International Journal of Acarology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/taca20

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To cite this article: Tobias Pfingstl, Shimpei F. Hiruta, Iris Bardel-Kahr, Yuito Obae & Satoshi Shimano (2022) Another mite species discovered via social media - *Ameronothrus retweet* sp. nov. (Acari, Oribatida) from Japanese coasts, exhibiting an interesting sexual dimorphism, International Journal of Acarology, 48:4-5, 348-358, DOI: 10.1080/01647954.2022.2074538

To link to this article: https://doi.org/10.1080/01647954.2022.2074538

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INTERNATIONAL JOURNAL OF ACAROLOGY
2022, VOL. 48, NOS. 4–5, 348–358
https://doi.org/10.1080/01647954.2022.2074538

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Another mite species discovered via social media - *Ameronothrus retweet* sp. nov. (Acari, Oribatida) from Japanese coasts, exhibiting an interesting sexual dimorphism

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ABSTRACT
The recent discovery of the oribatid mite *Ameronothrus twitter* via a social media platform resulted in a considerable media response and raised the awareness of the public for these tiny organisms. As a direct consequence, another new marine associated ameronothroid species was now discovered via the same social media service. Moreover, the record of this new species, *Ameronothrus retweet* sp. n., represents the first report of an ameronothroid taxon from the Sea of Japan coast, indicating that this coastline was successfully colonized by these organisms and that further species could be present there. *Ameronothrus retweet* sp. n. shows an extraordinary sexual dimorphism with females having relatively shorter legs and a strongly folded notogastral integument. Based on morphological characteristics, it is suggested that the new species is closest related to *Ameronothrus lineatus* and *Ameronothrus nigrofemoratus*. A molecular genetic investigation of selected ameronothroid taxa, using the *18S* rRNA gene, shows that all *Ameronothrus* species are closely related and represent a distinct monophyletic genus. In a larger phylogenetic context, the Fortuyniidae and Selenoribatidae are given as sister taxa with a monophyletic origin, whereas certain members of Ameronothridae are placed in paraphyletic positions, supporting theories of an independent origin of the marine associated lifestyle in ameronothroid mites.

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ARTICLE HISTORY
Received 18 March 2022
Accepted 21 April 2022
Published online 20 May 2022

KEYWORDS
Littoral; Honshu island; cool temperate zone; Ameronothridae; Twitter

Introduction

Marine-associated oribatid mites are adapted to live in the littoral environment. They may occur from the intertidal zone to supralittoral areas far above the tidal regime and are known to feed on algae, fungi, or lichen (Schulte 1976; Pfingstl 2017). Most of these mites belong to the superfamily of Ameronothroidea, which include four marine associated families, the Ameronothridae, Fortuyniidae, Podacaridae, and Selenoribatidae. Their distribution strongly correlates with climate, the Ameronothridae are confined to northern hemispheric polar and cold temperate regions, the Fortuyniidae and Selenoribatidae are restricted to the tropics and subtropics, and the Podacaridae occurs only on southern hemispheric polar and cold temperate coasts (e.g. Pfingstl 2017). The phylogenetic relationships among these families are a controversial issue. Several authors claim the Podacaridae to be Ameronothridae and do not challenge the monophyly of the superfamily (Schulte 1975; Weigmann and Schulte 1977). Others (Procheş 2001; Pfingstl 2017) suggest that the Ameronothroidea represent a paraphyletic taxon, as they may have evolved their littoral lifestyle independently in three distinct latitudinal bands with the Ameronothridae in the northern cold-temperate, the Fortuyniidae and Selenoribatidae in the tropical, and the Podacaridae in the southern cold-temperate region.

Apart from this controversy, the northern hemispheric Ameronothridae are an unproblematic taxon because they only consist of the genus *Ameronothrus*, which presently contains 14 valid species. In the Asian Pacific region, only four known species were reported so far (Pfingstl et al. 2019a), *Ameronothrus nidicola* Sitnikova, 1977 and *Ameronothrus oblongus* Sitnikova, 1977 from the Russian Far East coast of Kamchatka, the Kuril and Sakhalin Islands (Sitnikova 1977; Klimov 1998; Ryabinin 2015), and *Ameronothrus yoichi* Pfingstl & Shimano, 2019 and *Ameronothrus twitter* Pfingstl & Shimano, 2021 from Japanese coasts of Hokkaido and Honshu, respectively (Pfingstl et al. 2022).

Generally, these mites are only of interest for a small part of the scientific community, but the unusual discovery of *A. twitter* via a social network platform resulted in a large media response with international news raising the awareness of the public for these tiny inconspicuous animals. When a user (herein included as co-author, YO, see supplementary material) of this social networking site saw the news about *A. twitter*, he noticed that a mite he had previously photographed strongly resembled *A. twitter*, and immediately posted a photo of the animals with the message “Is this mite *A. twitter*?” As the photographs were taken on the Sea of Japan coast, where no *Ameronothrus* records existed before, the interest of one of the authors (SS) was immediately caught and subsequent sampling (by YO) and investigations verified the report and moreover revealed again an unknown species that even shows a remarkable sexual dimorphism.

The aim of the present paper is to describe this species and its dimorphism in detail, provide first molecular genetic data of this species, and assess its position in a larger phylogenetic context.

Material and methods

Mite specimens were collected by removing them with tweezers from depressions in the surface of the littoral rock. Afterwards, collected specimens were stored in ethanol (99.5%) for morphological and molecular genetic investigation.

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/01647954.2022.2074538

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Published online 19 May 2022

Sample location

Japan, Honshu, Tottori prefecture, Tottori City; Fukube, Iwado, Iwado Rock Beach; 31 March 2021, leg. OBAE Yuito.

Drawings and photographs

Preserved animals were embedded in Berlese mountant for microscopic investigation in transmitted light. Drawings were made with an Olympus BH-2 Microscope equipped with a drawing attachment. These drawings were first scanned, then processed, and digitized with the free and open-source vector graphics editor Inkscape (https://inkscape.org).

For photographic documentation, specimens were air-dried and photographed with a Keyence VHX-5000 digital microscope using automated image stacking.

Morphological terminology used in this paper follows that of Grandjean (1953), Schubart (1975) and Norton and Behan-Pelletier (2009).

Molecular genetic analyses

Five specimens of *Ameronothrus retweet* sp. n. were used for genetic analysis. For that purpose, whole genomic DNA was extracted and two gene fragments were amplified and sequenced: region 2 of the mitochondrial cytochrome c oxidase subunit 1 (*COI*-2) and the nuclear *18S* rRNA gene (*18S*) – whole specimens were crushed in microcentrifuge tubes which contained 50 µL Chelex solution and 1.7 µL Proteinase K. Region 2 of *COI* (around 590 bp) was amplified using the primers Mite *COI*-2F and Mite *COI*-2R (Otto and Wilson 2001) with a two-step PCR. Reaction volume was 10.5 µL, containing 1 µL 10x reaction buffer, 1 µL of each primer (10 mM), 1 µL dNTP mix (10 mM), 0.75 µL $MgCl_2$ (25 mM), 0.05 µL of Taq polymerase (5 units μl^{-1}, BioThermRed), 3.5 µL deionized water, and 2 µL of DNA template. The program consists of a denaturation step at 94°C for 5 min, followed by 18 cycles of the first step (denaturation for 30 sec at 94°C, annealing for 30 sec at 47°C, extension for 1 min at 72°C), then 22 cycles of the second step (denaturation for 30 sec at 94°C, annealing for 30 sec at 50°C, extension for 1 min at 72°C), ending with a final extension step at 72°C for 7 min. The complete *18S* gene (~ 1.8 kbp) was amplified in overlapping fragments using the primer pairs *18S*fw/rev960 (I) and fw390/*18S*rev (II) (Dabert et al. 2010) in reaction volumes of 10.5 µL (same composition as *COI*-2). PCR conditions were 94°C for 5 min, then 45 cycles of denaturation (94°C, 30 s), annealing (46.5°C, 30 s), extension (72°C, 1 min), followed by a final extension step at 72°C for 7 min. Subsequent DNA purification steps included enzymatic ExoSAPIT (Affymetrix) and Sephadex G-50 resin (GE Healthcare). Cycle sequencing, using BigDye Sequence Terminator v3.1 kit (Applied Biosystems) was conducted in 10 µL reaction volume according to the protocol by ThermoFisher. The conditions in the thermocycler were 3 min at 94°C, followed by 35 cycles of denaturation (94°C, 30 sec), annealing (50°C, 30 sec), extension (60°C, 4 min), with a final extension step of 60°C for 7 min. For *COI*-2, the aforementioned primers were used. For the *18S* gene the primers rev480, fw390 (I), fw770, and fw1230 (II) (Dabert et al. 2010) were used. Automatic capillary sequencing and sequence visualization were operated on an ABI3500XL (Applied Biosystems) device. Additional *18S* sequences were produced from one *Ameronothrus twitter* specimen, two *Ameronothrus maculatus* specimens, one from Germany and the other from Portugal, and one *Halozetes capensis* individual, using the same protocol.

Phylogenetic analyses

The final *18S* alignment comprised four *Ameronothrus retweet* sp. n. *18S* sequences, as well as one *18S* sequence of *A. twitter, A. maculatus* (from Germany and Portugal), and *H. capensis*, respectively. For the phylogenetic analyses, we combined the generated sequences with 20 other *18S* Ameronothroidea sequences taken from GenBank (for details see Table 3) in one alignment. *Crotonia reticulata* and *Malaconothrus monodactylus* were used as outgroup.

All phylogenetic analyses were performed in PhyloSuite v1.2.2 (Zhang et al. 2020). First, the alignment was performed by MAFFT (Katoh and Standley 2013), using auto strategy and normal alignment mode. The alignment was then loaded into ModelFinder (Kalyaanamoorthy et al. 2017) to select the best-fit model using Akaike Information Criterion (AIC). For maximum likelihood (ML), the best-fit model was TIM2 + F+ R2, for Bayesian inference (BI), it was GTR +F + I+ G4.

ML trees were constructed using IQ-TREE (Nguyen et al. 2015), under the aforementioned model, for 5000 ultrafast (Minh et al. 2013) bootstraps, as well as the Shimodaira-Hasegawa-like approximate likelihood-ratio test (Guindon et al. 2010). BI phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al. 2012) under the best-fit model in 2 parallel runs, each with four chains and two million generations. The sample frequency was set to 100, and the initial 25% of sampled data were discarded as burn-in.

Results

Description of new taxa

Family Ameronothridae Vitzthum, 1942
Genus *Ameronothrus* Berlese, 1896
Type species – *Eremaeus lineatus* Thorell, 1871
Ameronothrus retweet Pfingstl and Shimano sp. nov.
[New Japanese name: Iwado-hamabe-dani]

Type material/locality

Holotype: adult female (length 844 µm, width 444 µm); allotype: adult male (length 641 µm, width 363 µm), Japan, Honshu, Tottori prefecture, Tottori City; Fukube, Iwado, Iwado Rock Beach; 31 March 2021, leg. OBAE Yuito. Preserved in ethanol and deposited at the Collection of Arachnida, Department of Zoology, National Museum of Nature and Science, Tokyo (NMST). Four paratypes (2 males, 2 females) from the same sample deposited in the collections of the Senckenberg Museum für Naturkunde Görlitz (SMNG).

Etymology

The specific name '*retweet*' is given as noun in apposition. "Retweet" is used as both a verb and noun on the social media application Twitter (twitter Inc.) and means repost or forward a message. The present work does not represent a direct act of retweeting in a strict sense, but the species was discovered by a post as a response to the message about the discovery of *A. twitter*.

Differential diagnosis

The colour is dark brown, nearly black. Body length is 641–859 µm. In centrodorsal notogastral cuticle with dense granulation, lateral parts are covered with larger granules. Prodorsal lamellar keels are converging. Short clavate sensilli are present. Interlamellar and exobothridial setae are absent. Labiogenal articulation is complete. One pair of adanal setae located posteriorly of anal orifice. Remarkable sexual dimorphism is present, females with strongly folded gastronotic integument and considerably shorter epimeral, genital, and aggenital setae. Male spermatopositor conspicuously elongated, female ovipositor very short. Primilateral setae *pl* on tarsus I are present. Dorsal companion seta *d* on genu I, II, and III and all tibiae are present. Tarsal distal setae end with a small nodule. Juveniles is unknown.

Description

Measurements. Females (N = 4), length: 813–859 µm (mean 844 µm) and width: 444–475 µm (mean 456 µm); males (N = 10), length: 641–719 µm (mean 698 µm) and width: 363–413 µm (mean 390 µm).

Integument. Cuticle was thin and easily deformable. Cerotegument shows overall dense granulation. The colour is dark brown, almost black in stereomicroscope.

Prodorsum (Figures 1(a,c)). Rostrum is rounded in dorsal view, demarcated from remainder of prodorsum by faint transverse caudally arched ridge *ct*. Pair of converging lamellar keels (*cl*), reaches slightly beyond insertion of lamellar seta (*le*). Area between lamellar keels shows several irregular smaller ridges. Rostral seta (*ro*) spiniform is long and smooth (52–63 µm). Lamellar seta (*le*) is short, thickened, blunt and smooth (approx. 16 µm). Interlamellar seta (*in*) and exobothridial seta (*ex*) are absent. Bothridium is cup-like, orifice wide, and circular. Sensillum (*ss*) is short (approx. 25 µm), strongly clavate, globular head (diameter ca. 17 µm) (Figures 2).

Gnathosoma. Palp pentamerous 0-2-1-3-9 (solenidion not included), trochanter very short, femur by far longest segment, genu, tibia, and tarsus of almost equal length (Figure 3(a)). Solenidion *ω* on palptarsus is loosely associated with eupathidium *acm*, tips close to each other. Atelebasic rutellum: Distal part with wide and darker sclerotized external tooth followed by a smaller dark sclerotized tooth merging into a series of three lobe-like projections forming an undulating membranous edge (Figure 3(b)). Setae *a* (approx. 30µm) and *m* (approx. 23µm) is spiniform, robust, and smooth. Mentum regular, seta *h* is long, setiform, robust (approx. 46µm). Labiogenal articulation is complete. Chelicera chelate, mobile digit darker sclerotized; distinct strong interlocking teeth. Träghårdhs organ (*tg*) has slender blunt lamella, slightly upward orientated. Seta *cha*

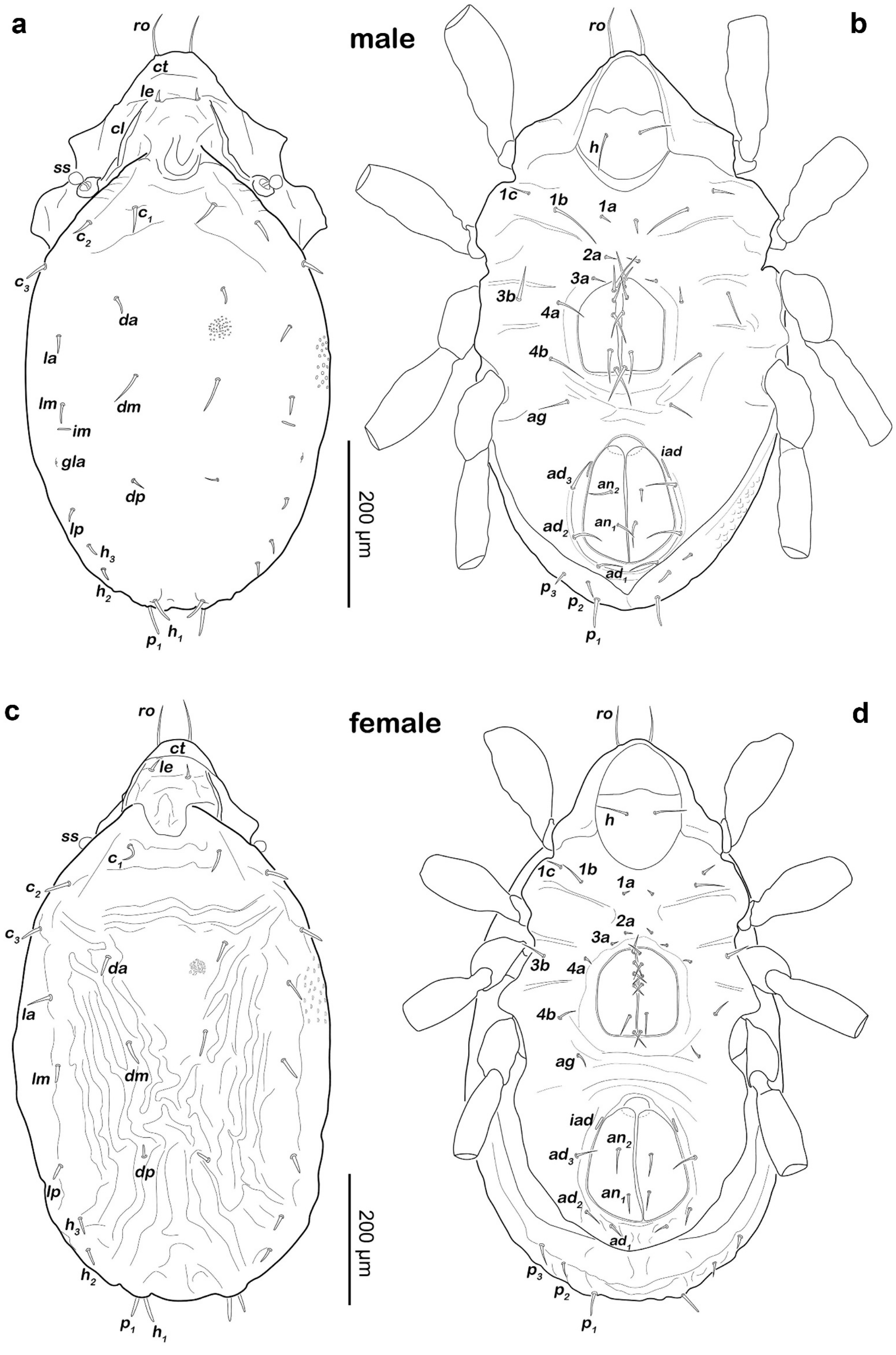

Figure 1. *Ameronothrus retweet* sp. n. adults. (a) Male, dorsal view, legs omitted. (b) Male, ventral view, distal leg segments and gnathosoma omitted. (c) Female, dorsal view, legs omitted. (d) Female, ventral view, distal leg segments and gnathosoma omitted.

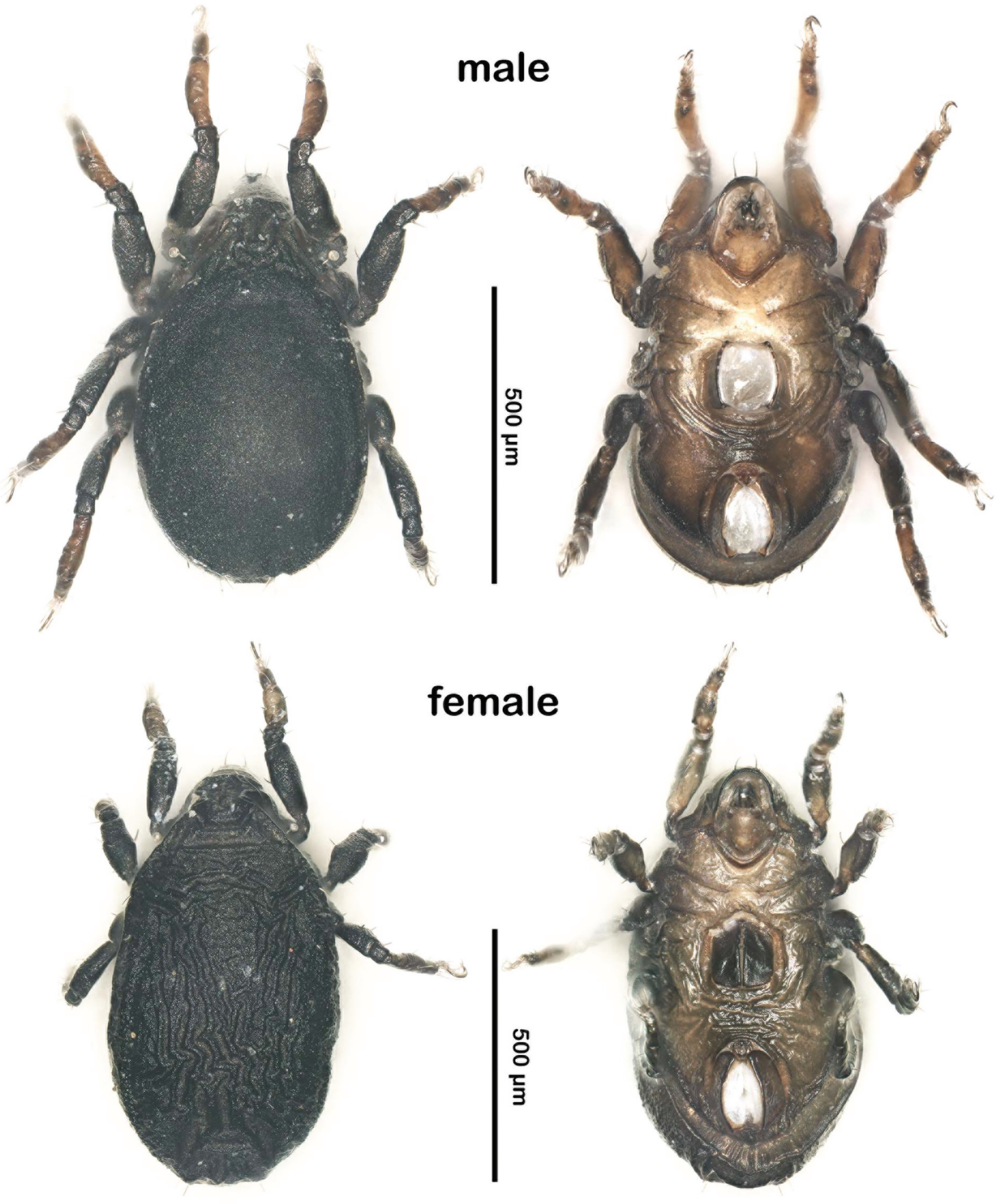

Figure 2. Photographs of male (upper row) and female (lower row) *Ameronothrus retweet* sp. n. specimens in dorsal (left side) and ventral view (right side).

and *chb* is robust and barbed, approximately the same length (59–63 µm) (Figure 3(c)). Large porous area is present on chelicera.

***Gastronotic region* (Figures 1(a, c)).** Oval and slender in dorsal view, slightly convex in lateral view; no distinct border between anterior median notogastral and prodorsal region, instead large U-shaped fold extending from posterior prodorsal area into anterior gastronotic region. Centrodorsal area with dense and fine granulation, lateral and posterior edges with conspicuously larger granulation. Fifteen pairs of slightly thickened and blunt notogastral setae (15–30µm), c_{1-3}, *da, dm, dp, la, lm, lp,* h_{1-3},p_{1-3}; seta *dp* shortest and setae p_1 and h_1 longest.

Dimorphic characters: Males with domed even dorsal gastronotic plate show a weak arch-like deepening in the anterior part (best seen on Figure 2). Five pairs of notogastral lyrifissures are present but difficult to trace due to rough cuticular surface; *ia* between seta c_2 and c_3, but closer to the latter; *im* between seta *lm* and *lp; 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*) is posterior to lyrifissure *im*. Females with strongly folded gastronotic plate (especially in the centrodorsal area) are largely overhanging in humeral areas so that bothridia are more or less completely covered in dorsal view. Strong folding of integument lyrifissures and orifice of opisthonotal gland is not traceable in females.

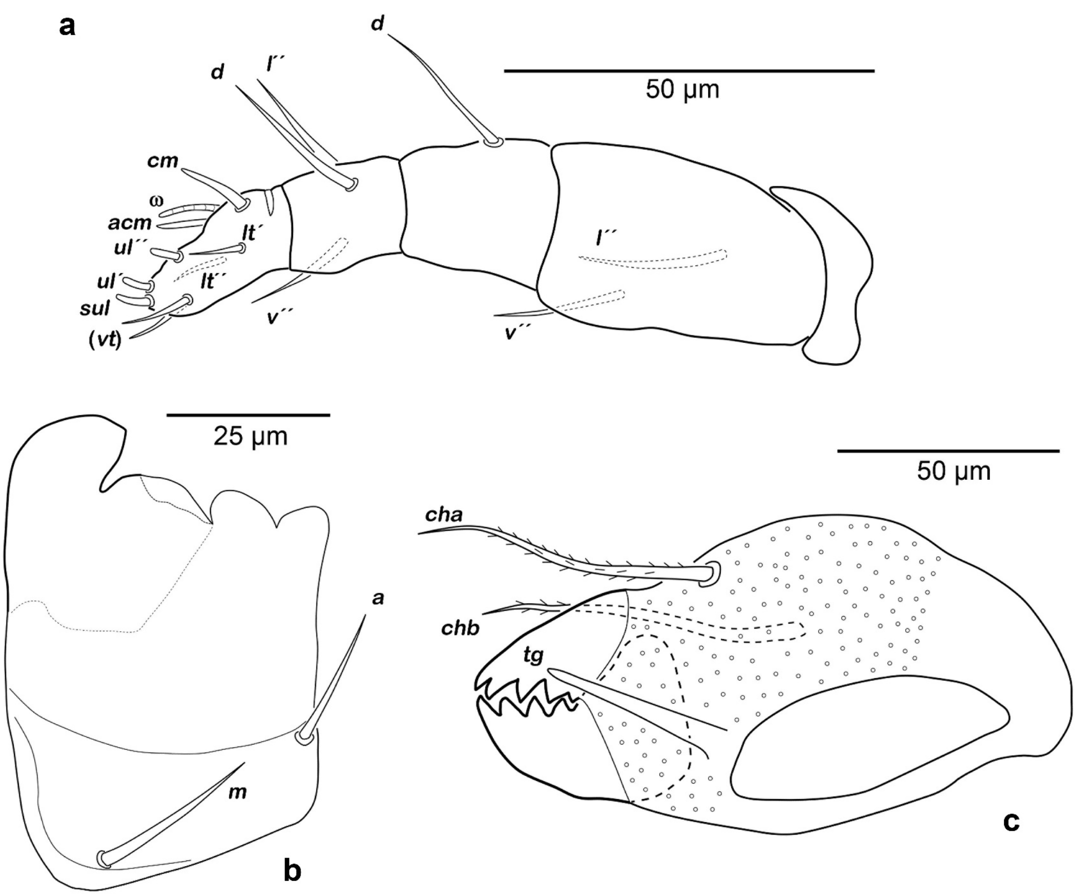

Figure 3. *Ameronothrus retweet* sp. n. mouthparts. (a) Right pedipalp, paraxial view. (b) Right rutellum ventral view. (c) Right chelicera, paraxial view.

Lateral aspect. Pedotectum I and II are absent. Discidium between acetabulum III and IV is developed as rounded ridge.

***Podosoma and venter* (Figures 1(b), 2(b)).** Epimeral setation 3-1-2-2, all setae are setiform and smooth, seta *1b* is conspicuously longer than others. Genital orifice is large, rectangular, anterior edges more rounded. Six pairs of spiniform genital setae arranged in longitudinal rows, first and last pair longest. One pair of setiform aggenital setae *ag*. Anal valves triangular but strongly rounded. Outer part of preanal organ is rectangular with rounded edges, inner part is shaped like a transverse bar. Two pairs of anal setae, $an_{1\text{-}2}$ (28–32µm) insert close to median border. Three pairs of adanal setae, $ad_{1\text{-}3}$ (39–42µm), $ad_{3\text{-}2}$ are located laterally and ad_1 posteriorly of anal orifice. Lyrifissure *iad* flanking anterior third of anal plates.

Dimorphic characters: Males with more even ventral plate show only faint ridges or folds. Epimeral, genital, and aggenital setae conspicuously are longer than in female. Epimeral setae *1a, 2a, 3a* (8–13µm), *1b* (ca. 63µm), *3b* (ca. 47µm), *4a* (31µm), *4b* (45µm); genital setae (25–55µm) and aggenital seta (31µm). Females with strongly folded ventral plate (see Figure 2) and shorter epimeral, genital and aggenital setae. Setae *1a, 2a, 3a* (8–10µm), *1b* (ca. 26 µm), *3b* and *4b* (ca. 22µm), *4a* (16µm); genital setae (19–31µm) and aggenital seta (ca. 20µm).

Legs. Ambulacrum tridactylous, median claw broad and strong, lateral claws weaker developed and dorsally slightly dentate. Extensive brachytracheae with slit-like stigmata on dorsal paraxial face of all femora and tracheal sacculi ventrally on all tibiae and dorsally on trochanter III and IV. Dorsal companion setae *d* associated with solenidia on genu I, II, III, and all tibiae are present. Primilateral setae of tarsus I present. Tectal (*tc*) and iteral (*it*) setae as well as most other terminal tarsal setae are with spoon-shaped or nodular tips (difficult to observe) (Figure 4). Famulus on tarsus I rod-like, blunt and next to solenidion ω_1, solenidion ω_2 shorter. Solenidia ω_1 and ω_2 on tarsus II adjacent. For Chaetome and solenidia, see Table 1.

Dimorphic characters: Legs of females are shorter than their body width, while legs of males are considerably longer than body width and therefore males possess relatively longer legs than females.

Reproductive organs. Male spermatopositor elongated consisting of a proximal and a distal smooth tube, latter is fitted in the former when retracted. Distal part is three lobes containing darker sclerotized plates. Posterior lobe bearing setae ε_ε and c, lateral lobes bearing setae $\varepsilon_{1,\ 1}$,a and b (Figure 5(a)). Female ovipositor, very short, tube-like structure strongly plicated, allowing strong increase of diameter. Three short terminal lobes are present, posterior lobe bearing setae ε_ε and c, lateral lobes bearing setae $\varepsilon_{1,\ 1}$,a and b (Figure 5(b)), k setae is absent.

Remarks

The new species *A. retweet* sp. n. can be easily distinguished from all congeners by its conspicuous sexual dimorphism, with males showing a completely different notogastral surface structure. Apart from this dimorphism, *A. retweet* sp. n. differs distinctly from *A. bilineatus, A. marinus* and *A. schneideri* in the presence of a sensillum (vs. absence) and from *A. nigrofemoratus* by the presence of 3 claws (vs. 1 claw). *Ameronothrus maculatus* possesses only one pair of anal setae (instead of two in *A. retweet* sp. n.), *A. lineatus* lacks the dorsal setae on all tibiae (these are present in *A. retweet* sp. n.), and *A. schusteri* and *A. schubarti* show an incomplete labiogenal articulation (vs. complete). *Ameronothrus lapponicus* and the Russian *A. dubinini, A. oblongus,* and *A. nidicola* show different femoral surface patterns (either reticulate or smooth versus granular in *A. retweet* sp. n.), and the Japanese *A. yoichi* and *A. twitter* exhibit strongly nodular notogastral integuments (vs. granular and folded

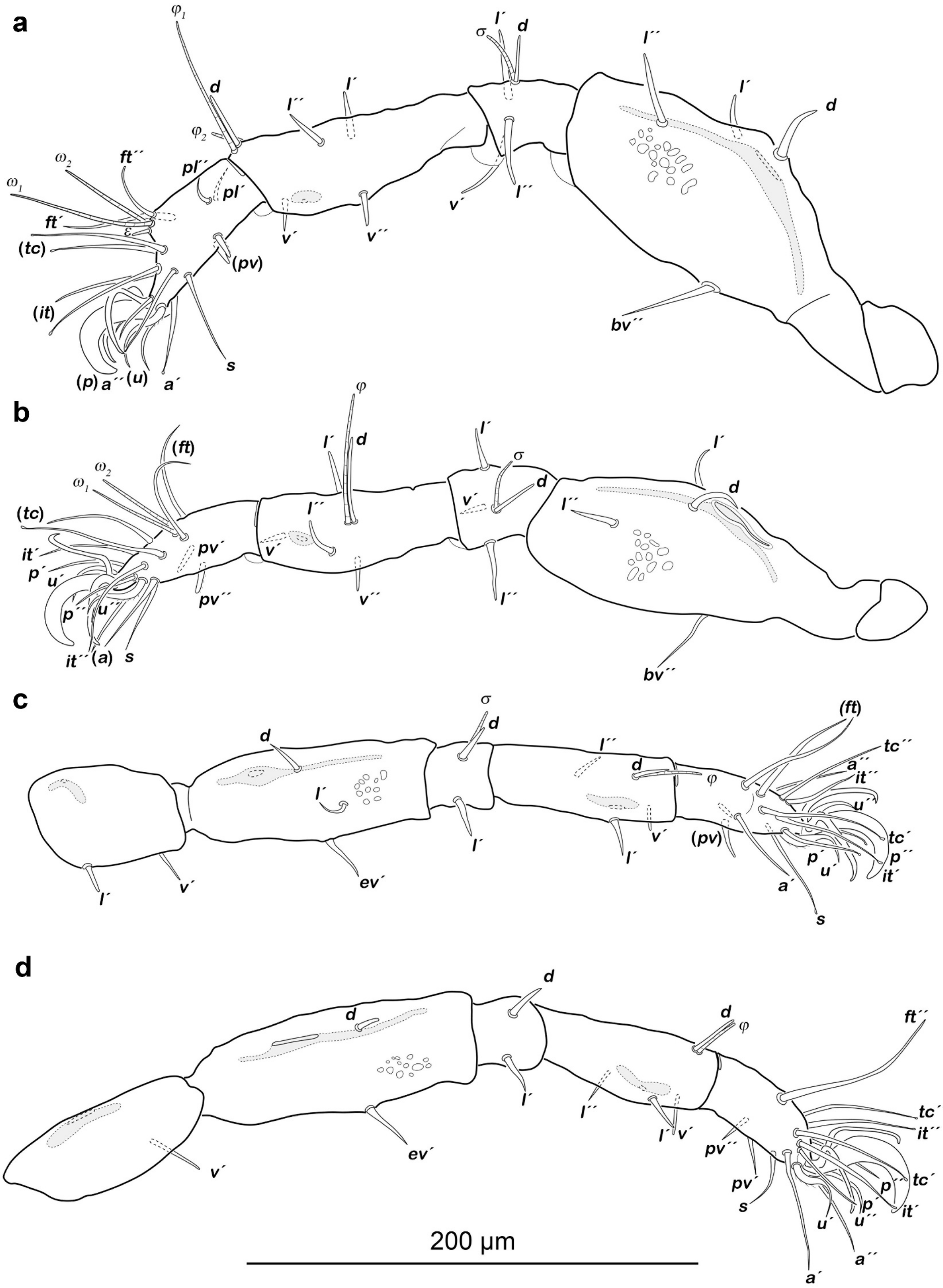

Figure 4. *Ameronothrus retweet* sp. n. adult male left legs, antiaxial view. (a) Leg I. (b) Leg II. (c) Leg III. (d) Leg IV.

Table 1. Leg setation and solenidia of *Ameronothrus retweet* sp. n.

	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	-	*bv´´, d, (l)*	*d, (l), v´*, σ	*d, (l), (v)*, φ_1, φ_2	*(pv), (pl), s, (a), (u), (p), (it), (tc), (ft)*, ω_1, ω_2, ε	0-4-4-5-18	1-2-2
Leg II	-	*bv´´, d, (l)*	*d, (l), v´*, σ	*d, (l), (v)*, φ	*(pv), s, (a), (u), (p), (it), (tc), (ft)*, ω_1, ω_2	0-4-4-5-15	1-1-2
Leg III	*l´, v´*	*ev´, l´, d*	*d, l´*, σ	*d, (l), v´*,φ	*(pv), s, (a), (u), (p), (it), (tc), (ft)*	2-3-2-4-15	1-1-0
Leg IV	*v´*	*ev´, d*	*d, l´*	*d, (l), v´*,φ	*(pv), s, (a), (u), (p), (it), (tc), ft´´*	1-2-2-4-14	0-1-0

in *A. retweet* sp. n.). These are just the most important distinctive characters, a detailed comparison of diagnostic traits of all *Ameronothrus* species is given in Table 2.

Genetic data

Mitochondrial *COI* as well as nuclear *18S* rRNA sequence data (Table 3) confirm all investigated dimorphic *Ameronothrus* specimens as a single distinct species and thus support their description as new species *Ameronothrus retweet* sp. n. A maximum likelihood tree and a Bayesian inference tree based on nuclear *18S* rRNA produced identical topologies, whereas node support was higher in the latter and thus only this tree is shown (Figure 6). All *Ameronothrus* species are closely related and form a monophyletic clade. Interestingly, the two *A. maculatus* specimens, one from the North Sea coast of Germany and the other from the coast of Portugal, are placed as separate taxa. *Paraquanothrus grahami*

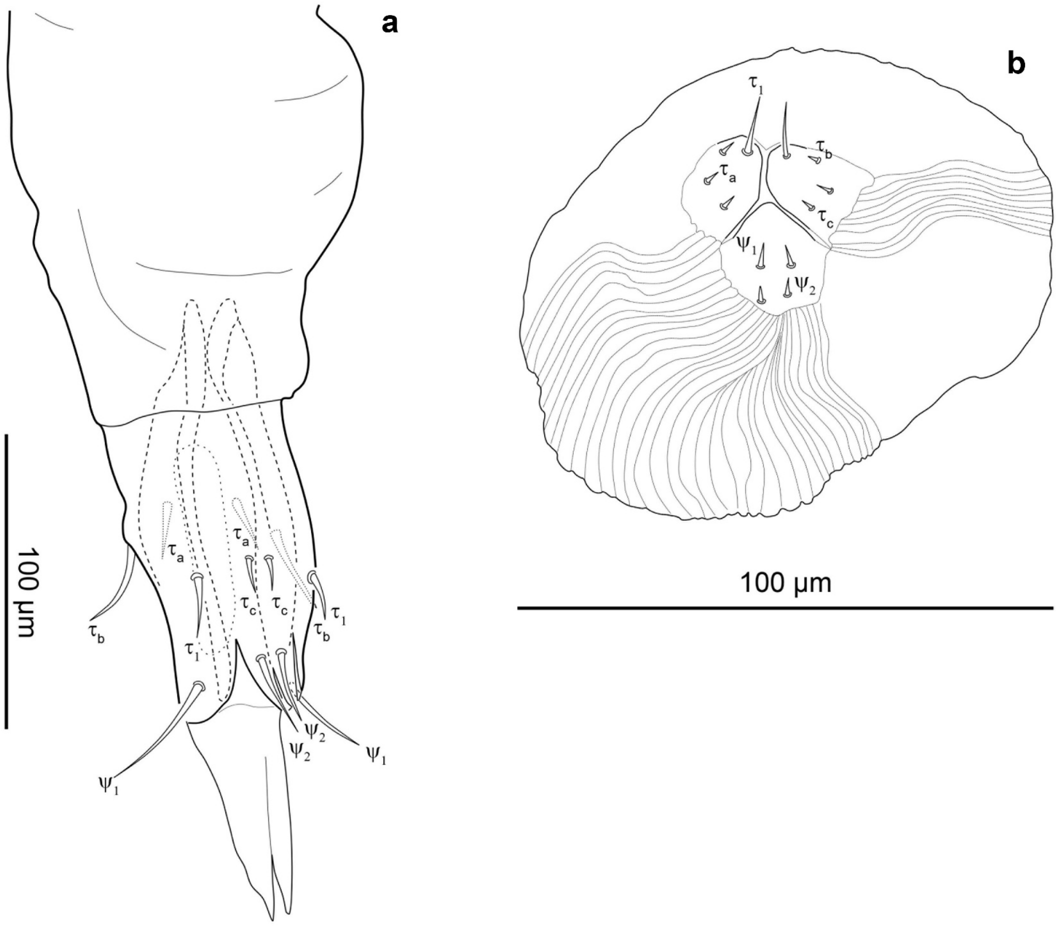

Figure 5. *Ameronothrus retweet* sp. n. reproductive organs. (a) Male, extruded spermatopositor in lateroposterior view. (b) Female, ovipositor, ventral view.

Table 2. Comparison of diagnostic morphological characteristics of *Ameronothrus* species. + = present, − = absent, ? = no information available.

	Trichobothrium	Ambulacra	Tarsal setae *pl*	Tibial setae *d*	Notogaster structure	Femora integument	Spermato-positor	Epimeral setation	Anal setation
A. retweet sp. n.	+	3	+	+	granules/ridges	granular	long	3-1-2-2	2
A. bilineatus	-	1	+	+	granules/ridges	reticulate	short	3-1-2-2	2
A. dubinini	+	3	?	?	ridges	reticulate	?	?	2
A. lapponicus	+	3	+	+	ridges	reticulate	?	3-1-2-2	2
A. lineatus	+	3	+	-	ridges	granular	long	3-1-2-2	2
A. maculatus	+	3	-	+	ridges	granular	short	3-1-2-2	1
A. marinus	-	3	+	+	granules	reticulate	short	3-1-2-2	2
A. nidicola	+	3	?	?	ridges	smooth	?	3-1-3-1	2
A. nigrofemoratus	+	1	+	-	ridges	granular	long	3-1-2-2	2
A. oblongus	+	3	?	?	ridges	reticulate	?	?	?
A. schneideri	-	1	-	+	granules	granular	short	3-1-2-2	1
A. schubarti	+	3	+	-	granules	granular	long	3-1-2-2	2
A. schusteri	+	3	+	+	nodules	granular	short	3-1-2-2	2
A. twitter	+	3	+	+	nodules	granular	short	3-1-2-2	2
A. yoichi	+	3	-	-	nodules	granular	short	3-1-2-2	2

(GenBank synonym *Aquanothrus* sp.) and *Halozetes capensis*, which are supposed by most authors as members of Ameronothridae, are placed in apparent paraphyletic positions (Figure 6). Marine-associated Fortuyniidae and Selenoribatidae are given as monophyletic families representing sister groups in the phylogenetic tree.

Discussion

Systematics

Based on synapomorphic characters, Schubart (1975) classified the *Ameronothrus* species into four groups, (I) the *A. marinus* group (*A. marinus, A. bilineatus, A. schusteri, A. schubarti*), (II) the *A. maculatus* group (*A. maculatus, A. schneideri*), (III) the *A. lineatus* group (*A. lineatus, A. nigrofemoratus*) and (IV) the *A. lapponicus* group (monotypic). Similar to the other two recently discovered Japanese species, *A. yoichi* and *A. twitter* (Pfingstl et al. 2019a, 2021a), the new species cannot be unequivocally assigned to one of these groups, because it diverges at least in one of the respective synapomorphic characters. In the *A. marinus* group, the solenidia on tarsus II are associated with the seta *ft″*, the tarsal setae (*tc*) and (*it*) show hook-like tips and the labiogenal articulation is incomplete and *A. retweet* sp. n. shows none of these traits. In the *A. maculatus* group the primilateral setae of tarsus I (*pl*) are absent, there is only one pair of anal setae, the ascleritic incision of notogaster is strongly reduced or lacking and the labiogenal articulation is complete. *Ameronothrus retweet* sp. n. shares the latter two characteristics but clearly differs in the former two. The *A. lineatus* group lacks dorsal setae on all tibiae, shows an incomplete labiogenal articulation, and possesses an elongated penis or spermatopositor, but apart from the long reproductive organ all these characters differ in *A. retweet* sp. n. Finally, the *A. lapponicus*

Table 3. GenBank accession numbers for *COI* and *18S* rRNA sequences used in this study. PRT – Portugal, DEU – Germany, ZA – South Africa.

	ID	*COI*	*18S*	Reference
Ameronothrus retweet sp. n.	JP_92_Am_01	ON382291	ON391750	This study
	JP_92_Am_02	ON382292	ON391751	
	JP_92_Am_04	ON382293	ON391752	
	JP_92_Am_05	ON382294	ON391753	
Ameronothrus twitter	JP_89_Am_01	ON382290	ON391749	
Ameronothrus maculatus (PRT)	PRT_Am_01	ON382296	ON391755	
Ameronothrus maculatus (DEU)	DE_01_Am_01	ON382295	ON391754	
Halozetes capensis (ZA)	ZA27_H_01	ON382297	ON391756	
Ameronothrus yoichi			MK880170	Pfingstl et al. (2019a)
Fortuynia smiti			MH285694	Pfingstl et al. (2019b)
Indopacifica pantai			MH285692	
Paraquanothrus grahami[a]			KX397627	Krause et al. (2016)
Hydrozetes lacustris			KX397631	
Limnozetes onondaga			KX397635	
Limnozetes rugosus			KX397636	
Tectocepheus velatus sarekensis			KX397637	
Hydrozetes confervae			AB818523	Iseki & Karasawa (2014)
Fortuynia rotunda			AB818525	
Eremaeozetes sp.			EU432187	Maraun et al. (2009)
Cymbaeremaeus cymba			EU432201	
Tectocepheus sarekensis			EF093776	Laumann et al. (2007)
Tectocepheus velatus			EF093780	
Crotonia reticulata			KR081605	Pachl et al. (2017)
Malaconothrus monodactylus			KR081621	
Schusteria littorea			HM070345	Pepato et al. (2010)
Scapheremaeus palustris			EU433989	Schaefer et al. (2010)
Scapheremaeus nakanoshimensis			LC367334	Bayartogtokh et al. (2018)
Scutovertex sculptus			GQ864305	Dabert et al. (2010)

[a] GenBank synonym *Aquanothrus* sp.

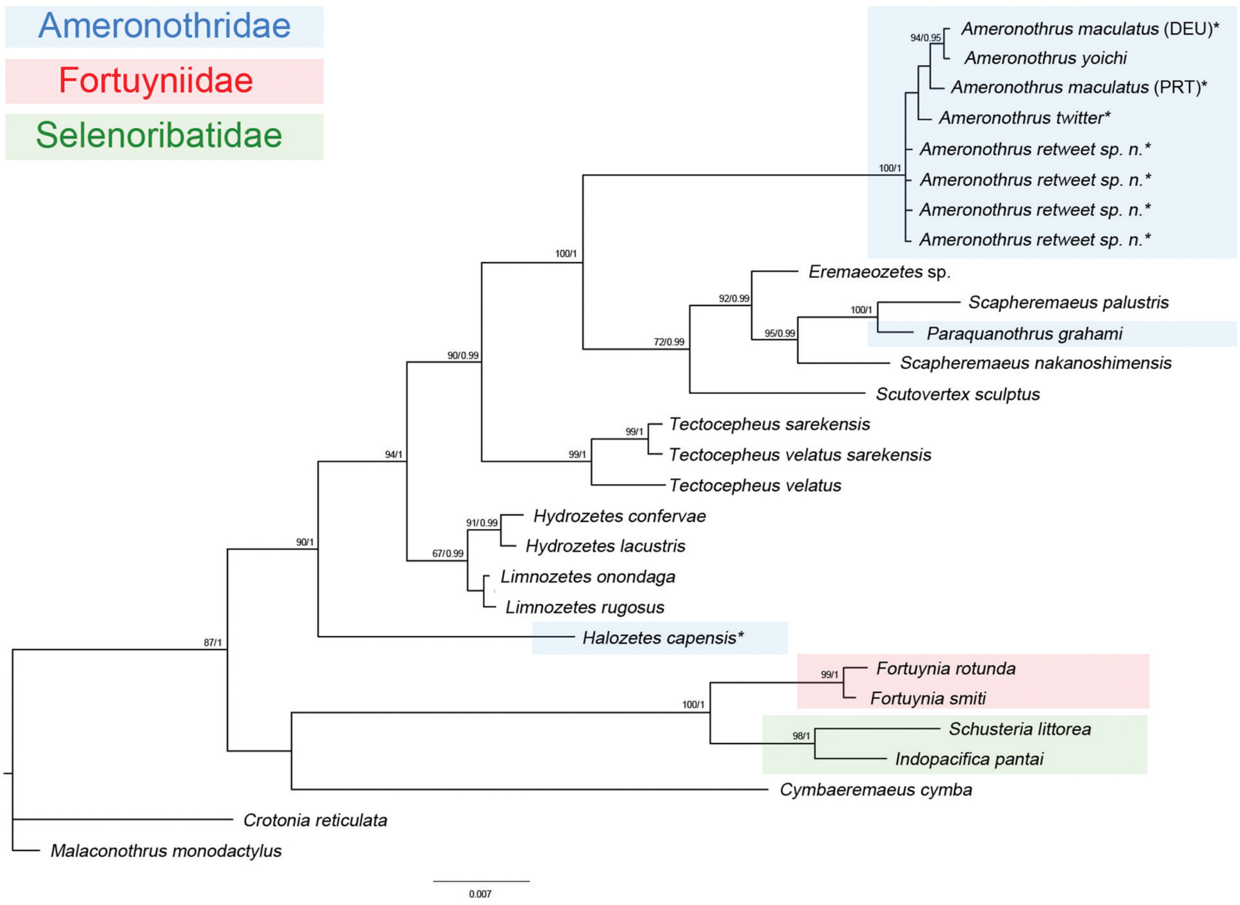

Figure 6. Bayesian inference tree of marine associated ameronothroid mites and selected terrestrial taxa based on *18S* rRNA gene sequences. Bootstrap values (>50) and posterior probabilities (>0.9) are shown near nodes. Sequences generated in this study are marked by *, all others were taken from GenBank and are listed in Table 3. Abbreviations: PRT – Portugal, DEU – Germany.

group shares the complete labiogenal articulation with *A. retweet* sp. n. but diverges strongly in the morphology of pedipalp. Consequently, no clear classification is possible using Schubart's (1975) synapomorphies. Nevertheless, the strongly elongated spermatopositor shared by *A. retweet* sp. n. and the *A. lineatus* group represents a rare and unique character indicating a closer relationship between these species. Moreover, the specific cuticular pattern of these three species is very similar, all possess granulated femora and a conspicuously folded gastronotic integument. Males of *A. retweet* sp. n. deviate from this pattern by lacking these folds, but males of *A. lineatus* and *A. nigrofemoratus* were also reported to show weaker developed gastronotic ridges or folds (Schubart 1975), and although the sexual dimorphism of the latter two species is by far not as pronounced as in *A. retweet* sp. n., the reduction of the folded integument may be seen as another synapomorphic character. Moreover, males of *A. lineatus* and *A. nigrofemoratus* show relatively longer legs than females, i.e. the basically smaller males exhibit the same leg length than the larger females, and this kind of sexual dimorphism is also shown in *A. retweet* sp. n.

The Russian *A. nidicola* may represent a further close relative of the *A. lineatus* group as it shows a similar notogastral integumental structure (Sitnikova 1977). However, *A. nidicola* is difficult to classify and problematic for various reasons: (1) the description of this species (Sitnikova 1977) is incomplete, as it provides only a dorsal depiction and lacks details about important morphological features, such as the legs, mouthparts, and reproductive organs; (2) only female specimens are known yet in this species (Sitnikova 1977; Klimov 1998) and therefore it is unknown if a distinct sexual dimorphism is present or not; and (3) *A. nidicola* should be distinguishable from *A. retweet* sp. n., *A. lineatus,* and *A. nigrofemoratus* by the smooth podosomal and femoral surface structure (vs. granular) and by an epimeral setation of 3-1-3-1 (vs. 3-1-2-2), but depictions or details of the ventral aspect and the femora are lacking and the epimeral formula could be based on an erroneous notation (numbers of setae are equal and if one of the setae on epimeron III is assigned to epimeron IV, there is no difference anymore). If further specimens of this species are found in the future, a detailed redescription and possibly molecular genetic data should be provided to clarify the systematic position of this species.

Generally, molecular genetic data of *Ameronothrus* species are scarce and thus a phylogenetic reconstruction based on these characters is not yet feasible. However, the present study included genetic data of at least the Japanese species and of *A. maculatus*, showing that all species are closely related and form a distinct monophyletic genus. *Ameronothrus maculatus* specimens are placed in different positions in the phylogenetic tree, indicating a high genetic divergence within this morphospecies. Cryptic diversity is a quite common phenomenon among marine associated oribatid mites (e.g. Pfingstl et al. 2021b) and this could also be the case here. The specimens were sampled from far distant locations at the North Sea coast of Germany and the Atlantic coast of Portugal (>2000 km) and due to this distance gene flow may have been restricted and resulted in strong genetic divergence. Future studies on *Ameronothrus* species from these areas should consider this possibility and thus include comprehensive molecular genetic data.

In a larger phylogenetic context, members of Ameronothridae are placed in paraphyletic positions whereas the Fortuyniidae and Selenoribatidae are given as sister taxa with a monophyletic origin. These results support the theory of an independent evolutionary origin of marine associated Ameronothroidea (e.g. Pfingstl 2017) and justify the family Podacaridae (with *H. capensis*) as a distinct taxon outside Ameronothridae.

Sexual dimorphism

Only 1% of bisexual oribatid mites are distinctly sexually dimorphic and this dimorphism seems to be an evolutionary response to intermittent dryness or aquatic habitats (Behan-Pelletier 2015). The intertidal environment clearly represents such an environment; therefore, it is not surprising to find sexually dimorphic species there. Nevertheless, only a minority of intertidal oribatid mites is known to exhibit an obvious sexual dimorphism. Males of the podacarid *Halozetes belgicae* (Michael, 1903), *Alaskozetes antarcticus* (Michael, 1903), and *Podacarus auberti* Grandjean, 1955 show aggenital neotrichy, whereas males of the latter additionally show epimeral neotrichy and larger claws (summarized in Behan-Pelletier 2015). Males of the fortuyniid *Fortuynia yunkeri* Hammen, 1963 possess modified tibiae on the fourth pair of legs, *Fortuynia atlantica* Krisper & Schuster, 2008 males exhibit modified anterior notogastral setae and lateral notogastral protuberances (summarized in Behan-Pelletier 2015), and male *Fortuynia dimorpha* Pfingstl, 2015 specimens show a large porous area on their posterior notogastral region (Pfingstl 2015). Males of *A. lineatus* and *A. nigrofemoratus* show relatively longer legs (Schubart 1975; Behan-Pelletier 2015), a morphological condition that is also shown in the new species. The specific function of these different sexually dimorphic structures is unknown for each species and consequently only a matter of conjecture. Pfingstl (2015) assumed that the modifications in Ameronothridae and Podacaridae allow a special mode of spermatophore deposition or transfer while the dimorphism of Fortuyniidae is supposed to be involved in some kind of mating behaviour. The long spermatopositor in connection with longer legs of *A. retweet* sp. n., *A. lineatus* and *A. nigrofemoratus* indeed indicates that these species may show different spermatophore deposition strategies. Moreover, we observed that the distal part of the extruded spermatopositor of preserved male *A. retweet* sp. n. specimens was always bent backwards at an almost right angle. A similar condition is shown in *Collohmannia gigantea* Sellnick, 1922 and *Collohmannia johnstoni* Norton & Sidorchuk, 2014, where males deposit a nuptial fluid with their backwards bent spermatopositor on their fourth pair of leg, which is then presented to the female (Schuster 1962; Norton and Sidorchuk 2014). However, if a nuptial gift is also presented in these *Ameronothrus* species can only be verified by observations of living specimens.

The strongly folded notogastral cuticule of female *A. retweet* sp. n. is a unique dimorphic character among marine associated oribatid mites and its function is also unknown. Considering the leathery and flexible nature of the cuticle in the genus *Ameronothrus* (e.g. Schubart 1975), it is assumable that females may increase their body volume considerably, so maybe they are able to either produce more eggs or larger eggs at a given time. However, among the *A. retweet* sp. n. specimens investigated here, there was not a single female carrying eggs or larvae and thus there is yet no indication supporting such an assumption.

Biogeographic aspects

Ameronothrus retweet sp. n. is the third species of Ameronothridae to be reported from Japanese landmasses. *Ameronothrus yoichi* is known to occur on the coasts of Hokkaido (Pfingstl et al. 2019a), *A. twitter* was found at the Pacific coast of Honshu in a port east of Tokyo (Pfingstl et al. 2021a) and *A. retweet* sp. n. was discovered at the Sea of Japan coast of Honshu. Indeed, the latter represents the recent and first record of an *Ameronothrus* from the Sea of Japan coast. Apart from that, no other record of any ameronothroid taxon is known yet from this coastline. Pfingstl et al. (2022) already mentioned the presence as "*Ameronothrus* sp." from the latter coast near Tottori and this report referred to *A. retweet* sp. n. Moreover, Pfingstl et al. (2022) assumed that cold adapted Ameronothridae are not able to persist above a mean annual average air temperature of 17°C and a mean annual average of 20°C sea surface temperature and these temperatures are not exceeded in Tottori which confirms their assumption and classifies this presence as the most southern occurrence of an *Ameronothrus* species on this specific coastline. In this respect, the report of *A. retweet* sp. n. in this area may shed further light on the factors that determine the distribution of Ameronothroidea. However, north of this occurrence, the Sea of Japan coastline is still completely uncharted in terms of intertidal mites and thus a wider distribution of *A. retweet* sp. n. along this coastline should be considered. Further faunistic studies on Japanese shores are clearly needed to assess the real number of present taxa and their real distribution areas.

Social media and Citizen science

About 1.22 million species have been described but it is estimated that the Earth is home to approx. 8.7 million species (Mora et al. 2011). According to the IPBES, one million of these species are endangered at the current rate of extinction (IPBES 2019). Considering these numbers, many species may be gone before we knew about them and even with the greatest effort of all taxonomists of the world, extinction presently outpaces the discovery of new species. However, modern taxonomy can use additional tools, as for example Citizen science and social network services (SNS), to increase the number of named and known species. Only a handful of species, e.g. a green lacewing (Wintertorn et al. 2012), a sundew (Gonella et al. 2015), a pygmy grasshopper (Skejo and Caballero 2016), a dipteran fly (Jaume-Schinkel et al. 2020), a fungus (Santamaria et al. 2020), a snake (Zeeshan et al. 2021), and a mite (Pfingstl et al. 2021a), have been discovered with the use of social networks so far. The discovery of *A. retweet*, which resulted as a consequence of the discovery of the *A. twitter* mite via social media (Pfingstl et al. 2021a) and the associated media response, shows that involving the public in biodiversity research can speed up the discovery of new species and raise the awareness for the yet unknown biodiversity and its protection. It shows the possibility and hopes that the citizen can contribute to zoological taxonomy through frequent communication via SNS, in the same way that new stars are discovered in astronomy (e.g. Fujii et al. 2021) or new facts are discovered in palaeontology (e.g. Macfadden et al. 2016). Presently, citizen science plays only a minor role in zoological taxonomy, but if proper ways and rules of communication between science and public are established in the near future (Dowthwaite and Sprinks 2019), its contribution may increase considerably.

Acknowledgments

The authors would like to thank Dr. Ken-ichi Okumura (National Museum of Nature and Science, Tokyo) for the deposition of type specimens. Thanks also to Steven Weiss and his Portuguese colleagues for providing us with the *Ameronothrus* specimen from Portugal.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This investigation was funded by the Austrian Science Fund (FWF): [I 3815] for TP and by bilateral Programs, Joint Research Projects (JSPS 17K07271,18K06392) and JSPS KAKENHI Grant Numbers 17K07271, 18K06392 for SS and SFH.

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