Description of a new species of *Rhombognathus* (Halacaridae, Acari), its spermiogenesis and spermatozoa

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Abstract

This is the first record of the subfamily Rhombognathinae on the Brazilian coast. A new species is described, *Rhombognathus levigatoides* sp. nov., which shares most diagnostic features with *R. levigatus* Bartsch, 2000, but differs from it by measurements of ds-1, dorsal plates, and spermatophorotype. A detailed account is provided of its spermiogenesis and sperm cell morphology. *Rhombognathus* sperm cells show features that should be regarded as probable plesiomorphies if contrasted with those found in the other two halacarid spermatozoa studied until now, *Halacarellus thomasi* and *Thalassarachna basteri*, such as the almost unmodified mitochondria, type of nuclear condensation similar to that observed in most Actinedida mites, complete acrosomal complex, and presence of a single kind of globular secretion.

Keywords: *Acari*, comparative spermatology, *Halacaridae*, *Rhombognathus*, new species, sperm cells, spermiogenesis

Introduction

The genus *Rhombognathus* comprises about 10% of all Halacaridae species, and has a world-wide distribution in marine algal beds. *Rhombognathus*, with the less diversified genera *Metarhombognathus*, *Rhombognathidés* (both restricted to North Atlantic), and *Isobactrus* belong to the algivorous subfamily Rhombognathinae.

Rhombognathines are often numerically dominant in intertidal and estuarine halacarid assemblages. They are readily recognized when sorting marine mite samples because of their dark greenish idiosomal contents and short gnathosoma. However, their position as a monophylum is poorly supported by their external morphology. In his revision on Rhombognathinae, Abé (1998) found only two synapomorphies uniting the rhombognathine genera: the dark greenish idiosomal contents (a consequence of feeding on algae) and filamentous pharyngeal apodemes. Bartsch (2003a) could not find conclusive evidence either to dismiss or to support rhombognathine monophyletism. Therefore, only the addition of new morphological and molecular data will improve our comprehension of their phylogenetic position among the halacarids.
Because of their relative phylogenetic stability through taxonomical levels higher than species category, spermatological data are a candidate for providing the requirements of character resolution needed to clarify the position of *Rhombognathus* among the Halacaridae and Rhombognathinae, as well as for contributing to the resolution of other problems concerning Halacaridae phylogeny.

Spermatozoa combine a set of characteristics that make these cells suitable for comparative studies. First, they are cells with several well-defined characters; second, sperm morphology is shaped by the reproductive biology of animals, a decisive factor in defining the evolutionary trends. Finally, as a complete series of stages of cell differentiation can often be observed in a single male, doubts on the homology of cell structures can be easily settled. Sperm cell morphology has been studied in all major groups of Acari. The sperm cells are rather diversified within mites, although all are aflagellate. Spermatological results fit well with the division of Acari into Anactinotrichida and Actinotrichida (revisions in Alberti 1991 and Alberti and Coons 1999). To date, testes and spermiogenesis have been studied in only two species of halacarids, *Thalassarachna basteri* (Johnston, 1836) and *Halacarellus thomasi* (Newell, 1984) (Alberti 1980; Alberti and Meyer-Rochow 2002). In the present work the sperm cell morphology and spermiogenesis of *Rhombognathus levigatoides* sp. nov is described along with its species description.

**Material and methods**

The specimens were collected from intertidal rocky shore algae at Baleia Beach, 23°46′S, 45°40′W; Pitangueiras Beach, 23°49′S, 45°25′W (both localities in São Sebastião, São Paulo State); Martim de Sá Beach and Island of Massaguacu, 23°38′S, 45°24′W (Caraguatatuba, São Paulo State), and Lázaro Beach, 23°30′04.5′′S, 45°08′17.2′′W (Ubatuba, São Paulo State). Intertidal algae were sorted under a stereoscopic microscope and the material obtained was fixed in 4% formalin. Mites were cleared in lactic acid and mounted in glycerin jelly (Green and Macquitty 1987). The holotype was deposited in the Museu de Zoológia of the University of São Paulo (MZUSP). Drawings were made with the aid of a camera lucida.

Abbreviations used in the description: AD, anterior dorsal plate; AE, anterior epimeral plate; ds, dorsal setae, from anterior to posterior: ds-1 to ds-5; ER, endoplasmatic reticulum; GA, genitoanal plate; GO, genital opening; gp, gland pores; OC, ocular plate; PD, posterior dorsal plate; PE, posterior epimeral plate; RER, rough endoplasmatic reticulum; legs numbered I–IV and the segments, in distal to proximal, named: tarsus, tibia, genu, tefofemur, basifemur, and trochanter; palpal segments in same order numbered P4–P1; VS, ventral shield; ω, solenidion; ε, famulus.

Chaetotaxy formula was given without solenidia and parambulaclral setae, from trochanter to tarsus. The position of certain structures was described according to Newell (1984), using the decimal system.

For transmission electron microscopy, males belonging to *Rhombognathus levigatoides* sp. nov. were collected from intertidal algae at Pitangueiras Beach. The gnathosoma was pulled out and legs extracted from living mites with a fine entomological needle in ice-cold fixative (2.5% glutaraldehyde buffered to pH 7.2 in 0.1 M cacodylate buffer). Following 2 h in cold fixative, the mites were rinsed in buffer solution and postfixed in 2% OsO4 for 2 h, rinsed again with buffer solution, immersed in uranyl acetate for 12 h and dehydrated in a graded series of ethanol. Material was embedded in Spurr’s resin with propyleneoxide as intermedium. Polymerization took 12 h at a temperature of 70°C.
Semi-thin sections were stained with toluidine-blue and observed under light microscope in order to allow general orientation. Ultra-thin sections through selected regions were obtained with the aid of a Leica Ultracut R ultramicrotome, stained with lead citrate and observed under a MET LEO 906E Zeiss transmission electron microscope.

**Systematic account**

**RHOMBOGNATHINAE** Viets, 1927

Idiosoma dark green or black. Ocular plates with one or two corneae. Short palps, three- or four-segmented, attached laterally and compressed laterally against gnathosoma. Both tritorostral and basirostral setae on rostrum. Carpite present between end of tarsus and central sclerite.

**Genus Rhombognathus** Trouessart, 1888

Dorsal plates well-developed, sometimes fused. Ocular plates with two setae and two corneae. Posterior dorsal plates with one or two pairs of setae. Adanal setae on anal plate. Ventral plates often fused. Epimeral plates often with adjunct setae. Adults with two, rarely one pair of subgenital setae. Palp four-segmented, P2 with single dorsal setae, P3 without setae, and P4 with three setae. Tarsus I with dorsolateral solenidion and famulus. Tarsus II with a dorsolateral solenidion. Males with plumose parambularal setae on tarsus IV. All tarsi with lateral claws only and without ventral setae. Two or three nymphal stages. If only two nymphal stages present, they are proto- and tritonymph.

**Rhombognathus levigatoides** sp. nov.

(Figures 1–8)

**Material examined**

Holotype: female (MZUSP), on intertidal algae at Massaguacu Island, Caraguatatuba, 16 March 2001, coll. BIOTA/FAPESP. Paratypes: three females (Author’s collection), on intertidal algae at Massaguacu Island, Caraguatatuba, 16 March 2001, coll. BIOTA/FAPESP; 12 females (Author’s collection), on intertidal algae at Massaguacu Island, Caraguatatuba, 16 March 2001, coll. BIOTA/FAPESP; three males (MZUSP) on intertidal algae at Massaguacu Island, Caraguatatuba, 16 March 2001, coll. BIOTA/FAPESP; 14 males (Author’s collection), on intertidal algae at Massaguacu Island, Caraguatatuba, 16 March 2001, coll. BIOTA/FAPESP; three tritonymphs (MZUSP) on intertidal algae at Massaguacu Island, Caraguatatuba, 16 March 2001, coll. BIOTA/FAPESP; six tritonymphs (Author’s collection), on intertidal algae at Massaguacu Island, Caraguatatuba, 16 March 2001, coll. BIOTA/FAPESP; female (Author’s collection), on intertidal rock shore at Martim de Sá Beach, Caraguatatuba, 19 September 2001, coll. BIOTA/FAPESP; female (Author’s collection), on intertidal rocky shore at Baleia Beach, São Sebastião, 16 October 2001, coll. BIOTA/FAPESP; tritonymph (Author’s collection), on *Sargassum cymosum* C. Agardh, 1820 at Lázaro Beach, Ubatuba, July 1991, coll. R. Curvelo; female (Author’s collection), on *Sargassum cymosum* C. Agardh, 1820 at Lázaro Beach, Ubatuba, July 1991, coll. R. Curvelo.

**Description**

Measurements as shown in Table I.
Female. Dorsal plates almost smooth, lateral portions of PD, medial AD and OC pierced by canaliculi (Figure 1A). Medial PD slightly reticulated as shown in Figure 1B. Anterior dorsal plates with ds-1 at 0.45–0.56 of AD length, such setae 23–25 μm long. First pair of gland pores at same level as leg I insertion. Posterior line of muscle scars at 0.79–0.84 of AD overall length. Pairs of ds-2, ds-3, gp-2 and gp-3 on OC, which also bears a couple of corneae and a pore canaliculus. Length/height ratio of OC 1.80–2.34. Posterior dorsal plate with only pair of ds-4 at 0.11–0.18 of its length, and pair of gp-4 at its posterior margin. Anterior dorsal plate 1.00–1.18 as broad as PD. Adanal setae dorsal on anal papilla.

Gnathosoma short, length: width ratio equal to 1.00–1.23. Rostrum 26–30 μm long, 15–18 μm wide, shorter than gnathosoma basis and as long as 0.36–0.41 times gnathosoma length.

Ventral plates AE, PE, and GA fused in a ventral shield, apart from anal plate by a band of membranous cuticle. Both AE and PE with single pair of adjunct setae. Genital area with five pairs of perigenital setae. Genital sclerites with two pairs of subgenital setae. Ovipositor 57–61 μm long, with three pairs of posterior and two pairs of anterior eugenital setae (only three individuals with everted ovipositor). Eugenital setae are strong dorsally pectinate spines (Figure 1E).

Figure 1. Rhombognathus levigatoides sp. nov. (A) Idiosoma, dorsal; (B) ornamentation at medial portion of PD; (C) genital opening; (D) idiosoma, ventral; (E) ovipositor; (F) gnathosoma, medial; (G) gnathosoma, ventral. (A, B, D–G) Female; (C) male. Scale bars: 50 μm (A, D); 25 μm (B, C, E–G).
Leg chaetotaxy, bipectinate setae referred with roman numerals: leg I, 1,2,7,5,5(II),3; leg II, 1,2,7,5,5(I),3; leg III, 1,2,4,3,5(I),4; leg IV, 0,2,4,3,5(II),3. Telofemora I–IV with 5/2, 5/2, 3/1, and 3/1 dorsal/ventral setae; length: height ratio of telofemora I–IV: 1.94–2.17; 1.90–2.36; 1.88–2.39; 1.77–2.29. Tarsus I with papiliform famulus, setiform solenidion and pair of doublet eupathidia (Figure 2B). Tarsus II with a setiform solenidion and a pair of doubled eupathidia (Figure 2H). Tarsus III with a single eupathid and a faintly pectinated spine. Tarsus IV with double slender setae and spine similar to that on tarsus III. Lateral claws well-developed, medial one lacking. Dorsal accessory process pectinate, with five to seven teeth.

**Male.** Similar to female in most features. Anterior: posterior dorsal plates width ratio 1.00–1.21. Posterior line of muscle scars on AD at 0.74–0.79 of its length. Genital area with 18–23 branched perigenital setae (Figure 1C). Genital sclerites with two pairs of subgenital setae. Spermatophorotype 40–49 μm long, 35–50 μm wide, surpassing anterior edge of GO by 16–22 μm. Tarsus IV with a plumose setae and a spine as parambulacral setae.

**Tritonymph.** Dorsal plates reduced, ventral plates AE, PE, and GP separated from each other by bands of striated cuticle. Chaetotaxy of epimal plates similar to adults, although
adjunct seta is lacking asymmetrically in some individuals. On genital plate, three pairs of setae, the medial one tiny and close to the primordial genital opening.

Leg chaetotaxy, bipectinate setae as Roman numerals: leg I, 1,2,6,5,5(II),3; leg II, 1,2,6,5,5(I),3; leg III, 1,2,4,3,5(I),4; leg IV, 0,2,2,3,5(II),3. Telofemora I–IV with 4/2, 4/2, 3/1, and 2/0 dorsal/ventral setae.

Remarks

*Rhombognathus levigatoides* sp. nov. shares with *R. levigatus* Bartsch, 2000 all diagnostic traits presented in the original description of the latter species: dorsal plates faintly
ornamented; PD with a single pair of dorsal setae; AE, PE, and GP fused in a ventral shield; only an adjunct setae on AE and PE; female with five pairs of perigenital setae; male with 10–12 pairs of branched perigenital setae; gnathosoma short; telofemora I–IV with 5/2, 5/2, 3/1, 3/1 dorsal/ventral setae; accessory process with five to six teeth in *R. levigatus* and five to seven in the species described herewith. *Rhombognathus levigatus* was described from the Great Barrier Reef, Queensland, and the Dampier Archipelago, Western Australia (Bartsch 2000, 2003b).

Figure 4. Two early stages of spermiogenesis. (A) First stage with batches of heterochromatin, and dense cytoplasm; (B) second stage without heterochromatin, picture shows single crest mitochondria (arrow) and Golgi body [G]; (C) second spermatid stage. Scale bars: 1 μm (A, C); 0.5 μm (B).
However, the Brazilian specimens differ from the Australian species in some measurements, allowing us to consider it to be a new species. Whereas ds-1 is 12 μm in the holotype of *R. levigatus*, it is 19–25 μm long in males and 23–25 μm long in females of *Rhombognathus levigatoides* sp. nov.; AD: PD width ratio is 0.85 in *R. levigatus* and 1.00–1.21 in the new species described here; and, finally, in the Brazilian species the spermatophorotype is 40–49 μm long whereas in *R. levigatus* it measures 60 μm.

Figure 5. (A) Intermediate spermatids: note the plasmalemmal infoldings; (B) spermatids with heterochromatin almost fully condensed: note mitochondria [M] of the somatic tissue between spermatids, acrosomal vesicles [AV] and thick and linear acrosomal filament [AF]; (C) mature sperm cells within cytoplasm of the somatic cells of germinative portion of testis. Scale bars: 1 μm.
Sperm cells, spermatogenesis, and accompanying secretions

Testis

The testis, similarly to other Actinotrichida and Solifugae (Alberti and Peretti 2002), consist of a dorsal germinative portion with spermatids and a ventral glandular, RER-rich portion (Figure 6A, B). Between them, a lumen contains mature spermatozoa and accompanying secretions. Spermatids are roughly ordered from earlier to later stages from dorsal to ventral regions of the germinative portion.

Figure 6. (A) Lumen of testis. Mature sperm cells are surrounded by somatic tissue and are delivered in testis lumen [Lu]. Then spermatozoa are coated with secreted material produced in the glandular portion: note microvilli and dense apico-lateral cell borders indicative of zonulae adherens among cells; (B) detail of a cell from the secretory portion of testis. N, nucleus. Scale bars: 1 μm.

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(1) Earliest spermatids have large nuclei containing patches of heterochromatin (Figure 4A). Cytoplasm is electron-dense, with scattered mitochondria. Plasmalemma is folded at one side of the spermatids. Similar to all later stages, mitochondria are small, most of them with a single medial crest. In the following stage (Figure 4B, C), heterochromatin has disappeared. Besides mitochondria, ribosome, and ER, a Golgi body can be found midway between the nucleus and the cell membrane (Figure 4B). No centrioles were found.

(2) Nuclear condensation is of the fibrillar type. At the beginning of nuclear condensation, the cell membrane folds deeply and approaches the nuclear membrane. Infolds are not evenly distributed, but restricted to one half of the spermatid. The acrosomal complex is complete, including a flattened vesicle and a thick acrosomal filament (Figure 5A, B).

(3) Sperm cell maturation is completed at the ventral portion of the germinal part, close to the testicular lumen (Figure 6A). As a final step in spermiogenesis, cytoplasm of later spermatids undergoes an intense condensation. Mature spermatozoa are cells with irregular shape prior to inclusion in their individual coats of secretions. Dissimilar to all earlier stages, cells are separated from each other by broad spaces filled with somatic cell cytoplasm (Figure 5C). When enclosed by their coats of secretion, sperm cells assume a globular shape. After condensation, membrane pleats become a “striated body” on the side opposite to the acrosomal complex (Figure 7B).

(4) Accompanying secretions originate from the glandular portion of testis, where microvilli-rich areas could be observed (Figure 6A, B). Three kinds of secretions were found: a thick individual coat surrounding each sperm cell; globular bodies of
Figure 8. (A) Vas deferens; (B) ductus ejaculatorius, the wall is composed by a thin epithelium associated with muscle fibers (arrows): note amorphous secretion on the left side of the picture and spermatozoa surrounded by globular bodies of secretion; (C) light micrograph of a cross-section through a male *Rhombognathus*: note general aspect of prospective spermatophore, with a secreted center upon which the sperm is laid. MG, excretory portion of midgut; N, nucleus of epithelial cell. Scale bars: 2 μm (A); 1 μm (B); 25 μm (C).

Table I. Measurements (in μm) from individuals of *Rhombognathus levigatoides* sp. nov.

|            | Female Length | Female Width | Male Length | Male Width | Tritonymph Length | Tritonymph Width |
|------------|---------------|--------------|-------------|------------|------------------|------------------|
| Idiosoma   | 273–288       | 183–193      | 243–263     | 150–178    | 228–265          | 140–170          |
| Gnathosoma | 70–74         | 71–60        | 64–69       | 50–61      | 56–60            | 45–51            |
| AD         | 82–97         | 93–98        | 83–94       | 80–91      | 63–79            | 62–80            |
| PD         | 118–125       | 82–95        | 108–127     | 77–85      | 80–90            | 56–69            |
| OC         | 65–75         | 31–37        | 61–72       | 34–44      | 47–60            | 20–27            |
| VS         | 198–233       | 183–195      | 180–200     | 150–178    | –                | –                |
| AE         | –             | –            | –           | –          | 59–70            | 143–123          |
| GA         | –             | –            | –           | –          | 35–41            | 31–40            |
| GO         | 56–62         | 22–31        | 32–35       | 17–25      | –                | –                |
secretion filling interstices between them, and an amorphous material. The sperm cells were also found inside the vas deferens (Figure 8A) and ductus ejaculatorius (Figure 8B, C), both thin-walled ducts consisting of a single-layered epithelium. The latter also had associated muscle fibres (Figure 8B). Inside it, the above-mentioned amorphous secretion constitutes a core, and sperm cells and secretion bodies are deposited around it (Figure 8A–C).

Discussion

Spermiogenesis and sperm cell morphology have been described for only two species of Halacaridae mites, Thalassarachna basteri (Johnston, 1836) and Halacarellus thomasi (Newell, 1984) (Alberti 1980; Alberti and Meyer-Rochow 2002). Using the out-group criterion, and considering current knowledge on Actinotrichida spermatology, the sperm cells, accompanying secretions, and spermiogenesis described above have several traits that should be regarded as plesiomorphies, suggesting that Rhombognathus belongs to an early branch of the Halacaridae stem.

The nuclear condensation process in both T. basteri and H. thomasi begins close to the nuclear envelope and progresses centripetally. The pattern found in Rhombognathus is similar to that found in most Actinotrichida (Alberti 1980).

Surface modifications have been reported in several other Actinotrichida mites and were regarded by Alberti (1991) as a characteristic feature of this taxon. Membrane infoldings in Rhombognathus are similar to those found in Cyta latirostris (Herrmann, 1804) and Tetranychus urticae Koch, 1836, and resemble simple pleats of plasmalemma. In Halacarellus thomasi, the periphery of the spermatozoa has thin centripetally pointing tubes that resemble those pleats. However, both Halacarellus and Thalassarachna species have electrodense tubules crossing the cytoplasm. These tubes and the ring-like infolding dividing the cell into two distinct halves in T. basteri are different structures. Indeed, there is the possibility that these structures appear inside the cytoplasm, arising from vesicular structures of spermatid cytoplasm and fuse with the cell membrane later (Alberti and Meyer-Rochow 2002). Therefore, the infoldings of Rhombognathus spermatozoa are probably plesiomorphic, while the presence of electrodense tubules and ring-like infolds in Thalassarachna should be regarded as apomorphies.

The presence of a complete acrosomal complex and mitochondria are undoubtedly plesiomorphic traits. Halacarellus thomasi contains a structure that remotely resembles an acrosomal vesicle, although the actual nature of this remains to be established. The more striking difference between Rhombognathus and the other two Halacaridae species is the division of the sperm cells into two halves (Alberti and Meyer-Rochow 2002). Although pleats of plasmalemma arise only on one side of the early spermatid membrane, these do not become a clearly distinct portion in the mature spermatozoa. The other known halacarid mature sperm cells lack mitochondria.

Both Halacarellus and Thalassarachna species have the spindle-shaped secretion termed “complex body” by Alberti and Meyer-Rochow (2002), besides globular electro translucid-bodies of secretion. A rather structured secretion, which shelters the sperm aggregates, could be recognized beside an amorphous secretion. This structured secretion is lacking in Rhombognathus levigatoides sp. nov. Bodies of secretion in Rhombognathus belong to a single class, all globular and with granulose aspect. There are no sperm aggregates, and the core of the “sperm droplet” is amorphous.
The spindle-shaped bodies of secretion are a possible apomorphy of a subset among Halacaridae since no equivalent material has been found among sperm aggregates in other Acari. Regarding the presence of sperm aggregates, however, out-group comparison does not allow an unambiguous conclusion: other Actinotrichida present both conditions.

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