

Phoretic Mexican macrochelids on high altitude ecosystems (Acari, Mesostigmata)

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Abstract. – In the general frame of studies on phoretic behavior and consequences on fauna and diversity, the authors have studied the Mexican macrochelids (Acari, Macrochelidae) phoriont of dung beetles in high altitudes (1700-3500 m). On the 1483 dung beetles collected, solely forty individuals, belonging to large beetle species, were found with mites attached. Among the nine species of the genus *Macrocheles* identified, six of them are new to science. Some of them belong to “*dimidiatus*” species group which is an American endemic, and more or less specialized as phoretic on the American Phanaeid beetles. Here, the sampling was carried on above the upper limit of these beetles. Six new species, *Macrocheles imeldae* n. sp., *M. violetae* n. sp., *M. simplissimus* n. sp., *M. simplisetosus* n. sp., *M. neomexicanus* n. sp. and *M. perciliatus* n. sp. are described and illustrated. Complements are given to the description of *M. filipponii* Evans & Hyatt.

Résumé. – Les Macrochélides phorétiques des écosystèmes d’altitude du Mexique (Acari, Mesostigmata). Dans le cadre d’une étude des comportements phorétiques et de leurs conséquences sur la faune et sa diversité, les Macrochélides mexicains (Acari, Macrochelidae) phorétiques des bousiers à haute altitude (1700-3500 m) ont été étudiés. Neuf espèces du genre *Macrocheles* ont été identifiées sur 40 des 1483 bousiers examinés, toutes phorétiques d’Insectes de grande taille. Six sont nouvelles pour la science. Certaines appartiennent au groupe d’espèces “*dimidiatus*” qui est considéré comme un groupe endémique américain, plus particulièrement inféodé au genre *Phanaeus*, alors que notre échantillonnage a été effectué au-dessus de la limite altitudinale de ce genre. Les nouvelles espèces *Macrocheles imeldae* n. sp., *M. violetae* n. sp., *M. simplissimus* n. sp., *M. simplisetosus* n. sp., *M. neomexicanus* n. sp. et *M. perciliatus* n. sp., sont décrites et illustrées. Des compléments sont donnés à la description de *M. filipponii* Evans & Hyatt.

Keywords. – Macrochelidae, phoretic mites, taxonomy, dung beetles, Mexico, Transverse Mexican volcanoes belt.

Many organisms use phoresy for reaching remote resource. Thus, most coprophilous or fimicolous macrochelid mites use dung beetles or winged insects to find the numerous preys hosted in dung pads, notably the nematodes and fly larvae, or eggs of small coprophilous organisms. Two main strategies are observed.

– The generalists: in few days, the gravid macrochelid females are attracted by the host, the eggs laid in the new dung pad giving females, giving themselves parthenogenetic males, and the newly mated females, attracted by insect host, start colonizing new pads.

– The specialists: when the beetles bury the dung in soil, the phoretic species may colonize this dung and stay, and thus they depend closely on the phoriont for leaving the nest with the new imagos. The specialists are hosted by selected phoriont.

Among the American macrochelids, some are American endemics, as well at the generic level, *i.e.* the genus *Holocelaeno* Berlese, 1910 (KRANTZ, 1967), or at infrageneric level as the *dimidiatus* group (genus *Macrocheles* Latreille, 1829) (KRANTZ, 2007). Several species of this latter taxon were described from the phanaeine beetles that are American endemic scarabaeoid coleopterans (KRANTZ, 2007).

EVANS & HYATT (1963) have distinguished three groups of macrochelids:

- the American *mitis* group (cheliceral brush long, filamentous and extending up to or beyond the distal end of the movable digit of the chelicera; dorsal shield with 29 pairs of setae; genu IV with seven setae);
- the cosmopolitan *glaber*-group (dorsal shield with 28 pairs of setae, *J2* absent);
- the *bregetovae*-group (dorsal shield with 29 pairs of setae, *J2* present).

The *mitis* group is now synonymous with *Holocelaeno* and it is an American endemic genus (KRANTZ, 1967); the *glaber*-group is the main group, with an imprecise definition, wide enough to accept a large amount of species; the *bregetovae* group was redefined. The latter was reconsidered, redefined and augmented with some species previously described as belonging to the *glaber* group by EVANS & HYATT (1963). These species share morphological general pattern and form a “group of species”: the *dimidiatus* species-group (KRANTZ, 2007). All these species originated from North, Central or South America. Further, MACHADO-ALLISON (1964) and MÉNDEZ-OLIVÓ (1968) identified and described some Mexican species (table I). The species belonging to the *dimidiatus* group are mainly associated with phanaeid phorionts.

During the survey on dung-beetle communities more or less linked with gophers at high altitude in the Transverse Volcanoes Belt (ARRIAGA *et al.*, 2012), several species of Macrochelidae were collected, with representatives of the *dimidiatus*-group, bore by dung beetles. This paper gives the first result of the study, with the description of six species new for science, above the upper limit of distribution of the usual host of the *dimidiatus*-group which is about 2400 m (ARRIAGA *et al.*, 2012).

Table I. – The Mexican species of Macrochelidae (genus *Macrocheles*) and their phorionts (*: *dimidiatus* group, **: cosmopolitan species; ***: Mexican *Phanaeus* species that were revised and partially synonymized by EDMONSON, 1994).

Species	Mexican hosts	References
<i>Macrocheles austroamericanus</i> *	<i>Phanaeus telamon</i> , <i>P. scintillans</i> ***	EVANS & HYATT, 1963
<i>M. boneti</i> Méndez, 1968	<i>Dichotomius carolinus</i> , <i>Copris lugubris</i> Boheman, 1858	MÉNDEZ-OLIVÓ, 1968
<i>M. dimidiatus</i> *	<i>Phanaeus spp.</i> , <i>P. amithaon</i> Harold, 1875***	EVANS & HYATT, 1963
<i>M. filipponii</i> *	<i>Dichotomius carolinus</i> , <i>Eurysternus claudicans</i>	EVANS & HYATT, 1963
<i>M. halffteri</i> Machado-Allison, 1964 *	<i>Phanaeus mexicanus</i> Harold, 1863***	MACHADO-ALLISON, 1964
<i>M. hechti</i>	<i>Canthon humectus</i> (Say, 1831)	MACHADO-ALLISON, 1964
<i>M. hoffmannae</i> Méndez, 1968 *	<i>Dichotomius carolinus</i> , <i>Phanaeus mexicanus</i> ***	MÉNDEZ-OLIVÓ, 1968
<i>M. jalisciensis</i> Méndez, 1968	<i>Dichotomius carolinus</i>	MÉNDEZ-OLIVÓ, 1968
<i>M. mexicanus</i>	<i>Phanaeus palliatus</i> Sturm, 1843***	EVANS & HYATT, 1963
<i>M. muscaedomesticae</i> **	<i>Aphodius subterraneus</i> (Linnaeus, 1758), <i>Onthophagus sp.</i> , <i>Geotrupes stercorarius</i> (Linnaeus, 1758), <i>Scarabeus sp.</i> , <i>Silpha obscura</i> Linnaeus, 1758	MÉNDEZ-OLIVÓ, 1968
<i>M. insignitus</i> **	Nests of <i>Neotoma albigula</i> Hartley, 1894 (Rodentia, Cricetidae)	QUINTERO <i>et al.</i> , 2001
<i>M. merdarius</i> **		
<i>M. penicilliger</i> **		

MATERIALS AND METHODS

In the general frame of the study of the distribution of dung beetles in high altitude environment, four volcanic mountains were sampled, each at two different altitudes between 2500 to 3500 m with ten pitfall traps baited with dung per site; the trap sampling was completed

with direct active collection method. Field work was done from June to August 2012 in the mountains of the east region of the Transmexican Volcanic Belt: Pico de Orizaba (5636 m, last eruption: 1846), Sierra Negra (4585 m), Cofre de Perote (4282 m, last eruption: 1150) and La Malinche (4461 m, last eruption: 3000 years ago) (fig. 1). The vegetation cover of the sampled sites differs: in Pico de Orizaba forestal environment is characterized by *Pinus montezumae* Lamb., *Alnus acuminata* Kunth and *Juniperus monticola* Martinez, alpine meadows and a mosaic of forest and abandoned croplands; in Sierra Negra, sampling sites were in *Cupressus* sp. forest and in the shrublands surrounded by *Pinus* forest; in Cofre de Perote, the traps were placed in shrublands surrounded by *Pinus teocote* Schiede ex Schltdl. & Cham. forest. Each dung beetle was checked for mites and then determined by G. Halffter. Once separated, the mites identified as Macrochelids were cleared in lactic acid and mounted for microscopy on slides, then identified by M. Bertrand. Half of the sampled mites was preserved for future molecular investigation. Holotypes are conserved in the Colección Nacional De Acaros UNAM, Mexico. The reference collection is maintained at the Laboratory of Zoogeography, Montpellier III University. Microscopic studies were carried on with Wild EB microscope, measures using calibration with Motic camera in temporary preparations in lactic acid. Dissected specimens were mounted in Hoyer's liquid.

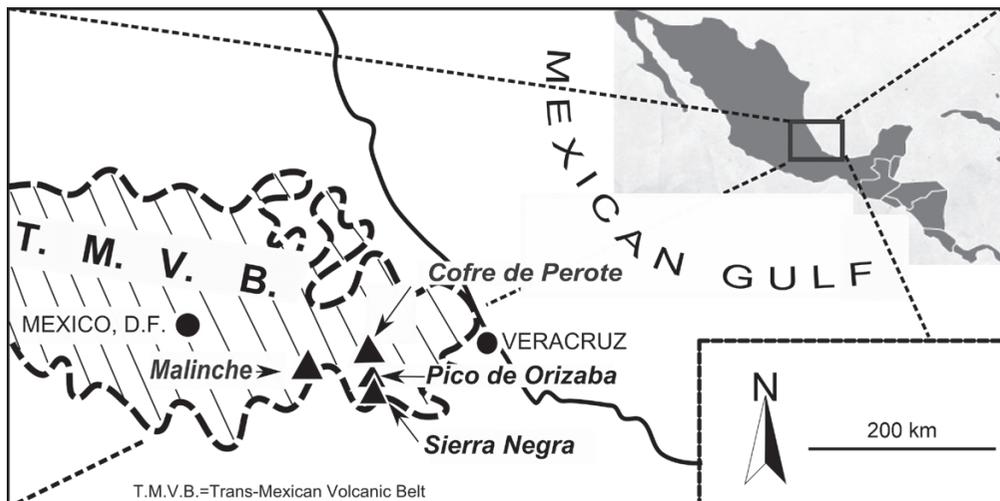


Fig. 1. – Situation map of the sampled volcanoes in the South-Eastern Transmexican Volcanic Belt.

The description of the species follows the general nomenclature of Macrochelids as established by BERLESE (1918), HALLIDAY (1986), KRANTZ (2007), LINDQUIST *et al.* (2009) and WALTER (2005) (fig. 2-5).

Used abbreviations. – *ad1*, *ad2*, *al*, antero-dorsal and anterolateral setae (antiaxial = “alpha” and paraxial = “pi” in the IVth leg genual); *ar1*, *ar2*, arthrodial brushes; *cj3*, anterior cell-like depression; *d*, dorsal; *j1-j6*, centro-dorsal setae of anterior dorsal shield; *J1-J6*, centro-dorsal setae of posterior dorsal shield; *Jv1*, *Zv2*, *Jv3*, preanal setae; *Jv1-Jv5*, posterior hysterosomal setae; *l.ang.*, *linea angulata*; *l.m.t.*, *linea media transversa*; *l.o.a.*, *linea oblique anteriore*; *l.o.p.*, *linea oblique posteriore*; *ly1*, *ly2*, antiaxial and paraxial fissure of the chelicera; *m.s.*, metasternal shield; *p. dent.*, *pilus dentilis*; *p.d.*, paradactylus; *p*, pore; *pd1*, *pd2*, *pdl*, postero-dorsal and postero-dorso-lateral setae of the genual IV; *PI-PIV*, coxal opening of 1st, 2nd, 3rd, 4th pairs of leg; *PS*, peritremal shield; *pZ5*, dorsal pore of the Z5 seta; *r1-r6*, marginal setae of anterior dorsal shield (*r5-r6* being out of the shield); *R1-Rx*, *Rpd*, *RpA*, dorso-lateral setae of the opisthosomal integument; *S*, stigmata; *s1-s6*, lateral setae of anterior dorsal shield; *SI-S6*, lateral setae of

posterior dorsal shield; *sl*, tarsal slit organ; *st1*, *st2*, *st3*: anterior, median and posterior sternal setae; *st4*, metasternal seta; *st5*, epigynal seta; *z1-z6*, mediolateral setae of anterior dorsal shield; *Z1-Z5*, mediolateral setae of posterior dorsal shield; *Zv1*, *Zv3*, anterior opisthogastric setae.

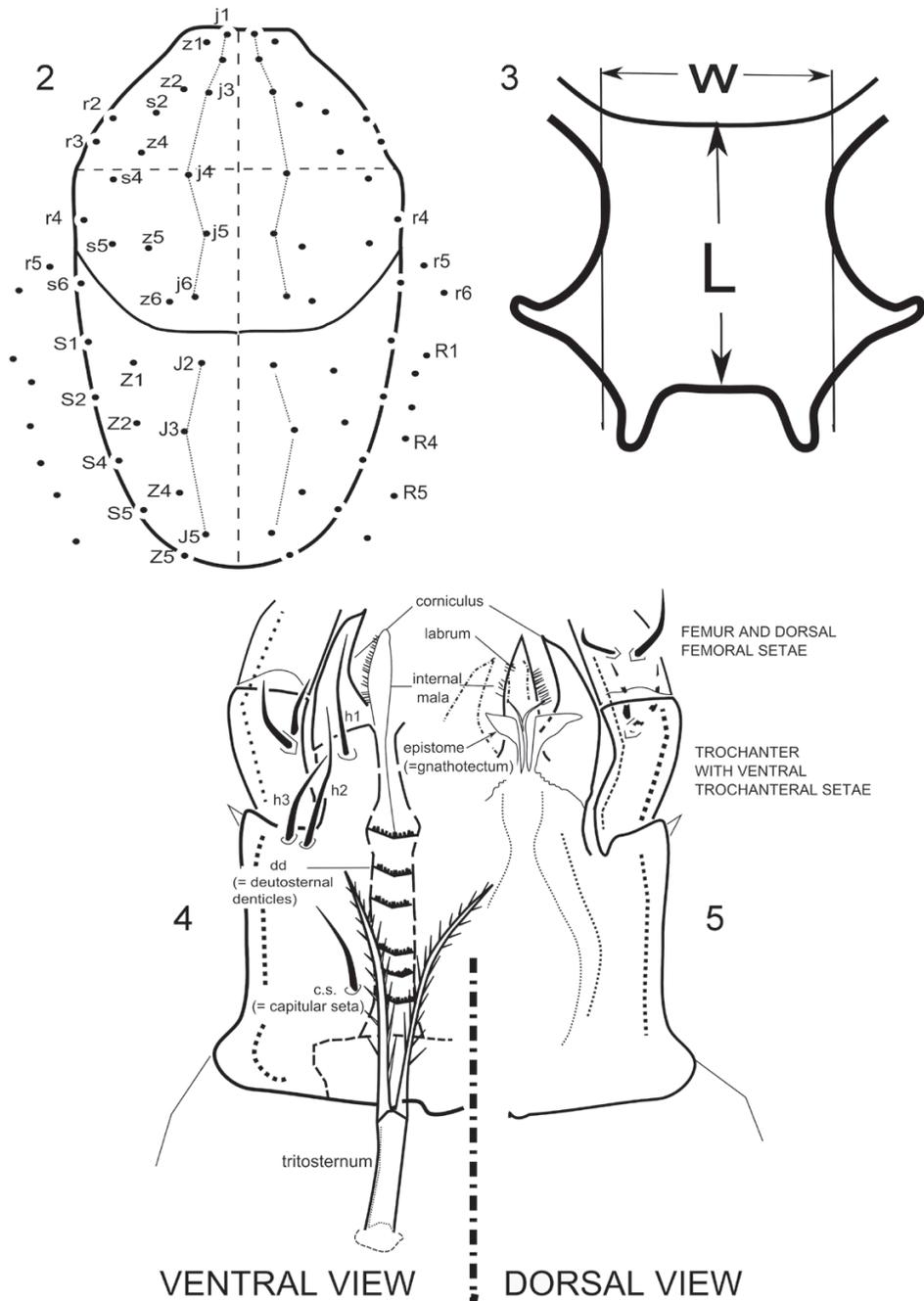


Fig. 2-5. – Macrochelidae, general nomenclature and anatomic organization. – 2, Dorsal setation. – 3, Measures of the sternal shield (length: L; width :W). – 4-5, Archetype of mouth parts (capitulum) morphology in macrochelids, ventral (4) and dorsal view (5). Note that chelicerae are not figured.

RESULTS

Phoretic mites were collected on dung beetles from all mountains under scrutiny, except from the Malinche. The total capture in the four mountains was of 1483 dung beetles; forty were found with mites attached (2.6 %) these specimens belonging to 5 species from a total of 26. The mites were found on dung beetles belonging to the genera *Onthotrupes* Jekel, 1865, *Onthophagus* Latreille, 1802, *Copris* Geoffroy, 1762, and *Geotrupes* Latreille, 1796. The carriers (dung beetles carrying at least one *Macrocheles* mite individual) were distributed on three of the four mountains (table II). Note that in samples over 3200 m, dung beetles were represented by two large size species, *Halffterius rufoclavatus* Jekel, 1866, and *Copris armatus* Harold, 1869, as well as *Onthophagus chevrolati* Harold, 1869, but macrochelids were only associated with *H. rufoclavatus* and *O. chevrolati* (table II).

Table II. – Distribution of the host collected (only the beetles with phoretic mites are noted).

Dung beetles	Site	Altitude	Coordinates	Date
<i>Onthophagus incensus</i> Say, 1835	Xalapa	1400 m	14.32°N - 96.54°W	VI.2012
<i>Onthotrupes nebulorum</i> Howden, 1964	Pico de Orizaba, Cuiyachapa	2709 m	19°02.19'N - 97°10.16'W	VII.2012
<i>Copris armatus</i> Harold, 1869	Sierra Negra	2766 m	18°59'25.9"N - 97°24.26'W	VI.2012
<i>Halffterius rufoclavatus</i> Jekel, 1866 <i>Copris armatus</i> Harold, 1869	Cofre de Perote, Carabinas	3237 m	19°30'6.3"N - 97°07'20.2"W	VII.2012
<i>Onthophagus chevrolati chevrolati</i> Harold, 1869	Sierra Negra, Texmalaquilla	3406 m	18°57'43.9"N - 97°17'39.4"W	VI.2012

The phoretic macrochelids. – All the macrochelids belong to the genus *Macrocheles* and the largest species to the *dimidiatus* group. The identity of the *dimidiatus* species group is based on the American species described by BERLESE (1918) and gathered in this group redefined by KRANTZ (2007). In application to the rules of the International Code of Zoological Nomenclature about the names of aggregates of species, above cited species groups (as well as complexes of species) will be denoted by interpolating in parentheses the specific name between the genus name and the specific name (Article 6.2. Names of aggregates of species or subspecies, and Article 45. The species group. ICZN, 1999).

Preliminary note on the dimidiatus group of species. – BERLESE (1918) described *Macrocheles dimidiatus* as belonging to the Xth “*penicillati* phalanx” gathering Argentinian (nine species or subspecies) and North America (one species) taxa, plus Java (one species). EVANS & HYATT (1963) defined the *bregetovae* group by the presence of 29 pairs of dorsal setae; then, KRANTZ (2007) reconsidered the species closely allied to *M. dimidiatus* and proposed to delineate four “complexes of species” within the *dimidiatus* species-group (table III): *hirsutissima*, *quadriareolatus*, *bregetovae* and *dimidiatus* complexes, with the respective eponym type-species : *M. hirsutissima* (Berlese, 1910), redescribed by KRANTZ (1988), *M. quadriareolatus* Berlese, 1918, *M. bregetovae* Evans & Hyatt, 1963, *M. dimidiatus* Berlese, 1918. The *bregetovae* and *dimidiatus* complexes differ notably in having the anterior dorsal setae (*j1*) similar or not to (*j2*), expanded or not and by absence or presence of procurved dorsal line.

KRANTZ (2007) considers that the *dimidiatus* complex may be divided into three main “clusters”: *woodruffi* (setae *J2* pectinate), *matthewsi* (*j1* greatly expanded), and *edmondsi* clusters (table III).

Table III. – Characters of the species belonging to the complexes of the species-group *dimidiatus* (according to KRANTZ, 2007).

	<i>hirsutissima</i>	<i>quadriareolatus</i>	<i>bregetovae</i>	<i>dimidiatus</i> (3 clusters)		
				<i>woodruffi</i>	<i>matthewsi</i>	<i>edmondsi</i>
Extramarginal setae	14-24	Less than 14 extramarginal setae				
Procurved line of dorsal shield	Absent	Present or absent				
		None	present or not	present		
Dorsal setae	29 pairs	28 all pectinate	28-29 or 30			
Sternal shield		As long as broad. Quadriareolate pattern	If quadriareolate ornamentation, thus the sternal setae are smooth and the sternal shield is broader than long			
<i>cj3</i>		Weak or absent				
Genu IV		Seven setae				
Basitarsus IV		Shorter than podomere				
Setae <i>j1-j2</i>		similar	<i>j1</i> expanded, longer than <i>j2</i>			
Setae <i>J2</i>		<i>J2</i> pectinate	<i>J2</i> smooth			
Setae <i>j1</i>		Elliptical, expanded	Not elliptical			
<i>cj3</i>		Developed and closed	Weakly formed or $j5 = 2 \times z5$			
Dorsal shield		Rounded posteriorly	Narrowed posteriorly			

SPECIES BELONGING TO THE GROUP *DIMIDIATUS****Macrocheles (dimidiatus) imeldae* Arriaga & Bertrand, n. sp.** (fig. 6-15)

HOLOTYPE : ♀, Pico Orizaba, Cuiyachapa, Veracruz (19°02'14.0"N - 97°10'15.3"W), 2709 m, *A. Arriaga col.*, *Pinus* and *Alnus* forest, VII.2012, host: *Onthotrupes nebularum* Howden, 1964 (UNAM).

PARATYPES: 2 ♀, *idem* holotype (UNAM).

Description of the female.

Idiosoma. Dorsal shield 850 µm long, maximal width 513 µm, attenuate and narrowed at the posterior end. Setae *j1* are broad and flat, densely pectinate. The major part of the dorsal 28 pairs of setae are pilose, rather long (> 80 µm) with exception *z1*, *z5*, *z6*, *j6*, that are smooth and shorter, *J2* are simple or weakly plumose, the pair (*J5*) (fig. 6) is plumose but reduced in length if compared with plumose dorsal or marginal setae (70 µm vs. about more than 100 µm). The dorsal shield is clearly divided by the procurved line. Between the pair *j3*, the cellular depression *cj3* is visible delimiting a curved ridge that connects the insertion base of the *j3* setae. On the opposite end, one pair of depression continued by a ridge visible around the subterminal pore *pZ5*. Surface of the dorsal shield with reticulate pattern, with large alveolae, larger and irregular in shape near the procurved line, less regular in the central dorsal zone between (*z6*) and (*j4*), and weak and stumped in the medially. The peritrematic shield long, reaching the level of lateral setae (*s6*). The dorsal pores are visible, those of the anterior idiosoma elongated and lyriform (*ly*, fig. 6). On each side of the dorsal shield, on the soft integument, ten shorter than the shield setae lined and drawing a large V, the first being the setae (*r5*) placed at a short distance of the peritrematic shield (fig. 6).

Ventral view. Fig. 7. Tritosternum (190-200 µm long) typical for the genus, with base about 0.33× the length of the branches, that are slightly ciliate. Sternal shield broader than long: minimal width between PII 180 µm, length along the sagittal line: ca. 115 µm. Sternal lines *l. ang.* and *l.o.a.* visible, as *l.m.t.* underlined by discrete punctures and *l.o.p.*; (*st1*) longer than *st2* and *st3*, distance between anterior pores,

quite identical to the minimal width measured at PII. Epigynal shield short (*ca.* 60 μm long), enlarged at the posterior extremity, distance between epigynal setae is *ca.* 80 μm . Metasternal shield close to the epigynal shield, with metasternal pore and (*st4*). At the level of the epigynal setae, a lateral pore present on each side on the soft cuticle. Ventrianal shield subtriangular in shape, longer than wide (190-220 μm in maximal length, 100-120 μm for the anterior limit), well separated from the epigynal shield, three pairs of preanal setae, pore post PIV well visible. Cribrum developed with pores (figs. 7-8). All the ventral setae bore by shields are simple, contrarily to the opisthosomal setae, external to the ventrianal shield, that are generally slightly plumose. Paranal and postanal setae simple.

Gnathosoma. Fig. 8-10. The structure of the gnathosoma is constant in the family and conform to the description already given (EVANS, 1992) (see fig. 4-5). Epistome (= gnathotectum) tripartite (fig. 9) with central part forked, simple and lateral expanded parts. Hypostome with three setae as in the group, conform to what currently observed in macrochelids (VAN DER HAMMEN, 1964, 1989) (fig. 4). Palp as for the family, terminal sensory setae with at least 5 long setae surrounding two shorter ones that are terminal. The hypognathal denticles (= deutosternal denticles) show six rows of small teeth-like projections (fig. 14). Chelicerae show fixed digit strong and armed by the large pyramidal tooth opposed to the shorter and clearly smoother tooth on the movable digit. Arthrodistal brush with *ar1* shorter than the half movable digit. *Pilus dentilis* inserted close to the distal end of the fixed digit, internal lyrifissure *ly2* elongated.

Legs (fig. 11-12) as in the genus. The genua IV with 7 setae as most species of the *dimidiatus* group, *pd1* and *pd2* ciliate, *a1*, *a2*, *al*, *pd* slightly plumose. Basitarsus IV with the four setae ciliate, ventral being 1.5 \times longer than the dorsal. Ambulacrum: normal for the genus, paradactyli distally divided. Tarsi II with subterminal setae which are similar to *M. austroamericanus*.

Etymology. – This species named in honor of G. Imelda Martínez Morales, researcher in the Instituto de Ecología, in Xalapa, for her support during the formation and development of the thesis of the first author.

Remarks. – Among the species already described, *M. imeldae* n. sp. could be confused with *M. hechti* Machado-Allison, 1964, that was described from the Veracruz region. However, in the original description and in the more consequent description by MÉNDEZ-OLIVÓ (1968),

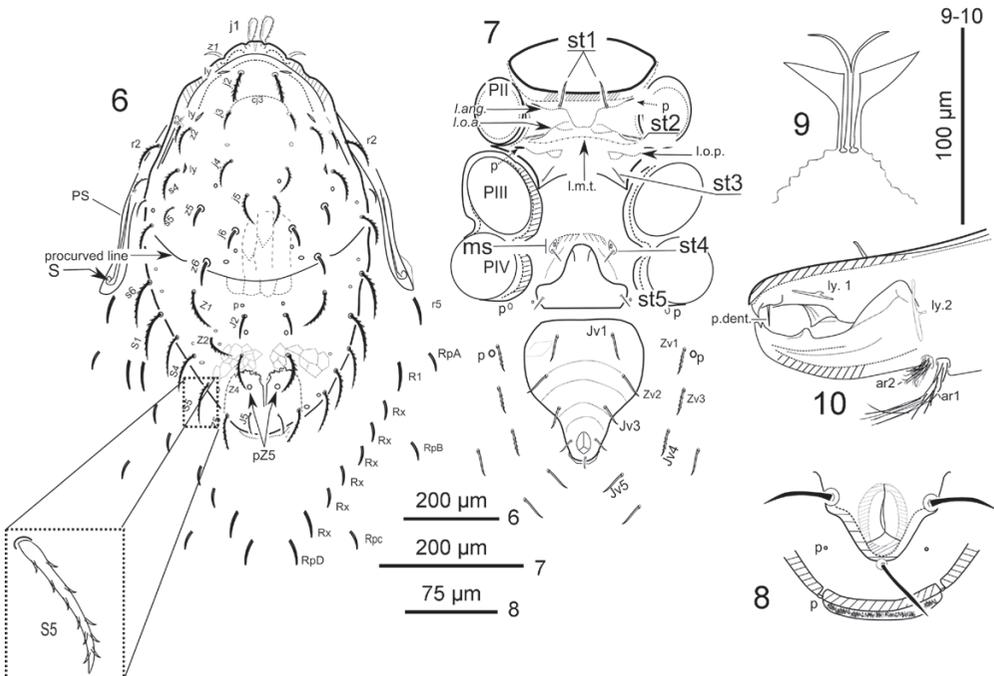


Fig. 6-10. – *Macrocheles imeldae* n. sp., ♀. – 6, Dorsum and detail of S5 seta. – 7, Venter. – 8, Ventrianal shield, detail. – 9, Epistome (syn. gnathotectum). – 10, Left chelicera, lateral view. (Abbreviations: see text).

M. hechti differs from *M. imeldae* on the dorsal chaetotaxy (presence of j_2 plumose setae j_5 , j_6 , J_5 , vs. simple setae) and by the chelicerae [in *M. hechti*: “dedo fijo mucho más grueso que el móvil” (MÉNDEZ-OLIVÓ, 1968)]. The sternal shield with long sternal setae $st1-st3$ but also $st4$ (metasternal setae). The presence of the seventh seta of the genu IV separates the new species from the species previously described. MÉNDEZ-OLIVÓ (1968) has remarked significant differences between populations of *M. hechti* collected either on the genera *Phanaeus* MacLeay, 1819, or on *Dichotomius* Hope, 1838. This may indicate that several species may be sympatric, hypothesis that could be verified by description of male specimens. About the characteristics of the j_1 , j_2 , and z_1 , analogous features were found in some species of the *dimidiatus* group, notably *Macrocheles bryanti* Evans & Hyatt, 1963, or *M. browningi* Evans & Hyatt, 1963, or

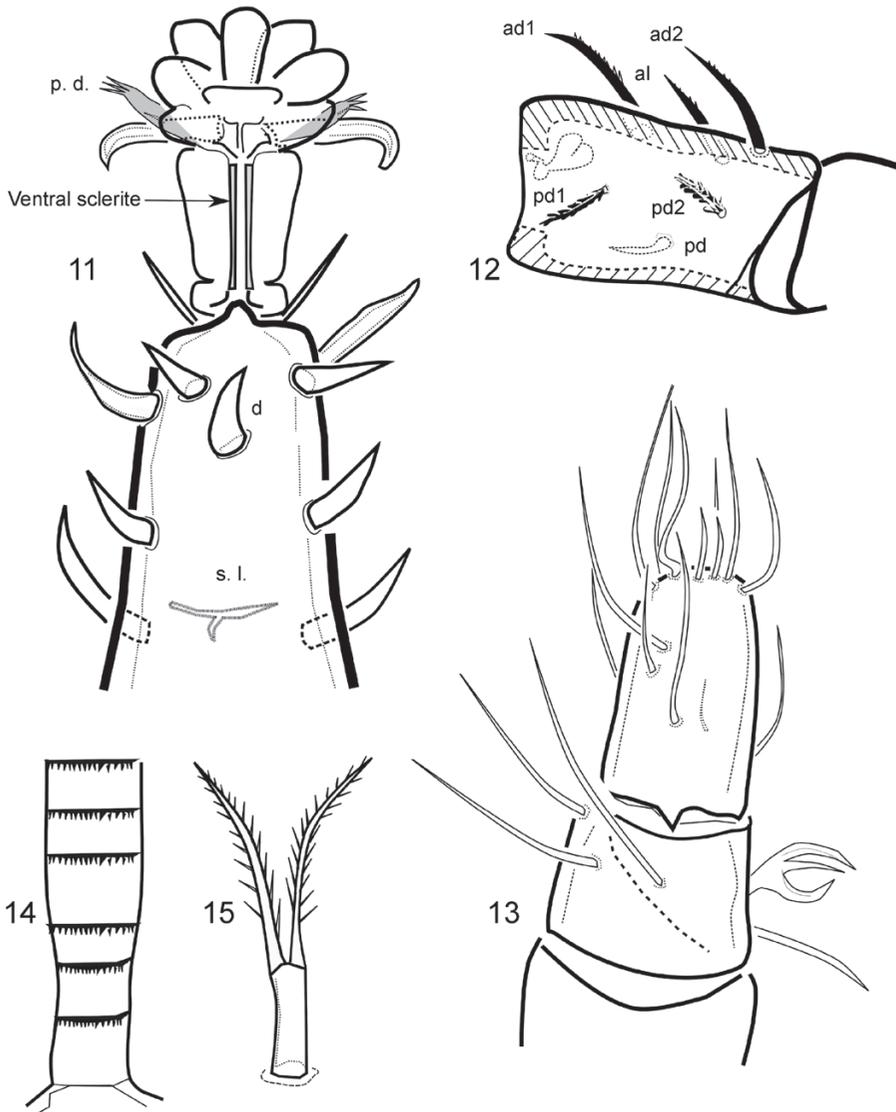


Fig. 11-15 – *Macrocheles imeldae* n. sp., ♀. – 11, Tarsus II and ambulacrum, dorsal view. – 12, Genu IV lateral view. – 13, Palpal distal part. – 14, Pharynx, ventral view. – 15, Tritosternum.

M. dimidiatus and *M. laciniatus* Krantz, 1988. As *M. dimidiatus*, the setae *j6*, *z6*, *z5*, *J2* are simple and short and *J5* is short too (KRANTZ, 2007). The new species differs by absence of marked lateral ridges on the posterior dorsal shield that figure a row of successive ridges. Ventrally, *l.o.a.* is very similar to that of *M. dimidiatus* or *M. austroamericanus* Evans & Hyatt, 1963, and *l.o.p.* is medially interrupted as in *M. hechti*. By the characters given here above, the new species must be placed in the *dimidiatus* complex *sensu* KRANTZ (2007).

This species could be confused with *M. dimidiatus* that was illustrated by EVANS & HYATT (1963: 347), MÉNDEZ-OLIVÓ (1968: fig. 33-36, lámina III) and KRANTZ (2007: 298). The new species differs by ornamentation of the sternal shield, shortness of setae *J5*, the simple median tooth of the mobile digit of the chelicerae, setae *Z2* smooth. *M. imeldae* n. sp. is characterized by the distance *j3-j4* longer than *j3*. The descriptions of *M. dimidiatus* by KRANTZ (2007) or EVANS & HYATT (1963) and the drawing by MÉNDEZ-OLIVÓ (1968) present some differences. The species identified by MÉNDEZ-OLIVÓ as *M. dimidiatus* exhibits long setae *j5*, longer than the distance *j5-j6*, contrarily of the species drawn by KRANTZ (2007) with short *j6*, *j5* being shorter than the distance *j5-j6*. *M. imeldae* has simple *z6*, and *z6* is slightly shorter than or as long as *j6*. This pair of setae is pilose in *M. dimidiatus*, and longer than *j6* in the descriptions by KRANTZ (2007) or EVANS & HYATT (1963).

***Macrocheles (dimidiatus) violetae* Arriaga & Bertrand, n. sp. (fig. 16-18)**

HOLOTYPE : ♀, Sierra Negra, Cd. Serdan, Puebla (18°59'25.9"N - 97°24.26'W), 2766 m, *A. Arriaga col.*, *Pinus* and *Cupressus* forest, VI.2012, host: *Copris armatus* Harold, 1869 (UNAM).

PARATYPE: 1 ♀, *idem* holotype (UNAM).

Description of the female.

Idiosoma. Fig. 16. Dorsal shield 900 µm long, maximal width 520 µm, the procurved line is visible and divides the dorsal shield in anterior and posterior part of equal length along the sagittal axis. Setae

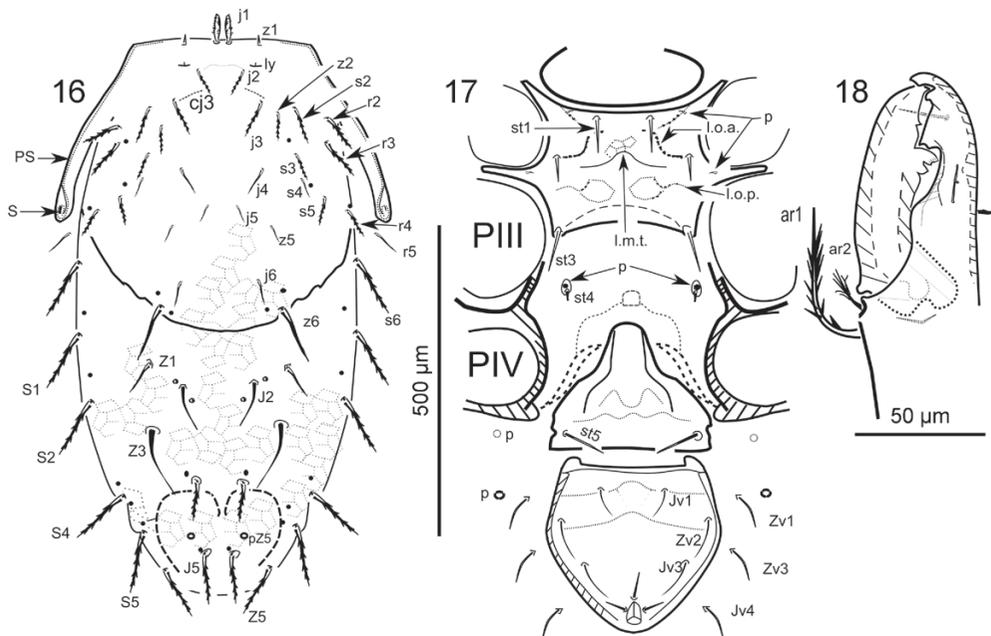


Fig. 16-18 – *Macrocheles violetae* n. sp., ♀. – 16, Dorsum. – 17, Venter. – 18, Left chelicera, lateral view.

j1 plumose, *ca* 70 μm long. Peripheral setae of the dorsal shield are rather long and plumose ($> 100 \mu\text{m}$) whereas the aspidosomal centro-dorsal setae smooth and shorter (30-60 μm) with exception of *z6* that are the longest, as long as the peripheral setae, *j5* being the shortest. The pairs *z1*, *j4*, *s4*, *j5*, *s5*, *z5*, *z6*, *J2*, *Z1*, *Z3*, are simple (fig. 16), setae *z1* short. Between (*j3*), the cellular depression *cj3* is visible delimiting the curved ridge between these setae. Anterior pores clearly elongated. The depression around the sub-terminal pore *pZ5* is very well marked surrounded by a ridge. Dorsal pattern with reticulate ornamentation, with large alveoli, sub-regular in shape. The peritrematic shields are rather short, not surpassing the anterior limit of the procurved line, at the level of setae *z4*. Setae *r5*, short and simple, are placed near the posterior end of the peritrematic shield.

Ventral view. Fig. 17. Sternal shield broader than long — 177 μm wide and 150 μm long — with setae *st1* and *st3* rather long and simple, *st2* shorter (44, 35, 30 μm in respect). Metasternal shield with setae *st4* (15 μm), and metasternal pore well visible. Epigynal shield sub-triangular in shape (160 μm long, 200 μm wide, *st5* 35 μm long). The ventrianal shield (longer than wide: 285 vs. 215 μm) is not immediately contiguous to the epigynal shield; ventrianal lateral edges convex. Ventrianal setae simple, 45 μm long, paranal setae 35-40 μm long. The ornamentation of the three ventral shields is characterized by the sinuous *l. m. t.*, sinuous cuticular pattern on the epigynal shield, and parallel the two anterior transverse ridges on the ventrianal shield (fig. 16). Tritosternum 190 μm in total length with ciliate branches 135 μm long.

Gnathosoma. Fig. 18. Chelicerae with long *pilus dentilis* (*ca.* 25-30 μm), mobile digit with a very small but sharp distal tooth and a large pyramidal median tooth but divided in two (fig. 17). Dorsal split organ located anterior to the dorsal cheliceral seta. Palpi with rather short terminal seta (40 μm vs. 60 μm in *Macrocheles imeldae* n. sp.).

Legs. Genua IV with 7 setae. Terminal setae on tarsi I relatively long (setae 110 μm long and tarsi 145 μm long).

Etymology. – This species named in honor of Violeta (Marcet) Halffter, an outstanding human being and extraordinary researcher, for all her support, inspiration and a model of life to the new generation of researchers.

Differential diagnosis. – This species is clearly distinct from the other Mexican species by the sternal ornamentation, the shape of genital and ventrianal shields and the dorsal setation with smooth *j4-j5*, *J6*, and *J2* simple shorter than *Z3*. Following the rules given by KRANTZ (2007), this species must be placed in the “cluster” *edmondsi* of the complex *dimidiatus* (table III).

***Macrocheles (dimidiatus) simplissimus* Arriaga & Bertrand, n. sp.** (fig. 19-22)

HOLOTYPE: ♀, Cofre de Perote near Carabinas, Municipio. Xico, Veracruz (18°59'25.9"N - 97°24.26'W), 3237 m, *A. Arriaga col.*, shrubland surrounded of *Pinus teocote*, VII.2012, host: *Halffterius rufoclavatus* (Jekel, 1866) (UNAM).

PARATYPES: 4 ♀, *idem* holotype (UNAM).

Description of the female.

Idiosoma. Fig. 19. Dorsal length 800-850 μm , width 450 μm at the level of humeral angles. Dorsal shield ornamented with polygonal penta or hexagonal pattern in shape, walls of alveoli and punctures being more visible and stronger in the fields comprised between the rows “s” and “j” of the anterior dorsal shield. Anterior and medial part of the dorsal shield well visible, 29 pairs of dorsal setae, all simple except *J5* which is pectinate. Anterolateral pair of setae *z1* are smaller in length than setae *j1* which are simple and divergent. The procurved line slightly sinuate marks a rupture in the polygonal pattern, notably in central field of the shield. The cell-like depression *cj3* is visible; however the posterior clunal depression *pZ5* depression is attenuated, usual pores present. The sclerotization of the shield defines behind the setae *S4* irregular limits (fig. 19).

Ventral view. Fig. 20. The sternal shield is 190-200 μm long and 200-225 μm wide, with the lines *l.o.a.*, *l.m.t* and *l.o.p.* visible, the two latter slightly sinuose and homothetic in shape. Posteriorly, the sternal shield ends are sharpened and in subterminal part slightly irregular. Setae *st1*, *st2* and *st3* similar in length (*ca.* 25 μm) are rather short if compared with the species described here above. The metasternal plates, with *st4* behind the third coxae, quite as the same level than the anterior edge of the epigynal

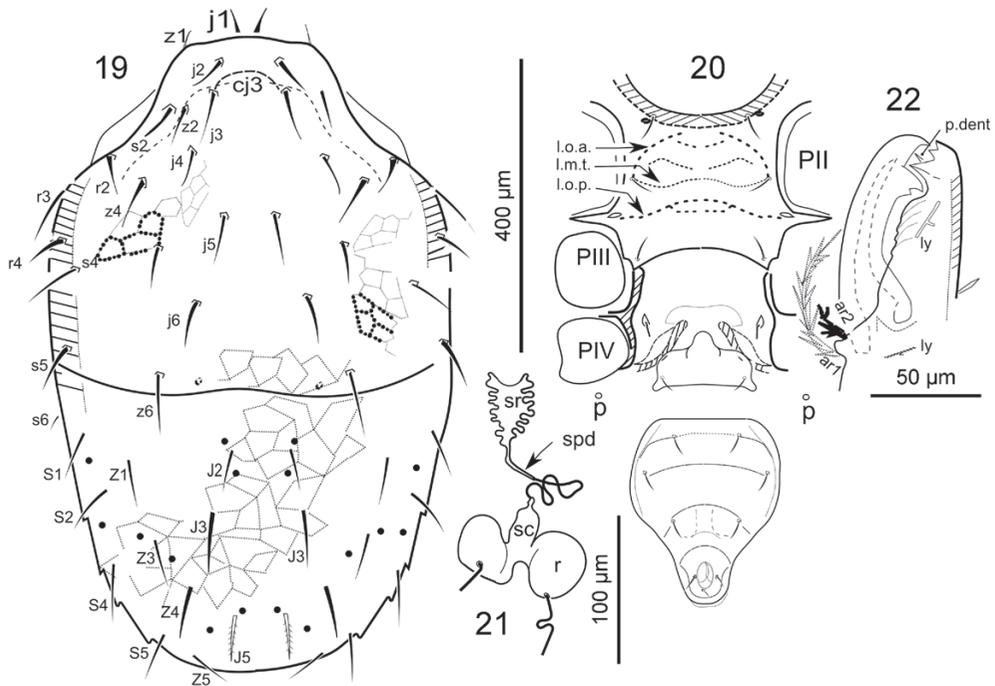


Fig. 19-22 – *Macrocheles simplissimus* n. sp., ♀. – 19, Dorsal shield. – 20, Venter. – 21, Sacculus foemineus (r, ramus; sc, sacculus; spd, spermiducte; sr, receptaculum). – 22, Chelicera, lateral view.

shield. Epigynal shield with posterior edge prorogued laterally and posterior by irregular and smooth ends. Ventrianal and epigynal shields well separated. Ventrianal shield longer than broad (270 µm long, maximal width 190 µm). Ornamentation with four arched lines, the three anterior bears the three pairs of ventrianal setae. On the soft integument, the post-coxal pore (*p*, fig. 19) is well visible. Paranal and post anal setae smooth, cribrum straight.

Gnathosoma. Chelicerae (fig. 22) with the *pilus dentilis* inserted between the subterminal, strong triangular tooth and a tiny and acute tooth. Movable digit with a large biacuminate tooth. Arthrodial brush with *ar2* short (less than 12 µm) and *ar1* reaching the half of the movable digit (about 75 µm long). Palpi typical for the genus. Genua IV with six setae. Epistome as for *M. imeldae* n. sp. (fig. 8)

Sacculus foemineus. *Ramus* globular, followed by bottle-like *sacculus*, *spermiductus* relatively short (less than 150 µm) ended by a well-developed and wrinkled seminal *receptaculum* of 40-55 µm long, 15 µm of maximal width (fig. 21).

Differential diagnosis. – *M. simplissimus* n. sp. is a medium large species characterized by simple dorsal setae with exception of the pennate *J5*. By the presence of a well-marked *cj3* and the number of dorsal setae, it could correspond to a member of the *dimidiatus* group, and ventrally the global arrangement pattern of the shields is very similar to that was described in the *dimidiatus* group. Further investigation should permit to give a more robust diagnostic.

Macrocheles (dimidiatus) filipponii Evans & Hyatt, 1963 (fig. 23-24)

This species was previously described as a “large species with areas of granulation and faint sparse reticulations around the margins”, with 29 pairs of dorsal setae strongly bipectinate, *j6* and *J5* being the shortest of the dorsal setae (EVANS & HYATT, 1963). Original description was carried on Guatemalan or Costa Rican specimens, collected on *Dichotomius carolinus* (Linnaeus, 1767) and *Eurysternus claudicans* Kirsch, 1871. Specimens of this species have

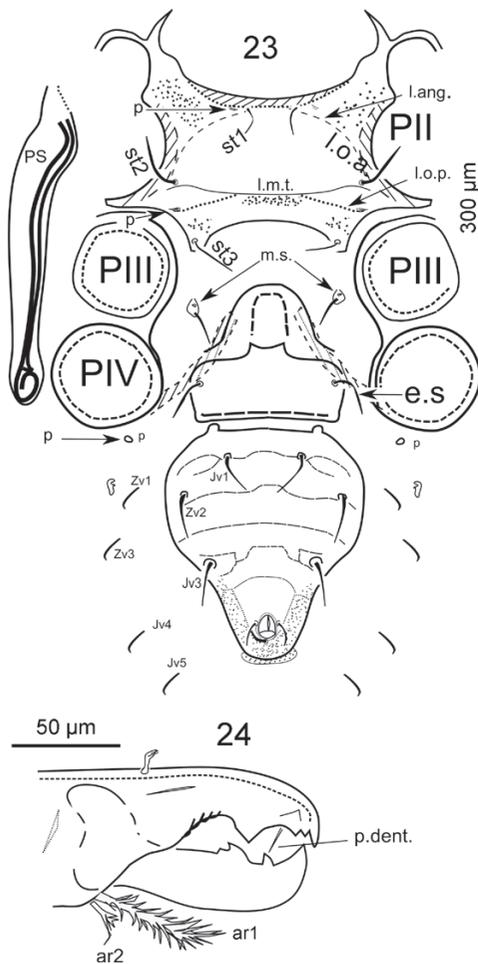


Fig. 23-24. – *Macrocheles flipponii* Evans & Hyatt, ♀. – 23, Venter. – 24, Distal end of chelicera.

been collected by J.-P. Lumaret and G. Halffter in 2006 from the Cofre de Perrote region, on Coprid beetles (*Copris armatus*).

The specimens here examined are similar to the original description by EVANS & HYATT (1963). This species was collected in the Guatemalan site near Cobán (elevation: more than 1300 m).

In complement to the original description, our specimens are larger than the type (dorsal shield: 1160 µm long, 691 µm wide vs. 1060 × 670 µm). The sternal shield is clearly wider than long (143 µm following the sagittal line, and 213 µm in the minimal distance between coxae II). The *l.m.t.* is concave forward (vs. convex forward in *M. dimidiatus*) and the *st3* setae are inserted at the end of the posterior angles of the sternal shield. Distance between *st3* is about 150 µm; distance between *st1* is about 50 µm. The anterior edge of the ventrianal shield is not linear but presents two and symmetrical expansions.

Chelicerae are very similar to that of *M. dimidiatus* (KRANTZ, 2007).

Macrocheles (dimidiatus) austroamericanus
Evans & Hyatt, 1963

M. austroamericanus is a species with large distribution, described from Mexico and South America (Paraguay, Argentina, Brazil, etc.). It is present in Bolivia (KRANTZ, 2007). It is very similar to *M. cordiger* (Berlese, 1918) and *M. spinosus* Berlese, 1918, by the dorsal chaetotaxy and the sculpture of the sternal shield. The latter is identifiable by the ventrianal shield six times longer than wide. In Mexico it was already reported from Phaneides beetles *P. scintillans* Bates, 1887, and *P. telamon* (Erichson, 1847). It was collected (by the first author) here from *Onthotrupes nebulorum*. Complements to the description were given by KRANTZ (2007), with the description of a male specimen.

SPECIES NOT BELONGING TO THE *DIMIDIATUS* GROUP

***Macrocheles simplisetosus* Arriaga & Bertrand, n. sp.** (fig. 25-29)

HOLOTYPE : ♀, Xalapa (19°31'32"N - 96°55'23"W), 1400 m, *A. Arriaga col.*, Urban vegetation, VI.2012, host: *Onthophagus incensus* Say, 1835 (UNAM).

PARATYPES: 2 ♀, *idem* holotype (UNAM).

Description of the female.

Idiosoma. Fig. 25. Large species with dorsal shield 1200-1300 µm long, 850-925 µm wide at level of humeral angles. Dorsal shield divided by regular procurved line, ornamented by polygons slightly

punctuate in the center of alveoli, well visible on the lateral part of the shield, whereas polygons in the central region become elongated according the symmetric axis. Posterad to *S4* the sclerification defining an irregular edge of the posterior end of the shield. All dorsal setae are simple except *j1* (50-60 μm long) that are plumose distally. Setae *j5* asymmetrically disposed. The cell-like depression *cj3* is attenuate and not clearly distinguishable. Central setae slightly shorter than peripheral setae on the anterior shield, but setae *J2* to *J5* and *Z2* to *Z4* are longer than the setae of the peripheral row S. Large dorsal pores visible. Posterior clunal depression *pZ5* faded.

Ventral view. Fig. 26. Tritosternum 265 μm long, branches 250 μm . Sternal shield (260 μm long, 210 μm wide) well divided in anterior part and posterior one, which is ornamented with quasi-circular depressions, by the line *l.m.t.* with its concavity directed forward. *l.ang.* directed forward and medially continued backward, the anterior angles being quasi aligned with *st1* that are close to the proximal sternal pores. Metasternal sclerites (55 μm long) are rather strong with the pore anteriorly and *st4*. Epigynal shield wider than long (210 \times 260 μm) but sclerotization attenuated forward, finishing backward well behind the coxae IV. Ventrianal shield large (475 μm long, 420 μm wide but only 260 μm for the anterior edge) indented latero-anteriorly, ornamented by large polygonal pattern, punctuations visible all along the lateral margin from the anal region to *ZV2*. On the soft integument, the first posterior to coxa IV pore and the second one between *Zv1* and *Zv3* clearly visible as the chitinized ventral platelet between *Zv1* and the second pore.

Legs. Fig. 28. Typical for the genua IV with 7 setae.

Gnathosoma. Typical for the genus. Chelicerae strong with fixed digit ended by a proximal tooth nipple like with the *pilus dentilis* and a strong pyramidal tooth directed backward (fig. 27). Movable digit with from distal to proximal part two small teeth, the first being the larger, a stronger tooth, acute, and a smaller proximal one. Arthrodistal brush with very short seta *ar2* and brief seta *ar1* (65 μm), half length of the fixed digit that is about 110 μm long. Very small proximal lyriform organ *ly*. Palp (fig. 29): tarsi with a sinuate subterminal sensitive seta and a long terminal seta (95 μm) which correspond to chemioreceptors.

Etymology. – Reference to the character of the non-plumose setae.

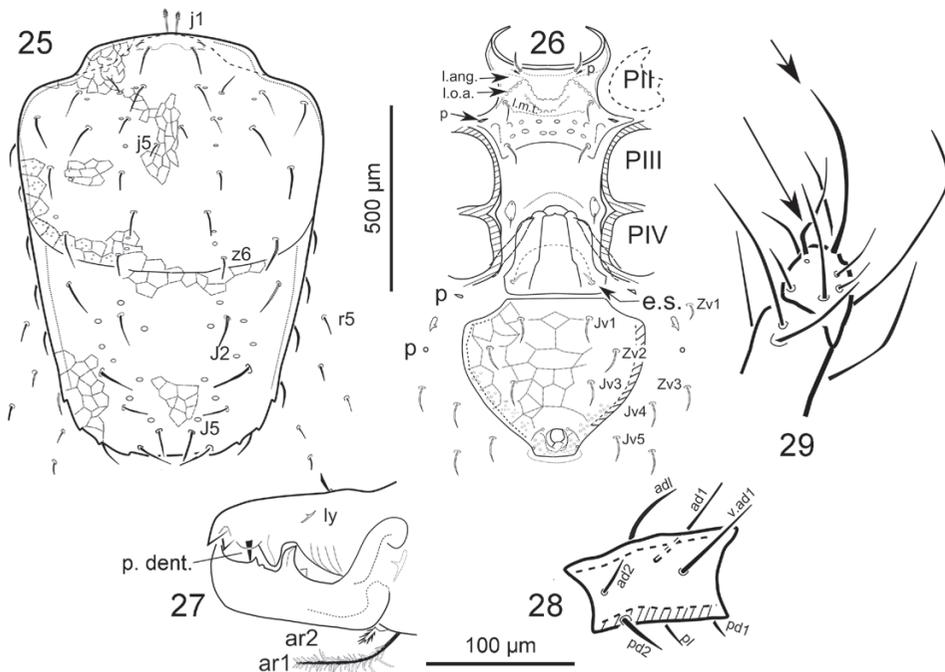


Fig. 25-29. – *Macrocheles simplisetosus* n. sp., ♀. – 25, Dorsum. – 26, Venter. – 27, Chelicera, lateral view. – 28, Genu IV, lateral view. – 29, Right palp, distal end, ventral view.

Differential diagnosis. – This species cannot be confused with the other species described from Mexico by the typical shape of the ventrianal shield, the pattern of the sternal shield, and the seven setae of the genua IV.

***Macrocheles neomexicanus* Arriaga & Bertrand, n. sp.** (fig. 30-33)

HOLOTYPE: ♀, Xalapa (19°31'32"N - 96°55'23"W), 1400 m, *A. Arriaga col.*, urban vegetation, VI.2012, host: *Onthophagus incensus* Say, 1835 (UNAM).

PARATYPE: 1 ♀, *idem* holotype (UNAM).

Description of the female.

Idiosoma. Fig. 30. Dorsal length 650-700 µm, width 370-425 µm at level of humeral angles. Dorsal shield with large reticular pattern, disappearing in the central zone in the anterior part of the shield notably between *j6* and *j4*. Twenty eight pairs of dorsal setae on the shield, with *j4*, *s1*, *s3*, *r2*, *S1*, *Z4* plumose distally, *r2* long (more than 125 µm), plumose setae longer than simple setae in the anterior part of the shield, in the posterior half, setae *J2* and *Z4* short, but longer than peripheral setae *S2* to *S5* and than *Z5*. Setae *j1* simple. Setae *z1* short, and the anterior lyrifissure is visible. Dorsal shield with indistinct procurved line.

Ventral view. Fig. 31. Tritosternum rather short (125 µm long). Sternal shield 175 µm long, 123 µm wide, poorly ornamented with solely *l.o.a.* and *l.ang.* central part densely punctate. Central part finely punctate, very similar to *M. mexicanus*. Metasternal shields rather large with the setae *st4* and a pore at the level of the *PIII*. Epigynal and sternal shields well separate from each other, the distance between these shields about 180 µm, the epigynal shield very close to the ventrianal. On each side the epigynal seta inserted near the corner. Ventrianal shield elongate (220 µm long, and 185-190 µm in maximal width, 100-110 µm for the anterior end), with the usual setae, the anterior pair being the shortest. Near the post coxal seta *Zv1*, on soft integument, the post coxal pore visible.

Gnathosoma. Fig. 33. Chelicerae similar to that of *M. mexicanus* with a short cheliceral brush shorter than the half of the mobile digit. Epistome classic for the genus, with bifid and finely ciliate central branch.

Sacculus foemineus. Fig. 32. Typical with a short spermiductus opening in a tiny vesicle.

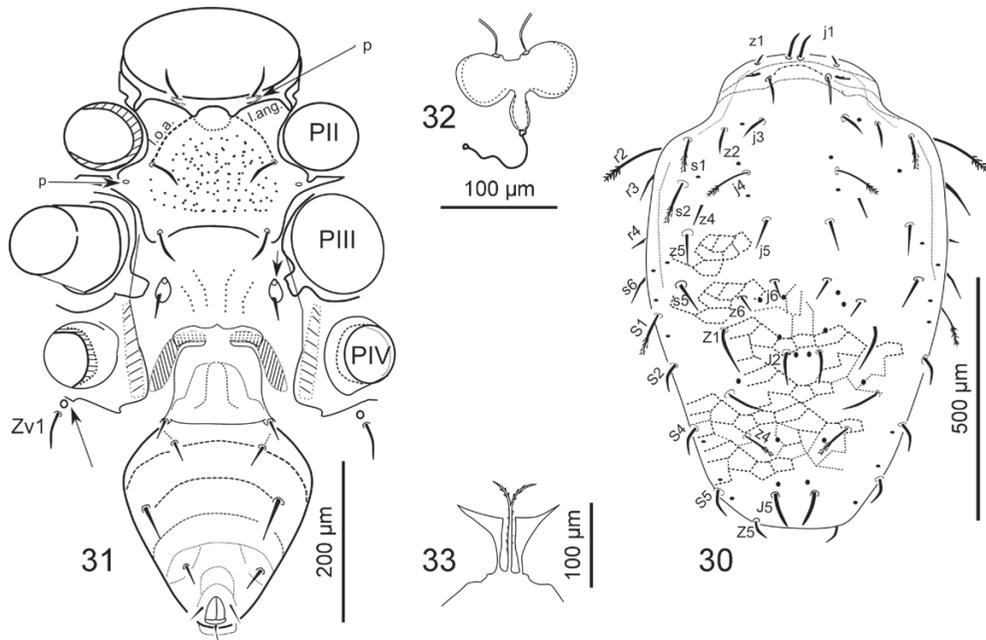


Fig. 30-33. – *Macrocheles neomexicanus* n. sp., ♀. – 30, Dorsal shield. – 31, Venter. – 32, Sacculus foemineus. – 33, Epistome.

Etymology. – In reference to the morphologically close species *M. mexicanus*.

Differential diagnosis. – The characters to differentiate this species from *Macrocheles mexicanus* Evans & Hyatt, 1963, are essentially in dorsal view: the character “pilose” or “simple” of setae (*S5*, *Z4* are pilose in *M. mexicanus*); the relative length of setae (*J5* is long in *M. neomexicanus*, short and simple in *M. mexicanus*); the ornamentation of the ventrianal shield (symmetrical and regular in *M. neomexicanus*); *l.o.a.* (visible in *M. neomexicanus* on the sternal shield vs. obsolescent in *M. mexicanus*).

***Macrocheles perciliatus* Arriaga & Bertrand, n. sp.** (fig. 34-36)

HOLOTYPE: ♀, Sierra Negra, Cd. Serdan, Puebla (18°59'25.9"N - 97°24'26"W), 2766 m, *A. Arriaga col.*, *Pinus* and *Cupressus* forest, VI.2012, host: *Copris armatus* Harold, 1869 (UNAM).

PARATYPE: 1 ♀, *idem* holotype (UNAM).

Description of the female.

Idiosoma. Fig. 34. Large species about 1000 µm long vs. 600-700 µm wide of the dorsal shield. Dorsal shield elongated, remarkable distance between setae *j2* that are shorter, and *j3*, that are longer, distance *j2-j3* longer than distance *j3-j3*. Frontal edge of the dorsal shield ended by setae *j1*, pilose distally. Anterior pore between *z1* and *j2* well visible and elongated. Dorsal shield ornamented with large polygonal pattern vanished centrally. Procurved line visible. Anterior setae *r2*, *r3*, *s4*, *s5* distally pilose. Dorsal rows *j2* to *j6* short and simple, *j5* and *j6* being the shortest. Posterad to the procurved line, *J2* are simple and short, *Z1-Z5*, *S2-S5* pilose.

Ventral view. Fig. 35. Sternal shield is 235 µm long medially, and 170 µm wide between the coxae II. The interval between setae *st2* is short, less than 140 µm, and *l.m.t.* is also shortened. Median line *l.o.p.* interrupted medially; median pores visible, the distance between them quite identical to the distance of *st3*. Epigynal and sternal shield shortly separated by soft integument, large metasternal plates very near the sternal shield. Epigynal shield wider than long (180 µm long and 245 µm wide). Ventrianal shield wider than long (490-500 µm wide, 370 µm long, length of the anterior edge only 220 µm).

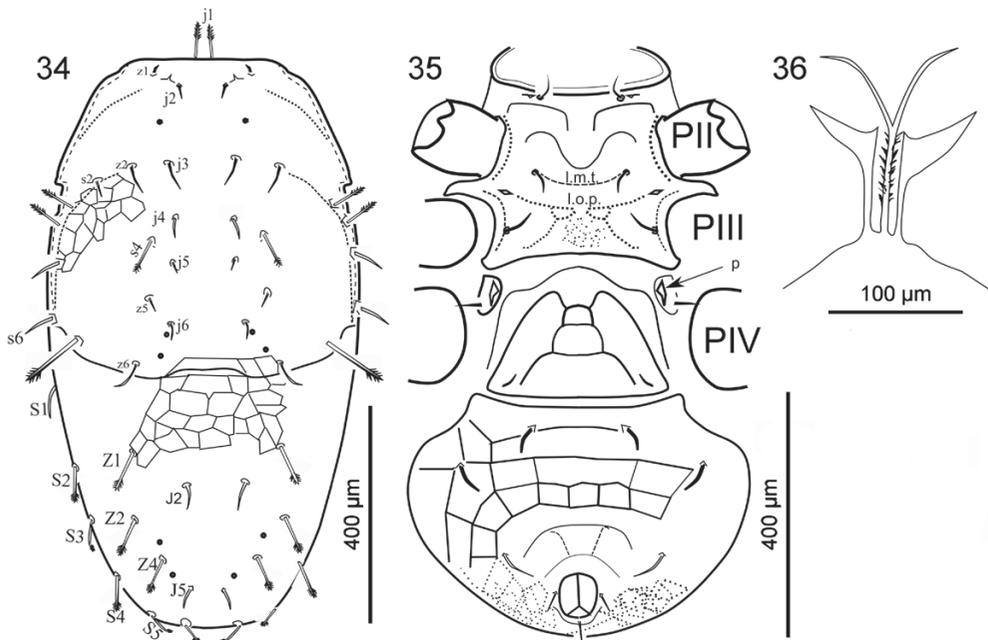


Fig. 34-36. – *Macrocheles perciliatus* n. sp., ♀. – 34, Dorsal shield. – 35, Venter. – 36, Epistome.

Gnathosoma. Chelicerae as for the genus, strong (65 µm thick) with strong mobile digit (95 µm long) and long arthrodial brush (*ar1*: 73 µm long). Epistome (fig. 36) with medial branch ciliate beneath the division into two glabrous branches. Tarsi I long (177 µm long) with long lateral setae (65-70 µm) and terminal seta (80 µm long) contrarily to the rather short terminal seta on palp tarsi (41 µm), if compared with *M. simplisetosus* n. sp. (92 µm long).

Etymology. – In reference to the character “ciliate” of the dorsal setae.

Differential diagnosis. – This species is characterized by the shape of the dorsal setae, plumose in *z-Z*, and *s-S* and simple in *j-J* series. Ventrally the shape of the ventrianal shield is characteristic as the sculpture of the sternal shield.

Macrocheles muscaedomesticae (Scopoli, 1772)

Material examined. – Xalapa (19°31'32"N - 96°55'23"W), 1400 m, *A. Arriaga col.*, urban vegetation, VI.2012, hosted by *Onthophagus incensus* Say, 1835.

This species is a cosmopolitan species and specialized on flies, *Musca domestica* Linnaeus, 1758. We also often collected it on the other cosmopolitan common host *Stomoxys calcitrans* (Linnaeus, 1758), the stable fly, from many part of world. It was already collected from Mexico (MÉNDEZ-OLIVÓ, 1968).

DISCUSSION

Among the species collected on large beetles, the *dimidiatus* group is well represented. This group of species needs special attention: 1) because in the current knowledge of the American fauna, the species group is an American endemic and having followed the dung beetles during the long period of the colonization of Central and South America by mammals (KRANTZ, 2007); and 2) because above 2000 m, notwithstanding the absence, due to the altitude of the supposed preferential host, the genus *Phanaeus*, it constitutes a large part of the species and of the individuals. These large mites were found associated with large beetles, on the genus *Copris* or Geotrupinae (*Halffterius* Zunino, 1984) sharing the analogous digger behavior with the phanaeine species, and neglecting apparently the smaller potential hosts, and the “non-digger species”. Their “concentration” on these hosts, trapped during the favorable season for beetles, corresponds to the single annual peak of activity of the Mexican beetles above 3000 m of altitude, whereas several peaks have been demonstrated at lower altitude (*i. e.* *Halffterius rufoclavatus*) (TROTТА-MOREU *et al.*, 2007). Undoubtedly, the coprophilous macrochelids exploit the seasonal peak of these most attractive carriers (TROTТА-MOREU *et al.*, 2007), and profit of the attractive and available hosts (GLIDA *et al.*, 2003).

We noted too the presence of “cosmopolitan” species. This conjunction could be consecutive to two main causes.

– Since a long time, the cosmopolitan species are specialized on unique or few cosmopolitan hosts: *i. e.* *Macrocheles muscaedomesticae* Scopoli, 1772, and followed the host’s distribution. Note that *Musca domestica* is thought having expended its territory since Pleistocene and undoubtedly originated from Asia (LEGNER & MCCOY, 1966; MARQUEZ *et al.*, 2003).

– The cosmopolitan fimicolous or coprophilous species have been widely spread by the pastoral activities throughout the historic times: macrochelids may have followed the increasing of the anthropization.

In Americas, the later condition can be called “trivial post-Colombian colonization”: it could ease to explain the presence of some worldwide distributed species. Opportunistic or specialized species were previously described from European countries (without any presumption

of their origin!); *Macrocheles insignitus* Berlese, 1918, was historically reported from Maryland on ceratopogonids (GROGAN, 1977); *Macrocheles merdarius* (Berlese, 1889), a common European species, and *Macrocheles penicilliger* (Berlese, 1904) which could be associated to the cosmopolitan host *Trox scaber* (Linnaeus, 1767) (BROWN, 1966), were reported from Mexico (QUINTERO *et al.*, 2001), as of course *M. muscaedomesticae*, following its preferential host in the conquest of all the continents.

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