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Traditional and geometric morphometrics supporting the differentiation of two new *Retracrus* (Phytoptidae) species associated with heliconias

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Abstract Cryptic diversity has been confirmed for several phytophagous mites in the Eriophyoidea superfamily previously considered as presenting low host specificity. Among generalist eriophyoids is the phytoptid *Retracrus johnstoni* Keifer, which has been reported in 19 palm species belonging to 11 genera, causing severe damage on some of them. Surprisingly this species was recently reported on another monocot family, Heliconiaceae, infesting *Heliconia* plants in Costa Rica and Brazil, being the only in the tribe Mackiellini to not be associated with palm trees. This study aimed to investigate the occurrence of cryptic species in *R. johnstoni* and to clarify the taxonomic status of populations associated with heliconias in the Americas. With this purpose traditional and geometric morphometric analyses were conducted as well as a detailed morphological study. Measurable trait data were analysed via univariate and multivariate analyses. Shapes of specimens from different populations were compared via geometric morphometric landmark methods. Morphometric analysis supported occurrence of at least two cryptic species previously identified as *R. johsntoni* and suggested occurrence of cryptic species among populations associated with different palm trees. Taxonomic descriptions of two new taxa associated with heliconias, namely *Retracrus costaricensis* n. sp. Ferreira and Navia and *Retracrus heliconiae* n. sp. Ferreira and Navia are presented. Morphometric traits that can be useful in the taxonomic identification are noted and their value is discussed. Results of the traditional morphometry and geometric methods were compared and the advantages of their joint use for Eriophyoidea systematics are discussed.

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Introduction

Among the plant-feeding mites, the Eriophyoidea are the second most economically important group of pests (Lindquist and Amrine 1996). Several species are known to cause considerable damage in agroecosystems and forestry regions worldwide (Lindquist et al. 1996; Castagnoli et al. 2010; Duso et al. 2010). They are responsible for yield losses via direct damage or virus transmission (Lindquist et al. 1996; Duso et al. 2010) and are subject to quarantine regulations due to their potential as invasive species (Navia et al. 2010).

Misidentification of crop pests may have serious negative implications, i.e., leading to adoption of inappropriate prevention measures or to ineffective control strategies (Armstrong and Ball 2005; Bickford et al. 2007). Elucidation of the cryptic structure of species complexes of pests can mitigate serious negative consequences caused by ignorance of their existence (Bickford et al. 2007; Arthur et al. 2011; Boykin et al. 2012; Rafter et al. 2013; Skoracka et al. 2013). Eriophyoid mite identification is hampered as a result of their small size, structural simplicity (Lindquist and Amrine 1996), and the occurrence of cryptic lineages (Skoracka et al. 2012).

Cryptic diversity has been detected in almost all taxonomic groups (e.g. Hebert et al. 2004; Bickford et al. 2007) and among eriophyoid mites it has been uncovered specially in taxa reported as generalists (Skoracka et al. 2012; Miller et al. 2013). Most of eriophyoid mites have high host specificity (Oldfield 1996; Skoracka et al. 2010); approximately 80 % of the known taxa infest a single plant species and only 5 % of known species are reported infesting plants of different genus or family (Oldfield 1996). Morphometric and molecular studies have showed that two eriophyid taxa previously recognized as generalists, *Aceria tosichella* Keifer and *Abacarus hystrix* (Nalepa), both associated with monocots in the Poaceae family, actually comprises a cryptic species-complex, in which some species or lineages have high host specificity (Skoracka and Kuczynski 2006; Carew et al. 2009; Skoracka 2009; Skoracka and Dabert 2010; Skoracka et al. 2012; Miller et al. 2013).

Among generalist eriophyoid mites a Phytoptidae in the Mackiellini tribe, *Retracrus johnstoni* Keifer, has been reported in 19 palm tree species (Arecaceae) belonging to 11 genera in the Americas—Mexico, Costa Rica and Brazil (Keifer 1965; Ochoa et al. 1994; Santana et al. 1994; Santana and Flechtmann 1998; Gondim Jr. 2000; Furiatti 2001; Abreu 2004; Navia et al. 2007) and also in Africa–Egypt (El-Halawany et al. 2001) (Table 1). In addition to *R. johnstoni*, currently the genus *Retracrus* presents two more species, both also reported from palm trees—*Retracrus elaeis* Keifer and *Retracrus pupunha* Reis and Navia (Keifer 1975; Reis et al. 2012). *Retracrus johnstoni* and *R. elaeis* can occur in large populations, causing severe symptoms and damaging their hosts (Genty and Reyes 1977; Genty 1980; Ochoa et al. 1991).

Prior to 2012, mites of the tribe Mackiellini had only been reported to be associated with palms (see Chetverikov et al. 2014). Surprisingly, *R. johnstoni* was recently reported on another monocot family, Heliconiaceae, infesting and causing damage on *Heliconia latispatha* Bentham in Costa Rica (Aguilar and Murillo 2012). Populations identified as *R. johnstoni* were also found to be associated with *Heliconia pendula* Wawra in Bahia State, Brazil (A. R. Oliveira, personal communication). In Costa Rica, symptoms of mite

Table 1 Palm tree host plants and localities of occurrence of mites in the genus *Retracrus*

Retracrus species	Palm host plant	Country, State	References
R. johnstoni Keifer	*Astrocaryum aculeatissimum* (Schott)	Brazil, São Paulo	Gondim Jr. (2000)
	Bactris gasipaes Kunth	Brazil, São Paulo	Gondim Jr. (2000)
	Bactris setosa Mart	Brazil, São Paulo	Gondim Jr. (2000)
	Chamaedorea sp.[a]	Mexico (intercepted at USA)[b]	Keifer (1965)
	Chamaedorea costaricana Oersted	Costa Rica	Ochoa et al. (1994)
	Chamaedorea sp.	Costa Rica	Ochoa et al. (1994)
	Cocos nucifera L.	Brazil-Bahia, Ceará, Paraíba, Pernambuco, Rio de Janeiro, Sergipe	Santana et al. (1994), Santana and Flechtmann (1998)
	Elaeis guineensis Jacquin	Brazil, Pernambuco	Gondim Jr. (2000)
	Euterpe edulis Mart.	Brazil, São Paulo	Gondim Jr. (2000)
	Euterpe oleracea Mart.	Brazil, São Paulo	Navia et al. (2007)
	Euterpe precatoria Mart.	Brazil, Amazonas	Navia et al. (2007)
	Euterpe sp.	Brazil, Pernambuco	Gondim Jr. (2000)
	Geonoma gamiova Barb. Rodr.	Brazil, São Paulo	Gondim Jr. (2000)
	Geonoma pohliana Mart.	Brazil, São Paulo	Gondim Jr. (2000)
	Geonoma schottiana Mart.	Brazil, São Paulo	Gondim Jr. (2000)
	Mauritia flexuosa L.	Brazil, Amazonas	Navia et al. (2007)
	Phoenix dactylifera L.	Egypt	El-Halawany et al. (2001)
	Scheelea sp.	Brazil, São Paulo	Navia et al. (2007)
	Syagrus romanzoffiana (Cham.)	Brazil, Rio de Janeiro, São Paulo	Santana et al. (1994), Gondim Jr. (2000)
R. elaeis Keifer	*Elaeis guineensis* Jacquin[a]	Colombia, Bucaramanga[b]	Keifer (1975)
	Bactris gasipaes Kunth	Costa Rica	Navia et al. (2007)
	Chamaedorea costaricana Oersted	Costa Rica	Navia et al. (2007)
R. pupunha Reis and Navia	*Bactris gasipaes* Kunth	Brazil, Roraima	Reis et al. (2012)

[a] Type host plant

[b] Type locality

infestation have been very severe, consisting of generalised chlorosis, rust-coloured damage, or uniform brown-coloured spots that can extend throughout the entire leaf blade (Aguilar and Murillo 2012). Aesthetic damage caused by *Retracrus* infestations in heliconias certainly compromises the market value of cut flowers, wherein the flowers are packed together with leaves. In Brazil, *Retracrus* populations are low, and up to now no damage has been observed (A. R. Oliveira, personal communication).

It is possible that populations currently identified as *R. johnstoni* associated with plants of the genus *Heliconia* in Costa Rica and Brazil comprise cryptic species, i.e., different taxa in the *johnstoni* complex, as observed for other "generalists" eriophyoid mites. Compared with other eriophyoids, the taxonomic identification of *Retracrus* mites is especially difficult. This is due to the simplified prodorsal shield ornamentation; the absence of longitudinal lines in the female coverflap; the greatly reduced empodium, which hinders ray counting; and the body often covered by wax, hindering taxonomic traits

(Keifer 1965, 1975). A reduced number of diagnostic traits are available for distinguishing species (see Keifer 1965, 1975).

"Traditional morphometrics" which consist of univariate and multivariate statistical analyses of sets of quantitative variates, are extremely useful for describing patterns of shape variation within and among groups (Marcus 1990). These morphometric methods have been successfully used in acarology for identifying new species, uncovering cryptic species, differentiating geographic populations, and revealing synonymy of taxa (Baker and Schwarz 1997; Skoracka et al. 2002; Klimov et al. 2006; Navia et al. 2009; Pfingstl et al. 2010; Vidović et al. 2010; Stekol'nikov and Klimov 2010; Wang et al. 2011). As linear distance measurements are usually highly correlated with size (Bookstein et al. 1985), it is interesting to associate analyses of quantitative variates with size-free shape variates using methods that allow for capturing the geometry of the morphological structures and preserving this information throughout the analyses (Adams et al. 2004). The idea of standardising the shape of structures, comparing seta positions using "deformation grids", and quantifying the variation of these positions is old in the context of acarology (see Rowell et al. 1978) and it preceded the development of modern geometric morphometric techniques. Most studies employing these modern tools have been conducted on ticks (Pretorius and Clarke 2000; Clarke and Pretorius 2005), water mites (Becerra and Valdecasas 2004), oribatida (Baran et al. 2011), and scutacarid (Jagersbacher-Baumann 2014). For the tiny eriophyoid mites, geometric morphometric methods have been poorly explored (Navia et al. 2006; Vidović et al. 2014), although initial results indicate the extreme promise of these techniques (Navia et al. 2006).

This study aimed to investigate the hypothesis of cryptic species occurrence in the genus *Retracrus* and to clarify the taxonomic status of populations associated with two heliconia species in the Americas by evaluating morphological differences across populations. For this purpose traditional and geometric morphometric analysis as well as a detailed morphological study were conducted. Measurable trait data (linear measurements or counts) were analysed via univariate and multivariate analyses. The shapes of specimens from different populations were compared via geometric morphometric landmark methods. The results of the traditional morphometry and geometric methods were compared. Taxonomic descriptions of the taxa identified as new to science are presented and the most remarkable morphometric differences are presented.

Materials and methods

Material examined

Specimens of seven populations preliminarily identified as *R. johnstoni* were studied. Two populations were collected from *Heliconia* (Heliconiaceae) plants, and five populations were collected from palms (Arecaceae) (Table 2). Samples of heliconia populations were sent by collaborators; Brazilian population was collected by Dr. Anibal Ramadan Oliveira, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil; Costa Rican population was collected by Dr. Hugo Aguilar, Universidad de Costa Rica, São José, Costa Rica. Number of specimes collected from each population varied from 30 to 60. Whenever possible, the same individuals were used to obtain both traditional and geometric morphometric data.

Mites were collected through direct examination using a stereomicroscope and preserved in 70 % ethyl alcohol. *Retracrus* mites are wax producers, and their bodies can be

Table 2 Studied populations of *Retracrus* mites, host plants and collection localities

Host family	Host species	Country	State, locality	Coordinates
Arecaceae	*Cocos nucifera* L.	Brazil	Alagoas, Maragogi	8°55′23.45″S 35°9′32.25″W
			Paraíba, Pitimbu	7°32′9.19″S 34°50′0.20″W
			Rio Grande do Norte, Búzios	6°6′50.08″S 35°9′32.00″W
			Pernambuco, Itamaracá	7°46′11.33″S 34°51′5.51″W
	Syagrus romanzoffiana (Cham.)	Brazil	São Paulo, Piracicaba	22°42′31.57″S 47°37′54.62″W
Heliconiaceae	*Heliconia pendula* Wawra	Brazil	Bahia, Ilhéus	14°47′45.66″S 39°10′01″W
	Heliconia latispatha Bentham	Costa Rica	San José, San José	9°55′37.66″N 84°4′55.24″W

completely covered by dense wax layers, hindering visualisation of taxonomic structures when examined under a microscope. To remove the wax, the mites were maintained for 1 min in Nesbitt's fluid before mounting on slides in modified Berlese medium (Amrine and Manson 1996).

Traditional univariate and multivariate morphometrics

The morphological parameters obtained were subjected to multivariate analysis of variance (MANOVA) with populations as the independent variate and, if significant, to univariate analysis of variance (ANOVA; GLM procedure); means were compared using Student–Newman–Keuls test. Two multivariate analyses were applied to the data set: canonical variate analysis (CVA) (PROC CANDISC), and discriminant function analysis (PROC DISCRIM). Each population (same host plant and locality) was a priori defined as a group in the discriminant function analysis. All of the analyses were performed using the SAS statistical program (SAS Institute 2002).

Twenty females in dorsoventral position were selected from each population and studied. A total of 39 traits were evaluated for the linear morphometric analyses (Table 3). The characters evaluated were those commonly used and considered important in Eriophyoidea systematics (Amrine and Stasny 1994), excluding some that were difficult to visualise or that could not be measured reliably because (1) were no clearly visualized or were bent (e.g., number of microtubercles of the ventral rings; length of very long setae); (2) were considered to be less important for morphometry, since they are commonly invariable among species; or (3) were difficult to standardise their measurement (e.g., length of the leg segments). The terminology follows Amrine and Stasny (1994). Measurements were conducted according to de Lillo et al. (2010) with the following exceptions: (1) body length was measured from the tip of the frontal lobe to the rear end of the anal lobe, not considering pedipalps; (2) the scapular seta (*sc*) tubercle distance (between internal tubercle margins) was used instead of base setae distance; (3) empodium length was measured including its basal portion inserted in the tarsus. The count of ventral opisthosomal annuli starts from the first full annulus behind the genitalia. Dorsal opisthosomal annuli were counted from the first full annulus behind the middle of the

Table 3 Measurements of *Retracrus* females (n = 20) used in the statistical analysis, mean, standard error and range

Traits	Costa Rica (*H. latispatha*)		Bahia, Brazil (*H. pendula*)		São Paulo, Brazil (*S. romanzoffiana*)		Pernambuco, Brazil (*C. nucifera*)	
	Mean ± SE	Min–max	Mean ± SE	Min–max	Mean ± SE	Min–max	Mean ± SE	Min–max
Id L	160.7 ± 3.50c	128–178	148.2 ± 2.23d	129–168	153.0 ± 3.48d	126–182	165.0 ± 1.19bc	152–173
Id W	80.2 ± 2.30c	62–98	83.4 ± 1.73c	70–97	85.3 ± 1.58bc	70–98	82.3 ± 0.44c	78–85
PSh L	63.4 ± 0.87d	57–69	66.5 ± 0.76c	62–72	62.9 ± 1.06d	57–71	63.4 ± 0.18d	62–65
PSh W	72.8 ± 1.94d	59–86	77.0 ± 1.73bcd	66–93	75.4 ± 1.06cd	65–99	73.1 ± 0.37d	70–75
FLb L	9.9 ± 0.24cd	8–12	11.4 ± 0.18a	10–13	10.9 ± 0.16b	9–12	9.0 ± 0.0e	9–9
FLb W	26.4 ± 0.4c	24–30	26.5 ± 0.35c	24–29	26.7 ± 0.43c	24–30	28.3 ± 0.23b	27–30
sc L	15.0 ± 0.25d	13–16	17.5 ± 0.42b	14–21	19.5 ± 0.36a	17–22	16.9 ± 0.06bc	16–17
sc Sp	36.2 ± 0.80a	30–45	30.2 ± 0.56c	26–34	33.7 ± 0.75b	28–41	35.8 ± 0.21a	34–37
ve L	18.2 ± 0.26e	15–20	19.4 ± 0.21d	18–21	25.2 ± 0.38a	22–28	22.9 ± 0.16b	22–24
ve Sp	41.6 ± 0.63b	30–45	40.0 ± 0.36c	37–43	42.5 ± 0.52b	38–46	44.9 ± 0.26a	44–47
LI L	32.6 ± 0.66b	27–37	28.1 ± 0.33c	26–31	32.9 ± 0.64b	27–36	34. 1 ± 0.25ab	31–36
*bv*I L	12.1 ± 0.19d	10–13	11.9 ± 0.12d	10–12	12.9 ± 0.25c	11–15	14.3 ± 0.21b	13–16
l′ L	15.9 ± 0.37d	13–19	10.5 ± 0.18e	9–13	18.6 ± 0.42c	16–23	23.6 ± 0.18a	22–25
φ L	7.8 ± 0.15e	8–10	7.1 ± 0.16f	6–8	8.4 ± 0.09d	8–9	9.0 ± 0.05ac	9–10
ft″I L	14.8 ± 0.33d	13–18	16.9 ± 0.34c	15–19	18.4 ± 0.33b	16–20	19.9 ± 0.22a	17–22
ft′I L	9.4 ± 0.30e	8–15	11.6 ± 0.27d	9–14	14.2 ± 0.04c	14–15	18.9 ± 0.19a	18–21
*ω*I L	4.7 ± 0.0e	5–5	5.4 ± 0.11d	5–7	6.6 ± 0.04a	6–7	6.0 ± 0.0b	6–6
EI L	4.7 ± 0.0c	4–5	4.1 ± 0.1d	4–5	5.0 ± 0.15b	5–7	5.0 ± 0.0bc	5–5
EI ray	6.0 ± 0.0b	6–6	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8
LII L	28.5 ± 0.44d	25–32	26.1 ± 0.27e	24–29	32.0 ± 0.28a	29–34	31.6 ± 0.16ab	30–33
*bv*II L	13.9 ± 0.18d	12–16	12.5 ± 0.17e	11–14	18.2 ± 0.27b	16–21	17.6 ± 0.15c	16–19
ft″II L	11.1 ± 0.22d	9–13	9.8 ± 0.32e	8–12	15.8 ± 0.27c	13–17	18.0 ± 0.20b	16–19
ft′II L	3.8 ± 0.04d	4–5	3.8 ± 0.06d	4–5	4.7 ± 0.0b	5–5	5.0 ± 0.0a	5–5
*ω*II L	4.6 ± 0.06d	4–5	4.8 ± 0.13c	4–6	5.7 ± 0.0b	5–6	5.95 ± 0.05a	5–6

Table 3 continued

Traits	Costa Rica (*H. latispatha*)		Bahia, Brazil (*H. pendula*)		São Paulo, Brazil (*S. romanzoffiana*)		Pernambuco, Brazil (*C. nucifera*)	
	Mean ± SE	Min–max	Mean ± SE	Min–max	Mean ± SE	Min–max	Mean ± SE	Min–max
EII L	3.8 ± 0.04d	4–5	4.3 ± 0.10c	4–5	4.9 ± 0.07ab	5–6	5.0 ± 0.0a	5–5
EII ray	6.0 ± 0.0b	6–6	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8
1b L	5.4 ± 0.20c	4–8	4.7 ± 0.0d	5–5	4.9 ± 0.10d	5–6	7.2 ± 0.22a	6–9
1b Sp	15.3 ± 0.28bc	13–19	16.3 ± 0.38b	14–19	18.7 ± 0.40a	15–21	14. 6 ± 0.19c	13–16
1a Sp	11.12 ± 0.38b	8–14	10.6 ± 0.27b	8–12	12.4 ± 0.31a	10–15	8.7 ± 0.14d	8–10
2a Sp	32.7 ± 0.64b	29–41	34.5 ± 0.74b	29–42	36.4 ± 0.76a	31–43	30.2 ± 0.29c	29–35
Gen L	16.2 ± 0.35c	12–18	15.7 ± 0.27cd	13–17	17.6 ± 0.27b	16–20	15.3 ± 0.22d	14–17
Gen W	23.7 ± 0.76a	19–29	22.9 ± 0.48a	19–27	19.8 ± 0.36b	18–24	22.95 ± 0.11a	22–24
c2 L	19.2 ± 0.56b	14–24	16.6 ± 0.29c	14–19	23.4 ± 0.71a	18–30	24.9 ± 0.33a	22–28
e L	13.3 ± 0.35b	10–17	12.0 ± 0.13c	11–13	14.9 ± 0.27a	13–17	14.95 ± 0.16a	14–16
e Sp	16.4 ± 0.50c	13–22	14.3 ± 0.39d	11–17	16.0 ± 0.48c	13–20	16.45 ± 0.19c	15–18
f L	19.5 ± 0.37e	17–26	17.3 ± 0.22f	16–19	23.4 ± 0.35d	21–27	26.4 ± 0.23b	24–28
f Sp	20.7 ± 0.51d	16–24	17.3 ± 0.43e	14–22	23.1 ± 0.44c	20–27	26.2 ± 0.22b	24–28
D Ann	13.0 ± 0.0a	13–13	13.0 ± 0.0a	13–13	13.0 ± 0.0a	13–13	13.0 ± 0.0a	13–13
V Ann	45.0 ± 0.0a	45–45	44.8 ± 0.13a	43–45	45.0 ± 0.0a	45–45	45.0 ± 0.0a	45–45

Traits	Rio Grande do Norte, Brazil (*C. nucifera*)		Paraíba, Brazil (*C. nucifera*)		Alagoas, Brazil (*C. nucifera*)		Holotype *R. johsntoni*
	Mean ± SE	Min–max	Mean ± SE	Min–max	Mean ± SE	Min–max	
Id L	170.6 ± 1.56b	155–179	168.3 ± 2.36bc	142–184	178.3 ± 1.29a	167–185	170–185
Id W	91.5 ± 0.91a	84–99	89.9 ± 1.26ab	80–100	89.2 ± 0.78ab	82–94	70–80
PSh L	68.8 ± 0.39b	65–71	69.3 ± 0.83b	61–75	71.7 ± 0.43a	69–75	80
PSh W	82.1 ± 0.96a	75–93	81.3 ± 1.31ab	72–96	79.5 ± 0.84abc	72–88	75
FLb L	9.5 ± 0.13de	8–10	9.4 ± 0.04de	8–10	10.15 ± 0.18c	9–11	*
FLb W	28.3 ± 0.20b	27–30	28.3 ± 0.13b	27–29	30.1 ± 0.33a	27–35	*

Table 3 continued

Traits	Rio Grande do Norte, Brazil (*C. nucifera*)		Paraíba, Brazil (*C. nucifera*)		Alagoas, Brazil (*C. nucifera*)		Holotype *R. johsntoni*
	Mean ± SE	Min–max	Mean ± SE	Min–max	Mean ± SE	Min–max	
sc L	16.3 ± 0.15c	15–18	17.1 ± 0.0bc	17–17	16.4 ± 0.15c	15–17	14
sc Sp	35.7 ± 0.17a	34–38	35.1 ± 0.23ab	33–38	36.0 ± 0.29a	33–38	40
ve L	21.8 ± 0.35c	18–25	21.7 ± 0.26c	20–24	22.3 ± 0.22bc	21–24	20
ve Sp	44.4 ± 0.31a	41–46	44.8 ± 0.42a	43–50	45.9 ± 0.29a	44–49	45
LI L	34.7 ± 0.26a	32–36	35.3 ± 0.38a	33–38	35.6 ± 0.23a	34–38	35
*bv*I L	14.5 ± 0.45b	12–19	13.9 ± 0.20b	12–16	15.4 ± 0.24a	13–17.0	*
l′ L	21.0 ± 0.23b	18–23	21.7 ± 0.44b	18–24	23.9 ± 0.33a	21–27	25
φ L	9.4 ± 0.06b	8–10	9.5 ± 0.0b	9–9	9.8 ± 0.08a	9–10	*
ft″I L	18.4 ± 0.16b	16–19	18.4 ± 0.27b	17–21	20.0 ± 0.00a	20–20	*
ft′I L	17.2 ± 0.22b	15–19	16.6 ± 0.10b	16–17	18.6 ± 0.29a	16–21	*
*ω*I L	5.7 ± 0.00c	6–6	5.7 ± 0.0c	6–6	6.0 ± 0.00b	6–6	*
EI L	4.7 ± 0.0c	4–4	4.7 ± 0.0c	5–5	6.0 ± 0.00a	6–6	*
EI ray	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8	6
LII L	30.2 ± 0.28c	28–32	30.7 ± 0.31bc	28–33	32.3 ± 0.34a	30–36	33
*bv*II L	17.2 ± 0.20c	16–19	17.3 ± 0.20c	16–19	19.3 ± 0.17a	18–22	*
ft″II L	15.8 ± 0.31c	14.2–19.0	16.1 ± 0.23c	14–18	19.2 ± 0.29a	16–20	*
ft′II L	4.6 ± 0.07c	3.8–4.7	3.8 ± 0.0d	4–4	5.0 ± 0.00a	5–5	*
*ω*II L	5.7 ± 0.04b	6–-7	4.7 ± 0.0c	5–5	6.0 ± 0.00a	6–6	*
EII L	4.7 ± 0.0b	5–5	4.7 ± 0.0b	5–5	5.0 ± 0.00a	5–5	*
EII ray	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8	8.0 ± 0.0a	8–8	6
1b L	5.1 ± 0.10cd	5–6	6.6 ± 0.0b	7–6	7.0 ± 0.0ab	7–7	*
1b Sp	16.1 ± 0.0b	16–16	15.6 ± 0.35bc	12–19	16.2 ± 0.19b	15–18	*
1a Sp	10.5 ± 0.21b	8–12	9.5 ± 0.0c	9–9	10.6 ± 0.19b	9–12	*
2a Sp	33.5 ± 0.43b	30–40	33.8 ± 0.57b	30–40	34.5 ± 0.37b	32–38	*

Table 3 continued

Traits	Rio Grande do Norte, Brazil (*C. nucifera*)		Paraíba, Brazil (*C. nucifera*)		Alagoas, Brazil (*C. nucifera*)		Holotype *R. johsntoni*
	Mean ± SE	Min–max	Mean ± SE	Min–max	Mean ± SE	Min–max	
Gen L	19.0 ± 0.21a	17–21	19.2 ± 0.16a	19–22	19.8 ± 0.13a	18–21	20
Gen W	23.9 ± 0.20a	22–26	23.7 ± 0.17a	22–27	23.8 ± 0.23a	22–26	25
c2 L	20.0 ± 0.49b	16–24	20.9 ± 0.38b	19–24	24.0 ± 0.60a	20–30	26
e L	14.9 ± 0.24a	13–17	15.1 ± 0.08a	15–16	15.3 ± 0.17a	14–17	15
e Sp	20.7 ± 0.46a	17–27	18.7 ± 0.13b	17–19	19.4 ± 0.49b	17–24	*
f L	25,0 ± 0.33c	22–27	24.4 ± 0.71cd	19–28	28.4 ± 0.57a	25–35	25
f Sp	27.9 ± 0.32a	26–30	27.3 ± 0.32a	25–29	28.1 ± 0.31a	26–31	*
D Ann	13.0 ± 0.0a	13–13	13.0 ± 0.0a	13–13	13.0 ± 0.0a	13–13	13
V Ann	45.0 ± 0.0a	45–45	45.0 ± 0.0a	45–45	45.0 ± 0.0a	45–45	*

Id L—idiosoma length; Id W—idiosoma width; PSh L—prodorsal shield length; PSh W—prodorsal shield width; FLb L—frontal lobe length; FLb W—frontal lobe width; *sc* L—scapular seta length; *sc* Sp—space between tubercles bearing scapular setae; *ve* L—external vertical seta length; *ve* Sp—space between tubercles bearing external vertical seta; LI L—leg I length; *bv*I L—basiventral femoral seta I length; *l′*I L—paraxial tibial seta I length; *φ* L—tibial solenidion length; *ft″*I L—antaxial fastigial tarsal seta I length; *ft′*I L—paraxial fastigial tarsal seta I lenght; *ω*I L—tarsal solenidion I length; EI L-empodium I length; EI ray—number of rays in empodium I; LII L—leg II length; *bv*II L—basiventral femoral seta II length; *ft″*II L—antaxial fastigial tarsal seta II length; *ft′*II L—paraxial fastigial tarsal seta II lenght; *ω*II L—tarsal solenidion II; EII ray—number of rays in empodium II; *1b* L—anterolateral seta on coxisternum I lenght; *1b* Sp—space between anterolateral setae on coxisternum I; *1a* Sp—space between proximal setae on coxisternum I; *2a* Sp—space between proximal setae on coxisternum II; Gen L—genitalia length; GenW—genitalia width; *c2* L—lateral seta length; *e* L—ventral seta II length; *e* Sp—space between ventral setae II; *f* L—ventral seta III length; *f* Sp—space between ventral setae III; D Ann—number of dorsal annuli; V Ann—number of ventral annuli

prodorsal shield rear margin. As for *sc* setae distance, the tubercle distance between the external vertical setae (*ve*) was considered (not between setae insertions). When a clear difference in lengths was observed between the right and left homologue of the same structure in the same specimen, the longer was considered. When homologous ventral setae were inserted in different annuli, they were considered to be inserted on the anterior annulus. For canonical variate analysis, the numbers of rays of empodia I and II were not considered, as the data did not fit this analysis when these traits were included. All of the measurements and counts were performed under 100× magnification with an optical phase-contrast microscope (model BX41, Olympus).

Examination of the *R. johnstoni* type material was not possible. In consulting with the curator of the US. National Mite Collection in the United States, no information was obtained on the material's availability. Dr. James W. Amrine Jr. (West Virginia University), a systematics specialist in eriophyoid mites of the US, reported that there was no more type material preserved in slides that were in good enough condition to be studied but that dried material (dry leaves of the host type infested by *R. johnstoni*) had been provided for study to Dr. Philipp Chetverikov, Saint Petersburg State University, Russia. Dr. Chetverikov reported that some specimens have been successfully mounted from the dried material but that they were very damaged. Only a few structural traits could be observed (such as the number of rays of empodium), but it would not be possible to take measurements from the specimens for morphometric studies. Information on the original description of *R. johnstoni* (Keifer 1965) is shown for comparison with the material under study (Table 3).

Landmark-based morphometric methods

Three body regions were separately analysed through landmark morphometric methods—ventral, coxigenital, and prodorsal shield. Fourteen landmarks in the ventral region, 13 in the coxigenital region, and 7 in the prodorsal shield were defined following Bookstein (1991) and its descriptions are presented in Fig. 1.

Females in dorsoventral position, well clarified, and with unbroken body were selected for these analysis. Images (2048 × 1536 pixels resolution) of body regions of the selected females were obtained using a video system consisting of a phase-contrast optical microscope (Eclipse 80i, Nikon) connected to a digital camera (12.7 megapixels, DS-Ri1, Nikon), both connected to a camera control unit (DS Controller, Nikon). Images of the ventral region were obtained using a 40× magnification objective, while those of the coxigenital and prodorsal shield regions were obtained with a 100× magnification objective. It was not possible to obtain the same number of good-quality images for each population and body region because some specimens/body regions were partially damaged or insufficiently clarified (very common for the coxigenital region). The number of images obtained for each population and body region are listed in Table 4.

Landmarks were recorded, and their positions were transformed into Cartesian coordinates (x and y) using the Tpsdig software (Rohlf 2010). The raw landmark coordinates were aligned by generalised procrustes analysis (GPA) to remove the variation due to the isometric effects of size, position, and orientation (Rohlf 1999). *Tpssmall* software was used to determine whether the shape variation of the studied body regions was sufficiently small for the application of the deformation analysis to be possible. This program helps to assess the accuracy of the approximation of shape space by the tangent space (Rohlf 1997).

Shape differences among the analysed populations were further explored using a PCA of the covariance matrix of the Procrustes coordinates averaged by population. In addition,

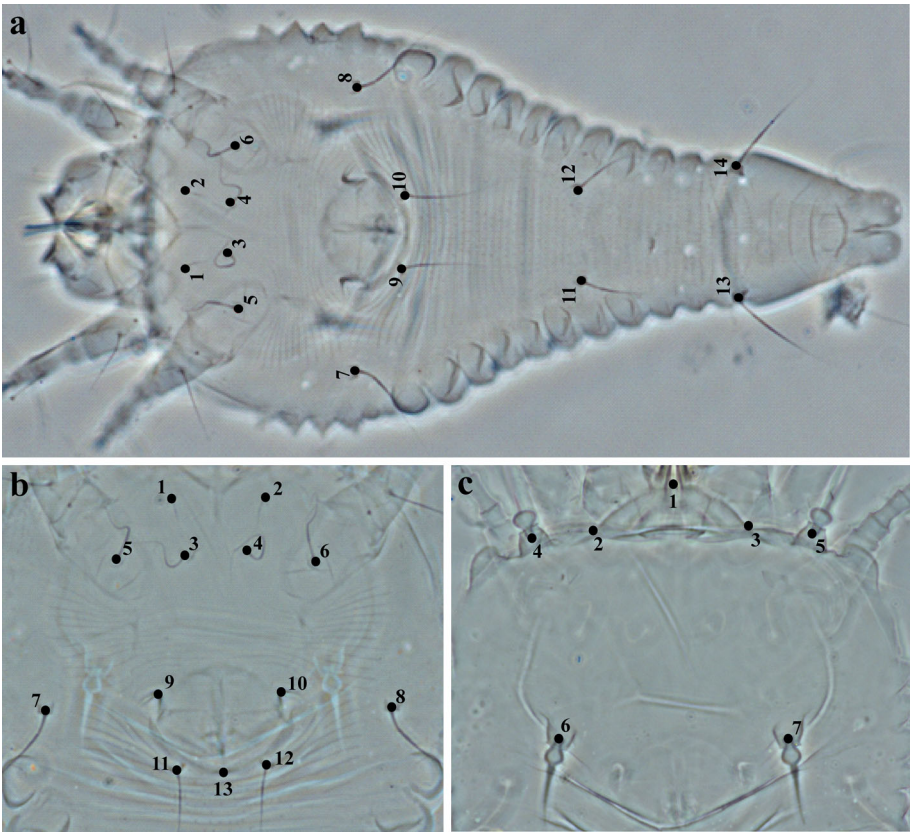


Fig. 1 Landmarks digitised on the ventral, coxigenital and prodorsal shield regions of *Retracrus* mites bodies. **a** Ventral region: *1* base of left coxal seta I (*1b*); *2* base of right coxal seta I (*1b*); *3* base of left coxal seta II (*1a*); *4* base of right coxal seta II (*1a*); *5* base of left coxal seta III (*2a*); *6* base of right coxal seta III (*2a*); *7* base of left lateral seta (*c2*); *8* base of right lateral seta (*c2*); *9* base of left genital seta (*3a*); *10* base of right left genital seta (*3a*); *11* base of left ventral seta II (*e*); *12* base of right ventral seta II (*e*); *13* base of left ventral seta III (*f*); *14* base of right ventral seta III (*f*). **b** Coxigenital region: *1* base of left of left coxal seta I (*1b*); *2* base of right coxal seta I (*1b*); *3* base of left coxal seta II (*1a*); *4* base of right coxal seta II (*1a*); *5* base of left coxal seta III (*2a*); *6* base of coxal seta III (*2a*); *7* base of left lateral seta (*c2*); *8* base of right lateral seta (*c2*); *9* left anterolateral margim of epigynium; *10* right anterolateral margim of epigynium; *11* base of left genital seta (*3a*); *12* base of right genital seta (*3a*); *13*. posterocentral tip of epigynium. **c** Prodorsal region: *1* anterior central tip of frontal lobe; *2* left base of frontal lobe; *3* right base of frontal lobe; *4* base of left external vertical seta (*ve*); *5* base of right external vertical seta (*ve*); *6* base of left scapular seta (*sc*); *7* base of right scapular seta (*sc*)

CVA was performed to reveal the variation among two or more groups of specimens relative to the average variation found within the groups. The overall significance test for CVA is also the appropriate significance test for a single classification multivariate analysis of variance (MANOVA). Distance matrixes were constructed by the generalised distance obtained through CVA. PCA and CVA were performed using MorphoJ software (Klingenberg 2011). Configurations of the anatomical landmarks were superimposed by the least-squares method, which transforms a landmark configuration by superimposing it on a reference configuration (consensus) and then translating, scaling and rotating one of them

Table 4 Number of digital images obtained for each body region and *Retracrus* population

Host, locality, country	Body region		
	Ventral	Coxigenital	Prodorsal shield
Heliconia latispatha, San José, Costa Rica	9	7	10
H. pendula, Ilhéus-BA, Brazil	10	10	11
Syagrus romanzoffiana, Piracicaba-SP, Brazil	12	11	20
Cocos nucifera, Itamaracá-PE, Brazil	20	20	20
C. nucifera, Búzios-RN, Brazil	11	12	16
C. nucifera, Pitimbu-PB, Brazil	20	20	20
C. nucifera, Maragogi-AL, Brazil	20	19	20

so that the sum of squares of the distances between the corresponding points of the configurations would as low as possible. The consensus configuration was separately obtained for each body region and population with the purpose of analysing differences between population averages using Relative Warp Analysis (RWA) in the Tpsrelw software (Rohlf 1998).

Taxonomic descriptions

Two new taxa identified as new to science were described based on morphometric analysis and detailed observations of their external morphology. Measurements were taken from females, males, and immature forms (larvae and nymphs). Drawings were made in a lucid chamber under a phase-contrast microscope (model BX41, Olympus) at 100× magnification. The drawings were scanned, digitised and elaborated using the Adobe Illustrator CS3 program. Measurements or counts were taken as aforementioned (univariate and multivariate morphometrics). All of the measurements are in micrometers (μm) unless otherwise noted. The measurements of the holotype precede the paratype ranges. Some measurements were not obtained due to the mite position in the slides. It was not possible to measure the cheliceral stylets due to overlap with other structures of the gnathosoma, such as palps and oral stylets. The terminology used was according to that proposed by Amrine and Stasny (1994). Morphometric traits with significant differences (SNK test) and without measurements overlapping with the other species in the group were considered as useful for taxonomic identification and are noted in the description remarks.

Results

Traditional univariate and multivariate morphometrics

The minimum and maximum values observed, with means and standard error of each of the 39 traits used in the morphometric analyses for the seven *Retracrus* populations from heliconias and palms, are exhibited in Table 3. The measurements/counts of the traits of the *R. johnstoni* holotype presented by Keifer (1965) in the original description are also presented.

The MANOVA showed significant differences among populations (GLnum/den = 222/584.16, Wilks' Lambda = 0.00000033 and F = 30; $P < 0.0001$). The univariate analyses

(Student–Newman–Keuls test) revealed significant differences among 37 of the 39 traits studied in the *Retracrus* populations; the only traits that did not significantly differ were number of dorsal and ventral rings. For several traits there was no variation (minimum–maximum) overlapping among the populations (Table 3). Fifteen traits were significant different between the heliconian populations and palm populations; 27 traits significantly differed among the two heliconia populations. In the comparison of the heliconia populations with those from the palms, the following traits exhibited significant differences with no or little overlap in variation ranges: setae and legs appendices lengths; length and distance between *ve*; and length and distances between opisthosomal ventral setae II (*e*) and III (*f*). In general, for these traits, the heliconia populations from both Brazil and Costa Rica exhibited lower values. Among the Brazilian and Costa Rican heliconia populations, the following traits exhibited significant differences with no or little overlap in variation ranges: length of paraxial tibial seta (l') and tibial solenidion (φ), and number of rays of the empodia of legs I and II. The *Retracrus* population from *H. pendula* from Brazil has a shorter body than all of the other populations studied and the *R. johnstoni* type material. The *H. latispatha* population from Costa Rica has six rays on the empodium, whereas eight rays were counted for all other populations.

The two first canonical variates (CV1 and CV2) explained 80.66 % of the total variation present in the covariance matrix among the traits of the populations analysed: CV1 explained 62.97 %, and CV2 explained 17.69 %. The projection graph of the individuals in space of the first two canonical variates (Fig. 2a) showed there was no overlap among the representatives of each of the heliconia populations or between these and the palm populations (*S. romanzoffiana* and *C. nucifera*); these populations were completely separate, revealing morphometric differentiation among them. Coconut tree populations from Pernambuco, Rio Grande do Norte, Alagoas and Paraíba were clustered, being overlapped or continuous, revealing morphometric proximity among them. The heliconia populations were differentiated from all palm tree populations along the CV1 axis. The *S. romanzoffiana* population was differentiated from all *C. nucifera* populations and from the Costa Rica heliconia population and along the CV2 axis. The two heliconia populations (Costa Rica and Brazil) were differentiated along both axes, but especially along the CV2 axis.

According to the CVA, the traits (eigenvectors) that contributed the most (higher eigenvalues loadings) to distinguishing the heliconia populations from all of the palm tree populations (Canonical variate 1) were the following, in decreasing order: lengths of the paraxial fastigial tarsal seta (ft') of legs I and II, of the l' seta on leg I, of the basiventral femoral seta (*bv*) on leg II, and of the tarsal solenidion (ω) on leg I; length and distance between the ventral setae III (*f*); and length of the antaxial fastigial tarsal seta (ft'') on leg II. Similarly, the traits that contributed most for distinguishing the two heliconia populations, as well as for distinguishing the *S. romanzoffiana* population from the coconut tree populations (Canonical variate 2) were as follows: lengths of the ω solenidion on leg I, of the ft' seta on leg I, and of the *ve* seta; distance between *sc* seta; and length of the idiosoma.

In comparing the measurements of the morphometric traits of the *Retracrus* populations obtained in this study and those of the type material presented by Keifer (1965) (Table 3), the *C. nucifera* populations are closest to the original description. Although it was not possible to conduct statistical analyses, it can be stated that marked differences are observed among the measurements of the *Heliconia* and *S. romanzoffiana* populations compared with the type material. The main differences were observed in the length of the idiosoma and the prodorsal shield; in the length and distance of the *sc* setae; in the length of the legs and legs setae; in the length and width of the genitalia; and in the length of the opisthosomal setae.

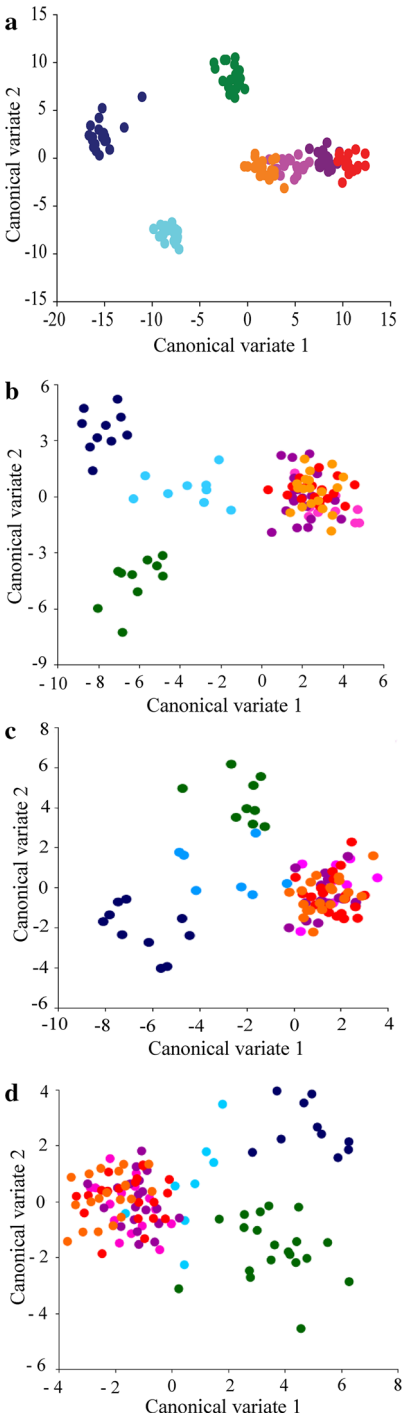


Fig. 2 Canonical variate analysis (CVA) of females morphometric traits of *Retracrus* populations from palm trees and heliconias from the Americas. **a** CVA of traditional morphometric traits (measurements and counts), **b** CVA of shape coordinates of the ventral region, **c** CVA of shape coordinates of the coxigenital region and **d** CVA of shape coordinates of the prodorsal shield. Individuals plotted against their values for the first two canonical variates. *Red circle*: *Cocos nucifera*, Alagoas, Brazil; *Orange circle*: *C. nucifera*, Paraíba, Brazil; *Violet circle*: *C. nucifera*, Pernambuco, Brazil; *Pink circle*: *C. nucifera*, Rio Grande do Norte, Brazil; *Light blue circle*: *Heliconia latispatha*, San José, Costa Rica; *Dark blue circle*: *H. pendula*, Bahia, Brazil; *Green circle*: *Syagrus romanzoffiana*, São Paulo, Brazil. (Color figure online)

Discriminant function analysis, through which the classification of the specimens was predicted, showed that all of the individuals were correctly classified in their populations of origin based on morphological similarities, except for one specimen from *H. pendula* from Bahia, Brazil, which was classified as belonging to the population from *S. romanzoffiana* from São Paulo, Brazil; and two specimens from *C. nucifera* from Rio Grande do Norte, Brazil, which were classified as belonging to the *C. nucifera* population from Paraíba. The correct prediction of most specimens in its respective populations corroborate CVA results, showing morphometric differentiation among studied populations and that coconut populations are the closest morphometrically.

Landmark-based morphometric methods

Analyses were conducted to obtain information on the morphological variations among *Retracrus* populations. The variation in shape found in each dataset was small enough to allow the statistical analyses to be performed in the tangent space (which is linear) approximate to Kendall's shape space (which is nonlinear).

The PCA performed on shape coordinates of 14 landmarks in the ventral region of 100 specimens from the seven studied populations resulted in 24 principal components, with the first two components explaining 67.25 % of the total variation (PC1 47.52 %, PC2 19.73 %). CVA performed on the same dataset showed that the first two canonical variates explained 90.26 % of the total variation (CV1 73.46 %, CV2 16.8 %). In the RWA performed on the population consensus configuration, the two first relative warps (RW1 and RW2) explained 92.99 % of the total variation (RW1 70.58 %, RW2 explained 22.41 %).

The PCA performed on shape coordinates of 13 landmarks in the coxigenital region of 100 specimens from the seven studied populations resulted in 22 principal components, with the first two components explaining 75.86 % of the total variation (PC1 62.78 %, PC2 13.08 %). CVA performed on the same dataset showed that the first two canonical variates explained 82.23 % of the total variation (CV1 60.83 %, CV2 21.39 %). In the RWA performed on the population consensus configuration, the two first relative warps explained 95.10 % of the total variation (RW1 82.66 %, RW2 12.44 %).

The PCA performed on shape coordinates of seven landmarks in the prodorsal shield region of 117 specimens from the seven studied populations resulted in 10 principal components, with the first two components explaining 52.3 % of the total variation (PC1 30.91 %, PC2 21.47 %). CVA performed on the same dataset showed that the first two canonical variates explained 91.92 % of the total variation (CV1 77.86 %, CV2 14.06 %). In the RWA performed on the population consensus configuration, the two first relative warps explained 88.89 % of the total variation (RW1 48.77 %, RW2 40.12 %).

The PCA and CVA scatterplots of the three body regions of *Retracrus* mites—ventral (Figs. 2b, 3), coxigenital (Figs. 2c, 4) and prodorsal shield (Figs. 2d, 5) from seven populations from heliconias and palm trees showed similar patterns, though in the CVA plots, specimens from each population were more clustered, and groups could be better segregated. The analysis revealed a clear distinction of populations related to the host plant. Specimens from all coconut tree populations were widely overlapped, whereas those from the palm tree *S. romanzoffiana* and from the two heliconias—*H. latispatha* and *H. pendula*—were completely separated or presented reduced overlap with the coconut specimens and also with one another. The population from *H. latispatha* was the most similar to the coconut tree populations, and for all body regions these specimens were plotted in an intermediate position between the coconut tree, *H. pendula* and *S. romanzoffiana* populations. Coxigenital and prodorsal shield CVA scatterplots (Fig. 2c, d) revealed the total

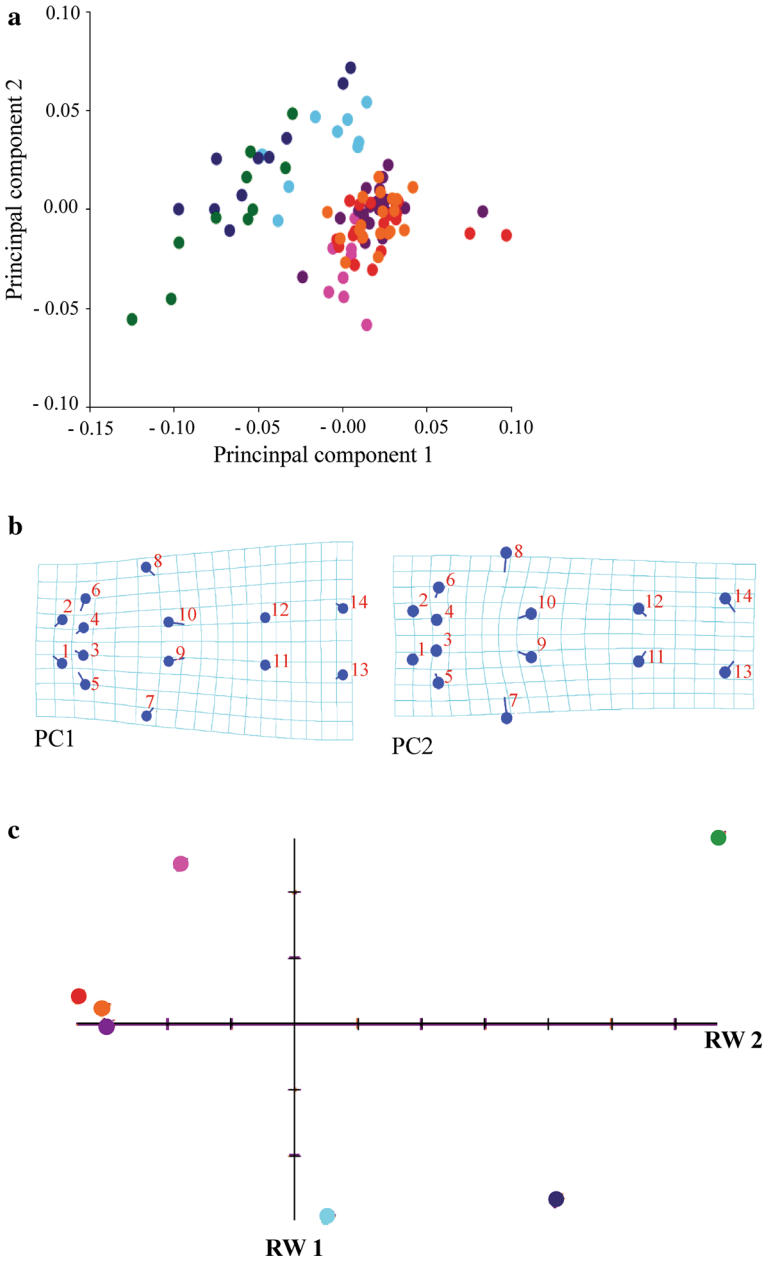


Fig. 3 Morphometric geometric analysis for the ventral region of *Retracrus* females from population associated with palm trees and heliconias in the Americas. **a** Principal component analysis (PCA). Individuals plotted against their values for the first two principal components. **b** Variations in shapes are presented in the form of transformation grids along the principal components 1 and 2 axis. **c** Relative warps (RW) for values $\alpha = 0$. Population consensus plotted against their values for the first two relative warps. *Red circle*: *Cocos nucifera*, Alagoas, Brazil; *Orange circle*: *C. nucifera*, Paraíba, Brazil; *Violet circle*: *C. nucifera*, Pernambuco, Brazil; *Pink circle*: *C. nucifera*, Rio Grande do Norte, Brazil; *Light blue circle*: *Heliconia latispatha*, San José, Costa Rica; *Dark blue circle*: *H. pendula*, Bahia, Brazil; *Green circle*: *Syagrus romanzoffiana*, São Paulo, Brazil. (Color figure online)

distinction of *H. pendula* and *S. romanzoffiana* populations; however, they also revealed that the *H. latispatha* population was not completely distinct, showing some proximity especially with the coconut tree and *S. romanzoffiana* populations. The CVA results showed that among the body regions studied, the ventral region (Fig. 2b) best distinguished specimens/populations from different host plants. CVA scatterplot of the ventral region is the most similar to that of the traditional morphometric analyses (Fig. 2a, b).

The consensus RWA showed that coconut tree populations were plotted along the negative RW1 axis, whereas populations from the other host plants were plotted along the positive axis (Figs. 3c, 4c, 5c). Within the coconut tree populations, this analysis revealed that those from Alagoas, Paraíba and Pernambuco are more similar to each other with respect to the ventral and coxigenital regions (Figs. 3c, 4c), while for the prodorsal shield region, those from Alagoas, Pernambuco and Rio Grande do Norte are the more similar (Fig. 5c). RWA scatterplots showed that the two heliconia populations are more similar with respect to the ventral and coxigenital regions than the prodorsal shield (Figs. 3c, 4c, 5c). The *S. romanzoffiana* population is very distinct from all other coconut tree populations, particularly in the ventral and coxigenital region (Figs. 3c, 4c).

The main ventral shape differences among populations revealed through PCA include genitalia position, which was shifted or not from the coxal area; coxal region compression, reflected by the distances between coxae and the posterior opisthosoma width; lateral seta position, which can be more or less shifted from the genitalia; and posterior opisthosoma constriction at the level of *e* and *f* setae, reflected by the distances between setae. PCA ventral deformation grids indicated differences in body shape between populations (see Supplementary material 1); in some populations, the body is relatively shorter and wider, while in others, they are larger and narrow. Ventral deformation grids from the coconut tree populations are quite similar, while for the *Retracrus* mites from heliconia populations (*H. pendula* and *H. latispatha*) and from *S. romanzoffiana*, some shape differences were quite remarkable. For these populations, the posterior opisthosoma is narrower than the anterior opisthosoma. In the *S. romanzoffiana* population, the body is wider at the level of the genitalia and lateral seta (*c2*); another difference is in the distance between proximal setae on coxisternum I (*1a*). In *H. pendula* population, the genitalia are nearer to the coxae (reflected by the base of the genital setae (*3a*) being closer to the genitalia). In *H. latispatha* population, the *1a* setae are more distant than in *H. pendula* population.

For the coxigenital region, the main shape differences include the lateral compression of the genital area, reflected by the distance between *c2* setae, and the length of the genitalia, reflected by the relative position of the posterocentral tip of the epigynium. Compared with palm populations, in heliconia populations, the genitalia are shorter; this difference was more notable in *H. pendula* population. As visualised in the ventral grids (see Supplementary material 1) but more evident in the coxigenital grids (see Supplementary material 2), in populations from heliconias and *S. romanzoffiana*, the body is narrower at the level of the genitalia (reflected by distance between *c2* setae) than in coconut tree populations.

For the prodorsal shield region, the main differences include the frontal lobe length, reflected by the distance between the frontal lobe tip and bases; the relative position of *ve* setae which can be anterior, posterior or on the level of the frontal lobe base; and the width of the frontal lobe (see Supplementary material 3). In coconut tree populations, frontal lobe lengths are quite similar, and *ve* seta bases are at the level of the frontal lobe base (insertion). Distinctly in the *H. latispatha* and in *S. romanzoffiana* populations, the *ve* bases are slightly posterior to the frontal lobe base, whereas they are shifted anteriorly in the populations from *H. pendula*. In *S. romanzoffiana* population the frontal lobe is longer and narrower than in the other populations.

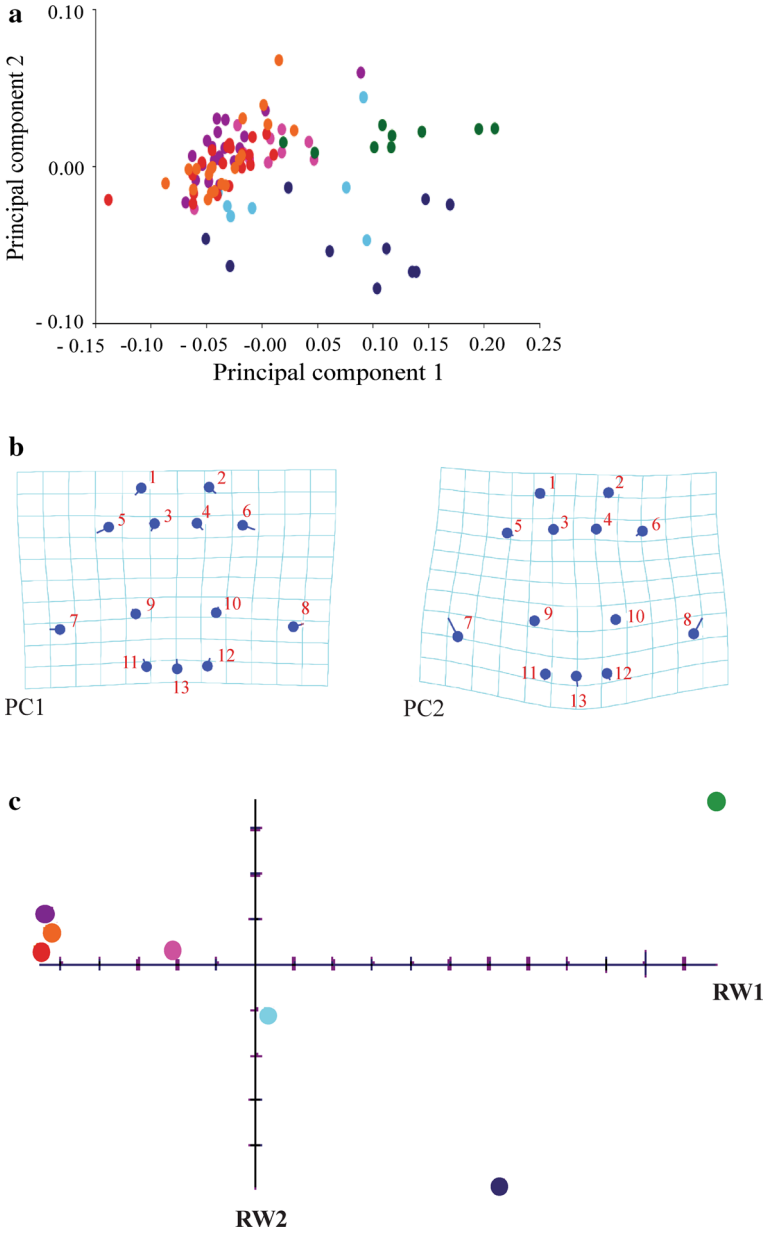
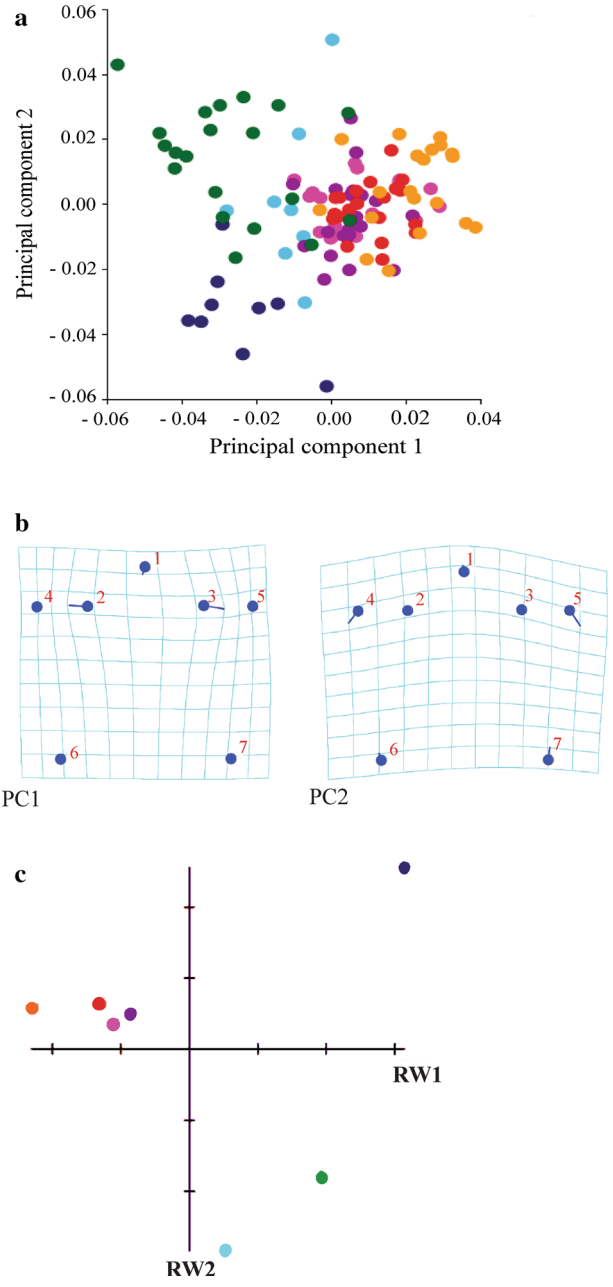


Fig. 4 Morphometric geometric analysis for the coxigenital region of *Retracrus* females from population associated with palm trees and heliconias in the Americas. **a** Principal component analysis (PCA). Individuals plotted against their values for the first two principal components. **b** Variations in shape s are presented in the form of transformation grids along the principal components 1 and 2 axis. **c** Relative warps (RW) for values $\alpha = 0$. Population consensus plotted against their values for the first two Relative Warps. *Red circle*: *Cocos nucifera*, Alagoas, Brazil; *Orange circle*: *C. nucifera*, Paraíba, Brazil; *Violet circle*: *C. nucifera*, Pernambuco, Brazil; *Pink circle*: *C. nucifera*, Rio Grande do Norte, Brazil; *Light blue circle*: *Heliconia latispatha*, San José, Costa Rica; *Dark blue circle*: *H. pendula*, Bahia, Brazil; *Green circle*: *Syagrus romanzoffiana*, São Paulo, Brazil. (Color figure online)



Discussion

Phenotypic variability may be related to partial or total genetic isolation among populations, as in the case of speciation (Skoracka et al. 2002). In this study, detailed morphological studies were performed using traditional morphometry and geometric methods to

◀**Fig. 5** Morphometric geometric analysis for the prodorsal shield of *Retracrus* females from population associated with palm trees and heliconias in the Americas. **a** Principal component analysis (PCA). Individuals plotted against their values for the first two principal components. **b** Variations in shape s are presented in the form of transformation grids along the principal components 1 and 2 axis. **c** Relative warps (RW) for values $\alpha = 0$. Population consensus plotted against their values for the first two relative warps. *Red circle*: *Cocos nucifera*, Alagoas, Brazil; *Orange circle*: *C. nucifera*, Paraíba, Brazil; *Violet circle*: *C. nucifera*, Pernambuco, Brazil; *Pink circle*: *C. nucifera*, Rio Grande do Norte, Brazil; *Light blue circle*: *Heliconia latispatha*, San José, Costa Rica; *Dark blue circle*: *H. pendula*, Bahia, Brazil; *Green circle*: *Syagrus romanzoffiana*, São Paulo, Brazil. (Color figure online)

evaluate phenotypic differences among populations that have been preliminarly identified as *R. johnstoni* from different hosts. The occurrence of morphometric variability or similarity among populations can add clarity to the evaluation of their taxonomic status. The results of the different morphometric analyses were extensively consistent. The morphometric analyses, both traditional and geometric morphometrics, revealed significant differences among the populations that allowed for differentiating the populations studied. A morphometric pattern associated with the host plant was observed. Populations most morphometrically similar were those associated with a same host plant, coconut trees, collected from different Brazilian states—Alagoas, Paraíba, Pernambuco, and Rio Grande do Norte. The populations associated with the two heliconia species were morphometrically different from the palm tree populations and also from one another. Surprisingly, the population from *S. romanzoffiana*, also a palm tree species, is morphometrically distinct from the *C. nucifera* populations.

The morphometric differences observed support the hypothesis of the existence of a cryptic species-complex among the populations that have been identified as *R. johnstoni* associated with different host plants. The populations associated with *H. latispatha* from Costa Rica and *H. pendula* from Bahia, Brazil are identified as new to science; their taxonomic descriptions were prepared and presented below in this study. In addition to the morphometric variability found among the heliconia populations, our detailed morphological study revealed differences that may be used as diagnosis traits for the new taxa.

Besides morphometric studies granting higher confidence for redefining the taxonomic status of the *Retracrus* populations associated with heliconias, they also allowed note some morphometric traits that can be helpful to identifying these species. A set of significant morphometric differences, for which there was no overlap in the variation range, were highlighted in the remarks. Future taxonomic studies of *Retracrus* mites should also consider morphometric traits to enrich descriptions in this genus.

Morphometric traits can be particularly useful in Eriophyoidea taxonomy in the case of "cryptic species" or when identification of species in a genus is difficult due to its morphological simplicity (e.g., reduced prodorsal shield or genitalia ornamentation). For several groups of mites, morphometric traits are commonly used as taxonomic characters, as for example for Phytoseiidae (Chant and McMurtry 2007), Tetranychidae (Baker and Schwarz 1997), or Trombiculidae (Stekol'nikov 2008). Also for Eriophyoidea taxonomy morphometric traits have already been used to differentiate species (Ozman-Sullivan et al. 2006; Reis et al. 2014). Whenever possible definition of taxonomic morphometric traits for Eriophyoidea should result from morphometric studies evolving enough number of specimens and populations to ensure its reliability.

In comparing populations studied and the original description of *R. johnstoni* (Keifer 1965), the measurements of the body and setae lengths of the *C. nucifera* populations were closer to the holotype, except for the number of rays of the empodium higher in the *C.*

nucifera individuals (Table 3). Unfortunately, it was not possible to access the *R. johnstoni* type material (see "Materials and methods"), but the information sent by Dr. Chetverikov allowed for some considerations about this character for which there was a discrepancy between the observations and the original description. According to Keifer (1965), *R. johnstoni* has an undivided empodium with six rays. In this study, only the Costa Rican *H. latispatha* population exhibited six rays in the empodium. All of the other populations analysed—from *C. nucifera*, *S. romanzoffiana*, and *H. pendula*—exhibited eight rays in the empodium. Although the *R. johnstoni* material obtained by Dr. Chetverikov was not well preserved, investigations revealed that there were eight rays in the empodium I of the female, not six as reported in the original description (Chetverikov, pers. comm.). The empodium of the mites of the genus *Retracrus* is very short, and under optical microscope observation counting the number of rays can be extremely difficult. It is possible that the microscopy resources available when the species *R. johnstoni* was described did not allow for accurately counting the number of rays of the empodium by Keifer (1965). It is thus suggested that the presence of eight rays in the empodium be considered as a taxonomic trait of *R. johnstoni*, not six as cited in the original description. Thus, the morphological traits of the studied *C. nucifera* populations align with those of *R. johnstoni*.

The *S. romanzoffiana* population of São Paulo State, Brazil, which has also been identified as *R. johnstoni*, was morphometrically different from the *C. nucifera* populations, which are closest to the type material presented by Keifer (1965). These results suggest that this population also comprises a cryptic species in the group *R. johnstoni*. It is possible that *R. johnstoni* populations identified from different palm trees do not consist of a single taxon but rather a species-complex. To clarify this hypothesis, given the unavailability of preserved *R. johnstoni* type material, obtaining topotype material of the species will be essential for comparing the populations from the diverse palms that have been reported as hosts. In addition to morphometric comparisons, as performed in this study, it will be important to conduct comparative studies using biological parameters and molecular data.

Among the performed analysis, the traditional CVA morphometric analyses allowed for better distinction among the populations studied (see Fig. 2). In addition to separation of the populations by host plant, supporting the identification of cryptic species in the genus, these analyses allowed for characterising the variability among populations of the same host, in the case of coconut tree populations from different states in Brazil; these populations entirely overlapped in the geometric morphometric analyses. Although the traditional CVA morphometric analyses has allowed the best discrimination among populations/species, we observed that results of the CVA applied to landmarks of the ventral region was very similar to that of the traditional CVA (Fig. 2a, b). This high similarity allowed us considering both analysis as presenting comparable efficiency for *Retracrus* species differentiation.

In this study despite the populations being better distinguished via traditional morphometric analyses than by geometric morphometric analyses, the use of landmark-based morphometric methods for mites of the genus *Retracrus* should be considered successful, as it allowed for separating populations/species and revealed interesting shape differences among them. Equally interesting results in studies of eriophyoid mites were obtained for species of the genus *Aceria* associated with Asteraceae of the genus *Cirsium* from Europe and the USA (Vidović et al. 2014) and for *Aceria guerreronis* Keifer populations from different continents (Navia et al. 2006). This is in contrast to what has been observed for other mite groups, such as Scutacariidae or Opiidae, for which geometric morphometry analyses have not proven useful in revealing interspecific differences but were useful for

identification to the genus level (Baran et al. 2011; Jagersbacher-Baumann 2014). Thus, geometric morphometry methods should be considered useful for the eriophyoid mite systematics. The geometric morphometry analyses reveal and allow for recording differences which are often perceived by the taxonomist but difficult to express. Without the use of geometric morphometry methods, explanations for the different shapes of the taxa/populations may not be appropriate due to its subjectivity. However, through the application of shape morphometric methods, these differences may be illustrated and recorded via deformation grids, subjected to multivariate analyses and graphically expressed, and, in addition, allow for future comparisons. In an integrative approach, these methods may be used together with other tools, including traditional morphometric analyses or molecular data.

Phytoptidae mites of the tribe Mackiellini belong to a Sierraphytoptini lineage of putatively archaic mites evolving on palm trees (Sukhareva 1994; Chetverikov and Sukhareva 2009). Until recently, all of the Mackiellini were thought to only associate with plants of family Arecaceae. The association of Mackiellini mites with Heliconiaceae is recent information and interesting from the perspective of the group's evolution. Chetverikov et al. (2014) suggested that the association of *Retracrus* with *Heliconia* plants may be a result of a host shift from arecacean to heliconiacean hosts, as the order Zingiberales (to which Heliconiaceae belongs) is phylogenetically quite remote from the order Arecales. Studies of the phylogenetic relationships among the species of *Retracrus* associated with heliconias described in this study and the species associated with palms could clarify this hypothesis. Given the new information, it would also be interesting to direct efforts for new collections of eriophyoids associated with numerous heliconia species—approximately 250 species are currently known (Mosca et al. 2004, de Castro et al. 2007), especially in their areas of natural occurrence in the Americas, as it is possible that many *Retracrus* species are associated with them.

The damage caused by new *Retracrus* species associated with *H. latispatha* in Costa Rica (Aguilar and Murillo 2012) has been quite severe. In addition to aesthetic damage to the foliage, it is possible that the species cause a run-out in the plants, compromising flower production. It will be extremely important to adopt quarantine measures to avoid the spread of *Retracrus* mites via international trade of materials for the vegetative propagation of heliconias, whether they be for commercial purposes (cut flowers, seedlings) or the exchange of genetic material (germplasm). It is possible that the distribution of the new species that has been observed causing damage to heliconias in Costa Rica is not restricted to this Central American country, and thus it will also be important to determine its current geographical distribution to suport adoption of appropriate quarantine measures.

Taxonomic descriptions

Retracrus costaricensis n. sp. Ferreira and Navia (Figs. 6, 7, 8) (Phytoptidae, Sierraphytoptinae, Mackiellini)

Diagnosis The new species *R. costaricensis* presents undivided empodium with six rays; one longitudinal line in the central basal area of the female genitalia; prodorsal shield with a sub-parallel line to the frontal lobe that continue as curved lines in the anterior shield; faint shield design, consisting in two irregular opposite curved lines (flat "U" lines) linked in the lateral area by curved longitudinal lines; dorsal ridge pronounced in the 3/4 posterior opisthosoma (except telosomal rings).

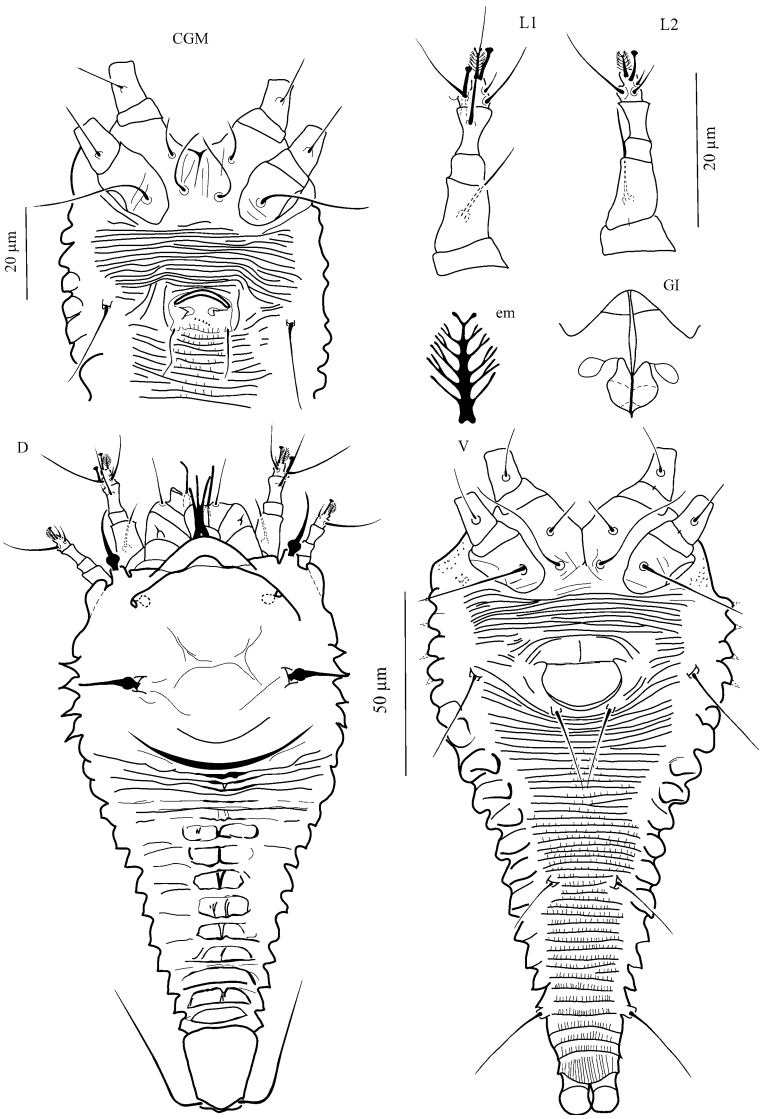


Fig. 6 *Retracrus costaricensis* n. sp. Ferreira and Navia, adult. *D* dorsal habitus, female; *V* ventral habitus, female; *CGM* coxigenital region, male; *em* empodium enlarged, leg I, female; *GI* internal genitalia, female; *L1* leg I, female; *L2* leg II, female

Remarks The new species differs from all other *Retracrus* species by the undivided six-rayed empodium. (undivided empodium with eight rays in *R. johnstoni* (see "Discussion"), *R. pupunha* and *R. heliconiae* n. sp.; divided and apparently seven rays in *R. elaeis*). It is similar to *R. johnstoni* and to *R. heliconiae* n. sp. in the presence of only one central longitudinal line in the basal area of the female genitalia; in *R. elaeis* and *R. pupunha* this area presents a transversal band of short longitudinal lines. *R. costaricensis* differs from all other species in the opisthosomal dorsal ridge that is attenuate in the first annuli and well

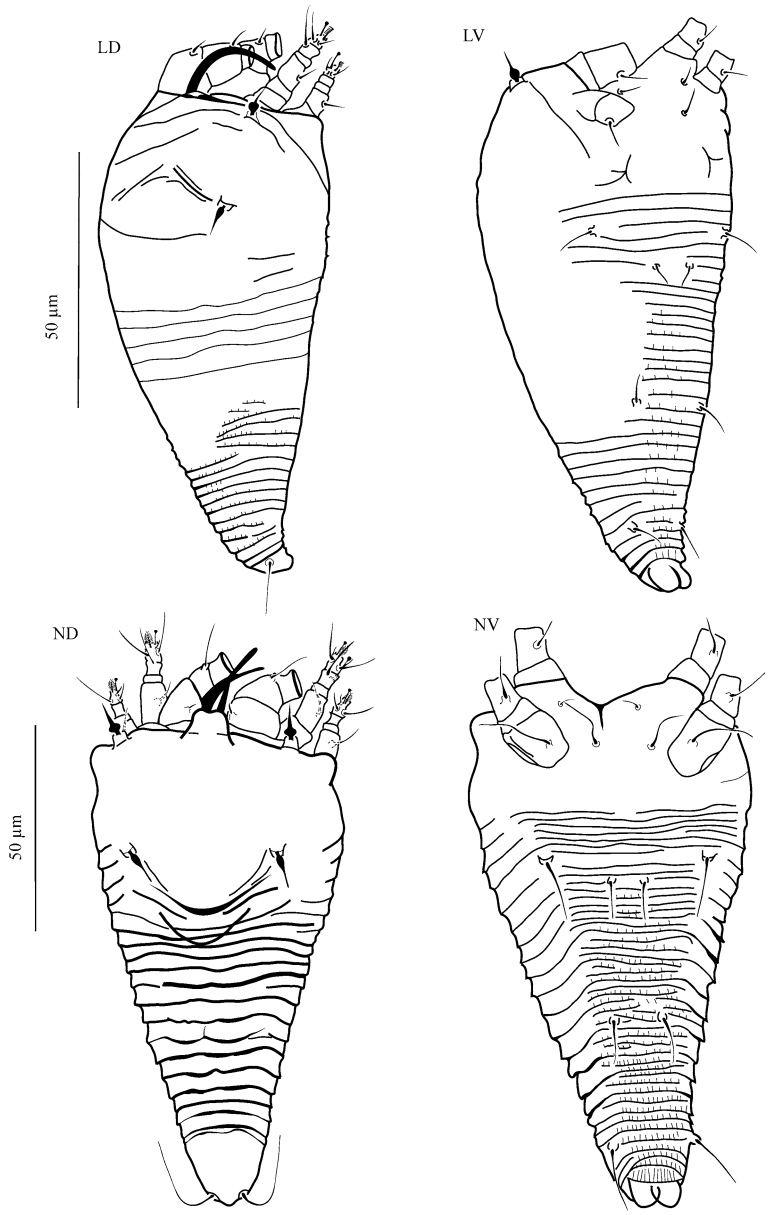


Fig. 7 *Retracrus costaricensis* n. sp. Ferreira and Navia, immatures. *LD* dorsal habitus, larva; *LV* ventral habitus, larva; *ND* dorsal habitus, nymph; *NV* ventral habitus, nymph

pronounced in the posterior opisthosoma (in *R. elaeis* (drawing) dorsal ridge is evenly pronounced in the whole opisthosoma; in *R. johnstoni* dorsal ridge is attenuate and more visible on anterior opisthosoma; in *R. pupunha* it extends on anterior opisthosoma, around eight first annuli; in *R. heliconiae* sp. n. it is attenuate and more visible on posterior opisthosoma). The new species is similar *R. johnstoni, R. elaeis* and *R. heliconiae* n. sp. in

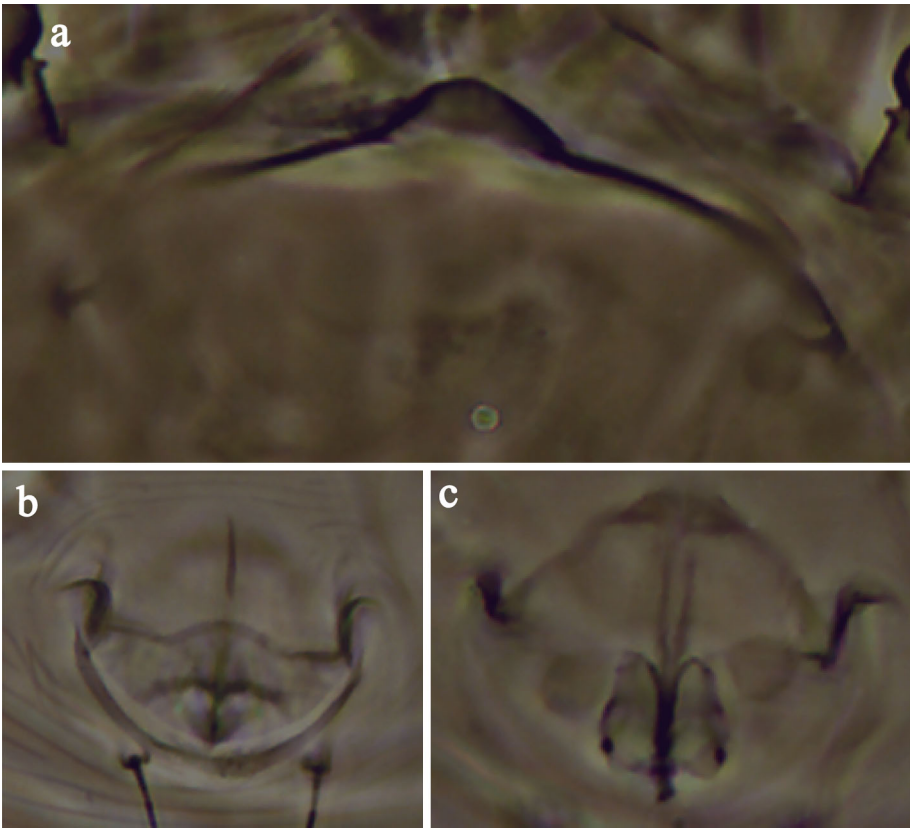


Fig. 8 *Retracrus costaricensis* n. sp. Ferreira and Navia, female phase contrast micrographs. **a** Anterior prodorsal shield, **b** external genitalia and **c** internal genitalia

the shape of prodorsal shield scapular (*sc*) and external vertical setae (*ve*), with a bulbous base and tapering gradually; however it differs from *R. pupunha* in these traits since *sc* and *ve* setae presents bulbous base followed by another dilatation.

The ratio between the body length and width provide information on the body shape and it can differentiate the new species from *R. elaeis* and *R. pupunha*. In *R. costaricensis* n. sp. this ratio is around 2. It is lower than in *R. elaeis* (2.5–2.7) and in *R. johnstoni* type material (2.4), and higher than in *R. pupunha* (1.7).

Some morphometric traits allow differentiate *R. costaricensis* n. sp. from *R. heliconiae* n. sp.. The first species presents longer paraxial tibial seta (l') and tibial solenidion (φ) than *R. heliconiae* (in *R. costaricensis* l' lenght mean is 15.9 ranging from 13 to 19 while in *R. heliconiae* this mean is 10.5 ranging from 9 to 13; in *R. costaricensis* φ lenght mean is 7.8 ranging from 8 to 10 while in *R. heliconiae* this mean is 7.1 ranging from 6 to 8).

Female (n = 10) Body fusiform, 175 (161–178) and 87 (67–96) wide. *Gnathosoma* downcurved, 26 (22–33); pedipalp coxal seta (*ep*) 3 (3); dorsal pedipalp genual seta (*d*) 13 (12–14); cheliceral stylets 24 (23–30). *Prodorsal shield* subquadrangular, 68 (62–69) (measured from the top of frontal lobe to the first complete opisthosoma annuli), 82 (62–82) wide (measured from the lateral spine from prodorsal shield). Frontal lobe wide-

based, rounded, 10 (9–12), 29 (24–30) wide. Scapular seta (*sc*) 16 (13–16), with bulbous base, inserted on prominent tubercles near the median-lateral margin of the shield, directed backwards, 33 (31–39) tubercles apart; external vertical seta (*ve*) 19 (17–20), with bulbous base on prominent tubercles inserted into the anterolateral margin of the prodorsal shield, directed forward, 41 (30–45) tubercles apart. Shield design consisting in a subparallel line to the frontal lobe and then extending on the 1/4 anterior shield. In some specimens "balloons" like structures were observed on he anterior shield as rearing from this anterior concave line; these structures seems to be superficial but internal. Central shield design faint, consisting in two irregular opposite curved lines (flat "U" lines) linked in the lateral area by curved longitudinal lines. Posterior shield with a convex line restricted to the median area. *Legs* with all segments; all setae present except for paraxial tibial seta (l') on leg II and antaxial genual seta (l'') in legs I and II. *Leg I* 35 (28–37); femur 10 (10), basiventral femoral seta (*bv*) 13 (11–13); genu 3 (3); tibia 8 (7–9), l' 17 (14–19), φ 8 (8–10); tarsus 5 (5), antaxial fastigial tarsal seta (ft'') 14 (13–17), paraxial fastigial tarsal seta (ft') 8 (8–15), paraxial unguinal tarsal seta (u') 4 (4), tarsal solenidion (ω) 5 (5), tarsal empodium 5 (5), simple, six-rayed. *Legs II* 31 (26–31); femur 10 (10), *bv* 14 (12–16); genu 3 (3); tibia 6 (6); tarsus 5 (5), ft'' 12 (10–13), ft' 4 (4–5), u' 3 (3), ω 5 (5); tarsal empodium 4 (4–5), simple, six-rays. *Coxigenital region* with 10–11 annuli. Sternal line 12–13. *Coxisternal plate*: coxisternum I and II mostly smooth, few short lines between proximal seta on coxisternum I (*1a*) and on coxa II; anterolateral seta on coxisternum I (*1b*) 6 (5–7), 16 (13–16) apart; proximal seta on coxisternum I (*1a*) 20 (12–24), 12 (10–14) apart; proximal seta on coxisternum II (*2a*) 18 (10–26), 33 (29–41) apart. *Genitalia* 17 (12–17), 27 (19–28) wide, one longitudinal line in the central basal area, coverflap smooth; genital seta (*3a*) 17 (13–19). Spermathecal apparatus presenting a subtrapezoidal or subtriangular (in horizontal-projection) anterior genital apodeme; ovoid spermathecae directed laterad, thick sausage-like spermathecal tubes. *Opisthosoma* 14 (13–14) dorsal annuli, smooth, dorsal ridge pronounced in the 3/4 posterior opisthosoma (except telosomal rings); 46 (45–46) ventral annuli, with thin elongated microtubercles visible from the ninth ventral ring until anal lobe. Lateral seta (*c2*) 21 (17–24), on ventral annulus 1 (1); ventral seta II (*e*) 15 (11–15), on annulus 27 (26–27), 14 (13–19) apart, 9 (9–10) microtubercles apart; ventral seta III (*f*) 19 (19–26), on annulus 42 (41–42), 24 (19–24) apart, 21 (20–21) microtubercles apart. Caudal seta (*h2*) 58 (46–58), accessory seta (*h1*) absent.

Male (n = 5) Smaller than female, 140–157, 62–85 wide. *Gnathosoma* 20–25; *ep* 2–3; genual seta *d* 7–11; cheliceral stylets 15–26. Prodorsal shield as in female, 60–69, 56–74 wide. *sc* 12–17, 29–35 tubercles apart; *ve* 15–17, inserted under prominent tubercle on the margin of anterior prodorsal shield and 38–51 tubercles apart; frontal lobe 9–12, 20–26 wide. *Legs* as in females. *Leg I* 23–29; femur 9–10, *bv* 6–11; genu 3; tibia 6–7, l' 9–18, φ 7–8; tarsus 4–5, ft'' 10–15, ft' 7–11, u' 3–4, ω 5; tarsal empodium 4, simple, six-rayed. *Leg II* 24–28; femur 10–12, *bv* 11–14; genu 2–3; tibia 5; tarsus 4, ft'' 9–14, ft' 3–4, u' 3–4, ω 4, tarsal empodium 4, six-rayed. *Coxigenital region* with 14–16 annuli, smooth. Sternal line 13–14. *Coxisternal plate*: coxisternum I and II mostly smooth, faint longitudinal or diagonal lines, *1b* 2–5, 13–22 apart; *1a* 10–16, 8–11 apart; *2a* 10–18, 26–40 apart. *Genitalia* 6–8, 15–19 wide, eugenital seta as in the figure; seta *3a* 12–15. *Opisthosoma* as in female, 14–15 dorsal annuli; 38–40 ventral annuli. *c2* 10–22, on anullus 1; *e* 8–15, on annulus 20–22, 8–15 apart, 8–12 microtubercles apart; *f* 14–20, on annulus 34–36, 20–24 apart, 22–28 microtubercles apart. *h2* 18–51; *h1* absent.

Nymph (n = 5) Body fusiform, 108–139, 51–64 wide. *Gnathosoma* 21–25; *ep* 2; pedipalp seta *d* 6–8; cheliceral stylets 18–26. *Prodorsal shield* subrectangular and smooth, 44–56, 51–64 wide. *sc* in different position that in adults, near rear shield margin, 8–10, 28–34 tubercles apart; *ve* as in adults, 8–9, 32–44 tubercles apart. Frontal lobe 4–6, 21–23 wide, with different shape than in adults, narrower, subquadrangular, with subparalell sides, slightly emarginated in apical central area. Prominent projections lateral to *ve* seta tubercles. No shield design observed. *Legs* as in adults. *Leg I* 15–20; femur 6–8, *bv* 4–6; genu 2; tibia 2–4, l' 8–13, φ 5–6; tarsus 4, ft'' 7–10, ft' 7–10, ω 4–5; tarsal empodium 3–4, simple, not possible to count rays. *Leg II* 15–18; femur 6–8, *bv* 5–7; genu 2; tibia 3; tarsus 4, ft'' 8–9, ft' 2–4, ω 4–5; tarsal empodium 3–4, simple, no possible counting rays. *Coxigenital region* with 7–9 annuli anterior to seta *3a*. Sternal line 13–14. *Coxisternal plate*: coxisternum I and II smooth, *1b* 2, 13–20 apart; *1a* 6–12, 8–13 apart; *2a* 9–12, 22–30 apart. Genitalia absent; *3a* 6–7. *Opisthosoma* 15–16 dorsal annuli; 36–37 ventral annuli. As in adults dorso-ventral differentiation, with dorsal annuli less numerous than ventral ones. Dorsal ridge not pronounced as in adults; attenuate relief along the whole opisthosoma. *c2* 11–14; *e* 6–11, on annulus 19–20, 9–11 apart, 4–5 microtubercles apart; *f* 10–14, on annulus 32–33, 11–12 microtubercles apart. *h2* 12–19; *h1* absent.

Larva (n = 2) Body slightly fusiform, 109–110, 47–56 wide. *Gnathosoma* 18–22; *ep* 2; pedipalp seta *d* 4–5; cheliceral stylets 22–23 long. *Prodorsal shield*, subrectangular with lines between and above *sc*, 31–41, 47–56 wide. *sc* as in adults, 5–6, 26–30 tubercles apart; *ve* as in adults, 7, 22–24 tubercles apart. Frontal lobe not distinguishable. Shield design not visible except for some diagonal and curved lines between *sc* setae. *Legs* as in adults, except for φ solenidion absent. *Leg I* 13–15; femur 6, *bv* 4; genu 2; tibia 3, l' 7–8; tarso 3, ft'' 6, ft' 4–6, ω 4; tarsal empodium 3, simple, no possible counting rays. *Leg II* 13; femur 6, *bv* 4; genu 2; tibia 3; tarsus 3, ft'' 4, ft' 3, ω 3; tarsal empodium 3, no possible counting rays. *Coxigenital region* with 5–6 annuli anterior to seta *3a*. Sternal line 9–10. *Coxisternal plate*: coxisternum I and II smooth, *1b* 3, 6 apart; *1a* 4–5, 5 apart; *2a* 5–6, 7 apart. Genitalia absent; *3a* 3–4. *Opisthosoma* differs from adults, dorsal annuli not completely formed, no dorso-ventral differentiation, with dorsal annuli continuous with ventral ones; not possible to count dorsal annuli, 24–25 ventral annuli. *c2* 6; *e* 6–7, on annulus 12, 10–12 apart, four microtubercles apart; *f* 8, on annulus 22, 11–12 microtubercles apart. *h2* 10–15; *h1* absent.

Type material Female holotype, 56 female, male, larva e nymph paratypes from *Heliconia latispatha* Bentham (Heliconiaceae), colected in Campus de la Universidad de Costa Rica, São José, Costa Rica (9°44′58.92″N; 83°45′12.53″O), May 17 of 2010, by Prof. Dr. Hugo Aguilar. Holotype and paratype (38 specimens, 19 females, 8 males, 2 larvae and 5 nymphs in four microscope slides) deposited in the mite collection of Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, Brazil. Paratypes (19 specimens, 9 females, 3 males, 6 nymphs and 1 larva in six microscope slides) also deposited in the collection of the Laboratório de Acarologia, Departamento de Agronomia, Universidade Federal Rural de Pernambuco, Recife, PE, Brazil.

Relation to host plant Vagrant on the upper leaf surface. Numerous colonies, causing general chlorosis and/or rusty-brownwish spots, which can extends along the whole leaf blade.

Etymology The specific name "*costaricensis*" is derived from Costa Rica, the name of the country where the mite was collected from.

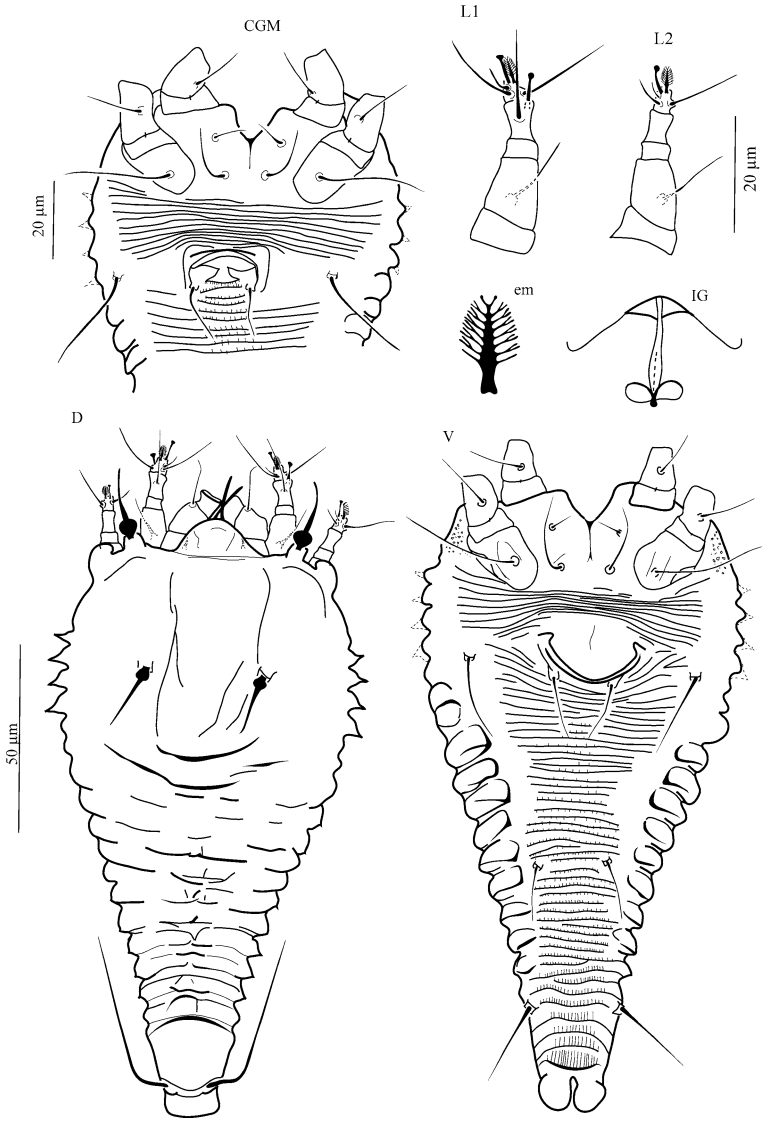


Fig. 9 *Retracrus heliconiae* n. sp. Ferreira and Navia, adult. *D* dorsal habitus, female; *V* ventral habitus, female; *CGM* coxigenital region, male; *em* empodium enlarged, leg I, female; *GI* internal genitalia, female; *L1* leg I, female; *L2* leg II, female

Retracrus heliconiae n. sp. Ferreira and Navia (Figs. 9, 10) (Phytoptidae, Sierraphytoptinae, Mackiellini)

Diagnosis The new species *R. heliconiae* presents undivided empodium with eight rays; one longitudinal line in the central basal area of the female genitalia coverflap; faint shield design consisting in irregular parallel longitudinal lines on the central area close and internal to scapular seta (*sc*) tubercles, extending from frontal lobe base to near rear shield

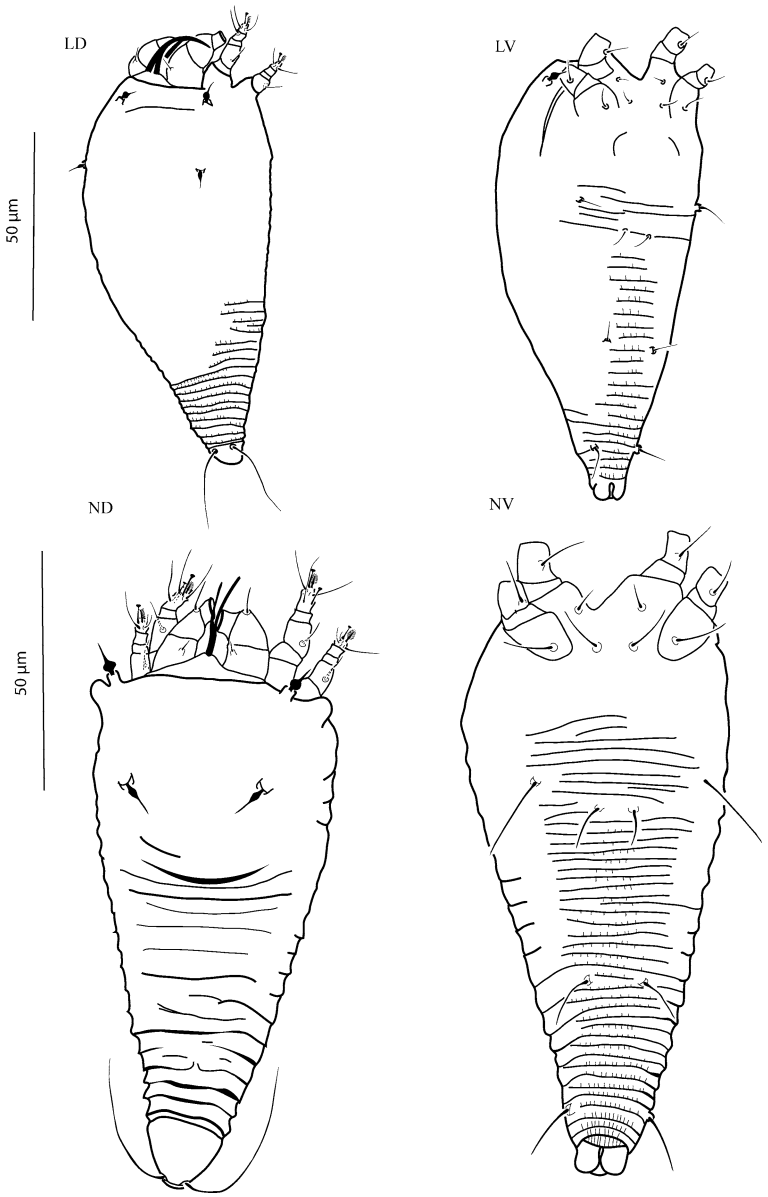


Fig. 10 *Retracrus heliconiae* n. sp. Ferreira and Navia, immatures. *LD* dorsal habitus, larva; *LV* ventral habitus, larva; *ND* dorsal habitus, nymph; *NV* ventral habitus, nymph

margin; faint or irregular delimitation of first dorsal annuli; and dorsal ridge attenuate, noticeable only in the 1/2 posterior opisthosoma (except telosomal rings).

Remarks The new species is similar to *R. johnstoni* and *R. pupunha* in the undivided eight-rayed empodium (undivided empodium with six rays in *R. costaricencis* sp. n.;

divided and apparently seven rays in *R. elaeis*). It is also similar to *R. johnstoni* and to *R. costaricencis* sp. n. in the presence of only one central longitudinal line in the basal area of the female genitalia; in *R. elaeis* and *R. pupunha* this area presents a transversal band of short longitudinal lines. *Retracrus heliconiae* n. sp. resembles *R. johsntoni* in the dorsal ridge that is discernible only on the posterior opisthosoma differing from other species in this trait (in *R. costaricencis* it is attenuate on the anterior annuli and well pronounced on the posterior opisthosoma; in *R. elaeis* (drawing) it is evenly pronounced in the whole opisthosoma; in *R. pupunha* extends on anterior opisthosoma, around eight first annuli). The new species is similar *R. johnstoni, R. elaeis* and *R. costaricencis* n. sp. in the shape of prodorsal shield setae (*sc* and *ve*), with a bulbous base and tapering gradually (in *R. pupunha sc* and *ve* setae presents bulbous base followed by another dilatation).

The ratio between the body length and width in the new species (around 1.8) is closer *R. pupunha* (1.7) (in *R. costaricensis* n. sp. it is around 2; in *R. elaeis* vary from 2.5 to 2.7; in *R. johnstoni* type material is 2.4).

Some morphometric traits allow differentiate *R. heliconiae* n. sp. from *R. costaricencis* n. sp.; the first species presents shorter paraxial tibial seta (l') and tibial solenidion (φ) on leg I than *R. costaricencis* (in *R. heliconiae* l' lenght mean is 10.5 ranging from 9 to 13 while in *R. costaricencis* this mean is 15.9, ranging from 13 to 19; in *R. heliconiae* φ lenght mean is 7.1 ranging from 6 to 8 while in *R. costaricencis* this mean is 7.8 ranging from 8 to 10).

Female (n = 10) Body fusiform, 168 (150–168), 87 (70–97) wide. *Gnathosoma* downcurved, 26 (20–27); pedipalp coxal seta (*ep*) 3 (3); dorsal pedipalp genual seta (*d*) 11 (11–13); cheliceral stylets 22 (19–27). *Prodorsal shield* subquadrangular, 69 (62–70) (measured from the top of frontal lobe to the first complete opisthosoma annuli), 76 (76–93) wide (measured from the lateral spine from prodorsal shield), frontal lobe wide-based, rounded, 11 (10–13), 24 (24–29) wide. Scapular seta (*sc*) 21 (16–21), with bulbous base, inserted on prominent tubercles near the median-lateral margin of the shield, directed backwards, 30 (27–34) tubercles apart; external vertical seta (*ve*) 21 (19–21), with bulbous base on prominent tubercles inserted into the anterolateral margin of the prodorsal shield and directed forward, 43 (40–43) tubercles apart. Faint shield design consisting in irregular parallel longitudinal lines on the central area close and internal to *sc* tubercles, extending from frontal lobe base to near rear shield margin; irregular short lines in the frontal lobe area; faint or irregular delimitation of first dorsal annuli. *Legs* with all segments; all setae present except for l' on leg II and antaxial genual seta (l'') in legs I and II. *Leg I* 29 (27–30); femur 10 (10), basiventral femoral seta (*bv*) 12 (10–12); genu 3 (3); tibia 9 (8–10), l' 12 (10–12), tibial solenidion (φ) 8 (6–8); tarsus 4 (4), antaxial fastigial tarsal seta (ft'') 18 (15–18), paraxial fastigial tarsal seta (ft') 12 (10–12), tarsal solenidion (ω) 7 (5–7), empodium 5 (4–5), simple, eight-rayed. *Legs II* 27 (24–29); femur 10 (10–11), *bv* 14 (11–14); genu 3 (3); tibia 6 (5–6); tarsus 4 (4), ft'' 11 (9–11), ft' 5 (4–5), paraxial unguinal tarsal seta (u') 3 (3), ω 6 (4–6); empodium 5 (4–5), simple, eight-rayed. *Coxigenital region* with 9–11 annuli. Sternal line 6–8. *Coxisternal plate*: coxisternum I and II smooth, anterolateral seta on coxisternum I (*1b*) 5 (5), 18 (15–19) apart; proximal seta on coxisternum I (*1a*) 19 (17–22), 11 (10–12) apart; proximal seta on coxisternum II (*2a*) 13 (10–15), 35 (29–42) apart. *Genitalia* 16 (13–17), 24 (22–27) wide, one longitudinal line in the central basal area, coverflap smooth; genital seta (*3a*) 16 (14–17). Spermathecal apparatus presenting a subtrapezoidal or subtriangular (in horizontal-projection) anterior genital apodeme; ovoid-rounded spermathecae directed postero-laterad, attached to longitudinal bridge (spermathecal tubes very short), half posterior longitudinal bridge

thickened. *Opisthosoma* 12 (12–13) dorsal annuli, smooth; dorsal ridge attenuate, noticeable only in the 1/2 posterior opisthosoma (except telosomal rings); 46 (44–46) ventral annuli, with thin, slightly elongated microtubercles visible from the seventh ventral ring until the anal lobe. Lateral seta (*c2*) 19 (14–19), on annulus 1 (1); ventral seta II (*e*) 11 (11–13), on annulus 27 (26–27), 16 (12–16) apart, 13 (13) microtubercles; ventral seta III (*f*) 18 (16–19), on annulus 46 (43–46), 21 (15–21) apart, 21 (21–26) microtubercles. Caudal seta (*h2*) 57 (35–67); acessory seta (*h1*) absent.

Male (n = 5) Same size or somewhat longer than female, 150–178, 78–88 wide. *Gnathosoma* 20–25; *ep* 3; pedipalp seta *d* 11–13; cheliceral stylets 19–27. *Prodorsal shield* as in female, 64–76, 70–81 wide. Frontal lobe as in female, 10–13, 25–30 wide. *sc* as in female, 15–18, 28–38 tubercles apart; *ve* as in female 19–20, 38–47 tubercles apart. *Legs* as in females. *Leg I* 27–30; femur 11–12, *bv* 9–12; genu 3; tibia 8–10, l' 9–13, φ 7–8; tarsus 4–5, ft'' 9–16, ft' 5–9, ω 5–6; tarsal empodium 4–5, simple, eight-rayed. *Leg II* 26–28; femur 10–12, *bv* 12–14; genu 3; tibia 6–7; tarsus 4–5, ft'' 7–13, ft' 4, ω 4–5; tarsal empodium 4–5, simple, eight-rayed. *Coxigenital region* with 14–17 annuli. Sternal line 11–12. *Coxisternal plate*: coxisternum I and II smooth, *1b* 5–6, 15–18 apart; *1a* 15–20, 9–15 apart; *2a* 11–15, 32–38 apart. *Genitalia* 5–9, 13–19 wide, eugenital seta as in the figure; *3a* 11–14. *Opisthosoma* 14–15 dorsal annuli; 42–44 ventral annuli. *c2* 18–24, on anullus 1; *e* 11–13, on annulus 23–24, 12–13 apart, 7–13 microtubercles apart; *f* 14–22, on annulus 38–39, 16–20 apart, 19–25 microtubercles apart. *h2* 49; *h1* absent.

Nymph (n = 2) Body fusiform 121–131, 56–61 wide. *Gnathosoma* 21–24; *ep* 2; pedipalp seta *d* 7–8; cheliceral stylets 19–22. *Prodorsal shield* subquadrangular, smooth, 52–55, 56–61 wide. *sc* as in adults, 8–9, 29–35 tubercles apart; *ve* as in adults, 8–9, 36–37 tubercles apart. Frontal lobe 4–5, 20–21 wide, with different shape than in adults, wider base, subtriangular, apically rounded. Prominent projections lateral to *ve* seta tubercles. No shield design observed. *Legs* as in adults. *Leg I* 19–20; femur 7, *bv* 6–7; genu 2; tibia 3, l' 10–14, φ 5; tarsus 4, ft'' 9–11, ft' 9, ω 5; tarsal empodium 4, simple, no possible counting rays. *Leg II* 16–18; femur 6–8, *bv* 6–7; genu 2; tibia 3; tarsus 4, ft'' 6–9, ft' 4, ω 4; tarsal empodium 4, not possible to count rays. *Coxigenital region* with 9–10 annuli anterior to seta *3a*. Sternal line 14–15. *Coxisternal plate*: coxisternum I and II smooth, *1b* 3–4, 13 apart; *1a* 8, 9 apart; *2a* 9–12, 26–27 apart. Genitalia absent; *3a* 6–9. *Opisthosoma* 14 dorsal annuli; 34–37 ventral annuli. As in adults dorso-ventral differentiation, with dorsal annuli less numerous than ventral ones. Dorsal ridge very attenuate, noticeable only on the last dorsal annuli (except telosomal rings); anterior annuli almost flat. *c2* 13–18; *e* 6–10, on annulus 18, 11 apart, 5–7 microtubercles apart; *f* 13–15, on annulus 30–33, 16–17 apart, 12–13 microtubercles apart. *h2* 27–28; *h1* absent.

Larva (n = 2) Body slightly fusiform, 114–115, 45–57 wide. *Gnathosoma* 23–26; *ep* 2; pedipalp seta *d* 4; cheliceral stylets 25. *Prodorsal shield* not possible to distinguish porterior margin, 45–57 wide. *sc* 6, on small tubercles, 30–31 tubercles apart; *ve* 5–7, on small tubercles, on the anterior prodorsal shield, 23 tubercles apart. Frontal lobe 4, broad based, apically rounded. Shield design not visible except for a transversal line on anterior shield. *Legs* as in adults, except for the tibial solenidion φ absent. Leg I 14–16; femur 5–6, *bv* 4–5; genu 2; tibia 3, l' 6–7; tarsus 3, ft'' 6–7, ft' 6–7, ω 4; tarsal empodium 4, simple, not possible to count rays. Leg II 13–14; femur 5–6, *bv* 3–4; genu 2; tibia 3; tarsus 3, ft'' 7–6, ft' 4, ω 4; tarsal empodium 4, not possible to count rays. *Coxigenital region* not possible to count annuli anterior to seta *3a*. *Coxisternal plate*: coxisternum I and II smooth, *1b* 3–4, 9–12 apart; *1a* 6–8, 6–7 apart; *2a* 6, 19–21 apart. Genitalia absent; *3a* 4. *Opisthosoma*

differs from adults, dorsal annuli not completely formed, no dorso-ventral differentiation observable, apparently dorsal annuli continuous with ventral ones; not possible to count dorsal annuli; 24 ventral annuli. *c2* 8; *e* 5–7, on annulus 11, 11 apart, 4–5 microtubercles apart; *f* 8–10, on annulus 19–20, 10 apart, 4–5 microtubercles apart. *h2* 12–16; *h1* absent.

Type material Female holotype, 36 females, male, larvae and nymph paratypes from *Heliconia pendula* (Heliconiaceae), colected in campus of Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil (14°47′45.66″S; 39°10′01″O), September of 2010, colected by Anibal Ramadan Oliveira. Holotype and paratype (16 specimens, 11 females, 4 males and 1 larvae in 2 microscope slide) deposited in the collection of mites of Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, Brazil. Paratypes (21 specimens, 9 females, 4 males, 4 nymphs and 4 larvae in 2 microscope slides) deposited in the collection of the Laboratório de Acarologia, Departamento de Agronomia, Universidade Federal Rural de Pernambuco, Recife, Brazil, PE.

Relation to host plant Vagrant on the upper leaf surface without aparent injuries, found in low population density.

Etymology The species name "heliconiae" is derived from the genus of the host plant *Heliconia.*

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