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REVISION OF THE GENUS *GAUDALGES* (ACARI: PSOROPTIDAE), PARASITES OF MALAGASY LEMURS

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ABSTRACT: The mite genus *Gaudalges* Fain, 1963 (Acari: Psoroptidae), species of which are permanent parasites of Malagasy lemurs belonging to the families Lemuridae and Indridae, is revised. An emended diagnosis of the genus and key to four presently recognized species of the genus is given. The phylogenetic relationships of the genus *Gaudalges* with other genera of the subfamily Makialginae are briefly discussed and evidence for its monophyly are provided. *Gaudalges* is supported as a monophyletic group by the presence in males of a dorso-apical spur on tibia III and a dorso-basal projection on tarsus IV. A new species, *Gaudalges brevisetosus* Bochkov et OConnor, sp.n. from *Eulemur coronatus* (Gray, 1842) (Lemuridae) is described. This new species differs from other species of the genus *Gaudalges* in both sexes by the absence of ornamentation on the propodonotal shield; in males, by short setae *c1, d1, d2*, and *e1* (less than 30 long), the position of setae *c1* and *d2* off the hysteronotal shield, the hysteronotal shield covered by transverse striations only in the posterior part, and by the short lobes of the idiosoma.

KEY WORDS: acari, Malagasy lemurs, systematics, *Gaudalges*, Psoroptidae, Makialginae

INTRODUCTION

The mite subfamily Makialginae Gaud et Mouchet, 1959 (Acari: Psoroptidae) includes six genera whose ten species are permanent parasites of African and Malagasy primates (OConnor 1984). Among them, nine species of five genera are associated with Malagasy lemurs of the families Cheirogalidae, Daubentoniidae, Lemuridae, Indridae, and Megaladapidae (see Table), while of the monobasic genus *Galagalges* Fain, 1963 (*G. congolensis* Fain, 1963) was described from an African host, *Galago moholi* Smith, 1836 (Galagonidae) from the Democratic Republic of Congo (Fain 1963c).

Fain (1963b, 1972) included four genera in the subfamily Makialginae: *Gaudalges* Fain, 1963 and *Makialge*s Gaud et Till, 1957 each with three species, and the monobasic *Lemuralges* Fain, 1963 and *Daubentonialges* Fain, 1972. OConnor (1984) synonymized the monobasic psoroptid subfamily Cheirogalginae Fain, 1973 (the genus *Cheirogalges* Fain, 1963) and the family Galalgidae (*Galagalges*) with Makialginae and conducted the first analysis of phylogenetic relationships among makialgine genera.

Gaudalges is the most taxonomically problematic genus of the subfamily. The monophyly of this genus was questioned by OConnor (1984), who suggested that *Gaudalges caparti* Fain, 1963 was more closely related to the genus *Makialges*. Of the three known species of this genus, the type species *G. propitheci* (Gaud et Till, 1957) has not been redescribed nor fully illustrated since the original description (Gaud and Till 1957). *Gaudalges haymani* Fain, 1963 was briefly described from the female but not figured, while the male of this species remains unknown (Fain 1963b).

In the present paper we redescribe all three previously named species from both sexes and describe a new species, *G. brevisetosus* Bochkov et OConnor, sp.n. An emended diagnosis of the genus and key to its species are provided. We also briefly discuss the phylogenetic relationships of this genus with other members of the subfamily Makialginae and provide evidence for its monophyly.

MATERIAL AND METHODS

Most specimens examined in this study were collected by AVB from dried host specimens in the American Museum of Natural History, New York, USA. In the descriptions below, idiosomal chaetotaxy follows Griffiths et al. (1990) with modifications of Norton (1998) for coxal setae. The leg chaetotaxy follows Grandjean (1939). All measurements are given in micrometers (μm) and were taken as follows: body length = the total length from the anterior extremity of the gnathosoma to the posterior border of the body; body width = maximum width taken at whatever level it occurs; length of dorsal shields = maximum length, measured in the mid-line of the shields; length of the posterior legs = length from the most basal point of the trochanter to the apex of the tarsus, excluding pretarsal ambulacrum; length of the tibiotarsus = length from most basal point of this segment to the apex of the tarsus, excluding pretarsal ambulacrum. Names of hosts follow Groves (2005). Specimen

Table
Psoroptid mites of the subfamily Makialginae Gaud et Mouchet, 1959
associated with Malagasy lemurs

Mite species	Host species	Host family	Locality	Reference
Cheirogalalges Fain, 1963				
** *C. evansi* Fain, 1963	* *Cheirogaleus medius* Geoffroy, 1812	Cheirogaleidae	Tôlanäro (=Fort Dauphin), 25° 02′ S, 47° 00′ E	Fain 1963b, 1966
	Cheirogaleus major Geoffroy, 1812	Cheirogaleidae	?	Fain 1963b, 1966
Daubentonialges Fain, 1972				
** *D. brygooi* Fain, 1972	* *Daubentonia madagascariensis* (Gmelin, 1788)	Daubentoniidae	Maroantsetra, 15° 26′ S, 49° 44′ E	Fain 1972
Gaudalges Fain, 1963				
** *G. pitheci* (Gaud et Till, 1957)	* *Propithecus verreauxi* Grandidier, 1867	Indriidae	Toliara, 23° 21′S, 43° 40′ E; Sud Majunga, ?	Gaund and Till 1957; Fain 1963 a, b; our data
G. brevisetosus Bochkov et OConnor, sp.n.	* *Eulemur coronatus* (Gray, 1842)	Lemuridae	Antsiranana Prov., 26 km N Vohimarina, 13° 08′ 52″ S, 49 °55′ 03″ E	our data
G. caparti Fain, 1963	* *Eulemur coronatus* (Gray, 1842)	Lemuridae	Nosy-Be Isl., 13° 20′ S, 48° 15′ E	Fain 1963a, b
	Hapalemur griseus (Link, 1795)	Lemuridae	Fianarantsoa Prov., Manombo, 23° 02′ S, 47° 44′ E; Toamasina Prov., 20 km SW Maroantsetra, Manombia, 15° 31′ S 49° 38′ E	our data
G. haymani Fain, 1963	* *Eulemur fulvus* (Geoffroy, 1796)	Lemuridae	Tôlanäro (=Fort Dauphin), 25° 02′ S, 47° 00′ E	Fain 1963b
	Eulemur coronatus (Gray, 1842)	Lemuridae	Antsiranana Prov., 26 km N, Vohimarina, 13° 08′ 52″ S, 49° 55′ 03″ E	our data
Lemuralges Fain, 1963				
** *L. intermedius*	* *Lepilemur ruficaudatus* Grandidier, 1867	Lepilemuridae	Tôlanäro (=Fort Dauphin), 25° 02′ S, 47° 00′ E	Fain, 1963b, 1966
	Eulemur fulvus (Geoffroy, 1796)	Lemuridae	Tôlanäro (=Fort Dauphin), 25° 02′ S, 47° 00′ E	Fain, 1963b, 1966
	Hapalemur griseus (Link, 1795)	Lemuridae	Tôlanäro (=Fort Dauphin), 25° 02′ S, 47° 00′ E	Fain, 1963b, 1966
	Propithecus verreauxi Grandidier, 1867	Indriidae	Tôlanäro (=Fort Dauphin), 25° 02′ S, 47° 00′ E	Fain, 1963b, 1966
Makialges Gaud et Till, 1957				
** *M. lepilemuri* Gaud et Till, 1957	* *Lepilemur mustelinus* Geoffroy, 1851	Lepilemuridae	Ambatolampy, (? many localities with this name)	Gaud and Till 1957, Fain 1963b, 1966
	Lepilemur ruficaudatus Grandidier, 1867	Lepilemuridae	Ambolisaka, 21° 54′ S, 43° 35′ E	Fain 1963b, 1966

Table continued

Mite species	Host species	Host family	Locality	Reference
Makialges Gaud et Till, 1957				
M. lobatus Fain, 1966	*Lepilemur ruficaudatus* Grandidier, 1867	Lepilemuridae	Tôlanäro (=Fort Dauphin), 25° 02′ S, 47° 00′ E	Fain 1966
M. sternodons Gaud et Till, 1957	*Lepilemur* sp.	Lepilemuridae	Toliara, 23° 21′ S, 43° 40′ E	Gaud and Till 1957, Fain 1963b, 1966

* — type host; ** — genotype; ? — unknown locality or geographical coordinates; all geographical coordinates are approximate (centroids).

depositories and reference numbers are cited using the following abbreviations:

AMNH — American Museum of Natural History, New York, USA

BMOC # — B.M. OConnor reference number

FMNH — Field Museum of Natural History, Chicago, USA

MNHN — Muséum national d'Histoire naturelle, Paris, France

MRAC — Musée royal de l'Afrique Centrale, Tervuren, Belgium

NHM — Natural History Museum, London, England

UMMZ — Museum of Zoology, University of Michigan, Ann Arbor, USA

ZISP — Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia.

SYSTEMATICS

Family Psoroptidae Canestrini, 1892

Subfamily Makialginae Gaud et Mouchet, 1959

Genus *Gaudalges* Fain, 1963

Fain 1963a: 154, 1963b: 56, OConnor 1984: 188.

Type species: *Makialges propitheci* Gaud et Till, 1957 by original designation.

Diagnosis. Both sexes. Subcapitulum with pair of distinct, retrorse ventral apophyses. Propodonotal shield with or without ornamentation, bearing setae *vi, se,* and *si*. Openings of opisthonotal glands (*o.g.*) distinctly sclerotized. Setae *h2* and *h3* whip-like. Coxal fields I–II each with ventral retrorse spur. Coxal apodemes I separated from each other. Genu I–II each with ventral retrorse spur. Tibia I–II each with antixial retrorse spur and ventral spur. Tarsi I–II each with straight dorso-apical process and ventral retrorse spur. Famulus bifurcate. Spur-like setae *ba*I–II and solenidia *ω1*I–II situated in median part that of respective tarsi. Solenidion *ω3* situated in apical part of tarsus I. Solenidion σI about 2 times longer than σII. Idiosomal setation: *scx, vi, si, se, c1–c3, cp, d1, d2, e1, e2, f2, h1–h3, ps2, ps3, 1a, 3a, 4a, 4b,* and *g*. Leg setation: *pR*I–II, *sR*III, *vF*I–II, *cG*I–II, *mG*I–II, *gT*I–II, *kT*III, *ba*I–II, *la*I–II, *s*I–III, *e*I–IV, *f*I–IV, and *d*I–IV, *ω1*I–II, *ω3*I, φI–IV, and σI–III.

Male. Hysteronotal shield distinctly ornamented. Paired dorso-lateral apodemes and U-shaped apodeme (=supraanal concavity) of hysterosoma present, distinctly developed (Fig. 1). Coxal fields III "closed" by apodemes. Aedeagus minute, situated at level of coxal fields IV. Adanal shields present. Adanal membrane with protuberances present. Opisthosomal lobes present, widely separated from each other. Para-anal suckers distinctly developed. Setae *3a* whip-like. Legs III about 2 times longer than legs IV. Tibia III with apically directed, dorso-apical spur. Tarsus III straight, with pointed apex. Tarsus IV with dorso-basal projection. Setae *d*IV and *e*IV modified into suckers; setae *s*III membranous knife-shaped.

Female. Hysteronotal shield absent. Hysterosomal setae, excluding whip-like *h2* and *h3,* relatively short (not longer than 30). Epigynum distinctly developed, situated between coxal fields II and III or I and II. Bursa-copulatrix opened ventroterminally. Basal cap and walls of inseminatory canal indistinct. Tibiae and tarsi III–IV each with ventro-apical spurs. Setae *d*III–IV whip-like.

Other species included: *G. caparti* Fain, 1963, *G. haymani* Fain, 1963, and *G. brevisetosus* Bochkov et OConnor, sp.n.

Host ranges and distribution. Malagasy lemurs of the families Lemuridae and Indridae.

Remarks. The genus *Gaudalges* Fain, 1963 was established for two species *G. propitheci* and *G. caparti* (Fain 1963a). Almost simultaneously Fain (1963b) described the third species of the genus, *G. haymani*. The description of the fourth species of this genus, *G. brevisetosus* sp.n. is given in the present work.

This genus mainly differs from the genus *Makialges* in males, by the presence of an adanal

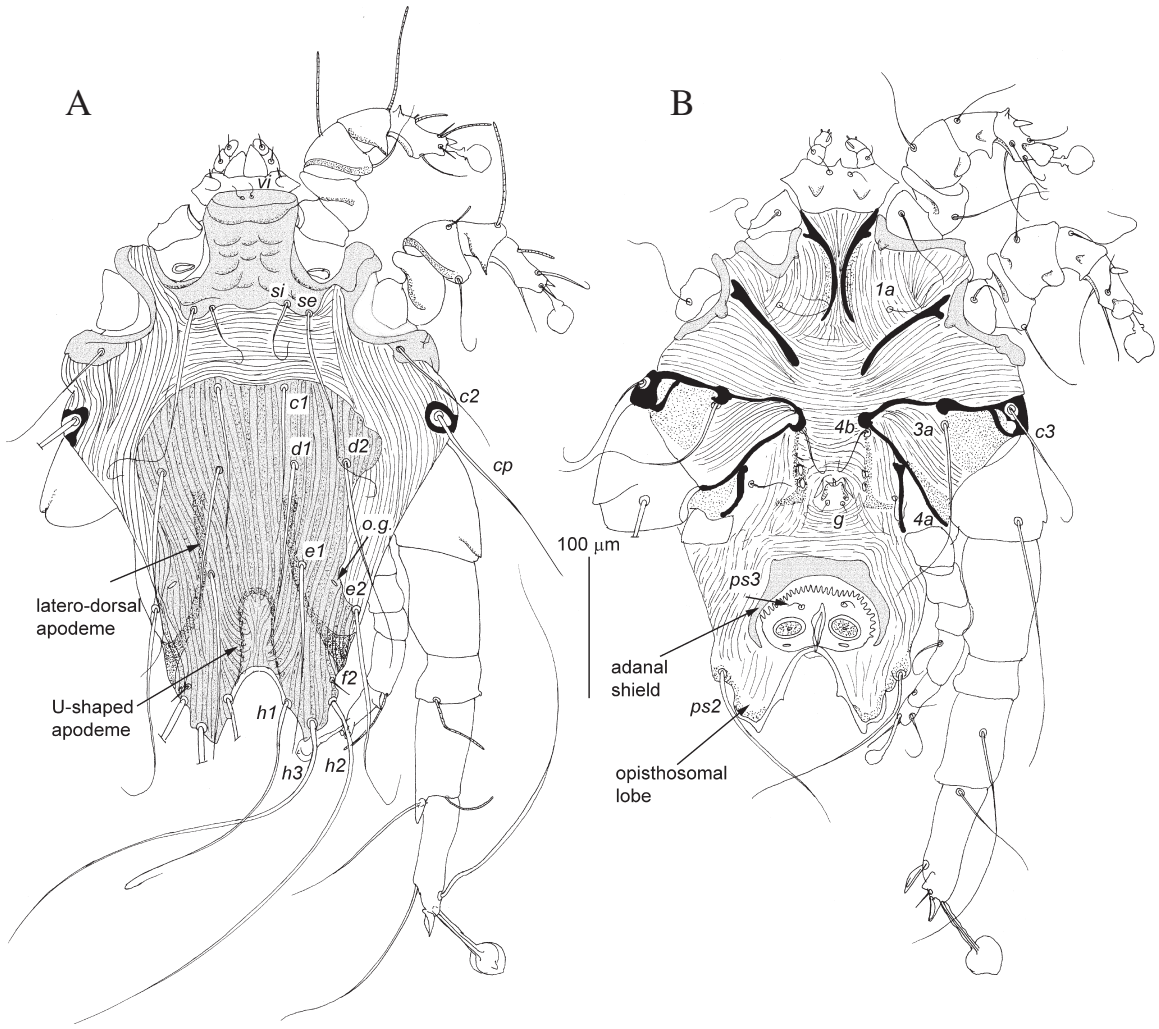

Fig. 1. *Gaudalges propitheci* (Gaud et Till, 1957), male. A — dorsal view; B — ventral view.

membrane bearing hyaline protuberances, the dorso-apical spur of tibiae III, and the dorso-basal projection of tarsi IV, by closed coxal fields III, membranous setae *s*III, and by the widely separated opisthosomal lobes; in females, by the absence of the hysteronotal shield, the distinctly developed epigynum, and by the relatively short hysterosomal setae (excluding whip-like *h2* and *h3*). In males of the genus *Makialges*, the adanal membrane, the dorso-apical spur of tibiae III, and the dorso-basal projection of tarsi IV are absent, coxal fields III open, setae *s*III are filiform, and the opisthosomal lobes are close to each other; in females, the hysteronotal shield is present, the epigynum is reduced, and the hysterosomal setae are relatively long.

The genus *Gaudalges* differs from the genus *Lemuralges* in both sexes, by the presence of ventral retrorse spurs on the subcapitulum [and coxal fields I–II; in males, by the presence of the dorso-apical spur of tibiae III and the dorso-basal projection of tarsi IV; in females, by the presence of well-developed retrorse antero-ventral spurs on tibiae and tarsi III–IV and by the epigynum not fused with coxal apodemes I. In both sexes of *Lemuralges*, the retrorse spurs of the gnathosoma and coxal fields I–II are absent; in males, the dorso-apical spur on tibiae III and the dorso-basal projection on tarsi IV are absent; in females, tibiae III bear an indistinct apico-ventral spur, tibiae IV and tarsi III–IV lack spurs, and the epiginum is fused with the anterior apodemes of coxal fields I.

The genus *Gaudalges* differs from the genus *Daubentonialges* in both sexes, by the presence of retrorse spurs on coxal fields I–II; in males, by the presence of the dorso-apical spur of tibiae III and the dorso-basal projection of tarsi IV. These structures are lacking in *Daubentonialges*.

The genus *Gaudalges* differs from the genus *Cheirogalalges* (known only from males and tritonymphs) in males, by the presence of retrorse spurs on coxal fields I–II, the adanal membrane, the dorso-apical spur of tibiae III, the dorso-basal projection of tarsi IV, by the absence of ventral spurs on trochanters I–II, by whip-like setae *h3*, and by

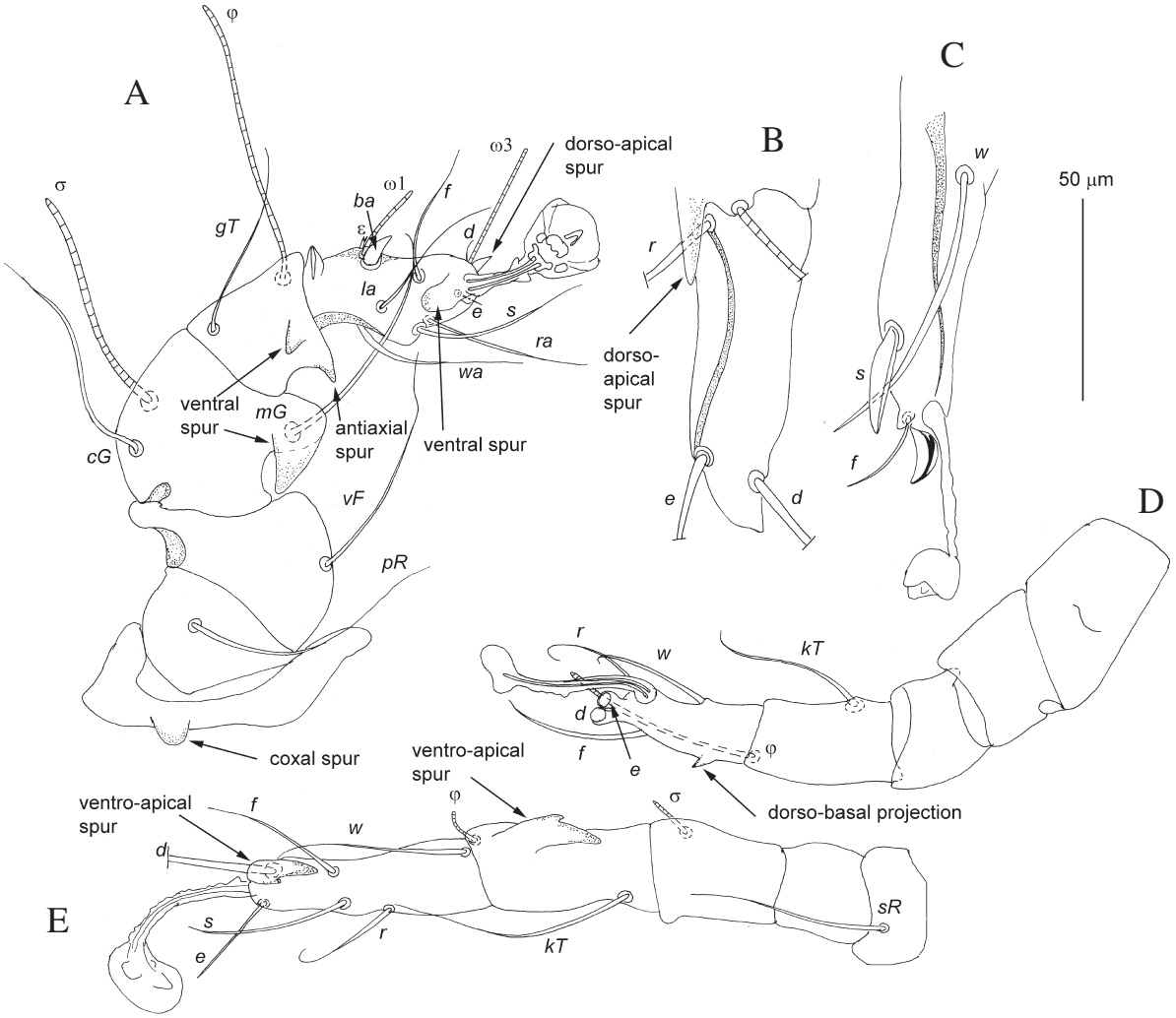

Fig. 2. *Gaudalges propitheci* (Gaud et Till, 1957), details. A — leg I of male in ventral view; B — tarsus III of male in dorsal view; same in ventral view; C — same in ventral view; D — leg IV of male in ventral view; E — leg III of female in ventral view.

membranous setae *s*III. In males of *Cheirogalalges,* the retrorse spurs of coxal fields I–II, the adanal membrane, the dorso-apical spur on tibiae III, the dorso-basal projection of tarsi IV are absent, ventral spurs are present on trochanters I–II, setae *h3* are short, and setae *s*III are filiform.

Gaudalges propitheci **(Gaud et Till, 1957)**

Figs 1–3.

Makialges propitheci Gaud and Till 1957: 142, fig. 2D, photos 7, 8.

Gaudalges propitheci, Fain 1963a: 155; Fain 1963b: 57.

Redescription: Male (2 specimens, Figs 1, 2A–D). Body, including gnathosoma, 440–470 long, 290–315 wide. Propodonotal shield 70–75 long, 120–125 wide, with elevations in median part. Hysteronotal shield 200–220 long in midline, completely covered by longitudinal striations. Anterior margin of hysteronotal shield only slightly concave. Length of setae *c1, d1, d2*, and *e1* greater than 70. Idiosomal striations between dorsal shields without verruccae. Dorso-lateral apodemes 150–160 long. Aedeagus about 5 long. Adanal shields completely fused to each other anteriorly. Protuberances surrounding anal area distinctly developed. Diameter of para-anal suckers about 25. Opisthosomal lobes distinctly developed, opisthosomal cleft about 45 long. Legs III about 370 long, legs IV about 160 long. Dorso-apical spurs of tarsi I–II about 5 long. Ventral spurs of coxal fields I–II 10–11 long. Spurs of genua and tibiae I–II moderately developed. Dorso-apical spur of tibia III about 20 long. Tarsi III about 90 long without pretarsus. Dorso-basal spur on tarsi IV about 6 long. Lengths of setae: *vi* 8–9, *si* 30–40, *se* 155–165, *c1* 120–125, *c2* 80–90, *cp* 210–220, *c3* 90–95, *d1* 125–130, *d2* 135–150, *e1* 155–165, *e2* 180–185, *f2* 18–20, *h1* 220–235, *h2* 310–320, *h3* 330–350, *1a* 45–48, *3a* 110–115, *4a* 37–40, *4b* 40–45, *ps3* 11–12, *ps2* 150–155, *ω3*I 38–40, *ω1*I 22–23, *φ*I–II 80–85, *σ*I 55–60, *σ*II 16–18, and *σ*III 45–50.

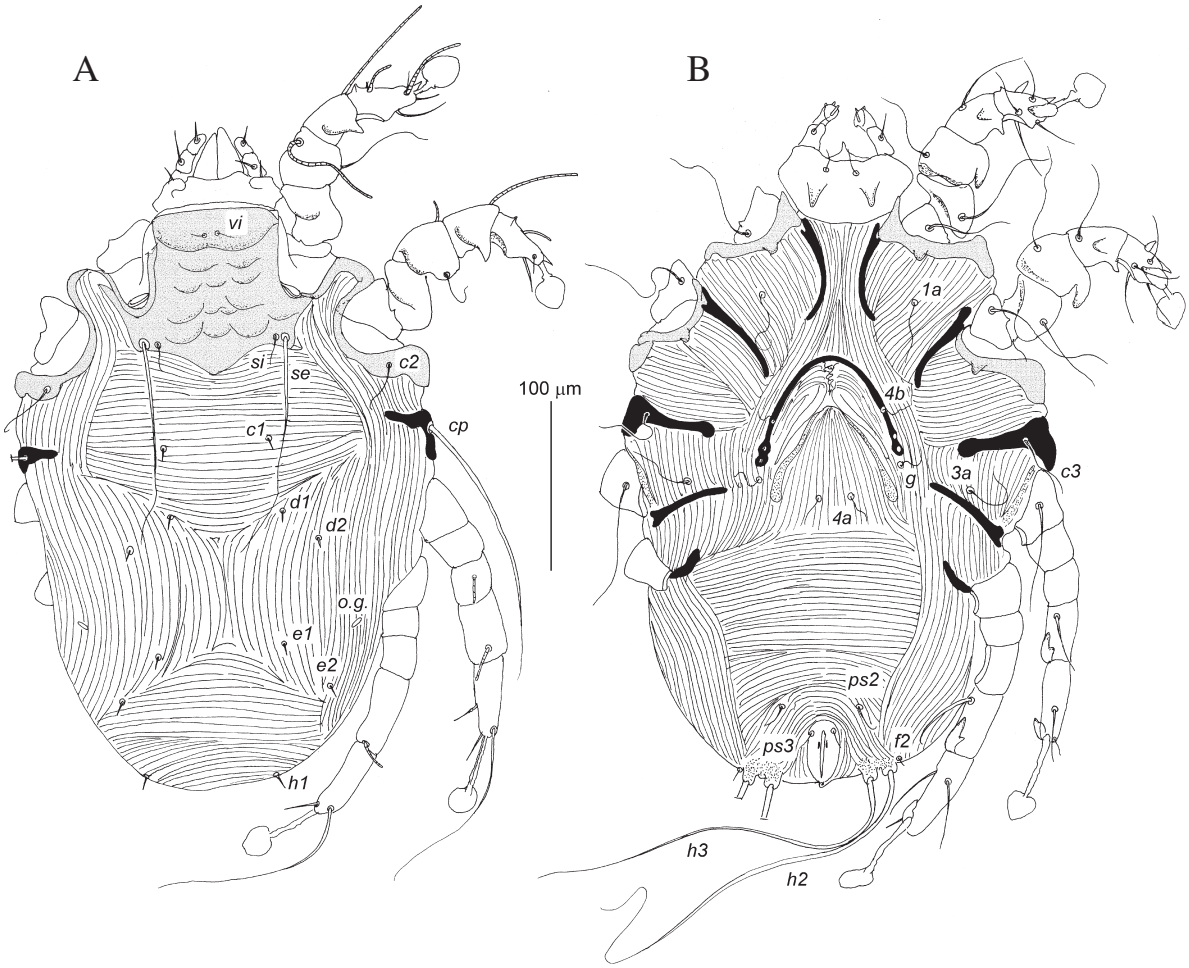

Fig. 3. *Gaudalges propitheci* (Gaud et Till, 1957), female. A — dorsal view; B — ventral view.

Female (3 specimens, Figs 2E, 3). Body, including gnathosoma, 420–440 long, 280–290 wide. Propodonotal shield 100–110 long, 130–135 wide, in median part. Dorsal idiosomal striations without verrucae. Epigynum situated between levels of coxal fields II and III. Genital papillae situated on epigynum. Legs III–IV about 180 long. Dorso-apical spur of tarsi I–II about 4 long. Ventral spurs of coxal fields I–II about 9 long. Tarsi III–IV about 65 long without pretarsus, subequal in length to pretarsi. Ventro-apical spurs on tibiae III–IV about 18 long, spurs on tarsi III–IV about 8. Lengths of setae: *vi* 8–9, *si* 12–15, *se* 125–130; *c1*, *d1*, *d2*, *e1*, and *e2* about 10, *c2* 22–25, *cp* 95–100, *c3* 35–38, *f2* and *h1* about 5, *h2* 250–260, *h3* 240–260, *1a* 35–40, *3a* 30–35, *4a* 23–25, *4b* 25–27, *g* 23–25, *ps3* 18–22, *ps2* 15–18, *ω3*I 30–33, *ω1*I 13–16, *φ*I–II 55–60, *σ*I 60–65, *σ*II 12–13, and *σ*III 12–14.

Material examined. 2 males and 3 females (UMMZ), ex *Propithecus verreauxi* Grandidier, 1867 (Primates: Lemuridae), MADAGASCAR: W. Madagascar, Sud Majunga, 26 June 1960, coll. unknown.

Type depository. Type series in MNHN.

Host ranges and distribution. This species is known only from the original record from *P. verreauxi* captured on Madagascar (Gaud and Till 1957) and the material cited above.

Gaudalges haymani Fain, 1963

Figs 4–7.

Gaudalges haymani Fain 1963: 113.

Redescription. Male (4 specimens, Figs 4, 5). Body, including gnathosoma, 440–470 long, 275–310 wide. Propodonotal shield 80–85 long, 120–130 wide, with elevations in median part. Hysteronotal shield 250–265 long in midline, completely covered by longitudinal striations. Anterior margin of hysteronotal shield moderately concave. Length of setae *c1, d1, d2*, and *e1* greater than 70. Idiosomal striations between dorsal shields with verrucae. Dorso-lateral apodemes 170–175 long. Aedeagus about 5 long. Adanal shields completely fused to each other anteriorly. Protuberances surrounding anal area distinctly developed. Diameter of paraanal suckers about 25. Opisthosomal lobes distinct-

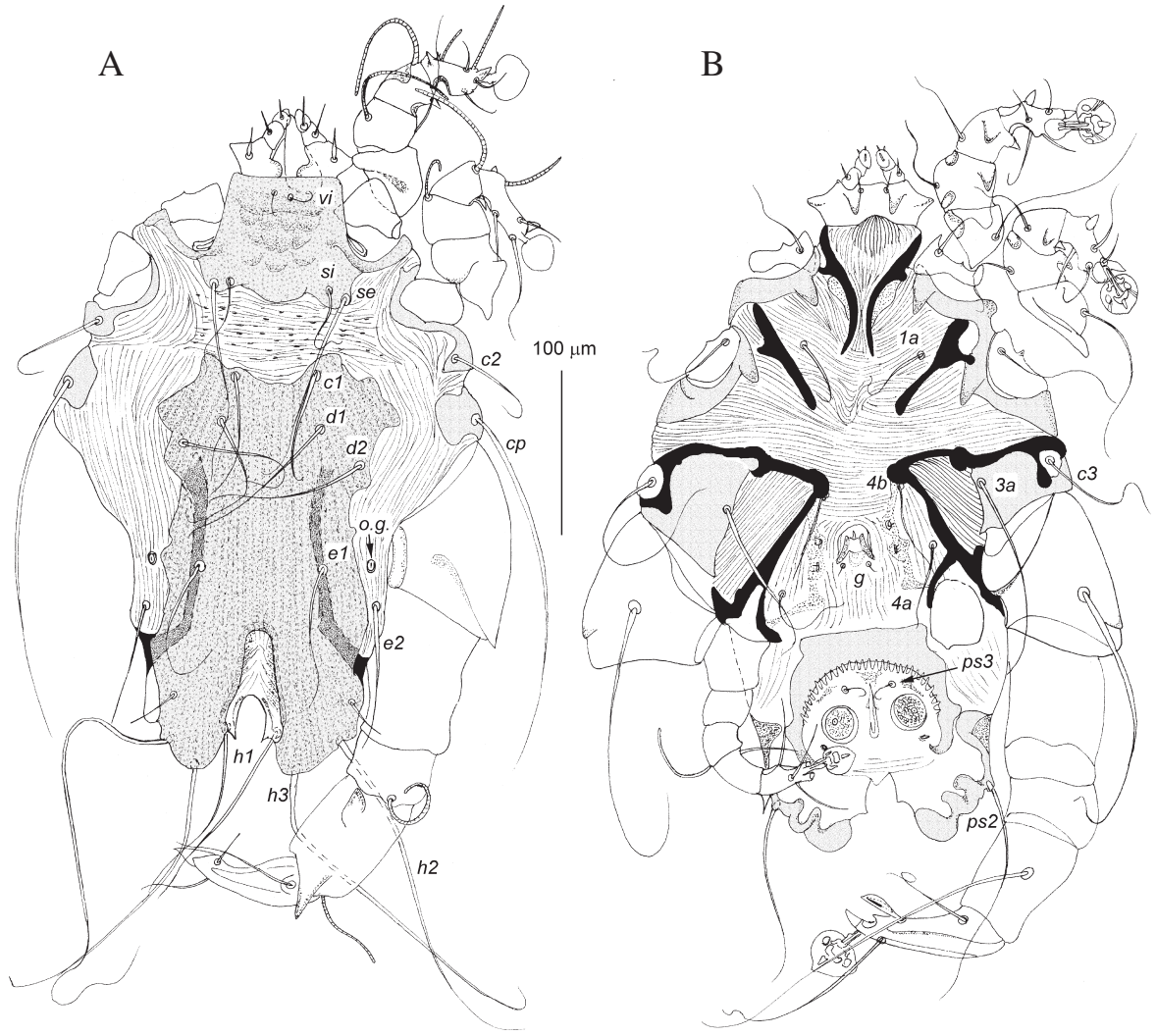

Fig. 4. *Gaudalges haymani* Fain, 1963, male. A — dorsal view; B — ventral view.

ly developed, opisthosomal cleft about 50 long. Legs III about 410 long, legs IV about 220 long. Dorso-apical spurs of tarsi I–II about 9 long. Ventral spurs of coxal fields I–II 17–18 long. Spurs of genua and tibiae I–II weakly developed. Dorso-apical spur of tibia III about 25 long. Tarsi III about 95 long without pretarsus. Dorso-basal spur on tarsi IV about 7 long. Lengths of setae: *vi* 9–10, *si* 28–32, *se* 120–125, *c1* 80–85, *c2* 75–80, *cp* 210–220, *c3* 110–115, *d1* 95–110, *d2* 100–115, *e1* 70–85, *e2* 100–105, *f2* 20–22, *h1* 200–210, *h2* 360–370, *h3* 325–340, *1a* 60–65, *3a* 120–130, *4a* 40–45, *4b* 50–55, *ps3* 18–20, *ps2* 100–110, *ω3*I 37–40, *ω1*I 25–28, *φ*I–II 65–70, *σ*I 40–50, *σ*II 12–13, and *σ*III 45–50.

Female (1 specimen; Figs 6, 7). Body, including gnathosoma, 445 long, 265 wide. Propodonotal shield 95 long, 110 wide, with elevations in median part. Idiosomal striations dorsally without verrucae. Epigynum situated between levels of coxal fields II and III. Genital papillae situated on epigynum. Legs III–IV about 180 long. Dorso-apical spur of tarsi I–II about 5 long. Ventral spurs of coxal fields I–II about 18 long. Tarsi III–IV about 50 long without pretarsus, subequal in length to pretarsi. Ventro-apical spur on tibiae III–IV about 13 long, spurs on tarsi III–IV about 9 long. Lengths of setae: *vi* 9, *si* 15, *se* 130; *c1*, *d1*, *d2*, *e1*, and *e2* about 15, *c2* 25, *cp* 95, *c3* 35, *f2* and *h1* about 5, *h2* and *h3* broken, *1a* 40, *3a* 27, *4a* 25, *4b* 26, *g* 25, *ps3* 22, *ps2* 20, *ω3*I 30, *ω1*I 13, *φ*I–II about 60, *σ*I 55, *σ*II 12, and *σ*III 18.

Material examined. 3 males and 1 female (BMOC 06–0324–003) ex *Eulemur coronatus* (Gray, 1842) (AMNH 100609) [anterior-dorsal body], MADAGASCAR: Antsiranana Prov., 26 km N Vohimarina, 13°08′52″S, 49°55′03″E, 27 September 1930, coll. A.L. Rand (# 1086). 1 male (BMOC 06–0324–005) from *E. coronatus* (AMNH 100615), same data, coll. A.L. Rand (# 1072). Voucher specimens are deposited in AMNH and UMMZ.

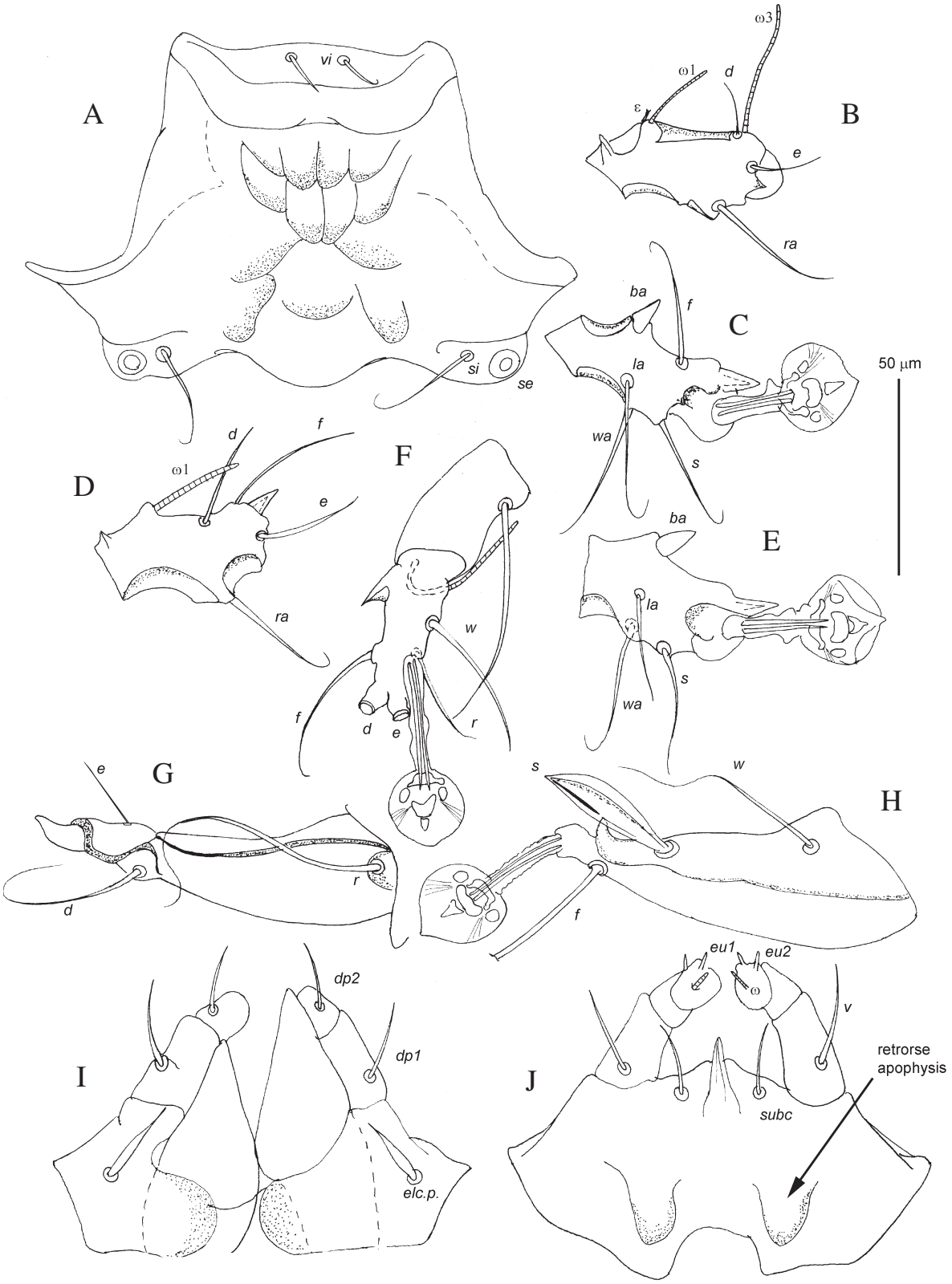

Fig. 5. *Gaudalges haymani* Fain, 1963, details of male. A — propodonotal shield; B —tarsus I in dorsal view; C — same in ventral view; D — tarsus II in dorsal view; E — same in ventral view; F — tibia and tarsus IV in ventral view; G — tarsus III in dorsal view; H — same in ventral view; I — gnathosoma in dorsal view; J — same in ventral view.

Type depository. Holotype in NHM.

Host ranges and distribution. This species was described from an alcohol preserved specimen of *Eulemur fulvus* (Geoffroy, 1796) (B.M. 91.11. 30.31) originating from Madagascar (Fort Dauphin) and housed in NHM. *E. coronatus* is a new host record for this species.

Fig. 6. *Gaudalges haymani* Fain, 1963, female. A — dorsal view; B — ventral view.

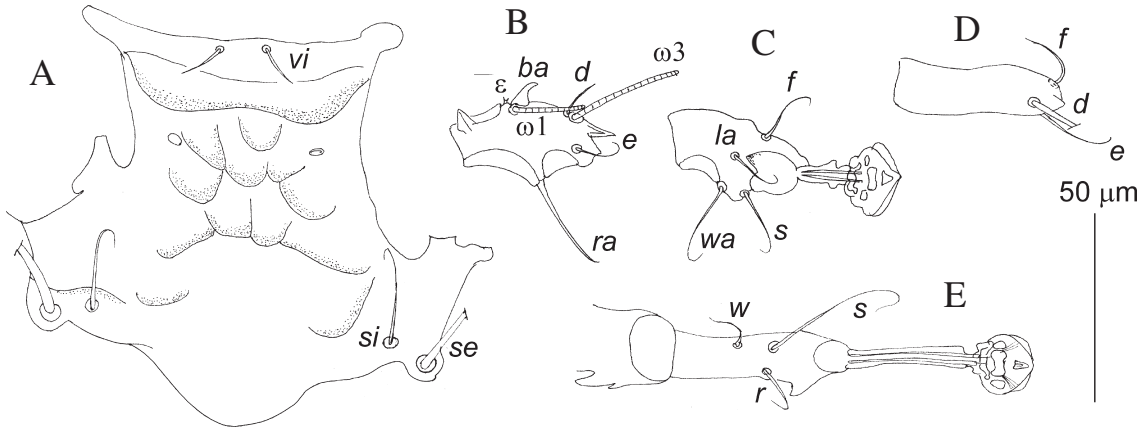

Fig. 7. *Gaudalges haymani* Fain, 1963, details of female. A — propodonotal shield; B —tarsus I in dorsal view; C — same in ventral view; D — tarsus III in dorsal view; E — tarsus and part of tibia III in ventral view.

Gaudalges caparti Fain, 1963

Figs 8–11.

Gaudalges carparti Fain 1963a: 155; Fain 1963b: 57, figs 36–39.

Redescription. Male (10 specimens, Figs 8, 10A–F). Body, including gnathosoma, 380–400 long, 260–270 wide. Propodonotal shield 70–80 long, 90–100 wide, bearing arched fold in median part. Hysteronotal shield 130–145 long in midline, completely covered by longitudinal striations. Anterior margin of hysteronotal shield only slightly concave. Setae *c1* and *d2* situated on hysteronotal shield. Length of setae *c1, d1, d2* greater than 60. Idiosomal striations between dorsal shields without verrucae. Dorso-lateral apodemes 110–120 long. Aedeagus 6–8 long. Adanal shields separated from each other or fused anteriorly by narrow band. Protuberances surrounding anal area distinctly developed. Diameter of paraanal suckers about 13. Opisthosomal lobes dis-

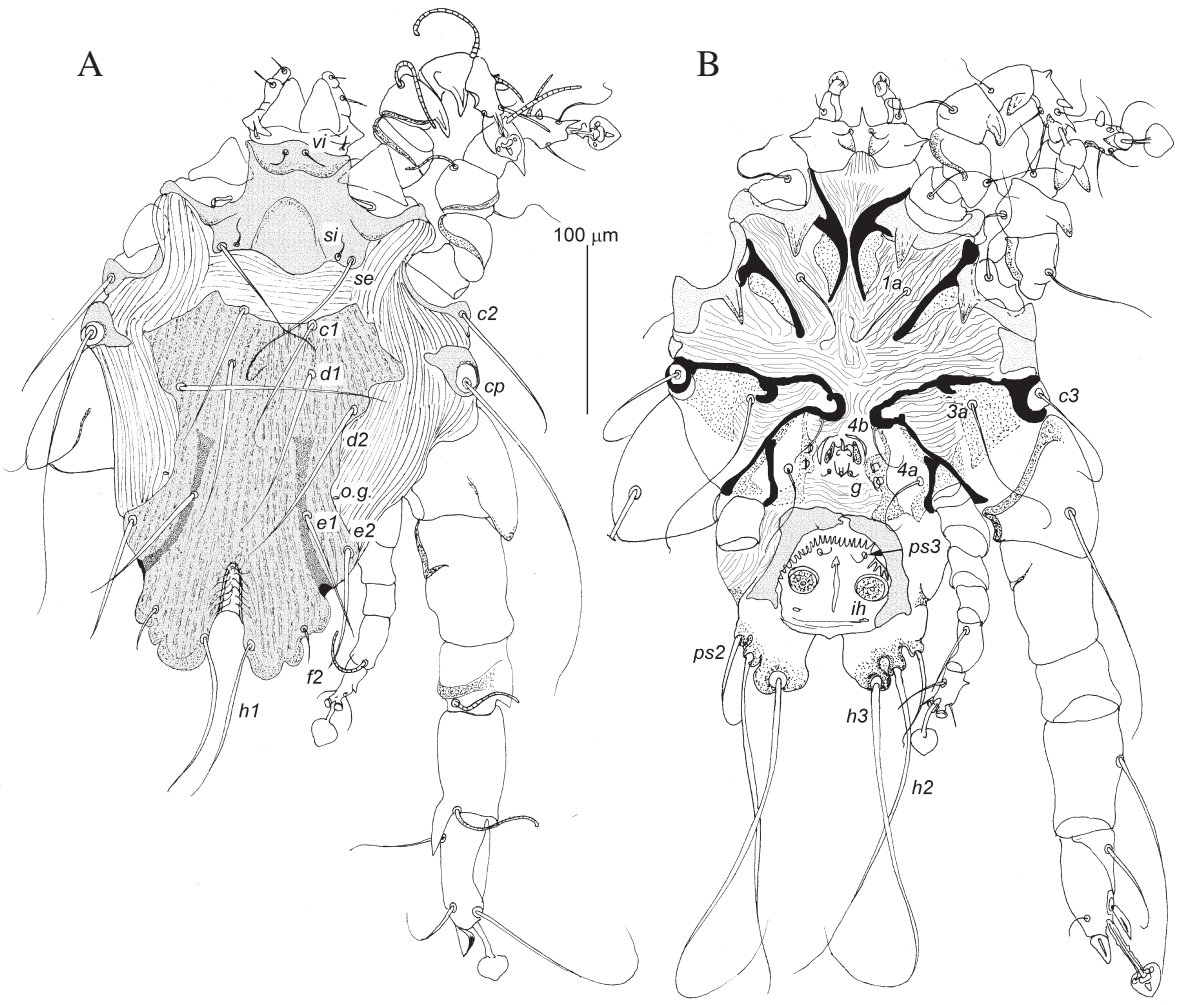

Fig. 8. *Gaudalges caparti* Fain, 1963, male. A — dorsal view; B — ventral view.

tinctly developed, opisthosomal cleft about 45 long. Legs III about 330 long, legs IV about 130 long. Dorso-apical spurs of tarsi I–II about 8 long. Ventral spurs of coxal fields I–II 18–19 long. Spurs of genua and tibiae I–II distinctly developed, about 13 long. Dorso-apical spur of tibia III about 20 long. Tarsi III about 75 long without pretarsus. Dorso-basal spur on tarsi IV about 5 long. Lengths of setae: *vi* 9–10, *si* 15–17, *se* 140–150, *c1* 65–70, *c2* 80–90, *cp* 165–180, *c3* 55–65, *d1* 130–140, *d2* 140–150, *e1* 60–65, *e2* 65–70, *f2* 20–25, *h1* 100–120, *h2* 220–230, *h3* 250–260, *1a* 55–60, *3a* 90–110, *4a* 30–35, *4b* 50–55, *ps3* 12–15, *ps2* 80–85, *ω3*I 37–40, *ω1*I 18–20, *φ*I–II 60–70, *σ*I 70–75, *σ*II 13–15, and *σ*III 40–45.

Female (10 specimens, Figs 9, 10G–J). Body, including gnathosoma, 330–350 long, 200–220 wide. Propodonotal shield 75–85 long, 105–110 wide, bearing arch-like fold in median part. Dorsal idiosomal striations with rounded protuberances, median hysterosomal striations thickened. Epigynum situated between levels of coxal fields I and II. Genital papillae situated posterior to epigynal arch. Legs III–IV about 150 long. Dorso-apical spur of tarsi I–II about 5 long. Ventral spurs of coxal fields I–II about 20 long. Tarsi III–IV about 45 long without pretarsus, 1.5 times longer than pretarsi. Ventro-apical spur on tibiae III–IV about 15 long, tarsi III–IV about 12. Lengths of setae: *vi* 8–9, *si* 10–12, *se* 110–120; *c1*, *d1*, *d2*, *e1*, and *e2* about 17, *c2* 22–25, *cp* 80–90, *c3* 20–22, *f2* and *h1* about 5, *h2* 55–60, *h3* 65–75, *1a* 40–50, *3a* 30–35, *4a* 17–20, *4b* 23–25, *g* 20–22, *ps3* 15–18, *ps2* 14–18, *ω3*I 35–38, *ω1*I 17–18, *φ*I–II about 45–50, *σ*I 25–30, *σ*II 13–15, and *σ*III 15–18.

Protonymph (2 specimens, Fig. 11A–C). Body, including gnathosoma, 210–230 long, 130–135 wide. Propodonotal shield 57–60 long, 45–48 wide, with indistinct tuberculate ornamentation in posterior part. Posterior margin of propodonotal shield triangular in outline. Setae *si* and *se* situated off propodonotal shield. Dorsal striations of idiosoma with rounded protuberances. Setae *h1, 4a, 4b, pR*I–II, *sR*III, *e*IV, *f*IV, *φ*IV, and one pair of genital

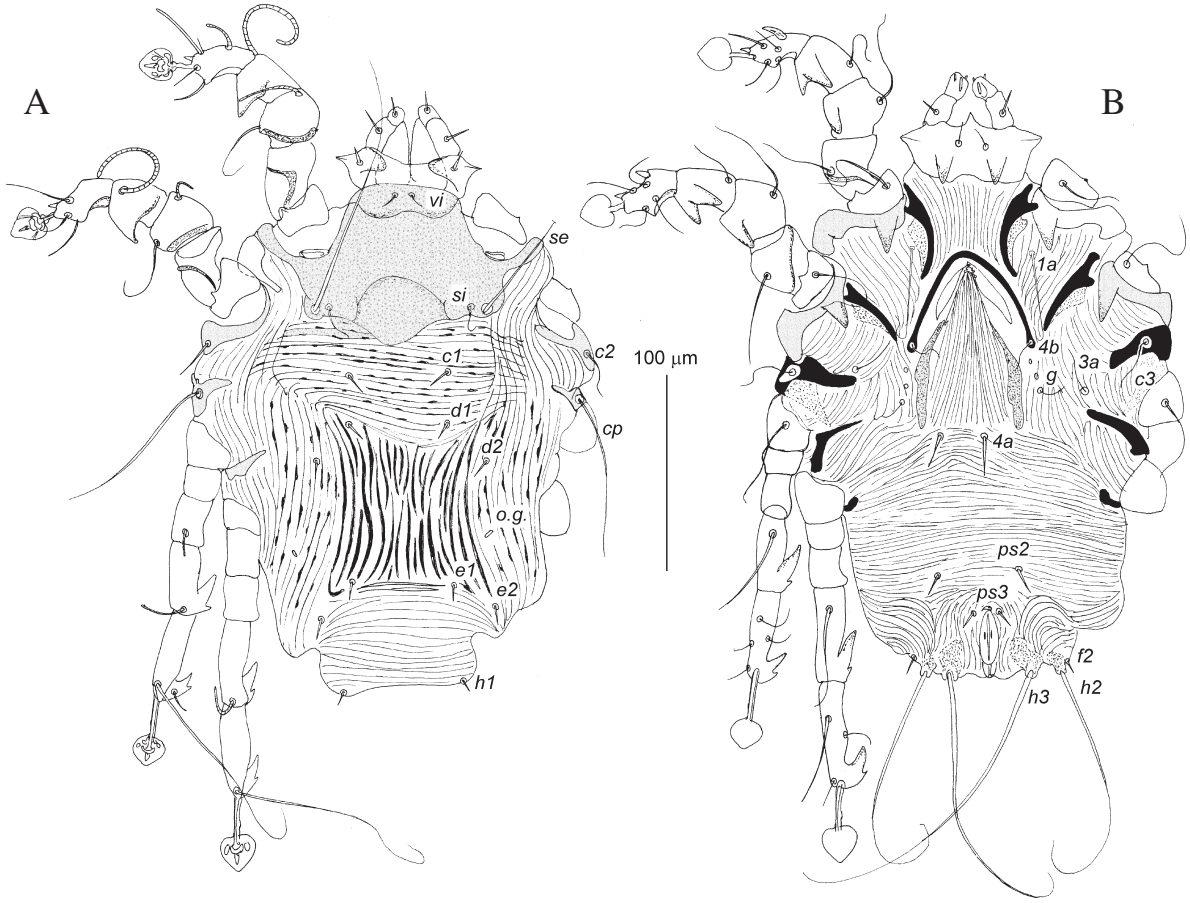

Fig. 9. *Gaudalges caparti* Fain, 1963, female. A — dorsal view; B — ventral view.

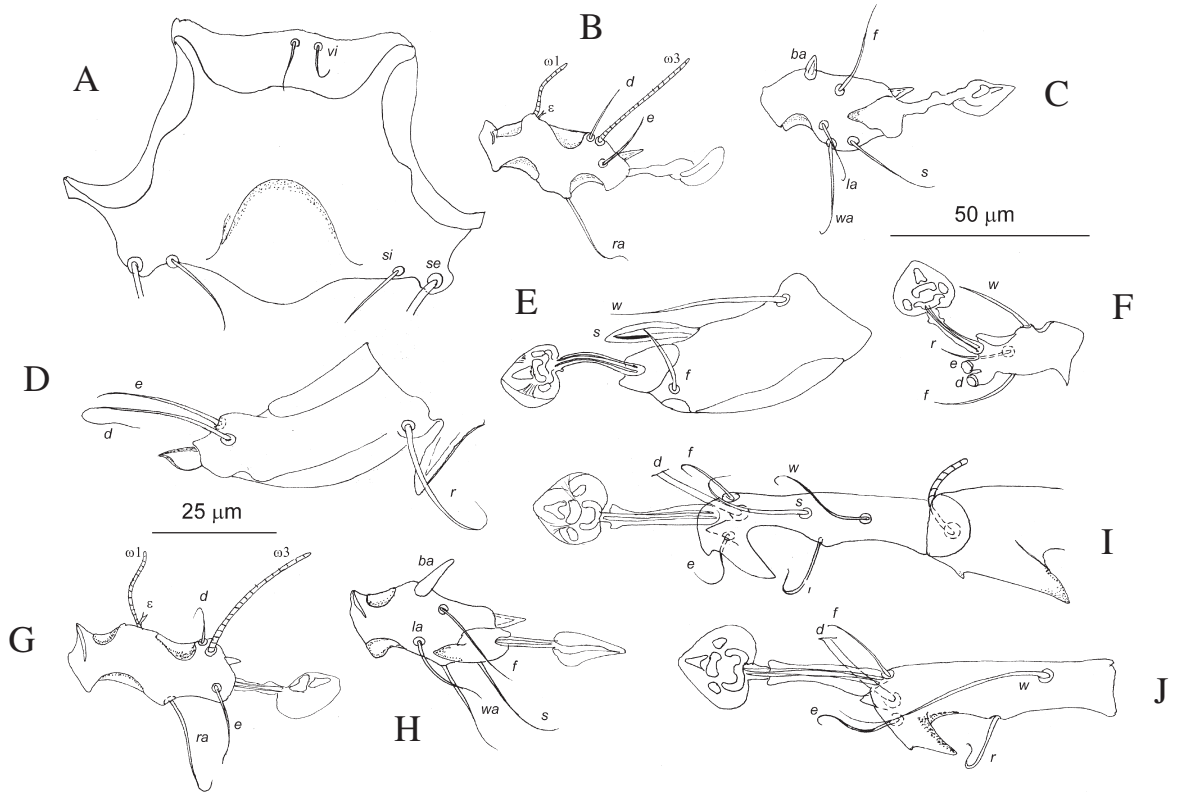

Fig. 10. *Gaudalges caparti* Fain, 1963, details. A — propodonotal shield of male; B —tarsus I of male in dorsal view; C — same in ventral view; D — tarsus III of male in dorsal view; E — same in ventral view; F — tibia and tarsus IV of male in ventral view; G — tarsus I of female in dorsal view; H — same in ventral view; I — tarsus and part of tibia III of female in ventral view; J — tarsus IV of female in ventral view.

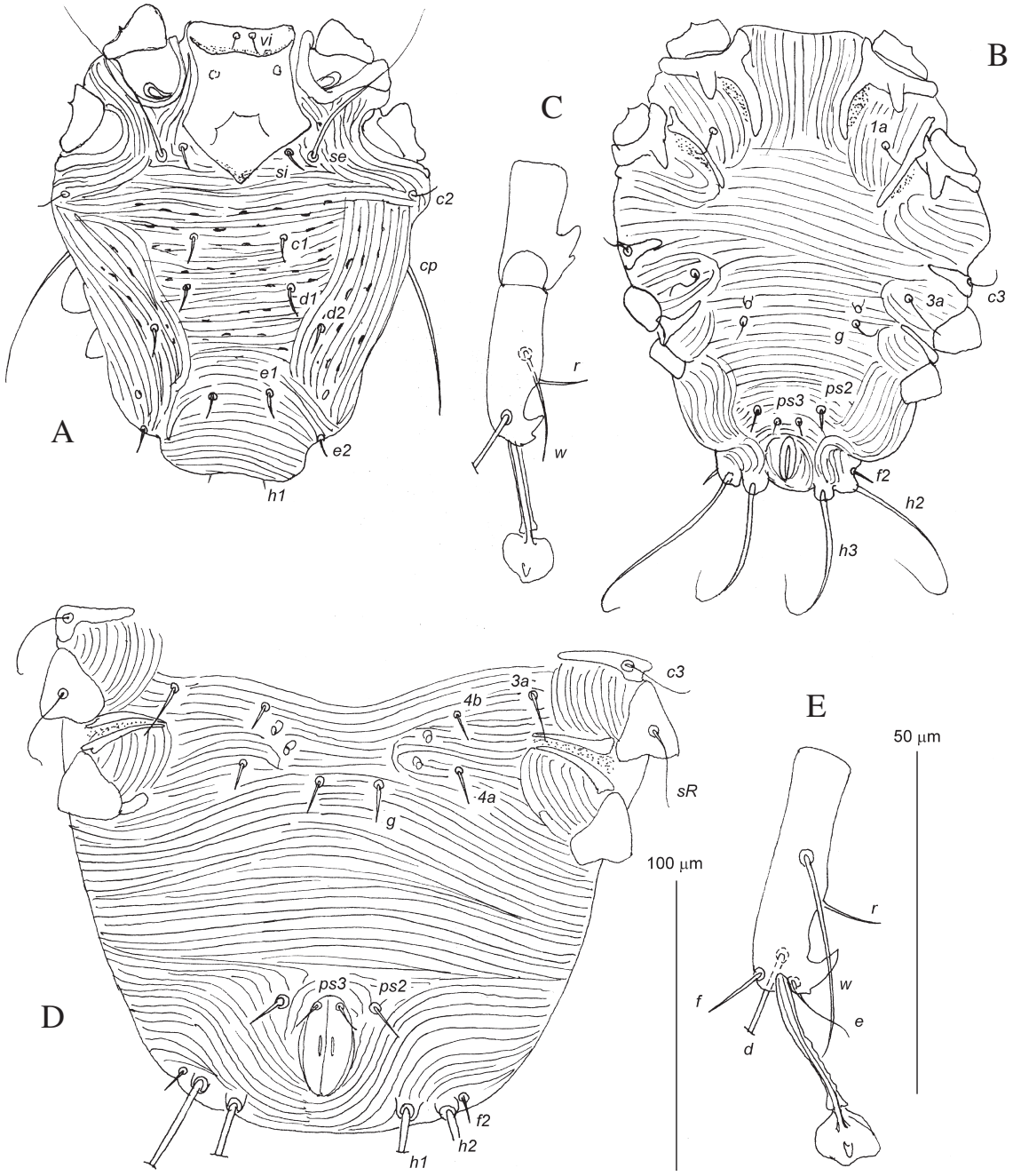

Fig. 11. *Gaudalges caparti* Fain, 1963, nymphs. A — protonymph in dorsal view; B —same in ventral view; C — tibia and tarsus of protonymph in ventral view; D — opisthosoma of tritonymph in ventral view; E — tarsus IV in ventral view.

papillae lacking. Lengths of setae: *si* 5–7, *se* 65–70, *c1, c2, c3, d1, d2, e1, e2* about 10, *cp* 35–40, *h2* 70–75, *h3* 60–70, *1a* 15–18, *3a* 14–16, *g* 10–11, *ps2* 6–7, *ps3* 10–11.

Tritonymph (1 specimen, Fig. 11D, E). Body, including gnathosoma 360, 215 wide. Similar to protonymph, but setae *h1, 4a, 4b, pR*I–II, *sR*III, *e*IV, *f*IV, *φ*IV, and second pair of genital papillae added. Lengths of setae: *si* 7, *se* 95, *c1, d1, d2, e1, e2* — all 10–12, *c2* 18, *cp* 70, *c3* 18, *h1* and *f2* 6, *h2* 50, *h3* 65, *1a* 25, *3a* 22, *4a, 4b*, and *g* — all 15–16.

Material examined. 27 males and 11 females (BMOC 06–0324–001) from *Hapalemur griseus griseus* (Link, 1795) (Primates: Lemuridae) (AMNH 100536) [anterior dorsum], MADAGASCAR: Fianarantsoa Prov., Manombo, 23°02′S, 47°44′E, 25 September 1929, coll. A.L. Rand (#406); 14 males, 9 females, 3 protonymphs, and 1 tritonymph (BMOC 06–0324–002) from *H. g. griseus* (AMNH 100630) [anterior dorsum], MADAGASCAR: Toamasina Prov., 20 km SW Maroantsetra, Manombia, 15°31′S, 49°38′E, 4 June 1930, coll. A.L. Rand. Voucher

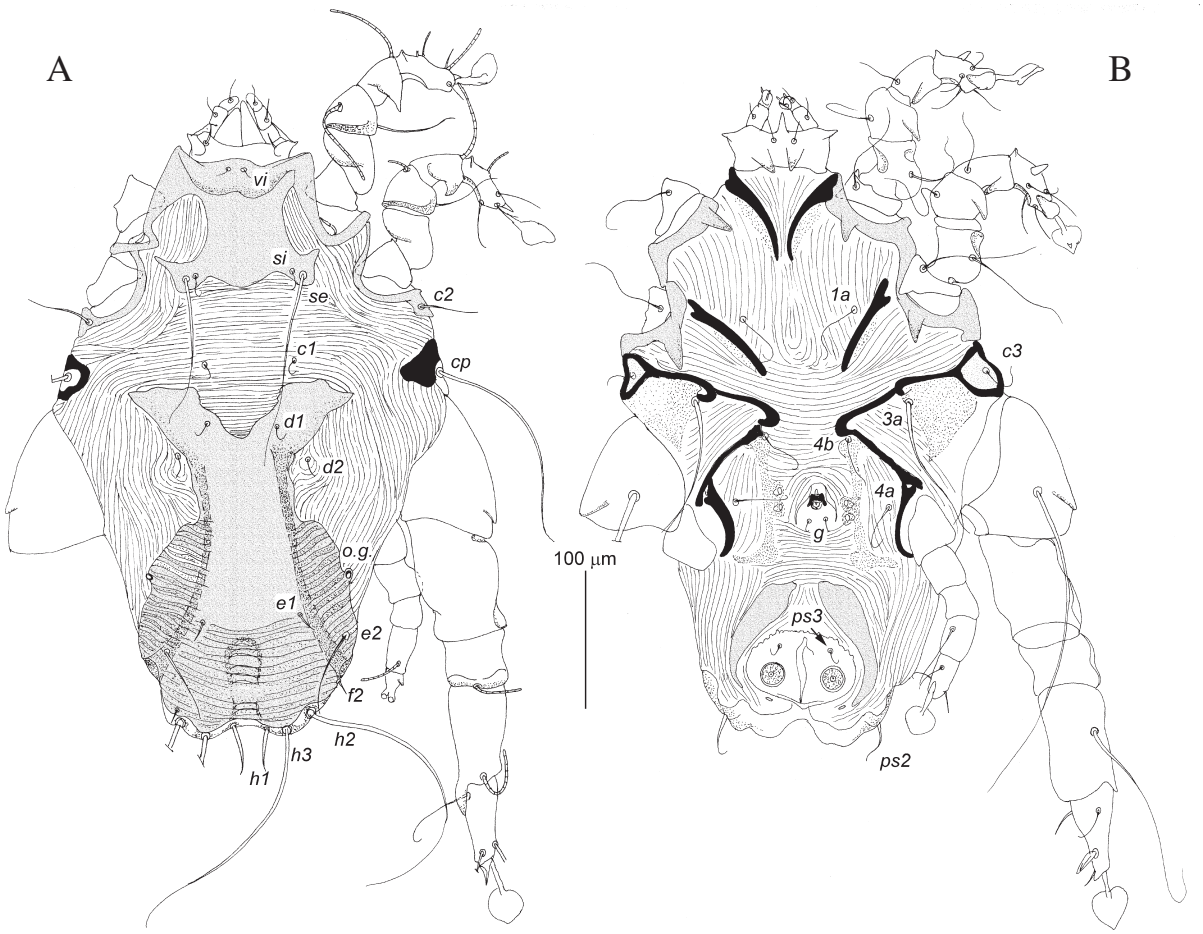

Fig. 12. *Gaudalges brevisetosus* Bochkov et OConnor, sp.n., male. A — dorsal view; B — ventral view.

specimens are deposited in AMNH, UMMZ, FMNH, and ZISP.

Type depository. Holotype in MRAC.

Host ranges and distribution. This species was described from *E. coronatus* from Madagascar (Nossi-Be) (Fain 1963a, b). *H. griseus* is a new host of this species.

Gaudalges brevisetosus Bochkov et OConnor, sp.n.

Figs 12–14.

Description. Male (holotype, Figs 12, 13). Body, including haetotaxy, 490 (420–470 in 2 paratypes) long, 315 (270–280) wide. Propodonotal shield 90 (90–95) long, 115 (110–120) wide, without ornamentation. Hysteronotal shield 210 (215–220) long in midline, covered by transverse striation posterior to level of setae *e1* and in lateral parts distally of dorso-lateral apodemes. Anterior margin of hysteronotal shield with wide median incision reaching level of setae *d1*. Setae *c1, d1, d2*, and *e1* very short, not longer than 30. Idiosomal striations between dorsal shields without verrucae. Dorso-lateral apodemes 175 (155–165) long. Aedeagus about 5 long. Adanal shields completely separated from each other. Protuberances surrounding anal area indistinct. Diameter of para-anal suckers about 20. Opisthosomal lobes weakly developed, opisthosomal cleft about 8 long. Legs III about 365 long, legs IV about 165 long. Dorso-apical spurs of tarsi I–II about 10 long. Ventral spurs of coxal fields I–II 18–20 long. Spurs of genua and tibiae I–II distinctly developed. Dorso-apical spur of tibia III about 20 long. Tarsi III about 75 long without pretarsus. Dorso-basal spur on tarsi IV about 5 long. Lengths of setae: *vi* about 9, *si* 15 (12–13), *se* 130 (130–145), *c1*, *d1, d2*, and *e1* 20–25 long, *c2* about 50, *cp* 185 (190–200), *c3* 45 (40–50), *e2* 65 (47), *f2* about 10, *h1* 35 (30–40), *h2* 180, *h3* 200 (175), *1a* about 55, *3a* 110 (100–125), *4a* and *4b* 35–40, *ps3* about 12, *ps2* about 55, *ω3*I 35–40, *ω1*I 23–25, *φ*I–II 55–60, *σ*I 25, *σ*II about 12, and *σ*III about 40.

Female (1 specimen, Fig. 14). Body, including haetotaxy, 380 long, 210 wide. Propodonotal shield 95 long, 110 wide, without ornamentation. Dorsal idiosomal striations without verrucae. Epigynum situated between levels of coxal fields II and III.

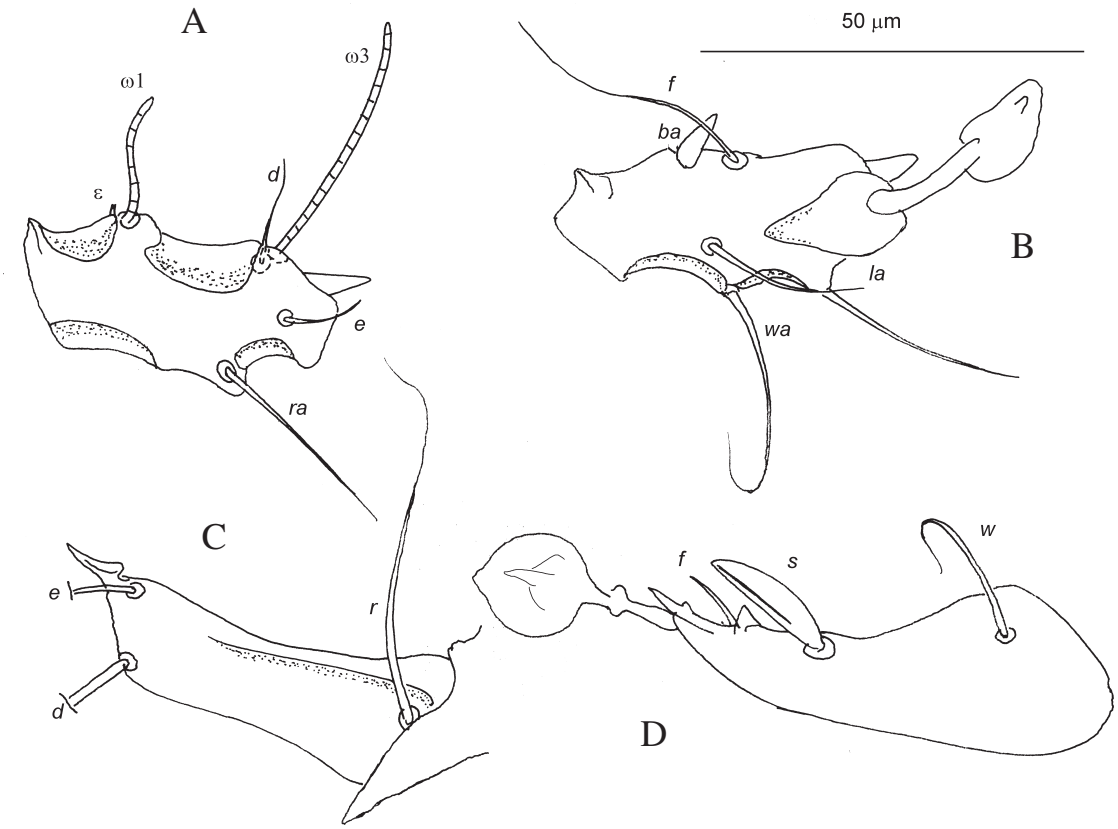

Fig. 13. *Gaudalges brevisetosus* Bochkov et OConnor, sp.n., details of male. A — tarsus I in dorsal view; B — same in ventral view; ventral view; C — tarsus III in dorsal view; D — same in ventral view.

Anterior pair of genital papillae situated on epigynal arch. Legs III–IV 150 and 175 long, respectively. Dorso-apical spur of tarsi I–II about 5 long. Ventral spurs of coxal fields I–II about 20 long. Tarsi III–IV about 50 long without pretarsus, 1.5 times longer than pretarsi. Ventro-apical spurs on tibiae III–IV about 10 long, spurs on tarsi III–IV about 8 long. Lengths of setae: *vi* 8, *si* 12, *se* 120; *c1*, *d1*, *d2*, *e1*, and *e2* about 13, *c2* 25, *cp* 90, *c3* 12, *f2* and *h1* about 5, *h2* and *h3* broken, *1a* 35, *3a* 25, *4a*, *4b*, and *g* about 15, *ps3* 6, *ps2* 70, *ω3*I 17, *ω1*I 30, *φ*I–II about 40, *σ*I 30, *σ*II 8, and *σ*III 11.

Type material. Male holotype and male paratype (BMOC 06–0324–004) from *Eulemur coronatus* (AMNH 100618) [dorsum], MADAGASCAR: Antsiranana Prov., 26 km N Vohimarina, 13°08′52″S, 49°55′03″E, 27 September 1930, coll. A.L. Rand (# 1072); male paratype (BMOC 06–0324–003) from *E. coronatus* (AMNH 100609), same data, coll. A.L. Rand (# 1086); 1 female paratype (BMOC 06–0324–005) from *E. coronatus* (AMNH 100615), same data, coll. A.L. Rand (# 100615).

Type depositories. Holotype and male paratype (BMOC 06–0324–004) in AMNH; male paratype (BMOC 06–0324–003) and female (BMOC 06–0324–005) paratypes in UMMZ.

Etymology. This species name is an adjective derived from the Latin words *brevis* (short) and *saeta* (seta) referring to the short hysteronotal setae of males in this new species.

Host ranges and distribution. This species so far known only from *E. coronatus* from Madagascar (Vohemar).

Differential diagnosis. This new species differs from other species of the genus *Gaudalges* in both sexes, by the absence of ornamentation on the propodonotal shield; in males, by short setae *c1, d1, d2*, and *e1* (less than 30 long), the position of setae *c1* and *d2* off the hysteronotal shield, the hysteronotal shield covered by transverse striations in the posterior part, the anterior margin of the hysteronotal shield with a wide median incision reaching the level of setae *d1*, the minute protuberances of the adanal membrane, and by the short lobes of the idiosoma. In both sexes of the three other species, the propodonotal shield is ornamented; in males, setae *c1, d1, d2,* and *e1* are at least 60 long, setae *c1* and *d2* are situated on the hysteronotal shield, the hysteronotal shield is completely covered by longitudinal striations, the anterior margin of the hysteronotal shield is only slightly concave, the adanal membrane bears the distinct hyaline protuberanc-

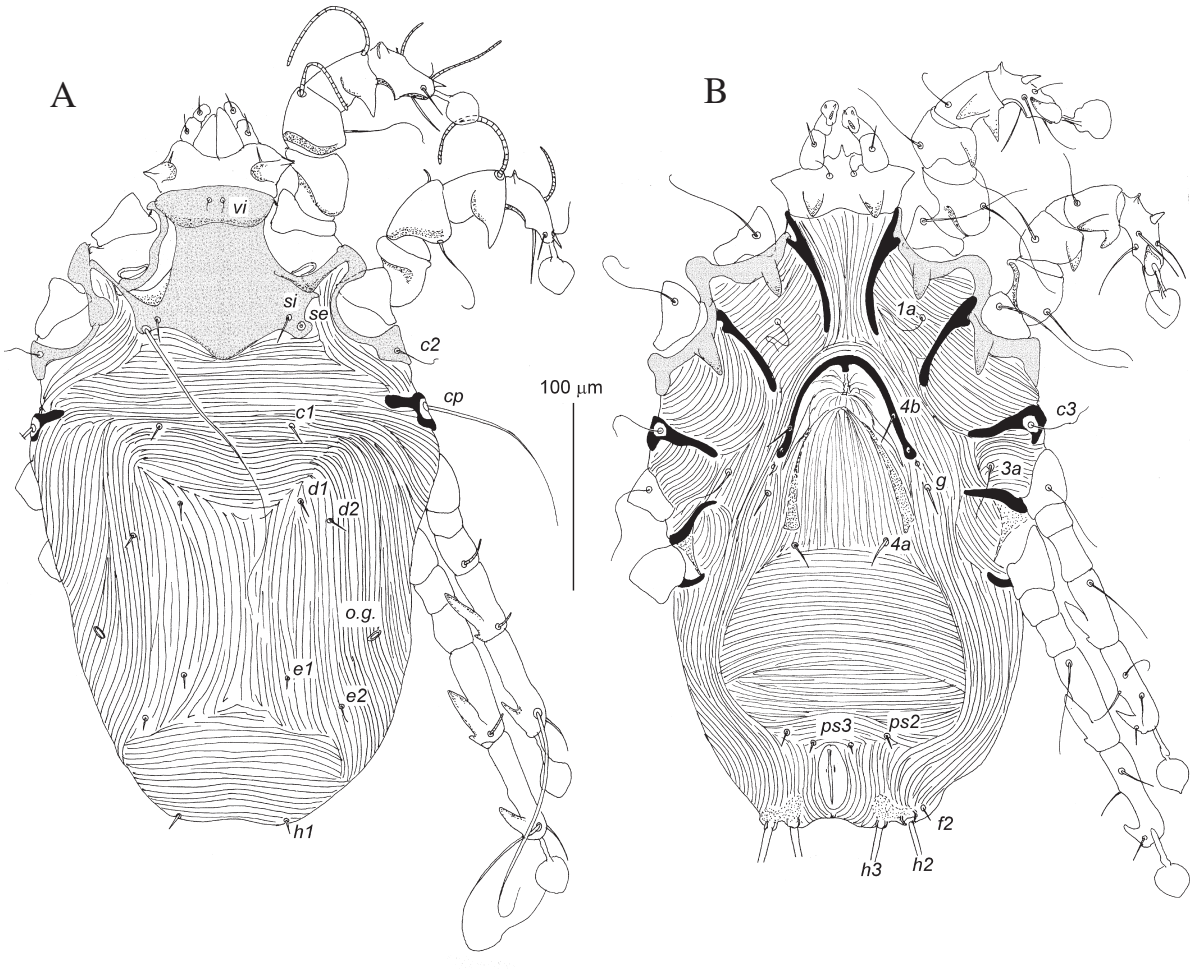

Fig. 14. *Gaudalges brevisetosus* Bochkov et OConnor, sp.n., female. A — dorsal view; B — ventral view.

es, and the opisthosomal lobes are distinctly developed. In addition, it differs from *G. propitheci* and *G. haymani* in males, by the absence of verrucae on the striations between the dorsal shields, the adanal shields completely separated from each other, and by short setae *h1* (30–40 long); in females, by the epigynal apodeme bearing only one pair of genital papillae. In males of *G. propitheci* and *G. haymani*, the cuticle between the dorsal shields bears rounded verrucae on the striations, the adanal shields are fused to each other anteriorly, setae *h1* are about 200 long; in females, the epigynal apodeme bears both pairs of genital papillae. *G. brevisetosus* sp.n. differs from *G. caparti* in males, by short setae *h1*; in females, by the epigynum situated between the levels of coxal fields II and III and bearing a single pair of genital papillae. In males of *G. caparti*, setae *h1* are 100–120 long; in females, the epigynum is situated between the levels of coxal fields I and II, and the genital papillae are situated posterior to the epigynum.

Key to species of the genus *Gaudalges* Fain, 1963

Males

1. Propodonotal shield ornamented. Setae *c1, d1, d2,* and *e1* at least 60 long; setae *c1* and *d2* situated on hysteronotal shield; setae *h1* longer than 60. Hysteronotal shield completely covered by longitudinal striations; anterior margin of hysteronotal shield only slightly concave. Anal area surrounded by distinct protuberances. Opisthosomal lobes distinctly developed; opisthosomal cleft longer than 30. 2
— Propodonotal shield without ornamentation. Setae *c1, d1, d2*, and *e1* less than 30 long; setae *c1* and *d2* situated off hysteronotal shield; setae *h1* 30–40 long. Hysteronotal shield covered by transverse striations only in posterior part; anterior margin of hysteronotal shield with wide median incision reaching level of setae *d1*. Anal area surrounded by indistinct protuberances. Lobes of idiosoma short; opisthosomal cleft less than 10 long. .... *G. brevisetosus* sp.n. (Fig. 12)

2. Propodonotal shield with elevations in median part (Fig. 5A). Striations between dorsal shields with verrucae. Adanal shields completely fused to each other anteriorly. Spurs on genu and tibia I–II weakly developed. 3
— Propodonotal shield with arch-like fold in median part (Fig. 10A). Striations between dorsal shields without verrucae. Adanal shields separated from each other or jointed by narrow sclerotized band. Spurs on genu and tibia I–II distinctly developed. ..... *G. caparti* (Fain, 1963) (Fig. 8)

3. Ventral spurs of coxal fields I–II 10–11 long. ..... *G. propitheci* (Gaud et Till, 1957) (Fig. 1)
— Ventral spurs of coxal fields I–II 17–18 long. ..... *G. haymani* (Fain, 1963) (Fig. 4)

Females

1. Idiosomal striations dorsally without verrucae. Propodonotal shield without ornamentation or with elevations. Epigynum situated between levels of coxal fields II and III, bearing 1 or 2 pairs of genital papillae. 2
— Idiosomal striations dorsally with verrucae. Propodonotal shield with median arch-like fold. Epigynum situated between levels of coxal fields I and II, genital papillae situated posterior to epigynum. ..... *G. caparti* (Fain, 1963) (Fig. 9)

2. Propodonotal shield with elevations. Epigynum bearing 2 pairs of genital papillae. Spurs on genu and tibia I–II weakly developed. Tarsi III–IV subequal in length to respective pretarsi. 3
— Propodonotal shield without ornamentation. Epigynum bearing 1 pair of genital papillae. Spurs on genu-tibia I–II distinctly developed. Tarsi III–IV about 1.5 longer than respective pretarsi. ..... *G. brevisetosus* sp.n. (Fig. 14)

3. Ventral spurs of coxal fields I–II about 9 long. ..... *G. propitheci* (Gaud et Till, 1957) (Fig. 3)
— Ventral spurs of coxal fields I–II about 18 long. ..... *G. haymani* (Fain, 1963) (Fig. 6)

DISCUSSION

OConnor (1984) conducted the first phylogenetic analysis of the subfamily Makialginae based on 21 morphological characters derived from published literature and using simple Hennigian argumentation. We have subsequently reevaluated some of these characters after examining specimens of some of these taxa. OConnor (1984) considered the genus *Gaudalges* as polyphyletic. *G. haymani* was inadequately described and, therefore, not included in that analysis. In his cladogram, *G. caparti* is the sister group of the genus *Makialges*. This branch is supported by two synapomorphies of females, enlarged apophyses of tibiae-tarsi III–IV and short pretarsi III–IV. *G. propitheci* was considered the sister group of the clade joining *Daubentonialges* and *Lemuralges*. OConnor regarded the presence of coxal apophyses as ancestral in makialgines because they are present in *Galagalges* and regarded their reduction or absence as derived states. The node linking *G. propitheci* with *Daubentonialges* and *Lemuralges* was supported by a single synapomorphy, the reduction and subsequent loss of the apophyses of coxal fields I–II. The apophyses of coxal fields and legs in all four *Gaudalges* species have the same principal structure and differ only in relative sizes. In *Galagalges*, coxal fields I–II each bears a pair of posterolaterally directed spurs (vs. only one posteriorly directed spur per coxal field in *Gaudalges*), so these spurs are possibly not homologous in these two taxa. The presence of coxal apophyses varies in *Makialges*, being present in *M. sternodons* but absent in *M. lepilemuri*. In *Daubentonialges* and *Lemuralges,* coxal apophyses are absent, as are the apophyses of tibiae IV and tarsi III–IV in females of *Lemuralges*. Concerning the relative lengths of pretarsi III–IV in females, these are not actually significantly different. In *G. propitheci,* female tarsi III–IV are subequal in length to the respective pretarsi, and in *G. caparti*, they are 1.5 longer than the pretarsi.

Given these reinterpretations, we now think that *Gaudalges* is a monophyletic group. Monophyly is supported by two unique synapomorphies in males, tibia III has a dorso-apical spine and tarsus IV bears a dorso-basal projection. There are no unique synapomorphies for this genus in the female.

Among genera of the subfamily Makialginae, the genera *Gaudalges*, *Daubentonialges*, and *Lemuralges* can be considered as a monophyletic group that can be characterized by the following synapomorphies: in males, closed coxal fields III, the presence of an adanal membrane bearing hyaline protuberances, and the relatively widely separated opisthosomal lobes; in females, the absence of the hysteronotal shield. Within this lineage, *Gaudalges* shares with *Lemuralges* the membranous form of seta s of tarsus III in males (filiform in *Daubentonialges*).

The genus *Makialges* is the sister group of this lineage, sharing with them the latero-dorsal and U-shaped apodemes of the male hysterosoma are distinctly developed and legs I and II have

similarly positioned and probably homologous spurs and projections that are strongly reduced but, nevertheless, recognizable in *Lemuralges*. The very long dorsal opisthosomal setae consistitute synapomorphies of the *Makialges* species.

The genus *Cheirogalalges* differs from all other Malagasy makialgines by the structure of the leg's spurs and projections and in males, by the indistinct dorso-lateral and U-shaped apodemes. Setae *ba*I–II of *Cheirogalalges*, however, are spur-like, and legs III–IV of tritonymphs have the same structure as in the genera *Makialges* and *Gaudalges*. The adult female remains unknown in this genus.

The morphology of the genus *Galagalges,* known only from males and tritonymphs should be re-examined. OConnor (1984) considered this genus being the sister group to the genus *Cheirogalalges* basing on the following synapomorphies: elongation of the body, the presence of ventral opisthosomal and post-aedeagal sclerites in males, and the absence of pretarsus III in males. Some of these synapomorphies, however, seem questionable. In *Galagalges*, the idiosoma is 3 times longer than wide (vs. 2 times in *Cheirogalalges* and 1.5 times in other makialgines); the ventral opisthosomal sclerite is clearly homologous to the adanal shields that are present and even fused in many different psoroptids, including makialgines, thus the actual synapomophy shared by *Galagalges* and *Cheirogalalges* is the shape of the sclerite, which is longer than wide. This, however, is likely related to the relative elongation of the body in these taxa and not independent of it. The male pretarsus III, while completely absent in *Cheirogalalges*, is represented in *Galagalges* by a reduced ambulacral stalk. These states may represent a transformation series. Finally, the presence of a post-aedeagal (postgenital) sclerite is not unique. A postgenital sclerite is present in males of many different psoroptid taxa, including the genus *Makialges*. OConnor (1984) did not note the absence of coxal apophyses in *Cheirogalalges*, the presence of which he regarded as ancestral in Makialginae (see above).

Galagalges is well characterized by a number of unique apomorphies including fused apodemes I, legs III and IV subequal in length, absence of the opisthosomal lobes, the strongly elongated idiosoma, and the absence of the adanal suckers. The tarsal setation must be reexamined (the published illustrations of the male show only 6 setae on tarsus I) to determine the form of seta *ba*. The spine-like form of this seta is diagnostic of the Makialginae, but the possible homologue of this seta in *Galagalges* is filiform. The form and position of the apophyses of the legs are also somewhat different from the other Makialginae. Discovery of the females of *Galagalges* and *Cheirogalalges* may provide additional evidence concerning the possible relationships between these genera and the position of *Galagalges* with respect to the other Makialginae or other psoroptid lineages associated with Primates. At this time, there is good support for the monophyly of the psoroptid genera parasitizing Malagasy lemurs. These hosts themselves form a monophyletic group, the common ancestor of which presumably colonized Madagascar in the early Tertiary period (Karanth et al. 2005).

ACKNOWLEDGEMENTS

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