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Redescription of *Damaeus* (*Eudamaeus*) pomboi Pérez-Iñigo, 1987 on the basis of type material

(Acari, Oribatida, Damaeidae)

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The oribatid mite *Damaeus* (*Eudamaeus*) *pomboi* Pérez-Iñigo, 1987 (Oribatida, Damaeidae), is redescribed and illustrated in detail on the basis of paratypes. The main morphological traits for this species are summarized. The subgeneric status of *Damaeus* (*Eudamaeus*) Pérez-Iñigo, 1987 is confirmed. The differences between the subgenera of *Damaeus* Koch, 1835 (*Adamaeus* Norton, 1978, *Eudamaeus* and *Paradamaeus* Bulanova-Zachvatkina, 1967) are discussed.

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Introduction

The genus *Damaeus* (Acari, Oribatida, Damaeidae) was proposed by Koch (1835) with *Damaeus auritus* Koch, 1835 as type species. Main generic morphological characters were summarized by Miko (2015). The genus comprises three subgenera (Miko 2015): *Adamaeus* Norton, 1978, *Eudamaeus* Pérez-Iñigo, 1987, and *Paradamaeus* Bulanova-Zachvatkina, 1967.

The subgenus *Damaeus* (*Eudamaeus*) Pérez-Iñigo, 1987 is monotypic with one known species, *Damaeus* (*Eudamaeus*) *pomboi* Pérez-Iñigo, 1987, from the Azores. The confusion, emergence and support of the subgeneric name was explained by Miko (2015, p. 177). The original description of adult *D.* (*Eudamaeus*) *pomboi* is incomplete in the sense of modern morphological characterization (Pérez-Iñigo 1987) because information on morphology and measurements of some morphological structures and on identification of chaetome of legs is absent, and only brief figures of the dorsal and ventral sides of the body and leg genua are presented (Pérez-Iñigo 1987). A detailed morphology of the prodorsum and

the identification of leg the setae and solenidia are very important for the classification of the family Damaeidae, therefore a redescription of *D.* (*Eudamaeus*) *pomboi* has been long overdue to have a complete understanding of all the diagnostic traits of this species and the correct placement of the taxon *Eudamaeus* within the damaeid system.

A main goal of the paper is to present a redescription of *D.* (*Eudamaeus*) *pomboi* on the basis of the type material (paratypes), to summarize the main morphological traits, which will help with the identification of this species in the future, and to confirm clearly the subgeneric status of *Eudamaus*. Also, the differences between the subgenera of *Damaeus* are presented.

Material and methods

Material examined

The type material (paratypes) of *Damaeus* (*Eudamaeus*) pomboi Pérez-Iñigo, 1987 was presented (in ethanol) from the Museum of Zoology, University of Navarra,

Pamplona, Spain. Ten paratypes (sample SMA-10) according to Pérez-Iñigo (1987); the holotype was selected from same sample: Azores, Isla de Santa María, Alto Nascente, 28.VI.1986 (Dalberto Teixeira Pombo). Eight paratypes (sample SMA-13): Azores, Isla de Santa María, Carcereira, 16.VI.1986 (Dalberto Teixeira Pombo).

Methods

Specimens were mounted in lactic acid on temporary cavity slides for measurement and illustration. Body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the notogaster. Notogastral width refers to the maximum in dorsal aspect. Lengths of body setae were measured in lateral aspect. All body measurements are presented in micrometers. Formulas for leg setation are given in parentheses according to the sequence trochanterfemur-genu-tibia-tarsus (famulus included). Formulas for leg solenidia are given in square brackets according to the sequence genu-tibia-tarsus.

Drawings were made with a camera lucida using a Leica transmission light microscope "Leica DM 2500". Images were obtained with an AxioCam ICc3 camera using a Carl Zeiss transmission light microscope "Axio Lab.A1". SEM photos were made with the aid of a JEOL–JSM-6510LV SEM microscope.

General morphological terminology used in this paper mostly follows that of F. Grandjean: see Travé & Vachon (1975) for references, Norton (1977) for leg setal nomenclature, and Norton & Behan-Pelletier (2009) for overview. Particular traits of Damaeidae follow terminology used by Miko (2015).

The following abbreviations are used: apt – prodorsal tectum; *ibr* – interbothridial ridge; *P* – propodolateral apophysis; ro, le, in, ex - rostral, lamellar, interlamellar and exobothridial setae, respectively; bs – bothridial seta (sensillus); bo – bothridium; Da, Ba, Bp – prodorsobasal tubercles; c, la, lm, lp, h, p - notogastral setae; sa - spina adnata; im, ih, ips – notogastral lyrifissures; gla – opisthonotal gland opening; sm - subcapitular mentum; a, m, h – subcapitular setae; or – adoral setae; v,l,d,cm,acm,ul,sul,vt,lt – palp setae; ω – palp and leg solenidion; cha, chb - cheliceral setae; Tg - Trägårdh's organ; Sa, Sp – parastigmatic tubercles; dis – discidium; dep – depression; 1a,1b,1c,2a,3a,3b, 3c,4a,4b,4c,4d – epimeral setae; vlr – ventrolateral ridge; E2a, E2p – epimeral tubercles; Va, Vp – ventrosejugal tubercles; g,ag,an,ad – genital, aggenital, anal and adanal setae, respectively; iad - adanal lyrifissure; po – preanal organ; Tr, Fe, Ge, Ti, Ta – leg trochanter, femur, genu, tibia, tarsus, respectively; $pa - \log porose area$; $\sigma, \varphi - \log solenidia$; $\varepsilon - \log solenidia$ famulus; v, ev, bv, l, d, ft, tc, it, p, u, a, s, pv, pl - leg setae.

Systematics

Family Damaeidae Genus Damaeus Koch, 1835 Subgenus Damaeus (Eudamaeus) Pérez-Iñigo, 1987 Type species Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987

Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987 Figs 1-12

Measurements. Body length: 1012–1128 (18 paratypes, 8 females and 10 males); notogaster width: 664–730 (18 paratypes). No distinct differences between females and males in body size.

Integument (Figs 1A-D; 2B,C; 3B; 4B; 5A). Natural body colour brown to dark brown. Surface of body and legs densely microgranulate, partially covered by spherical, bacilliform, vermicular and filamentous cerotegument.

Prodorsum (Figs 2A-C; 3A,B; 4A; 5A; 6; 8A-C; 12A,B). Rostrum rounded. Rostral part slightly hump-like. Prodorsal tectum present, interrupted medially. Costulae, transcostula, anterobothridial ridges and prodorsal enantiophyses absent. Propodolateral apophyses large, pedotectum-like. Indistinct transverse ridge observed between bothridia, indicating anterior margin of bothridial protuberances. Bothridia placed quite close to each other and at a distance from lateral edges of prodorsum. Three pairs of prodorsobasal tubercles present (Da, Ba and Bp), all separated, similar in size; Dp and La absent. Longitudinal interbothridial ridges present, connected basally with Da. Rostral (114-127) and lamellar (196-205) setae setiform, slightly barbed, directed anteromedial. Interlamellar setae (73-82) thickened, barbed, directed posteriad. Bothridial setae (155-164) bacilliform, barbed. Exobothridial setae (53-61) setiform, barbed.

Notogaster (Figs 2A–C; 3A,B; 4A; 6; 7; 8B,D). Oval, often covered by residual parts of exuviae (Fig. 3A). Spinae adnatae (45–53) thorn-like, straight. Dorsal notogastral setae inserted in two arched rows, with tips radially oriented; c_1 , c_2 , la, lm, lp, h_1 , h_2 and h_3 (184–205) light grey, elongate, thorn-like, roughened; p_1 , p_2 and p_3 (102–123) setiform, barbed. Lyrifissures im, ih, ips and opisthonotal gland openings distinct; lyrifissures ia and ip not observed.

Gnathosoma (Figs 4A; 9A–C). Characteristic for Damaeidae (Miko et al. 2017, Ermilov 2018, Miko & Ermilov 2019). Subcapitulum longer than wide (232–246×164–172). Subcapitular setae setiform, slightly barbed, a (41–53) shorter than m (61–73) and h (61–73). Adoral setae (20) setiform, thin, smooth. Palps (209–213) with setation 0–2–1–3–9($+\omega$). Solenidion bacilliform, pressed to palptarsal surface, reaching

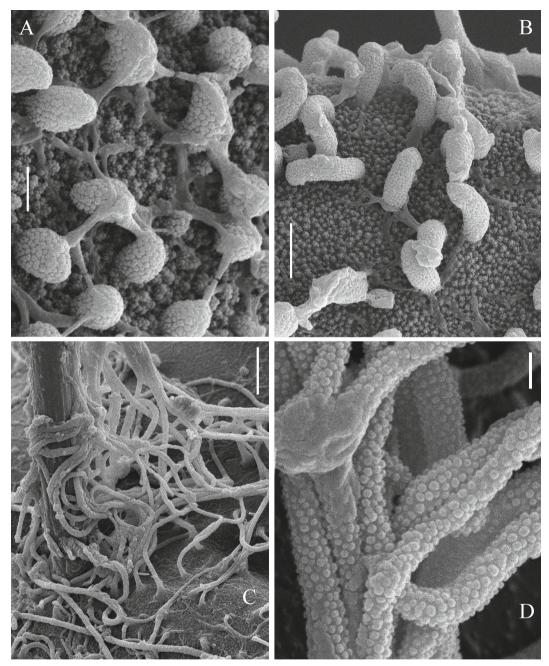


Fig. 1. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult, SEM photos: A. spherical cerotegument; B. bacilliform and vermicular cerotegument; C. filamentous cerotegument; D. filamentous cerotegument under high magnification. Scale bar 2 μ m (A), 5 μ m (B), 10 μ m (C), 1 μ m (D).

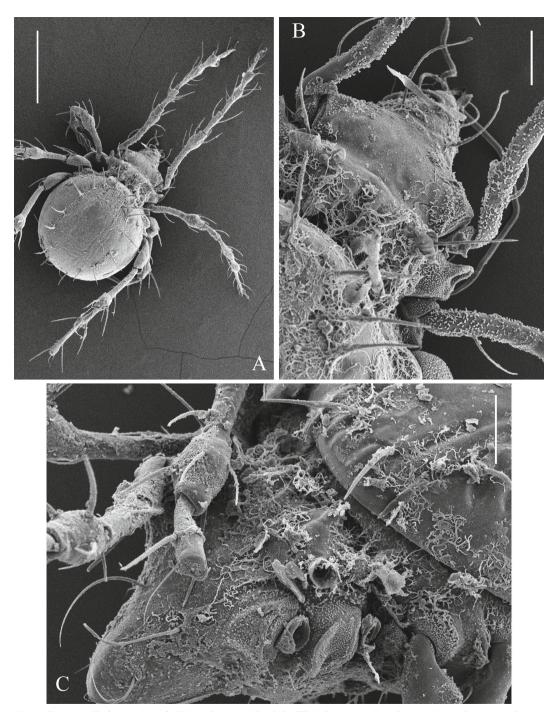


Fig. 2. *Damaeus* (*Eudamaeus*) *pomboi* Pérez-Iñigo, 1987, adult, SEM photos: **A.** dorsal view; **B.** prodorsum and anterior part of notogaster, dorsal view; **C.** prodorsum and anterior part of notogaster, dorsolateral view. Scale bar 500 μm (A), 100 μm (B,C).

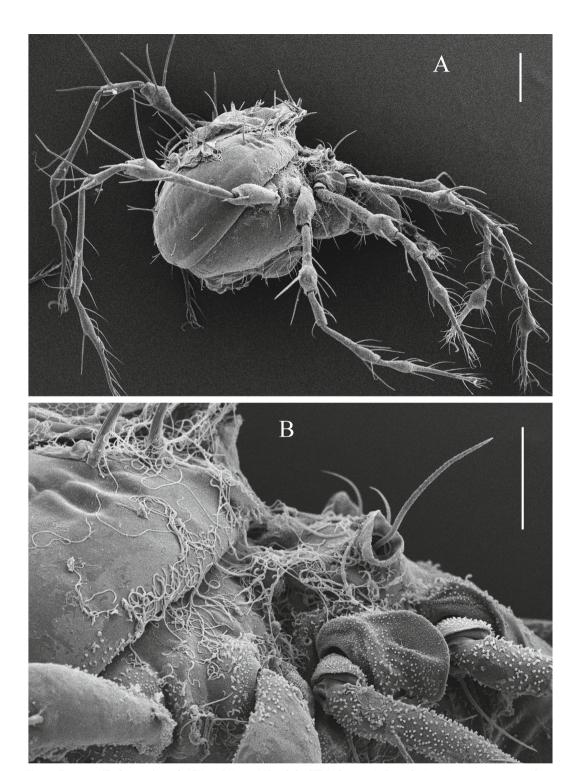


Fig. 3. *Damaeus (Eudamaeus) pomboi* Pérez-Iñigo, 1987, adult, SEM photos: **A.** lateral view; **B.** posterior part of notogaster, anterior part of notogaster and part of lateral podosomal region, lateral view. Scale bar 200 μ m (A), 100 μ m (B).

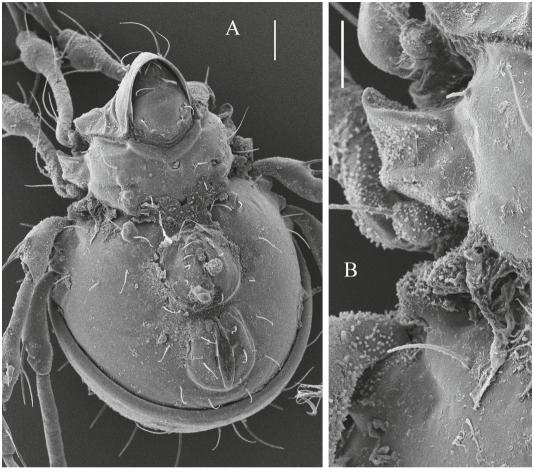


Fig. 4. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult, SEM photos: **A.** ventral view; **B.** part of epimeral and lateral podosomal regions, ventral view. Scale bar 100 μm (A), 50 μm (B).

basal part of seta *acm*. Postpalpal setae (8) thorn-like, smooth. Chelicerae (232–246) with two setiform setae, *cha* (69–73) barbed, *chb* (53–61) shortly ciliate unilaterally in mediodistal part. Trägårdh's organ of chelicerae elongate triangular.

Epimeral and lateral podosomal regions (Figs 3 A, B; 4 A, B; 8E; 12D). Epimere I with median ring-like structure (posterior and close to apodeme I) which is represented by slightly visible depression. Parastigmatic apophyses *Sa* strong, elongate triangular, *Sp* large, quadrangular in ventral view. Epimeral and ventrosejugal tubercles well-developed, rounded distally. Ventrolateral longitudinal ridges slightly visible, ventrolateral tubercles not observed. Epimeral setal formula: 3–1–3(or 4)–4. Epimeral setae setiform, slightly barbed to roughened, *1b* (131–143) longer than *1a*, *1c*, *2a*, *3a* (69–82) and others (94–102);

3b inserted on tubercles Vp, 4b inserted at bases of Vp. Discidia present, small, triangular.

Anogenital region (Figs 3A; 4A,B; 5B; 7; 8D,E, 12C). Six pairs of genital (g_1 , 94–102; g_2 – g_6 , 69–82), one pair of aggenital (69–82), two pairs of anal (69–82) and three pairs of adanal (69–82) setae setiform, slightly barbed to roughened. Adanal lyrifissures diagonal, located close to anal aperture and anteriorly to ad_3 .

Legs (Figs 2A; 3A; 5C; 10A,B; 11A,B; 12E–J). All legs longer than body length (Table 1). Claw of tarsi roughened on dorsal side. Porose areas on all femora and on trochanters III and IV slightly visible. Formulas of leg setation and solenidia: I(1–7,8,9–4–7,8–23)[1–2–2],II(1–6,7–3–5–19)[1–1–2], III (2–6,7–2,3–5–20) [1–1–0], IV (1–6–4–5–17) [0–1–0]; homologies of setae and solenidia indicated in

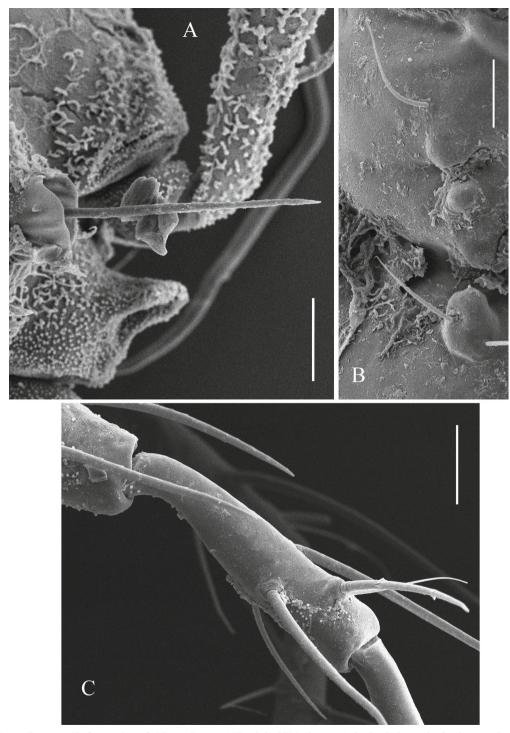


Fig. 5. *Damaeus (Eudamaeus) pomboi* Pérez-Iñigo, 1987, adult, SEM photos: **A.** bothridial seta, bothridium and propodolateral apophysis, dorsal view; **B.** epimeral and ventrosejugal tubercles, ventral view; **C.** leg genu I. Scale bar 50 μm.

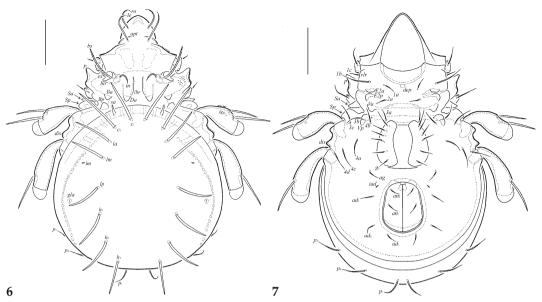


Fig. 6. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult: dorsal view (legs except trochanters not shown). Scale bar 200 μm.

Fig. 7. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult: ventral view (gnathosoma and legs except trochanters not shown). Scale bar 200 μm.

Table 2. Setae d on leg genua I setiform, longer than coupled solenidion. Femora, tibiae and tarsi with variable number of accessory ventral setae. All tarsi with setae v_1' , v_1'' , v_2'' , v_2'' ; in addition, tarsi III and IV with seta v_3' .

Discussion

1. Based on our redescription and on the original description (Pérez-Iñigo 1987) of adult *Damaeus* (*Eudamaeus*) *pomboi*, we propose the following diagnostic morphological traits for this species. Body size: 1012–1200×664–780. Cerotegument present,

Table 1. Leg mean lengths (micrometers) of two paratypes of Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987

Leg	Tr	Fe	Ge	Ti	Та	All segments	Leg:body length
I	41, 41	498, 531	199, 199	298, 315	415, 431	1451, 1517	≈1.37-1.38
II	41, 41	415, 431	166, 182	215, 232	415, 431	1252, 1317	≈1.19-1.20
III	232, 199	365, 365	166, 182	265, 282	431, 448	1459, 1476	≈ 1.34-1.38
IV	249, 265	464, 498	199, 199	448, 464	514, 531	1874, 1957	≈1.77-1.78

Table 2. Leg setation and solenidia of adult *Damaeus* (*Eudamaeus*) *pomboi* Pérez-Iñigo, 1987. Roman letters refer to normal setae, Greek letters to solenidia (except ε = famulus); $\underline{d\sigma}$, seta and solenidion coupled. Single prime (') marks setae on the anterior and double prime (") setae on the posterior side of a given leg segment. Parentheses refer to a pair of setae.

Leg	Tr	Fe	Ge	Ti	Ta
I	v'	d ,(l), bv ",(v_1), v_2 ', v_2 "*, v_3 "*	(l),v', <u>dσ</u>	$(l), (v_1), (v_2), v_3', v_3''*,$	(ft),(tc),(it),(p),(u),(a),s,(pv),(pl),l",
				ϕ_1, ϕ_2	$(v_1),(v_2),\varepsilon,\omega_1,\omega_2$
II	v'	$d,(l),bv'',(v_1),v_2'^*$	$(l),v',\sigma$	$(l), (v_1), v_2', \varphi$	$(ft),(tc),(it),(p),(u),(a),s,(pv),(v_1),(v_2),\omega_1,\omega_2$
III	l',v'	$d,(l),bv'',(v_1),v_2'^*$	l',l''^*,v',σ	$(l), (v_1), v_2', \varphi$	$(ft),(tc),(it),(p),(u),(a),s,(pv),(v_1),(v_2),v_3$
IV	v'	$d,(l),bv^{\prime\prime},(v)$	d,(l),v'	$(l),(v_1),v_2',\varphi$	$ft'',(tc),(p),(u),(a),s,(pv),(v_1),(v_2),v_3'$

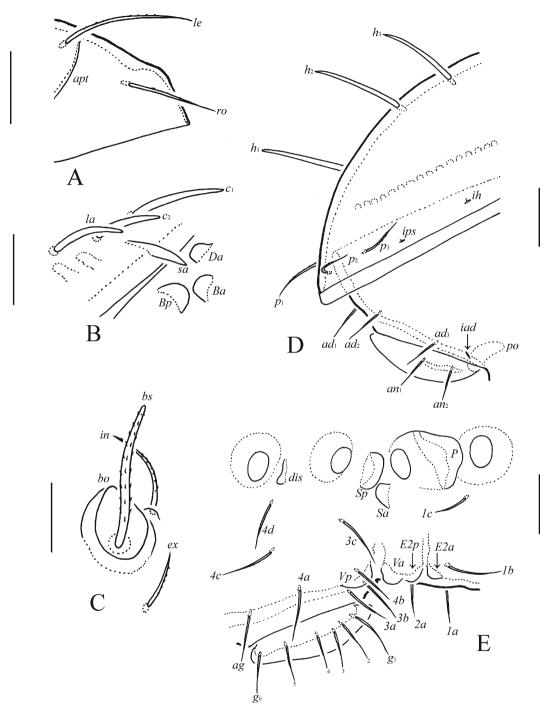


Fig. 8. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult: **A.** anterior part of prodorsum, lateral view; **B.** prodorsobasal tubercles and anterior part of notogaster, lateral view; **C.** bothridial, interlamellar and exobothridial setae, and bothridium, lateral view; **D.** posterior part of notogaster, lateral view; **E.** epimeral, lateral podosomal and genitoaggenital regions (legs not shown). Scale bar 100 μm (A,B,D,E), 50 μm (C).

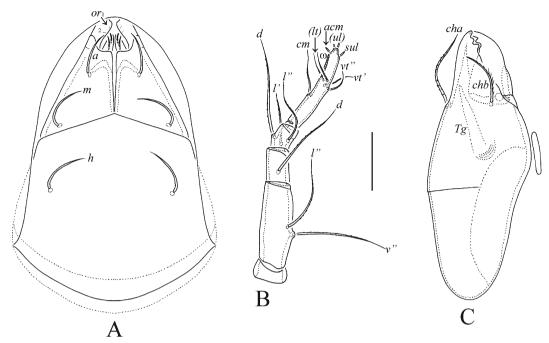


Fig. 9. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult: A. subcapitulum, ventral view; B. palp, right, antiaxial view; C. chelicera, right, antiaxial view. Scale bar 50 μm.

spherical, bacilliform, vermicular and filamentous. Notogaster often covered by parts of exuviae. Costulae absent. Interbothridial ridges present. Three pairs of prodorsobasal tubercles developed (Da, Ba and Bp). Rostral and lamellar setae setiform, slightly barbed, ro of medium size, le long. Interlamellar setae of medium size, thickened, barbed. Bothridial setae long, bacilliform, barbed. Spinae adnatae short, thorn-like. Dorsal notogastral setae long, elongate thorn-like, roughened, p_1 , p_2 and p_3 of medium size, setiform, barbed. Parastigmatic apophyses Sa triangular, Sp quadrangular. Epimeral and ventrosejugal tubercles developed. Epimeral and anogenital setae short, setiform, slightly barbed to roughened. Discidia present. All legs longer than body length, with variable numbers of additional ventral setae on femora, tibiae and tarsi beyond standard setation. Formulas of leg segments (I-IV): femora 7,8,9-6,7-6,7-6; genua 4-3-2,3-4; tibiae 7,8-5-5-5; tarsi 23-19-20-17.

2. The genus *Damaeus* includes, except of nominal subgenus, three subgenera, differing mutually by one main morphological trait (presence or absence of dorsal seta *d* coupled with solenidion on leg genua I-III): *Adamaeus* has genua I-III with free solenidion, without coupled seta *d*; *Eudamaeus* has genua I with seta *d* coupled with solenidion, genua II and III with free solenidion, without coupled seta *d*; and

Paradamaeus has genua I and II with seta d coupled with solenidion, genua III with free solenidion, without coupled seta d.

In addition, *Damaeus* (*Adamaeus*) is characterized by the presence of propodolateral tubercles *La* (versus absent in the other subgenera); and *Damaeus* (*Eudamaeus*) by the high number of leg setae on tarsi, with formula 23–19–20–17 with extra setae v (versus usually 21–18–18–15 in the other subgenera), and on genua IV, with four setae including l" (versus three setae, l" absent in the other subgenera).

Thus, the morphological differences between *Adamaeus*, *Paradamaeus* and *Eudamaeus*, as it is listed above, are well defined. However, the general morphology and, in particular, the development of prodorsum (rugged surface with protuberances and ridges, presence of prodorsal tectum, size and development of propodolateral apophyses, position and distance of bothridia, form and length of bothridial setae), suggest closer mutual relations of these taxa and their placement into the common genus *Damaeus* rather than splitting into separate genera. Hence, we agree with subgeneric statuses of *Adamaeus*, *Paradamaeus* and *Eudamaeus* into *Damaeus* as it was proposed earlier by Miko (2015).

3. Increased and variable leg setation of *D.* (*E.*) *pomboi* is interesting, but not completely unique because additional setae may be found in



 $\textbf{Fig. 10.} \ \textit{Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult: } \textbf{A.} \ \text{leg I, right, antiaxial view; } \textbf{B.} \ \text{leg II, without trochanter, left, paraxial view. Scale bar 100 } \mu\text{m}.$

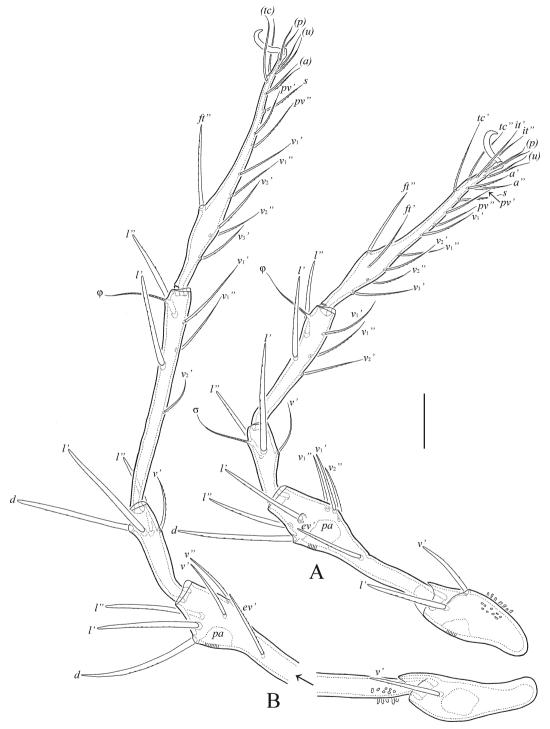


Fig. 11. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult: A. leg III, left, antiaxial view; B. leg IV, left, antiaxial view. Scale bar 100 μ m.

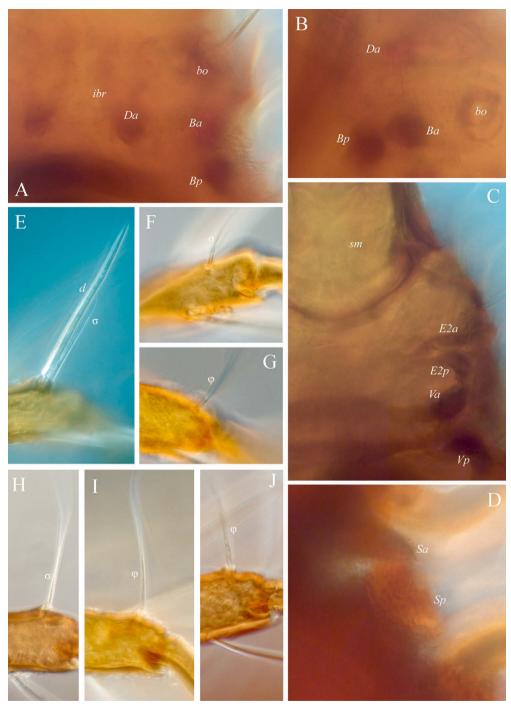


Fig. 12. Damaeus (Eudamaeus) pomboi Pérez-Iñigo, 1987, adult, microscope images: A. prodorsobasal tubercles, dorsal view; B. prodorsobasal tubercles and bothridium, lateral view; C. epimeral and ventrosejugal tubercles, ventral view; D. parastigmatic apophyses, ventral view; E. coupled seta and solenidion of leg genu I; F. solenidion of leg genu II; G. solenidion of leg tibia II; H. solenidion of leg genu III; J. solenidion of leg tibia IV.

some other related species. For example, Damaeus (Damaeus) arvernensis Grandjean, 1960 has femoral setal formula 10-9-7-7; Tamdamaeus staryi Miko & Ermilov, 2017 has six setae on femora III and IV. Damaeus species from the angustipes-group (Norton 1978) have the increased number of setae on tibiae (up to six setae on tibiae I-III, up to 11 setae on tibia IV). All these taxa were characterized by very long legs (longer than body) and together with Norton (1978) we assume that increased numbers of leg (tibial) setae may be related to increased length of legs. Similarly, D. (E.) pomboi has all legs prolonged (longer than body), even if not to the same extent as species from the angustipes-group. From observed distribution of additional leg setae it may be concluded that their presence is more linked to body size and length of legs, i.e. may occur across the genera within Damaeidae. The presence of additional leg setae is therefore insufficient morphological trait at the generic level and should be always considered in combination with other, more stable, traits.

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