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Ontogeny of *Megalolaelaps colossus* sp. nov. (Acari: Megalolaelapidae), an enigmatic symbiont of dung beetles (Coleoptera: Scarabaeidae) in Colombia

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Abstract

Post-embryonic development of *Megalolaelaps colossus* **sp. nov.**, is described and illustrated. This unusually large species of mite is closely associated with the dung beetle *Oxysternon conspicillatum* (Weber) (Coleoptera: Scarabaeidae) in Colombia. All instars of the mite occur on the beetle, except for the larva. This is the first description of all instars for a species in this genus.

Key words: Permanent association, CCLC, Amazon, relative size, dependence

Introduction

All things being equal, large organisms usually attract more attention than small ones. In that context, mites in the genus *Megalolaelaps* Berlese may be a bit of an anomaly. They are extremely large mites (up to 4 mm in body length) (Mašán & Halliday 2014), which is larger than some adults ticks (Fonseca 1946)), and they occur on (relatively) common dung beetles (Figure 1). They have been known since the early 1900'rds and all six recognizable species were described over 50 years ago. Since that time, there have been no revisionary studies, post-embryonic development has never been documented, and nothing is known about behavior and general life-history, although there are a few pieces of anecdotal information. For example, specimens of *Megalolaelaps* may carry parasitic fungi of the genus *Rickia* and other genera of Laboulbeniales (Paoli 1911; Elsen & Fain 1973; Proaño-Castro & Rossi 2008).

The immediate goal of this study is to address one of the deficiencies in the knowledge of the genus by describing all instars of a new species of *Megalolaelaps*. Studies on the life history of these mites, and a systematic revision of the genus are in progress.

Materials and methods

Initial collections of specimens from *Oxysternon conspicillatum* (Coleoptera: Scarabaeidae) were made in 2013–2014 in the Coffee Cultural Landscape of Colombia (CCLC)[1]. Additional specimens were obtained from the same host species in May 2015, from the Amazon region.

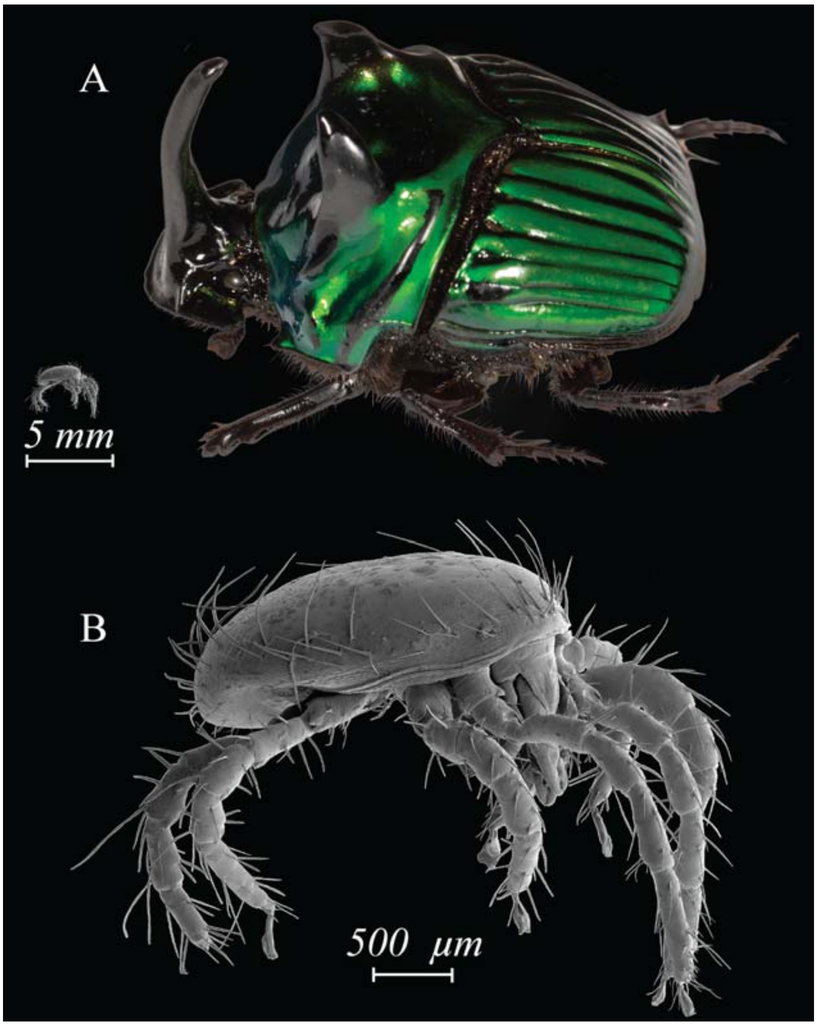

FIGURE 1. A. *Oxysternon conspicillatum* (Scarabaeidae) and *Megalolaelaps colossus* **sp. nov.**, at the same scale. B. Female *Megalolaelaps colossus* **sp. nov.**, magnified (LT-SEM).

Beetles were collected using non-lethal pitfall traps (Cultid Medina *et al.* 2012). Mites were removed from the beetles using forceps or a small brush under a dissecting scope and preserved in 96% ethanol. Some mites were cleared in 55% lactic acid, and studied as temporary preparations in cavity slides or dissected and prepared as permanent slides using Hoyer's medium (Walter & Krantz 2009).

Identifications, photographs, and measurements were made using a Nikon Eclipse 90i microscope equipped with DIC illumination and a motorized head with a PC controlled digital camera Ds-5M-U1. Most images were taken using the automatic Z-stack feature in the NIS-Elements microscope imaging software (Nikon Instruments Inc., Melville, NY). When needed, partial images from different parts of the body were combined using the photomerge function in Adobe Photoshop, vs CC 2015 (Adobe Systems Inc., San Jose, CA). Digital drawings were prepared in Adobe

1. CCLC, is comprised of the departments of Quindío, Risaralda and Caldas and was declared a World Heritage site by UNESCO in 2011 as http://whc.unesco.org/en/list/1121

Illustrator, vs CC 2015 (Adobe Systems Inc., San Jose, CA), using a Wacom Cintiq 21UX (Wacom, Vancouver, WA) drawing tablet, with the Adobe Photoshop combined pictures as templates.

All measurements are in micrometers (µm). Idiosomal length measured along the midline of the body, and width taken at the level between coxa III and IV. The gnathosoma is excluded from the length measurements. Length of sternal and anal shields measured along the midline of the body, width for sternal shield at level of setae *st2* and for anal shield at greatest measurement anterior to the para-anal (*pa*) setae. Length for metapodal shield measured as greatest length (roughly 35° off the midline of the body), width as greatest measurement at 90° angle to the shield length axis. Some average values are included in the description, and all averages, as well as minimum and maximum values, are given in Table 1. Most anatomical notations and idiosomal chaetotaxy follow, respectively, Evans & Till (1979) and Lindquist & Evans (1965); palp chaetotaxy follows Evans (1963a) and leg chaetotaxy Evans (1963b). Designations for lyrifissures and glands (Figures 2–3) follow Athias-Henriot (1971, 1975) as adapted by Kazemi *et al*. (2014). Notably, additional lyrifissures and glands may be present; despite the size of these mites, lyrifissures and especially glands proved difficult to see even when examining multiple specimens.

Paratypes of other species of *Megalolaelaps*, held in the collections of the U. S. National Museum of Natural History (NMNH) and Ohio State University Acarology Collection (OSAL), were examined directly, while additional specimens in the Berlese Acaroteca (Istituto Sperimentale per la Zoologia Agraria, Florence, Italy) and Instituto Butantan (São Paulo, Brazil) were examined indirectly based on images.

Abbreviations for specimen depositories: ICN: Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Bogotá, Colombia; OSAL: Ohio State University Acarology Collection, Columbus, Ohio, U.S.A. ANIC: Australian National Insect Collection, Canberra, Australia.

SYSTEMATICS

Family Megalolaelapidae Fonseca, 1946

Megalolaelaptidae Fonseca, 1946: 179.
Type genus *Megalolaelaps* Berlese, 1892: 72, by monotypy.
Type species *Megalolaelaps haeros* Berlese, 1888, by subsequent designation (Vitzthum 1931; 26)

The familial assignment of the genus *Megalolaelaps* is unclear and needs further study. Provisionally, this manuscript follows Mašán and Halliday (2014), who judged Fonseca’s (1946) proposal to place the genus in its own family “reasonable”.

Diagnosis, adults only (modified from Mašán and Halliday (2014)):

Female. Large mites, idiosomal length 2000–4000. Dorsal shield entire, almost completely covering idiosoma. Dorsal setation hypertrichous. Epigynal shield separated from anal shield by a wide area of soft integument, ventral shield absent; exopodal platelets absent. Lateral and ventral opisthogastric setation hypertrichous. Palp pretarsal claw 2-tined; palp trochanter with a large antero-ventral horn-like projection. ***Male***: spermatodactyl long, tightly coiled, and inserted medially in antiaxial surface of movable digit. Cheliceral segments larger and more robust than those of female. Sternal and genital shields fused, separated from anal shield.

Notes. Megalolaelapidae are most similar to Pachylaelapidae and members of the genus *Neopodocinum* Oudemans (Macrochelidae). In females of Megalolaelapidae the genital and anal shields are free, the ventral shield is absent, and they lack a pair of sclerites lateral to the genital shield. Females of Pachylaelapidae may have the anal and ventral shields fused forming a ventrianal shield (in Pachyseiinae), or the genital shield is fused with the ventral or ventrianal shields. In

Neopodocinum and in general in Macrochelidae, females have one pair of sclerites next to the lateral borders of the genital shield. The spermatodactyl in males of Megalolaelapidae is long and strongly coiled, while it is short and erect in *Neopodocinum* and long and well developed, but not coiled, in Pachylaelapidae.

Additionally, adults of Megalolaelapidae have a hypertrichous dorsal shield with minute setae (>100 pairs of setae), while adults of Pachylaelapidae are hypotrichous (with exception of *Pachysphaerolaelaps* Mašán, which is hypertrichous with about 80 pair of setae), usually bearing 30 pairs of setae, (29 pairs of setae in *Neopachylaelaps* Mašán, and *Pachyglobolaelaps* Mašán, or 33–37 pairs in *Elaphrolaelaps* Berlese, and *Pachyseiulinae*). In *Neopodocinum* the dorsal shield may have between 28–31 pair of setae. Also, *Neopodocinum* (and in general macrochelids), have well developed arthrodial brushes while the arthrodial articulation in *Megalolaelaps* lacks distinct arthrodial processes or brush like structures.

Species included: For the purpose of this paper *Megalolaelaps* includes six valid, recognizable species: *M. haeros* Berlese, 1888, described from Brazil, host unknown; *M. hirtus* Berlese, 1904 described from Brazil on *Passalus interruptus* and also reported in Ecuador; *M. mexicanus* Stoll, 1893, described from Mexico, unknown host; *M. enceladus* Berlese, 1910a described from North America, on *Dichotomius carolinus* (probably includes *M. ornatus* (Keegan 1946)); *M. immanis* Berlese 1910b described from Venezuela, host unknown, also reported in Brazil; *M. athleticus* Berlese, 1888 described from Paraguay under the bark of a tree.

***Megalolaelaps colossus* Cómbita-Heredia & Quintero-Gutierrez sp. nov.**
(Figures 2–17)

Diagnosis (Adults). Anal shield (*An*) 2–2.5 times longer than wide, expanded anteriorly, and with a lateral constriction (Figures 3D, 3E). Very long setae on margins of idiosoma. Posterior marginal setae long and wavy. Ventral setae anteriorly and antero-laterally surrounding anal shield slightly shorter than para-anal (*pa*) setae. One pair of setae between peritrematal and metapodal shields (*imp* seta 3D, 3E), similar in length to those surrounding anal shield. Metapodal shields (*Mt*) relatively large, semi-oval in shape; peritrematal shields terminating posteriorly with a broad, rounded tip (Figures 3D, 3E, 4). Males with setae *av1* on femora, genua, and tibiae of legs II modified as short spines inserted on distinct tubercles (Figure 15); setae pd_1 on genua and tibiae of legs III-IV distinctly elongated and wavy (in all instars) (Figures 16–17). Gland *gv3* extending in an external, long, and conspicuous tube-like structure which is almost as long as the para-anal setae.

Description

Idiosoma (Figures 2–8)

Larva. Length 1381, width 943 (N=2). Shape slightly rounded.
Dorsum (Figure 2A). Dorsal shields absent. Setation holotrichous, consisting of 20 pairs of long, simple setae of subequal length (229): *j-J* row *j1*, *j3–6*, *J2–5*; *z-Z* row, *z2*, *z4–5*; *Z3–5*; and *s-S* row *s4*, *s6*, *S–5*.

Venter (Figure 3A). Tritosternum weakly sclerotized, base not clearly differentiated from laciniae (245). Bases of setae *St1* (159) inserted on a pair of oval-shaped sternal shieldlets; no other ventral shields observed. Setation: three pairs of sternal, four pairs of ventral *Jv1–2*, *Jv5*, *Zv6*, one pair of para-anal (*pa*), plus unpaired postanal (*po*) seta. Sternal and ventral setae of subequal length, setae *pa* very long (384), seta *po* long (301). No lyrifissures or glands were observed in the specimens available.

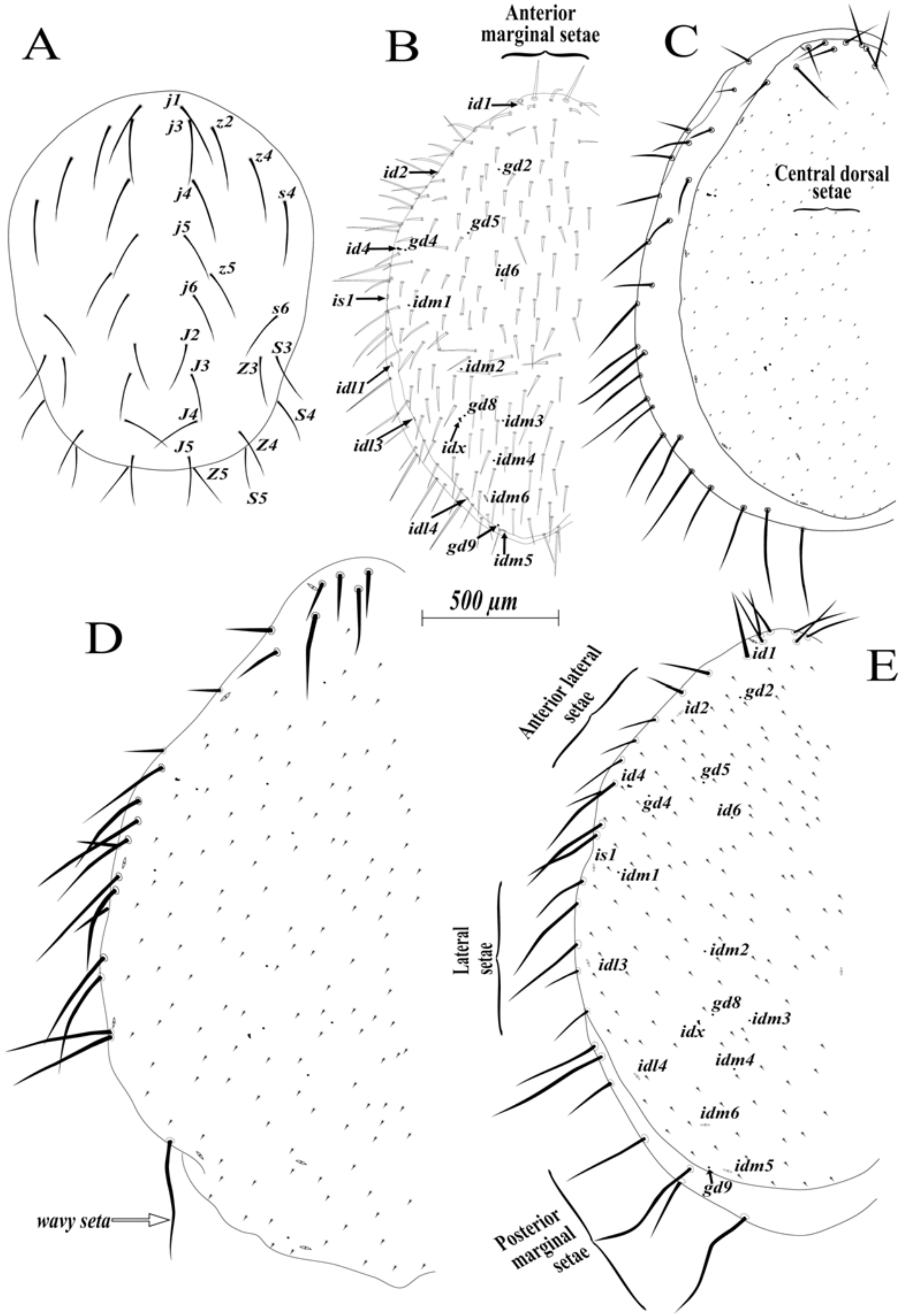

FIGURE 2. *Megalolaelaps colossus* **sp. nov.** Dorsal idiosoma: A. Larva; B. Protonymph; C. Deutonymph; D. Male; E. Female.

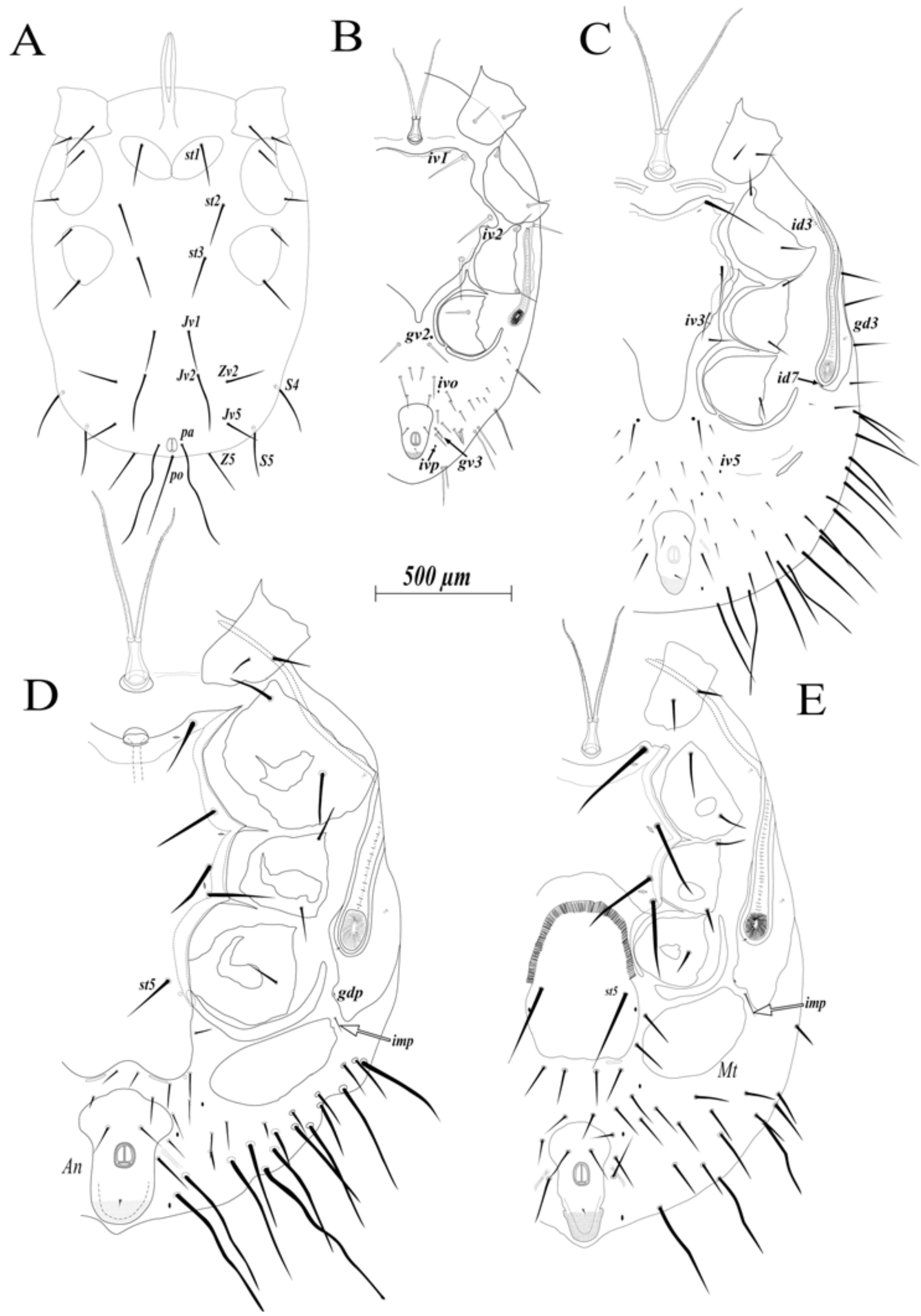

FIGURE 3. *Megalolaelaps colossus* **sp. nov.** Ventral idiosoma: A. Larva; B. Protonymph; C. Deutonymph; D. Male; E. Female.

Protonymph. Length 1675, width 1048 (N=8). Shape ovoid, posterior end more pointed.

Dorsum (Figure 2B). Holodorsal shield with finely granulated ornamentation conserved ontogenetically (Figure 6), length 1522, width 946, leaving only thin marginal and posterior areas with soft cuticle. Setation hypertrichous; marginal setae slightly longer than central setae. Central dorsal shield setae variable in length, but shorter than in larva (82); anterior marginal setae, including

4–5 pairs plus, occasionally, a single unpaired seta, inserted on shield (94); anterior lateral (135), lateral (182) and posterior marginal setae (173) mostly inserted off shield. Dorsum with a total of 15 pairs of lyrifissures *id1–2*, *id4*, *id6*, *is1*, *idl1* (off dorsal shield), *idl3–4*, *id6*, *idm1*–3, *idx*, *idm5* and *idm6*, and five pairs of gland pores *gd2*, *gd4–5*, *gd8–9*.

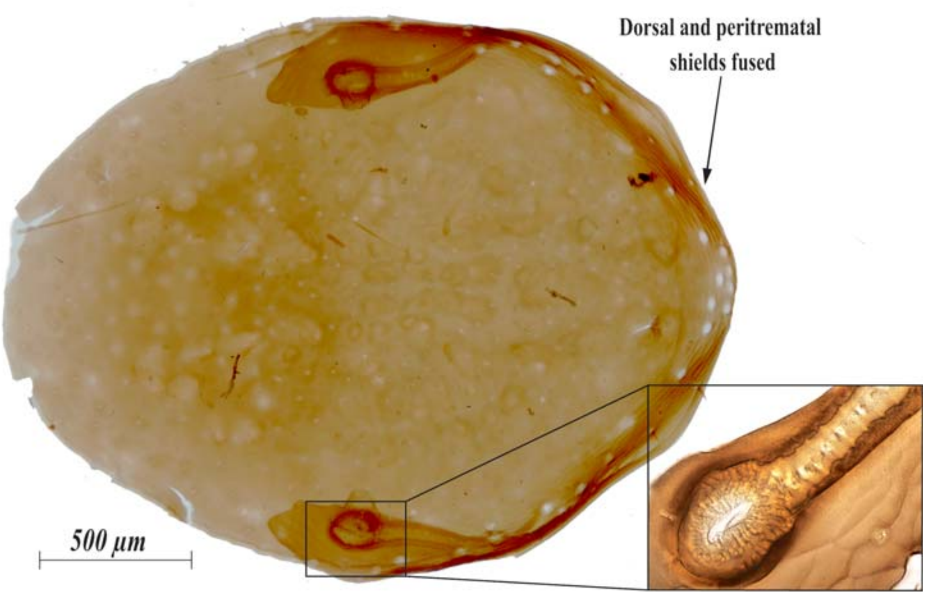

FIGURE 4. *Megalolaelaps colossus* **sp. nov.** Stigma and fused dorsal and anterior peritrematal shields. Male.

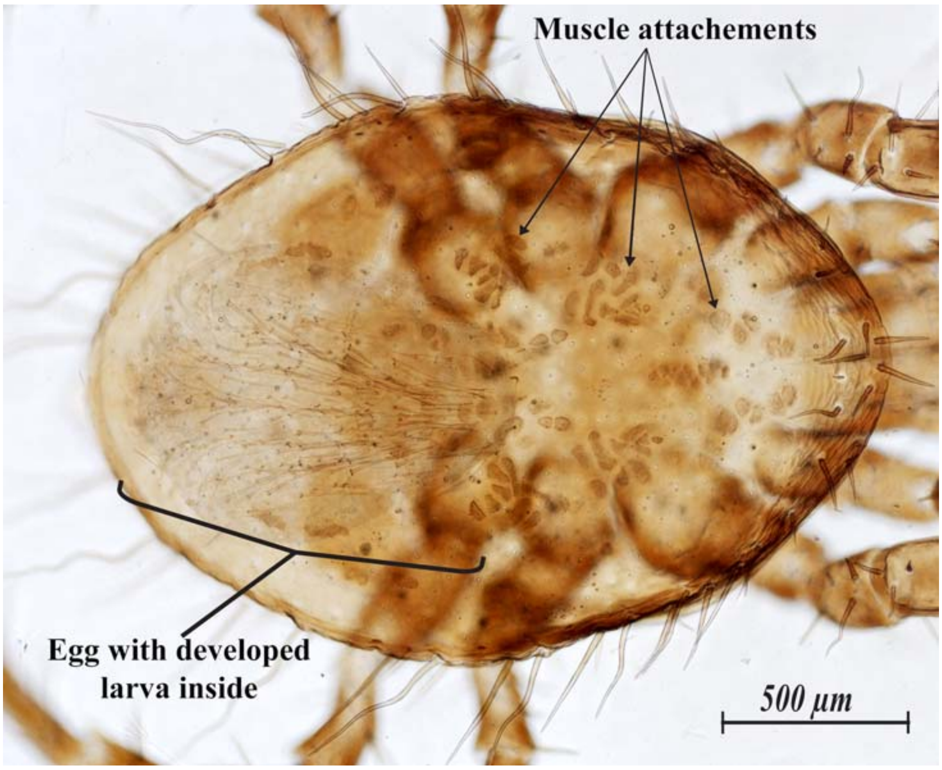

FIGURE 5. *Megalolaelaps colossus* **sp. nov.** Female. Dorsal idiosoma.

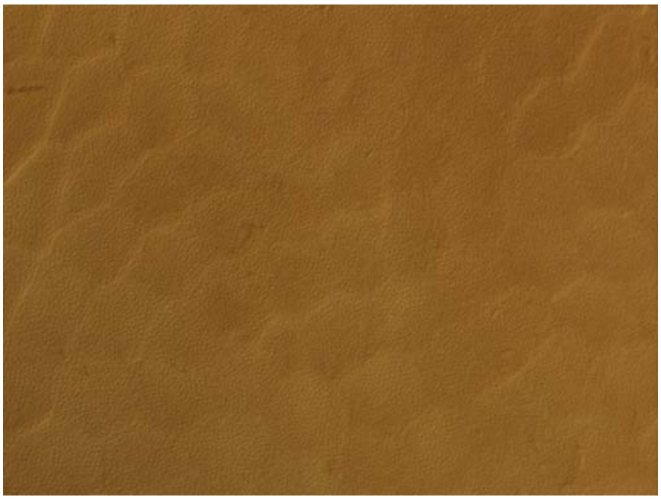

FIGURE 6. *Megalolaelaps colossus* **sp. nov.** Male. Dorsal shield ornamentation.

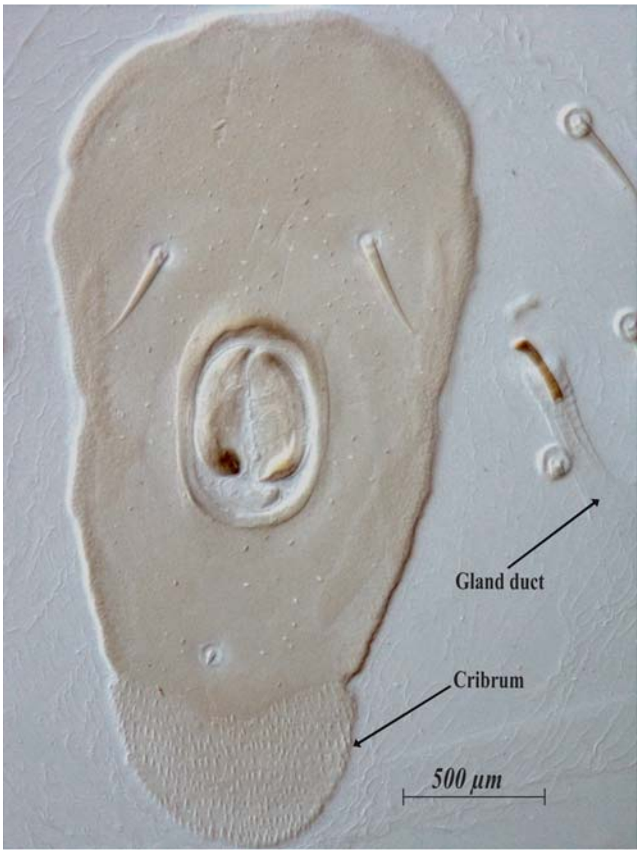

FIGURE 7. *Megalolaelaps colossus* **sp. nov.** Deutonymph. Anal shield.

Venter (Figure 3B). Tritosternum with a discrete base (91) that is one third of the length of the long relatively thin, laciniae (386). Sternal shield slightly concave anteriorly, tapering to a pointed tip posteriorly, not extending beyond coxae IV; length 574, width 523; shield reticulate marginally. Setae *St1–3* (146) inserted on cuticular thickenings (Figure 8) on sternal shield. Lyrifissures *iv1–2* slit-like, adjacent to setae *St1* and *St2*. Setae *St5* inserted on soft cuticle. Separate endopodal shields partially surrounding coxae III–IV. Inguinal shields free, strongly sclerotized and surrounding posterior part of coxae IV. Exopodal and peritrematal shields poorly developed. Peritremes short, extending anteriorly to posterior border of coxae II (Figure 3B). Opisthogaster hypertrichous, marginal setae long (as on dorsum), ventral setae short. Setae *pa* (33) inserted anterior to anus, seta *po* short (19). Anal shield free, longer (193) than wide (83) (Figures 3B–E). Cribrum well developed (Figure 7). With two pairs of lyrifissures, *ivo* ovoid, between anal shield and coxae IV, and *ivp* ovoid, next to posterior edge of anal shield, and two pairs of glands, *gv2* ovoid, adjacent to coxae IV, and *gv3* next to anal shield, extending externally in a tube-like structure. Gland pores *gv3* present in all post-larval instars (Figure 7), tube subequal in length to *pa* setae.

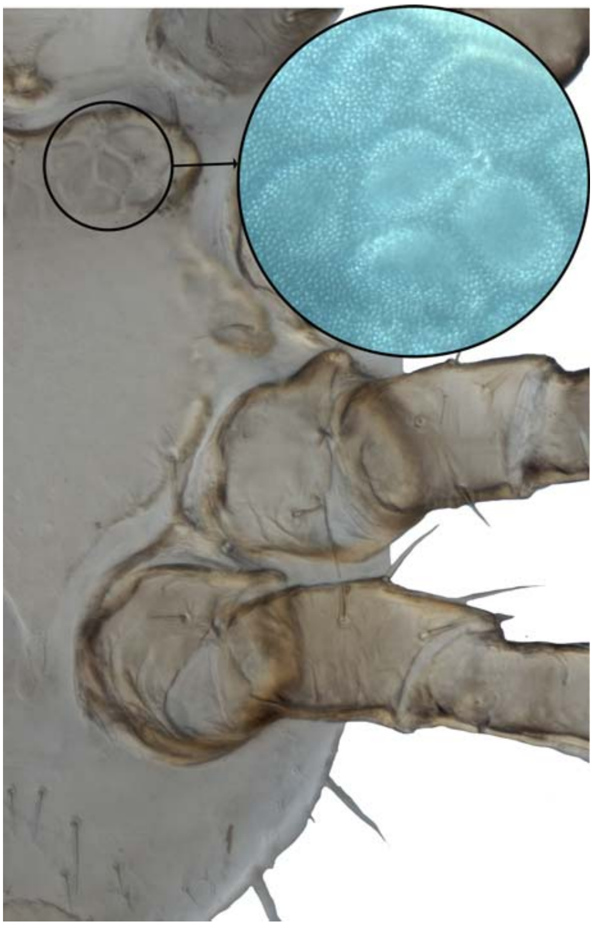

FIGURE 8. *Megalolaelaps colossus* **sp. nov.** Ornamentation on sternal shield. Protonymph.

Deutonymph. Length 1896, width 1276 (N=8). Shape slightly rounded.

Dorsum (Figure 2C). Holodorsal shield, length 1790, width 1079. Setation hypertrichous. Setal size distribution as in protonymph, but size differences more extreme: central dorsal setae very short (13), anterior marginal (195), anterior lateral (146), lateral (208), and posterior marginal (340) setae long and wavy. Lyrifissures and glands as in protonymph but *idl1* not observed.

Venter (Figure 3C). Tritosternal base (177) one third of lacinial length (510). Sternal shield concave anteriorly, tapering to a blunt tip posteriorly, not extending beyond posterior end of coxae

IV, length 750, width 558, shield with strong reticulate patterns anterior and lateral, weak patterns on the remainder area of shield. Sternal setae *St1–3* (180) inserted on cuticular thickenings on sternal shield. Lyrifissures *iv1–2* as in protonymph, plus lyrifissure pair *iv3* adjacent to setae *St3*. Setae *St4* and *St5* inserted on soft cuticle. Endopodal shields between coxae II-IV fused, free from sternal and well sclerotized inguinal shields. Peritremes extending to anterior margin of coxae II. Peritrematal shields more developed than in protonymph, extending to the anterior border of coxa II (Figure 3C) and bearing two pairs of lyrifissures *id3*, *id7* and one pair of glands *gp3*. Metapodal shields present as thin strips length 132, width 17. Opisthogaster hypertrichous (as in protonymph). Anal shield as in protonymph, shield length 292, width 127; length of setae *pa* 48, *po* 29. Lyrifissures and glands as in protonymph, plus lyrifissures *iv5* between *ivo* and coxae IV.

*Male***.** Length 3023, width 2242 (N=9). Shape ovoid.

Dorsum (Figure 2D). Holodorsal shield covering entire dorsum; dorsal setation pattern similar to deutonymph but differing in setal length distribution: central dorsal setae short (21), anterior marginal setae (208), anterior lateral (146), lateral (372), and posterior marginal (494) setae very long and wavy (not straight) (Figure 2D). Posterior marginals generally off shield. Lyrifissures and glands as in deutonymph.

Venter (Figure 3D). Tritosternal base (172) one third of the laciniae (524). Sternito-ventral shield well sclerotized, extending beyond coxa IV posteriorly, anterior and posterior margins concave, length 1157, width 644; shield ornamentation pattern as on dorsum, bearing setae *St1–5*, all of similar length (218); lyrifissures *iv1–3* as in deutonymph but *iv3* aligned longitudinally. Endopodal elements developed between coxae I–IV, fused throughout with sternito-ventral shield. Inguinal shields free, sclerotized and surrounding the posterior portion of coxae IV. Peritremes extending beyond anterior margin of coxae I. Peritrematal shields well developed, extended slightly beyond posterior border of coxae IV with well-developed peritremes and large stigmatal openings (Figure 4); fused anteriorly with dorsal shield at level of coxae II; posterior end extending into broad point (Figure 4), lyrifissures and glands as in deutonymph plus gland pair *gdp*. Metapodal shields large, suboval in shape, external border directed towards the peritrematal shield semi-truncate, with somewhat irregular margin, length 528, width 221. Opisthogastral setation pattern as in deutonymph, but marginal setae longer. Anal shield length 481, width 26; setae *pa* (27), *po* (25). Lyrifissures and glands as in deutonymph.

Female. Length 2520, width 1875 (N=8). Shape ovoid.

Dorsum (Figure 2E). Holodorsal shield length 2352, width 1875, covering most of idiosoma, except posterior margin of body. Ornamentation pattern similar to male; muscle attachments conspicuous (Figure 5). Central dorsal setae short (19), anterior marginal seta (213), anterior lateral (156), lateral (310), and posterior marginal (451) setae very long. Posterior marginal setae off shield. Lyrifissures and glands as in male.

Venter (Figure 3E). Tritosternal base (140) one third of the laciniae (434). Sternal shield well sclerotized, anterior and posterior margins concave, length 365, width 636; shield ornamentation limited to anterior and lateral margins, central area smooth. Setae *St1*, *St2*, *St3*, *St4* similar in length (343), all inserted on sternal shield. Lyrifissures *iv1–3* as in male. Epigynal shield length 544, width 431, ornamentation as on dorsum; setae *St5* inserted on genital shield. Peritrematal shields and inguinal shields more slender than in male. Peritrematal lyrifissures and glands as in male. Metapodal shields shorter (430) and wider (273) than in male. Setal pattern as in male. Anal shield length 435, width 168, setae *pa* (128), *po* (23). Lyrifissures and glands as in deutonymph.

Gnathosoma (Figures 9A–E, 10A–E)

The gnathosoma of *Megalolaelaps* was previously studied in detail for *M. enceladus* by Flora Gorirossi Bourdeau (Gorirossi-Bourdeau 1956).

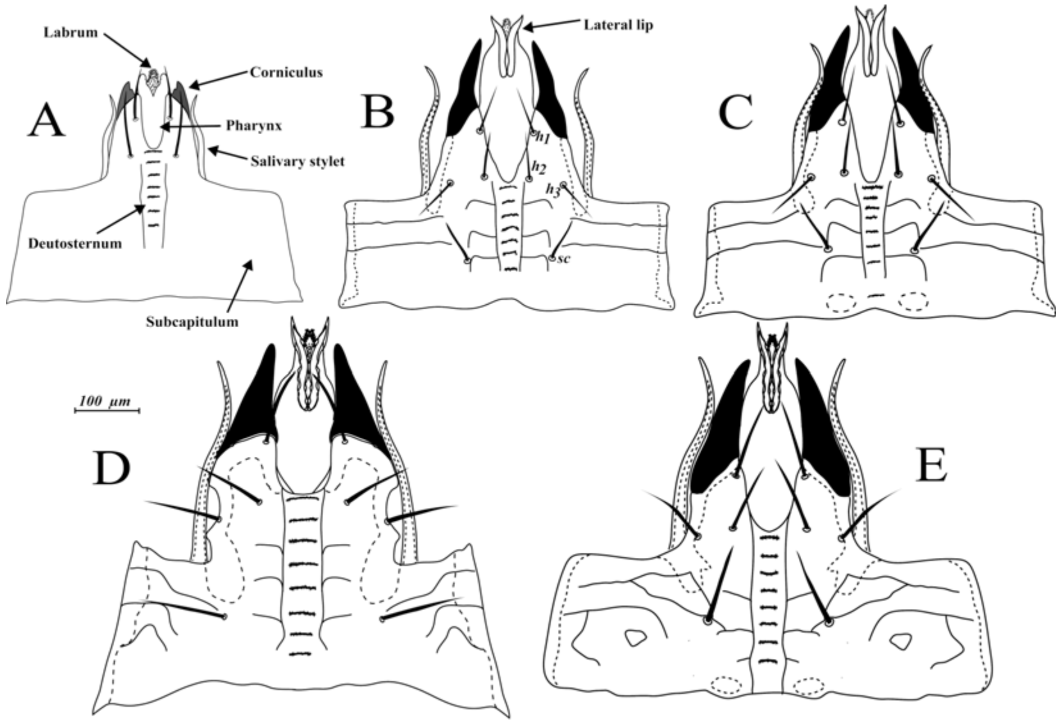

FIGURE 9. *Megalolaelaps. colossus* **sp. nov.** Subcapitulum: A. Larva; B. Protonymph; C. Deutonymph; D. Male; E. Female.

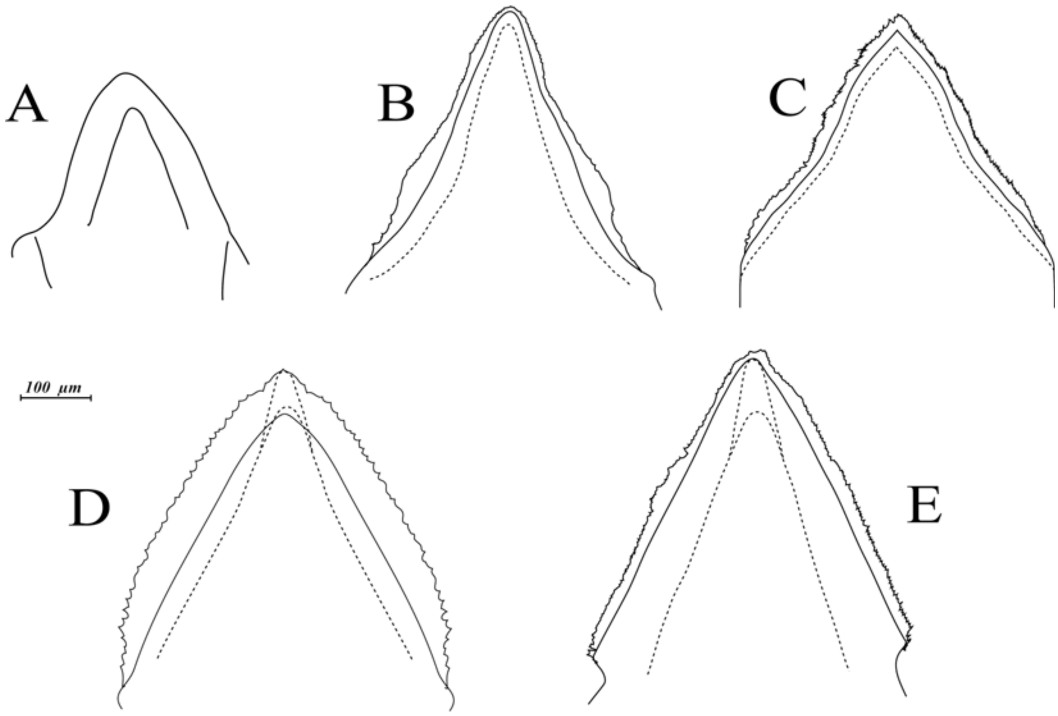

FIGURE 10. *Megalolaelaps colossus* **sp. nov.** Gnathotectum: A. Larva; B. Protonymph; C. Deutonymph; D. Male; E. Female.

Larva. Subcapitulum smooth, deutosternum with seven rows of denticles; hypostomatal setae *h1–2* present and similar in length (87); corniculi short, with medial dentations; salivary stylets long, extending to mid-level of corniculi (Figure 9A). Gnathotectum triangular in shape, without any evident ornamentation, anterior margin smooth (Figure 10A).

Protonymph. Deutosternum as in larva. Two distal transverse lines and three short lines close to deutosternum; hypostomatal setae *h1–3* and *sc* all similar in length (74), corniculi long and heavily sclerotized, without dentations (Figure 9B). Shape of gnathotectum as in larvae, but with a thin anterior flange bearing small marginal denticles (Figure 10B).

Deutonymph. Subcapitulum mostly as in protonymph, but with a pair of ovoid ornamentations flanking base of deutosternal groove; deutosternum with eight rows of denticles; hypostomatal setae as in protonymph, similar in length (80) (Figure 9C). Gnathotectum as in protonymph (Figure 10C).

Male. Subcapitulum ornamentation more reticulate and variable; deutosternum as in deutonymph; hypostomatal setae longer (119); corniculi slightly shorter and thicker than those in deutonymph; salivary stylets as in protonymph (Figure 9D). Gnathotectum as in deutonymph, but more sclerotized (Figure 10D).

Female. Subcapitulum ornamentation as in male; deutosternum as in deutonymph, hypostomatal setae long (117); corniculi as in deutonymph; salivary stylets and hypopharyngeal process as in male (Figure 9E). Gnathotectum (Figure 10E) as in deutonymph.

Chelicera (Figures 11A-F)

Larva. Chelicera weakly sclerotized; fixed and movable digits with very small, poorly developed teeth; fixed digit with lateral lyrifissure, simple dorsal seta present, digit semi-membranous (Figures 11A, 11B).

Protonymph. Chelicera strongly sclerotized; fixed digit with a basal molar shape tooth, well developed medial and distal hook, pilus dentilis present; movable digit with a strong medial tooth that fits between molar and medial teeth of fixed digit, with one small and a strong distal tooth; dorsal seta, lateral and dorsal lyrifissures present (Figure 11D); arthrodial articulation well developed, with a small hyaline flap.

Deutonymph. As in protonymph, but more sclerotized (Figure 11D).

Male. Chelicerae strongly sclerotized, fixed digit with a bidentate tooth, and two small subapical teeth, pilus dentilis reduced. Movable digit with large proximal process and a large subapical tooth. Coiled spermatodactyl on medial side of movable digit with a complex 3D configuration reaching up to 1200 in length.

Female (Figure 11G). Fixed digit as in protonymph, but more sclerotized; hyaline basal flap more conspicuous than that of male (Figure 11F, arrow).

Legs (Figures 13–17).

Leg length (Table 1) measured from proximal border of trochanter to tip of claw. Leg setal formula for all instars listed in Table 2 (comments on leg setation limited to unusual morphology of specific setae). Nearly all leg setae setiform and smooth. Tarsal setae *ad1* and *ad2* on legs II-IV in all instars small and thin, while *al1* and *pl1* in legs II-III form thin spines in nymphs and female. Tibial and genual setae *pd1* in legs III-IV distinctly elongated and wavy in all instars. Setae *av1* on femora, genua, and tibia of legs II in males modified as short spines on distinct tubercles (Figure 15).

Type deposition. Holotype female in ICN. Paratypes in ICN, OSAL, ANIC.

Material examined. Colombia, Quindío, Santo Domingo municipality, farm El Bosque. 4.5194 N -75.6266 W. 29 September 2014, Quintero E. & Romero, N. ex. *O. conspicillatum* (Coleoptera: Scarabaeidae). **Holotype:** female, in 95% ethanol in ICN (ICN-Ac 460). **Paratypes**: same collection data, all fluid preserved, 3 females (ICN-Ac 461, ICN-Ac 462, ICN-Ac 463), 3 males (ICN-Ac 471, ICN-Ac 464, ICN-Ac 465), 3 deutonymphs (DN) (ICN-Ac 466, ICN-Ac 467, ICN-Ac 468), 1 protonymph (PN) (ICN-Ac 469). 2 females in OSAL (OSAL 0099747, OSAL 0110289), 2 males (OSAL 0110302, OSAL 0099893), 1 DN (OSAL 0110304). 1 PN (OSAL 0110308). 5 females in ANIC (ANIC 51-006344 - 48). 5 males (ANIC 51-006349 - 53). 5 DN (ANIC 51-006354 - 58). 4 PN (ANIC 51-006359 - 62). Colombia, Quindío, Universidad del Quindío (4.5339 N -75.6742 W), reared in lab. 10 November 2014, Quintero, Edwin, Romero, Nicole, ex. *O. conspicillatum,* 1 larva (L), slide mounted in ICN (ICN 470). Same collection data, fluid preserved, 1 L in OSAL (OSAL 0102231). 1 L in ANIC (ANIC 51-006364). **Other material review:** Esteban Carillo's farm, Km 11 Tarapacá road, Leticia, Amazonas, Colombia (4°05'44.7" S 69°57'00.9" W). 21 May 2015, Keeney, G., Combita, O. & Bohorquez, R. ex. *O. conspicillatum* (Coleoptera: Scarabaeidae). 2 females, 2 PN in OSAL (OSAL 0115453), all fluid preserved.

Etymology. *Colossus* is Latin for giant statue, but the term has been generalized to a "huge, massive, enormous, gigantic" thing. Hence the character "Colossal Titan" of the anime series "Attack on Titan"[2], a manga series written and illustrated by Hajime Isayama[3]. The large size of this mesostigmatid mite, plus its ferocious appearance, resembles the "Colossal Titan" character.

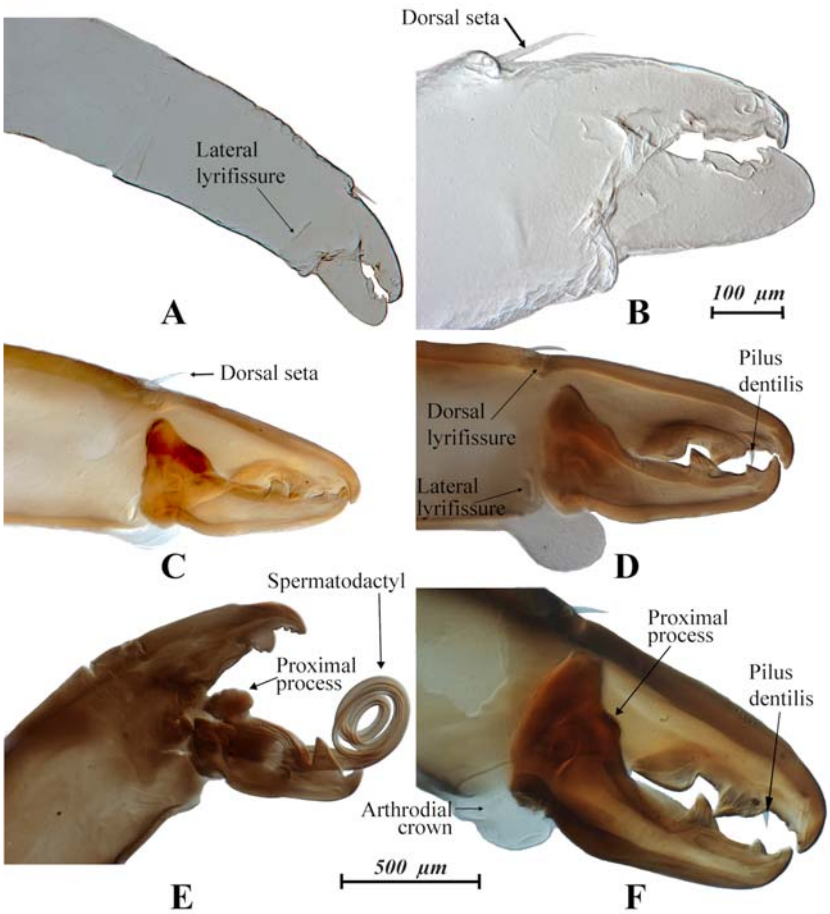

FIGURE 11. *Megalolaelaps colossus* **sp. nov.** Chelicerae: A. Larva; B. Larva, detail of tip chelicera (different scale); C. Protonymph; D. Deutonymph; E. Male; F. Female.

2. http://shingeki.tv/movie_season2/
3. https://twitter.com/hajime_isayama?lang=en

Remarks.

1. Differential characters. Megalolaelaps colossus **sp. nov.** differs from *M. hirtus* in that the latter has the peritrematal shield fused with the metapodal shield, while *M. colossus* **sp. nov.** has the peritrematal shield free. Also, *M. hirtus* lacks the long setae on the margins of the idiosoma. *Megalolaelaps colossus* **sp. nov.** differs from *M. mexicanus* and *M. athleticus* in that the latter two species lack metapodal shields entirely. Also, the anal shield in *M. athleticus* is wider than long. *Megalolaelaps colossus* **sp. nov.** differs from *M. enceladus* by a large, oval, metapodal shield (small, strap-like, approximately as wide as the inguinal shield in *M. enceladus*). The new species differs from *M. haeros* by the insertion of setae *st4* on the sternal shield (inserted on soft cuticle in *M. haeros*). Finally, the new species differs from *M. immanis* by the long marginal setae on the idiosoma (absent in *M. immanis*).

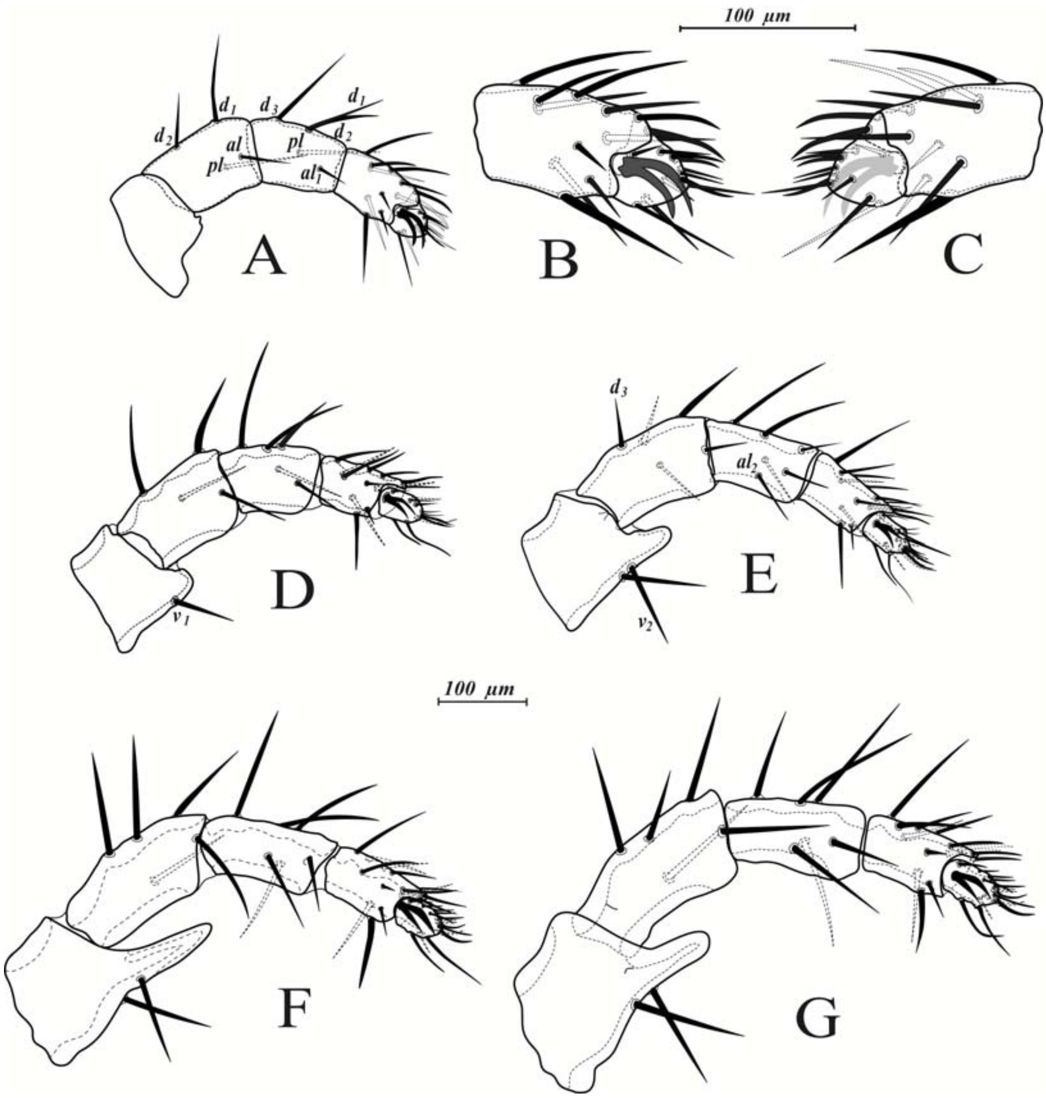

FIGURE 12. *Megalolaelaps colossus* **sp. nov.** Palp: A. Larva, overview; B. Larva, medial view of tibia and tarsus; C. Larva, lateral view of tibia and tarsus (B-C different scale); D. Protonymph; E. Deutonymph; F. Male; G. Female.

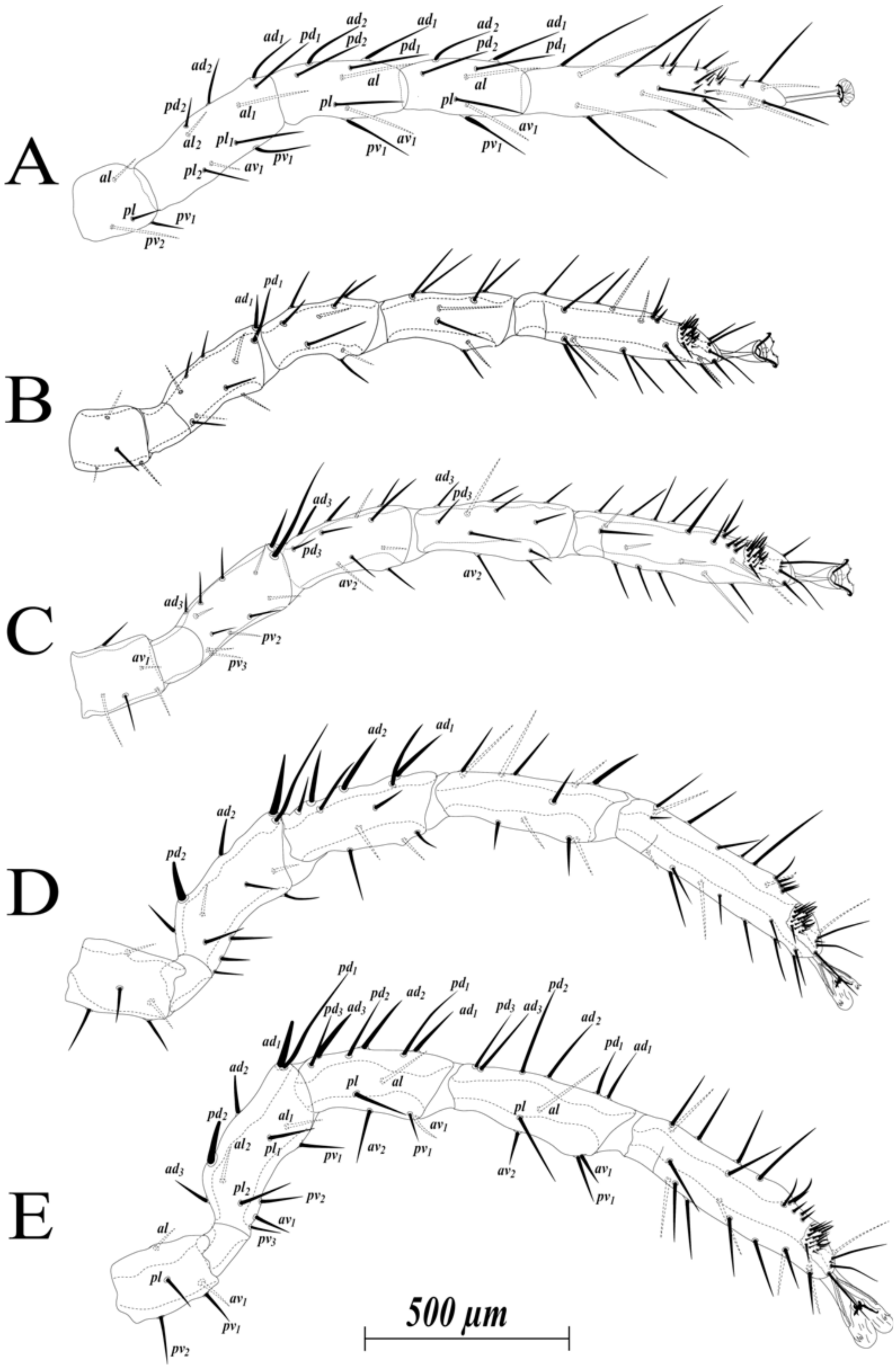

FIGURE 13. *Megalolaelaps colossus* **sp. nov.** Leg I, excluding coxa, lateral view. A. Larva; B. Protonymph; C. Deutonymph; D. Male; E. Female.

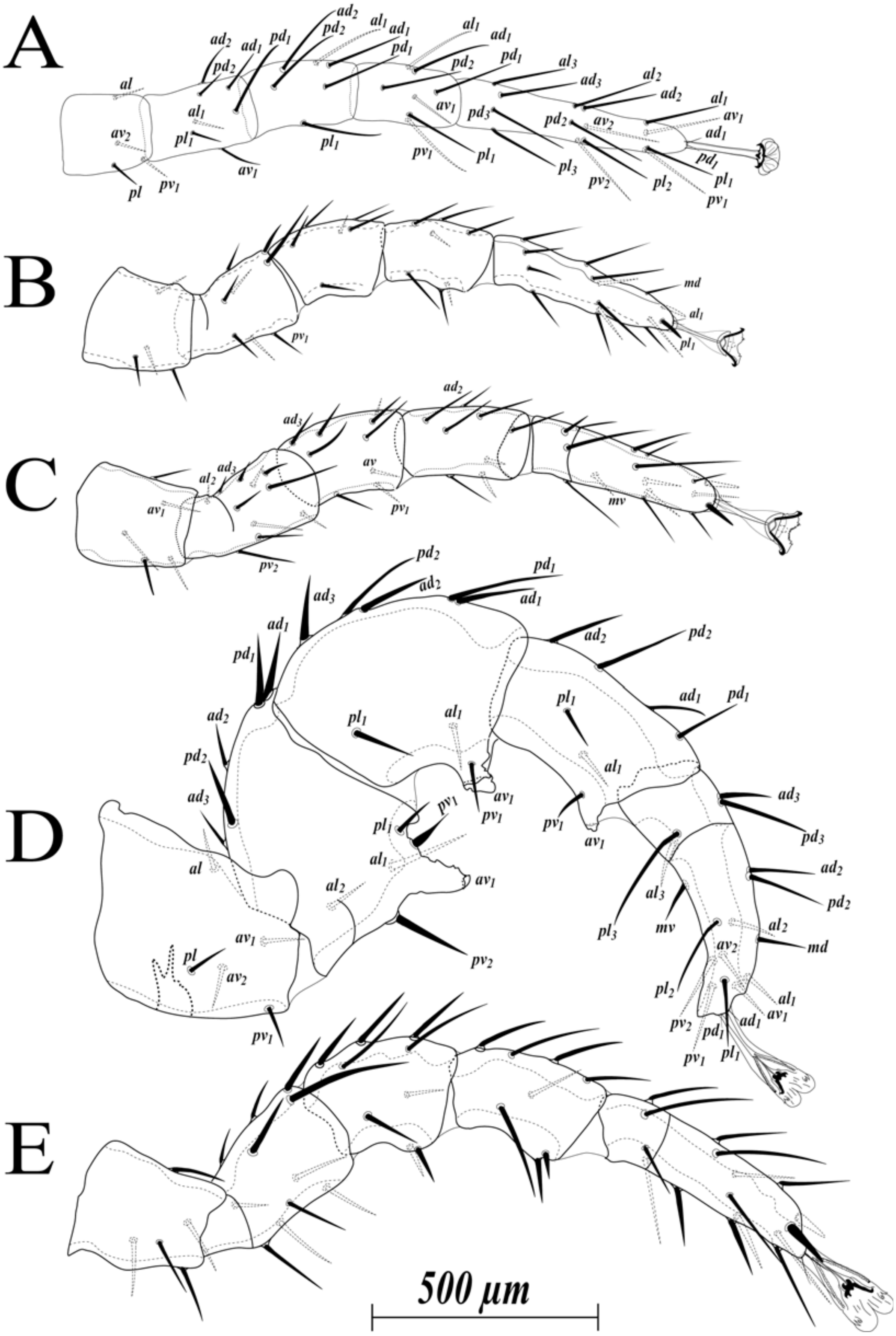

FIGURE 14. *Megalolaelaps colossus* **sp. nov.** Leg II, excluding coxa. A. Larva; B. Protonymph; C. Deutonymph; D. Male; E. Female.

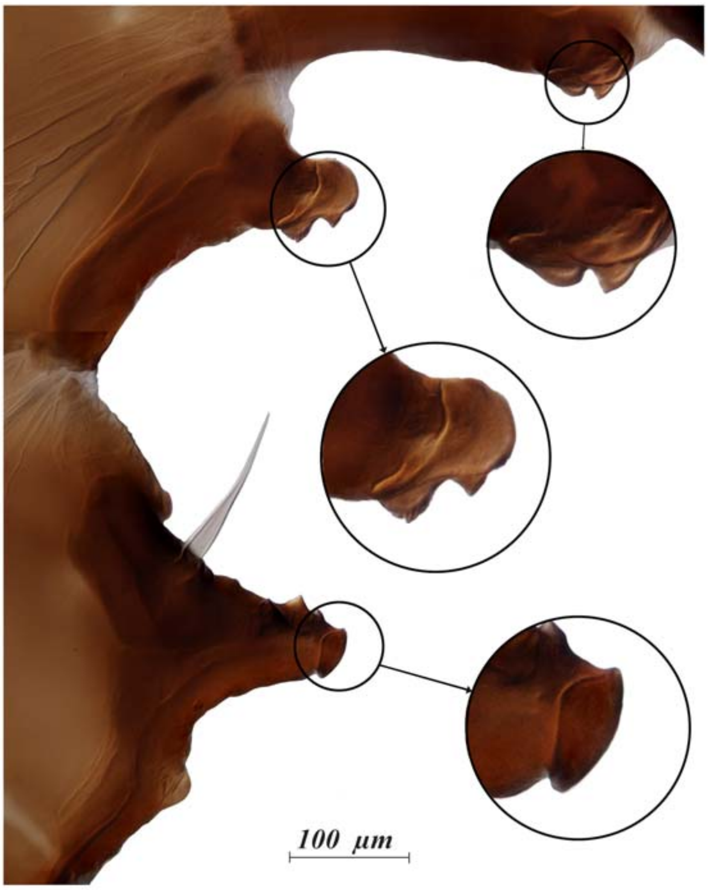

FIGURE 15. *Megalolaelaps colossus* **sp. nov.** Leg II. av_1 modified setae on femur, genu and tibia. Male.

2. Chaetotaxy and familial affiliations. The idiosomal setal arrangement in the larva matches that of the larva of *Lasioseius* Berlese (Lindquist & Evans 1965), but the post larval stages are hypertrichous, preventing meaningful comparisons. The larval leg chaetotaxy is identical to the standard pattern outlined for *Pergamasus* Berlese (Evans 1963a). For the adults, the following comparative observations can be made. *Megalolaelaps* does not add a sixth seta, *ad1*, on trochanter I, an unusual characteristic shared with Macrochelidae, Phytoseiidae and some Eviphididae (*Thinoseius* Berlese). The femoral setation on all legs matches the most common patterns for Gamasina including Eviphidoidea. The patterns for the genua and tibiae are more unusual. Genu I setation is similar to that in Eviphididae and Macrochelidae but reduced relative to Pachylaelapidae (11 setae vs. 12–13). Genu II setation is shared with some Phytoseiidae. It is clearly reduced, with one (relative to *Thinoseius*) or two (relative to other Eviphididae, Macrochelidae, Pachylaelapidae) fewer added setae than in other Eviphidoidea (absent setae, respectively, *pl2* and *al2*). Genu III setation is similar to Macrochelidae and some Pachylaelapidae and Eviphididae (most Gamasina carry 1–2 additional setae (probably *al2* and *pv1*) on genu III). Setation of genu IV retains the addition of *pd3*, not added in Eviphididae and Pachylaelapidae and *pl1*, not added in many *Macrocheles* Latreille 1829. Both setae *pd3* and *pl1* are added in deutonymphs and adults of most Gamasina. Tibia I setation is similar to that in Eviphididae but reduced relative to Macrochelidae and Pachylaelapidae (*al2* not added) and most other Gamasina (setae *al2*, *pl2*, and *av2* not added). Tibia II setation is also reduced, with one (*Thinoseius*) or two (Macrochelidae, Pachylaelapidae, most

Eviphididae) less setae added (respectively, *pl2*, and *al2* plus *pl2*). Tibia III setation matches that of all other Eviphidoidea. Tibia IV setation is enriched relative to Eviphididae, Macrochelidae, and Pachylaelapidae, by adding two more dorsal setae (*ad2*, *pd3*), both of which added in the majority of Gamasina.

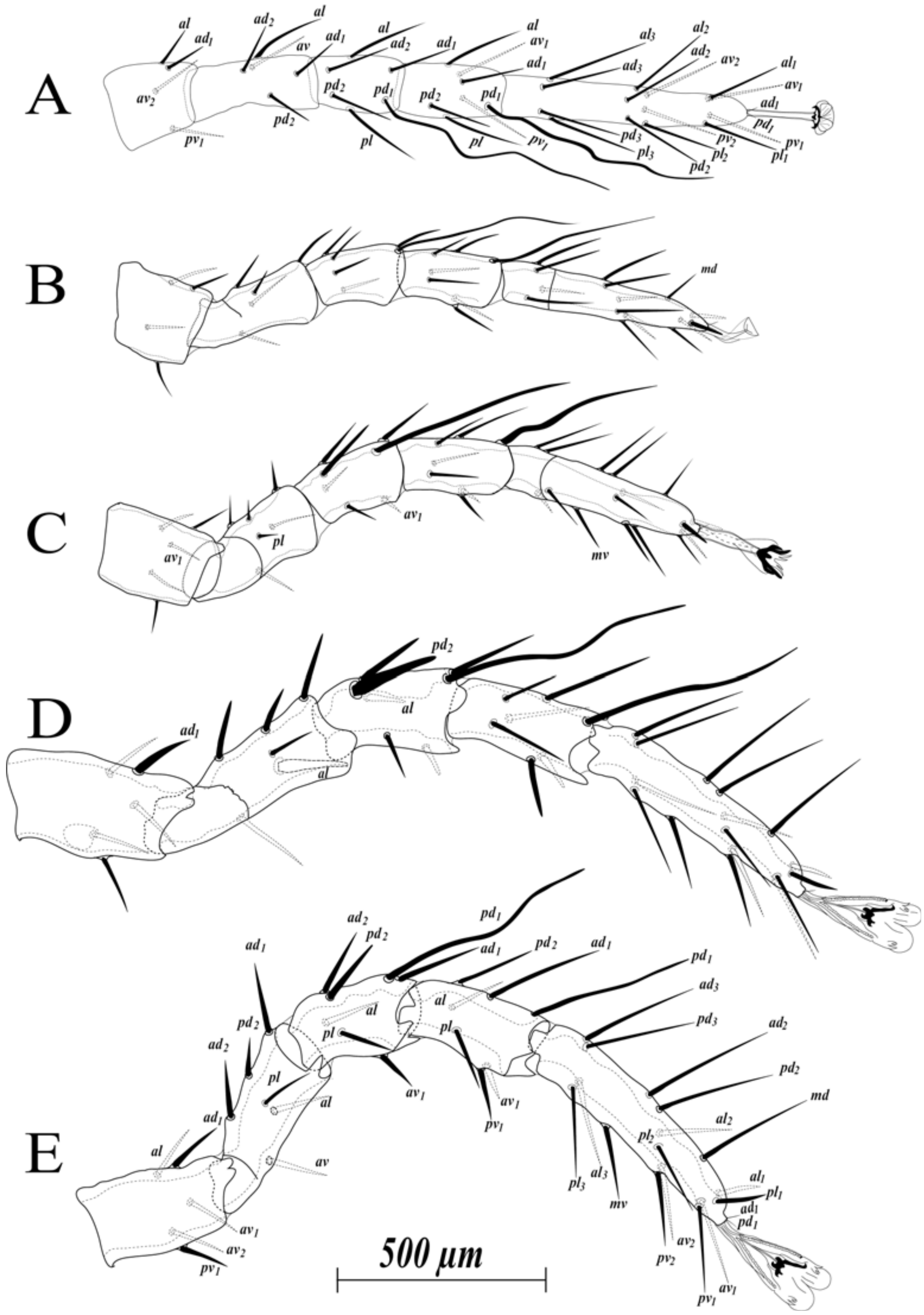

FIGURE 16. *Megalolaelaps colossus* **sp. nov.** Leg III, excluding coxa. A. Larva; B. Protonymph; C. Deutonymph; D. Male; E. Female.

TABLE 1. Comparative measurements for all active instars of *Megalolaelaps colossus* **sp. nov.**

	LARVAE N=2			**PROTONYMPH N=8**			**DEUTONYPMH N=8**			**MALE N=9**			**FEMALE N=8**		
	Ave	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave	Min	Max	Ave	Min	Max
Idiosoma length	1381	1254	1507	1675	1479	1775	1896	1825	1999	3023	2878	3285	2520	2314	2928
width	943	813	1073	1048	967	1160	1276	1200	1342	2242	2090	2482	1875	1803	1968
Dorsal shield length	-	-	-	1522	1351	1613	1798	1688	1940	3023	2878	3285	2352	2083	2782
width	-	-	-	946	878	1042	1079	980	1169	2242	2090	2482	1875	1803	1968
Central dorsal shield setae	229	179	243	82	52	114	13	11	15	21	18	25	19	17	22
Anterior marginal setae	-	-	-	94	51	163	195	159	266	208	157	315	213	192	272
Anterior lateral setae	-	-	-	135	93	174	146	91	187	146	107	174	156	134	210
Lateral setae	-	-	-	182	117	217	208	153	297	372	304	434	310	228	354
Posterior marginal setae	-	-	-	173	146	204	320	257	397	494	417	610	451	336	525
Sternal shield length	-	-	-	574	539	609	750	736	766	1157	1090	1279	365	308	440
width	-	-	-	523	491	556	558	527	558	644	605	700	636	620	656
Sternal setae	159	153	167	146	137	156	180	108	264	218	199	240	343	318	392
Genital shield ♀ length	-	-	-	-	-	-	-	-	-	-	-	-	544	494	583
width	-	-	-	-	-	-	-	-	-	-	-	-	431	401	452
Metapodal shield length	-	-	-	-	-	-	17	15	20	528	465	615	430	417	454
width	-	-	-	-	-	-	132	113	158	221	182	282	273	263	283
Anal shield length	-	-	-	193	180	204	292	274	310	481	441	514	435	428	440
width	-	-	-	83	74	93	127	108	142	226	203	251	168	160	177
Para-anal setae	384	380	388	33	28	37	48	43	52	107	101	114	128	124	135
Postanal setae	301	293	309	19	17	21	29	24	37	25	24	27	23	22	27
Total length Leg I	1618	1357	1879	1762	1615	1929	2121	1996	2195	2737	2327	3242	2377	2342	2406
Leg II	1391	1127	1655	1530	1365	1768	1774	1577	1937	2862	2381	3604	2027	1972	2076
Leg III	1496	1256	1736	1570	1488	1660	1751	1530	2003	2583	2543	2980	2178	2115	2238
Leg IV	-	-	-	2016	1900	2101	2258	2046	2474	3027	2814	3363	2724	2629	2836
Macro setae Genu leg III	555	384	725	483	462	500	530	493	560	693	637	765	562	557	571
Tibia leg III	557	420	694	357	342	370	394	387	397	418	394	444	401	337	459
Genu leg IV	-	-	-	669	657	682	711	621	838	838	614	1003	936	912	952
Tibia leg IV	-	-	-	555	548	654	57	255	40	601	423	731	714	680	733

- inapplicable or structure absent

The pattern noted above shows some distinct similarities between *Megalolaelaps* and (many) Eviphidoidea, e.g. lack of addition of tibia III seta *al2*, genu III setae *al2*, *pl2*, and *pv1*, and genu IV seta *pv1*, but also clear differences. Notably, those differences do not follow a single pattern: the chaetome of genua and tibiae II (and to some degree I) is reduced compared to other Eviphidoidea (and other Gamasina), the chaetome of those leg segments for legs III is near identical to that in other Eviphidoidea, and the chaetome for genua and tibiae IV is enriched, more strongly resembling addition patterns in other Gamasina than other Eviphidoidea.

3. Life-history notes. The larvae are very large compared to the size of the female (mean length of the larval idiosoma is 55% of the females' mean idiosomal length). The largest larva measured had a fully developed protonymph inside. Females of *M. colossus* **sp. nov.**, carry only one (large) egg at the time. Fully formed larvae may be visible inside the egg inside the female (Figure 5). It is unknown whether this species is ovi- or larviparous, but free eggs have not been observed in cultures. All post-larval individuals of *M. colossus* **sp. nov.** were found exclusively on the dung beetle *Oxysternon conspicillatum*. Larvae were obtained by laboratory rearing: they were found in the medium of the rearing container. Within 24 hours they molt to protonymphs and attach to the host.

Post-larval instars could not be kept alive without a host. This particular dependence on the beetle has not been reported in any other species of *Megalolaelaps* associated with beetles.

TABLE 2. Leg chaetotaxy for all instars of *Megalolaelaps colossus* **sp. nov.** (L: larvae, PN: protonymph, DN: deutonymph, M: male, F: female; NE: not examined). Numbers in red and bold represent the added setae.

Leg	Coxa	Trochanter	Femur	Genu	Tibia	Tarsus
I	L, PN DN, M, F: $0\frac{0\,0}{1\,1}0$	L, PN: $1\frac{0\,0}{0\,2}1$ DN, M, F: $1\frac{0\,0}{\mathbf{1}\,2}1$	L, PN: $2\frac{2\,2}{1\,1}2$ DN, M, F: $2\frac{2\,\mathbf{3}}{1\,\mathbf{3}}2$	L, PN: $1\frac{2\,2}{1\,1}1$ DN, M, F: $1\frac{\mathbf{3}\,\mathbf{3}}{\mathbf{2}\,1}1$	L, PN: $1\frac{2\,2}{1\,1}1$ DN, M, F: $1\frac{\mathbf{3}\,\mathbf{3}}{\mathbf{2}\,1}1$	NE
II	L, PN DN, M, F: $0\frac{0\,0}{1\,1}0$	L, PN: $1\frac{0\,0}{1\,1}1$ DN, M, F: $1\frac{0\,0}{\mathbf{2}\,1}1$	L: $1\frac{2\,2}{1\,0}1$ PN: $1\frac{2\,2}{1\,\mathbf{1}}1$ DN, M, F: $\mathbf{2}\frac{\mathbf{3}\,2}{1\,\mathbf{2}}1$	L, PN: $1\frac{2\,2}{0\,0}1$ DN, M, F: $1\frac{\mathbf{3}\,2}{\mathbf{1}\,\mathbf{1}}1$	L, PN: $1\frac{1\,2}{1\,1}1$ DN, M, F: $1\frac{\mathbf{2}\,2}{1\,1}1$	L: $3\frac{3-0-3}{2-0-2}3$ PN: $3\frac{3-\mathbf{1}-3}{2-0-2}3$ DN, M, F.: $3\frac{3-1-3}{2-\mathbf{1}-2}3$
III	L, PN DN, M, F: $0\frac{0\,0}{1\,1}0$	L, PN: $1\frac{1\,0}{1\,1}0$ DN, M, F: $1\frac{1\,0}{\mathbf{2}\,1}0$	L, PN: $1\frac{2\,1}{1\,0}0$ DN, M, F $1\frac{2\,1}{1\,0}\mathbf{1}$	L, PN: $1\frac{2\,2}{0\,0}1$ DN, M, F: $1\frac{2\,2}{\mathbf{1}\,0}1$	L, PN, DN, M, F: $1\frac{1\,2}{1\,1}1$	L: $3\frac{3-0-3}{2-0-2}3$ PN: $3\frac{3-\mathbf{1}-3}{2-0-2}3$ DN, M, F.: $3\frac{3-1-3}{2-\mathbf{1}-2}3$
IV	PN, DN, M, F: $0\frac{0\,0}{0\,1}0$	PN: $1\frac{1\,0}{2\,0}0$ DN, M, F: $1\frac{1\,0}{2\,\mathbf{1}}0$	PN: $1\frac{2\,1}{0\,0}0$ DN, M, F $1\frac{2\,1}{\mathbf{1}\,0}\mathbf{1}$	PN: $1\frac{2\,2}{0\,0}1$ DN, M, F: $1\frac{2\,\mathbf{3}}{\mathbf{1}\,0}1$	PN: $1\frac{1\,2}{1\,1}1$ DN, M, F: $1\frac{\mathbf{2}\,\mathbf{3}}{1\,1}1$	PN: $3\frac{3-\mathbf{1}-3}{2-0-2}3$ DN, M, F.: $3\frac{3-1-3}{2-\mathbf{1}-2}3$

Discussion

At least five species of *Megalolaelaps* have been found associated with dung beetles (Scarabaeidae), *M. enceladus*, *M. haeros*, recently found by the authors in the Amazon Region of Colombia, *M. colossus* **sp. nov.**, and two new species of *Megalolaelaps* from Caldas and Boyacá departments in Colombia. This, plus the observation that all instars (except the larvae) of *M. colossus* **sp. nov.** are associated with its host *O. conspicillatum*, suggests that species in the genus *Megalolaelaps* may be obligate and permanent associates of scarab beetles. Host presence, rather than off-host habitat, may therefore be the most important factor for survival of these mites. For example, *O. conspicillatum* is quite common in disturbed areas such as coffee, plantain and bamboo crops, but also occurs, though sometimes less commonly, in tropical forest below 1500 m. The authors have recovered *M. colossus* **sp. nov.** from this host in both habitats. If *M. colossus* **sp. nov.** is indeed a specific associate of *O. conspicillatum*, it may be able to infer the possible distribution of *M. colossus* **sp. nov.** from the distribution of its host.

The geographical distribution of *O. conspicillatum* covers much of northern South America, excluding areas of very high elevation. It includes records from Colombia, Panama, Venezuela, Ecuador, Brazil, Peru, Bolivia, and Paraguay (Edmonds & Zídek 2004). In Colombia, this species is distributed in the west across the Chocó Biogeographical region and in the east across a vast portion of the Amazonia and Oriniquia regions (Fig. 18). It shows both nocturnal and diurnal activity. *Oxysternon conspicillatum* is a tunneler or paracoprid, which means that they dig tunnels under the dung pile. Eggs are deposited on dung assembled in the tunnels (Cultid Medina *et al.* 2012). It is unknown how this behavior affects *Megalolaelaps* mites.

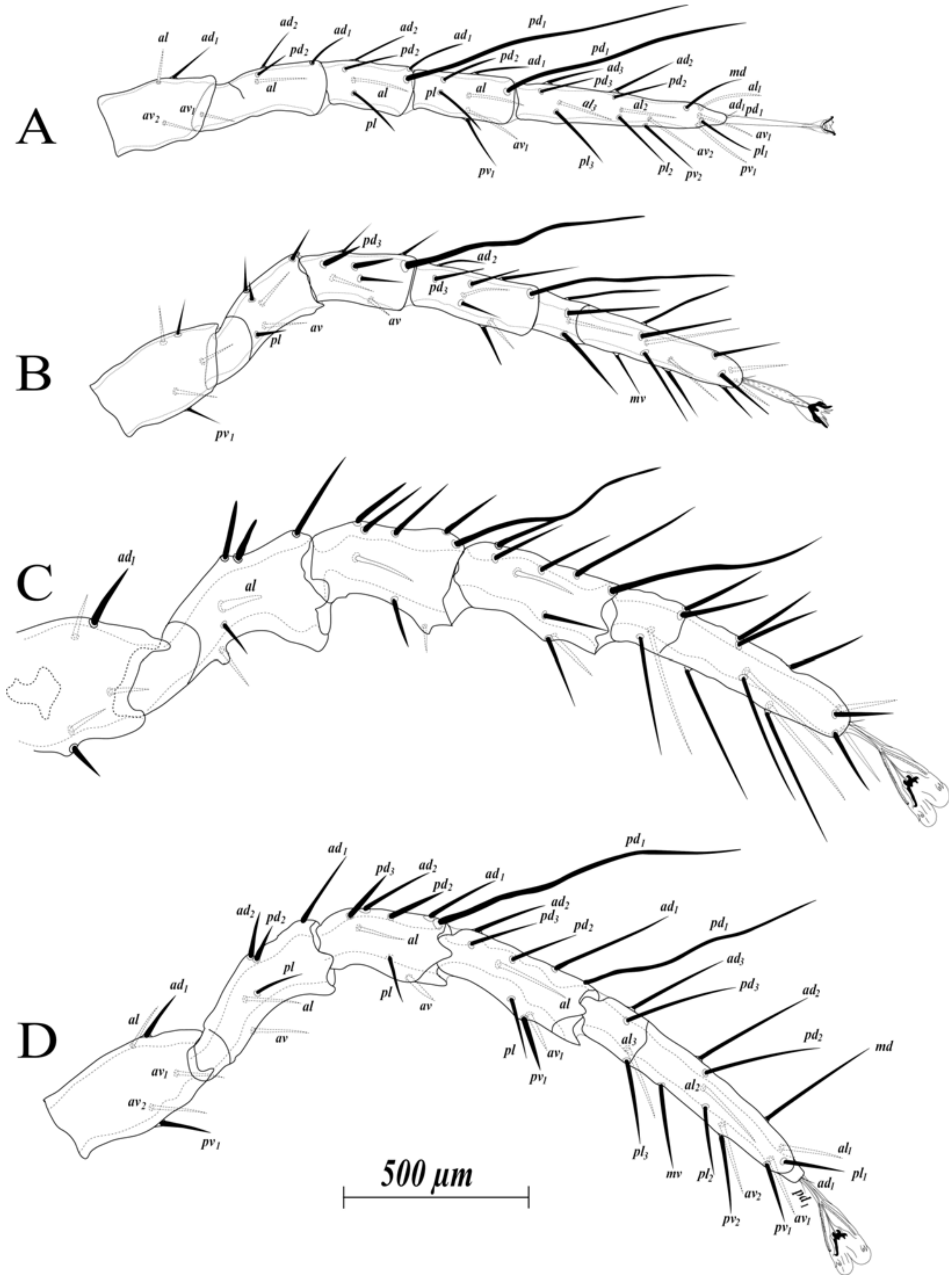

FIGURE 17 *Megalolaelaps colossus* **sp. nov.** Leg IV, excluding coxa. A. Protonymph; B. Deutonymph; C. Male; D. Female.

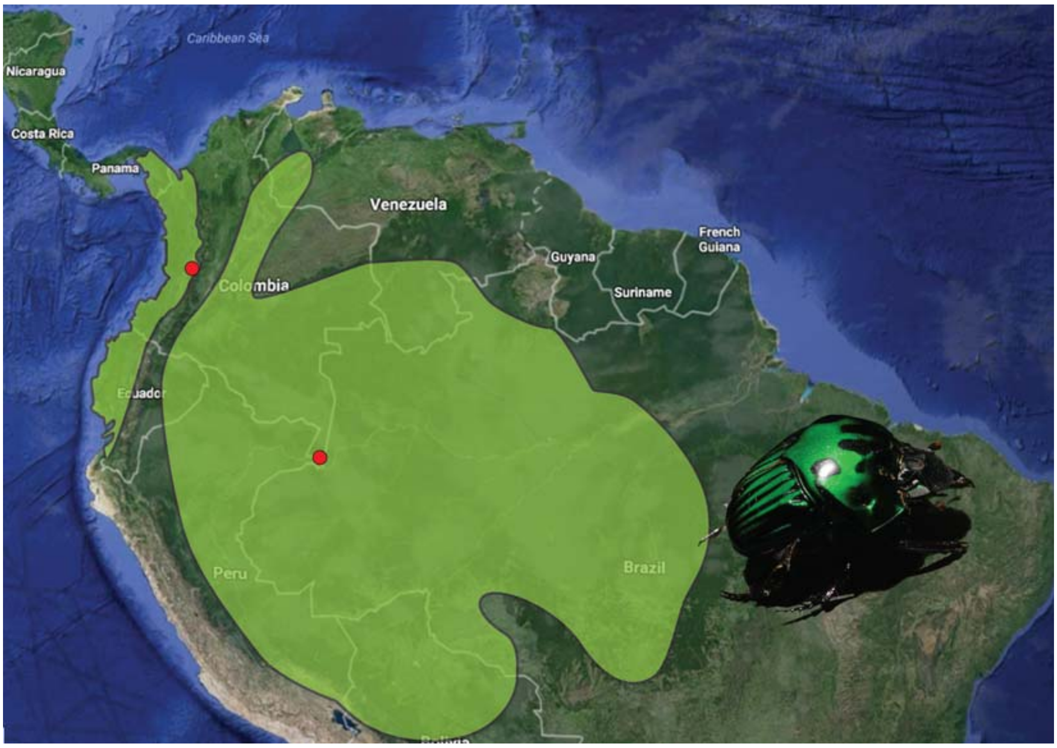

FIGURE 18. Distribution of *Oxysternon conspicillatum* (based on Edmonds & Zídek 2004). Red dots represent collection records of *Megalolaelaps colossus* **sp. nov.**

Acknowledgements

The first author would like to dedicate this manuscript to the memory of his friend, the late Juan Manuel Campo-Kurmen #unbosqueparajuan[4]. Thanks to Juan Manuel for the image of the female of *O. conspicillatum* in Fig. 18, and for dedicating his life to protect and study the forests in Colombia. Many thanks to Bruce Halliday for his contributions on the manuscript process. To Gary Bauchan and Ronald Ochoa for their help with the LT-SEM images (Fig. 1) and for the loan of paratypes of some *Megalolaelaps* from the U. S. National Museum of Natural History. To Huayan Chen for the picture of *O. conspicillatum* in Fig. 1. To Nicole Romero for her contributions in the initial phase of the project. To Marcel Santos de Araújo and Valeria Castilho Onofrio for providing images of some type specimens in, respectively, the Berlese Acaroteca and the Instituto Butantan. Special thanks to the anonymous reviewers and the editor, Shahrooz Kazemi, for all of their suggestions. This project was partially funded by the fellowship "Doctorados Exterior" 568-2012-80048516 Colciencias, Colombia (JOCH).

References

Berlese, A. (1888) Acari austro-Americani quos collegit Aloysius Balzan. Manipulus primus. Species novas

4. https://unbosqueparajuan.wordpress.com

circiter quinquaginta complectens. *Bolletino della Società Entomologica Italiana*, 20, 171–222 + Plates V–XIII.

Berlese, A. (1892) *Acari, Myriopoda et Scorpiones hucusque in Italia reperta*. *Ordo Mesostigmata (Gamasidae).* (Sumptibus Auctoris, Patavii). 143 pp.

Berlese, A. (1904) Acari nuovi. Manipulus II. *Redia*, 1, 258–280.

Berlese, A. (1910a) Liste di nuovi specie e nuovi generi di Acari. *Redia*, 6, 242–271.

Berlese, A. (1910b) Brevi diagnosi di generi e specie nuovi di Acari. *Redia*, 6, 346–388.

Cultid Medina, C.A., Medina Uribe, C.A., Martínez Quintero, B.G., Escobar Villa, A.F., Constantino, L.M. & Betancur Posada, N.J. (2012) Escarabajos coprófagos (Scarabaeinae) del eje cafetero. Guía para el estudio ecológico. *WCS, Colombia, CENICAFÉ y Federación Nacional de Cafeteros. Villa María. Colombia.* 196 pp.

Edmonds, W.D. & Zídek, Y.J. (2004) Revision of the Neotropical dung beetle genus *Oxysternon* (Scarabaeidae: Scarabaeinae: Phanaeini). *Folia Heyrovskyana, Supplementum*, 11, 1–58.

Evans, G.O. (1963a) Some observations on the chaetotaxy of the pedipalps on the Mesostigmata (Acari). *Annals and Magazine of Natural History (13th series), London*, 6, 513–527.

Evans, G.O. (1963b) Observations on the chaetotaxy of the legs in free-living Gamasina (Acari: Mesostigmata). *Bulletin of the American Museum of Natural History* (*Zoology*), 10(5), 277–303.
https://doi.org/10.5962/bhl.part.20528

Evans, G.O. & Till, W.M. (1979) Mesostigmatic mites of Britain and Ireland (Chelicerata: Acari–Parasitiformes).An introduction to their external morphology and classification. *Transactions of the Zoological Society of London*, 35, 139–270.
http://dx.doi.org/10.1111/j.1096-3642.1979.tb00059.x

Fonseca, F.d. (1946) Notas de acareologia. XXXV. Descrição do macho de *Megalolaelaps immanis* Berlese, 1910, e comentarios sobre a família Pachylaelaptidae Vitzthum, 1931 (Acari). *Livro de Homenagem a R. F. d'Almeida*, 16, 177–186.

Gorirossi-Bourdeau, F.E. (1956) The gnathosoma of *Megalolaelaps ornata* (Acarina - Mesostigmata - Gamasides). *The American Midland Naturalist*, 55(2), 357–362.
http://dx.doi.org/10.2307/2422597

Keegan, H.L. (1946) Six new mites of the superfamily Parasitoidea. *Transactions of the American Microscopical Society*, 65, 69–77.
https://doi.org/10.2307/3223286

Kazemi, S., Rajaei, A. & Beaulieu, F. (2014) Description of three *Gaeolaelaps* (Acari: Mesostigmata: Laelapidae) mites from Iran, including two new species, a revised generic concept, and notes on significant morphological characters. *Zootaxa*, 3861(6), 501–530.
http://dx.doi.org/10.11646/zootaxa.3861.6.1

Lindquist, E.E. & Evans, G.O. (1965) Taxonomic concepts in the Ascidae, with a modified setal nomenclature for the idiosoma of the Gamasina (Acarina: Mesostigmata). *Memoirs of the Entomological Society of Canada*, 47, 1–64.
http://dx.doi.org/10.4039/entm9747fv

Mašán, P. & Halliday, B. (2014) Review of the mite family Pachylaelapidae (Acari: Mesostigmata). *Zootaxa*, 3778, 1–66.
https://doi.org/10.11646/zootaxa.3776.1.1

Paoli, G. (1911) Nuovi Laboulbeniomiceti parassiti di Acari. *Redia*, 7, 283–295 + plate XII.

Stoll, O. (1893) Arachnida Acaridea. Biologia Centrali-Americana. R.H. Porter, London, 55 pp + Plates 1–21.

Vitzthum, H. (1931) Acarinen. *In*: Résultats Scientifiques du Voyage aux Indes Orientales Néerlandaises. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique, Hors Série*, 3(5), 1–55.

Walter, D.E. & Krantz, G.W. (2009) Collecting, rearing and preparing specimens. *In*: Krantz, G.W. & Walter, D.E. (eds.) *A Manual of Acarology*, 3rd ed. Texas Tech University Press, Lubbock, TX. pp. 83–95.

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