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New Fortuyniidae and Selenoribatidae (Acari, Oribatida) from Bonaire (Lesser Antilles) and morphometric comparison between Eastern Pacific and Caribbean populations of Fortuyniidae

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Abstract

Two new intertidal oribatid mite species were found on the coast of Bonaire. *Litoribates bonairensis* **sp. nov.** can be distinguished from its only congener, *L. caelestis*, by the cerotegumental pattern and shape of sensillus. This is also the first record of the genus from the Caribbean region. *Thasecazetes falcidactylus* **gen. nov., sp. nov.** is characterized by conspicuous longitudinal notogastral ridges and sickle shaped claws and represents a new selenoribatid genus that probably shows a wider distribution within the Caribbean. Both species were found in mangrove habitats. An ecological preference for this environment may be considered. A morphometric investigation of *Litoribates* and *Alismobates* populations from the Galápagos Archipelago in the Eastern Pacific, several Caribbean areas and the Western Atlantic Bermuda Islands revealed certain remarkable facts: First, *Litoribates* species show a conspicuous higher size variation between the different locations than *Alismobates* species; second, the geographic distance between the populations is reflected in the extent of divergence and third, similar variation patterns shown in *Litoribates* and *Alismobates* indicate that both taxa have experienced similar evolutionary histories in the respective geographic regions. An additional molecular genetic analysis provides barcoding sequences for the new taxa and confirms their taxonomic distinctness.

Keywords: *Litoribates*; *Alismobates*; *Thasecazetes* gen. nov.; juveniles; Galápagos; 18S rDNA

Introduction

Fortuyniidae and Selenoribatidae represent oribatid mites exclusively living in the intertidal zone and being distributed on nearly all subtropical and tropical coasts (e.g. Schuster 1989; Pfingstl & Schuster 2014). Their preferred habitats are rocky shores, boulder beaches and mangrove forests, where they feed on different kinds of littoral algae (e.g. Schuster 1966; Pfingstl 2013a). For a long time most studies on these two taxa were limited to species descriptions or records, mainly from the Indo-Pacific region (e.g. Luxton 1992, Karasawa & Aoki 2005, Bayartogtokh *et al.* 2009). Only during the last two decades research focused on other topics, such as ecology, dispersal and reproduction (e.g. Karasawa & Hijii 2004a, b; Pfingstl 2013b, c), and on other geographic regions, for instance the Eastern Pacific and the Caribbean (Schatz 1998; Pfingstl & Jagersbacher-Baumann 2016; Pfingstl *et al.* 2016; Pfingstl & Schatz 2017).

Fortuyniid and selenoribatid mites are known from the Eastern Pacific since the sixties (Hammen 1963) and in the Caribbean since the seventies of the last century (Schuster 1977). Most of the few records were only determined to family level (e.g. Schuster 1977, 1989) and hence the true diversity of these taxa remained largely uncovered. Hammen (1963) described *Fortuynia* *yunkeri* from the Pacific coast of Panama, Schuster (1966, 1977, 1989) provided records of higher taxa from Ecuador, San Salvador, Mexico and the Pacific shore of Costa Rica, and Schatz (1998) found two fortuyniid and one selenoribatid species on the Galápagos islands. Nearly twenty years later, Pfingstl and Schuster (2014) added records from the Pacific coast of Colombia and the archipelago of Hawaii. The Hawaiian specimens were described recently as *Fortuynia hawaiiensis* (Pfingstl & Jagersbacher-Baumann 2016) and the fortuyniid specimens from Galápagos as *Alismobates galapagoensis* and *Litoribates caelestis* (Pfingstl & Schatz 2017).

Schuster (1977, 1989) was the first author who reported the occurrence of Selenoribatidae in the Caribbean Sea, namely in Dominica and St. Lucia but again provided only records at family level. Later, Pfingstl (2013d) described *Thalassozetes barbara* from Barbados. Pfingstl and Schuster (2014) added records of Selenoribatidae and Fortuyniidae from Jamaica and the Dominican Republic, and Pfingstl *et al.* (2016) confirmed the occurrence of one fortuyniid and two selenoribatid species in the Dominican Republic.

The records mentioned above demonstrate that Fortuyniidae and Selenoribatidae may be a common part of the intertidal fauna of both, the Caribbean and the Eastern Pacific coasts. Moreover, the intertidal oribatid mite faunas of both oceanic regions may share several characteristics as the two oceans were linked prior to the closure of the Central American Isthmus about three million years ago (Coates 1996). The assumed close relationship of the Eastern Pacific species *Alismobates galapagoensis* to the Western Atlantic *A. inexpectatus* (Pfingstl & Schatz 2017) may reflect this former geographic connection, and new species discoveries from the Antillean Island of Bonaire may further support this assumption.

Bonaire (294 km²) is situated in the Leeward Lesser Antilles about 80 km off the north coast of Venezuela. The basement of Bonaire is mainly composed of volcanic and sedimentary rocks of the Washikemba formation from the Late Cretaceous and Paleogene during accretion of the Leeward Antilles ridge (Hippolyte & Mann 2011). The climate is semi-arid tropical, with little seasonal variation and almost constant north easterly trade winds. Lac Bay, where the new species were collected, is a sheltered shallow inland bay on the windward shore in southeastern Bonaire with a flooded area of approximately 7.5 km², and is protected as a RAMSAR wetland site of international importance. Lac Bay comprises Bonaire’s only significant mangrove and seagrass ecosystem. The mangrove belt is dominated by *Rhizophora mangle* and includes also *Avicennia germinans*, *Laguncularia racemosa* and *Conocarpus erectus*. The mangrove stands are particularly important as nesting and roosting areas for birds, and the seagrass beds form nursery grounds for some reef fish as well as foraging area and breeding ground for sea turtles. It is also a well-known habitat for the endangered Caribbean Queen Conch *Lobatus gigas* (De Meyer 1998; Debrot *et al.* 2010).

In the course of ongoing studies on the intertidal oribatid mite diversity of the Caribbean, one of the authors (HS) collected samples from Bonaire which yielded a further new *Litoribates* species as well as a new selenoribatid species for which a new genus is proposed. Based on these findings the present paper intends to (1) describe the new taxa, (2) distinguish the new *Litoribates* species from its congeners based on morphometric analyses, (3) validate the genus *Litoribates* based on molecular genetic data, (4) analyse Caribbean and Eastern Pacific populations of *Litoribates* and *Alismobates* morphometrically and (5) compare the morphological diversification patterns between the two oceanic regions.

Material and Methods

Preparation of specimens: For investigation in transmitted light preserved animals were embedded in Berlese mountant (for drawings) or lactic acid (for measurements). Drawings were made with an Olympus BH-2 Microscope equipped with a drawing attachment.

Morphometric measurements: Measurements were performed using the above mentioned microscope and an ocular micrometre. Fifteen continuous variables were measured in *Litoribates* and *Alismobates* populations from the Eastern Pacific, the Western Atlantic and Caribbean (Fig. 1). These variables were chosen because they were already successfully used in an earlier study (Pfingstl & Baumann 2017). For the comparison between Eastern Pacific (EP) and Caribbean (C) populations, a total of 39 *Litoribates* (20EP/19C) and a total of 117 *Alismobates* (59EP/58C) specimens were analysed, with populations from each marine region being pooled for the analyses. Additionally, 20 *Alismobates inexpectatus* specimens from Bermuda were added to the analyses. Details of population localities are given below.

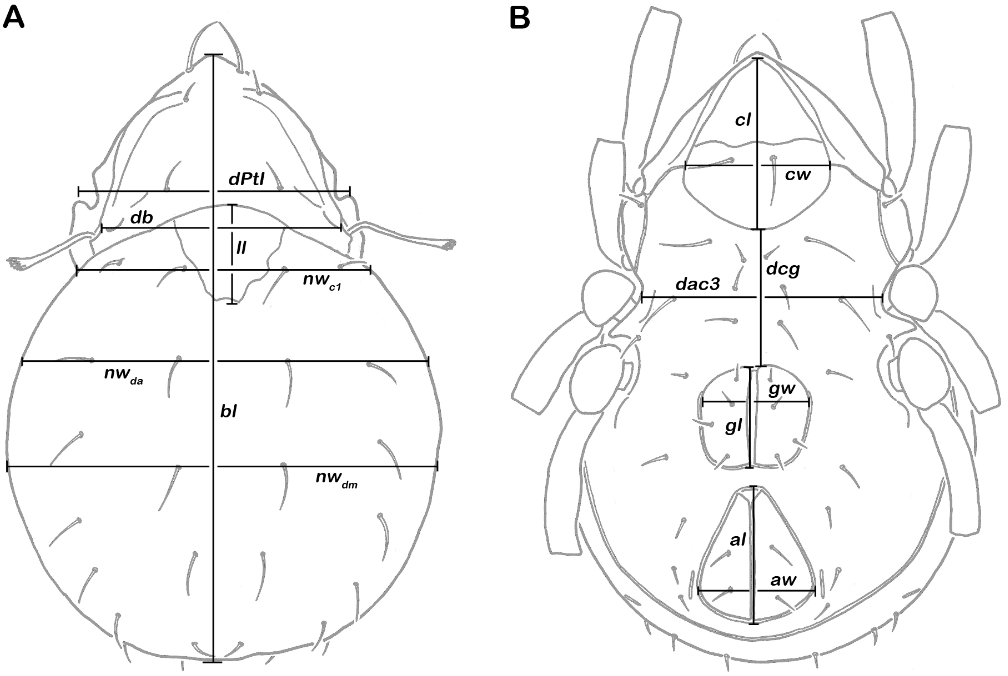

FIGURE 1. Graphic illustration of measured continuous variables shown on simplified drawings of *Litoribates bonairensis* **sp. nov.** A) Dorsal aspect: *bl*—body length, *dPtI*—distance between pedotecta I, *db*—distance between bothridia, *ll*—lenticulus length, nw_{c1}—notogastral width on level of seta c_1, nw_{da}—notogastral width on level of seta *da*, nw_{dm}—notogastral width on level of seta *dm*. B) Ventral aspect: *cl*—camerostome length, *cw*—camerostome width, *dcg*—distance between camerostome and genital orifice, *dac3*—distance between acetabula 3, *gl*—genital orifice length, *gw*—genital orifice width, *al*—anal opening length, *aw*—anal opening width.

Statistics: All statistical analyses were performed with the freeware program PAST 3.04 (Hammer *et al*. 2001).

Mean, standard deviation and coefficient of variation (*cv*) were calculated for *Litoribates*, and the Mann-Whitney-U test was used for comparing the means of variables between the two groups from Galápagos and Bonaire. The data were size corrected by dividing each variable through the geometric mean of the respective specimen, and thereafter the raw data as well as the size-corrected data were ln(x+1) transformed for performing multivariate analyses. A Principal Component Analysis (PCA) was conducted to reveal the pattern of morphological variation in *Litoribates* and a Discriminant Analysis (LDA) was performed for determining the variables contributing most to the differentiation between the two species from Galápagos and the Caribbean. The performance of the classification by the discriminant function was calculated by all samples and Leave-One-Out Cross-Validation. For testing the equality of means of the two groups, a Bonferroni-corrected Hotelling's T^2 test was conducted.

For the comparison between the Eastern Pacific and Atlantic populations of *Litoribates* and *Alismobates*, a PCA and Canonical Variates Analysis (CVA, equivalent to LDA when more than two groups are analysed) were conducted. The performance of the classification by CVA was tested by calculating the number of specimens correctly classified by all-samples CVA and Leave-One-Out Cross-Validation CVA. Multivariate Analysis of Variance (MANOVA) and pairwise Bonferroni-corrected Hotelling's T^2 tests were conducted in order to test the equality of means of the groups.

Molecular genetics

Extraction of genomic DNA was carried out using the Chelex method (Casquet *et al.* 2012) with some adjustments for small arthropods (Lienhard & Schäffer in prep.). Total genomic DNA was extracted from single specimens preserved in absolute ethanol. The complete 18S rDNA (~1.8 kb) was amplified in two overlapping fragments according to the PCR protocol of Dabert *et al.* (2010) using the recommended primers (Skoracka & Dabert 2010). DNA purification- and sequencing steps were conducted after the methods developed and published by Schäffer *et al.* (2008). Alignments were generated by means of the program MEGA6 (Tamura *et al.* 2013). All available ameronothroid 18S rDNA GenBank (www.ncbi.nlm.nih.gov/genbank/) sequences were used to construct a Bayesian 50 % majority rule consensus tree. For this, a MC^3 simulation with 50 million generations (5 chains, 2 independent runs, 10 % burn-in) was performed by means of MrBAYES 3.1.2 (Ronquist & Huelsenbeck 2003). Sequences gained in this study are available in GenBank (accession numbers see Table 1).

TABLE 1. Species identification, taxonomy and GenBank accession numbers shown for all individuals investigated in genetic studies.

Species ID	Taxonomy (family)	GenBank (accession nrs.)	Source
Alismobates reticulatus Luxton, 1992	Fortuyniidae	AB818526.1	Iseki & Karasawa 2014
Aquanothrus sp.	Ameronothridae	KX397627.1	Krause *et al*. 2016
Fortuynia rotunda Marshall & Pugh, 2002	Fortuyniidae	AB818525.1	Iseki & Karasawa 2014
Litoribates bonairensis sp. nov. (1)	Fortuyniidae	MF997503	this study
Litoribates bonairensis sp. nov. (2)	Fortuyniidae	MF997502	this study
Schusteria littorea Grandjean, 1968	Selenoribatidae	HM070345.1	Pepato *et al*. 2010
Thalassozetes shimojanai (Karasawa & Aoki, 2005)	Selenoribatidae	AB818524.1	Iseki & Karasawa 2014
Thasecazetes falcidactylus sp. nov.	Selenoribatidae	MF997501	this study

Sampling locations (Fig. 2):

Western Atlantic/ Caribbean populations

Litoribates bonairensis **sp. nov.**, **Bonaire** Lesser Antilles (BON 16-15.HS); mangroves north of Lac Bay, mangrove leaves and leaf litter under *Rhizophora mangle* at low tide; 24 Apr. 2016, leg. H. Schatz.

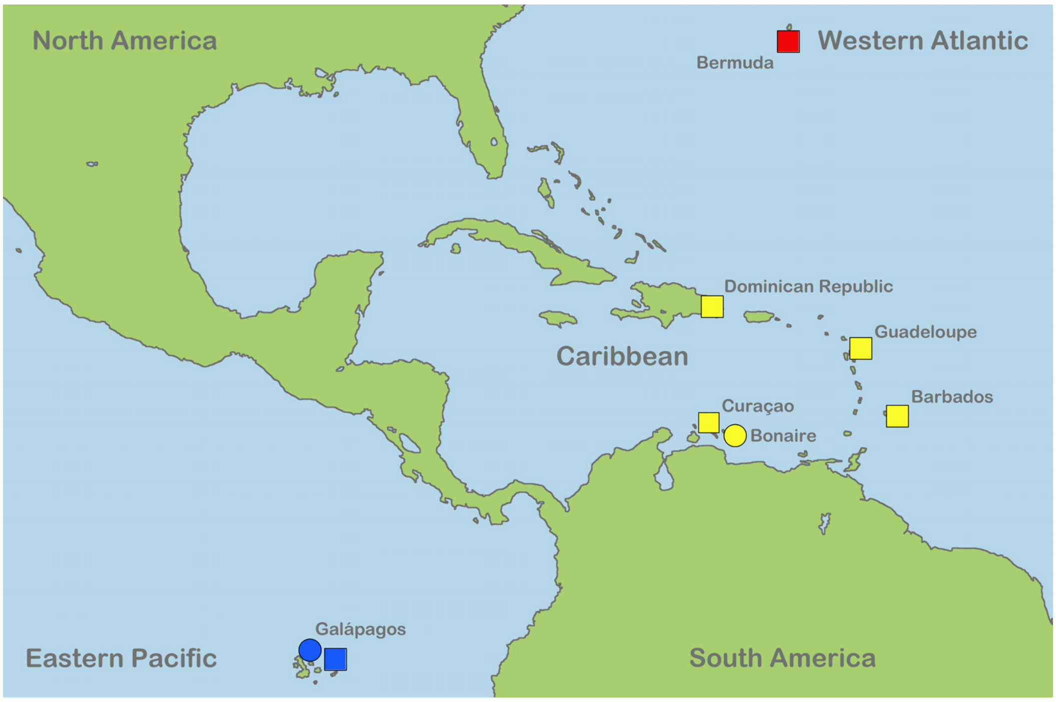

FIGURE 2. General map of Central America and adjacent oceanic regions showing locations of sampled populations. Different colors refer to different oceanic areas; square = *Alismobates*, circle = *Litoribates*.

Alismobates inexpectatus Pfingstl & Schuster, 2012, **Bermuda**, Building Bay (BE_11.TP); intertidal algae on rocks; 17 Aug. 2011, leg. T. Pfingstl.

Alismobates sp., **Dominican Republic** (1) Río San Juan, Playa Grande (RS-1609), intertidal algae growing on rock; May 1993, leg. A. Hlebajna. (2) Boca Chica (DR_03.PL); intertidal algae on rocks; 8 Febr. 2016, leg. T. Pfingstl and A. Lienhard. (3) Samaná, Puerto Santa Bárbara (DR_10.PL); intertidal algae on rocks; 11 Febr. 2016, leg. T. Pfingstl and A. Lienhard (for more details about Dominican Republican samples see Pfingstl *et al.* 2016). **Curaçao**, Lesser Antilles, Boca Ascención (CU_15.PL); intertidal algae on rocks; 5 Febr. 2016, leg. T. Pfingstl and A. Lienhard. **Barbados**, Bathsheba (BA_05.TP); intertidal algae on rocks; 29 Aug. 2012, leg. T. Pfingstl. **Guadeloupe**, Capesterre-Belle-Eau, intertidal algae on rocks; 19 Febr. 2016, leg. T. Pfingstl and A. Lienhard.

Thasecazetes falcidactylus **gen. nov., sp. nov.**, **Bonaire** (BON 16-15.HS); same location and date as *Litoribates bonairensis*.

Eastern Pacific populations (see also Pfingstl & Schatz 2017)

Litoribates caelestis Pfingstl & Schatz, 2017, **Galápagos**, (1) Bartolomé Island, Pinnacle Rock (GAL 85-137, GAL 87-424); decaying leaf litter and mud under *Maytenus octogona*; 12 Febr. 1985 and 26 Dec. 1986, leg. H. Schatz. (2) Santa Cruz Island, Puerto Ayora (GAL 87-434); decaying mangrove litter under *Rhizophora mangle*; 30 Dec. 1986, leg. H. Schatz.

Alismobates galapagoensis Pfingstl & Schatz, 2017, **Galápagos**, (1) Bartolomé Island, Pinnacle Rock (GAL 85-138); mangrove leaf litter; 12 Febr. 1985, leg. H. Schatz. (2) Santa Cruz Island, south of Puerto Ayora (GAL 87-431, GAL 87-432); intertidal algae from rocks and mangrove roots; 29 Dec. 1986, leg. H. Schatz. (3) San Cristóbal Island, south of Wreck Bay (GAL 87-476); decaying mangrove leaf litter; 4 Jan. 1987, leg. H. Schatz. (4) Isabela Island, Punta García (GAL 87-702); leaf litter and soil; 21 Febr. 1987, leg. H. Schatz.

Results

Descriptions of new taxa

Family Fortuyniidae Hammen, 1963

Genus *Litoribates* Pfingstl & Schatz, 2017

Type species—*Litoribates caelestis* Pfingstl & Schatz, 2017

Litoribates bonairensis sp. nov.

(Figs 3–8)

Type material—Holotype: Adult male, BON 16-15: Bonaire Lesser Antilles, preserved in ethanol, deposited in the collections of the Senckenberg Museum für Naturkunde Görlitz (SMNG) (56670), 4 Paratypes from the same sample, deposited at the Naturhistorisches Museum Wien/NHM Vienna (2 males - NHMW 29148, 2 females - NHMW 29149), and additional specimens in the collections of the Institute of Zoology, University of Graz.

Etymology. The species name refers to the type locality, the Antillean island of Bonaire.

Diagnosis. Adult instar brown sclerotized mites. Average length 364 µm, average width 240 µm. Notogaster rounded, almost circular in dorsal view. Slender lamellar ridges anteriorly bent medially, not reaching the transversal ridge behind the rostrum. Sensillus slightly clavate and spinose at tip. Cerotegument finely granular, larger granules only in areas flanking lenticulus. Fourteen pairs of setiform, notogastral setae. Epimeral setation 3-1-2-2, setae *1b* and *3b* longest. Tibia IV with 2 setae.

Description of adult. Females (N=15), length: 351–382 µm (mean 365 µm), width: 228–252 µm (mean 240 µm); males (N=4), length: 345–367 µm (mean 360 µm), width: 228–246 µm (mean 237 µm).

Integument. Colour brown. Prodorsal cerotegument finely granular, larger granules next to bothridia and anterior notogastral border. Notogastral cerotegument also finely granular, obviously larger granules in areas flanking lenticulus laterally. Larger granules in areas surrounding acetabula. Fine granules in ventral region. Leg cerotegument generally finely granular, larger granules only on distal third of all femora.

Prodorsum (Figs 3A, C). Rostrum nearly triangular in dorsal view, projecting anteroventrally in lateral view. Rostrum demarcated from remainder of prodorsum by faint transverse ridge. Pair of two converging, slender lamellar ridges in slightly lateral position, reaching from bothridium to lamellar seta. Rostral seta (*ro*) robust, setiform, smooth (approx. 30 µm). Lamellar seta (*le*) setiform, short and smooth (approx. 10 µm). Interlamellar seta (*in*) setiform (approx. 15 µm), exobothridial seta (*ex*) minute. Bothridium hardly protruding, borders not clearly defined; orifice narrow and circular. Sensillus (*ss*) long (approx. 70 µm), slightly curved caudally, slightly clavate and spinose at tip.

Gnathosoma. Typical for the genus. Palp pentamerous 0-2-1-3-8 (solenidion not included), trochanter very short, femur by far longest segment, genu, tibia and tarsus of almost equal length. Large porose area on ventral paraxial face of femur. Solenidion ω on palptarsus not associated with eupathidium *acm*. Chelicera chelate, mobile digit darker sclerotized; distinct teeth interlocking. Seta *cha* and *chb* of approximately same length (approx. 15 µm), both dorsally slightly pectinate. Gena well sclerotized. Distal part of rutellum developed as thin triangular membrane, slightly curved inward with longitudinal incision. Setae *a* and *m* long (approx. 30 µm), robust and smooth. Mentum regular, seta *h* setiform, thin (approx. 17 µm).

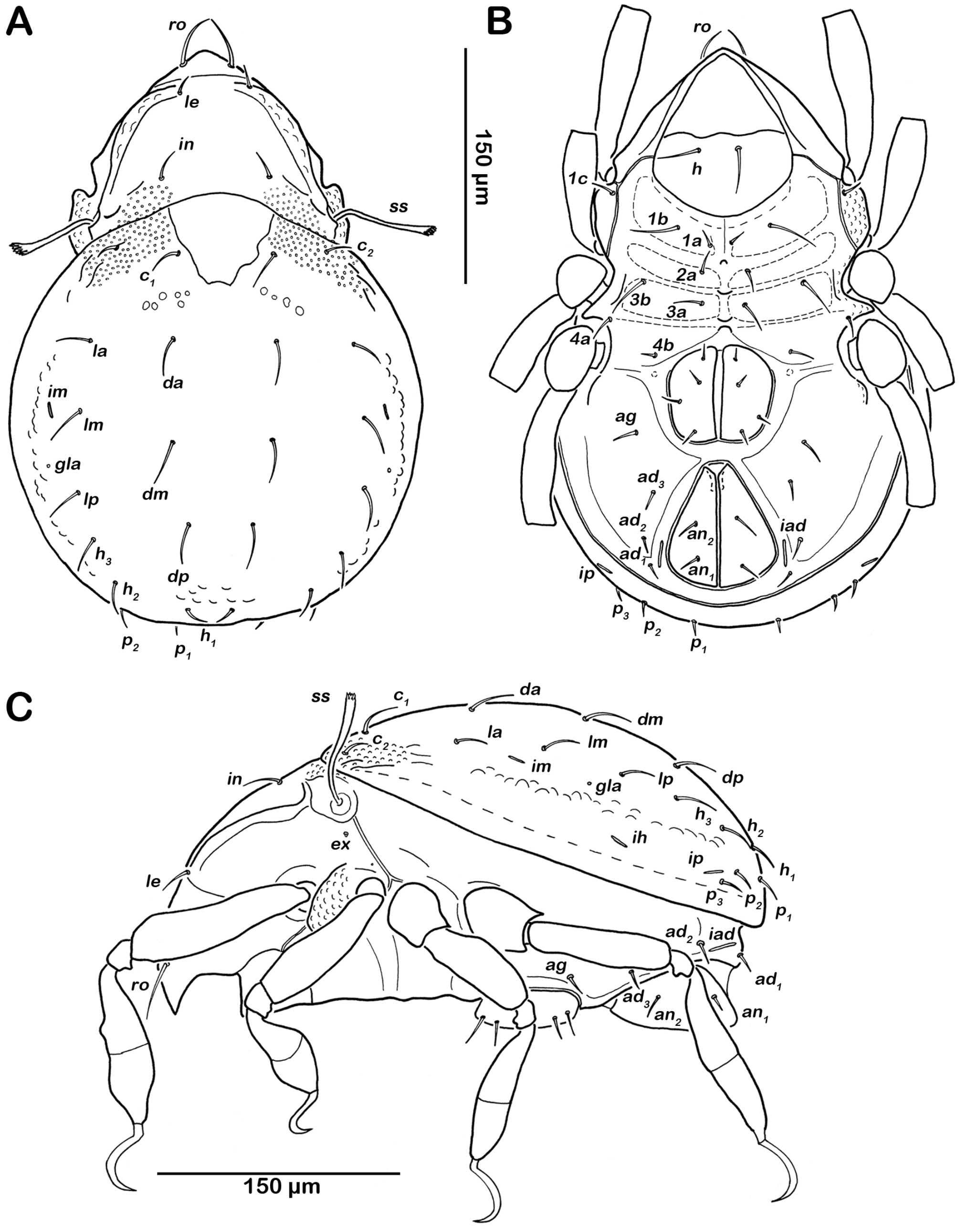

FIGURE 3. *Litoribates bonairensis* **sp. nov.** adult. A) dorsal view; B) ventral view, distal leg segments omitted; C) lateral view.

Gastronotic region (Figs 3A–C). Conspicuously rounded in dorsal view, convex in lateral view; anterior notogastral margin distinct, forming a slightly overhanging bulge. Lenticulus nearly triangular with slightly irregular borders. Several small circular light spots posterior to seta c_1. Fourteen pairs of setiform notogastral setae (10–17 µm), c_{1-2}, *da*, *dm*, *dp*, *la*, *lm*, *lp*, h_{1-3}, p_{1-3}; seta c_3 absent. Five pairs of notogastral lyrifissures present; *ia* laterad of seta c_2, hardly discernible due to strong cerotegumental granulation; *im* slightly anterior and laterad of seta *lm*; *ih* laterad and anterior to h_3; lyrifissures *ip* and *ips* laterally of seta p_3 and p_2 respectively. Orifice of opisthonotal gland (*gla*) between seta *lm* and *lp*.

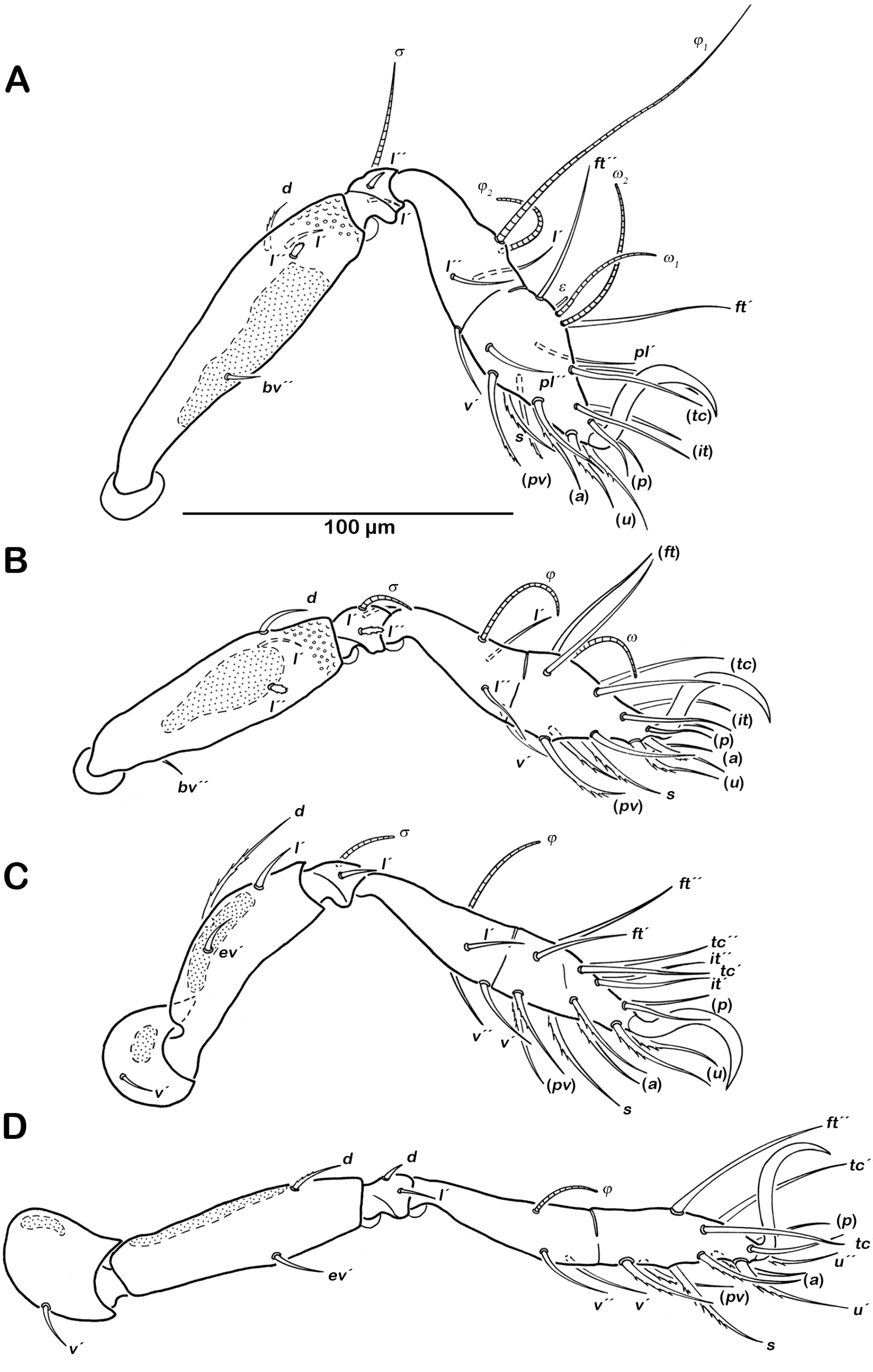

FIGURE 4. *Litoribates bonairensis* **sp. nov.** adult legs antiaxial view. A) right leg I; B) right leg II; C) left leg III; C) left leg IV.

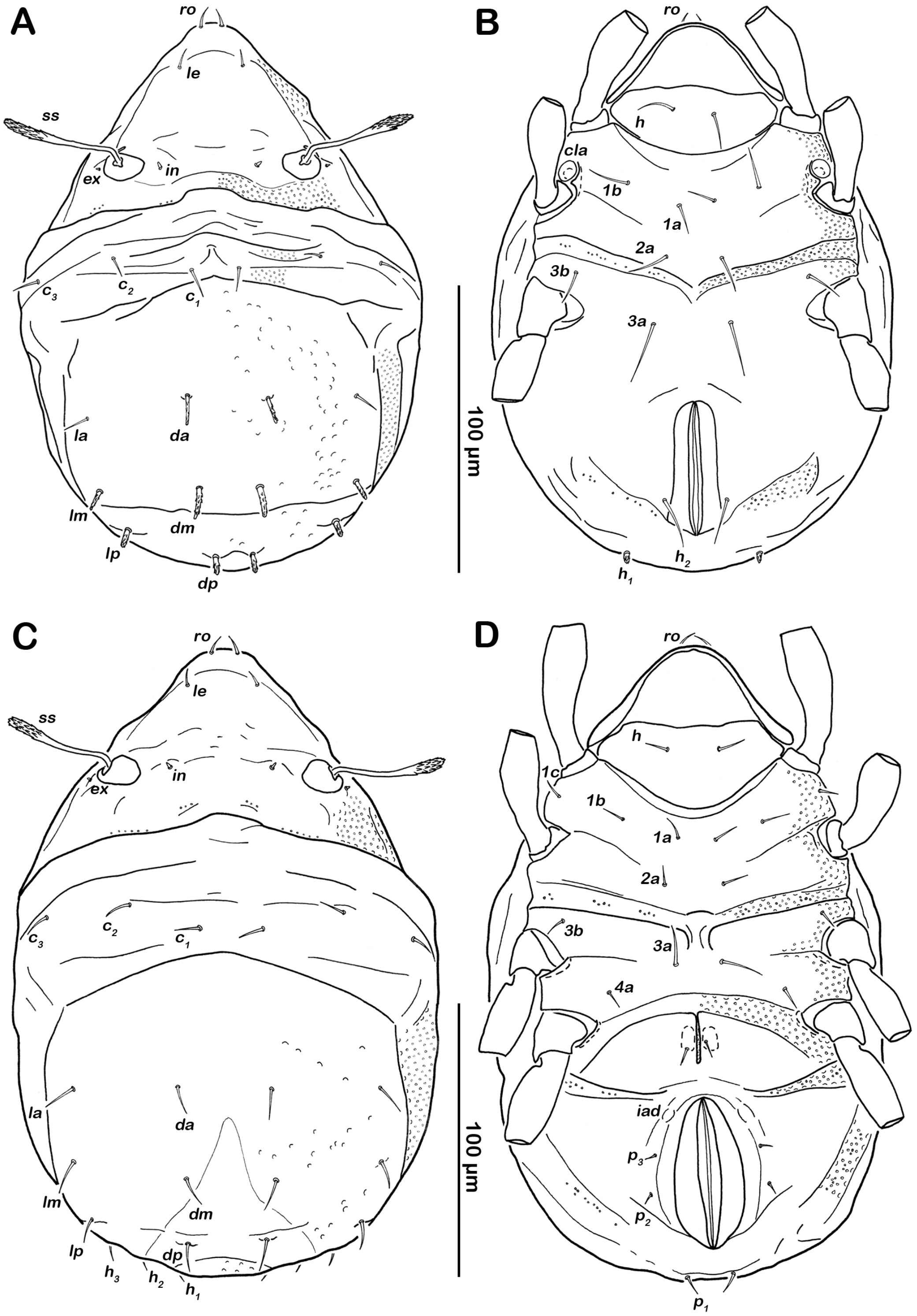

FIGURE 5. *Litoribates bonairensis* **sp. nov.** juveniles. A) larva dorsal view; B) larva ventral view, distal leg segments omitted; C) protonymph dorsal view; D) protonymph ventral view, distal leg segments omitted.

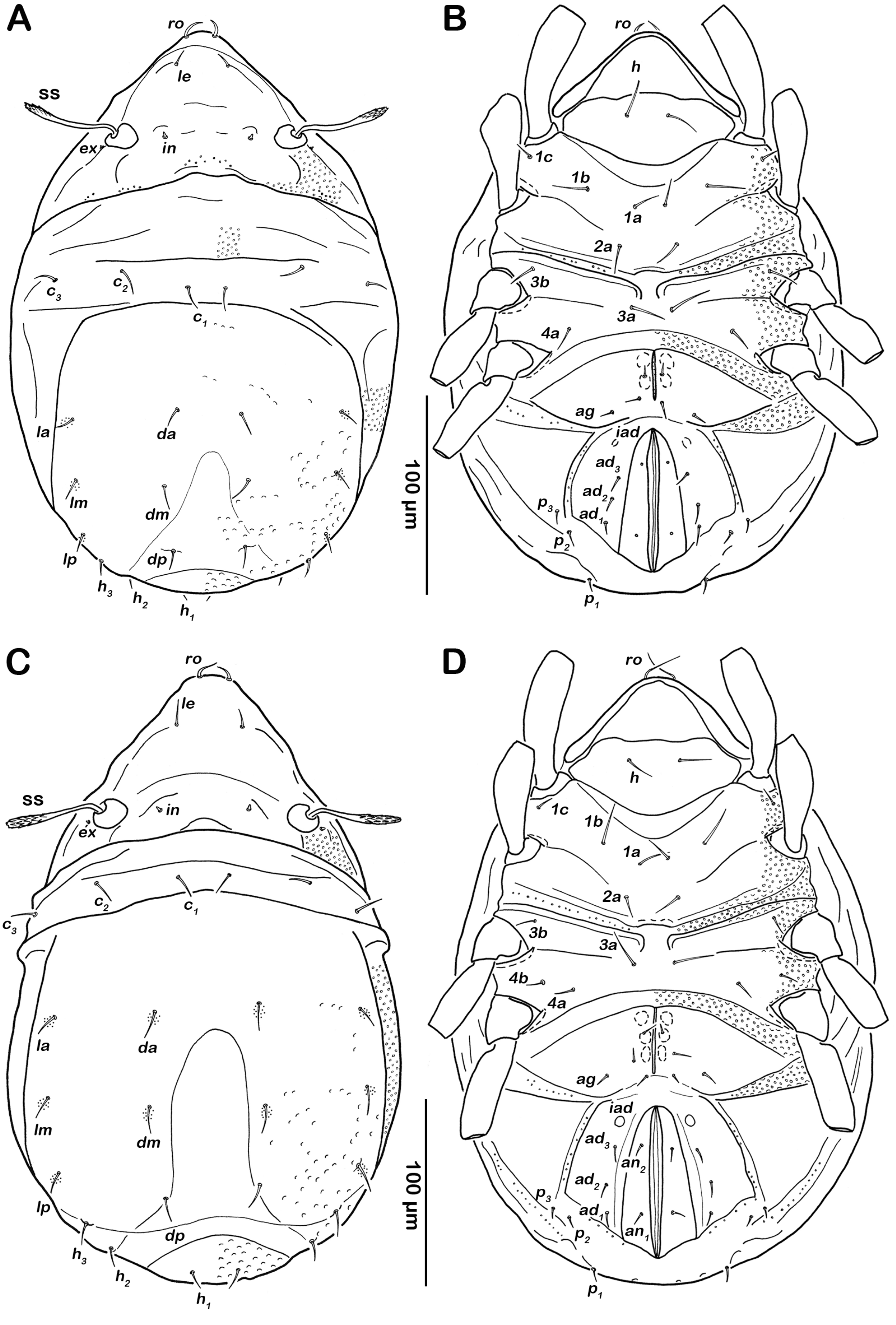

FIGURE 6. *Litoribates bonairensis* **sp. nov.** juveniles. A) deutonymph dorsal view; B) deutonymph ventral view, distal leg segments omitted; C) tritonymph dorsal view; D) tritonymph ventral view, distal leg segments omitted.

Lateral aspect (Fig. 3C). Pedotectum I small rounded, slightly projecting. Pedotectum II absent. Discidium present, not conspicuously expressed. Van der Hammen's organ present; typical for genus (Pfingstl & Schatz 2017).

Ventral region of idiosoma (Figs 3B, C). Epimeral setation 3-1-2-2, all setae setiform and smooth. Setae *1b* and *3b* longest (approx. 23 µm), others shorter (10–12 µm). Internal borders of all epimera well visible. Sternal apodemes slightly protruding with small indentations at each transition from one epimeral segment to other. Genital and anal opening closely adjacent, both surrounded by slightly darker cuticle. Rounded genital plates with four pairs of fine filiform setae (approx. 10 µm). First two pairs near medial margin of plates, third pair close to lateral margin of plates and fourth pair median on posterior edge of plates. Tendon β well visible as dark dot laterad of genital orifice. One pair of setiform aggenital setae *ag*. Anal valves triangular. Outer part of preanal organ rectangular with rounded edges, inner part shaped like a transverse bar. Two pairs of short anal setae, $an_{1\text{-}2}$ (approx. 9 µm). In few specimens asymmetrical variation with three pairs on one plate. Three pairs of short adanal setae, $ad_{1\text{-}3}$ (approx. 9 µm). Lyrifissure *iad* flanking posterior third of anal plates.

Legs (Fig. 4). Monodactylous and slender. Long, strong hook-like claws. Trochanter III and IV with obvious dorsal spur. Femoral carinae on legs I and II absent. All genua with ventral transversal ridge. All tarsi with proximal lyrifissure. Large irregularly shaped porose areas on ventral paraxial side of femora I and II, elongated proximal porose areas on paraxial dorsal aspect of femora III and IV, kidney-shaped porose areas on paraxial dorsal side of trochanters III and IV. Dorsal seta *d* on all femora slightly thickened and serrate dorsally. Lateral setae of genua I and II short, broadened and slightly serrate. Ventral setae of all tibiae and tarsi long and strongly serrate ventrally. Tibia IV with 2 setae. Solenidia $\varphi_{1\text{-}2}$ on tibia I borne on small apophysis. For chaetome and solenidia see Table 2.

Sexual dimorphism. Females of *Litoribates bonairensis* **sp. nov.** slightly larger, most of them bearing one or two large eggs. Apart from adult size, no external sexual dimorphism could be observed.

Common features of juvenile stages. Apheredermous. Colour brown. Integument plicate and soft, except for centrodorsal plate. Habitus typical for the family. Prodorsum triangular, anterior part finely granular, rostrum rounded. Rostral (*ro*) and lamellar seta (*le*) short. Interlamellar seta (*in*) very short, exobothridial seta (*ex*) minute. Sensillus slightly clavate, distally spinose. Bothridium small, cup-like, laterally opened. Hysterosomal edges slightly convex. Centrodorsal plate large with slightly uneven surface and semicircular median depression on posterior part in nymphal stages. Cerotegument of ventral aspect finely granular, larger granules in acetabular regions and ventral furrows. Ventral furrows typical for family. In nymphal stages no distinct genital sclerites developed, genital opening only a thin longitudinal slit, inner margins showing small granules. Respiratory system typical for family. Legs monodactylous. Porose areas present in all immature stages showing same positions as in adults. Setation and solenidia for all stages see Table 2.

Larva. Length (N=4): 185–197 µm (mean 190 µm).

Gastronotic region (Fig. 5A). Eleven pairs of notogastral setae; $c_{1\text{-}3}$, *da*, *dm*, *dp*, *la*, *lm*, *lp*, $h_{1\text{-}2}$; h_3 absent; *da*, *lm*, *lp*, *dm*, *dp* and h_1 slightly thickened and serrate; seta h_2 setiform and smooth, next to anal opening (Fig. 5B). Transverse ridge on centrodorsal plate passing posterior line of setae *dm* and *lm*.

Ventral region of idiosoma (Fig. 5B). Epimeral setation 3-1-2, epimeral setae of normal length, except for seta *1c* minute, valve-like protecting Claparède's organ *cla*.

Protonymph. Length (N=9): 219–252 µm (mean 234 µm).

Gastronotic region (Fig. 5C). Fifteen pairs of notogastral setae; $c_{1\text{-}3}$, *da*, *dm*, *dp*, *la*, *lm*, *lp*, $h_{1\text{-}3}$ and $p_{1\text{-}3}$, all setae setiform and thin.

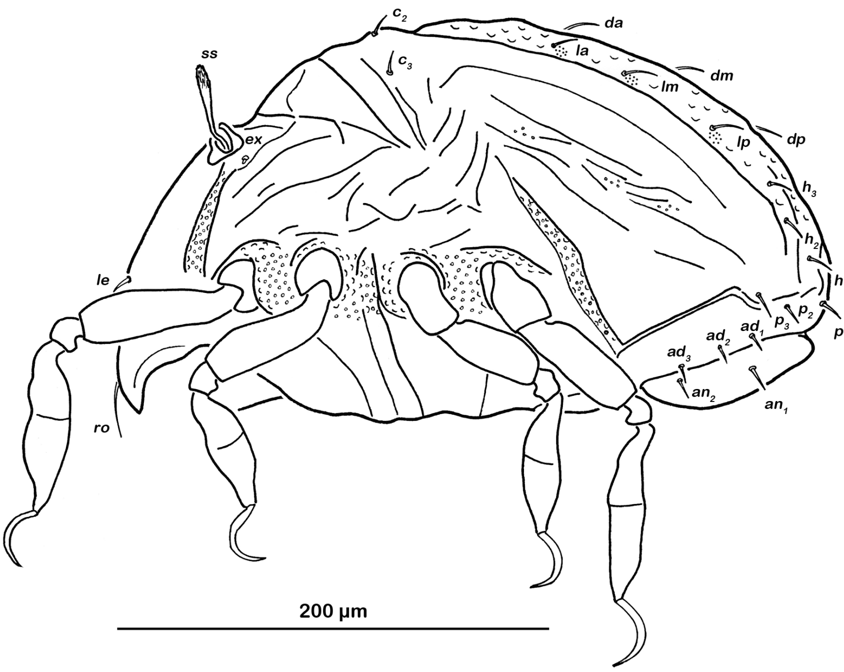

FIGURE 7. *Litoribates bonairensis* **sp. nov.** tritonymph lateral view.

TABLE 2. *Litoribates bonairensis* **sp. nov.** Chaetome and solenidia from larva to adult. First development of setae characterized by letters. ( ) = pairs of setae, - = no change with regard to preceding stage.

	Instars	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	larva	-	*d*, *bv´´*	(*l*), σ	(*l*), *v´*, φ_1	(*pl*), (*pv*), *s*, (*a*), (*u*), (*p*), (*tc*), (*ft*), ε, ω_1	0-2-2-3-16	1-1-1
	protonymph	-	*l´*	-	-	ω_2	0-3-2-3-16	1-1-2
	deutonymph	-	*l´´*	-	φ_2	-	0-4-2-3-16	1-2-2
	tritonymph	-	-	-	-	(*it*)	0-4-2-3-18	1-2-2
	adult	-	-	-	-	-	0-4-2-3-18	1-2-2
Leg II	larva	-	*d*, *bv´´*	(*l*), σ	*l´*, *v´*, φ	(*pv*), *s*, (*a*), (*u*), (*p*), (*tc*), (*ft*), ω	0-2-2-2-13	1-1-1
	protonymph	-	*l´*	-	-	-	0-3-2-2-13	1-1-1
	deutonymph	-	*l´´*	-	-	-	0-4-2-2-13	1-1-1
	tritonymph	-	-	-	-	(*it*)	0-4-2-2-15	1-1-1
	adult	-	-	-	*l´´*	-	0-4-2-3-15	1-1-1
Leg III	larva	-	*d*, *ev´*	*l´*, σ	*v´*, φ	(*pv*), *s*, (*a*), (*u*), (*p*), (*tc*), (*ft*)	0-2-1-1-13	1-1-0
	protonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	deutonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	tritonymph	*v´*	-	-	-	(*it*)	1-2-1-1-15	1-1-0
	adult	-	*l´*	-	*l´*, *v´´*	-	1-3-1-3-15	1-1-0
Leg IV	protonymph	-	-	-	-	(*pv*), (*u*), (*p*), *ft´´*	0-0-0-0-7	0-0-0
	deutonymph	-	*d*, *ev´*	*d*, *l´*	*v´*, φ	*s*, (*a*), (*tc*)	0-2-2-1-12	0-1-0
	tritonymph	*v´*	-	-	-	-	1-2-2-1-12	0-1-0
	adult	-	-	-	*v´´*	-	1-2-2-2-12	0-1-0

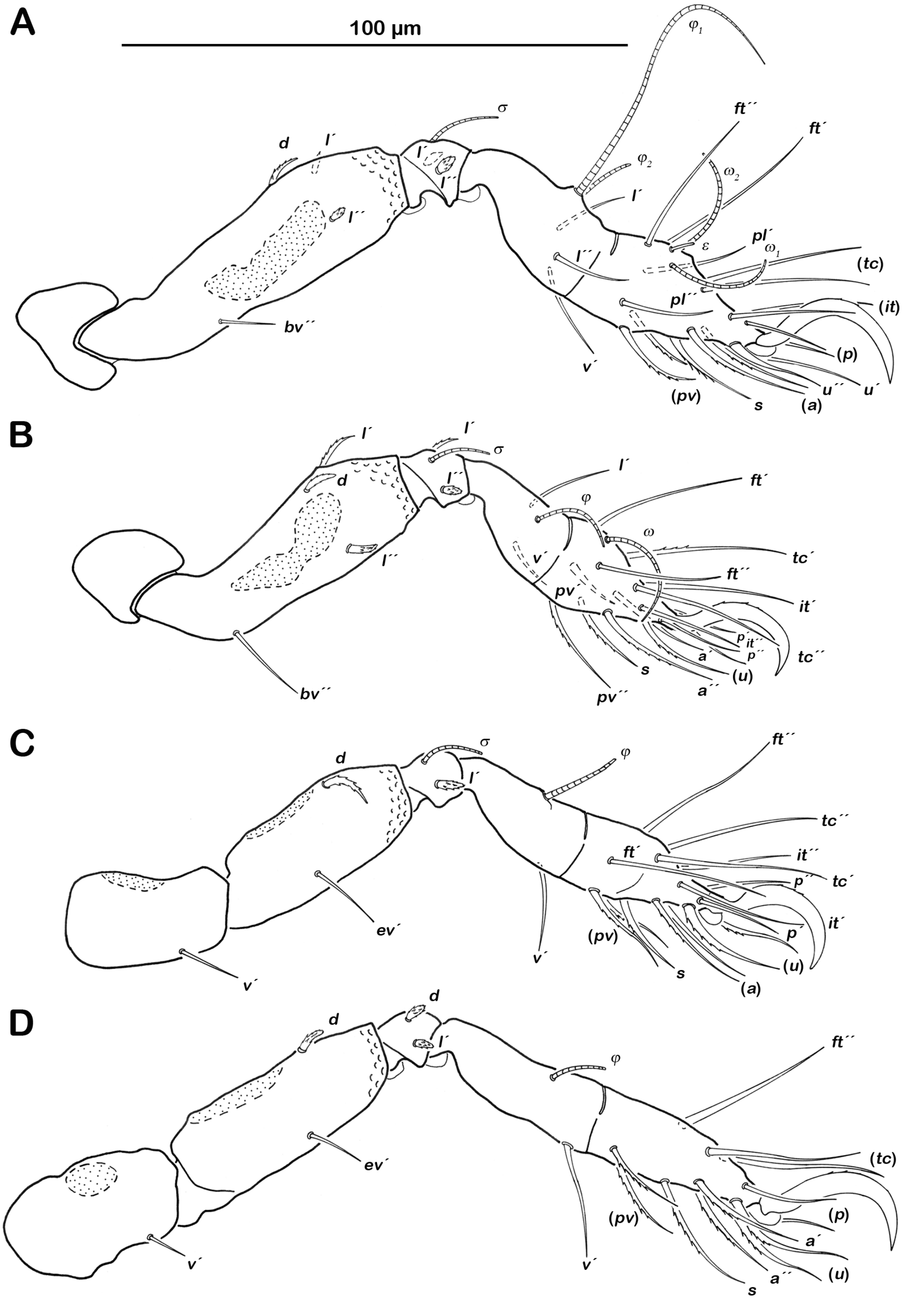

FIGURE 8. *Litoribates bonairensis* **sp. nov.** tritonymph legs, antiaxial view. A) right leg I; B) right leg II; C) left leg III; D) left leg IV.

Ventral region of idiosoma (Fig. 5D). Epimeral setation 3-1-2-1. Seta *1c* developed normal, setiform, next to trochanter I, seta *4a* close to trochanter IV. One pair of short genital setae. Aggenital setae absent. Cupule *iad* next to anterior border of anal opening.

Deutonymph. Length (N=5): 268–299 µm (mean 286 µm).

Gastronotic region (Fig. 6A). Fifteen pairs of notogastral setae, same positions and shapes as in protonymph.

Ventral region of idiosoma (Fig. 6B). Epimeral setation 3-1-2-1. Two pairs of short genital setae arranged in longitudinal row. One pair of setiform, short aggenital setae *ag*. Three pairs of adanal setae $ad_{1\text{-}3}$ flanking anal valves.

Tritonymph. Length (N=5): 305–338 µm (mean 330 µm).

Gastronotic region (Figs 6C, 7). Fifteen pairs of notogastral setae, no difference to deutonymph. Ventral region of idiosoma (Fig. 6D). Epimeral setation 3-1-2-2, seta *4b* median on epimeral plate IV.

Three pairs of short genital setae. One pair of aggenital setae *ag*. Three pairs of adanal setae $ad_{1\text{-}3}$. Two pairs of anal setae $an_{1\text{-}2}$.

Legs (Fig. 8, Table 2). Slender, claws sickle-shaped. Femoral dorsal setae *d* serrate, basiventral setae *bv´´* short and blunt. Tibial lateral setae also short and blunt.

Family Selenoribatidae Schuster, 1963

***Thasecazetes* gen. nov.** (generic characters are highlighted in the discussion section)

Type species—*Thasecazetes falcidactylus* **sp. nov.**

Thasecazetes falcidactylus sp. nov.
(Figs 9-11)

Type material—Holotype: adult male, BON 16-15: Bonaire, Lesser Antilles. Paratypes: same locality as holotype. Preserved in ethanol. Deposited in the collections of the Senckenberg Museum für Naturkunde Görlitz (SMNG) (56671), 4 Paratypes from same sample, deposited at the Naturhistorisches Museum Wien/NHM Vienna (2 males—NHMW 29150; 2 females—NHMW 29151), additional specimens in the collections of the Institute of Zoology, University of Graz.

Etymology. As the new genus shares several characteristics with other selenoribatid genera, the generic name represents a combination of the first syllables of the generic names ***Tha****lassozetes*, ***Se****lenoribates* and ***Ca****rinozetes* and the greek word “zetes”. The specific name “*falcidactylus*” refers to the conspicuous sickle-shaped claws of this species.

Species diagnosis

Adults brown sclerotized. Average length 385 µm, mean width 251 µm. Slender prodorsal lamellar ridges in median position. Sensillus clavate, distally spinose. Bothridium with two triangular posterior projections. Notogaster rounded in dorsal view, convex in lateral view. Dorsosejugal suture incomplete. Small humeral projection present. Lenticulus absent. One pair of long, longitudinal notogastral ridges. Fifteen pairs of notogastral setae, p_1 slightly dorsally displaced. Epimeral setation 1-0-1-1, densely granulated median sternal cavity on epimeron I. Three pairs of genital setae. Lyrifissure *iad* transversally adjacent to anterior borders of anal opening. Five pairs of very short and fine adanal setae. One pair of anal setae. Legs slender, monodactylous, tibiae III and IV elongated. Claws sickle shaped with one proximoventral tooth.

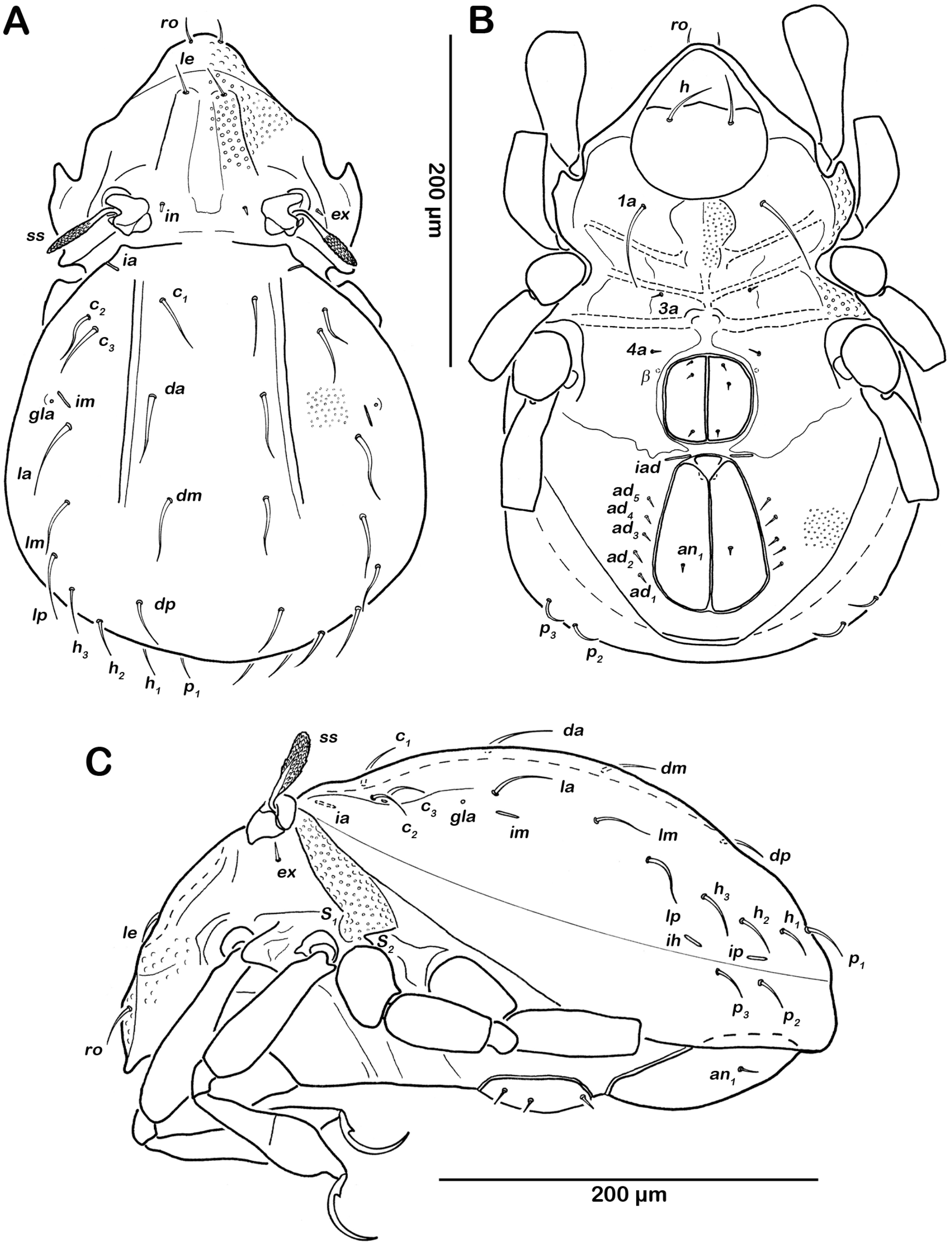

FIGURE 9. *Thasecazetes falcidactylus* **sp. nov.** adult. A) dorsal view; B) ventral view, distal leg segments omitted; C) lateral view, distal legs segments of leg III and IV broken off.

Description of adult. Females (N=3), length: 381–394 µm (mean 388 µm), width: 252–259 µm (mean 255 µm); males (N=6), length: 375–394 µm (mean 383 µm), width: 231–259 µm (mean 248 µm).

Integument. Colour dark brown. Prodorsal cerotegument granular, notogastral cerotegument finely granular. Fine granules in lateral and ventral areas but larger granules in lateral sejugal area and in areas surrounding acetabula. Leg cerotegument granular from trochanter to genu; finely granular on tibiae and tarsi.

Prodorsum (Figs 9A, C). Rostrum nearly triangular in dorsal view, projecting anteroventrad in lateral view. Rostrum demarcated from remainder of prodorsum by faint transverse ridge. A pair of two converging, slender lamellar ridges in median position, reaching lamellar seta. Rostral seta (*ro*) setiform, smooth (approx. 10 µm). Lamellar seta (*le*) setiform and smooth (approx. 10 µm). Interlamellar seta (*in*) blunt, short (approx. 6 µm), exobothridial seta (*ex*) minute. Bothridium prominent, strongly protruding, with two triangular posterior projections; orifice large orientated laterad. Sensillus (*ss*) robust (approx. 55 µm), curved caudally, clavate and spinose distally.

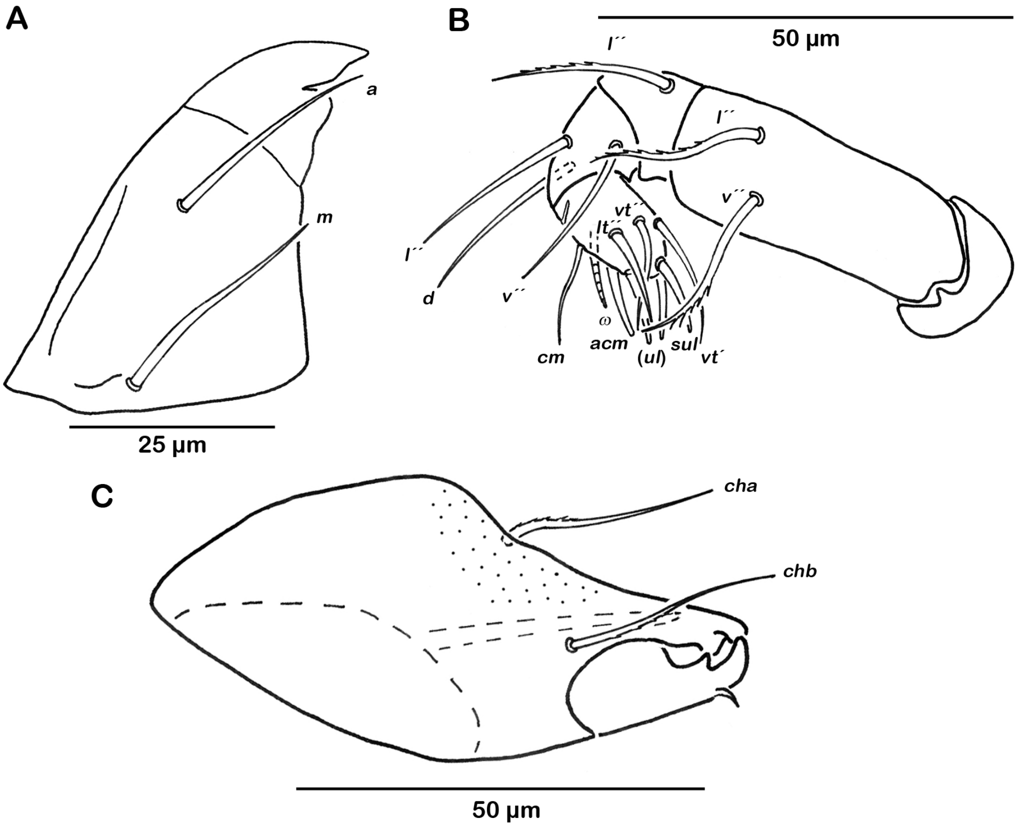

FIGURE 10. *Thasecazetes falcidactylus* **sp. nov.** adult mouthparts. A) right rutellum ventral view; B) left pedipalp, antiaxial view; C) right chelicera, antiaxial view.

Gnathosoma. Palp pentamerous 0-2-1-3-8 (solenidion not included), trochanter very short, femur by far longest segment, genu, tibia and tarsus of almost equal length (Fig. 10B). Solenidion ω on palptarsus not associated with eupathidium *acm*. Chelicera chelate, mobile digit darker sclerotized; distinct teeth interlocking (Fig. 10C). A small, faint and slightly curved dent-like projection on antiaxial ventral aspect of mobile digit. Seta *cha* and *chb* of approximately the same length (approx. 25 µm), both slightly pectinate. Gena well sclerotized. Distal part of rutellum developed as thin triangular membrane, slightly curved inward with longitudinal incision (Fig. 10A). Setae *a* and *m* long (approx. 30 µm), robust and smooth. Mentum regular, seta *h* setiform, thin (approx. 30 µm) (Fig. 9B).

Notogaster (Figs 9A–C). Rounded in dorsal view, convex in lateral view. Dorsosejugal suture incomplete, medially interrupted. Lenticulus absent. Small humeral projection on anterior notogastral border opposite of bothridium. Pair of two slightly anteriorly converging longitudinal notogastral ridges, reaching from anterior notogastral border to insertion of seta *dm*. Fifteen pairs of setiform notogastral setae (30–45 µm), c_{1-3}, *da*, *dm*, *dp*, *la*, *lm*, *lp*, h_{1-3}, p_{1-3}; p_1 slightly dorsad displaced. Five pairs of notogastral lyrifissures present; *ia* laterad of small humeral projection; *im* slightly anterior of seta *la*; *ih* laterad and anterior to h_3; lyrifissures *ip* and *ips* laterally of seta p_3 and p_2 respectively. Orifice of opisthonotal gland (*gla*) next to lyrifissure *im*.

Lateral aspect (Fig. 9C). Pedotectum I small triangular, slightly projecting. Pedotectum II absent. Discidium present, not conspicuously expressed. Lateral projections present, anterior projection S_1 triangular, blunt, posterior protrusion S_2 triangular and small.

Ventral region of idiosoma (Fig. 9B). Epimeral setation 1-0-1-1, all setae setiform and smooth. Setae *1a* longest (approx. 50 µm), others short (approx. 15 µm). Internal borders of all epimera well visible. Densely granulated median sternal cavity on epimeron I, lateral borders slightly concave. Another small circular median sternal cavity on epimeron III. Genital and anal opening closely adjacent, both surrounded by slightly darker cuticle. Strongly rounded genital plates with three pairs of fine very short filiform setae (approx. 3 µm). First two pairs closer together. Tendon β well visible as dark dot laterad of genital orifice. Aggenital setae absent. Anal valves almost triangular. Preanal organ rectangular with rounded edges. Five pairs of short adanal setae, ad_{1-5} (approx. 7 µm), in longitudinal row, all lateral to the anal plates. One pair of minute anal setae, an_1 (approx. 3 µm). Lyrifissure *iad* transversal adjacent to anterior corners of anal opening.

Legs (Fig. 11). Monodactylous and slender. Claws long, slender sickle-shaped with one proximoventral tooth. All tarsi with proximal lyrifissure. Porose areas not discernible. Femoral carinae on legs I and II absent. All genua with ventral transversal ridge. Dorsal seta *d* on all femora slightly thickened and unilaterally serrate. Lateral setae of genua I and II short, broadened and slightly serrate on leg III and IV. Ventral setae of all tarsi ventrally serrate. Chaetome and solenidia see Table 3.

Juvenile instars. Not found.

TABLE 3. *Thasecazetes falcidactylus* **sp. nov.** adult; leg setation, chaetome and solenidia ( ) = pairs of setae.

	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	-	*d*, *bv´´*, *l´*	(*l*), σ	(*l*), *v´*, φ_1, φ_2	(*pl*), (*pv*), *s*, (*a*), (*u*), (*p*), (*it*), (*tc*), (*ft*), ε, ω_1, ω_2	0-3-2-3-18	1-2-2
Leg II	-	*d*, *bv´´*, *l´*	(*l*), σ	(*l*), *v´´*, φ	(*pv*), *s*, (*a*), (*u*), (*p*), (*it*),(*tc*), (*ft*), ω	0-3-2-3-15	1-1-1
Leg III	*v´*	*d*, *ev´*	*l´*, σ	(*v*), φ	(*pv*), *s*, (*a*), (*u*), (*p*), (*tc*), (*ft*)	1-2-1-2-13	1-1-0
Leg IV	*v´*	*d*, *ev´*	*l´*	*l´*, (*v*), φ	(*pv*), *s*, (*a*), (*u*), (*p*), (*tc*), *ft´´*	1-2-1-3-12	0-1-0

Morphometrics

Univariate Statistics of *Litoribates bonairensis* **sp. nov.** and *L. caelestis*

The two *Litoribates* species from Galápagos and the Caribbean/Bonaire differ highly significantly ($p < 0.001$) in all variables except *ll* when compared by Mann-Whitney U-test (Table 4). *Litoribates bonairensis* specimens show higher values in all measured variables. The variability as indicated by the coefficient of variation (cv) is moderate in both groups, with a maximum value of 0.10. In *L. caelestis* from Galápagos, the most variable characters are *dcg* (cv = 0.08), *gl* (0.07) and *gw* (0.08), in *L. bonairensis* from Bonaire they are *dcg* (0.07) and *ll* (0.10). Except *ll*, these variables are related to the genital orifice and thus their variability represents a moderate sexual dimorphism.

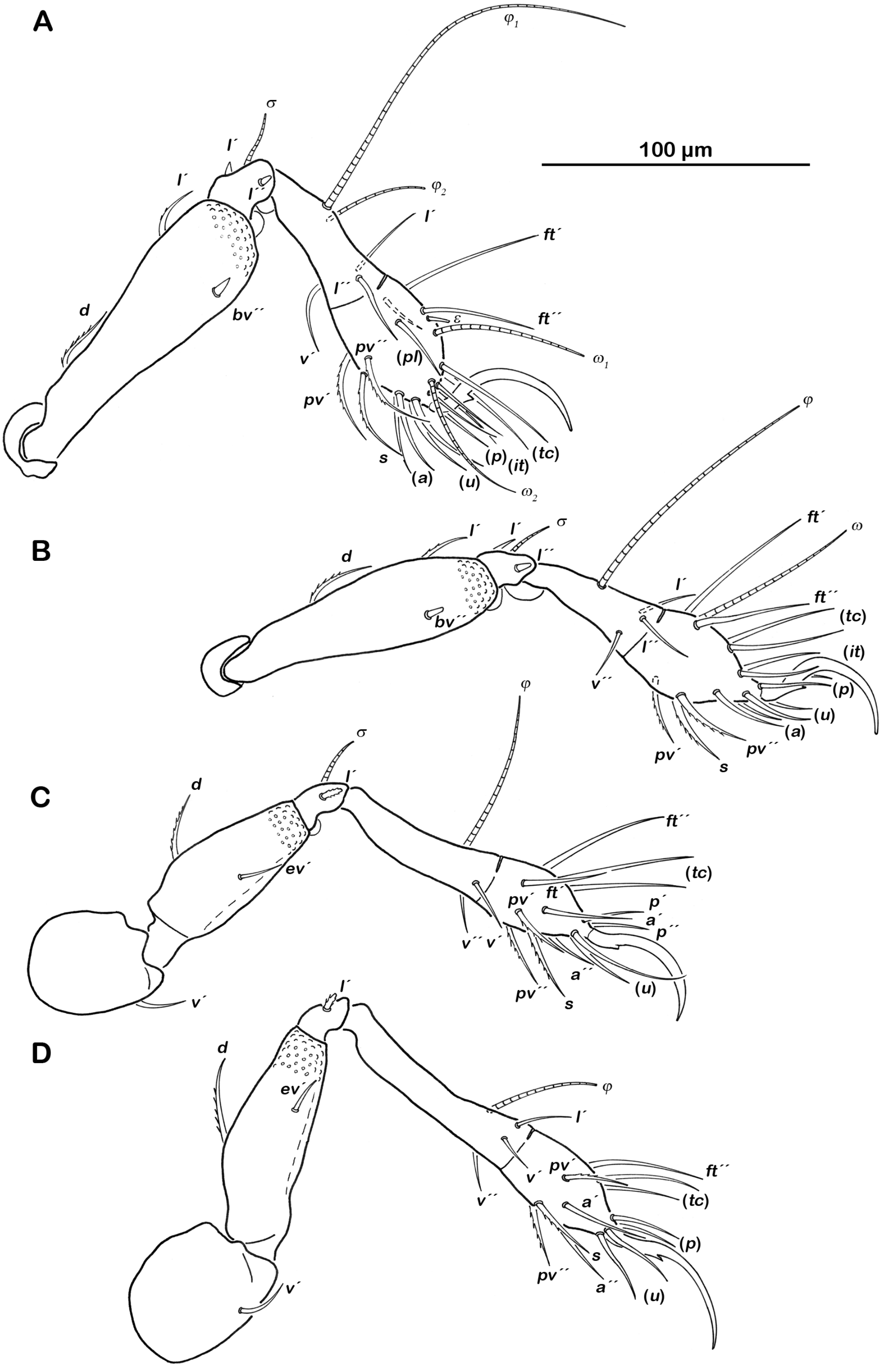

FIGURE 11. *Thasecazetes falcidactylus* **sp. nov.** adult legs antiaxial view. A) right leg I ; B) right leg II; C) left leg III; D) left leg IV.

TABLE 4. Mean (x), standard deviation (sd) and coefficient of variation (cv) of *Litoribates caelestis* and *L. bonairensis* **sp. nov.** Results of Mann-Whitney-U test are given.

	Galapagos (n=20) *L. galapagoensis*			Bonaire (n=19) *L. bonairensis* **sp. nov.**			Mann-Whitney-U test
	x	sd	CV	x	sd	CV	* $p < 0.001$
bl	322	9.94	0.03	364	8.97	0.02	*
dPtI	143	2.82	0.02	157	3.75	0.02	*
db	129	2.58	0.02	138	4.98	0.04	*
ll	50	3.12	0.06	51	5.16	**0.10**	
nw_{c1}	153	9.07	0.06	176	9.33	0.05	*
nw_{da}	203	6.74	0.03	239	7.83	0.03	*
nw_{dm}	201	6.70	0.03	237	10.54	0.04	*
cl	95	4.49	0.05	99	5.63	0.06	*
cw	68	2.07	0.03	84	2.41	0.03	*
dcg	75	5.67	**0.08**	81	5.86	**0.07**	*
dac3	110	2.32	0.02	135	3.66	0.03	*
gl	46	3.07	**0.07**	58	3.63	0.06	*
gw	54	4.27	**0.08**	64	3.10	0.05	*
al	69	2.17	0.03	81	1.82	0.02	*
aw	55	2.19	0.04	69	2.56	0.04	*

Multivariate analyses

1. *Litoribates bonairensis* **sp. nov.** and *L. caelestis*

The PCA on both raw and size-corrected data clearly separates the two *Litoribates* species from Galápagos and the Caribbean/Bonaire (Figure 12). In both cases, PC1 is the component responsible for separation, explaining 82% of the total variation. In the PCA on raw data, PC1 strongly correlates with size (r = 0.99), indicating that the *L. bonairensis* specimens are larger than *L. caelestis* specimens from Galápagos. Loadings with the highest values (> 0.3) and thus contributing most to separation are present in the variables *gl*, *aw*, *cw*, *dac3* and *gw* (Table 5). The decrease of the total variation after size correction was considerable (94%). Nevertheless, *L. caelestis* and *L. bonairensis* remain clearly separated by PC1 (explaining 46% of the total variation) in PCA on size-corrected data, and the variables with the highest loadings on this component are *cl*, *ll*, *db*, *gl* and *aw*.

The discriminant function on both raw and size-corrected data classified all specimens correctly in all samples as well as in Leave One Out Cross-Validation. Variables with the highest loadings were *gl* and *aw* in raw data and *cl* and *db* in size-corrected data. In both datasets, Bonferroni-corrected Hotelling's T^2 test revealed highly significant ($p < 0.001$) differences between *L. caelestis* and *L. bonairensis*.

2. *Litoribates* vs. *Alismobates (L. caelestis*, *L. bonairensis* sp. nov., *A. galapagoensis*, *A. inexpectatus*, *Alismobates* sp.)

In PCA on raw data, three separate groups are recognizable on PC1 versus PC2: *L. caelestis* from Galápagos, *L. bonairensis* from the Caribbean and one large group of *Alismobates* from

Galápagos, the Caribbean and Bermuda (Fig. 13). While the two *Litoribates* species are well separated by PC1 as well as PC2, the *Alismobates* groups overlap, forming one large cluster. The two genera *Litoribates* and *Alismobates* are clearly separated from each other by a combination of PC1 and PC2: in *Litoribates* from Galápagos the separation from *Alismobates* is caused by PC1, whereas in *Litoribates* from the Caribbean it is PC2. PC1 explains 67% of the total variation, PC2 explains 15%. PC1 is correlated with "size" (r = 0.94), and the variable with the highest loading on this component is *ll*. The specimens of *Alismobates* generally have higher values on PC1 than *Litoribates*, thus indicating that they are larger in terms of body size. On PC2, the variables with the highest loadings are *db* and *ll* (Table 6).

After size correction, the total variation is reduced by 88%. In PC1 versus PC2, the two genera *Litoribates* and *Alismobates* are still clearly separated from each other on PC1. PC1 explains 63% of the total variation and the variables with the highest loadings (> 0.45) are *db* and *ll*. The two species of *Litoribates* are still separated by the combination of PC1 and PC2, but there is a small overlapping area. Highest loadings on PC2 (explaining 9% of the total variation) can be found in the variables *dcg* and *dac3* (Table 6). The three groups of *Alismobates* still overlap, but there are some distinct clusters recognizable based on the combination of PC1 and PC2: *Alismobates galapagoensis* from Galápagos is separated from *A. inexpectatus* from Bermuda, and it is separated from *Alismobates* sp. from the Caribbean with an overlapping area. *Alismobates* from Bermuda and from the Caribbean cluster together.

After size correction, *Litoribates* and *Alismobates* show the same pattern of variation. In both genera, the specimens from Galápagos show higher values on PC1 as well as PC2 when compared to those from the Caribbean and/or Bermuda.

TABLE 5. Loadings of the two principal components PC1 and PC2 gained from PCA on ln(x+1) transformed raw and size corrected data of two different *Litoribates* species from Galápagos and the Caribbean. High loadings explaining differences between the groups are given in bold.

	raw data		size corrected	
	PC 1	PC 2	PC 1	PC 2
bl	0.21	0.02	0.12	0.10
dPtI	0.16	-0.03	0.22	0.23
db	0.12	0.04	**0.36**	0.19
ll	0.07	**0.79**	**0.39**	**-0.37**
nw_{c1}	0.23	**0.36**	0.11	**-0.50**
nw_{da}	0.27	0.04	-0.12	-0.06
nw_{dm}	0.27	-0.07	-0.16	0.19
cl	0.09	0.24	**0.44**	-0.11
cw	**0.33**	-0.15	-0.26	0.07
dcg	0.15	**-0.34**	0.19	**0.66**
dac3	**0.32**	-0.05	-0.28	-0.01
gl	**0.42**	-0.14	**-0.33**	0.03
gw	**0.31**	0.08	-0.14	-0.09
al	0.24	0.03	-0.05	-0.03
aw	**0.37**	-0.04	**-0.31**	-0.10

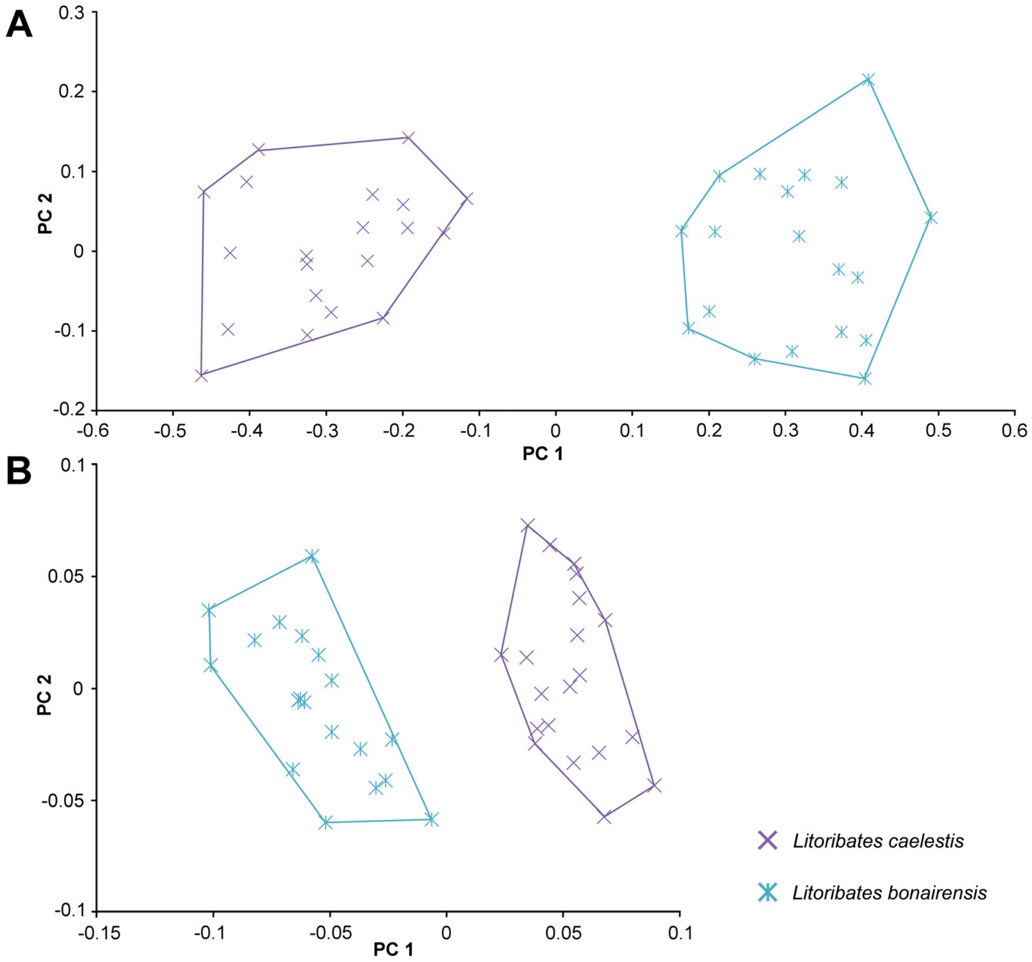

FIGURE 12. Scatter plots of PCA of *Litoribates caelestis* from Galápagos and the Caribbean *L. bonairensis* on ln(x+1) transformed A) raw data and B) size corrected data.

Classification by CVA always gave good results. In the raw data, all-samples CVA classified 96% and Leave-One-Out Cross-Validation classified 92% of all specimens correctly. Misclassified specimens always belonged to the genus *Alismobates*. After size correction, all samples CVA again classified 96% and Leave-One-Out Cross-Validation classified 93% of all specimens correctly, thus achieving slightly better results. Again, misclassifications only occurred in *Alismobates*. MANOVA as well as pairwise Bonferroni-corrected Hotelling's T^2 tests always revealed highly significant ($p < 0.001$) differences between all groups.

Molecular genetic analyses

The Bayesian inference tree based on 18S rDNA (Fig. 14) separates the genus *Litoribates* with a posterior probability of 93 from the genus *Alismobates*. The new genus *Thasecazetes* also represents a well-supported branch within the selenoribatid clade, consisting of *Thasecazetes*, *Schusteria* and *Thalassozetes*.

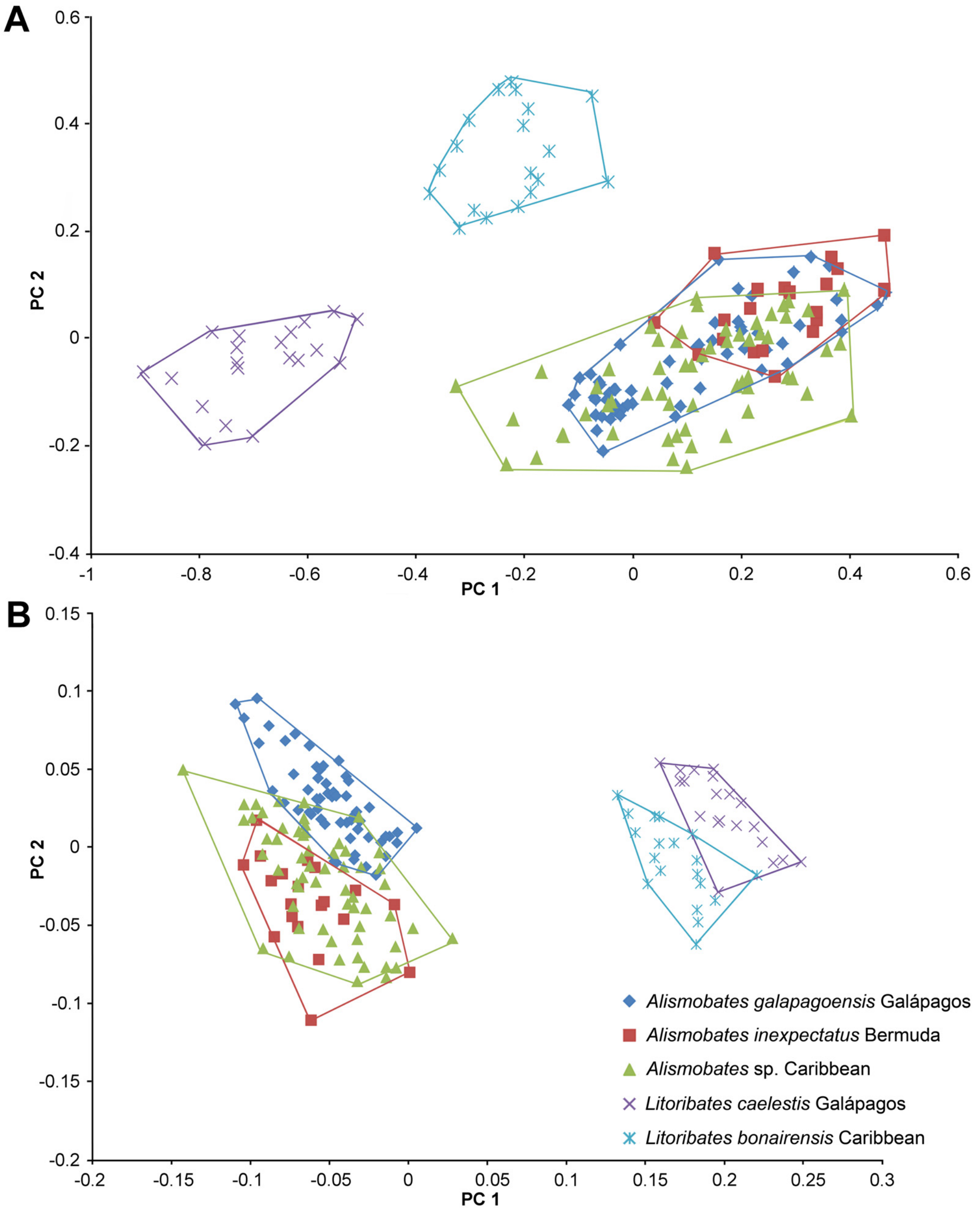

FIGURE 13. Scatter plots of PCA of *Litoribates* and *Alismobates* from the Atlantic and the Pacific on ln(x+1) transformed A) raw data and B) size corrected data.

TABLE 6. Loadings of the two principal components PC1 and PC2 gained from PCA on ln(x+1) transformed raw and size corrected data of *Litoribates* and *Alismobates* from the Atlantic and the Pacific. High loadings explaining differences between the groups are given in bold.

	raw data		size corrected data	
	PC 1	PC 2	PC 1	PC 2
bl	0.16	0.15	0.08	0.05
dPtI	0.11	0.15	0.13	-0.07
db	-0.23	**0.55**	**0.75**	0.36
ll	**0.54**	**-0.50**	**-0.47**	0.20
nw_{cl}	0.28	0.01	-0.19	0.33
nw_{da}	0.20	0.19	0.02	0.22
nw_{dm}	0.18	0.21	0.05	0.16
cl	0.11	0.01	0.08	0.18
cw	0.09	0.29	0.15	-0.10
dcg	0.05	0.21	0.18	**-0.54**
dac3	0.14	0.24	0.10	**-0.48**
gl	0.32	0.34	-0.08	0.18
gw	0.38	0.13	-0.21	-0.10
al	0.25	0.04	-0.10	0.01
aw	0.33	0.10	-0.16	-0.19

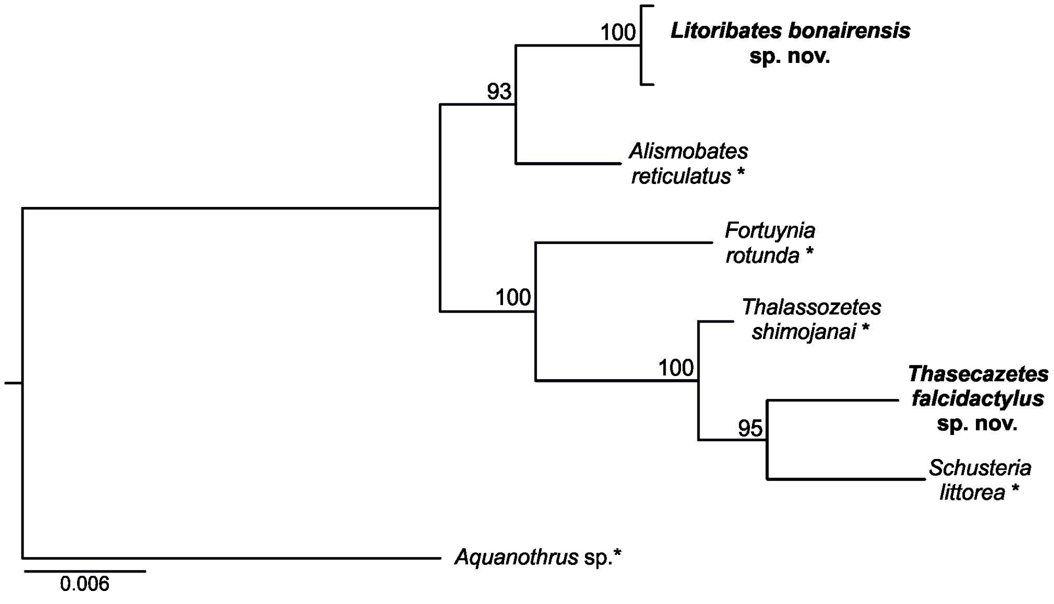

FIGURE 14. Bayesian inference tree based on 18S rDNA sequences (1768 bp) constructed by means of MrBayes applying the GTR+I+G model. Posterior probabilities (>90) are shown above the branches. Sequences obtained from GenBank are marked by *. For details see Table 1.

Discussion

Systematics

Litoribates bonairensis **sp. nov.** can be clearly differentiated from its Eastern Pacific congener *L. caelestis* by morphometric differences in size and shape, and it is also characterised by specific morphological features which confirm its distinct species status. *Litoribates bonairensis* shows slightly clavate sensilli whereas *L. caelestis* exhibits fusiform sensilli; this character distinctness also allows the assignment of juveniles to a particular species. In *L. bonairensis* the prodorsal lamellar ridges are more conspicuously bent medially and do not reach the transversal ridge demarcating the rostrum while in *L. caelestis* the lamellar ridges are more straight and fused with the transversal prodorsal ridge. Additionally, *L. bonairensis* shows only two setae on tibia IV instead of three. The most striking morphological difference between the two species is the different notogastral cerotegument structure; *L. caelestis* is characterized by the name giving “star chart” like cerotegumental pattern whereas *L. bonairensis* shows conspicuous cerotegumental granules in the humeral area flanking the lenticulus.

Apart from the different sensillus, the juveniles of both species exhibit only subtle differences: the centrodorsal plate is slightly more rough-textured in *L. caelestis* and in *L. bonairensis* the lateral setae of all genua are broader and barbed.

The finding of a second species showing the generic characters, e.g. incorporated bothridia, triangular anal valves (Pfingstl & Schatz 2017), justifies *Litoribates* again as distinct genus and this is also supported by morphometric and molecular genetic data. However, the same data also show that *Litoribates* is closely related to *Alismobates* and that both genera are likely sister taxa.

The new genus *Thasecazetes* shows all important characteristics of Selenoribatidae given by Grandjean (1966), namely the epimeral formula 1-0-1-1 and the partial fusion of tibia and tarsus on all legs and hence it is classified as a member of this intertidal family. *Thasecazetes* can be distinguished from the other selenoribatid genera by the following unique characters: long slender legs with tibia III and IV conspicuously elongated; claws sickle-shaped and thin and adanal hypertrichy. Other important morphological characters are shared with other selenoribatid genera, e.g. prodorsal ridges are also shown in *Thalassozetes*, 15 pairs of notogastral setae are also present in *Arotrobates*, *Carinozetes* and *Schusteria*, epimeral foveae are also exhibited in *Thalassozetes*, *Selenoribates* and *Carinozetes* etc. Accordingly, it is difficult to find the closest relative within the Selenoribatidae based on morphological characters. However, genetic data presently renders *Thasecazetes* as a sister taxon to *S. littorea* within the Selenoribatidae.

Distribution and Ecology

This is the first confirmed record of the genus *Litoribates* in the Caribbean and, although the specimens were only found in a single location on the Island of Bonaire, a much wider distribution can be expected. Indeed, an earlier record from Isla de Margarita, a Venezuelan offshore island, was published recently (Ermilov 2016) wherein the specimens were listed as an undetermined *Alismobates* species. These individuals are very similar to *L. bonairensis* (S.G. Ermilov, pers. comm.) which is not surprising as Bonaire is located only approx. 200 kilometres northwest of Isla de Margarita. Therefore an occurrence of this species or at least congeners along this part of the South American shoreline and its offshore islands may be assumed.

The genus *Litoribates* obviously shows a close ecological association with mangroves or other coastal trees and shrubs. Pfingstl and Schatz (2017) mentioned that *L. caelestis* was recorded almost exclusively in mangrove leaf litter on certain Galápagos Islands, the *L. bonairensis* specimens were also found in leaf litter under the red mangrove *Rhizophora mangle* and the specimens from Isla de Margarita were also extracted from leaf litter of unspecified origin (Ermilov 2016).

All specimens of *Thasecazetes falcidactylus* **gen. nov., sp. nov.** described in this paper, originate from a single location on Bonaire and so far no other records have been published. However, this taxon may also show a wider Caribbean distribution as indicated by unpublished records of one specimen from the Greater Antillean landmass of Hispaniola and of several specimens from the Florida Keys (Pfingstl & Lienhard unpublished). The genus *Thasecazetes* may also show a preference for mangrove habitats as all specimens from the above mentioned locations were either found in mangrove leaf litter or underneath mangrove trees.

The apparently close connection of *Litoribates*, *Thasecazetes* and several other Ameronothroidea species to mangroves underlines the high diversity of mangrove ecosystems down to the smallest arthropods, but also their vulnerability due to the endangerment of mangrove ecosystems. The mangroves of Lac Bay are threatened by an increasing number of visitors, eutrophication, sedimentation and reduction of water circulation in mangrove channels. The interruption of water inflow is mainly caused by dam building for road construction (Debrot *et al.* 2010, Wentink & Wulfsen 2011). A destruction of this unique ecosystem would also reduce, if not destroy, the population of these rare oribatid mite species.

Morphometric comparison Eastern Pacific versus Caribbean species

Multivariate analyses clearly separate the two fortuyniid genera *Alismobates* and *Litoribates*, but at the same time result in large overlaps of the different *Alismobates* populations (see Fig. 13). Pfingstl and Schatz (2017) already mentioned that *A. galapagoensis* shows to a large extent morphological conformity with the Bermudian *A. inexpectatus*, which is clearly reflected in the present data. The same applies to the undetermined Caribbean *Alismobates* populations; they also show large overlaps with *A. galapagoensis* and *A. inexpectatus* and hence are very similar in terms of size and shape.

The two studied *Litoribates* populations from Galápagos and Bonaire show conspicuously stronger divergence than the *Alismobates* populations (Fig. 13). They are clearly separated as proved by univariate and multivariate statistics, confirming their distinct species status. Both species, *Litoribates bonairensis* and *L. caelestis* show a low degree of intraspecific variation and most of this can be attributed to sexual dimorphism. The interspecific variation, on the other hand, is high and affects nearly all characters. There is an obvious overall size difference between the two species, which is already evident in the univariate analysis: *Litoribates bonairensis* **sp. nov.** specimens are on average 40 µm longer and broader than *L. caelestis* individuals. Apart from this remarkable size difference, significant shape differences can be found in the camerostome, the bothridial and the genito-anal area.

Accordingly, almost all variation found in *Litoribates* from Galápagos and the Caribbean in the multivariate analysis can be attributed to size. After size correction, the total variation decreased by 94%, an unusually high value. In a recent paper, Pfingstl & Baumann (2017) analysed two populations of *L. caelestis* from Galápagos and found a decrease in total variation after size correction of 33%. In the same work, they also studied *Alismobates* from Galápagos and Bermuda and found a decrease in total variation of 45% in females and 50% in males. Differences in overall size are assumed to be influenced by environmental factors (e.g. Jungers *et al.* 1995) but in the present case we are not able to assess which factors are indeed responsible for the large size differences. Further ecological investigations would be necessary to answer this question.

In contrast to raw data, size-corrected data are supposed to better illustrate variation induced by genetic differences (e.g. Stekolnikov & Klimov 2010). The gained shape variation thus does not reflect phenotypic plasticity, but rather points to diverging genomes. As mentioned above, size correction decreased the total variation considerably, but still showed clear separation between *Alismobates* and *Litoribates* as well as between the populations of each genus (see Fig. 13). In

Alismobates, the geographic distance between populations is reflected by the PCA graph: specimens from Bermuda are more similar to the Caribbean individuals than the mites from Galápagos. This seems legitimate due to the larger distance between Galápagos and the Caribbean region and the complete isolation of the Eastern Pacific from the Caribbean Sea since approx. 3 my years.

The probably most interesting result is the similar pattern of shape variation between Eastern Pacific and Caribbean populations in both *Alismobates* and *Litoribates*. It indicates that both taxa are derived from the same point of origin and during their dispersal independently experienced similar morphological changes in their evolutionary history. These changes were most probably induced by similar selection pressures caused by the different environments according to geographic region. Indeed, the Eastern Pacific aerial and oceanic climate (e.g. water temperature, tidal range) differs considerably from the Caribbean (Fortunato 2008) and this may explain why *Litoribates* and *Alismobates* exhibit similar morphological shape changes in the same geographic region.

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