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Freshwater halacarid mites (Acari: Halacaridae) from Madagascar – new records, keys and notes on distribution and biology

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Abstract. Four freshwater halacarid species were previously recorded from Madagascar. They had been extracted from sandy deposits at the banks of streams and creeks. Recently another two species were found, namely *Porohalacarus alpinus* and *Soldanellonyx monardi*. On the basis of individuals of these two species, as well as of additional material of the four formerly recorded species (*Limnohalacarus cultellatus*, *Limnohalacarus novus*, *Lobohalacarus weberi*, and *Ropohalacarus pallidus*), morphological characters are added to previous descriptions and the male of *P. alpinus* is described. A key is given to adults of Madagascar freshwater halacarid genera. Morphological differences between the presently known African freshwater halacarids are outlined. Geographical and biological data of the six species from Madagascar are presented. All genera and most of the species have world-wide distributions.

Key words. Halacaroidea, riverine sediments, taxonomy, biology, geography.

INTRODUCTION

The database 'Freshwater Animal Diversity Assessment' (FADA) presents a list of 67 freshwater halacarid species and subspecies in 17 genera (Bartsch 2013d). Some of the species are related to marine genera but the majority belong to genera which are restricted to fresh or slightly saline brackish water. Eight truly freshwater halacarid species are recorded from continental Africa, i.e., *Limnohalacarus africanus* Walter, 1935; *L. fontinalis* Walter & Bader, 1952; *L. major* Bader, 1968; *L. marlieri* (Bader, 1968); *L. portmanni* Bader, 1967; *Lobohalacarus weberi* (Romijn & Viets, 1924); *Porohalacarus alpinus* (Thor, 1910); *Ropohalacarus uniscutatus* (Bartsch, 1982); and *Soldanellonyx monardi* Walter, 1919 (Walter 1935; Walter & Bader 1952; Bader 1967, 1968; Green 1984; Green et al. 1974; Bartsch 2008a, 2013a, b).

Collections of the freshwater mite fauna in sandy deposits at the banks of Madagascar streams and creeks, carried out by R. Gerecke and T. Goldschmidt, also included halacarid mites. Recently, records of four species were published (Bartsch 2013b). Sorting of additional samples brought to light another two species, namely *Porohalacarus alpinus* and *Soldanellonyx monardi*, and also several more individuals of the formerly mentioned *Limnohalacarus cultellatus* Viets, 1940; *Limnohalacarus novus* Bartsch, 2013; *Lobohalacarus weberi*; and *Ropohalacarus pallidus* Bartsch, 2013. Morphological characters of the six species from Madagascar are outlined, the male of *Porohalacarus alpinus* is described, biological details are added and discussed. The geographical distribution of the species is summarized in maps.

MATERIAL AND METHODS

The halacarid mites were extracted from banks of streams and creeks by digging pits into the sandy deposits and filtering the seeped water (Karaman-Chappuis Method). Collectors are Drs R. Gerecke and T. Goldschmidt. The MD numbers refer to those in the collectors' collection diary (unpublished). The halacarid mites were partly studied in a drop of glycerine, partly cleared in lactic acid, rinsed in glycerine and mounted in glycerine jelly. Voucher specimens are deposited in the Zoological Museum Hamburg (ZMH), Centrum für Naturkunde (CENAK), University of Hamburg; additional material in the author's collection.

The presentation of the species found on Madagascar starts with a bibliographical list which includes the first description of the species, papers which added morphological details, recent records or keys covering large-scale geographical areas (British Islands, Central Europe, North America) and synonyms. The geographical regions correspond to those outlined in Balian et al. (2008) and Bartsch (2009). These are the Afrotropical, Palaearctic,

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Oriental, Nearctic, Neotropical, and Australian Regions, the Pacific Islands and Antarctica. The latter region includes islands of the southern Atlantic (South Georgia) and southern Indian Ocean (Prince Edward Islands, Crozet Island, St Paul, and Kerguelen).

The illustrations and morphological and biological data are of individuals from Madagascar. Rarely occurring numbers of setae are in parentheses. A figure in square brackets indicates the number of cases involved. Decimal indices are added to notify the position of a structure with reference to anterior – posterior end of the idiosoma.

Abbreviations used in the descriptions, keys, and discussion: AD, anterior dorsal plate; AE, anterior epimeral plate; AP, anal plate; ds-1 to ds-6, first to sixth pair of dorsal idiosomatic setae, numbered from anterior to posterior; GA, genitoanal plate; gac, genital acetabula; glp, gland pore(s), numbered glp-1 to glp-5 from anterior to posterior; GO, genital opening; GP, genital plate; L:H, ratio length to height; LxW, data of length and width; L:W, ratio length to width; mxs, maxillary setae, mxs-1, mxs-2, basal and apical pair of maxillary setae, respectively; OC, ocular plate(s); P-1 to P-4, first to fourth palpal segment; pas, parambulacral seta(e); PD, posterior dorsal plate; PE, posterior epimeral plate(s); pgs, perigenital setae; sgs, subgenital setae. The legs, their segments and claws are numbered from I to IV from anterior to posterior. The leg segments are trochanter, basifemur, telofemur, genu, tibia, and tarsus. The number of setae on the tarsi includes the solenidion but excludes the parambulacral setae. In the illustrations, marginal setae are shown either in dorsal or in ventral aspect but not in both. Unless indicated otherwise, the given length of a segment is that along its dorsal margin.

SYSTEMATICS

Annotated key to adult Afrotropical freshwater halacarid genera and Madagascar species

1a. Genu and telofemur of leg I almost equal in length. Tarsus I with ventromedial spur and pair of short ventral setae. .... ***Lobohalacarus***
Remarks. In the Afrotropical region, the genus *Lobohalacarus* is represented by a single species, *L. weberi*. The majority of the individuals have a frontal spine whereas the anterior margin of the other freshwater species is arched or truncate.

1b. Genu of leg I shorter than telofemur I. Tarsus I with 0–1 ventral setae... 2

2a. Gland pores inconspicuous or absent. 3

2b. Dorsum with four to five pairs of distinct gland pores (glp), pair of glp-1 on AD, glp-2 marginally in striated integument, glp-4 and glp-5 in striated integument lateral to PD. 4

3a. With four dorsal plates (AD, pair of OC and PD) and four ventral plates (AE, pair of PE and GP). OC with cornea and large spot of black eye pigment (> 10 µm in diameter). .... ***Porohalacrus***
Remarks. The only *Porohalacarus* species known from Madagascar and Africa, *P. alpinus*, is characterized by its spots of dark eye pigment, a small one on the AD and a larger one on each OC. The other Madagascan freshwater halacarids have either faintly brown or no eye pigment.

3b. With dorsal shield (AD and PD fused, OC reduced or fused with PE) and ventral shield (AE, PE and GP fused). Neither cornea nor eye pigment present. .... ***Ropohalacarus***
Remarks. A single species is known from Madagascar, namely *Ropohalacarus pallidus*. A record of another species, *R. uniscutatus*, is from northern Africa (Bartsch 2013). Distinguishing characters are outlined below.

4a. Genital acetabula in posterior part of GP, none situated anterior to the level of GO. Length of anal sclerites about half that of female genital sclerites. .... ***Soldanellonyx***
Remarks. At present, *Soldanellonyx monardi* is the only *Soldanellonyx* species with records from the Afrotropical region. Worldwide nine species have been described.

4b. Genital acetabula arranged in line along lateral margin of GP (or area representing this plate), most anterior acetabula situated well anterior to GO. Anal sclerites less than 1/3 of the size of genital sclerites. 5

5a. OC not including platelet with gland pore. Ventral plates AE, PE and GA separated by striated integument. Claws I apically with few, delicate tines, basally with lamellar process with about four tines. .... ***Limnohalacarus cultellatus***

5b. OC including platelet with gland pore. All ventral plates fused. Claws I with J-shaped arranged pectines bearing at least 15 long tines. .... ***Limnohalacarus novus***
Remarks. These two *Limnohalacarus* species are recorded from Madagascar but further species are mentioned from Africa. All African species are outlined below, after the presentation of *L. novus.*

Madagascan and related halacarid species, notes on morphology, taxonomy, biology, and distribution

Limnohalacarus cultellatus Viets, 1940

L. cultellatus Viets, 1940: 194–200, figs 5–12.
L. cultellatus, Bartsch 2011: 491–493, fig. 2A–C, 2013a: 204–206, figs 1b–h, 2a–h; Pepato & Dos Santos Costa 2015: 5–7, fig. 4A–I.

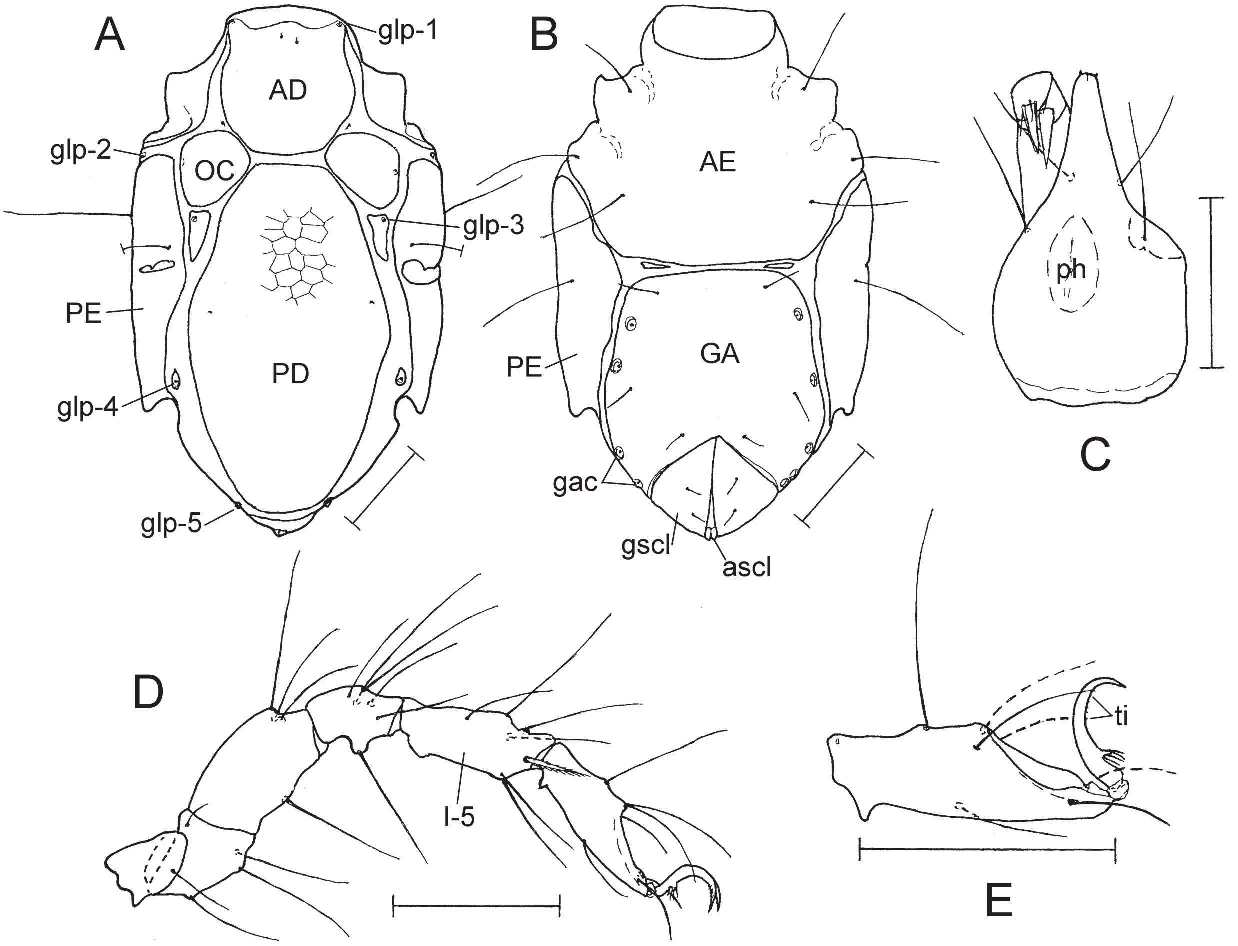

Fig. 1A–E. *Limnohalacarus cultellatus* Viets, 1940, female. **A.** idiosoma, dorsal; **B.** idiosoma, ventral; **C.** gnathosoma, ventral; **D.** leg I, medial; **E.** tarsus I, medial (lateral setae in broken line, lateral claw omitted). (Scale = 50 µm) (AD, anterior dorsal plate; AE, anterior epimeral plate; ascl, anal sclerite; GA, genitoanal plate; gac, genital acetabula; glp-1 to glp-5, first to fifth gland pore; gscl, genital sclerite; OC, ocular plate; PD, posterior dorsal plate; PE, posterior epimeral plate; ph, pharyngeal plate; ti, tines; I-5, tibia of leg I).

L. kakinadus Chatterjee & Chang, 2005: 23–27, figs 1A–H, 2A–D.

Collecting data. South-eastern Madagascar, Fianarantsoa, Ionilahy, stream draining area Marosaro (S from River Ionilahy), 220 m, 21°C, 0.072 mS/cm, 12 Aug. 2001, interstitial (MD 023). – South-eastern Madagascar, Fianarantsoa, Ionilahy, River Ionilahy, 200 m, 23°C, 0.059(11. Aug.)–0.088(13. Aug.) mS/cm, 11/13 Aug. 2001, interstitial (MD 026). – Northern Madagascar, Antsiranana, Antalaha, Marofinaritra, River Andranomenaheli, upstream confluence with River Ankavia (right affluent below MD 135), 70 m, 22.3°C, 0.009 mS/cm, riffle, 04 Nov. 2001 (MD136a).

Short description (Fig. 1A–E). *Female*: Length of idiosoma 255–290 µm [3]. OC and platelet with gland pore separated by striated integument (Fig. 1A), OC about 1.1 times longer than wide. Corneae and spots with eye pigment lacking. AE, PE and GA separated by striated integument (Fig. 1B). Pair of ds-6 present on anal cone (obscured by genital sclerites). GP with four to five pairs of gac, three to four pairs of pgs, genital sclerites with two pairs of sgs. Gnathosoma 1.5–1.7 times longer than wide; pharyngeal plate distinctly removed from basal margin of gnathosoma. Both pairs of maxillary setae slender (Fig. 1C). Legs shorter than idiosoma, length ratio leg I:idiosoma 0.7:1. Length of telofemur I 1.8 times the height (Fig. 1D). Basifemora I to IV with 4, 3, 2, 1 setae, tibiae I to IV with 7, 6, 7, 6 setae. Tibiae I and II each with one bipectinate seta, tibiae III with two bipectinate ventromedial setae, tibia IV with slender, smooth ventral setae. Claws on leg I slender, apically with few

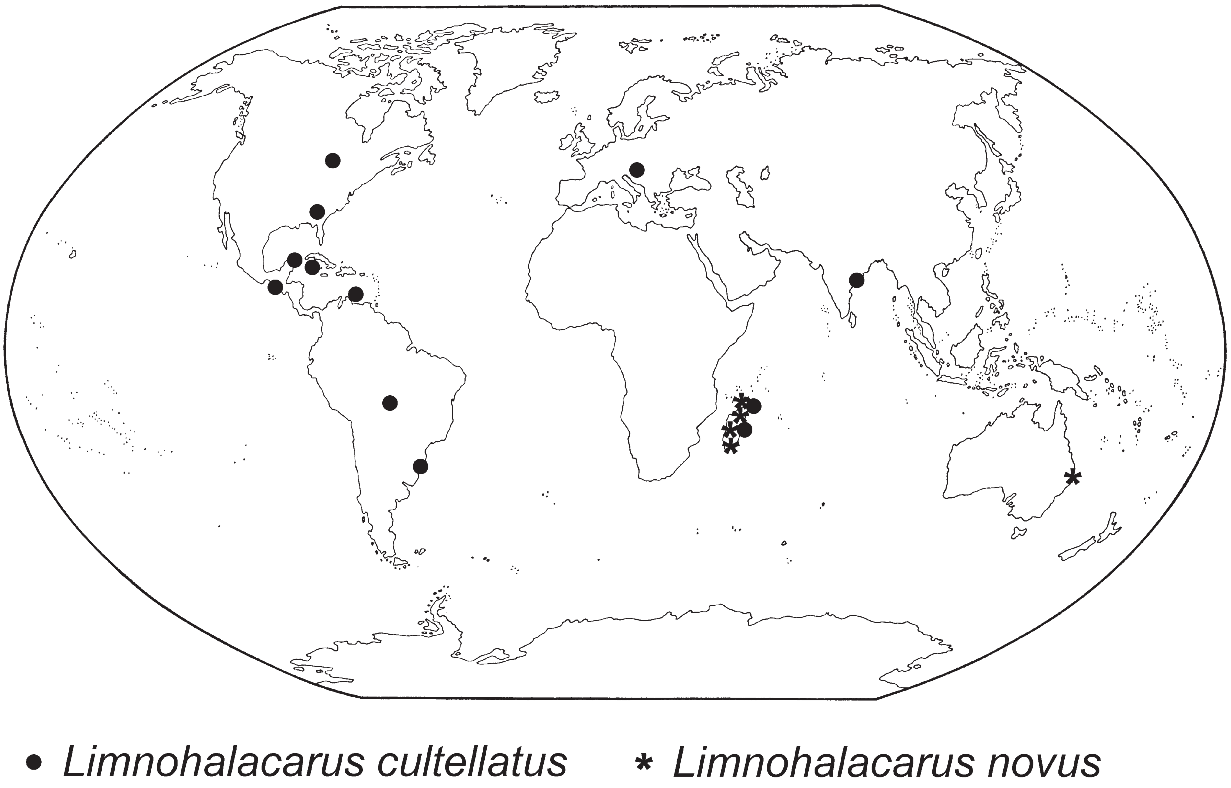

Fig. 2. Records of *Limnohalacarus cultellatus* Viets, 1940 (black spot) and *Limnohalacarus novus* Bartsch, 2013 (asterisk).

(8–10) minute tines (Fig. 1E), basal lamellar process with four tines.

Male: Not present.

Juveniles: Length of deutonymph, protonymph and larva 240 µm [1], 200 µm [1] and 155 µm [1], respectively. Dorsal aspect similar to that of females. AE of larva with pair of epimeral pores. In nymphs GP and anal plate separated by striated integument, in larvae GP lacking.

Remarks. *Limnohalacarus cultellatus* can be distinguished from the other African *Limnohalacarus* species by combination of: dorsal and ventral plates separated and pectines on claws I much more delicate than on claws II to IV. Notes on African *Limnohalacarus* species are given below.

Biology. At present there is no record of a male, neither from Africa nor from other parts of the world.

One of the females included an ovoid excretory body, 125 µm long, 60 µm wide, the centre (10 µm in diameter) is dark, the margin hyaline and delicately stratified. One of the females held an egg, 50 µm long, 55 µm wide.

Geographical distribution (Fig. 2) (cf. Bartsch 2011, 2013a; Pepato & Dos Santos Costa 2015; Ojeda et al. 2016):

Afrotropical Region. – Madagascar;
Palaearctic Region. Europe: – Hungary;
Oriental Region. – India (Andhra Pradesh);
Nearctic Region. – United States (Georgia, Wisconsin ?);
Neotropical Region. – Brazil (Mato Grosso, Rio Grande do Sul) – Cayman Islands (Grand Cayman) – El Salvador – Mexico (Quintana Roo) – The Netherlands Antilles (Bonaire, Curaçao) – Venezuela (Margarita Island).

Limnohalacarus novus Bartsch, 2013

L. novus Bartsch, 2013a: 206–210, figs 3a–h, 4a–g.
L. billabongis, Bartsch 2008b: 127, 128.

Collecting data. Central Madagascar, Antananarivo, Anjazorobe, River Ranonisoanavola (larger stream E from main mountain chain), 1200 m asl, 13.2°C, 0.058 mS/cm, interstitial, 23 Jul. 2001 (MD 012). – South-eastern Madagascar, Fianarantsoa, Ionilahy, stream draining area Marosaro (S from River Ionilahy), 220 m, 21°C, 0.072 mS/cm, interstitial, 12 Aug. 2001 (MD 023). – South-eastern Madagascar, Fianarantsoa, Ionilahy, River Ionilahy,

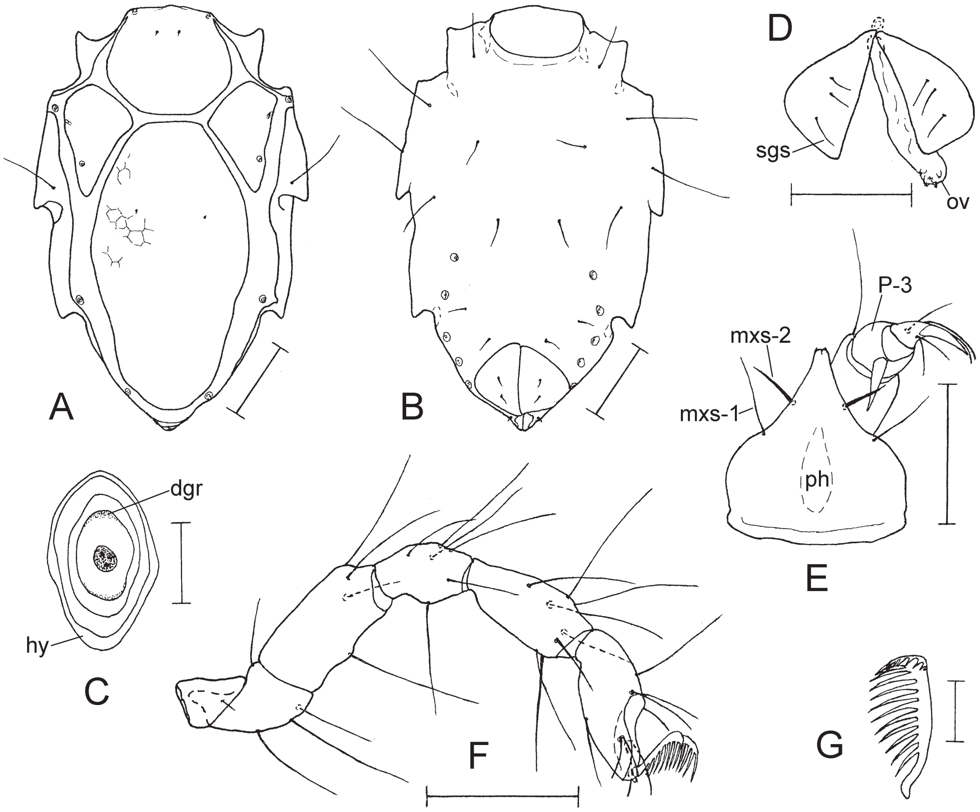

Fig. 3A–G. *Limnohalacarus novus* Bartsch, 2013, female. **A.** idiosoma, dorsal; **B.** idiosoma, ventral; **C.** excretory body, ventral; **D.** genital area with ovipositor; **E.** gnathosoma, ventral; **F.** leg I, medial; **G.** claw I, ventral. (A–F, scale = 50 µm; G, scale = 10 µm) (dgr, dark granules; hy, hyaline part; mxs-1 and mxs-2, basal and apical maxillary seta, respectively; ov, ovipositor; ph, pharyngeal plate; P-3, third palpal segment; sgs, subgenital seta).

200 m, 23°C, 0.059(11. Aug.)–0.088(13. Aug.) mS/cm, interstitial, 11/13 Aug. 2001 (MD 026). – South-eastern Madagascar, Fianarantsoa, Ionilahy, small stream crossing the railroad east from village, 200 m, 19.9°C, 0.083 mS/cm, 15 Aug. 2001 (MD027). – Southern Madagascar, Tulear, Tsimelahy, River Antarantsa, ca 1 km upstream from village, 300 m, 20.4°C, 0.171 mS/cm, interstitial, 04 Sep. 2001 (MD 058). – Central Madagascar, Antanarivo, Ankaratra, Reserve Manjakatompo, left affluent of River Mahiavona, EM Mantsina, 1750 m, 14.1°C, 0.003 mS/cm, interstitial, 08 Oct. 2001 (MD107). – North-western Madagascar, Majunga, Adjamangirana, stream in dry forest, upstream, rice field area (road to the village of Tsaratanana), 220 m, 30.8°C, 0.008 mS/cm, interstitial, 19 Oct. 2001 (MD115). – Northern Madagascar, Antsiranana, Antalaha, Marofinaritra, River Antsohibe, upstream confluence with River Ankavia (5 km NE Amparihimena), 70 m, 25.2°C, 0.008 mS/cm, riffle, 03 Nov. 2001 (MD135). – Northern Madagascar, Antsiranana, Antalaha, Marofinaritra, River Andranomenaheli, upstream confluence with River Ankavia (right affluent below MD 135), 70 m, 22.3°C, 0.009 mS/cm, riffle, 04 Nov. 2001 (MD136a). – Northern Madagascar, Antsiranana, Maroambihy (Sambava), left affluent of River Lokoho upstream from the village, 90 m, 26.0°C, 0.010 mS/cm, interstitial, 12 Nov. 2001 (MD149). – Northern Madagascar, Antsiranana, Joffreville (M. d'Ambre), River Antomboka, downstream large cascade, 850 m, 20 Nov. 2001 (MD163). – Northern Madagascar, Antsiranana, Joffreville (Montagne d'Ambre), River Manques in Reserve Fontenay, 580 m, interstitial, 21 Nov. 2001 (MD 165).

Short description (Fig. 3A–G). *Female*: Length 206–289 µm [20]. OC including platelet with glp-3 (Fig. 3A), L:W of OC 1.4–1.6:1. Length ratio of PD:AD 2.6–2.7:1. Pair of ds-2 absent. Ventral plates AE, PE and GP fused (Fig. 3B). Area corresponding to GP with three pairs of pgs, five to six pairs of gac and on each genital sclerite two (three) sgs. Ovipositor short and narrow (LxW 74 x 10 µm), very faintly sclerotized, genital spines very delicate and short, 2 µm in length, and arising from minute papillae (Fig. 3D). Anal slit less than 10 µm long and guarded by pair of short anal sclerites. Gnathosoma about 1.1 times longer than wide. Pair of mxs-2 shorter but wider than mxs-1 (Fig. 3E). Legs shorter than idiosoma, length ratio leg I:idiosoma 0.7:1. Length of telofemur I 2.1–2.3 times the height (Fig. 3F). Tibiae I to IV with 8, 7, 7, 6 setae [14]. Ventromedial seta on tibia II and both ventromedial setae of tibia III bipectinate; setae on legs I and IV smooth. Claws I to IV with J-shaped arranged pectines (Fig. 3G), extending from apical lateral flank and along medial flank to basis of claw. On claws II to IV basal tines partly fused to a lamellar process.

Male: Not present.

Juveniles: Length of deuto-, protonymphs and larvae 231–275 µm [13], 180–226 µm [7] and 142–170 [5] µm, respectively. In contrast to adults, OC and posterior gland-bearing platelet separated by transverse striae. Ventral plates AE, PE and GP of nymphs separated from each other by striated integument, in larvae GP absent and AE with pair of epimeral pores.

Biology. Eleven of 15 females studied held an egg. The length x width of the eggs ranged from 35 x 35 to 100 x 50 µm. The eggs are not deposited in the substratum but attached to tibiae IV. One-third of the females had a single cocoon fixed with a slender stem, the latter 2–3 µm wide. The length of the cocoons was about 103–113 µm, the diameter 60–64 µm. Each one enclosed a single embryo.

Limnohalacarus species have the excretory material accumulated within an ovoid, compressed body (cf. Walter 1914; Petrova 1966; Ramazotti & Nocentini 1960; Pepato & Dos Santos 2015). In the material studied, 11 (73 %) of 15 females, 9 (22%) of 27 deutonymphs and one (22%) of six protonymphs held such a body, but none of four larvae. The body was dorsal to the gut, in some individuals it had a dark centre, surrounded by concentrically arranged more or less transparent layers (Fig. 3C). In one female the excretory body was almost uniformly dark, in another one hyaline, the body recognizable mainly because refraction of light. In one female (length 255 µm) this body was 108 µm long, 71 µm wide and 41 µm thick, the general size range in length was 95–158 µm, in width 50–92 µm. The length of the excretory body equalled 0.4–0.5 times the length of the female idiosoma. In deutonymphs the stratified body was 60–85 µm long, 45–95 wide, in a protonymph 50 µm long, 36 µm wide, i.e., a length of 0.3–0.4 and 0.2 of that of the nymphal idiosoma, respectively. Such a body was present/absent independent of the age of the instar, e.g. it was absent both in assumedly recently hatched females and in ovigerous ones and also in those carrying a cocoon (or their remnants) fixed to the tibiae.

Remarks. Adults of *Limnohalacarus cultellatus* and *L. novus*, the two species known from Madagascar, can easily be separated by (1) the shape of the ocular plates, namely OC hardly longer than wide (L:W 1.1:1) and not including the platelet with a gland pore versus OC 1.3 times longer than wide and including the platelet with gland pore, (2) the ventral plates, separated versus fused to a shield, (3) the length of the gnathosoma, at least 1.5 times longer than wide versus 1.1 times or less, and (4) the claws on tarsus I, with few delicate versus numerous long tines. Juveniles of both species have the ventral plates and the OC and gland-pore bearing platelet separated but can be distinguished by the shapes of gnathosoma and claw I.

Compared with African species, *L. novus* turns out to be most similar to *L. portmanni*. Both are of about the same size, their length 206–289 and 217–289 µm, respectively, but the PD of *L. novus* is not as slender as in *L. portmanni* and the length ratio PD:AD is 2.6–2.7:1 in *L. novus* but 3.1–3.3:1 in *L. portmanni* (Bartsch 2013a).

Geographical distribution (Fig. 2) (cf. Bartsch 2013a):

Afrotropical Region. – Madagascar;

Australian Region. – Australia (Queensland – Moreton Bay, North Stradbroke Island, not Moreton Island).

***Limnohalacarus* species from the Afrotropical Region**

The *Limnohalacarus* species recorded from the Afrotropical region are: *L. africanus*, *L. cultellatus*, *L. fontinalis*, *L. major*, *L. marlieri*, *L. novus*, and *L. portmanni*. Relying on often vague descriptions, the most specific morphological characters of the six African species are:

Limnohalacarus africanus. Characters (according to Walter 1935, Green 1984 and Bartsch 2013a): Length 330 µm, OC and gland pore-bearing sclerite separated, ventral plates separated, GA of female with 8–9 (up to 12 according to Green 1984) pairs of gac and three pairs of pgs, its genital sclerites with two pairs of sgs; L:W of female gnathosoma 1.6:1 (Walter 1935: p. 74), but distinctly less in the deutonymph (Walter 1935: fig. 4), none of setae on tibiae I bipectinate, pectines on claws I J-shaped and bearing numerous long tines. Distribution: Burkina Faso (Upper Volta) (well at Banfora) (Walter 1935), West Cameroon (Debundska Lake) (Green et al. 1974), South Sudan (Lake No) (Green 1984).

Limnohalacarus fontinalis. Characters (according to Walter & Bader 1952 and Bartsch 2013a): Length 310–370 µm, gland pore included in elongate OC; ventral plates fused, L:W of gnathosoma 1.1:1; tibiae I to IV with 8, 7, 7, 6 setae, respectively, claws I with numerous long tines. Distribution: Kenya (Mombasa, from well with slightly saline water) (Walter & Bader 1952), South Sudan (Lake No) (Green 1984).

Limnohalacarus major. Characters (according to Bader 1968): Length 465 µm, distinctly larger than the other species (their length 224–370 µm), gland pore included in elongate OC; ventral plates fused, gnathosoma slender, its L:W 1.6:1. Distribution: DR Congo (Zaire) (Lake Tanganyika) (Bader 1968).

Limnohalacarus marlieri. Characters (according to Bader 1968 and André & N'Dri 2012): Length of female 305 µm, of male 350 µm. OC elongate, 1.4 times longer than wide. Length ratio PD:AD 3.4:1. Ventral plates fused. Female with eight pairs of gac posterior and posterolateral to GO. Number of gac along margins of area representing GA not known. Gnathosoma short, L:W 1.1–1.2:1. *Limnohalacarus marlieri* is very similar to both *L. fontinalis* and *L. portmanni*, it is classified as a junior synonym and omitted in the following key. Distribution: DR Congo (Zaire) (Lake Tanganyika) (Bader 1968).

Limnohalacarus portmanni. Characters (according to Bader 1967 and Bartsch 2013a): Length of females 224–250 µm, of males 217–289 µm, gland pore included in elongate OC; length ratio PD:AD 3.1–3.3:1; ventral plates fused, L:W of gnathosoma 1.2:1. Female with up to seven pairs of gac and three pairs of pgs, each genital sclerite with (two to) four sgs. All claws with J-shaped arranged pectines. Distribution: DR Congo (Zaire) (Lake Tanganyika, from shallow water sediment) (Bader 1968).

Characters of *Limnohalacarus cultullatus* and *L. novus* are outlined above.

Key to adult Afrotropical *Limnohalacarus* species

1a. All ventral plates separated. 2
1b. All ventral plates fused to a single shield. 3
2a. Claws on tarsus I with numerous distinct tines. .... ***africanus***
2b. Claws I apically and in middle with a few delicate tines, basally with narrow lamella bearing tines. .... ***cultellatus***
3a. Length of idiosoma exceeding 450 µm. L:W of gnathosoma 1.6:1. .... ***major***
3b. Length of idiosoma between 200–400 µm. L:W of gnathosoma 1.1–1.2:1. 4
4a. Length of idiosoma about 300–400 µm. ... ***fontinalis***
4b. Length of idiosoma between 200 and almost 300 µm. 5
5a. L:W of PD 2.1:1. Length ratio of PD:AD 3.1–3.3:1. .... ***portmanni***
5b. L:W of PD 1.9:1. Length ratio of PD:AD 2.6–2.7:1. .... ***novus***

Lobohalacarus weberi (Romijn & Viets, 1924)

Walterella weberi Romijn & Viets, 1924: 217–220, figs 3–6.
Lobohalacarus weberi, Schwoerbel 1955: 147, fig. 1; Green and MacQuitty 1987: 162, fig. 68A–D; Bartsch 2006: 128–130, fig. 5-8a–f, 2007: 74–80, fig. 2, 2011: 493–494, fig. 3A–C.
Walterella weberi quadripora Walter, 1947: 236–237, fig. 35.
Lobohalacarus weberi quadriporus, Viets 1959: pl. 4, fig. 42, pl. 5, fig. 47.
Lobohalacarus weberi gotoensis Imamura, 1970: 455–457, figs 1 and 2.
Lobohalacarus weberi tristanensis Bartsch, 1995: 171–175, figs 1–13.

Species with vague descriptions but expected to belong to *L. weberi*:
Halacarus processifer Walter, 1919a: 21–23, fig. 1–3 (only protonymph known);
Lobohalacarus hummelincki Viets, 1940: 191–194, fig, 1,2I and II, 3III and IV, 4;
Lobohalacarus bucharensis Jankovskaja, 1967: 109–114, fig. 1(1–7), 2(1–7), 3(1–6) (only deuto- and protonymph known);
Lobohalacarus bunurong Harvey, 1988: 363–365, figs 1–6.

Collecting data. Central Madagascar, Antananarivo, Anjazorobe, River Ranonisoanavola (larger stream E from main mountain chain), 1200 m asl, 13.2°C, 0.058 mS/cm, interstitial, 23 Jul. 2001 (MD 012). – South-eastern Madagascar, Fianarantsoa, Ionilahy, stream draining area Marosaro (S from River Ionilahy), 220 m, 21°C, 0.072 mS/cm, interstitial, 12 Aug. 2001 (MD 023). – South-eastern Madagascar, Fianarantsoa, Ionilahy, small stream crossing the railroad east of village, 200 m, 15 Aug. 2001 (MD027). – South-eastern Madagascar, Fianarantsoa, Andrambovato, stream 3 km E from the village, upstream from the cascade, 900 m, 20 Aug. 2001 (MD 038). – Southern Madagascar, Tulear, Tsimelahy, River Antarantsa, ca 1 km upstream from village, 300 m, 20.4°C, 0.171 mS/cm, interstitial, 04 Sep. 2001 (MD 058). – Central Madagascar, Antanarivo, Ankaratra, Reserve Manjakatompo, left affluent of River Mahiavona, EM Mantsina, 1750 m, 14.1°C, 0.003 ms/cm, interstitial, 08 Oct. 2001 (MD107). – Northern Madagascar, Antsiranana, Andapa, right affluent of River Ambendrana downstream, large cascade, 600 m, 11 Nov. 2001 (MD147).

Short description (Fig. 4A–E). *Female*: Length (with frontal spine included) 249–304 [25] µm, 228–273 (if frontal spine excluded). All Madagascar specimens with frontal spine, spine generally slender (Fig. 4C) and about 21–31 µm long, one female with 19 µm-long spine. Dorsal plates uniformly foveate, foveae 3 µm wide. AD and anterodorsal part of AE fused (Fig. 4A). Opposing edges of AD and PD truncate. OC oblong, without cornea or eye pigment. Dorsal setae minute, seven pairs present, most posterior pair on PD. Ventral plates AE, PE and GA fused to a shield (Fig. 4B). A pair of epimeral pores about levelling with aperture of legs II. GO extending anteriad to the level of apertures of legs IV. Area corresponding to PE with one rather short dorsal and two long ventral

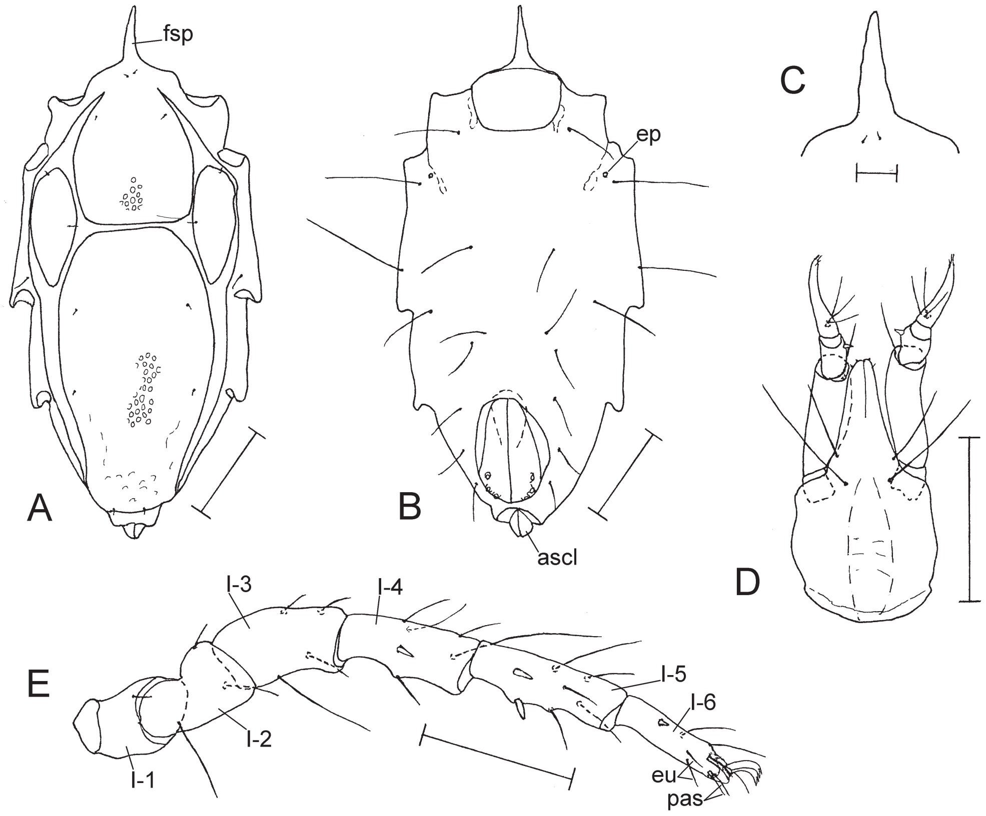

Fig. 4A–E. *Lobohalacarus weberi* (Romijn and Viets, 1924), female. **A.** idiosoma, dorsal; **B.** idiosoma, ventral; **C.** frontal spine; **D.** gnathosoma, ventral; **E.** leg I, medial. (A, B, D, E, scale = 50 µm; C, scale = 10 µm) (ascl, anal sclerite; ep, epimeral pore; eu, eupathid setae; fsp, frontal spine; pas, parambulacral setae; I-1 to I-6, trochanter, basifemur, telofemur, genu, tibia, and tarsus of leg I).

setae, genital area with four to five pairs of setae. Each genital sclerite with two to three gac. Gnathosoma slender, 1.8 times longer than wide. Rostrum almost extending to end of P-2 (Fig. 4D). P-2 with single dorsal seta, P-3 with medial spur. Length ratio leg I:idiosoma 0.8:1, following legs somewhat shorter. Telofemur and genu I equal in length (Fig. 4E). Telofemora III and IV with 2/0 dorsal/ventral setae. Genu I with two ventral setae, generally one seta spur-, the other seta-like, rarely both setae spur-like. Tibia I ventrally with two pairs of setae, one pair spiniform, one bristle-like; ventral flank of tibiae II to IV with (zero to) one smooth and (one to) two pectinate setae. Tarsus I with ventromedial spur, apically with pair of eupathidia (short sensory setae) and pair of doubled pas (Fig. 4E); tarsus III with 4/1 dorsal/ventral setae, and tarsus IV with 3/1 setae. Lateral fossa membrane of tarsus I enlarged, its length 7 µm, height 6 µm, on following tarsi lateral and medial fossa membrane small both in length and height. Claws on tarsus I smaller than those of following tarsi.

To get an idea of variants in respect to external characters, as commonly found in *Lobohalacarus weberi* (Bartsch 1995, 2007, 2011), details of 25 uncleared females were examined in a drop of glycerine, but some females were damaged or the characters in question obscured. The character studied were (1) frontal spine: present [25]; (2) number of gac per genital sclerite: 2 [12], 3 [38]; (3) number of pgs in each half of genital plate: 3 [1], 4 [22], 5 [26]; (4) combination of spines (sp) and bristles (br) on genu I: sp/br [49], sp/sp [1]; (5) number of dorsal/ventral setae on telofemur III: 2/0 [47], 2/1 [1]; (6) number of dorsal/ventral setae on telofemur IV: 2/0 [49], 2/1 [0]; (7) number of pectinate (p) + smooth (s) setae on tibia II: 2p+1s [46], 1p+1s [4]; (8) number of pectinate (p) + smooth (s) setae on tibia III: 2p+1s [31], 1p+1s [14]; (9) number of pectinate (p) + smooth (s) setae on tibia IV: 2p+1s [48], 1p+1s [0]; (10) number of dorsal/ventral setae on tarsus III: 4/1 [43], 4/0 [1], 3/0 [0]; (11) number of dorsal/ventral setae on tarsus IV: 4/1 [1], 3/1 [45], 3/0[2].

Male: Not present.

Juveniles: Length (frontal spine excluded) of deutonymphs 230–247 [3] µm, protonymphs 210 [2] µm and larvae 130–162 [4] µm. All instars with slender frontal spine, in one larva that spine very delicate. Ventral plates AE, PE and GA separated. Tarsus I with three dorsal setae, dorsolateral solenidion, enlarged lateral fossa membrane, ventromedial spur, and two ventral eupathidia.

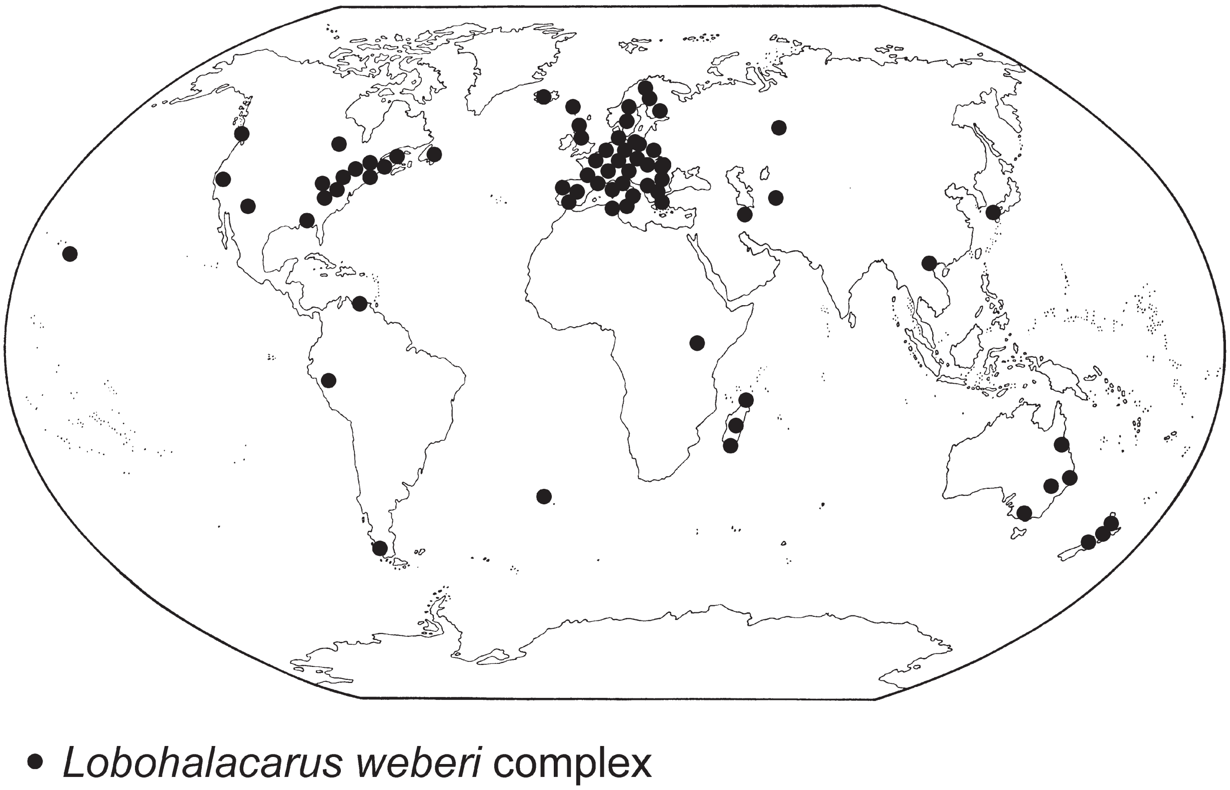

Fig. 5. Records of *Lobohalacarus weberi* (Romijn & Viets, 1924) and species of the *L. weberi* complex.

Biology. Eighteen of 26 females enclosed an egg, one female two eggs. The smallest egg was globular and had a size of 40 x 40 µm, the largest one reached a size of 110 x 56 µm.

No male was found in the material from Madagascar. Though *L. weberi* is one of the very wide-spread and commonly recorded species reliable records of males are lacking.

Remarks. Two easily recognized characters used for identification of *Lobohalacarus weberi* are the frontal spine and the ventral shield. These characters are known to vary, though rarely. In the samples from Madagascar, all individuals have a pointed frontal spine and a ventral shield. In almost all Madagascan specimens the frontal spine is very slender, similar to that illustrated by Schwoerbel (1955: fig. 1(4)). In general, the spine is somewhat shorter but wider (cf. Romijn & Viets 1924: figs 3 and 4; Bartsch 2006: fig. 5–8a and b). Among material from Inaccessible Island, Tristan da Cunha Islands, three out of six females had no frontal spine. In two of these three specimens the anterior margin of the idiosoma was evenly arched, in one the spine was reduced to a hood-like process (Bartsch 1995: figs 12 and 13). Out of 92 individuals from New Zealand, one female had no spine but an evenly rounded anterior margin, 91 females had a frontal spine (Bartsch 2007: fig. 2A–C). In the same material one of the females had no ventral shield, instead AE, PE and GA were separated (Bartsch 2007: fig. 2C). *Lobohalacarus weberi* is expected to be highly variable in its morphology rather than to be represented by several cryptic species. Studies on the influence of habitat parameters on character expression do not exist.

Geographical distribution of *Lobohalacarus weberi* and the *Lobohalacarus weberi* complex (Fig. 5) (cf. Bartsch 2008a, b, 2011, 2014a; Pešić et al. 2010; Fritz & Feminella 2011; Stolbov et al. 2018):

Afrotropical Region. – Kenya – Madagascar – Tristan da Cunha Islands;

Palaearctic Region. Europe: – Austria – Belgium – United Kingdom (England, Northern Ireland, Scotland) – Bulgaria – Denmark – Faeroerne – Finland – France – Germany – Greece – Hungary – Iceland – Italy – Macedonia – Monte Negro – Poland – Portugal – Romania – Switzerland – Spain – Sweden – The Netherlands. Northern Africa: – Tunisia. Asia: – Iran – Japan (*L. weberi gotoensis*—Imamura 1970) – Russia (Tyumen region) – Uzbekistan (*Lobohalacarus bucharensis*—Jankovskaja 1967);

Nearctic Region. – Canada (British Columbia, New Brunswick, Newfoundland, Ontario, Quebec). – United States (Alabama, Arizona, California, Colorado, Georgia, Illinois, New Hampshire, New Mexico, New York, North Carolina, Rhode Island, Tennessee, Virginia);

Neotropical Region. – Chile (Magallanes) – Peru (Lake Levandera, *Lobohalacarus processifer*) – Venezuela (near Higuerote, *Lobohalacarus hummelincki*);

Australian Region. – Australia (New South Wales (*Lobohalacarus* sp.), Queensland, Victoria (*Lobohalacarus bunurong* and *Lobohalacarus* sp.), the author expects these specimens to belong to the *L. weberi* complex). – New Zealand (North and South Island);

Pacific Islands. – Hawaiian Islands.

Porohalacarus alpinus **(Thor, 1910)**

Halacarus alpinus Thor, 1910. 348–351, figs 1 and 2.

Porohalacarus alpinus, Thor 1922: 110, 111; Bartsch 1973: 117–119, figs 1–21, 2007: 80–82, fig. 3, 2011: 497–498, fig. 6A–D; Green & MacQuitty 1987: 164, fig. 69A–D.

Porohalacarus alpinus alpinus Viets 1927: 465–469, figs 3–8.

Porohalacarus alpinus alpinus, Bartsch 1987: 85, 2006: 130–132, figs 5-9a–f.

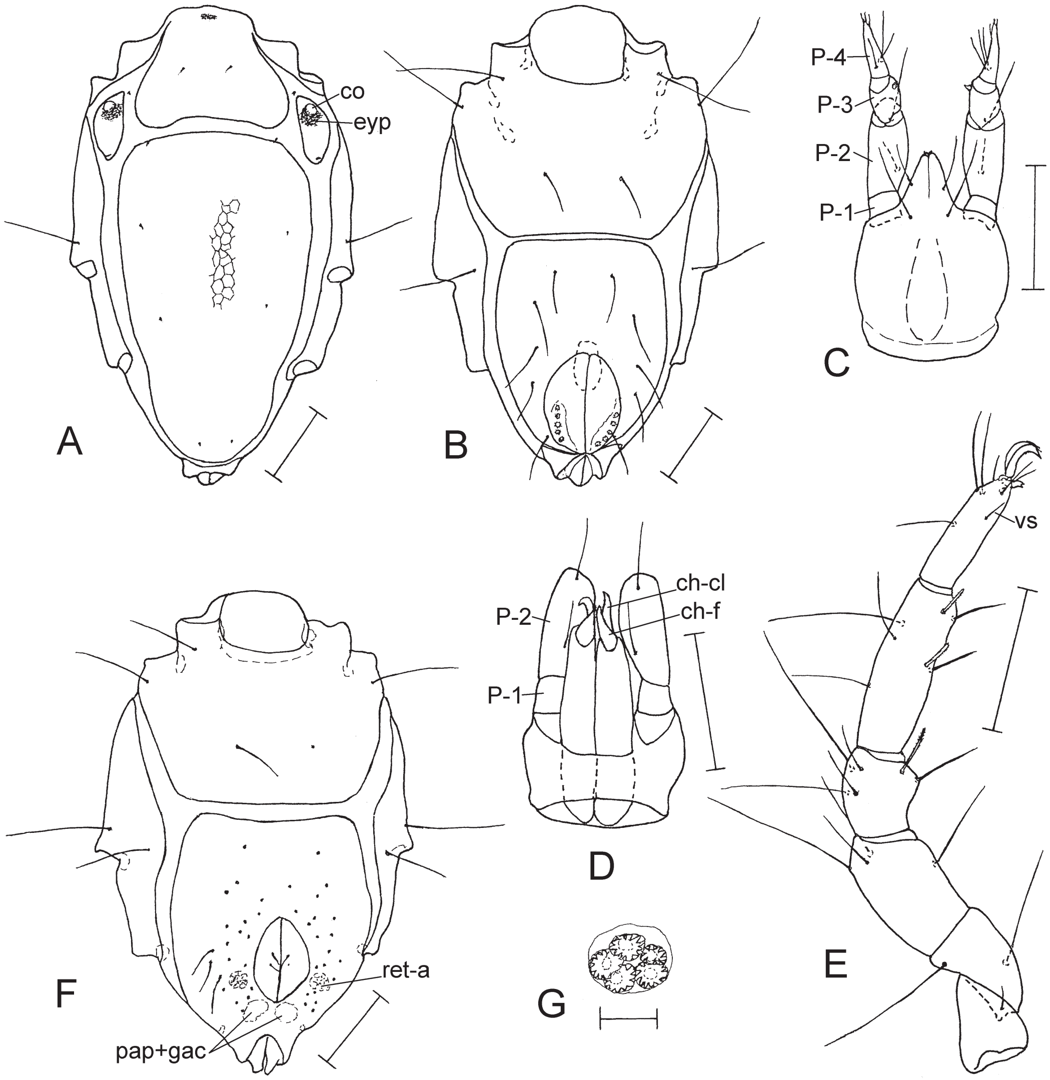

Fig. 6A–G. *Porohalacarus alpinus* (Thor, 1910). **A.** idiosoma, dorsal, female; **B.** idiosoma, ventral, female; **C.** gnathosoma, ventral, female; **D.** gnathosoma, dorsal (P-3 and P-4 omitted), female; **E.** leg I, medial, female; **F.** idiosoma, ventral, male; **G.** papilla with genital acetabula, male. (A–F, scale = 50 µm, G, scale = 10 µm) (ch-cl, cheliceral claw; ch-f, dorsal flap-like process of chelicera; co, cornea; eyp, eye pigment; pap+gac, papilla with genital acetabula; P-1 to P-4, first to fourth palpal segment; ret-a, reticulate area; vs, ventral seta).

Porohalacarus alpinus brachypeltatus Viets, 1927: 469, figs 9, 10.

Porohalacarus alpinus brachypeltatus, Bartsch 1987: 85–86, figs 2 and 3, 2006:132, 5-10a, b.

Collecting data. Southern Madagascar, Tulear, Tsimelahy, River Antarantsa, ca 1 km upstream from village, 300 m, 20.4°C, 0.171 mS/cm, interstitial, 04 Sep. 2001 (MD 058). – Northern Madagascar, Antsiranana, Sambava, Maroambihy, left affluent of River Lokoho upstream from the village, 90 m, 26.0°C, 0.010 mS/cm, interstitial, 12 Nov. 2001 (MD149).

Short description (Fig. 6A–G). *Female*: Length 280–318 µm [10]. Dorsal plates reticulate, in anterior part of PD reticulation honey comb-like, in posterior part presenting a longitudinal pattern. OC with cornea. AD and OC with spots of black eye pigment (Fig. 6A), that on AD narrow, 13 µm wide, spot on OC 15–18 µm in diameter. Dorsal setae very small, their position as illustrated in Fig. 6A, ds-6 on PD removed from posterior margin. Surface of ventral plates finely porose. Genital plate with (four to) five pairs of pgs, each genital sclerite with (four to) five external acetabula. Interval between anterior margin of GP and that of GO somewhat longer than the latter's length (Fig. 6B). Gnathosoma hardly longer than wide (Fig. 6C). Rostrum shorter than gnathosomal base and hardly extending to middle of P-2. Palps four-segmented, lateral to rostrum, i.e., distance between pair of P-1 more than their width. P-2 with two dorsal setae (Fig. 4D), P-3 with medial spur. Chelicera with claw and wide, flap-like dorsal process. Legs slender, shorter than idiosoma, length of legs I and IV 0.7 times that of idiosoma. Genu I much shorter than telofemur I (Fig. 6E). Tibiae I to IV with 4, 3, 2, 2 ventral setae, in addition tibiae III and IV with short, faintly pectinate mid-segmental medial seta. Tarsus I with single slender ventral seta (Fig. 6E), following tarsi without ventral setae. Paired claws with delicate tines.

Male: Length of idiosoma 286 µm, width 185 µm [1]. Dorsal aspect similar to that of females, plates similar in shape, length:width ratio and ornamentation. Length of AD 65 µm, width 93 µm, length of OC 40 µm, width 20 µm, length of PD 188 µm, width 130 µm. GP and AP fused to GA, length of that plate 148 µm, width 121 µm, GA slightly wider than female GP. Length of male GO 50 µm, width 33 µm, distance between GO and anterior margin of GA 58 µm, i.e., 1.1 times longer than GO. GA with 19 pgs on one side, 20 on the other side; one of genital sclerites with one, the other with two sgs. Lateral to posterior part of GO a circular area present, 10–12 µm in diameter, with internal bars forming reticulate ornamentation (Fig. 6F, ret-a). Posterior to GO a pair of dome-like areas, 12–14 µm in diameter, each with five gac (Fig. 6G). Each acetabulum, about 7 µm in diameter, with an inner central papilla, 3 µm in diameter, and surrounded by inward crooked teeth. Length of spermatopositor slightly more than that of GO. Shape of gnathosoma and legs similar to those of females.

Juveniles: With two nymphal and a larval instar. Length of deutonymphs 240–263 µm [6], of protonymphs 186–210 µm [6] and of larvae 140–185 [6] µm. All instars with dark spots of eye pigment.

Biology. Fifteen out of 20 females were ovigerous, the other five held no eggs. The size (length x diameter) of the eggs was between 55 x 63 µm and 88 x 75 µm.

Remarks. The females in the Madagascan material have five (rarely four) external acetabula on each genital sclerite. In populations from other parts of the world the number of acetabula is known to vary between four and nine (Bartsch 2011). In Europe two varieties are known, *P. a. alpinus* and *P. a. brachypeltatus*. Discriminating characters in females are the length of the idiosoma, i.e., 297–371 versus 248–270 µm, and the position of the GO in relation to length of the GP, namely distance from anterior margin of GO to that of GP about the same versus about half the length of GO, respectively (Viets 1927: fig. 6 versus fig 9; Bartsch 2006: fig. 5-9b versus fig. 5-10a). Similar, nymphs of *P. a. alpinus* have, in contrast to *P. a. brachypeltatus*, a larger distance between the area with genital acetabula and the anterior margin of GP. A rather inconspicuous difference is that the PD of *P. a. alpinus* is slightly longer than that of *P. a. brachypeltatus*. In the first mentioned the ds-3 insert immediately adjacent or in the margin of the PD, in the latter within the narrow band of striated integument. The Madagascan individuals belong to *P. a. alpinus*.

In general, all adults in populations of *P. alpinus* are females. The above mentioned male is one of the very rare exceptions. A former record of a male is one of *P. a. brachypeltatus*. It was found among more than 2500 slide-mounted adults, all extracted from a population living in Northern Germany which inhabited a small former peat ditch, now filled with rapidly growing *Sphagnum* sp. (Sphagnales) (Bartsch 1987). The water in the peat ditch was acidic, had a low ionic concentration and a sparse fauna (some few cladocerans, rotifers and testaceans). Differences between the males, from Madagascar (*P. a. alpinus*) and northern Germany (*P. a. brachypeltatus*), are the larger size, 286 µm versus 254 µm, and a higher number of pgs, namely 39 versus 20 pgs. The morphological differences between the two forms *P. a. alpinus* and *P. a. brachypeltatus* raises the question whether these are two separate species, subspecies or ecotypes? In northern Europe, *Porohalacrus a. alpinus* inhabits a wide range of substrata, slightly acidic to alkaline and even oligohaline brackish water, oligo- and mesotrophic lakes, ponds and banks of slow flowing rivers, substrata rich in microcaverns, e.g. dense colonies of small mussels (*Dreissena* sp.), colonies of sponges, bryozoans, mosses, and biofilms on vascular plants, all these habitats have a

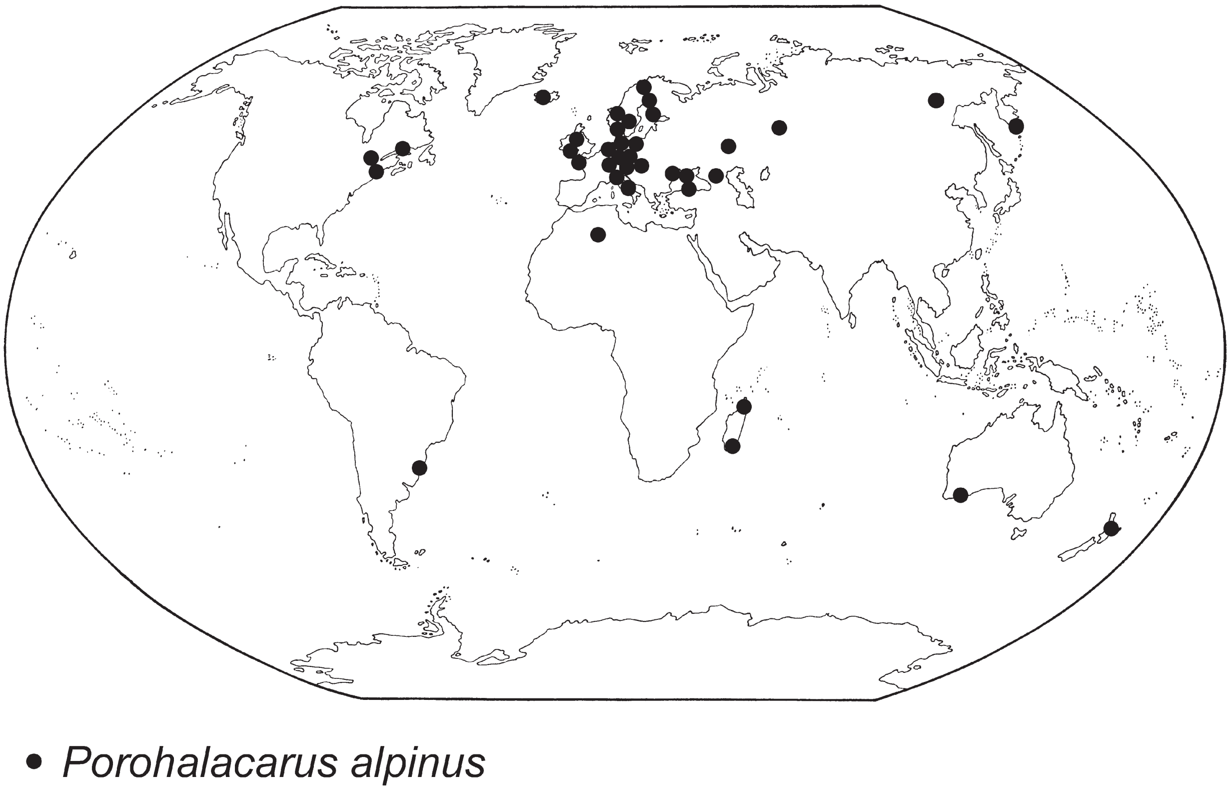

Fig. 7. Records of *Porohalacarus alpinus* (Thor, 1910) (*Porohalacarus alpinus brachypeltatus* included).

rich meio- and microfauna and -flora. In contrast, *P. a. brachypeltatus* has been taken only in strongly acidic *Sphagnum* peats with sparse associated meiofauna. Judging by the gut content of *P. a. alpinus*, namely brownish, with darker and lighter particles, these mites are carnivorous. In contrast, the gut content of *P. a. brachypeltatus* is greenish, suggesting that the mites are phytophagous. Is *P. alpinus brachypeltatus* a degenerate (impoverished) form, because of its life in an environment with low concentration of cations and meagre diet? Both molecular and experimental studies, namely rearing of the mites over several generations under different environmental conditions, may give an answer. Phenotypic plasticity in freshwater crustacea has been documented more than a century ago (Woltereck 1909), and plasticity is not restricted to arthropods, Cattau et al. (2018) recently described a rapid morphological change in a bird of prey.

Geographical distribution (Fig. 7) of both *P. a. alpinus* and *P. a. brachypeltatus* (Viets 1956; Green & MacQuitty 1987; Bartsch 2007, 2009, 2011; Tolstikov et al. 2005; Semenchenko et al. 2010; Stolbov et al. 2018; Pepato & da Silva Conceição 2019 in press):

Afrotropical Region. – Madagascar (new record);

Palaearctic Region. Europe: – Austria – Belgium – Great Britain (England, Scotland, Wales) – Denmark – Finland – France – Germany – Hungary – Iceland – Italy – Norway – Poland – Russia (Saratov—Volga Biological Station) – Sweden – Switzerland – The Netherlands – Ukraine. Northern Africa: – Algeria. Asia: – Turkey – Russia (Kamchatka, Sakha Republic, Tyumen region);

Australian Region. – Australia (Western Australia—Esperance). – New Zealand (North Island).

Nearctic Region. – United States (New Hampshire, Rhode Island). – Canada (Ontario, Quebec);

Neotropical Region. – Brazil (Rio Grande do Sul—*Porohalacarus* cf. *alpinus*).

Ropohalacarus pallidus Bartsch, 2013

Ropohalacarus pallidus Bartsch, 2013b: 80–84, figs 1a–h, 2a–g.

Collecting data. Central Madagascar, Antananarivo, Anjazorobe, River Ranonisoanavola (larger stream E from main mountain chain), 1200 m asl, 13.2°C, 0.058 mS/cm, interstitial, 23 Jul. 2001 (MD 012). South-eastern Madagascar, Fianarantsoa, Ionilahy, stream draining area Marosaro (S from River Ionilahy), 220 m, 21°C,

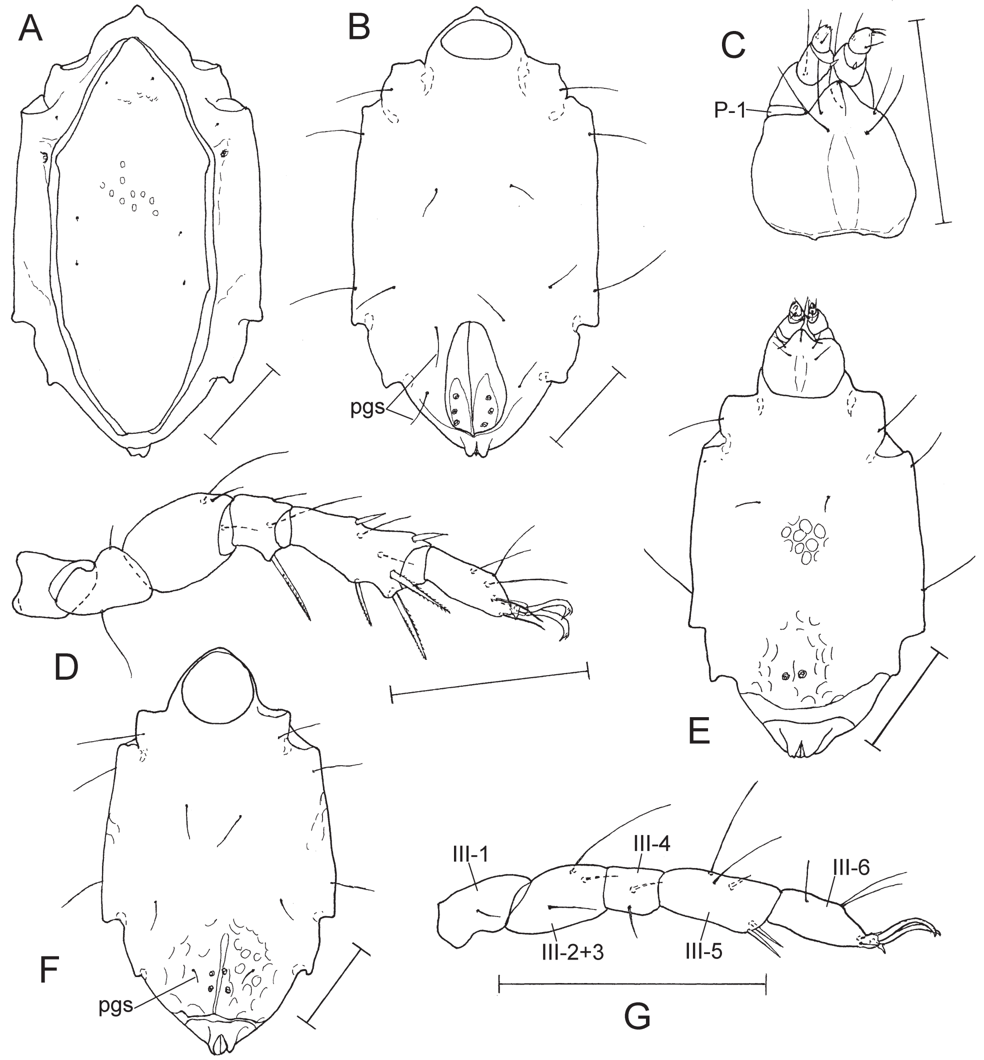

Fig. 8A–G. *Ropohalacarus pallidus* Bartsch, 2013. **A.** idiosoma, dorsal, female; **B.** idiosoma, ventral, female; **C.** gnathosoma, ventral, female; **D.** leg I, medial, female; **E.** idiosoma and gnathosoma, ventral, protonymph; **F.** idiosoma, ventral, deutonymph, **G.** leg III, lateral, larva. (Scale = 50 µm) (pgs, perigenital seta(e); P-1, first palpal segment; III-1, III-2+3, III-4, III-5, III-6, trochanter, femur, genu, tibia and tarsus of leg III).

0.072 mS/cm, 12 Aug. 2001, interstitial (MD 023). – South-eastern Madagascar, Fianarantsoa, Ionilahy, small stream crossing the railroad east from village, 200 m, 15 Aug. 2001 (MD 027). – South-eastern Madagascar, Fianarantsoa, Andrambovato, stream 3 km E from the village, upstream from the cascade, 900 m, 20 Aug. 2001 (MD 038). – Southern Madagascar, Tulear, Tsimelahy, River Antarantsa, ca 1 km upstream from village, 300 m, 20.4°C, 0.171 mS/cm, 04 Sep. 2001, interstitial (MD 058). – Tulear, Andohalela, Isaka, spring area S pass RIP 118 (km36), 700 m, 16.0–18.4°C, 0.055–0.060 mS/cm, 10 Sep. 2001, interstitial (MD 071). – Northern Madagascar, Antsiranana, Andapa, right affluent River Ambendrana downstream, large cascade, 600 m, 11 Nov. 2001 (MD147).

Short description (Fig. 8A–G). *Female*: Length 203–245 [30] µm, idiosoma pale, about 1.8 times longer than wide, its anterior and posterior part narrowed. Eye pigment lacking. AD and PD fused to an elongate dorsal shield (Fig. 8A). Ventral shield extending dorsad and including AE, PE, GA (Fig. 8B) and parts corresponding to OC. Integument of dorsal shield with delicate porosity and faint foveate ornamentation, ventral plates almost smooth. Dorsal setae very small, ds-1, ds-3 and ds-4 in dorsal shield, ds-2 in dorsal part of ventral shield. Adanal setae lacking. Gland pores lacking. Area of ventral shield

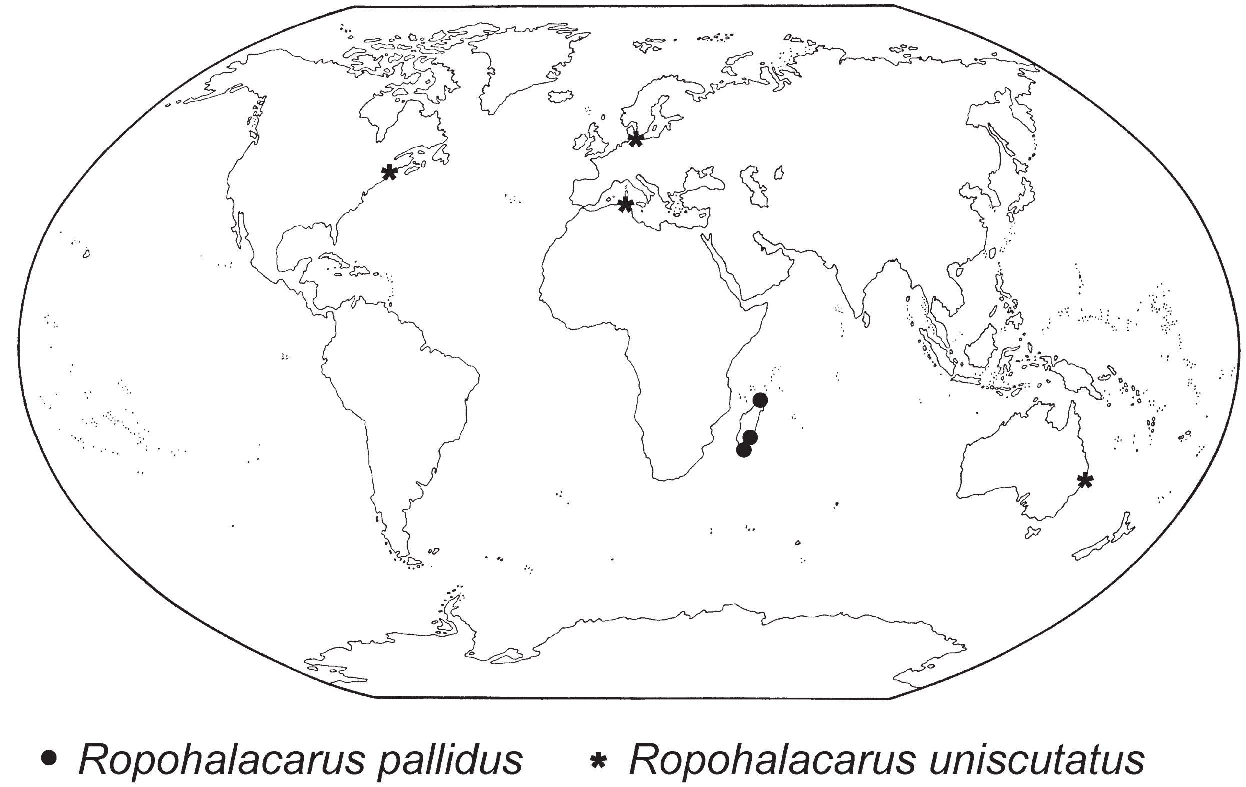

Fig. 9. Records of *Ropohalacarus pallidus* Bartsch, 2013 (black spot) and *R. uniscutatus* Bartsch, 1982 (asterisk).

representing AE with two pairs of marginal and one pair of ventral setae, areas of PE each with one marginal and one ventral seta, and that of GP with two perigenital setae. Marginal setae of idiosoma longer than ventral setae. Three pairs of genital acetabula arranged in posterior part of genital sclerites. Gnathosoma slightly wider than long (Fig. 8C). Palps four-segmented, extending beyond short, conical rostrum. Short palps and rostrum visible in dorsal aspect. Legs distinctly shorter than idiosoma (length ratio leg I:idiosoma equalling 0.5:1). Distance between apertures of pairs of legs II and III almost equal to half the length of idiosoma (in the other genera length of idiosoma more than twice the distance between these apertures). Trochanter I in one of the females studied with delicate medial seta, in general no seta present. Ventral setae on genu I and three ventral setae on tibia I bipectinate (Fig. 6D).

Male: Not present.

Juveniles: Length of deutonymph 173–226 μm [6], of protonymph 122–173 μm [3], of larva 113–128 μm [2]. Nymphs with AD and PD separated by striated integument, remnants of ocular plates and marginal part of epimeral plates fused. Ventral plates AE, PE and GP fused to a single ventral shield, no fissure between area representing AE and GP. Ventral plates delicate; ornamented with foveae. In both nymphal instars area representing AE with three pairs of setae (Fig. 8E and F). In deutonymph area representing PE with one pair of marginal and one of ventral setae (Fig. 8F) and area of GP with one pair of pgs. Protonymphal PE solely with pair of marginal setae. Larval tarsus III, just as tarsi III of following instars, with three dorsal setae, namely two fossary setae and one solenidion (Fig. 8G).

Biology. Of 32 females studied 13 (41%) were ovigerous. In general a single egg was present, its size (length x diameter) between 45 x 43 μm and 70 x 43 μm.

Remarks. As illustrated in Bartsch (2013b: fig. 2e), AD and PD of the deutonymphs, as also those of the protonymphs, are separated from each other by a narrow, transverse area of striated integument, but both deuto- and protonymphs have a ventral shield, including the anterior and posterior epimeral and the genital plate (AE, PE and GP). In contrast to Bartsch (2013b: fig. 2f, 2g), no transverse rupture was recognized in the new material studied (three deutonymphs, one protonymph). In the majority of halacarids the adults have solid exoskeletal plates. In several species these are fused to a dorsal or ventral shield. Sometimes, though rarely, both the dorsum and venter are covered by a solid shield whereas the juveniles have the plates separated by tensible striated integument. Consequently juveniles can grow due to expansion of the striated integument between the dorsal and the ventral plates (as illustrated in *Halacarellus subterraneus* — Bartsch 1972 fig. 28A, B versus C, D and E, F versus G, H) whereas the adults can hardly increase in size. An exception is *Ropohalacarus pallidus*. In the juveniles of this species, the foveate textured integument of the ventral plates is expected to allow a slight dilatation (cf. Bartsch 2013b). Data on the thickness of the pro- and epicuticula are lacking.

No males have ever been found, neither of *Ropohalacarus pallidus* nor of the second species, namely *R. uniscutatus*, but the number of specimens studied to date is small (< 50 individuals).

Compared with other Madagascar halacarids, *R. pallidus* is in its general shape most similar to *Porohalacarus alpinus*. Distinguishing characters are: the pale idiosoma (versus prominent spots of eye pigment), the dorsal and ventral shield (versus dorsum with AD, OC and PD, venter with AE, PE and GP), the ornamentation of dorsal shield or plates, delicately foveate versus reticulated with longitudinal polygons, the position of apertures of legs III, in posterior third of idiosoma (0.7) versus in its middle (0.5).

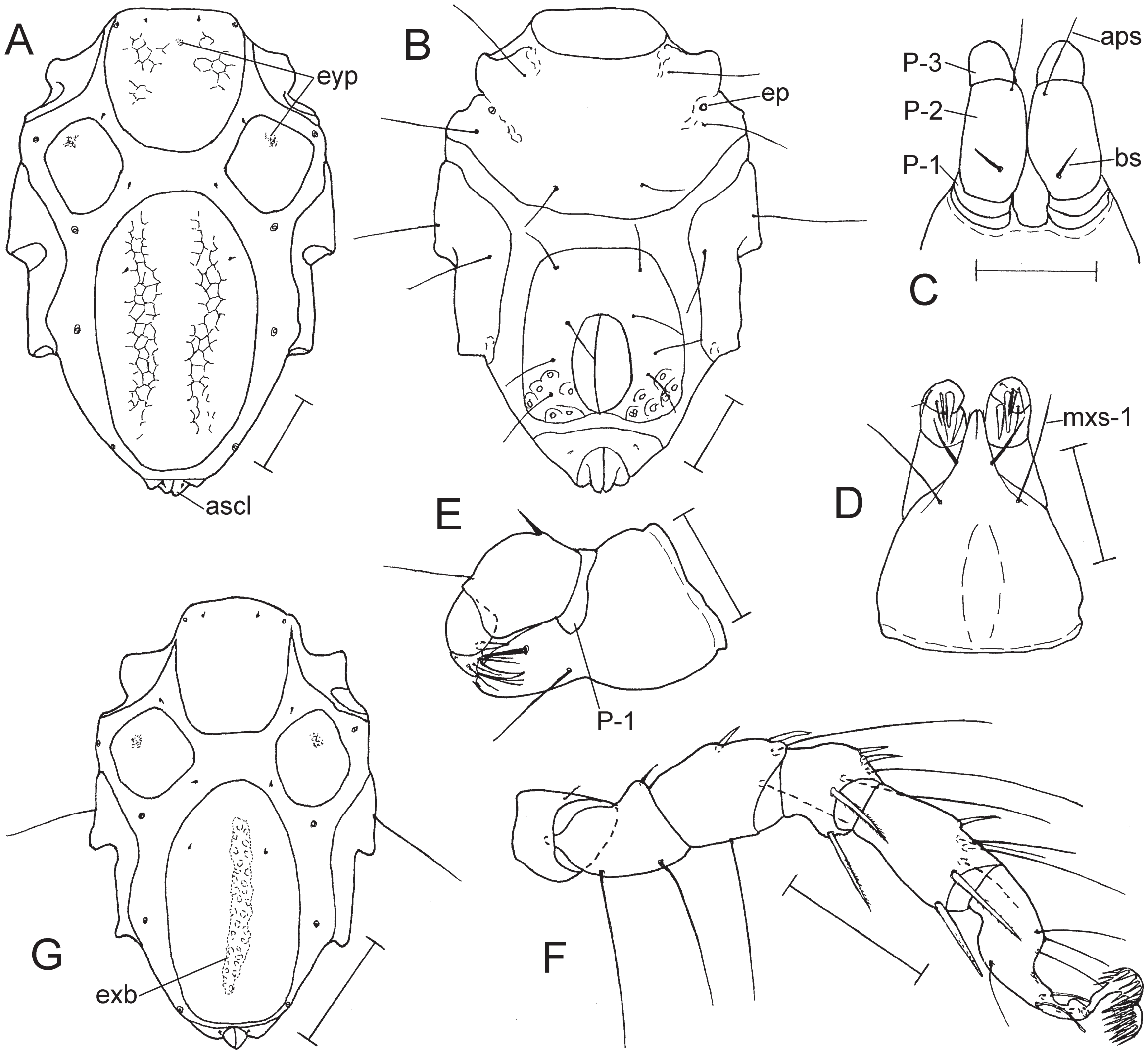

Fig. 10A–G. *Soldanellonyx monardi* Walter, 1919. **A.** idiosoma, dorsal, female; **B.** idiosoma, ventral, female; **C.** part of gnathosomal base with P-1, P-2 and P-3, female; **D.** gnathosoma, ventral, female; **E.** gnathosoma, lateral, female; **F.** leg I, ventromedial, female; **G.** idiosoma, dorsal, protonymph. (Scale = 50 µm) (aps, apical seta on second palpal segment; ascl, anal sclerite; bs, basal seta on second palpal segment; ep, epimeral pore; exb, excretory bar; eyp, eye pigment; mxs-1, basal maxillary seta; P-1, P-2, P-3, first, second and third palpal segment).

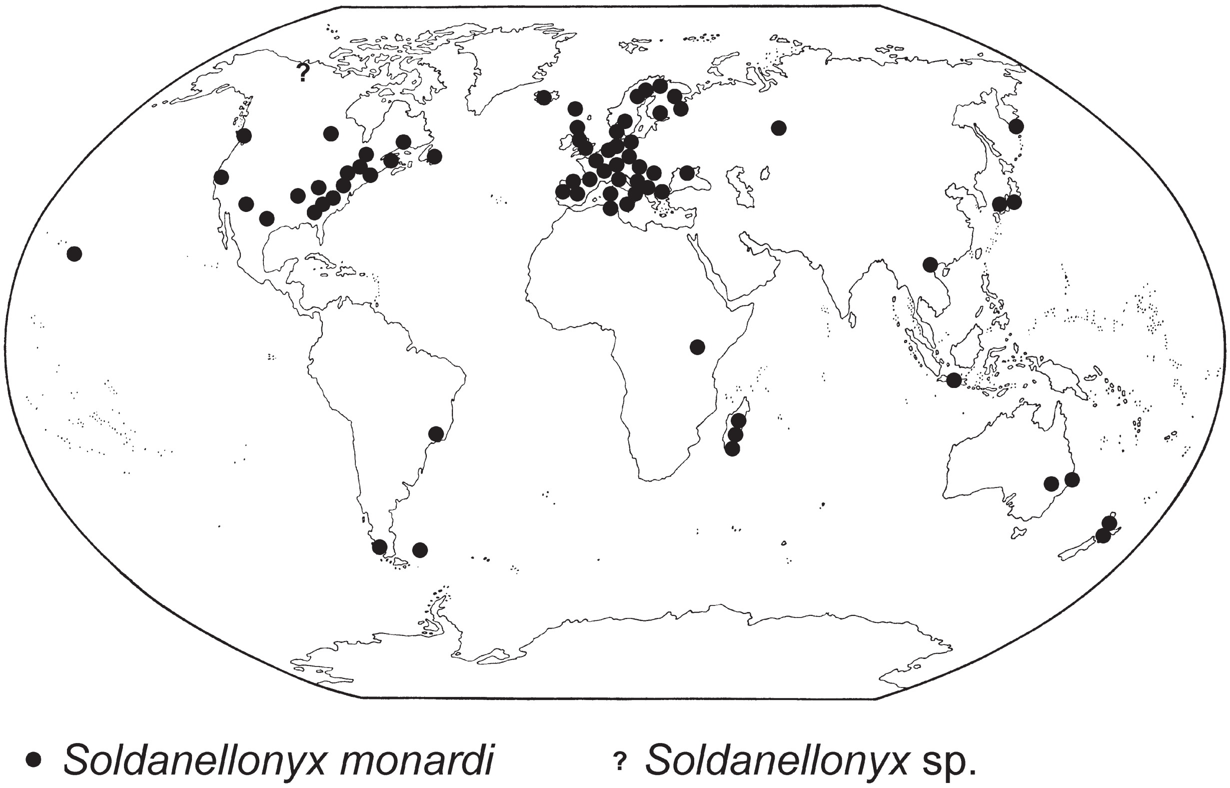

Fig. 11. Records of *Soldanellonyx monardi* Walter, 1919.

Geographical Distribution (Fig. 9):
Afrotropical Region. – Madagascar (Bartsch 2013b and present record).

***Soldanellonyx monardi* Walter, 1919**

S. monardi Walter, 1919b: 238–241, fig. 4–7.
S. monardi, Green & MacQuitty 1987: 156, fig. 65A–C; Bartsch 2006: 142, 143, fig. 5-19a–f, 2007: 82, 83, fig. 3, 2011: 502, fig. 11A–C, 2014a: 167–169, fig. 2A–K.
S. monardi sarangaensis Viets, 1929: 32–34, fig. 5–7(a, b).

Subspecies of uncertain position but expected to belong to *S. monardi* are:
S. monardi hyogoensis Imamura, 1981: 292 (described in Imamura 1959: 56, 57, fig. 2a–e).
S. monardi japonicus Imamura, 1971: 334–336, figs 2a–c, 3a–d.

Collecting data. Central Madagascar, Antananarivo, Anjazorobe, River Ranonisoanavola (larger stream E from main mountain chain), 1200 m asl, 13.2°C, 0.058 mS/cm, interstitial, 23 Jul. 2001 (MD 012). – South-eastern Madagascar, Fianarantsoa, Andrambovato, stream 3 km E from the village, upstream from the cascade, 900 m, 20 Aug. 2001 (MD 038). – Southern Madagascar, Tulear, Tsimelahy River Antarantsa, ca 1 km upstream from village, 300 m, 20.4°C, 0.171mS/cm, interstitial, 04 Sep. 2001 (MD 058). – Central Madagascar, Antananarivo, Ankaratra, Reserve Manjakatompo, left affluent of River Mahiavona, EM Mantsina, 1750 m, 14.1°C, 0.003 ms/cm, interstitial, 08 Oct. 2001 (MD 107).

Short description (Fig. 10A–G). *Female*: Length 270–335 µm [8]. With faint spots of brown eye pigment in anteromedian part of AD and anterior part of OC (Fig. 10A). AD, OC and PD with reticulate ornamentation, reticulation most distinct within pair of faint costae of PD. Pairs of glp-1 to glp-5 and ds-1 to ds-4 as illustrated, ds-5 lacking, ds-6 on anal cone. Delicate punctation of ventral plates presenting reticulate pattern. AE, PE and GP separated. AE with pair of epimeral pores (Fig. 10B). Each PE with one ventral and lateral but no dorsal seta. Gnathosoma somewhat wider than long (Fig. 10D). Pair of palps attached dorsally, distance between P-1 less than their width (Fig. 10C). P-2 somewhat flattened, length 1.3 times the height (Fig. 10E); basal seta on P-2 short; spiniform, distal seta long and slender. P-3 with large medial spine, its length 0.9 of that of P-3. P-4 ending with a similar wide spine. Legs shorter than idiosoma, length of legs I and IV about 0.6 and 0.7 times that of idiosoma, respectively. Length of telofemur I 1.5 times the height. In addition to long, slender setae, telofemur, genu and tibia of leg I with 2, 2 and 1 short and spiniform dorsal setae and 0, 2, 2 long ventral spines, respectively. Pair of ventral spines on genu I distinctly, on tibia I faintly bipectinate. Claws I with solid, mushroom-like arranged tines (Fig. 10F), tines on claws on following tarsi in J-shaped arrangement.

Male: Not present.

Juveniles: Length of deuto-, protonymphs and larvae 205–285 [8], 180–255 [7] and 143–148 µm [2], respectively.

Biology. Of eight females studied six held eggs. Size of eggs 10 x 10 to 40 x 45 µm (length x diameter). If present, the excretory material is in form of small, brown globuli. These are concentrated within a rod-like structure (Fig. 10G).

Remarks. *Soldanellonyx monardi* is presently the only *Soldanellonyx* species recorded from the Afrotropics. *Soldanellonyx chappuisi* Walter, 1917 and *S. visurgis* Viets, 1959, as *S. monardi* reported from several continents, have as yet not been taken but are expected to be found in future studies in Africa or the Afrotropical region. *Soldanellonyx chappuisi* and *S. visurgis* have, in contrast to *S. monardi*, more slender telofemora I (length more than 1.5 times the height), four ventral bristles or spines on tibia I (versus two), more slender and longer P-2 (length more than twice the height) and the two dorsal setae on P-2 are similar-sized (versus basal seta less than half the length of distal seta). In addition, no epimeral pores are seen in *S. chappuisi* and S. *visurgis* but these are present in *S. monardi*.

Another six *Soldanellonyx* species are described, one species has been collected in both southern Japan and Kamchatka, each one of the others from a single geographical region, four from Japan, one from the Lake Baikal.

In *Soldanellonyx monardi*, as also in *S. chappuisi* and *S. visurgis*, males are extremely rare or absent. Those recorded by Sokolov (1952), Efford (1959) and Imamura (1981) need confirmation. The author expects the males of *S. monardi* to differ from females by a high number (>20) of pgs arranged around the GO and, of course, the presence of the spermatopositor. Slight differences in the outline of the GA, as described by Sokolov (1952) and Imamura (1981), are commonly found in females. Sokolov (1952: fig. 91,4) presented an illustration of a male GA with a slightly larger number of genital acetabula (11–12 pairs) and pgs (5–6 pairs) but else similar to that of females, the typical spermatopositor is not illustrated. Imamura (1981) described the 'penis skeleton' as having four hook-shaped claws; the number of the genital acetabula is similar to that of females. Hook-shaped claws on the spermatopositor are else unknown in halacarid males and those mentioned by Imamura (1981) may represent the genital spines of an ovipositor. Efford (1959) did not present any morphological details.

Geographical distribution (Fig. 11) (of *S. monardi* and its subspecies) (Fig. 8) (Bartsch 2008a, 2011, 2014a; Tolstikov et al. 2005; Pešić et al. 2010; Stolbov et al. 2018; Pepato & da Silva Conceição, in press):

Afrotropical Region. – Kenya – Madagascar;
Palaearctic Region. Europe: – Austria – Belgium – United Kingdom (England, Northern Ireland, Scotland, Wales) – Bulgaria – Crimea – Croatia – Denmark – Faeroerne – Finland – France – Germany – Hungary – Iceland – Italy – Luxemburg – Macedonia – Monte Negro – Portugal – Romania – Russia (Karelia, Kola Peninsula, Lake Onega) – Switzerland – Spain – Sweden – The Netherlands. Northern Africa: – Tunisia. Asia: – Japan – Russia (Kamchatka, Tyumen region);
Oriental Region. – Indonesia (Java) – Vietnam;
Australian Region. – Australia (New South Wales, Queensland). – New Zealand (North Island);
Pacific Islands. – Hawaiian Islands;
Nearctic Region. – Canada (British Columbia, Manitoba, New Brunswick, Newfoundland, Ontario, Quebec). – United States (Alabama, Arizona, California, Georgia, Indiana, Missouri, New Hampshire, New York, North Carolina, Missouri, Oregon, Pennsylvania, Rhode Island, Texas, Tennessee, Virginia). The *Soldanellonyx* species, by Vinke (2013) mentioned from the Northwest Territories (Canada), may belong to *S. monardi* (in Fig. 11 marked by a question mark);
Neotropical Region. – Brazil (Sao Paulo) – Chile (Magallanes) – Falkland Islands (Malvinas).

DISCUSSION

Biogeography

The halacarid species extracted from shallow water sandy deposits at the banks of streams and creeks on Madagascar belong to six species in five genera. Considering that the knowledge regarding the freshwater halacarid fauna of the world is very sparse, it is striking that none of the genera is restricted to Madagascar or to the Afrotropical Region, all are cosmopolitans. At species level, a single one (*Ropohalacarus pallidus*) is at present only known from Madagascar, but this does not mean that the species is endemic since no similar habitats have been studied in adjacent parts of Africa. The three species *Lobohalacarus weberi*, *Porohalacarus alpinus* and *Soldanellonyx monardi* are the ones generally found in the course of similar studies in northern Europe, North America and

New Zealand (Husmann & Teschner 1970, Bartsch 2007, 2011). The three species are spread on all continents except for Antarctica from where no adequate substrata have been studied in respect to their freshwater halacarid fauna. The two *Limnohalacarus* species taken on Madagascar are wide-spread, too. Since most *Limnohalacarus* species have been found in warm-temperate and tropical regions, these may avoid cold-temperate waters. One exception, *Limnohalacarus wackeri* (Walter, 1914) is recorded from northern European and Asian waters, from southern Finland and Kamchatka, respectively (Paasivirta 1975; Tolstikov et al. 2005).

Madagascar, as well as New Zealand, is known to have a unique water mite fauna (Gerecke 2004; Sirvid et al. 2011). Gerecke (2004) presented a list of Hydrachnidia, collected on Madagascar, which included 63 species. Of these, 35 (or 56%) had only been taken on Madagascar, and 24 (or 38%) on both Madagascar and Africa; only four species (or 6%) proved to be wide-spread (Gerecke 2004). Since then more Madagascan species have been described (Goldschmidt 2008; Pešić et al. 2013). Similar, the New Zealand mite fauna is known to include a very high number of endemisms; in many well studied mite groups, terrestrial as well as aquatic mites, 80 % of the species and 35 of the 59 (59 %) of the freshwater genera are expected to be restricted to New Zealand (Sirvid et al. 2011). Because of the low reproduction rate of halacarids, absence of dispersal instars but unusual wide geographical distribution of not just one but several more or less syntopic living species, Bartsch (1996, 2007) expects these species to have colonized and spread on Pangea since the Mesozoic or even Pre-Mesozoic. Minor morphological differences between populations are assumedly due to phenotypic plasticity and no evidence of cryptic speciation.

***Limnohalacarus*: Characters not or rarely observed in other halacarid genera**

Species of the genus *Limnohalacarus* demonstrate two characters which are either restricted to this genus or only rarely found in other halacarid genera. Unique is that the eggs are fixed to the basal part of the tibiae IV (Viets 1940; Ramazotti & Nocentini 1960; Petrova 1966; Bartsch 1999) but the oviposition has not been observed. Up to 9 eggs, or their remnants, can be found per leg (Bartsch 1999). The embryos in the eggs are often in different states of development. In a population of *L. wackeri* from northern Italy, the development of the eggs took about one month (Ramazotti & Nocentini 1960). In general, halacarids deposit their eggs via the ovipositor into a substratum (Teschner 1963; Kirchner 1969; Bartsch 1972), either singly or in clusters. When at rest, the ovipositor is retracted and in most halacarid females it extends internally slightly or distinctly beyond the anterior margin of the genital foramen. The outline of the ovipositor and its genital spines are at least partly visible through the genital plate. The extruded ovipositor ends with genital spines. In some genera these spines are more or less spiniform, in others palmate, either faintly or distinctly sclerotized (cf. Bartsch 2015). In contrast to the majority of halacarid species, the ovipositor of *Limnohalacarus novus* is short and narrow (LxW 74 x 10 µm), the 1–2 µm-long genital spines at the end of the ovipositor are very faintly sclerotized, they arise from minute papillae.

Another detail often found in *Limnohalacarus* species is the combination of an ovoid, somewhat flattened body with accumulated excretory material, and small anal sclerites. Such an excretory body is already present in larvae but is most conspicuous in adults (Walter 1914; Petrova 1966; Ramazotti & Nocentini 1960; Pepato & Dos Santos 2015). In most of the other halacarid species, in larvae, nymphs and adults, the waste products are concentrated within a dorsomedian bar (cf. *Soldanellonyx monardi*—Fig. 10G; *Isobatrus uniscutatus* (Viets, 1939)—Bartsch 2014b: fig. 1). The length of the bar, if present, can correspond to about half or almost two-thirds of the idiosomal length, it is filled with white or light brown granulated material. The 'light mesial line', mentioned by Johnston (1836) in the description of *Thalassarachna basteri* (Johnston, 1836), and the 'dark line' in *Lohmannella falcata* (Hodge, 1863), described by Hodge (1863), may represent such bars. Halacarids have the excretory organ dorsal to the gut (Thomae 1926), defecation is through the anus which is guarded by the anal sclerites. Anatomical details in *Thalassarachna basteri* have been studied by Thomae (1926).

The presence of ovoid excretory bodies, in *Limnohalacarus novus* distinctly stratified, is not restricted to *Limnohalacarus* species but documented also from other halacarid genera. Examples are *Halacarus excellens* Lohmann, 1907 and *Rhombognathus amplus* Bartsch, 2013 (Bartsch 2010, 2013c) as well as other prostigmatid mite families, e.g. the Cunaxidae (Kielczewski & Wisniewski 1977). In halacarid species with such an excretory body the anal sclerites are unusual small, just as in *L. novus*. More species with small anal sclerites are *Bathyhalacarus anomalous* Bartsch, 2005, *Rhombognathus bulbosus* Bartsch, 2005, *R. cyrtonotus* Bartsch, 2000, *R. delicatulus* Bartsch, 2000 (Bartsch 2000c, 2005a, b) but in individuals of these species no ovoid bodies with excretory material were found. However, the number of mites studied is very small. At present it seems that halacarid species with a large ovoid excretory body (20–50 % of idiosomal length) have small anal sclerites, though not all mites with small anal sclerites have such an ovoid body.

Little is known about feeding, almost nothing about digestion and defecation in halacarid mites. Most halacarids, marine as well as freshwater species, are expected to be carnivorous. *Limnohalacarus wackeri*, for example, could be reared with a diet of small ciliates, *Lobohalacarus weberi* with pieces of oligochaetes (Teschner 1963; Ramazotti & Nocentini 1960). Larvae are known to show an excretory bar or ovoid body soon after commencement of feeding (Kirchner 1969; Ramazotti & Nocentini 1960). Rate, periods and frequency of defecation are not known. A general idea may give the studies by Bowman (2017a, b) who examined the feeding of the mesostigmatid *Pergamasus longicornis* (Berlese, 1906), a carnivorous species as *Limnohalacarus*, but terrestrial and with a length of almost 1300 µm distinctly larger than *Limnohalacarus*. In *P. longicornis* up to three weeks may be needed to clear the idiosoma of excretory material (Bowman 2017a, b).

Among halacarids most species have excretory bars, only a small number has ovoid bodies with concentrically arranged layers (e.g. *Rhombognathus amplus*). Among the few specimens studied of the latter species, collected in Singapore mangroves, each following instar had an excretory body almost similar or larger in size than that of the preceding stage. The length of the idiosoma (in parentheses) and LxW data of the excretory body are in protonymphs (209–235 µm) about 37 x 25 µm, in deutonymphs (242–284 µm) 37–75 x 25–30 µm, in tritonymphs (245–354 µm) 127 x 30 µm, and in adults (364–415 µm) 110–182 x 62–77 µm. For critical examination of taxonomic details, halacarid mites have to be cleared, i.e., the body content has to be removed. In *R. amplus* the stiff excretory body could only with difficulty be pressed through the camerostome, though the size of the latter (LxW about 70 x 100 µm) is much larger than that of the anal slit (length about 20 µm). How can such large excreta pass through the small anal opening? Do the mites accumulate excretory material during their lives, from the larval to the adult stage? This seems to be unlikely; the amount of excreta produced in the course of the mite's life is expected to be much larger than that enclosed in the ovoid body. Most halacarids studied have a life span of about 15 months, *Limnohalacarus* up to 24 months (Ramazotti & Nocentini 1960; Bartsch 1972, 1987), the major part takes the adult stage. About one quarter of the *Limnohalacarus novus* females studied had no excretory bodies. This quarter included stages from recently hatched to cocoon-carrying females, and accordingly we can expect that the small anal sclerites do not prevent defecation. Since quiescent or moulting stages were not represented in the samples, we do not know if at least partly the mites can defecate during or immediately after moulting, as long as the integument is not hardened yet.

The two just mentioned species differ in their life style which in turn will influence digestion and defecation. *Rhombognathus amplus* is phytophagous and restricted to the upper tidal zone, several hours a day emerged. The delicate algal film inhabited quickly desiccates. The mites studied were collected during low tide, consequently they were dehydrated and that certainly had an influence on the compactness of the waste products and the defecation. In contrast, *Limnohalacarus* species are carnivorous and live in an at least constantly waterlogged habitat. Feeding and metabolic activities are not hampered by desiccation and hence the wastes may be elastic enough to be pressed through the small and narrow anal slit.

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