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CARINOZETES NOV. GEN. (ACARI: ORIBATIDA) FROM BERMUDA AND REMARKS ON THE PRESENT STATUS OF THE FAMILY SELENORIBATIDAE

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ABSTRACT — Two new species, Carinozetes trifoveatus and C. bermudensis, are reported from intertidal habitats of the archipelago of Bermuda. These species represent a new genus of the family Selenoribatidae and are characterized by a pair of ventral keels crossing the anterior epimeral region longitudinally. The juvenile stages of Carinozetes show a centrodorsal plate framed by plicate integument, typical for selenoribatid immatures. The cerotegument of both, adults and juveniles, retains air to the body surface when flooded, enabling the animals to breathe underwater. The morphological comparison with other members of Selenoribatidae indicates the closest relation to the genus Schusteria. A review of the literature showed that Schuster, 1963, instead of Grandjean, 1966, must be quoted as author of the family Selenoribatidae. Further the present classification of the genus Schusteria is partly based on misinterpreted information and therefore questionable. A thorough revision will be needed to solve this problem and to assess the real biodiversity of this group.

KEYWORDS — Ameronothroidea; taxonomy; juveniles; plastron; zoogeography

INTRODUCTION

The marine littoral is one of the most interesting ecosystems as it represents an intersection of two completely different worlds. Only a few oribatid mites have successfully invaded this extreme ecotone and have managed to exist at the borders of both the terrestrial and marine realms.

The Selenoribatidae belong to this group of thalassobiotic mites and are distributed on shores of the tropics and subtropics. At present this family includes 14 species belonging to six genera, Arotrobates Luxton, 1992, Psednobates Luxton, 1992, Rhizophobates Karasawa and Aoki, 2005, Schusteria Grandjean, 1968, Selenoribates Stenzke, 1961 and Thalassozetes Schuster, 1963. The number of described species within this taxon tripled in recent years and the immense and rapid increase of the family resulted in certain unclear classifications and controversial taxonomic acts.

The present discovery of more new selenoribatid taxa on the small archipelago of Bermuda further increases the biodiversity of this group and raises the question whether relatively conservative diagnoses and keys are still suited to classify this number of new species.
**TABLE 1:** Detailed list of sample locations of *Carinozetes* species. Numbers in first column refer to Figure 22.

<table>
<thead>
<tr>
<th>Nr.</th>
<th>Location</th>
<th>Date</th>
<th>Collector</th>
<th>GPS coordinates</th>
<th>species</th>
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<td>1</td>
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<td>29 Aug. 1981</td>
<td>R. Schuster</td>
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<td>5</td>
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<td>9 Sep. 1981</td>
<td>R. Schuster</td>
<td></td>
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<tr>
<td>6</td>
<td>Devonshire Bay</td>
<td>15 Sep. 1981</td>
<td>R. Schuster</td>
<td></td>
<td><em>C. trifoveatus</em></td>
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<tr>
<td>7</td>
<td>Vine Cave</td>
<td>22 Sep. 1981</td>
<td>R. Schuster</td>
<td></td>
<td><em>C. bermudensis</em></td>
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<tr>
<td>8</td>
<td>Burnt Point Fort</td>
<td>5 Aug. 2011</td>
<td>T. Pfingstl</td>
<td>32°21´44´´N 64°42´56´´W</td>
<td><em>C. trifoveatus, C. bermudensis</em></td>
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<td>Concrete Beach</td>
<td>9 Aug. 2011</td>
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<td>32°22´10´´N 64°41´50´´W</td>
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<td>12 Aug. 2011</td>
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<td><em>C. bermudensis</em></td>
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<td>2 Feb. 2012</td>
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<td><em>C. trifoveatus</em></td>
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<tr>
<td>21</td>
<td>Church Bay</td>
<td>18 Apr. 2012</td>
<td>T. Pfingstl</td>
<td>32°14´57´´N 64°50´50´´W</td>
<td><em>C. trifoveatus</em></td>
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**MATERIALS AND METHODS**

For investigation in transmitted light all animals were stored in ethanol (70 % or absolute ethanol), then heated in lactic acid (80°C for about 20 minutes) and afterwards embedded in BERLESE mountant. Observations, photographs and drawings were made with an Olympus BH-2 Microscope and a WILD HEERBRUGG M20, both equipped with a drawing attachment. Image stacks were obtained by an Olympus E1 digital camera and layered with the Combine ZP software. Inscriptions of drawings were done according to Grandjean (1966, 1968).

Intertidal algae growing on sandy and rocky substrate, as well as on mangrove roots (*Rhizophora mangle, Avicennia germinans*) were collected during low tide and afterwards put in a Berlese-Tullgren apparatus for the extraction of mites. For a list of sample locations see Table 1.

**Type material:**


FIGURE 1: Carinozetes trifoveatus adult: A – dorsal view; B – ventral view; C – lateral view.
RESULTS

Carinozetes nov. gen.

Type species — Carinozetes trifoveatus n. sp.


Carinozetes trifoveatus n. sp.

Diagnosis — Brown sclerotized mites. Average length 321 µm, mean width 204 µm. Notogaster rounded. Sensillus clavate, spinose. Interlamellar setae short. Three depressions on anterior part of notogaster, separated by two X-shaped ridges. Fifteen pairs of simple, notogastral setae. Three pairs of adanal setae. Legs monodactylous with large claw. Leg setation (chaetome, solenidia): Leg I 0-4-2-3-18, 1-2-2; leg II 0-4-2-3-15, 1-1-1; leg III 1-2-1-2-13, 1-1-0; leg IV 1-2-1-3-12, 0-1-0. Juveniles plicate with large centrodorsal plate.
**FIGURE 3:** *Carinozetes trifoveatus* adult, LM-micrographs: A – characteristic notogastral foveae and ridges, scale bar = 25 µm; B – light areas surrounding bases of notogastral setae (dm) and (dp), scale bar = 15 µm.
Description

Adult

Females (N=3) — length: 322 – 335 µm (mean 326 µm), width: 200 – 212 µm (mean 206 µm); males (N=5), length: 316 – 322 µm (mean 318 µm), width: 194 – 212 µm (mean 202 µm).

Integument — Colour ranging from brown to dark brown, sometimes with a slight metallic shimmer.

Prodorsum — Cerotegument finely granular, larger granules on rostrum. Rostrum rounded in dorsal view, but slightly projecting anteroventrally in lateral view. Rostrum demarcated from remainder of prodorsum by a transverse ridge. Rostral setae (ro) short. Lamellar setae (le) simple, short and smooth. Interlamellar setae (in) very short and simple. One pair short and fine exobothridial setae (ex). Bothridia large cups with a lateral incision, strongly projecting, orifice circular and narrow. Sensilla of normal length (approx. 50 µm), with a clavate and spinose head. Tutorium absent. A pair of weaker sclerotized spots between interlamellar setae.

Gnathosoma — Pedipalp pentamerous 0-2-1-3-9 (including solenidion). Solenidion ω on palp—tarsus erect, not associated with eupathidium acm. Chelicerae chelate, mobile digit slightly darker sclerotized, both digits each with two teeth. Lateral porose area on proximal part of fixed digit. Seta cha and chb of approximately same length, both dorsally slightly pectinate. Distal part of rutellum developed as thin triangular slightly curved inward membrane. Seta a and m long and smooth. Mentum regular, seta h simple, thin and long.

Gastronomic region (Figures 1A, 2A) — Rounded, dorsosejugal suture complete. Cerotegument mainly finely granular, but darker spots distributed regularly over whole gastronomic region, resulting in a dotted pattern. Three depressions on anterior part of notogaster, separated by two X-shaped ridges (Figure 3A). Densely granulated cerotegument within depressions. Fifteen pairs of normal, smooth notogastral setae, c1-3, da, dm, dp, la, bm, lp, h1-3, p1-3. Lighter circular areas at bases of notogastral setae (Figure 3B). Porose areas or distinct pores absent. Five pairs of notogastral lyrifissures present; ia next to seta c1, close and rectangular to anterior notogastral border; im lateral of seta la; ih on lateral aspect of notogaster, slightly anterior to seta h3; lyrifissure ips next to seta p3 and ip between seta p3 and p2. Orifice of opisthonotal gland (gla) near seta la.

Lateral aspect (Figure 1C) — Cerotegument generally finely granular, larger granules in areas surrounding acetabula. Tutorium absent. Pedotectum I small but thick, pedotectum II absent. Discidium triangular and strongly projecting. Broad furrow with large granules running laterally from dorsal sejugal suture to ventral sejugal suture. Orifice of coxal gland II z well visible.

Ventral region of idiosoma (Figures 1B, 2B) — Cerotegument finely granular. Epimeral setation 1-0-1-1, seta 1b very long reaching trochanter III, setae 3b and 4a of normal length. Internal borders of all epimera well visible, sternal apodemes II, sejugal and III well developed. A pair of strongly projecting carinae running longitudinally from camerostome to ventral sejugal furrow. Anteriorly each carina forms a tooth-like projection. On level of apodeme II a densely granulated median sternal weak cavity. Genital and anal opening closely adjacent, both surrounded by stronger sclerotized and hence darker cuticle. Rounded genital plates with three pairs of fine genital setae. First two pairs on anterior half of genital valves, last pair close to posterior border of orifice, no equidistance between setae. Adjacent to anterior corners of genital opening, two obvious points of dark pigmentation, representing insertion of tendon β (Grandjean 1966). Aggenital setae absent. Anal valves nearly triangular. Preanal organ shaped like an inverted T in ventral view. Two pairs of short anal setae, an1-2. Three pairs of short and simple adanal setae a-id1-3, flanking anal opening. Lyrifissure iad long, orientated transversally.

Legs (Figure 4) — Monodactylous. Long hook-like claws with one proximoventral tooth. Cuticle heterogeneous, trochanter, femur and genu dark, heavily sclerotized, tibia and tarsus lighter, showing thinner cuticle. Femora with strongly projecting ventral carina, showing roughly granulated cerotegument. All tarsi with proximal lyrifissure. No porose areas detectable. Lateral seta l” on genu
FIGURE 4: Carinozetes trifoveatus adult: A – right leg I, paraxial view (femur and genu slightly distorted); B – right leg II, antiaxial view; C – left leg III, antiaxial view (seta tc'' broken off); D – right leg IV, antiaxial view.
I and II, as well as seta $l'$ on genu III and IV short, broad and conspicuously blunt. Solenidia on tibiae long always orientated backwards. Setae on genu I-II close to solenidion $\sigma$. Ventral setae on tarsi I and II ventrally slightly serrate. Solenidion $\omega$ long, inserting on antiaxial side of tarsus, orientated horizontally and parallel to claw. Famulus rod-like and short. Chaetome and solenidia see Table 2.

**Etymology** — The generic name is derived from the Latin word *carina* meaning “keel” and refers to the characteristic pair of longitudinal epimeral ventral keels. The species name *trifoveatus* refers to the three depressions on the anterior part of the notogaster.

**Juvenile stages — common features**

Apheroderous. Colour brown. Integument plicate, except for centrodorsal plate (Figure 5). Prodorsum triangular, anterior part strongly granular, rostrum rounded. Rostral ($ro$) and lamellar setae ($le$) short. One pair of short exobothridial setae ($ex$) and short interlamellar setae ($in$). Sensilla of normal length (depending on stage approx. 25 – 40 $\mu$m), clavate and distally spinose. Bothridia cup-like, laterally opened with a narrow circular orifice. Gnathosoma no obvious differences to adult stage. Opisthosomal dorum laterally carinate. Hysterosomal cupules not traceable in any stage. Large stronger sclerotized centrodorsal plate bearing centrodorsal setae. Centrodorsal plate slightly convex, plateau-like; lateral and posterior inner borders of plate deepened like a broad furrow, showing dense granulation. Median part of plate with less densely distributed granules. Large folds, with fine granular surface, framing centrodorsal plate completely. Orifice of opisthonal gland (glia) located lateroventrally on level of anal orifice. Ventral sejugal suture developed as distinct furrow, showing exceptional dense granulation. Genital valves hardly discernable, medially obviously finely granulated. In the anogenital area a complex of distinct and connected furrows, consisting of a short longitudinal branch flanking genital opening, a transversal branch running from acetabulum IV to area between genital and anal orifice and a further longitudinal branch flanking anal opening. All furrows showing an obvious dense granulation. Legs monodactylous. Dorsal setae of tibiae and genua absent in all stages.

**Larva (Figure 5A)**

Length (N=1) — 136 $\mu$m.

Gastronotic region — 11 pairs of short and simple notogastral setae; $c_{1-3}$, $da$, $dm$, $dp$, $la$, $lm$, $lp$, $h_{1-2}$; $h_{3}$ absent.
FIGURE 5: *Carinozetes trifoveatus* LM-micrographs, scale bar = 50 µm: A – larva lateral view, layered from 7 sequentially focused images; B – tritonymph dorsal view, 6 layered images; C – protonymph ventral view, layered from 5 images.
FIGURE 6: Carinozetes trifoveatus: A – protonymph dorsal view; B – protonymph ventral view; C – deutonymph dorsal view; D – deutonymph ventral view.
Figure 7: Carinocetes trifoveatus deutonymph, legs antiaxial view: A – right leg I; B – right leg II; C – left leg III; D – left leg IV.
Figure 8: Carinozetes trifoveatus tritonymph: A – dorsal view; B – ventral view; C – lateral view.
Figure 9: Carinozetes trifoveatus tritonymph, legs antiaxial view: A – right leg I; B – left leg II; C – right leg III; D – left leg IV.
Ventral region of idiosoma — Epimeral setation 1-0-1. Claparède organ bladder-like, framed by thickened cuticle, no protecting seta detectable. Complex of anogenital furrows consisting in this stage only of transversal parts.

Legs — Setation and solenidia see Table 2.

Protonymph

Length (N=1) — 194 µm.

Gastronotic region (Figure 6A) — 15 pairs of notogastral setae; $c_{1-3}$, $da$, $dm$, $dp$, $la$, $lm$, $lp$, $h_{1-3}$ and $p_{1-3}$, all setae normal and short.

Ventral region of idiosoma (Figure 6B) — Epimeral setation 1-0-1-1, seta $4a$ added in this stage. One pair of short genital setae.

Legs — Chaetome and solenidia see Table 2.

Deutonymph

Length (N=3) — 219 – 259 µm (mean 235 µm).

Gastronotic region (Figure 6C) — 15 pairs of notogastral setae, same positions and shapes as in protonymph.

Ventral region of idiosoma (Figure 6D) — Epimeral setation 1-0-1-1. Two pairs of short genital setae ar ranged in a longitudinal row. Three pairs of adanal setae $ad_{1-3}$ flanking anal valves.

Legs (Figure 7) — Chaetome and solenidia see Table 2.

Tritonymph

Length (N=23) — 237 – 308 µm (mean 287 µm).

Gastronotic region (Figures 8A and C) — 15 pairs of notogastral setae, same as deutonymph.

Ventral region of idiosoma (Figure 8B) — Epimeral setation 1-0-1-1. Three pairs of short genital setae in a longitudinal row. Three pairs of adanal setae $ad_{1-3}$.

Two pairs of short anal setae $an_{1-2}$.

Legs (Figure 9) — Chaetome and solenidia see Table 2.

Carinozetes bermudensis n. sp.

Diagnosis — Brown to dark brown sclerotized mites (Figure 10). Average length 357 µm, mean width 222 µm. Notogaster rounded. Sensillus clavate, spinose, short. Interlamellar setae normal. A pair of weak longitudinal ridges on anterior part of notogaster. Fifteen pairs of notogastral setae. Two pairs of adanal and two pairs of anal setae. Legs monodactylous with large claw. Leg setation (chaetome, solenidia): Leg I 0-4-2-3-18, 1-2-2; leg II 0-4-2-3-15, 1-1-1; leg III 1-2-1-2-13, 1-1-0; leg IV 1-2-1-3-12, 0-1-0. Juveniles plicate with large centroidorsal plate.

Description

Adult

Females (N=5) — length: 341 – 386 µm (mean 367 µm), width: 219 – 246 µm (mean 232 µm); males (N=10), length: 335 – 360 µm (mean 349 µm), width: 203 – 229 µm (mean 217 µm).

Integument — Colour ranging from light brown to dark brown. Cuticle appears matt under dissecting microscope.

Prodorsum — Cerotegument finely granular. Rostrum rounded in dorsal view, but slightly projecting anteroventrally in lateral view. Rostrum clearly demarcated from remainder of prodorsum by an obvious transverse ridge. Rostral setae ($ro$) simple and short. Lamellar setae ($le$) smooth, twice as long as ($ro$) and in most cases bent caudally. Interlamellar setae ($in$) short. One pair of short and fine exobothridial setae ($ex$). Bothridia large cups with a lateral incision, strongly projecting, orifice circular and narrow. Sensilla short, clavate and spinose. Tutorium absent.

Gnathosoma — Pedipalp pentamerous 0-2-1-3-9 (including solenidion). Solenidion $\omega$ on palp-tarsus erect, not associated with eupathidium acm. Distal part of rutellum developed as thin triangular slightly inward curved membrane (Figure 11A). Seta $a$ and $m$ long and smooth. Chelicerae (Figure 11B) chelate, mobile digit slightly darker sclerotized, both digits with two teeth, porose area on proximolateral part of fixed digit. Seta $cha$ and $chb$ of approximately same length, both dorsally slightly pectinate. Mentum regular, seta $h$ normal, thin and long.

Gastronotic region (Figure 12A) — Rounded, dorsosejugal suture complete, whereas median part weaker developed. Cerotegument finely granular (Figure 13A). A pair of, hardly discernable, median
Figure 10: Carinozetes bermudensis adult, LM-micrographs; scale bar = 100 µm: A – dorsal view, layered from 6 sequentially focused images; B – ventral view, 6 layered images; C – lateral view, 10 layered images.
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Figure 11: Carinozetes bermudensis adult: A – right rutellum, ventral view; B – left chelicera, paraxial view.

Longitudinal ridges on anterior part of notogaster (more obvious under dissecting microscope). Fifteen pairs of smooth notogastral setae, $c_{1-3}$, $da$, $dm$, $dp$, $la$, $lm$, $lp$, $h_{1-3}$, $p_{1-3}$, all bent caudally. Porose areas or distinct pores absent. Five pairs of notogastral lyrifissures present; $ia$ next to seta $c_{2}$ close and rectangular to anterior notogastral border; $im$ slightly anterior and lateral of seta $la$; $ih$ on lateral aspect of notogaster, slightly anterior to seta $h_{3}$; lyrifissure $ips$ anterior to seta $p_{3}$ and $ip$ between seta $p_{2}$ and $p_{1}$. Orifice of opisthonotal gland ($gla$) next to setae $la$.

Lateral aspect (Figure 12C) — Cerotegument generally finely granular, larger granules in areas surrounding acetabula. Tutorium absent. Pedotectum I small but thick, pedotectum II absent. Discidium a conspicuous triangular projection in lateral view. A broad lateral furrow with large granules reaching from dorsal sejugal suture to ventral sejugal suture. Orifice of coxal gland II ± well visible.

Ventral region of idiosoma (Figure 12B) — Cerotegument finely granular (Figure 13B). Epimeral setation 1-0-1-1, seta $1b$ very long reaching trochanter III, setae $3b$ and $4a$ of normal length (approx. 10 µm). Internal borders of all epimera well visible, sternal apodemes II, sejugal and III well developed. A pair of projecting carinae running longitudinally from camerostome to ventral sejugal furrow. Anteriorly each carina forms a weak tooth-like projection. Medially on level of apodeme II a densely granulated sternal cavity. Genital and anal openings closely adjacent, both surrounded by stronger sclerotized cuticle. Genital plates rounded with three pairs of short and fine genital setae. First two pairs on anterior half of genital plates, last pair close to posterior border of orifice. Adjacent to anterior corners of genital valves insertion of tendon represented by two conspicuously dark pigmented points. Aggenital setae absent. Anal valves triangular. Preanal organ in ventral view shaped like an inverted T. Two pairs of short anal setae, $an_{1-2}$. Two pairs of simple adanal setae $ad_{1-2}$, flanking anal opening in longitudinal rows (sometimes asymmetrical appearance of a third anterior adanal seta, as shown in Figure 12B). Lyrifissure $iad$ aligned transversally.

Legs (Figure 14) — Monodactylous. Long hook-like claws with one proximoventral tooth. Cuticle of trochanter, femur and genu dark, strongly sclerotized. Tibia and tarsus light, showing thinner cuticle. Femora with strongly projecting ventral carinae showing roughly granulated cerotegument. Porose areas absent. All tarsi with proximal lyrifissure. Antiaxial lateral setae $l$ on genu I-IV short, thick and conspicuously blunt. Solenidia on all tibiae always
Figure 12: Carinozetes bermudensis adult: A – dorsal view; B – ventral view; C – lateral view.
FIGURE 13: Carinozetes bermudensis adult, LM-micrographs: A – notogastral cerotegmental pattern in detail, scale bar = 10 µm; B – ventral cerotegument next to genital opening in detail, scale bar = 25 µm.
FIGURE 14: Carinozetes bermudensis adult, legs antiaxial view: A – left leg I; B – left leg II; C – right leg III; D – left leg IV.
Figure 15: Carinozetes bermudensis LM-micrographs: A – protonymph dorsal view, layered from 5 sequentially focused images, scale bar = 50 µm; B – deutonymph ventral view, 4 layered images, scale bar = 50 µm; C – tritonymph lateral view, layered from 6 images, scale bar = 100 µm.
Figure 16: Carinozetes bermudensis nymphs, LM-micrographs: A – longitudinal depression along lateral border of centrodorsal plate showing large granules, scale bar = 20 µm; B – cerotegumental pattern on centrodorsal plate near setal pair da, scale bar = 20 µm; C – cerotegument in lateral folds, scale bar = 10 µm; D – cerotegument in large ventral folds next to genital opening, scale bar = 10 µm.
Figure 17: *Carinozetes bermudensis*: A– larva dorsal view; B– larva ventral view; C– protonymph dorsal view; D– protonymph ventral view.
FIGURE 18: Carinozetes bermudensis larva, left legs antiaxial view: A – leg I; B – leg II; C – leg III.
orientated backwards. Setae $l'$ on genua I and II inserting close to solenidion $\sigma$. Ventral setae on tarsi I and II ventrally slightly serrate. Solenidion $\omega_2$ long, inserting on anti axial side of tarsus, orientated parallel to claw. Famulus short and rod-like. Chaetome and solenidia see Table 2.

Etymology — The specific epithet *bermudensis* refers to its type locality, the archipelago of Bermuda.

**Juvenile stages — common features**

Apheredermous. Colour brown. Integument plicate, except for centrodorsal plate (Figure 15). Prodorsum triangular, rostrum rounded and strongly granular. Rostral ($ro$) and lamellar setae ($le$) short and simple. One pair of short and fine exobothridial setae ($ex$). Interlamellar setae ($in$) short. Sensilla short, clavate and distally spinose. Bothridia large cups, laterally opened. Gnathosoma same as adult stage. Opisthosomal dorsum laterally carinate. Hysterosomal cupules not detectable in any stage. Large strong sclerotized centrodorsal plate bearing centrodorsal setae. Centrodorsal plate slightly convex, plateau-like; lateral and posterior inner borders of plate deepened like a broad groove, showing large granules, distributed densely (Figure 16A). Median part of plate finely granulated with a few large granules, dark spots respectively (Figure 16B). Large folds, with fine granular surface, framing centrodorsal plate completely (Figure 16C). Orifice of opisthonal plate (gla) located lateroventrally on level of anal orifice. Ventral sejugal su-
Figure 20: Carinozetes bermudensis protonymph, left legs antiaxial view: A – leg I; B – leg II; C – leg III; D – leg IV.
FIGURE 21: Carinozetes bermudensis: A – deutonymph dorsal view (right sensillus broken off); B – deutonymph ventral view; C – tritonymph dorsal view; D – tritonymph ventral view.
ture developed as distinct furrow, showing exceptional dense granulation. Genital valves hardly discernable, medially finely granulated. Anogenital area with a complex of distinct connected furrows; a short longitudinal part flanking genital opening, a transversal branch running from acetabulum IV to area between genital and anal orifice, turning into a further longitudinal furrow flanking anal opening. All furrows with an obvious dense granulation (Figure 16D). Legs monodactylous. Dorsal setae of tibiae and genua absent in all stage.

**Larva**
Length (N=11) — 145 – 188 \( \mu m \) (mean 170 \( \mu m \))
Gastronomic region (Figure 17A) — 11 pairs of short and setiform notogastral setae; \( c_{1-3}, da, dm, dp, la, lm, lp, h_{1-2}, h_{3} \) absent.
Ventral region of idiosoma (Figure 17B) — Epimeral setation 1-0-1. Claparède organ framed by thickened cuticle, no protecting seta detectable. Complex of anogenital furrows consisting in this stage only of transversal parts.
Legs (Figure 18) — Setation and solenidia see Table 2.

**Protonymph**
Length (N=31) — 200 – 253 \( \mu m \) (mean 235 \( \mu m \))
Gastronomic region (Figures 17C and 19) — 15 pairs of notogastral setae; \( c_{1-3}, da, dm, dp, la, lm, lp, h_{1-3} \) and \( p_{1-3} \).
Ventral region of idiosoma (Figure 17D) — Epimeral setation 1-0-1-1. One pair of short genital setae.
Legs (Figure 20) — Chaetome and solenidia see Table 2.

**Deutonymph**
Length (N=43) — 245 – 311 \( \mu m \) (mean 285 \( \mu m \))
Gastronomic region (Figure 21A) — 15 pairs of notogastral setae, same positions and shapes as in protonymph.
Ventral region of idiosoma (Figure 21B) — Epimeral setation 1-0-1-1. Two pairs of short genital setae arranged in a longitudinal row. Two pairs of adanal setae \( ad_{1-2} \) flanking anal valves. Two pairs of anal setae developed as vestiges.
Legs — Chaetome and solenidia see Table 2.

**Tritonymph**
Length (N=46) — 315 – 386 \( \mu m \) (mean 347 \( \mu m \))
Gastronomic region (Figure 21C) — 15 pairs of notogastral setae, same as deutonymph.
Ventral region of idiosoma (Figure 21D) — Epimeral setation 1-0-1-1. Three pairs of short genital setae. Two pairs of adanal setae \( ad_{1-2} \). Two pairs of vestigial anal setae.
Legs — Chaetome and solenidia see Table 2.

**Local distribution (Figure 22)**
The intertidal habitat of Bermuda is known to harbour the fortuyniid taxa *Fortunyia atlantica* Krisper and Schuster, 2008 and *Alismobates inexpectatus* Pfingstl and Schuster, 2012 and now two new species of the Selenoribatidae, *Carinozetes trifoveatus* and *C. bermudensis* are added as further characteristic elements of the littoral fauna of this archipelago. Schuster (1983, 1989) already mentioned the occurrence of selenoribatid species on Bermuda and the present study confirms that this landmass has been successfully colonized by various intertidal oribatid species. Both new selenoribatid species prefer sheltered shores, whereas *C. trifoveatus* occurs exclusively on rocky substrate, especially in sand accumulated in rock crevices and *C. bermudensis*, showing a wider range of habitats, can be found on sandy or boulder beaches, as well as on mangrove roots. Apart from the known records shown in Figure 22, both species presumably occur on all Bermudan coasts offering these conditions.

The biogeographical origin of the Selenoribatidae found on Bermuda is yet unknown and generic and specific endemism cannot be assessed given the prevailing incompleteness of records. But faunistic influences from Central-American and South-American shores must be considered. Moreover, the relatively high number of species on Bermuda (there are also yet unpublished records of at least two new *Selenoribates* species) may reflect a generally high biodiversity of intertidal oribatid mites within this part of the Atlantic Ocean. Sampling the coasts of the Caribbean Sea, we may face a further dramatic increase of new fortuyniid and selenoribatid taxa.

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DISCUSSION

The new taxon and its position within the present selenoribatid classification.

The new genus *Carinozetes* is a very interesting group showing a mixture of unique morphological features and characters typically shown in other taxa. *Carinozetes trifoveatus* possesses, the name giving, three foveae on the anterior part of the notogaster, which are very similar to those present in *Selenoribates* species (Stenzke 1961; Grandjean 1966; Abd-El-Hamid 1973). *Carinozetes bermudensis*, on the other hand, is lacking these structures completely and shows instead only a pair of weak longitudinal ridges. Nevertheless, the leg setation of both species is completely identical and they share an eye-catching trait, namely a remarkable pair of ventral carinae combined with a single median epimeral cavity. This character combination is specific for these two species; moreover the ventral aspects of both taxa are so similar that it is hard to tell them apart. It is unlikely that such a similarity is based on independent origins; therefore the ventral keels in combination with the sternal cavity are supposed a synapomorphy for *C. bermudensis* and *C. trifoveatus*. Apart from these remarkable morphological features and the presence of setae *k* on the ovipositor, the new genus *Carinozetes* shows in the majority of its characters, e.g. dorsal aspect, body setation, absence of setae (*it*) from tarsus III and IV, loss of setae *d* on genu and tibia in all stages and all legs, conformity with the genus *Schusteria* sensu Grandjean, 1968, indicating a close relation of both genera. Although none of the *Schusteria* species possesses epimeral ventral carinae, there is indication that a corresponding precursory structure within this genus may be present. Grandjean (1968, p. 123, 124) mentioned and depicted two weak ridges *cz* in *S. littorea*, having exactly the same position as the robust, strongly projecting keels of *Carinozetes*, accordingly they may represent a primitive stage of this character.

The genus *Arotrobates* is also characterized by a pair of ventral keels, similar to that of *Carinozetes*, but its members lack the epimeral cavity (Luxton 1992) and diverge conspicuously in other charac-

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**FIGURE 22:** Map of Bermuda showing distribution of *Carinozetes* species. Numbers refer to locations in Table 1.
ters, as for example the relative positions of the lyri-fissure iad and the adanal setae. Thus the generic distinctness of Carinozetes and Arotrobates are beyond question but a homologous origin of the ventral carinae of each group may still be considered.

The juvenile morphology of Carinozetes is well in accordance with those of other selenoribatid species. The typical habitus of selenoribatid juveniles, showing a smooth centrodorsal plate surrounded by large folds (Grandjean 1966, 1968; Schuster 1963), is also present in immatures of Fortuyniidae (van der Hammen 1963; Luxton 1992; Pfingstl and Schuster 2012) and Tegeocranellidae (Behan-Pelletier 1997). Although the basic pattern of plication within these taxa is similar, the detailed structure is specific for each family. Differences among the families can be found in the size and curvature of the centrodorsal plate and in the arrangement of ventral furrows (Pfingstl and Schuster 2012). In fortuyniid juveniles the large folds and furrows play an important role producing a plastron while being submerged (Pfingstl and Schuster 2012) and the same is true for immatures of Carinozetes. There is an extraordinary granulated cerotegument within the folds and furrows of the larva and nymphs of C. bermudensis and C. trifoveatus retaining air to the body surface when the animals are flooded. But in contrast to fortuyniid immatures, where respiration takes places across fine pores associated with tracheal tubes (Pfingstl and Schuster 2012), the oxygen transfer in these selenoribatid juveniles is presumably accomplished directly through the thin cuticle. Porose areas or pores have not been detected yet in Carinozetes juveniles but a respiration via such structures should not be excluded completely as electron-microscopic investigations may still reveal the existence of these organs.

The comparison of the instars of C. trifoveatus and C. bermudensis shows hardly any differences. The immatures of C. bermudensis are in each stage at an average of 50 µm larger, show more and larger granules on the centrodorsal plate, only two pairs of adanal setae and vestigial anal setae in the deutonymph. All the other aspects are completely identical and thus the juvenile morphology also confirms the discreteness of the genus Carinozetes.

**Special features of Carinozetes adults**

The adults of the genus Carinozetes are also able to use a plastron mechanism to breathe underwater (details of this plastron will be published in a separate paper). The fine granular cerotegument (shown in Figure 13) retains a layer of air to the body when the animals are submerged. Similar plastron structures were also observed in other littoral oribatid mites (Pugh et al. 1987), as for example in Ameronothrus marinus. However, this is the first report of a selenoribatid mite using plastron respiration to withstand tidal flooding. Conspicuous granular or foveate cerotegumental layers are known to occur in the majority of Selenoribatidae (e.g. Grandjean 1968; Marshall and Pugh 2000; Karasawa and Aoki 2005; Bayartogtokh and Chatterjee 2010), therefore similar plastron mechanisms must be assumed for most members of this family.

The genus Carinozetes exhibits a certain amount of morphological variability. As shown in several depictions (e.g. Figures 1A, 12A and B), asymmetrical positions or numbers of setal pairs may occur. Schuster (1963) demonstrated the existence of similar and other variations in Thalassozetes riparius, whereas this species is far more affected by this phenomenon. However, asymmetrical variations may be more common among further selenoribatid species, but a detailed analysis would be needed to assess the degree of this variation and to find out whether this variability is inherited or based on certain ecological factors.

**Problematic points in present selenoribatid systematics**

Although the Selenoribatidae are well delimited against other families of the Ameronthroidea, the actual status of the family and certain members represents a controversial and problematic issue. First of all, in literature there is confusion about the designation of the family. Three different authors made important scientific contributions leading to the erection of the Selenoribatidae, whereas each author was so humble, that he claimed the other
responsible for the family designation. Strenzke (1961) described the first species of this group, *Selenoribates foveiventris*, but delayed the definite designation of a new family until juveniles should be found. Two years later, Schuster (1963) discovered adults and juveniles of the second species of this taxon, *Thalassozetes riparius*, and consequently several authors (e.g. Balogh 1972; Subías 2004) quoted Schuster as scientific father of the family Selenoribatidae. But Schuster (1977) revoked and clearly assigned this merit to Grandjean (1966), who indeed had given a detailed diagnosis for the Selenoribatidae for the first time, accordingly some other resources (e.g. ION, 2012) quote Grandjean, 1966 as author of the family. But Grandjean (1966) himself had explicitly attributed the family designation to Strenzke (1961) and at that point the discussion is spinning round. However, Strenzke (1961) as well as Schuster (1963) clearly stated that they refrain from giving these taxa family status until further details are known and Grandjean (1966) made the first clear and diagnostic statement about the discreteness of the Selenoribatidae. But for all that, it was Schuster (1963, p. 402) who first named the group of these taxa “Selenoribatiden” and therefore made the name available. According to articles 10, 11 and especially 11.7.1.3 of the International Code on Zoological Nomenclature, Schuster, 1963 is the author of this family.

Apart from the family designation, there is confusion about the morphological distinctness of the Selenoribatidae caused by apparently intermediate specimens that have never been described. Schuster (1963) reported some mites from the Maldives representing a new species of the Selenoribatidae. Three years later the same animals were supposed to be members of a new intertidal oribatid mite family (Grandjean 1966; Schuster 1966) and after two more years, they were thought to be the missing link between Selenoribatidae and Fortuyniidae (Grandjean 1968). A decade later, Schuster (1977) even questioned the distinctness of both families based on the intermediate morphology of these specimens and stated that Fortuyniidae and Selenoribatidae may represent a single family. But since then the discussion about the systematic status of these intertidal mites has became silent, nevertheless the undetermined animals from the Maldives still appeared in literature (Schuster 1989; Procheş and Marshall 2001). The respective specimens were originally given to Schuster by Gerlach, the collector, and Schuster handed the material on to Grandjean, who had offered to perform a detailed morphological analysis of these animals. Unfortunately Grandjean died before he could finish this work. So, the real identity of these specimens has never been revealed and the deposition of the samples is now unknown. Due to these circumstance, they will remain some kind of taxonomic ghosts, always present in the literature but out of reach. Nevertheless, apart from these mysterious specimens the families Fortuyniidae and Selenoribatidae are well distinguishable and their validity should not be questioned.

Passing from family to generic level, the genus *Schusteria* Grandjean, 1968 was subject to other misinterpretations and therefore its taxonomic identity changed inappropriately over the years. When Grandjean described the type species *S. littorea*, he gave a clear diagnosis for the genus including the characters of two undescribed species, “espèce B du Brésil” and “espèce C d’El Salvador” (Grandjean 1968, p.142). The latter two species showed two instead of three pairs of adanal setae and two pairs of anal setae instead of one. Most subsequent authors, writing about *Schusteria*, ignored this fact for unknown reasons. Balogh and Balogh (1988) listed three pairs of adanal setae and one pair of anal setae as specific characters for this genus. Luxton (1992), providing a key to Ameronothroidea of the tropics and subtropics, also gave one pair of anal setae as a characteristic trait of *Schusteria* and the same was done by Karasawa and Aoki (2005). Marshall and Pugh (2000) found two new species of this taxon, *S. melanomerus* and *S. ugraseni*, which showed two pairs of adanal and two pairs of anal setae just like the species B and C of Grandjean (1968). The authors determined their species correctly but they stated that future diagnoses must include the above mentioned characters. Of course this statement was right but at the same time it was redundant as the original diagnosis of Grandjean (1968) was already
TABLE 3: Comparison of common diagnostic morphological features of all selenoribatid genera, showing variability within taxa as well as overlapping morphologies. Variations within genera are marked bold; ? = no information available, *= according to Grandjean, 1966.

<table>
<thead>
<tr>
<th>Selenoribatid Genera</th>
<th>Arotrobates</th>
<th>Carinozetes</th>
<th>Psednobates</th>
<th>Rhizophobates</th>
<th>Schusteria</th>
<th>Selenoribates</th>
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Based on these traits.

Some of Grandjean’s (1968) other definitions simply have been misunderstood or mistaken. Karasawa and Aoki (2005) wrote that Schusteria possesses distinct interlamellar ridges whereas Grandjean (1968, p. 143) stated "Pas de carène lamellaire" as specific character, which means the absences of lamellar ridges. Unfortunately Karasawa and Aoki (2005) described in the same publication two new Schusteria species, S. nagisa and S. saxea, partly based on the above-mentioned inaccurate premise. Further, Marshall and Pugh (2000) listed an incomplete dorsosejugal suture as diagnostic trait for the genus but Grandjean (1968, p. 143) originally wrote "Ligne de grande suture complète ou partiellement effacée", expressing that the suture may be complete as well. In sum all these inconsistencies and mistakes lead to a blurry picture of the genus Schusteria and may have caused certain ambiguous taxonomic acts. Karasawa and Aoki (2005) designated the litoral genus Rhizophobates based on the type species R. shimojanai and further transferred S. ugraseni and S. melanomerus to this new taxon. These authors provided four differences separating the genera Rhizophobates and Schusteria, whereas two of the divergences, the "distinct interlamellar ridges" and one pair of anal setae specified specific for Schusteria, are based on the imprecise information mentioned above. The third difference, an obliquely or horizontally aligned adanal lyrifissure present in Rhizophobates, had already been included into the slightly broadened concept of Schusteria given by Marshall and Pugh (2000). The only de facto remaining deviation is a glabrous or sparsely granulated body surface in Rhizophobates and the designation of a new genus based on this single character would be a very risky act. Besides the question about the validity of the genus itself, the inclusion of S. melanomerus and S. ugraseni into Rhizophobates (Karasawa and Aoki 2005) was not justified as both species are well in accordance with the original Schusteria-specific characters given by Grandjean (1968). However, Subías (2004, update 2011) also doubted the distinctness of the genus Rhizophobates and synonymized it with Thalassozetes, but in doing so he unfortunately just replaced one mistake with another. The genus Thalassozetes diverges conspicuously from R. shimojanai, S. melanomerus and S. ugraseni and there is no obvious reason or explanation for such a classification. The latter two species may have been subject to an "in for a penny, in for a pound" action as they were linked to Rhizophobates since the paper of Karasawa and Aoki (2005). Nevertheless, Subías (2004, update 2011) made the taxonomic rearrangement only in the online version of his catalogue, consequently this nomenclatural act is not valid as it does not represent a published work according to the International Code on Zoological Nomenclature (Article 8).

If valid or not, the above mentioned examples show that the systematics of this group are suffering from major problems, whereas not all of these are
based on misinterpretations of literature. The family itself shows a very heterogeneous morphology, a mosaic distribution of characters so to speak, complicating the clear assignment of some taxa. Grandjean (1966) stated that the genera of the Selenoribatidae are easy to distinguish and at that time he was right, but since then numerous species have been discovered and generic diagnoses have begun to overlap more and more. For instance, the number of notogastral setae was formerly used to determine the genera Schusteria, Selenoribates and Thalassozetes (Grandjean, 1968) but nowadays this number varies within the respective taxa (Table 3) losing its value as distinctive character. The same is true for many other morphological features, e.g. position of adanal lyrifissure, number of proximoventral teeth on tarsal claw (see also Table 3) and therefore it may be necessary to redefine certain diagnoses using character combinations or including other morphological features. Concerning the latter, there is no need to search for absolutely new traits or characters that have never been looked at because some authors already proposed important diagnostic traits. Schuster (1963) and Grandjean (1966) stated that Thalassozetes is characterized by a very short and round famulus, and Grandjean (1968) listed the absence of k setae on the ovipositor as specific for Schusteria. These morphological features, neglected by most authors, are very special and therefore may be of considerable taxonomic value. Missing information does not only represent gaps in our knowledge it also deters us from estimating the variability of a character within a respective taxon and thus from assessing its real diagnostic value. Therefore every author describing new taxa should provide as much information as possible.

In summary, the systematic status of the Selenoribatidae exhibits certain inconsistencies and uncertainties for various reasons. We do not intend to change the present classification, as there is still a lot of information lacking and work to be done. Additionally, the expectable growing number of new species and taxa within this family will necessitate a revision and accommodation of certain generic diagnoses in the near future. This undertaking requires the complement of so far incomplete information, e.g. features of the legs, ovipositor, and the inclusion of yet completely missing data, as for example developmental characteristics. Further, a phylogenetic reconstruction based on morphological as well as molecular genetic data would be an important next step revealing natural relationships of the Selenoribatidae.

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