (Fig. 3H). Family gall-inducer: Psyllidae
Leaf gall, globular on secondary veins, more obvious in upper side.
Cerro De La Torre. 18-VIII-98. J. L. Nieves *leg*
I. Ranchería. 19-VII-98. J. L. Nieves *leg*
Cima del Cerro de la Torre. 7-III-98. J. L Nieves *leg*.

MELASTOMATACEAE

Clidemia discolor (Triana) Cogn.

G29. Family gall-inducer: Eriophyidae
Bud gall, flowers.
Manglar De Sta. Cruz. 24-VII-98. J. L. Nieves *leg.*

Miconia lacera (Bonpl.) Naudin

G31. (Figs. 4K, 5E) Family gall-inducer: Eriophyidae
Gall on buds and stems, subspherical.
Cerro De La Torre. 7-III-98. A. Ibáñez *leg*.

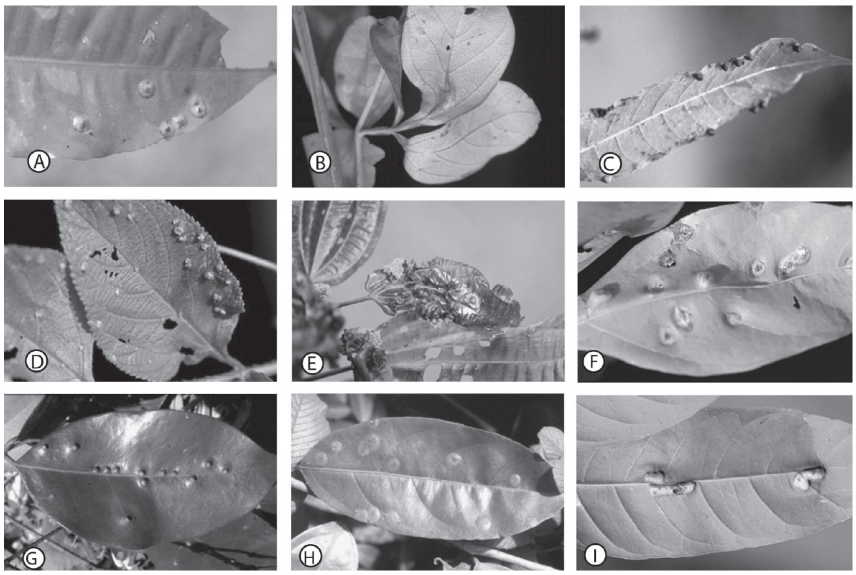

Fig. 4. Pictures of galls from Coiba: (A) gall midge on *Croton schiedeanus,* (B, F) gall midge on *Serjania mexicana,* (C) gall midge on *Pouteria foveolata,* (D) mite gall on *Lantana camara,* (E) mite gall on *Miconia lacera,* (G) gall midge on *Prioria copaifera,* (H) gall midge on Annonaceae, (I) gall midge on *Faramea occidentalis.*

Miconia minutiflora (Bonpl.) DC.

G32. Family gall-inducer: Eriophyidae
Dense erineum on underside of leaf, hairs red.
Cerro De La Equis. 26-VIII-97. J. L. Nieves *leg*
Estación Biológica. Otoño 98. A. Ibáñez *leg*
Sendero de Santa Cruz. 26-VIII-99. A. Ibáñez *leg.*

Miconia nervosa (Sm.) Triana

G30. (Fig. 3L) Family gall-inducer: Eriophyidae
Leaf gall, more obvious on underside, blades hair.
Rio Negro. 9-XII-97. A. Ibáñez *leg.*
Cerro De La Equis. 18-VII-98. J. L. Nieves *leg.*

MORACEAE

Ficus popenoei Standl.

G33. Family gall-inducer: Cecidomyiidae
Leaf gall, pouch on blades, small.
Cerro De La Equis. 21-III-98. A. Ibáñez *leg.*

Sorocea sp.

G35. Family gall-inducer: Psyllidae (Fig. 3N)
Leaf gall, spindle shaped, on blades abundant more obvious on upper side.
I. Ranchería. 7-IX-97. A. Ibáñez *leg*.

MYRISTICACEAE

Virola sp.

G36. Family gall-inducer: Cecidomyiidae

Leaf gall, spindle shaped, in blades, tiny.
Cerro De La Equis. 12VI-98. A. Ibáñez *leg.*

MYRSINACEAE

Ardisia sp.

G37. Family gall-inducer: Cecidomyiidae
Leaf gall, ovoid in blades medial size.
Manglar De Sta. Cruz. 24-VII-98. J. L. Nieves *leg.*

MYRTACEAE

Gen. Ind.

G38. Family gall-inducer: Cecidomyiidae
Leaf gall, ovoid, small.
Cerro De La Equis. 26-VIII-97. J. L. Nieves *leg*.

Gen. Ind.

G39 (Fig. 3P). Family gall-inducer: Phlaeotripidae
Bud gall on flower irregular spherical.
Manila. 23-VII-98. J .L. Nieves *leg*
I. Jicarón. 3-X-97. A. Ibáñez *leg*.

Gen. Ind. 1, Sp.3

G40 (Fig. 3O). Family gall-inducer: Coccidae
Leaf gall, blister shaped, with opening below.
Río Escondido. Otoño 97. A. Ibáñez *leg*.

Gen. Ind. 2, Sp. 1

G41. Family gall-inducer: Cecidomyiidae
Leaf gall subspherical irregular on blades.
La Falla. Otoño 97**.** A. Ibáñez *leg***.**

Gen. Ind. 3, Sp. 4

G42. Family gall-inducer: Eriophyidae
Gall leaf, blister shaped, small more obvious on upper side.
Playa Cerro De La Equis. Otoño 97. A. Ibáñez *leg*.

Sp. 5

G43. Family gall-inducer: Cecidomyiidae
Leaf gall, on blades, ovoid small.
Cima del Cerro De La Torre. 7-III-98. A. Ibáñez *leg*.

Gen. Ind. Sp. 6

G44. Family gall-inducer: Phlaeotripidae
Leaf gall, blades margin folded thick.

NYCTAGINACEAE

Neea sp.

G45. Family gall-inducer: Cecidomyiidae
Leaf gall, blister in blades, distinct in both sides of leaf.
I. Ranchería. 19-VII-98. J. L. Nieves *leg*
Rio Negro. 9-XII-97. A.Ibañez *leg.*

OCHNACEAE

Ouratea lucens (Kunth) Engl.

G46. Family gall-inducer: Indeterminate

Leaf gall, blister in blades.
Cerro De La Equis. VIII-97. J. L. Nieves *leg*
Subida a la Falla. 21-IX-99. A. Ibáñez *leg*.

PELLICIERACEAE

Pelliciera rhizophorae Triana & Planch.

G47 (Fig. 3Q). Family gall-inducer: Coccidae
Leaf gall, blister small, abundant.
Manglar De Sta. Cruz. IX- 98/ 26-VIII-99. A. Ibáñez *leg*.

RHAMNACEAE

Gouania lupuloides (L.) Urb.

G48. Family gall-inducer: Cecidomyiidae
Leaf gall, ovoid on blades with hairs.
I. Jicarón. 30-VIII-97. J. L. Nieves *leg*.

RHIZOPHORACEAE

Cassipourea elliptica (Sw.) Poir.

G49. Family gall-inducer: Cecidomyiidae
Leaf gall, spindle shaped, on mid vein, distinct on both sides of blade.
Sendero Yuma. 25-VIII-97. J. L. Nieves *leg*
Cerro De La Equis, 21-III-98. J. L. Nieves *leg*.
G50. Family Gall Inducer: Coccidae
Leaf gall, ovoid small on blade more obvious on upper side.
Cerro De La Equis, 21-III-98. J. L. Nieves *leg*.

RUBIACEAE

Faramea occidentalis (L.) A. Rich.

G51 (Fig. 4I). Family gall-inducer: Cecidomyiidae
Leaf gall, blister shaped on mid vein more obvious on underside.
Manila. 23-VII-98. J. L. Nieves *leg*
I. Ranchería. 7-IX-97. A. Ibáñez *leg*.

Psychotria horizontalis Sw.

G52 (Fig. 3R). Family gall-inducer: Cecidomyiidae
Leaf gall, blister irregular on mid vein and petioles.
Cerro De La Equis. VIII-97. J. L. Nieves *leg*
Catival. 18-X-97. A. Ibáñez *leg*.
Cerro De La Torre. 7-III-98. A. Ibáñez *leg*.

SAPINDACEAE

Serjania mexicana (L.) Willd.

G53 (Fig. 4 B, F). Family gall-inducer: Cecidomyiidae
Leaf gall on blades, petioles but, mainly on mid and secondary veins.
Camino de las Salinas. 27-VIII-99. A. Ibáñez *leg*.

SAPOTACEAE

Pouteria cf. foveolata T.D. Penn.

G54 (Fig. 4C). Family gall-inducer: Cecidomyiidae

Leaf gall, ovoid small, aligned on blades margin.
Manglar De Sta. Cruz. XI-97. A. Ibáñez *leg*
Cerro De La Equis. XI-97. A. Ibáñez *leg*
Cerro De La Torre. 22-VII-98. J. L. Nieves *leg*
Manglar De Sta. Cruz. 24-VII-98. J L. Nieves *leg.*
G55 (Fig. 3J). Family gall-inducer: Cecidomyiidae
Leaf gall, ovoid small on leaf blade.
Cerro De La Torre. 22-VII-98. J. L. Nieves *leg*
Manglar De Sta. Cruz. 24-VII-98. J L. Nieves *leg.*

STERCULIACEAE

Theobroma angustifolium Moç. & Sessé ex DC.

G56. Family gall-inducer: Cecidomyiidae
Leaf gall, small spindle in leaf blade.
I. Jicarón. 3-X-97. A. Ibáñez *leg.*

VERBENACEAE

Lantana camara L.

G57 (Fig.5D). Family gall-inducer: Eriophyidae
Leaf gall; a small pouch on leaf blades.
Camino de las Salinas. 27-VIII-99. A. Ibáñez *leg.*

VITACEAE

Cissus microcarpa Vahl

G58. Family gall-inducer: Cecidomyiidae
Leaf gall, ovoid abundant, distinct in both sides of blades, medial size.
Sendero de Santa Cruz. 26-VIII-99. J. L. Nieves *leg.*

DISCUSSION

Gall-inducing arthropods have been more thoroughly sampled in temperate regions than in tropical regions. Indeed, from the perspective of biodiversity inventories, we have barely scratched the surface of the tropical faunas (Hanson and Goméz-Laurito 2005). A global pattern in local number of gall-inducing insects was described recently (see Price *et al*. 1998). The study pointed to a greater richness of gall-inducing insects in warm dry regions, while temperate and tropical areas with humid, mesic vegetation showed lower gall richness indices. However, as recently acknowledged by Espírito-Santo and Fernandes (2007), these results could be affected by an under-sampling of tropical rain forests, where gall richness could be higher than predicted by Price *et al*. (1998).

Our results show than the moist and wet tropical forests of Coiba National Park revealed a rich diversity of gall-inducing arthropods, with species richness numbers higher than those registered in continental Panama (see Price *et al.* 1998) and other parts of the Neotropical region (see Cuevas *et al.* 2004a, Costa De Oliveira and Maia 2005) (Table 4). Although we did not collect all species in Coiba Island, the total of fifty nine species, with a range of one to nineteen gall inducer species per site, in Coiba National Park is more that the twelve proposed for mesic vegetation in the literature (see Price *et al.* 1998). Coiba National Park diversity is similar

TABLE 4
Comparison of gall inducing arthropods species richness of Coiba Nacional Park and literature data from the Neotropical Region

Region	Site	No. Gall inducers species	Average o range	Method	References
Coiba Island	17 sites	59	1-19	Two weeks per year for 3 years of intensive sampling	Present paper
Mainland Panama	9 sites		0-19	9 samples of 10 hours each one	Barrios & Medianero 1999
	Park. Nat. Metropolitano	50	2-15	Sampling of 138 plants species for 15 months	Medianero *et al*. 2003
	San Lorenzo	58	13-30	Sampling of 120 plants species for 12 months	Medianero *et al.* 2003
Mexico	Jalisco	39		30 transects of 50 x 5 m	Cuevas *et al.* 2004
			14-15	2 samples of 45 trees, 100 shrubs and 1000 herbs	Price *et al.* 1998
Brazil	Cerrado do Cipo		0-46	43 samples of 45 trees, 100 shrubs and 1000 herbs	Price *et al.* 1998
	Cerrado	49	17	3 samples of 45 trees, 100 shrubs and 1000 herbss	Gonçalves-Alvin & Fernandes 2001
	Campo sujo	31	13	3 samples of 45 trees, 100 shrubs and 1000 herbss	Gonçalves-Alvin & Fernandes 2001
	Cerradão	23	8	3 samples of 45 trees, 100 shrubs and 1000 herbss	Gonçalves-Alvin & Fernandes 2001
	Canga	33	13	3 samples of 45 trees, 100 shrubs and 1000 herbss	Gonçalves-Alvin & Fernandes 2001
	Río de Janeiro	43		6 sites collection of 30 minutes between 2002-2004	Costa de Oliveira & Maia 2005
	São Paulo	36			Urso-Guiamares & Scareli-Santos. 2006
	Minas Gerais	137		36 samples of 8 hours each one	Maia & Fernandes 2004
Costa Rica	Different sites	967		Sampling per 10 years	Hanson & Goméz-Laurito 2005

to that found at San Lorenzo ($\alpha = 9.3$), a six ha rain forest area on the Panamanian mainland (Medianero *et al*. 2003). Our results suggest that, according to insular biogeography theory (MacArthur and Wilson 1967), that Panama's continental territory, where close to 11000 species of plants have been identified (Correa 2001), as well as other sites in the Neotropical region, must be richer in arthropods than indicated by recorded data in literature. Certain climatic and edaphic factors can produce higher than expected gall-inducing species richness in certain warm temperature regions. Plant diversity is the predominant factor producing high gall-inducing species richness in wet tropical regions (Yukawa *et al.* 2001; Hanson & Gómez-Laurito 2005). Our results support the idea that it may be premature to conclude that species richness of gall inducers declines near the equator (Hanson and Gómez-Laurito 2005). Furthermore there is an urgent need for more investigation of gall-inducing arthropods in the Neotropics, a region where as many as 20.000 gall-midge species (Cecidomyiidae), could exist (Espírito-Santo and Fernandes 2007).

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RESUMEN

El interés por el estudio de las agallas y los artrópodos que las inducen ha crecido en todo el mundo en los últimos veinte años. Sin embargo, los artrópodos que inducen agallas en la región Neotropical son probablemente los menos estudiados. Un estudio de la riqueza y composición de artrópodos que inducen agallas fue desarrollado en el Parque Nacional Coiba en la Republica de Panamá. Los datos provienen de muestreos intensivos de dos semanas, efectuados entre agosto de 1997 y septiembre de 1999, en 17 sitios del área insular del Parque Nacional Coiba. Un total de 4942 agallas, que corresponden a 50 especies de insectos y nueve de ácaros, fueron colectadas en 50 especies de plantas vasculares de 30 familias. El 62.7% de las agallas correspondieron a especies de la familia Cecidomyiidae (Diptera), el 15.3% a ácaros de la familia Eriophyidae, el 8.5% a Psyllidae (Homoptera), un 6.8% a Coccidae y el 5.1% a Phlaeothripidae (Tysanoptera). Las familias de plantas con más especies de inductores de agallas fueron Myrtaceae con siete, Bignoniaceae con cinco y Euphorbiaceae, Fabaceae y Melastomataceae con cuatro. Las agallas formadas en hojas representaron el 93% del total. El número de inductores de agallas por sitio osciló entre uno y diecinueve. La riqueza de artrópodos inductores de agallas del Parque Nacional Coiba se discute con datos disponibles de la literatura para el área continental de Panamá y el Neotrópico. Nuestros resultados apoyan la idea de que es prematuro concluir que la riqueza de artrópodos que inducen agallas disminuye hacia el Ecuador.

Palabras clave: Coiba, insectos gallícolas, riqueza de agallas, plantas hospedadoras, interacción planta/insecto, Panamá.

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