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# A new species-group with new species of the genus *Lasioseius* (Acari: Mesostigmata: Blattisociidae) associated with Neotropical hispine beetles in furred leaves of *Heliconia*

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## ABSTRACT

A new species-group of *Lasioseius* is described from adults and immatures of four newly described and one undescribed species associated with hispine beetles of the genera *Cephaloleia* and *Chelobasis* and other gamasine mites in the furred leaf habitat of *Heliconia* and related Zingiberales plants. The species-group presents a suite of apomorphic attributes placing it in the subgenus *L.* (*Lasioseius*). Adults and immatures were found moving freely on and off the beetles when the latter were exposed from their habitat. Larviparity is indicated by adult females gravid with fully developed larvae. Limited data suggest considerable host specificity between mites and their beetle hosts, indicating that there may be a vast diversity of these mites associated with hundreds of species of hispine beetles in the Neotropical Region. Keys are provided to currently accepted species-groups of *Lasioseius* and to the species within the new species-group.

**Keywords** Gamasina, Phytoseioidea, Imatidiini/Cephaloleiini, Zingiberales

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## Introduction

A remarkable diversity of mesostigmatic mites have been found to coexist with Neotropical hispine beetles in furred leaves of *Heliconia* and related plants. Some represent a newly described family (Lindquist & Moraza 2014), and others, new genera of Melicharidae (Moraza & Lindquist 2015, 2016). Here, we describe a new species-group of the blattisociid genus *Lasioseius* based on adults and immatures of four newly described and one undescribed species associated with hispine beetles of the genera *Cephaloleia* and *Chelobasis* in Costa Rica. Beetles of these Neotropical genera often coexist and undergo their life histories together in the same furred leaves of *Heliconia* and other Zingiberales plants (Staines 2009, Schmitt & Frank 2013, Staines & Garcia-Robledo 2014). The associations of these mites and beetles are currently being studied by Garcia-Robledo and colleagues (e.g., Garcia-Robledo *et al.* 2013, 2015), and a need for descriptions, names, and identification keys for these mites is relevant to those studies. Although included in the key, one species is left undescribed, due to the available exemplars at hand being too few in number and in poor morphological condition. However, the description of the species-group accounts for its attributes.

*Lasioseius* is the most diverse and species-rich genus in the family Blattisociidae. Keys to 156 species were presented by Christian & Karg (2006), and some 195 species were

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recorded in the catalogue by Moraes *et al.* (2016). Yet, the real biodiversity of this genus remains unaccounted for. For example, based on the findings of the Arthropods of La Selva (ALAS) study in the 1990's, approximately 50 species of *Lasioseius* were collected, with slide preparations made of adults, from a wide variety of habitats in just one small area of lowland tropical rainforest in Costa Rica (Lindquist 2001). Most to nearly all of those species, other than those belonging to the species-group being described here, remain undescribed. Moreover, many of those species present remarkably distinctive morphological structures of the gnathosoma and legs, indicating specialized ways of life.

## Materials and methods

Living mites were discernible by hand lens on the hispine beetles when first removed from the unfurled leaves of the host plants at the La Selva Biological Station, Heredia Province, Costa Rica in 1994. Methods of collecting and observing living mites at the ALAS laboratory were the same as presented in our previous paper concerning these beetles and their associated mites (Moraza & Lindquist 2015). Mites along with their beetle hosts were preserved in 80% ethanol, with the mites subsequently mounted into Hoyer's medium on microslides and sealed with Glpt insulating varnish. Taxonomic concepts of the superfamilies of mesostigmatic mites, especially the Phytoseioidea and its component families, and the genera of Blattisociidae, follow those of Lindquist *et al.* (2009) and Lindquist and Moraza (2010, 2012). Morphological observations, measurements, and illustrations were made using compound microscopes equipped with differential interference contrast and phase contrast optical systems, drawing tubes and stage-calibrated eyepiece micrometers.

Setal notation for the idiosoma follows Lindquist & Evans (1965) as modified slightly by Lindquist (1994). Measurements of structures are given in micrometers ( $\mu\text{m}$ ), indicating the ranges among specimens measured. Dorsal shield lengths are midline from anterior margin anterior to bases of vertex setae *j1* to caudal margin posterior to bases of clunal setae *J5*. Lengths of ventral idiosomatic shields are midline, from the anterior margin to posterior edge of each structure, including the hyaline anterior extension of the epigynal shield and the posterior cribrum of the ventrianal shield. Sternal and sternitigenital shield widths are narrowest, between bases of legs II for the former, and sequentially between bases of legs II, III, IV for the latter. Notation for leg and palpal setation follows Evans (1963, 1964, 1969). Leg lengths are from base of the coxa to apex of the tarsus, excluding the pretarsus. As the forms of the leg segments and their chaetotaxy and form of setae are so similar among the species being described, complete illustrations are provided for the legs of only one species, but figures are provided for the tarsi of legs II and IV for each species. Distinction of pore-like structures on the idiosomal integument as either poroids (lyrifissures) or glandular openings (solenostomes), as distinguished morphologically by Athias-Henriot (1969, 1971b, 1975) and physiologically by Krantz & Redmond (1987), is presented stylistically in the illustrations; gland pores are shown in circular form, while poroids are shown in elliptical form. Notation for pore-like structures of the peritrematal region follows that of Johnston & Moraza (1991).

Identifications of the hispine beetles associated with the mites were made by Project ALAS parataxonomists Danilo Brenes and Ronald Vargas, or by Derek Johnson (see acknowledgments). Some of the identities of the beetles (and background plant substrate) presented for each mite species are not in accord with current molecular studies, which indicate that there is a complex of multiple cryptic species with similar morphology in the La Selva area (Carlos Garcia-Robledo, personal communications, June 2014). These issues are treated, as necessary, in a paragraph on host identifications following description of each mite species.

The holotypes and some of the paratypes of the new species are deposited in the Instituto Nacional de Biodiversidad (INBio) of Costa Rica, Santo Domingo de Heredia; additional paratypes of each new species are deposited in the Canadian National Collection of Insects and Arachnids (CNCI), Science & Technology Branch, Agriculture & Agri-Food Canada, Ottawa, and the Museum of Zoology, University of Navarra (MZUNAV), Pamplona, Spain.

## Systematics

Both subgenera and species-groups have been proposed by various authors for the genus *Lasioseius*. Five subgenera were proposed by Christian & Karg (2006), four of which were found to be based on unreliable homoplastic attributes, as reviewed by Moraza & Lindquist (2011), and synonymized under the nominate subgenus. Their subgenus *Lasioseius* (*Endopodalius*), for which Lindquist (1964) and Lindquist & Evans (1965) earlier had recognized the *scutalis* species-group, is well-based apomorphically, and constitutes one of the two subgenera of *Lasioseius* recognized by Moraza & Lindquist (2011) and included in their key to genera and subgenera of the subfamily Blattisociinae. Within the subgenus *Lasioseius* (*Lasioseius*) *sensu* Moraza & Lindquist, three species-groups have been proposed by various authors, based to some extent on distinctive apomorphic attributes. The *phytoseioides*-group was initially recognized by Lindquist (1964) and further characterized by de Moraes *et al.* (2015) to include about twenty named species, many of which remain inadequately described. The *porulosus*-group was first recognized by Walter & Lindquist (1997) to include seven species. The *floridensis*-group was proposed by Mineiro *et al.* (2009) and includes four described species. In contrast, Christian & Karg (2006) recognized five "species-complexes", all of which are based on shades of differences of adult female structures, rather than on apomorphic attributes, e.g., whether the metapodal plates are enlarged to some extent or not; whether the ventrianal shield has four versus five or six setae other than the circumanal setae; whether leg I is shorter or longer than the idiosoma; whether some of the setae on tarsus IV are long enough to be considered macrosetae; and whether the forms of dorsal shield setae are distinctively tricarinate or not. As a result, their species-complexes suffer from the same problems as their subgenera, by including species which could be grouped more meaningfully on the basis of other, more clearly apomorphic attributes, and are not recognized here. For example, *Lasioseius americanus* Chant, 1963, placed in their *inguinalis*-complex of their subgenus *Lasioseius*, shares other, more distinctively apomorphic attributes that are useful in redefining their subgenus *Endopodalius*, including the unusual convex form of the posterior margin of sternal shield and the peculiarly penicillate shape of setae Z4 or Z5. Based on those and other attributes, *L. americanus* was designated as a member of the *scutalis* species-group by Lindquist (1964) and Lindquist & Evans (1965), and is a member of the subgenus *L. (Endopodalius)* *sensu* Moraza & Lindquist (2011).

Here, we propose a new species-group, the *cassidini*-group, within the subgenus *Lasioseius* (*Lasioseius*), that is apomorphically and ecologically distinctive in its association with hispine beetles in rolled leaves of *Heliconia* and other Zingiberales plants. We include it in a tentative key to species-groups that we currently recognize within the subgenus *L. (Lasioseius)*, preceding a key to species of the *cassidini*-group itself. Although based at least in part on apomorphic attributes, such species-groups may represent different hierarchic levels among the many species in the subgenus, such that one group may eventually be shown to be a subset of another. Unquestionably, further studies will recognize other species-groups or even additional subgenera, for which names such as *Aceoseius* Sellnick (1941) and *Hyattella* Krantz (1962) may already be available.

**Diagnosis, *Lasioseius cassidini* species-group.** Dorsal shield setae collectively simple, imperceptibly or vestigially tricarinate (homoplasy); setae *j*2 aligned transversely with paravertical poroids *idj*1 nearly at level of setae *j*1 and *z*1 (apomorphy); humeral setae *r*3 erect, relative to adjacent setae *r*2 and *r*4 (plesiomorphy). Palptarsus with a hyaline anterolateral flap extending from base of apotele to base of cluster of apical setae (apomorphy). Peritremes short of reaching vertex area, extending at most to level slightly beyond setae *s*1 (homoplasy). Male subcapitulum dimorphic in having a pair of short fimbriated processes medial to and separate from corniculi (homoplasy).

## Description of species group

With the diagnostic attributes of genus and subgenus *Lasioseius* (*Lasioseius*) *sensu* Moraza & Lindquist (2011), but restricted and augmented as follows:

**Idiosomatic dorsum** — Dorsal shield setae collectively simple (imperceptibly or vestigially tricarinate), more elongated posterior setae sometimes slightly, sparsely barbed; setae *j2* aligned transversely with paravertical poroids *idj1*, nearly at level of setae *j1* and *z1*; dorsal shield holotrichous, setae *z3* present, humeral setae *r3* erect, *r5* on shield, *r6* on or off shield of females and *R1* on or off shield of males; idiosoma with setae *j1-j6*, *z1-z6*, *s1-s6*, *r2-r6*, *J1-J5*, *Z1-Z5*, *S1-S5*, *R1-R6* always present (seta in *R7* position designated as *ZV5*). Dorsal shield with complement of 23 pairs of discernible pore-like structures (10 podonotal, 13 opisthonotal), of which seven pairs (four podonotal, three opisthonotal) superficially appear secretory (gland pores) and 16 pairs (six podonotal, 10 opisthonotal) non-secretory (poroids).

**Idiosomatic venter** — Adult female. Tritosternum with laciniae pilose, their fused section and columnar base without elaborations. Presternal region lacking an unpaired platelet at base of tritosternum. Sternal shield entire, fully integrated with endopodal extensions between legs I-II and II-III, with posterior margin straight or slightly concave; apex of endopodal extension between legs I-II with gland pore *gbv*; shield with three pairs of setae (*st1-st3*) and two pairs of poroids (*iv1-iv2*); *st1* and *iv1* sometimes inserted in a less sclerotized region of shield. Setae *st4* and poroids *iv3* on tiny metasternal platelets or on soft cuticle. Endopodal strips by legs III-IV slender, distant from sternal shield. Epigynal shield with broadly to narrowly rounded hyaline anterior margin barely or not overlapping posterior edge of sternal shield. Postgenital furrow with transverse strip of four narrow platelets. Ventrianal shield with circumanal setae and usually four pairs of ventral setae, or rarely three pairs if *JV1* on soft cuticle; anal opening relatively small; postanal seta clearly longer than paranal setae. Soft opisthogastric integument with two pairs of small, sometimes partly coalesced metapodal platelets, four or five pairs of setae (*ZV1*, *ZV3*, *ZV5*, *JV5*, sometimes *JV1*, *ZV4*), and three or four pairs of poroids, flanked by posteriormost two pairs of *R*-setae; setae *ZV4* sometimes absent, *JV4* always absent; glandular pores *gv3* on or off shield posterolateral to anal opening. Minor duct of sperm access system without a distant secondary enlargement.

Adult male. Base of tritosternum biarticulate; other aspects of tritosternum and presternal region as in female, and with separate sternitigenital, ventrianal, peritrematal shields. Ventrianal shield capturing metapodal sigillae anterolaterally, with circumanal setae and usually seven pairs of ventral setae (rarely six pairs if *JV5* on soft cuticle), and two or three pairs of poroids; glandular pores *gv3* on margin of shield at level slightly behind posterior margin of anal opening; aspects of circumanal setae, anal opening and cribrum as in female; poroids *ivo3* on or off shield laterad setae *ZV3*. Soft opisthogastric integument with one (*ZV4*) or two pairs of setae (*ZV5* present or absent, *JV4* absent), and one or two pairs of poroids; setae *ZV5* often aligned with posterior flanking *R*-setae, so as to resemble *R7*. Postanal furrow present.

**Lateropeltidal region** — Peritrematal shields fused with dorsal shield at level of setae *s1* in females and level of *r2-r3* in males; pore-like elements *ips*, *gp3*, *ip3* on peritrematal shield posterior to stigma; peritremes well developed but reaching at most to level slightly beyond setae *s1*, well short of paravertical setae *z1*. Exopodal strip continuous and separate from peritrematal plate alongside coxae II-III, its extension between coxae I and II nearly touching apex of endopodal extension from sternal or sternitigenital shield.

**Gnathosoma** — Gnathotectum anterior margin denticulate, either truncate or with three branches of similar length. Chelicerae with movable digit usually tridentate in female, unidentate in male, with weakly fimbriated basal sheath; fixed digit with offset small subapical tooth, a row of 7-28 fine teeth of similar form along entire masticatory surface, and minute pilus

dentilis; dorsal seta simple; lateral hyaline rim along paraxial face of fixed digit smooth, lacking serration at level of base of movable digit. Male spermatodactyl digitiform, projecting freely, generally anteroventrally from movable chela, not elaborated in shape. Corniculi normal in hornlike form, entire, well sclerotized and separated from base to apex, lacking a paraxial process basally. Internal malae somewhat longer than corniculi, divided subapically into a shorter, lateral, fimbriated, bluntly pointed extension and a longer, medial, smooth, slender, sharply pointed one. Adult males with pair of short fimbriated processes medially beside corniculi, separate from internal malae. Subcapitulum with seven moderately wide, transverse rows of deutosternal denticles, the anterior six rows connected by lateral edges, seventh row free. Subcapitular setae simple in form, with *hp1* sometimes attenuated. Palpi normal in form and setation as described for Gamasina by Evans (1964); internal setae *al* of femur and *al-1*, *al-2* of genu strongly spatulate distally. Apical anterolateral margin of palptrochanter with or without one to several spinelike structures. Palptarsus with hyaline anterolateral flap extending from base of apotele to base of cluster of apical setae (Fig. 4G).

**Legs** — Leg I not elongated (about as long as dorsal shield); tarsus I with biarticulated pretarsus with normally developed claws. Leg IV approximately as long as dorsal shield, and with no setae differentiated as macrosetae by being more erect and longer than tibia. Tarsi II-IV without elongated whiplike setae; apical setal processes (*d-1*) shorter or nearly as long as length of pretarsus to base of claws; ventral setae (*v-1*) similar in form, or *av-1* longer and thicker than *pv-1*; seta *md* slightly more slender and attenuated, and slightly the longest of tarsal setae, or subequally so with (*d-2*); ventral apical process smoothly triangular, tapered to a blunt tip or with a wide, untapered, serrated apical margin; pretarsi with paracymbria symmetrically developed, or with anterior one asymmetrically larger on tarsi III and IV. Complement of setae on segments of legs I to IV holotrichous for genus *Lasioseius* as presented by Lindquist and Evans (1965); chaetotactic formulae for genera I-II-III-IV: (2 – 3/2, 3/1 – 2) (2 – 3/1, 2/1 – 2) (2 – 2/1, 2/1 – 1) (2 – 2/1, 3/0 – 1); tibiae: (2 – 3/2, 3/1 – 2) (2 – 2/1, 2/1 – 2) (2 – 1/1, 2/1 – 1) (2 – 1/1, 3/1 – 2). Legs II-IV of males sometimes with dimorphism evident in form of particular setae.

**Immature instars** — Descriptive notes for the larva and protonymph are based on one or two specimens of only one species, so they cannot be assumed to hold for members of the species-group as a whole. They are presented in the description of *L. serripes*.

**Remarks** — Although based on material representing only five species, four of which are described here, this species-group is anticipated to include a multitude of species, in view of evident preferences among host beetles and the tremendous diversity of these beetles in the Neotropics and other tropical regions.

**Morphological aspects** — Unless overlooked among some other members of the genus *Lasioseius* and other genera of Blattisociidae, the hyaline flap associated with the palptarsal apotele seems independently derivative to the new species-group. A similar structure, termed a ‘hyaline scale’, is found at the base of the palptarsal apotele, and characteristic of all members of the family Veigaiidae (Lindquist *et al.* 2009). It does not extend as far apically along the anterior edge of the palptarsus in veigaiids. A much smaller structure, termed a ‘small hyaline lobe’ has been noted as present or absent at the base of the palptarsal apotele among species of the melicharine genera *Proctolaelaps* and *Mucroseius* (Lindquist & Hunter 1965, Lindquist & Wu 1991).

Although characteristic of males of the new species-group, the presence of a pair of short fimbriated processes medially beside the corniculi, separate from the internal malae, has been noted and illustrated previously (Lindquist 1971) for the male of an unrelated species of *Lasioseius*, *L. corticeus* Lindquist. Therefore, this dimorphism is either homoplasious or apomorphic at a higher group level within the genus *Lasioseius*.

In contrast to the diversity of shapes evident among many other species of *Lasioseius* (e.g. Walter & Lindquist 1989, 1997), the forms of male spermatodactyls and female spermathecae are notably similar among the described members of this species-group. This may argue for a relatively recent diversification of species in this group or for other behavioral aspects that prevent species introgressions among coexistent species.

Within the *cassidini*-group, the absence or presence and number of spinelike structures on the apical anterolateral margin of the palptrochanter is a newly-noted, specific attribute. A few SEM images indicate the presence of such structures among some other species of *Lasioseius* (e.g., figs. 19E, G of Walter & Lindquist 1989), but their diagnostic usefulness in other groups of the genus is problematical.

Two aspects of leg IV of the protonymph, for which we have a single specimen of just one species, merit attention as possible species-group apomorphic attributes. First, the tarsus of leg IV differs from that of legs II and III in having seta *av-1* distinctively erect, longer and slightly thicker than all other tarsal setae (Fig. 12G). Except for the one undescribed species at hand, this is unlike its form on tarsus IV of the adult (no deutonymphs of this species were available for study), on which it is similar to that of tarsi II and III (Figs. 13C, 14B). As noted in the key to species, the adult female of the undescribed form at hand has seta *av-1* erect, and longer and thicker than other adjacent setae, though not less adjacent ones of the tarsus (Fig. 12H). This may be an ontogenetic retention of the aforementioned protonymphal condition of tarsus IV to adulthood. Such distinctiveness of protonymphal tarsus IV has not been noted for any other species of *Lasioseius* or other genera of the Blattisociidae, and we are not aware of something similar to this among other families of Gamasina. Second, the rudimentary presence of seta *av-1* on femur IV and the full presence of seta *pl-1* on genu IV are ontogenetic accelerations of setae that are typically first expressed in the deutonymph (Evans 1963). Although ontogenetic leg chaetotactic data are sparse for other species of the genus *Lasioseius* (e.g., Lindquist 1971, Britto *et al.* 2011) and for the family Blattisociidae as a whole (e.g., Lindquist 2003, Lindquist & Moraza 2016), such acceleration of usually deutonymphal setae has not been noted for other blattisociids (EEL, personal observations).

Increased descriptive and illustrative details are given to the form of setae on tarsi II to IV of members of the *cassidini*-group. Based on our experience in dealing with forms that are similar to previously described species, with less detailed descriptions and illustrations, we are often left uncertain as to their identities. Moreover, as species of the *cassidini*-group are to be involved in further studies at a more refined level, using molecular approaches to analyze for haplotypes and dietary preferences of the mesostigmatic mites associated with the two genera of rolled-leaf hispine beetles, we hope that a more detailed morphological approach will approximate those further findings.

### Key to species-groups of subgenus *Lasioseius* (*Lasioseius*): females.

For a key to the genus and subgenera of *Lasioseius*, see the key to the world genera and subgenera of the subfamily Blattisociinae by Moraza and Lindquist (2011).

1. Dorsal shield lacking vertical (*j1*) and paravertical (*z1*) setae, leaving setae *j2* as anteromedial-most pair, slightly behind level of paravertical poroids *idj1*; posterior region of dorsal shield with 10 or 11 pairs of setae, each of *J*, *Z*, *S* series with less than five pairs of setae; peritremes with anterior apices curving posteromedially above level of setae *j2*; female ventrianal shield with six pairs of opisthogastric setae; antiaxial face of fixed cheliceral digit with a subapical pointed process. . . . . *phytoseioides*-group *sensu* Lindquist, 1964 and de Moraes *et al.*, 2015 — Dorsal shield with setae *j1* and usually *z1* present, inserted at transverse level of poroids *idj1* anterior to setae *j2*; posterior region of dorsal shield with 13 to 15 pairs of setae, at least the *Z*-series and usually all series complete with five pairs of setae each; peritremes with anterior apices not curving posteromedially where ending at level beside or short of setae *z1*; female ventrianal shield with two to six pairs of opisthogastric setae; antiaxial face of fixed cheliceral

- digit usually lacking a subapical process ..... 2
2. Dorsal shield flanked by only two or three pairs of setae (marginals *r5*, *R1* and ventrolateral *ZV5*) on soft cuticle; dorsal shield with 16 pairs of setae, post-humeral pair *r4* absent; tritosternum with laciniae fused for more than half their length; genua of legs I, II, III with 12, 9 or 10, 7 or 8 setae, respectively, each lacking one or two ventral setae .....  
 ..... *porulosus*-group *sensu* Walter and Lindquist, 1997  
 — Dorsal shield flanked by five to twelve pairs of setae (elements of marginals *r5-6*, *R1-6*, submarginals *UR*, and ventrolateral *ZV5*) on soft cuticle; dorsal shield with 18 to 23 pairs of setae, usually including post-humeral pair *r4*; tritosternum with laciniae free for usually more than half their length; genua of legs I, II, III usually with 13, 11, 9 setae, respectively, each usually including holotrichous set of 3, 2, 2 ventral setae ..... 3
3. Dorsal shield setae collectively simple (imperceptibly or vestigially tricarinate); setae *j2* nearly aligned transversely with *j1* and *z1*; peritremes reach at most to level slightly beyond setae *s1* (but not to paravertical setae *z1*); palptarsus with hyaline anterolateral flap extending from base of apotele to base of cluster of apical setae ..... *cassidini*-group  
 — Dorsal shield setae variable in form, but with at least setae *j1*, *r3*, *Z5* usually tricarinate or tricarinate-pectinate; setae *j2* inserted clearly behind transverse level of setae *j1* and *z1*; peritremes variable in extent, but usually reaching to insertions of paravertical setae *z1*, anteriorly beyond setae *s1*; palptarsus lacking hyaline flap near base of apotele ..... 4
4. Dorsal shield with post-humeral seta *r4* short, simple, similar to *r2*, and not more than half as long as tricarinate seta *s4* neighboring it medially; most dorsal setae tricarinate and moderately long, nearly as long as longitudinal intervals between their bases; anterior pair of sternal setae on weakly sclerotized presternal area, just before anterior margin of sternal shield; sternal shield with anteromedial patch of reticula; tarsus II with one midlateral seta, *pl-2*, elongated, reaching nearly to base of pretarsus ..... *floridensis*-group *sensu* Mineiro *et al.*, 2009  
 — Dorsal shield with seta *r4* usually similar in weakly to strongly tricarinate form and over half as long as adjacent seta *s4*; dorsal setae variable in form and lengths; anterior pair of sternal setae on or off well sclerotized surface of sternal shield; sternal shield variably ornamented; tarsus II with or without one or two attenuated setae .....  
 ..... many other species and undescribed groups of subgenus *L. (Lasioseius)*

## Key to species of *Lasioseius cassidini* species-group: females.

1. Ventrianal shield with 3 pairs of ventral setae, *JV1* on soft cuticle (Fig. 5E); sternal shield reticulate over entire surface; setae *st4* and poroids *iv3* on soft cuticle (Fig. 5E); metapodal platelets connected or coalesced on each side (Fig. 5E); tarsi II-IV with ventroapical process truncate-spiculate apically (Figs 13G, 14B) ..... *L. serripes* **n. sp.**  
 — Ventrianal shield with 4 pairs of ventral setae, *JV1* on shield (Fig. 8D); sternal shield smooth, or weakly lineate along lateral margins; setae *st4* and usually poroids *iv3* on metasternal platelets; metapodal platelets separate on each side; tarsi II-IV with ventroapical process bluntly pointed, smooth apically (Figs 13H, 14A, C, D) ..... 2
2. Gnathotectum with three elongated tines (Fig. 8C); fixed chela with 9-13 teeth (Fig. 8E); smaller mites, dorsal shield length less than 470  $\mu\text{m}$  ..... *L. fuscina* **n. sp.**  
 — Gnathotectum with three short broad tines or irregularly truncate-serrate; fixed chela with 18-28 fine teeth (Fig. 10G); larger mites, dorsal shield length more than 530  $\mu\text{m}$  ..... 3
3. Setae *Z5*, *S5* thickened, blunt-tipped in distinction to other attenuated dorsal setae (Fig. 10A, B); gnathotectum with three short broad tines (Fig. 10D); poroids *iv3* and setae *st4* together on



slender metasternal platelets (Fig. 10C) ..... *L. duobtusiseta* n. sp.  
 — Setae *Z5*, *S5* not conspicuously thicker or blunter than other dorsal setae; gnathotectum truncate-serrate (Fig. 1D); poroids *iv3* alone on soft cuticle or with setae *st4* on slender metasternal platelets ..... 4

4. Sternal setae *st4* on tiny metasternal plates, leaving sternal poroids *iv3* on soft cuticle (Fig. 1C); sternal setae *st1* on weakly sclerotized presternal region (Fig. 1C); podonotal region of dorsal shield with 23 pairs of setae, including *r6*; tarsus IV with distal seta *av-1* ca 1.3 longer than *pv-1* and 2.5 times longer than slender setae (*l-1*) (Fig. 14A) ..... *L. cassidini* n. sp.  
 — Sternal poroids *iv3* with sternal setae *st4* on slender metasternal platelets (as in Fig. 8D); sternal setae *st1* on anterior margin of sternal shield; podonotal region of dorsal shield with 22 pairs of setae, *r6* on soft cuticle; tarsus IV with distal seta *av-1* enlarged, erect, 2.5 times longer than *pv-1* and 4 times longer than short, slender setae (*l-1*) (Fig. 12H) .....  
 ..... *Lasioseius* sp. (undescribed) ex *Chelobasis bicolor*

## Description of new species

### *Lasioseius cassidini* n. sp. (Figures 1, 2, 11A, 12C, 13A-B, 14A)

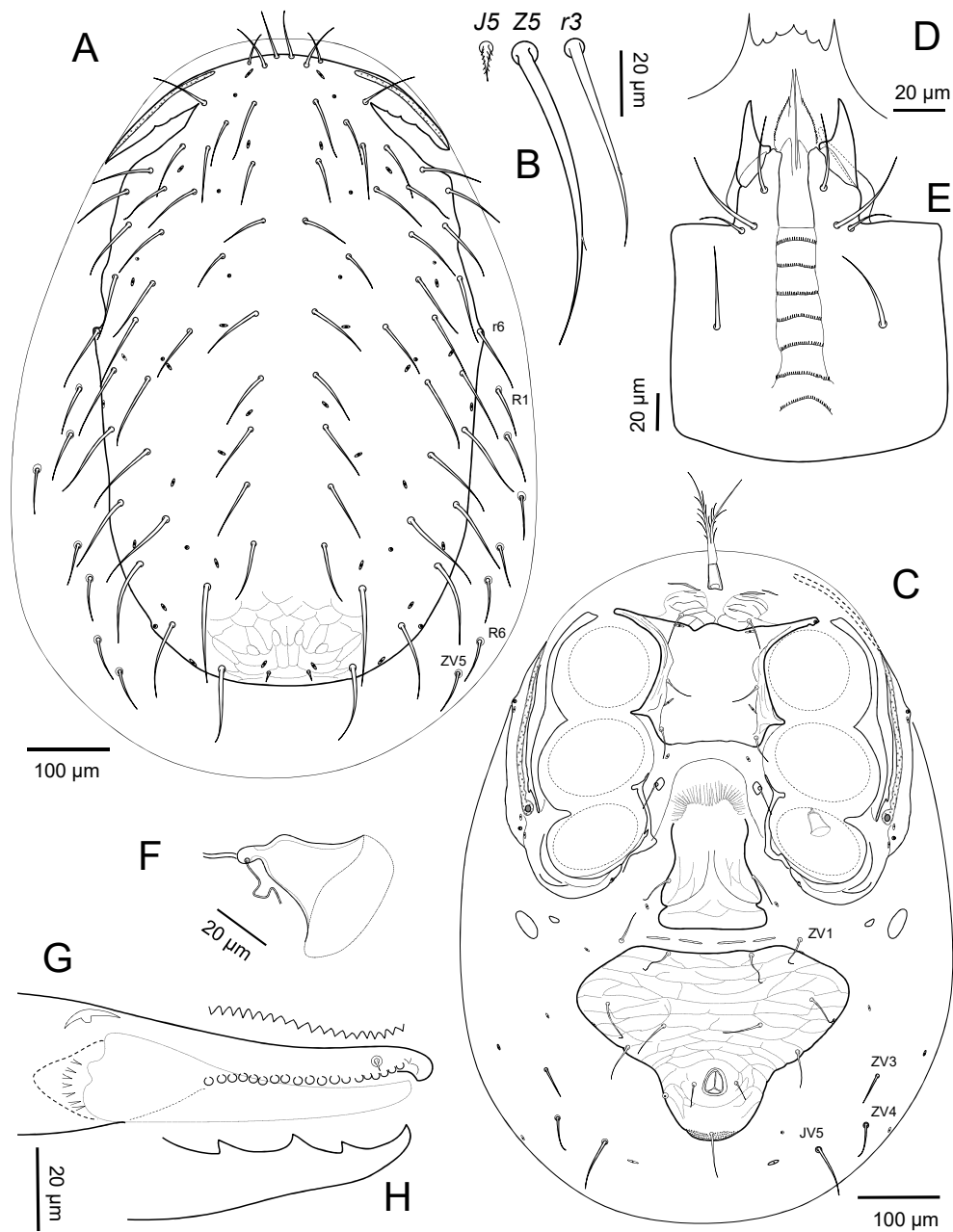
Zoobank: [EB77E489-1EB6-4120-9375-44E765ABEFF3](https://doi.org/10.21203/rs.3.rs-1111111/v1)

Diagnosis — Adult female: Sternal shield weakly lineate along lateral margins, smooth medially, its posterolateral corners not emarginated; poroids *iv3* alone, on soft cuticle, setae *st4* on tiny metasternal platelets; epigynal shield partially reticulated, its lateral margins concave, narrowed anterior to setae *st5*; ventrianal shield with posterolateral margins on either side of anus divergent anteriorly, and with four pairs of opisthogastric setae, *JVI* on shield; metapodal plates well separated on each side. Dorsal setae *r6* on edge of dorsal shield; *Z5*, *S5* attenuated like adjacent setae. Adult male: Dorsal shield setae *S5* dimorphically less attenuated. Sternitigenital shield incompletely reticulated, nearly smooth medially. Tibiae III-IV with setae (*v*) dimorphically spinelike, blunt; genu IV *av* similarly so. Adult attributes: Gnathotectum anterior margin truncate, irregularly denticulate. Fixed chela with file of ca 20 teeth in female, ca 18 in male. Sternal setae *st1* inserted in weakly sclerotized presternal region. Tarsi II-IV with ventral apical process bluntly pointed, smooth apically; tarsi II-III with seta *av-1* slightly longer than *pv-1*; pretarsi III-IV with anterior paradactylus asymmetrically elongate, twice as long as claws; tarsus IV with distal seta *av-1* clearly larger, thicker than adjacent setae.

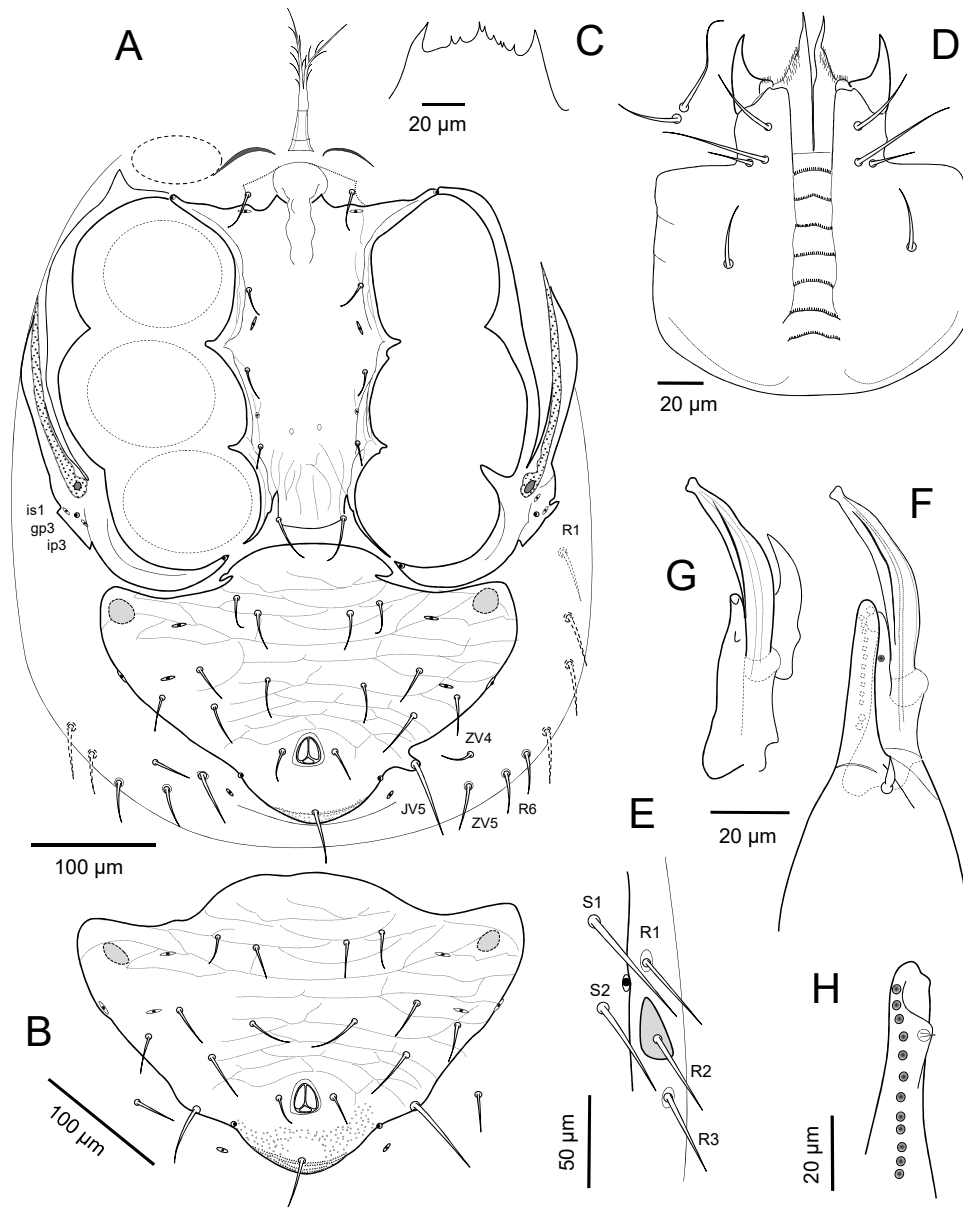
### Description

Idiosomatic dorsum — Adult female. Dorsal shield 703 – 757 long, 375 – 410 wide at level of *r3*, 428 – 477 wide at *r6* (n=9), lightly reticulated over entire surface, without puncta behind level of setae *Z4*; shield with 38 pairs of setae generally similar in size and acutely pointed form, *J1-J4* about as long or slightly longer than longitudinal intervals between their bases; *J5* minute, barbed (8 – 12): *j1*, *j2* (45 – 60), *j3* (67 – 76), *j4* (50 – 57), *j5* (56 – 62), *j6* (70 – 77), *z1* (37 – 42), *z2* (56 – 65), *z3* (60 – 68), *z4* (72 – 77), *z5* (52 – 62), *z6* (62 – 74); *s1* (58 – 75), *s2* (65 – 75), *s3* (70 – 75), *s4* (70 – 80), *s5* (82 – 92), *s6* (85 – 96), *r2* (62 – 74), *r3* erect (60 – 67), *r4* (75 – 80), *r5* (75 – 82), *r6* (70 – 79), *J1* (65 – 75), *J2* (68 – 77), *J3* (67 – 82), *J4* (70 – 75), *Z1*, *Z2* (92 – 103), *Z3* (100 – 112), *Z4* (107 – 122), *Z5* (93 – 110), *S1* (77 – 95), *S2*, *S3* (88 – 103), *S4* (97 – 110), *S5* (82 – 105). Lateral soft cuticle with seven pairs of smooth setae, including *R1-R3* (48 – 62), *R4-R6* (42 – 53) and *ZV5* (47 – 55) posteriorly (Figs. 1A, B, C).

Adult male. Dorsal shield 493 – 610 long, 315 – 342 wide at level of setae *r3*, 345 – 367 wide at *r6* (n = 8); shield ornamentation, complement of pore-like structures and setation as in female; posterolateral setae attenuated as in female. Setae *j1* (40 – 50), *j2* (35 – 47), *j3* (50 –



**Figure 1** *Lasioseius cassidini* n. sp. adult female: A – Idiosoma, dorsal view; B – Detail of denoted dorsal setae; C – Idiosoma, ventral view; D – Gnathotectum; E – Subcapitulum; F – Spermathecal structures; G – Fixed cheliceral digit in ventral view; H – movable cheliceral digit in partially lateral view.



**Figure 2** *Lasioseius cassidini* n. sp., adult male: A – Idiosoma, ventral view; B – Variant form of ventrianal shield; C – Gnathotectum; D – Subcapitulum and ventral setae of palptrochanter; E – Detail of denoted dorsal setae, showing R2 on variant platelet; F – Cheliceral digits and spermatodactyl, dorsal view; G – Cheliceral movable digit, spermatodactyl, and corniculi, dorsal view; H – Detail of fixed digit, ventral view.

60), *j*4 (38 – 45), *j*5 (43 – 47), *j*6 (53 – 62), *z*1 (28 – 38), *z*2, *z*3 (43 – 55), *z*4 (52 – 62), *z*5 (40 – 45), *z*6 (48 – 55), *s*1 (47 – 57), *s*2-*s*4 (50 – 65), *s*5, *s*6 (60 – 75), *r*2 (50 – 60), *r*3 erect (38 – 55), *r*4, *r*5 (53 – 67), *r*6 (45 – 57), *J*1, *J*2 (43 – 55), *J*3 (50 – 62), *J*4 (40 – 47), *J*5 (5 – 9), *Z*1 (63 – 80), *Z*2 (65 – 92), *Z*3 (66 – 98), *Z*5 (61 – 77), *S*1 (54 – 72), *S*2 (55 – 77), *S*3, *S*4 (60 – 78), *S*5 (50 – 70), *Z*4 longest (80 – 102) of opisthonotal setae. Lateral soft cuticle with five or six pairs of *R*-setae (33 – 48) (Fig. 2A), *R*2 sometimes on small platelet (Fig. 2E).

Idiosomatic venter — Adult female. Tritosternum base sometimes biarticulate, 38 – 43 long and 20 – 22 wide at its base, with paired laciniae fused for about 22 – 25 of entire length

(122 – 135). Presternal region with circumscribed pair of weakly granulated, lineated areas, flanked anteriorly by a pair of weak or distinct narrow strips on either side of tritosternal base, and with setae *st1* (33 – 37) inserted on this region, anterior to sternal shield. Sternal shield 127 – 135 long from anterior margin at transverse level with poroids *iv1* to slightly concave posterior margin, 125 – 136 wide, weakly lineated along lateral margins, smooth medially; sternal setae *st2*, *st3* of similar length (30 – 37). Sternal poroids *iv3* alone on soft cuticle, setae *st4* (28 – 35) on tiny metasternal platelets (13 – 15 x 8 – 11). Endopodal strips narrow between coxae III and IV. Epigynal shield sparsely reticulated, its broadly rounded hyaline anterior margin not overlapping posterior edge of sternal shield, its lateral margins slightly concave, narrowed anterior to setae *st5* (38 – 47), and its posterolateral corners emarginated behind *st5*; shield 208 – 225 long, 118 – 137 at widest level at posterior rounded corners, 80 – 87 at narrowest width between legs IV. Opisthosomatic venter with two pairs of well separated metapodal platelets, primary pair elongate-oval, 33 – 40 long, 15 – 19 wide, secondary pair small, 10 – 16 by 5 – 7. Ventrianal shield inversely subtriangular with angulose or rounded anterior corners, with posterolateral margins on either side of anus divergent anteriorly; surface entirely reticulate, and punctate on either side of postanal seta; shield wider (293 – 337) than long (212 – 232), width at anal level (130 – 155); poroids *ivo2* on shield anterior edge behind setae *ZV1*; gland pore *gv3* on or off shield posterior to anal opening; shield with four pairs of ventral setae: *JV1* (37 – 42), *JV2* (43 – 50), *JV3* (44 – 55), *ZV2* (35 – 48); with paranal setae (21 – 27) shorter than postanal seta (43 – 65). Soft cuticle with five pairs of simple opisthogastric setae, *ZV1* (35 – 44) anterior to ventrianal shield, *ZV3* (33 – 43), *ZV4* (37 – 44), *JV5* (55 – 67) flanking the shield, and *ZV5* aligned behind *R6*; three pairs of poroids on soft cuticle. Peritrematal-exopodal shield with lines extending from stigma into rounded posterior margin (Fig. 1C); peritreme extending to level between setae *s1* and *z1* (Fig. 1A). Spermathecal apparatus with cup-like calyx 28 – 29 long to embolus, 30 – 31 including it (Fig. 1F).

Adult male. Tritosternum much as in female, but with base biarticulate, longer (20 – 32) than wide (15 – 19), and with laciniae fused for only about 10 – 15 of entire length (88 – 107). Presternal region faintly sclerotized, with a pair of distinct narrow strips on either side of tritosternal base, and with setae *st1* inserted on this region on either side of genital opening. Sternitigenital shield length 225 – 267, narrowest widths 88 – 113 at level between coxae II, 77 – 95 between coxae III, 58 – 87 between coxae IV; shield slightly lineated along lateral margins and posteriorly between coxae IV, unornamented medially, with endopodal apices freely acuminate beside coxae IV; setae *st1* (28 – 32) and *st5* (28 – 37) longer, *st2-st4* (17 – 26); poroids *iv3* sometimes hardly discernible flanking faint pair of pits (Fig. 2A). Ventrianal shield well reticulated and with punctate fields in anal region as in female, its convex anterior margin sometimes excised near apices of exopodal strips behind coxae IV, and posterolateral margins slightly constricted in anal region; shield much wider (278 – 337) than long (170 – 228, including cribrum ca. 8 – 11 long, 58 – 65 wide); shield with six or usually seven pairs of opisthogastric setae, *JV5* asymmetrically on or off shield (Figs. 1A, B); *JV1* and *ZV1* (23 – 32), *JV2* (28 – 37), *ZV2* (28 – 32), *JV3* (28 – 42), *ZV3* (23 – 30), *JV5* (39 – 50); postanal seta smooth (39 – 47), about twice as long as paranal setae (15 – 22). Soft opisthogastric cuticle with two pairs of setae, *ZV4* (26 – 30), and *ZV5* (30 – 42) aligned behind *R6*, one pair of lyrifissures, *ivp*.

Gnathosoma — Adult female. Gnathotectum anterior margin broadly truncate, with two lateral smooth prongs and serrate medial edge (Fig. 1D). Cheliceral shaft, excluding basal section, 160 – 173 long, with slender digits; dorsal seta blunt (13 – 14); fixed digit with tiny offset subapical tooth and row of 18-22 very fine teeth (Fig. 1G), pilus dentilus minute, at level between 4<sup>th</sup>- 5<sup>th</sup> apical teeth; movable digit (71 – 75) tridentate (Fig. 1H). Subcapitulum rows of deutosternal denticles progressively slightly wider posteriorly, each with numerous (ca 30-35) fine denticles, 6th and sometimes 7th widest and with ca 40-45 and 35-40 teeth, respectively (Fig. 1E); subcapitular setae *hp1* (40 – 45) slightly shorter than *hp3* (48 – 52) and capitular seta *pc* (43 – 52), *hp3* much longer than *hp2* (23 – 27). Palp length (195 – 212); apical

margin of palptrochanter with a single spine anterolaterally; palptrochanter setae dissimilar in length,  $v1$  48 – 52,  $v2$  38 – 42.

Adult male. Gnathotectum as in female (Fig. 2C). Cheliceral shaft, excluding short basal section 105 – 130 long; fixed digit with offset subapical tooth followed by minute pilus dentilis inserted on small angular protrusion and row of 11–16 small teeth (Fig. 2H); movable digit (40 – 45) unidentate; spermatodactyl 45 – 54 long, 8 – 9 wide at medial region, extending anteriorly 28 – 37 beyond apex of digit, with narrowed neck and small bifid head apically (Figs. 2F, G). Corniculi more widely spaced but not more arched than in female, 33 – 37 long, and flanked medially by pair of short (7–10) spiculate processes (Figs 2D, 11A); internal malae and labrum as in female. Subcapitulum with seven rows of deutosternal denticles much as in female, sixth and seventh rows slightly widest; hypostomatic setae *hp1* (28 – 32) similarly as long as *pc* (25 – 37), *hp3* usually longest (30 – 50), *hp2* (12 – 20). Palpi (length 145 – 187) similar in structure, form of setae as in female; palptrochanter with inner seta longer (30 – 44) than outer seta (17 – 32) but not markedly whip-like.

Legs — Adult female. Legs I (707 – 755) about as long as legs IV (715 – 750), and about as long as dorsal shield; other leg lengths (excluding pretarsi): II (565 – 600), III (587 – 615). Leg I pretarsus with biarticulate shaft (38 – 42 to base of claws), tarsus (187 – 205) about 1.6 longer than tibia; other length ratios, femur (135 – 147): genu (112 – 118): tibia (117 – 125) about 1.15: 0.95: 1.0. Legs II–IV with tarsus/tibia length ratios about 2.0–2.3. Chaetotactic formulae of leg segments as given for species-group. Tarsi II–IV with ventroapical process (12 – 17) bluntly pointed, smooth apically (Figs 13A, H), and with setae (*d-1*) (23 – 30) slightly shorter than pretarsus to base of claws (28 – 37). Tarsi II–IV with paradactyli asymmetrical, anterior element increasingly extending beyond tip of claw from II to IV, its length 30 – 35, twice as long as claw (15) on leg IV (Fig. 14A). Tarsi II and III with setae (*l-1*) and (*v-1*) symmetrical in form, *pl-1* (32 – 35) and *av-1* (36 – 47) slightly longer than *al-1* (27 – 30) and *pv-1* (26 – 37), respectively. Tarsus IV with distal seta *av-1* (50 – 60) blunt, clearly larger, thicker than *pv-1* (37 – 45); adjacent setae (*l-1*) symmetrically short (20 – 27), slender (Fig. 14A). Tarsi II–IV with dorsal seta *md* nearly reaching base of claws, and nearly as long as smooth attenuated setae (*d-2*) (67 – 80 on II, 85 – 100 on III, 95 – 110 on IV).

Adult male. Legs I clearly longer than dorsal shield, not thicker than those of female; relative leg lengths, excluding pretarsi, similar to those of female, I 550 – 660, II 445 – 524, III 455 – 552, IV 575 – 675. Legs with segment length ratios as in female. Tarsus I with long pretarsus (25 – 37 to base of claws), claws 10 – 12 long. Tarsi II–IV with dorsoapical setal processes (*d-1*), ventroapical process and pretarsal structures formed as in female, pretarsus lengths 27 – 35 excluding claws (10) (Fig. 13B). Legs III–IV with tibial setae (*v*) and leg IV genual seta *av* dimorphically thicker, spinelike, less attenuate; length and form of other setae much as in female; seta *pl-3* of basitarsus II smooth, attenuate (36 – 38) (Fig. 13B), but *pl-3* of basitarsi III, IV (21 – 22) similar to *pl-2* in thicker, slightly shorter form than other three basitarsal setae.

Type material — Except the final one, noted below, all specimens collected at the La Selva Biological Station, Heredia Province, Costa Rica (10°26'N, 84°01'W, elevation 50–150 m): HOLOTYPE: adult female, 8 July 1997, ex adult *Cephaloleia bella* Baly on *Heliconia pogonantha* leaves, coll. M. Paniagua. PARATYPES: 1 adult female, 1 adult male, with same data as holotype; 2 adult females, 1 adult male, 12 June 1997, ex coexistent adults of *Cephaloleia belti* Baly and *C. ornatrix* Donckier from *Heliconia* leaves, coll. ALAS; 3 adult females, 2 adult males, 15 April 1994, ex adult Chrysomelidae, no host plant data, M. Paniagua coll.; 1 adult female, 1 adult male, June 1997, ex adult *Cephaloleia bella* Baly, no host plant data, coll. D. Johnson; 1 adult female (gravid with larva), 1 adult male, June 1997, ex adult *Cephaloleia belti* Baly, no host plant data, coll. D. Johnson; 2 adult males, February 1994, associated with adult *Chelobasis* sp. on leaves of *Heliconia pogonantha*, coll. E.E. Lindquist & ALAS; 1 adult female, 2 adult males, 18 February 1994, ex adult Chrysomelidae, no host plant data, coll.

ALAS; 3 adult females, 2 June 1997, with adult hispine beetles on Heliconiaceae leaves, coll. E.E. Lindquist; 2 adult females, June 1997, ex adult *Cephaloleia vicina* on *Heliconia pogonantha*, coll. not indicated; 1 adult male, February 1994, associated with adult *Cephaloleia vicina* on leaf of *Heliconia pogonantha*, coll. E.E. Lindquist & ALAS. Costa Rica, Osa Peninsula, Corcovado National Park (8°27.39'N, 83°25.45'W, elevation 10-500 m): 1 adult male, May 1997, ex adult *Chelobasis bicolor* Gray, no host plant data, coll. D. Johnson.

Host identifications — Some of the identities of the associated beetles given above are in accord with current molecular studies, *i.e.*, those as noted below for *Lasioseius serripes*. However, the following identities are discordant. *Cephaloleia vicina* does not occur at La Selva, and specimens identified as such from there are, in all cases checked by DNA barcodes, *C. bella*. Further, *C. bella* normally does not occur on *Heliconia pogonantha*; thousands of field diet records indicate it feeds only on *H. imbricata* (Garcia-Robledo *et al.*, 2017).

Etymology — The specific name is based on the chrysomelid subfamilial name Cassidinae, which includes the tribes Arescini and Imatidiini (or Cephaloleini) to which beetle associates of the genera *Chelobasis* and *Cephaloleia* belong, respectively. We have chosen this name for the species with the widest array of host associates and as the species-group name, anticipating that rolled-leaf beetles of other genera in these tribes will be found to live with these mites.

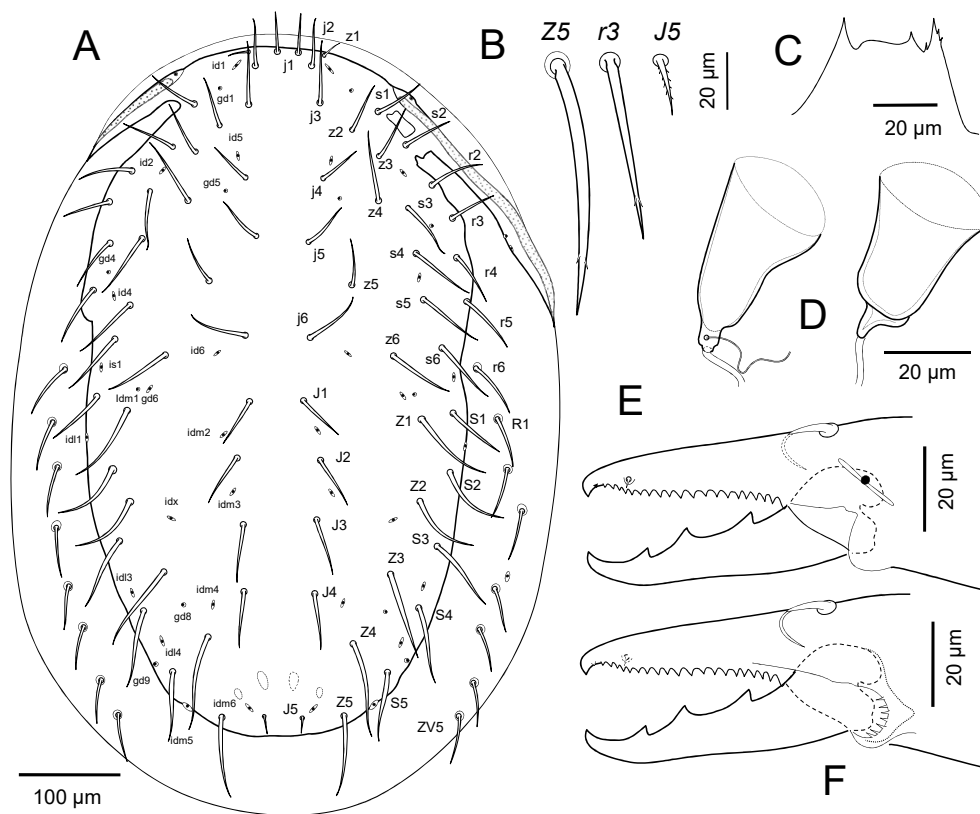
Remarks — The male from Corcovado measured ca 12-19% smaller in dimensions than seven males measured from La Selva; however, in other descriptive aspects it fully resembles those from La Selva. Two females are asymmetrical in having humeral seta *r3* inserted off the dorsal shield on one side, yet the aligned *r2* and *r4-r6* are on the shield. Two females show asymmetry in size and arrangement of the vertical cluster of setae *j1, j2, z1*; one male lacks one *j2*.

Collection records of this mite species associated with beetles of three different species of *Cephaloleia* and one of *Chelobasis* leave uncertainty as to host preferences, particularly as beetles of these species are often coexistent (Garcia-Robledo 2010, Staines 2011, Schmitt & Frank 2013, Moraza & Lindquist 2015). Adults of *Lasioseius cassidini* are clearly the largest of the described species of this group. However, the data available are inadequate to test whether a mite/beetle size correlation exists, such as was hypothesized for larger mites being associated with larger beetles, for species of *Hispiniphis* and *Makarovaia*, which are more intimate subelytral associates of these same beetles (Moraza & Lindquist 2015, 2016). Although there are records of a few specimens of *L. cassidini* with relatively large beetles of *Chelobasis*, including one from the Osa Peninsula, they are based only on adult male mites, which may not present inherent preferences phoretically. Tentatively, subject to further studies, we conclude that, at La Selva, *Lasioseius cassidini* may be associated regularly with small beetles of the host specialist *Cephaloleia bella* and to some extent with the host generalist *C. belti* on *Heliconia imbricata*.

## ***Lasioseius serripes* n. sp. (Figures 3-7, 11B, 12A, B, G, 13C-D, 14B)**

Zoobank: [F1A4EE0C-0031-410D-B993-20CDC3D08D71](https://doi.org/10.1111/1365-3113.12000)

Diagnosis — Adult female: Sternal shield reticulated over entire surface, its posterolateral corners emarginated lateral to setae *st3*; poroids *iv3* and setae *st4* on soft cuticle; epigynal shield fully reticulated, its lateral margins parallel anterior to setae *st5*; ventrianal shield with posterolateral margins on either side of anus divergent, and with three pairs of opisthogastric setae, *JVI* on soft cuticle; metapodal plates connected or coalesced on each side. Dorsal setae *r6* usually on soft cuticle; *Z5, S5* attenuated like adjacent setae. Adult male: Sternitigenital shield reticulated over entire surface. Leg II with dorsal setae dimorphically short, blunt on

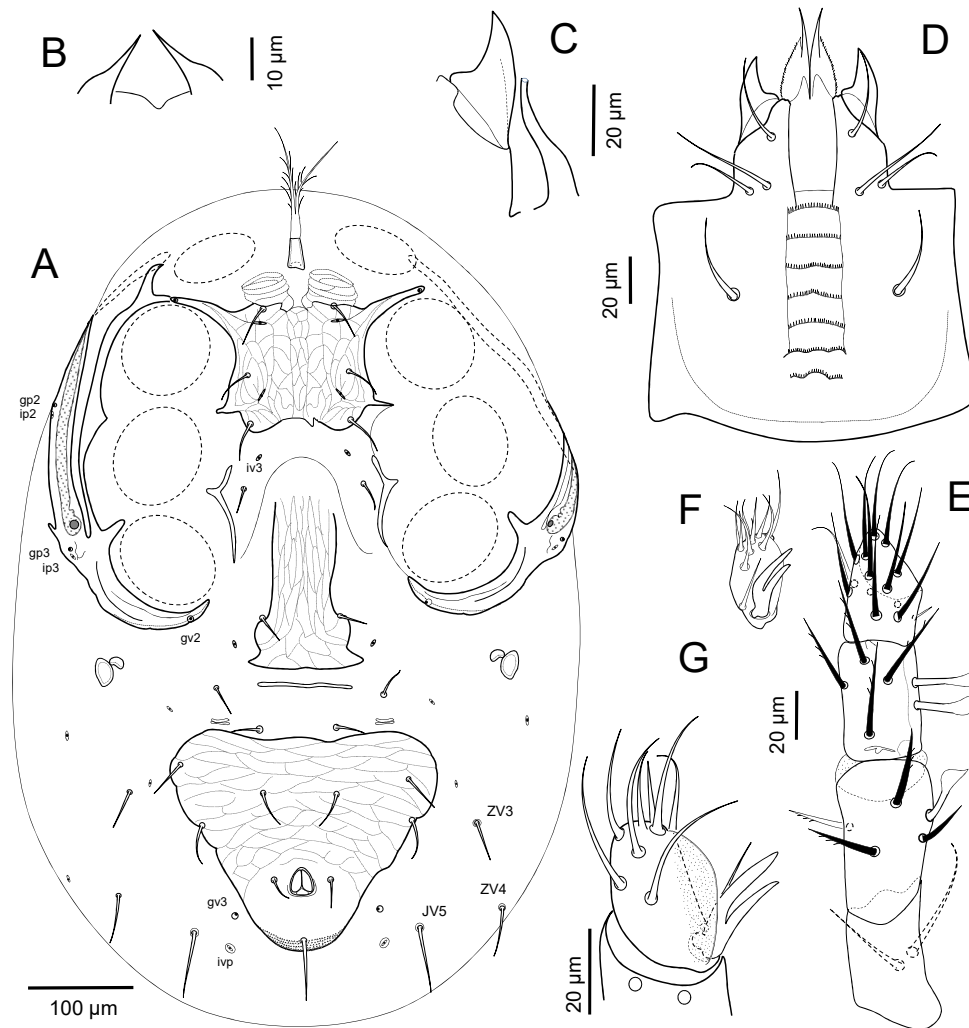


**Figure 3** *Lasioseius serripes* n. sp., adult female: A – Idiosoma, dorsal view; B – Detail of denoted dorsal setae; C – Gnathotectum; D – Spermathecal structures; E – Cheliceral digits, paraxial view; F – Cheliceral digits, antiaxial view.

genus, tibia, tarsus. Tibiae III-IV with seta *pv* dimorphically hooked, blunt. Adult attributes: Gnathotectum anterior margin truncate, irregularly denticulate. Fixed chela with file of ca 20 teeth in female, ca 18 in male. Sternal setae *st1* inserted on anterior edge of sternal shield. Tarsi II-IV with ventroapical process truncate-spiculate apically; tarsi II-III with seta *av-1* slightly longer and thicker at base than *pv-1* and both slightly longer than (*l-1*); tarsus IV with apical setae (*v-1*) symmetrically thicker than, and about twice as long as (*d-1*); pretarsal paradactyli small, symmetrical.

### Description

Idiosomatic dorsum — Adult female: Dorsal shield 651 – 695 long, 337 – 385 wide at level of *r3*, 368 – 397 wide at level of *r5* (n=9), lightly reticulated over entire surface, more faintly so behind setae *Z4*, where also faintly punctate. Shield with 37 pairs of setae, all acutely pointed (Figs. 3A, B), with few barbs, except *J5* short (15 – 17), clearly barbed; *J1-J4* about as long as longitudinal intervals between their bases, *Z1-Z4* and *S2-S4* longer than intervals between their bases; *r3* erect, similarly as long as *r2*, *r4*: *j1* (41 – 50), *j2* (45 – 55), *j3* (60 – 70), *j4* (43 – 50), *j5* (48 – 55), *j6* (58 – 63), *z1* (20 – 29), *z2* (50 – 55), *z3* (52 – 60), *z4* (64 – 70), *z5* (47 – 55), *z6* (60 – 70), *s1* (48 – 55), *s2* (50 – 60), *s3* (53 – 65), *s4* (64 – 70), *s5* (63 – 75), *s6* (57 – 72), *r2* (50 – 60), *r3* (54 – 62), *r4* (55 – 62), *r5* (56 – 67), *J1* (45 – 55), *J2-J4* (48 – 62), *Z1-Z3* (71 – 97), *Z4* (87 – 102), *Z5* (70 – 88), *S1* (57 – 70), *S2* (66 – 77), *S3* (64 – 75), *S4* (66 – 78), *S5* (64 – 75). Lateral soft cuticle with eight pairs of smooth setae, including *r6* (52 – 62), *R1* (48 – 55), *R2-R6* (44 – 52) and *ZV5* (43 – 47) posteriorly.

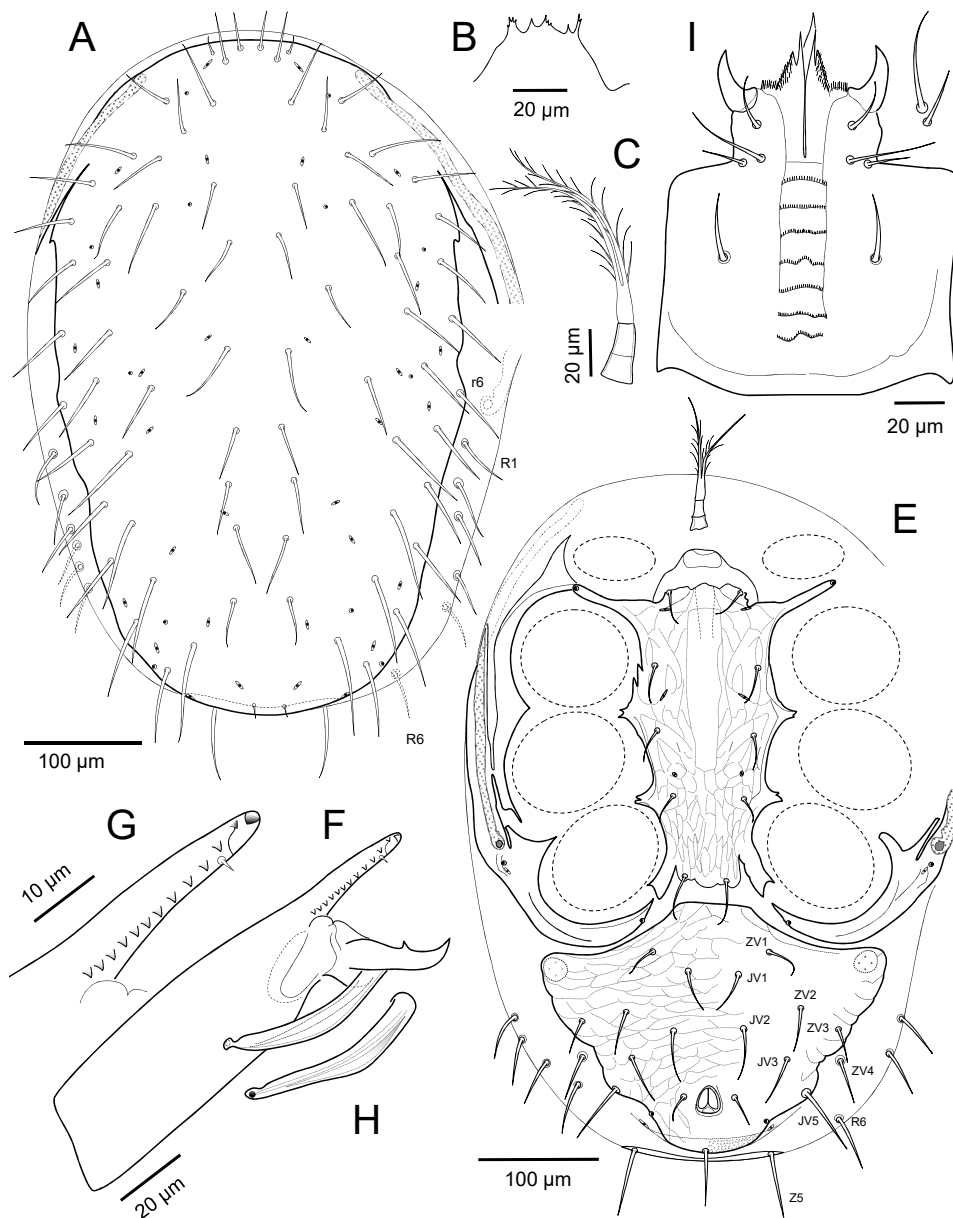


**Figure 4** *Lasioseius serripes* n. sp., adult female: A – Idiosoma, ventral view; B – Detail of parolabrum; C – Detail of corniculus and salivary stylus; D – Subcapitulum; E – Palp, dorsal view; F – Detail of palptarsus; G – Detail of hyaline anterolateral flap of palptarsus.

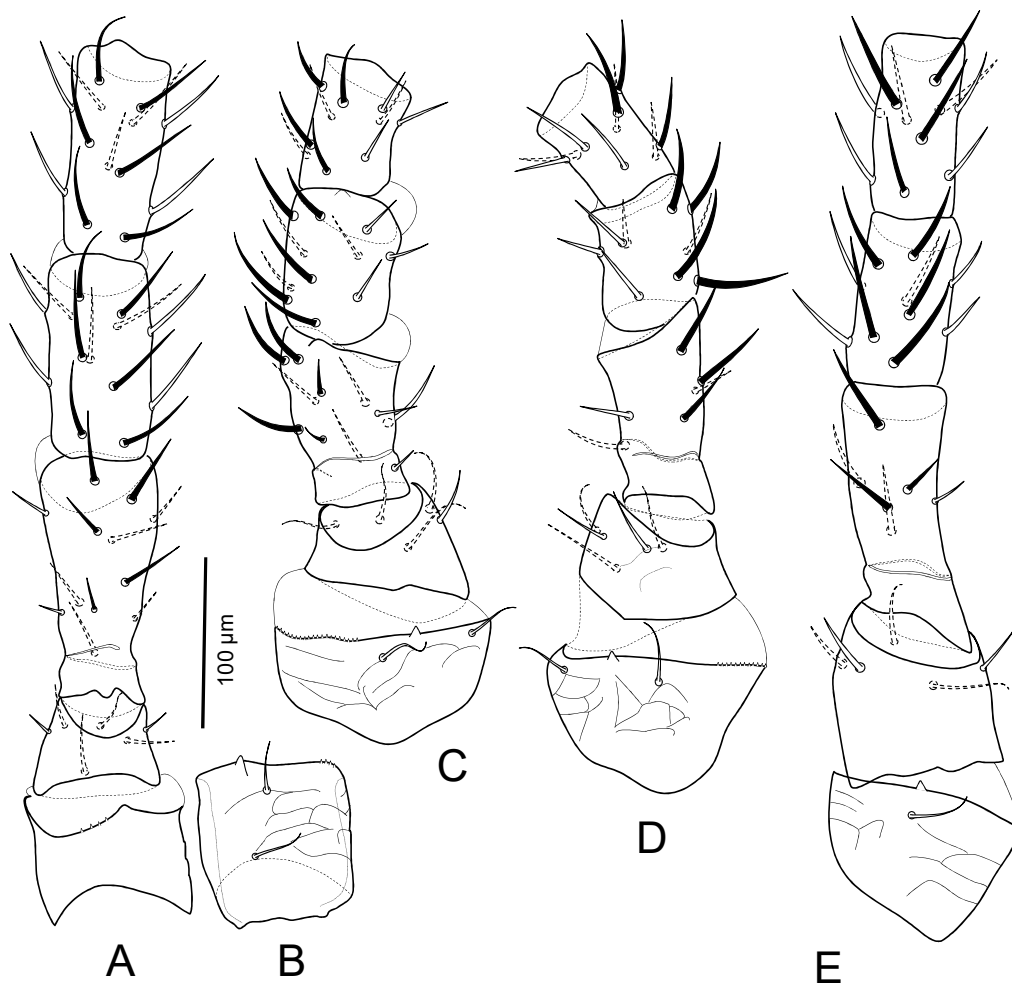
Adult male. Dorsal shield 557 – 587 long, 332 – 357 wide at level of setae *r3*, 325 – 353 wide at level of *r6* ( $n = 5$ ); shield ornamentation, complement of pore-like structures and setation as in female except slightly more expanded laterally so as to become united with peritrematal shields at level of setae *s2* and bear marginal setae *r6* and sometimes *R1* (Fig. 5A). Dorsal shield with 37-38 pairs of setae, their form and relative lengths as in female, except bases of *Z4*, *Z5*, *S4*, *S5* swollen sub-basally. Setae *j1* (28 – 33), *j2* (40 – 43), *j3* (53 – 60), *j4* (38 – 40), *j5* (38 – 47), *j6* (48 – 54), *z1* (17 – 20), *z2*, *z3* (45 – 50), *z4* (55 – 60), *z5* (38 – 44), *z6* (50), *s1* (46 – 48), *s2* (52 – 56), *s3* (50 – 61), *s4* (58 – 65), *s5* (58 – 65), *s6* (55 – 58), *r2-r4* (48 – 53), *r5* (57 – 60), *r6* (50 – 52), *J1-J4* (40 – 47), *J5* (9 – 12), *Z1-Z3* (66 – 75), *Z5* (61 – 72), *S1* (50 – 52), *S2* (55 – 57), *S3-S5* (57 – 66), *Z4* the longest opisthonotal setae (75 – 86). Lateral soft cuticle with usually six pairs of marginal setae (40 – 47). Form of peritrematal shields as in female.

Idiosomatic venter — Adult female. Tritosternum base 28 – 33 long, 16 – 20 wide at its base, with paired laciniae fused along basal 15 – 22 of entire length (95 – 115). Presternal



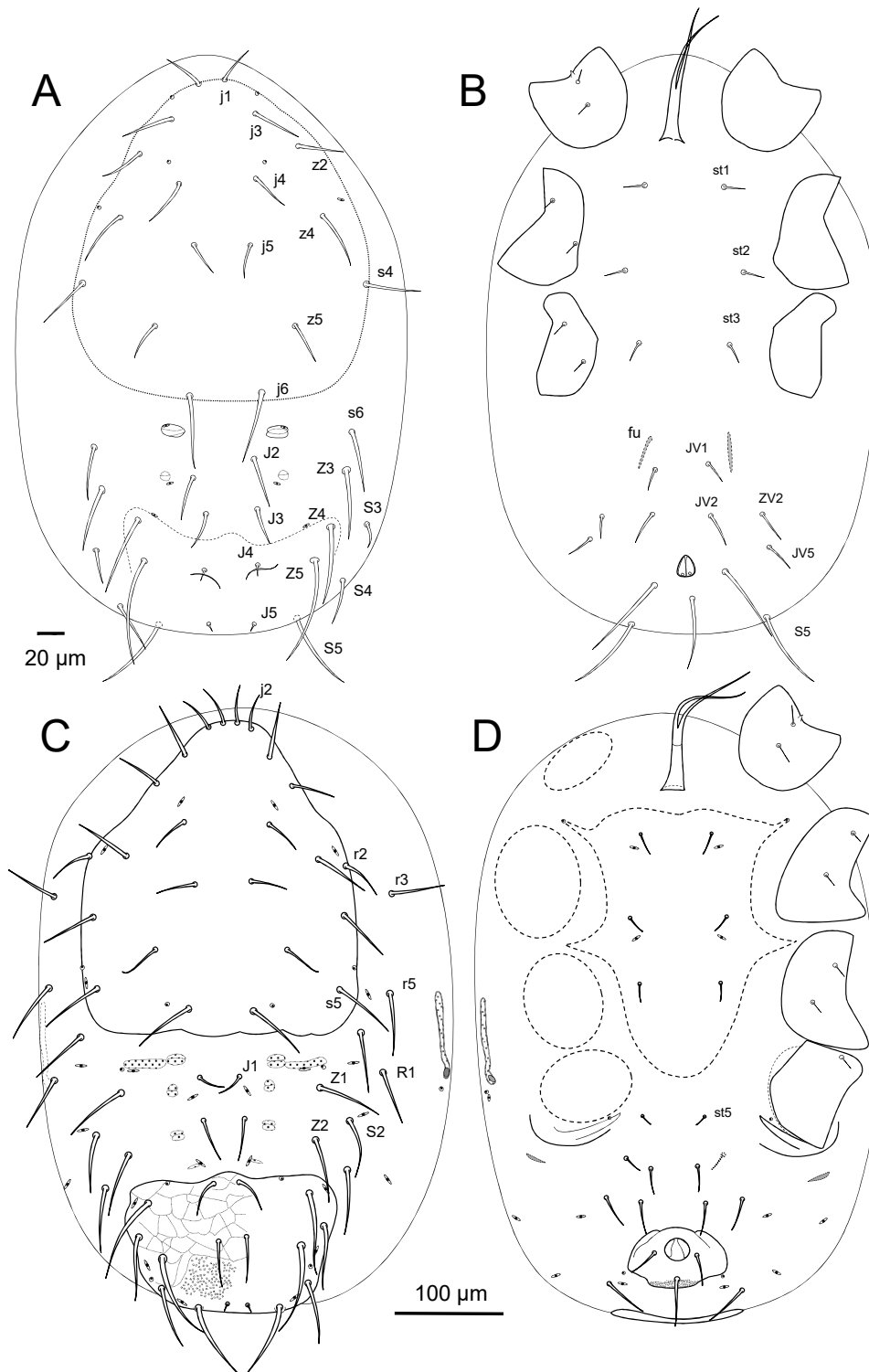


**Figure 5** *Lasioseius serripes* n. sp., adult male: A – Idiosoma, dorsal view; B – Gnathotectum; C – Tritosternum; D – Subcapitulum and ventral setae of palptrochanter; E – Idiosoma, ventral view; F – Chelicera and spermatodactyl, ventrolateral view; G – Detail of fixed cheliceral digit, ventral view; H – Detail of spermatodactyl.



**Figure 6** *Lasioseius serripes* n. sp., adult female, right legs I-IV (excluding tarsus): A – Leg I, dorsal view; B – Leg I coxa, ventral view; C – Leg II, posterodorsal view (coxa ventral view); D – Leg III, anterodorsal view (coxa ventral view); E – Leg IV, dorsal view (coxa ventral view). (Solid black setae indicate dorsal setae on segments).

region with circumscribed pair of weakly lineated granulated areas adhered to anterior margin of sternal shield. Sternal shield 100 – 112 long, with irregularly concave posterior margin, 118 – 125 wide, well reticulated over entire surface, midsurface with narrower reticula; sternal setae of similar length, *st1* (38 – 42), *st2* (33 – 39), *st3* (35 – 42). Sternal poroids *iv3* and setae *st4* (26 – 32) inserted on soft cuticle. Endopodal strips narrow between coxae III and IV. Epigynal shield well reticulated over entire surface, with narrower reticula anterior to insertion of *st5* (36 – 42), its broadly rounded hyaline anterior margin not reaching posterior edge of sternal shield, its lateral margins nearly parallel anterior to setae *st5*, and its posterolateral corners slightly to clearly emarginated behind *st5*; shield 188 – 210 long, 95 – 107 at widest level at posterior angulate margin, 62 – 70 at narrowest width between legs IV. Opisthosomatic venter with two pairs of metapodal platelets connected or coalesced on each side, primary pair ovate, 25 – 30 long, 13 – 17 wide, secondary pair with greatest dimension transverse, 13 – 22; one adjacent set of small, narrow platelets near anterior margin of ventrianal shield, lateral to *JVI*. Ventrianal shield inversely subtriangular with rounded anterior corners, with posterolateral margins on either side of anus divergent anteriorly; surface strongly reticulate except faintly in anal region where also faintly punctate on either side of postanal seta; shield wider (253 – 295)



**Figure 7** *Lasioseius serripes* n. sp.: A – Larva, idiosoma, dorsal view; B – Larva, idiosoma, ventral view; C – Protonymph, idiosoma, dorsal view; D – Protonymph, idiosoma, ventral view.

than long (179 – 205), including cribrum (8 – 12); shield with three pairs of ventral setae and sometimes pores *gv3*: *JV2* (33 – 40), *JV3* (35 – 45), *ZV2* (34 – 40); with paranal setae (20 – 27) shorter than postanal seta (49 – 62). Soft cuticle with six pairs of simple opisthogastric setae, *JV1* and *ZV1* (26 – 33) anterior to ventrianal shield, *ZV3* (32 – 40), *ZV4* (40 – 47), *JV5* (55 – 65) flanking the shield, and *ZV5* (43 – 47) aligned behind *R6*; three pairs of poroids (including *ivp*) and sometimes gland pore *gv3* on soft opisthogastric cuticle. Peritrematal-exopodal shield with lines extending from stigma to irregularly rounded posterior margin (Fig. 4A); peritreme extending to level slightly anterior to insertion of setae *s1* (Fig. 3A). Spermathecal apparatus with cup-like calyx ca. 30 – 35 long from atrium at base, 23 – 26 wide at distal margin (Fig. 3D).

Adult male. Tritosternum much as in female, but with base biarticulate, longer (21 – 24) than wide (13 – 17), and laciniae (78 – 88) fused along basal 10 – 12 of entire length (Fig. 5C). Presternal region weakly granulated, with or without pair of weakly sclerotized transverse strips anteriorly. Sternitigenital shield length 245 – 283 from anterior margin of genital opening, widths 104 – 110 at level between coxae II, 92 – 100 between coxae III, and 58 – 71 between coxae IV; shield nearly fully reticulated, but bare near posterior margin where endopodal apices freely truncated beside coxae IV; shield medial region more weakly ornamented but punctate between setae *iv1* and *st3*, and with poroids *iv3* appearing as distinctively rounded pits; setae *st1* on anterior margin of sclerotized region of shield; setae *st1-st5* of dissimilar lengths as in female, *st1-st3* (27 – 30), *st4* shortest (20 – 23) and *st5* longest (30 – 35). Ventrianal shield strongly reticulate as in female, its greatest width (282 – 305) larger than its length (178 – 220, including cribrum ca. 9 – 11 long, 75 – 86 wide); shield with seven pairs of opisthogastric setae; lateral margins irregular or eroded near where setae *ZV4* on adjacent soft cuticle; setae *JV1* (30 – 32), *JV2* (37 – 42), *JV3* (37 – 44), *ZV1* (27 – 30), *ZV2* (35 – 38), *ZV3* (28 – 33), *ZV4* (35 – 40), and *JV5* the longest (50 – 59) inserted in bluntly angled lateral corners; postanal seta smooth (40 – 48), about twice as long as paranal setae (19 – 25). Soft opisthogastric cuticle with two pairs of setae, including *ZV5* aligned behind *R6*, and one pair of lyrifissures, *ivp* (Fig. 5E).

Gnathosoma — Adult female. Gnathotectum anterior margin broadly truncate, variably with two lateral, short, smooth prongs or with few denticles, sometimes with smaller denticles between lateral prongs (Fig. 3C). Cheliceral shaft, excluding basal section, 136 – 148 long, with slender digits (Figs 3E, F); dorsal seta blunt (8 – 11); fixed digit with tiny offset subapical tooth and row of 19-24 very fine teeth (Fig. 3E), pilus dentilus minute (1 – 2) at level of 4<sup>th</sup> apical tooth; movable digit (62 – 72) tridentate. Subcapitulum rows of deutosternal denticles each with numerous (ca 25-40) fine denticles, those of most anterior row slightly coarser (ca 25-30), 2<sup>nd</sup>-5<sup>th</sup> rows with ca 35-40 teeth, 6<sup>th</sup> and sometimes 7<sup>th</sup> rows slightly wider and slightly more denticulate (Fig. 4D); subcapitular setae *hp1* (30 – 37) slightly shorter than capitular setae *pc* (36 – 42), *hp3* slightly longest (40 – 47), much longer than *hp2* (23 – 27). Salivary styli and corniculi as in figure 4C. Palp length (193 – 202); apical margin of palptrochanter without spines anterolaterally; palptrochanter setae dissimilar in length, *v1* 45 – 63 and *v2* 34 – 42 (Figs 4E, F).

Adult male. Gnathotectum as in female (Fig. 5C). Cheliceral shaft, excluding short basal section, 110 – 120 long (Fig. 5F); fixed digit with offset subapical tooth followed by pilus dentilis behind hollow area and row of 10-16 small-sized teeth (Figs. 5F, G); movable digit (42 – 45) unidentate; spermatodactyl 40 – 57 long, 6 – 7 wide at base, slightly wider (8) at medial region, extending anteriorly ca 35 beyond apex of digit, with narrowed neck and small head apically (Figs 5F, H). Corniculi slightly more widely spaced and arched inwardly than in female, 25 – 30 long, and flanked medially by pair of short (7 – 8) spiculate processes (Figs 5I, 11B); internal malae and labrum as in female. Subcapitulum with seven or rarely eight rows of deutosternal denticles formed much as in female; hypostomatic setae *hp1* not attenuated (21 – 27), slightly shorter than capitular setae *pc* (22 – 32), *hp3* (30 – 37) slightly longest, *hp2* shortest (15 – 20) (Fig. 5I). Palpi (length 173 – 188) similar in structure, form of setae

as in female; palptrochanter with inner seta longer (38 – 40) than outer seta (20 – 23) but not markedly whip-like (Fig. 5I).

Legs — Adult female. Legs I (669 – 715) nearly as long as legs IV (678 – 725), and slightly longer than dorsal shield; other leg lengths (excluding pretarsi): II 519 – 529, III 538 – 545 (Figs 6A-E). Leg I pretarsus with biarticulated shaft (38 – 45 to base of claws), claws 15 – 17 long; tarsus (173 – 182) about 1.4-1.5 longer than tibia; other length ratios, femur (137 – 145): genu (110 – 117): tibia (112 – 124) about 1.2: 0.95: 1.0. Legs II-IV with tarsus/tibia length ratio about 2.0-2.2 (Figs 6C, D). Chaetotactic formulae of leg segments as given for species-group. Tarsi II-IV with ventroapical process (15 – 17) truncate-spiculate apically (Figs 13C, 14B), and with setae (*d-1*) (25 – 30) shorter than pretarsus to base of claws (33 – 44). Tarsi II-IV with paradactyli nearly symmetrical, weakly developed, anterior element barely extending beyond tip of claw (Figs 13G, 14B). Tarsi II (Fig. 13C), III with setae (*l-1*) (44 – 48) shorter than (*v-1*) (50 – 65); dorsal seta *md* (77 – 85) longest of tarsal setae, (*d-2*) barbed, less attenuated (50 – 62). Tarsus IV with setae *av-1* (70 – 75) slightly longer than *pv-1* (60 – 65), both nearly twice as long as similarly slender (*l-1*) (38 – 42) (Fig. 14B).

Adult male. Legs I slightly thicker than those of female, and longer than dorsal shield; relative lengths similar to those of female, I 690 – 705, II 475 – 525, III 493 – 507, IV longest, 710 – 735. Legs with segment length ratios as in female. Tarsus I with long pretarsus (25 – 35 to base of claws), claws 15 long. Tarsi II-IV with spiculated form of ventroapical process (Fig. 13D), relative lengths of dorsoapical setal processes (*d-1*) (25 – 28) and pretarsal structures as in female; tarsi II-III with setae (*v-1*) (45 – 55) symmetrically longer than slender (*l-1*) (33 – 44), increasingly so on III; tarsus IV with *av-1* (70 – 75) and *pv-1* (55 – 67) asymmetrically longer than (*l-1*) (32 – 35) (Fig. 13D). Legs II with dorsal setae of genu, tibia, basitarsus and (*d-2*) of telotarsus (16, 23, 26, 27), distinctively shorter than in female and bluntly spine-like (Figs 12A, 13D); genu III and tibiae III-IV seta *pv* and tibia IV seta *av* dimorphically hooked, blunt (Fig. 12B). Length and form of other setae slightly thicker than in female.

Deutonymph. None available to study for comparative purposes.

Protonymph. General description, based on one specimen, without measurements, for species-group perspective. Dorsal idiosoma (Fig. 7C) with setae generally nearly aciculate, but with some setae acquiring slightly tricarinate or barbed form as in adult. Podonotal region holotrichous, with 15 pairs of setae (five pairs added to larval complement, including *j2*, *s5* amidst 11 pairs on podonotal shield and *r2*, *r3*, *r5* along with larval *s6* on lateral soft cuticle); *j2* inserted in nearly transverse alignment with *j1*. Opisthonotal region holotrichous, with 15 pairs of setae (five pairs added to larval complement, including *J1*, *Z1*, *Z2*, *S2*, *R1*, all on interscutal soft cuticle; pygidial shield expanded so as to include eight pairs of setae, including *J3*, *Z5*, *S4*, *S5* (all larval setae).

Ventral idiosoma (Fig. 7D) with all setae aciculate, with no postlarval podosomal additions except *st5*. Sternal poroids *iv1*, *iv2* present, *iv3* absent, and larval funicules suppressed. Anal shield oval, with paranal setae similar in length or slightly shorter than postanal seta; rudiments of euanal setae suppressed. Opisthogastric soft cuticle with four or five pairs of setae, with asymmetrical addition of *ZV5*, which usually deutonymphal; *JV5* relatively larger than in larva, and inserted more posteriorly, in transverse alignment with postanal seta.

Gnathosoma — Fixed cheliceral digit with even row of 12-13 teeth; movable digit tridentate. Gnathotectum similar in form to adult. Subcapitulum with four pairs of setae, hypostomatic *h1-h3* and capitular *pc*. Palpus with normal protonymphal complement of setae, including one on trochanter (Lindquist & Evans 1965); palptarsus with hyaline flap developed beside apotele as in adult.

Legs — Legs I-IV with claws, pretarsi and shape of setae similar to adult female; tarsi II-IV with ventroapical process similar in form, serrated apically, as adult. Legs I, II, III, IV with normal, holotrichous protonymphal chaetotaxy (Lindquist & Evans 1965), except genu IV with

accelerated presence of usually deutonymphal seta *pl-1*, and femur IV with accelerated alveolar indication of seta *v-1* near basal lyriform fissure: coxae 2, 2, 2, 1; trochanters 4, 4, 4, 4; femora 10 (2 2/1 2/2 1), 8 (1 2/1 2/1 1), 5 (1 2/1 1/0 0), 4 (1 2/0 1/0 0); genua 8 (1 2/1 2/1 1), 6 (1 2/0 2/0 1), 6 (1 2/0 2/0 1), 6 (1 2/0 2/0 1); tibiae 8 (1 2/1 2/1 1), 7 (1 1/1 2/1 1), 7 (1 1/1 2/1 1), 7 (1 1/1 2/1 1); tarsi II-IV each with 17 (*md* added to larval complement). Tarsus IV with seta *av-1* distinctively erect, longer and slightly thicker than all other tarsal setae (Fig. 12G), in contrast to its form on tarsi II, III of protonymph, and on tarsus IV of adult.

Larva. General description, based on two unborn specimens, without measurements, for species-group perspective. Dorsal idiosoma (Fig. 7A) with all setae aciculate. Podonotal shield holotrichous with typical nine pairs of setae (*j1*, *j3-j6*, *z2*, *z4*, *z5*, *s4*); setae *s6* on soft cuticle behind posterolateral margin of shield. Opisthonotal region holotrichous with 10 pairs of setae (*J2-J5*, *Z3-Z5*, *S3-S5*); pygidial shield margins mostly indiscernible on specimens at hand, but its surface with typical pair of arcuate lines near insertions of setae *J4*, and with typical complement of four pairs of setae, including tiny *J4*, *J5* and prominent *Z3*, *Z4*. Soft interscutal cuticle with two pairs of mesonotal scutellae and typical six pairs of setae, including moderately long *J2*, *J3*, *S3*, *S5*, prominent *Z5* (in ventrolateral position), and shorter *S4*.

Ventral idiosoma (Fig. 7B) with all setae aciculate. Sternal shield outline not distinguishable; setae *st1-st3* similarly short, *st4*, *st5* absent, but the typical pair of subcutaneous structures ('funicules' sensu Athias-Henriot 1971a) present posteromedial bases of legs III. Anal shield margins indistinguishable; anal valves with rudimentary pair of euanal setae; paranal setae slightly longer than postanal seta. Opisthogastric soft cuticle with typical four pairs of similarly short setae (*JV1*, *JV2*, *JV5*, *ZV2*).

Gnathosoma — Fixed cheliceral digit with even row of 10-11 teeth; movable digit bidentate. Gnathotectum triramous, branches shorter than in adult. Subcapitulum with two pairs of hypostomatic setae, *h1* longer than *h2*. Palpus with normal larval complement of setae (Lindquist & Evans 1965); palptarsus with hyaline flap not evident beside apotele.

Legs — Legs I-III with claws, pretarsi and shape of setae similar to adult female; tarsi II, III with ventroapical process similar in form, serrated apically, as adult, and with setae (*d-1*) more strongly developed, slightly longer than pretarsi to base of claws. Legs I, II, III with normal, holotrichous larval chaetotaxy (Lindquist & Evans 1965): trochanter 2, 2, 2; femora 10, 7, 5; genua 8, 6, 6; tibia 8, 7, 7; tarsi II, III each with 16.

Type material — All specimens collected at the La Selva Biological Station, Heredia Province, Costa Rica (10°26'N, 84°01'W, elevation 50-150 m): HOLOTYPE: adult female, 12 June 1997, ex *Heliconia* leaves, successional plots, coll. ALAS. PARATYPES: 5 adult females, 5 adult males, 1 protonymph, with same data as holotype; 3 adult females (2 gravid with larva), 6 adult males, 12 June 1997, ex coexistent adults of *Cephaloleia belti* Baly and *C. ornatrix* Donckier from *Heliconia* leaves, coll. ALAS; 1 adult female (CRI 002: 739027), 8 July 1997, ex adult *Chelobasis perplexa* Baly, no host plant data, coll. M. Paniagua; 3 adult females, 1 adult male, June 1997, ex adult *Cephaloleia ornatrix*, no host plant data, coll. D. Johnson.

Host identifications — The identities of the associated beetles given above are in accord with current molecular studies, which indicate that one haplotype of *Chelobasis perplexa* sensu stricto and records of *Cephaloleia belti* and *C. ornatrix* on *Heliconia pogonantha* are in accord with field diet records. While *C. belti* is a host generalist, *C. ornatrix* is a host specialist of *Heliconia pogonantha* (Staines & Garcia-Robledo 2014, Garcia-Robledo *et al.* 2017).

Etymology — The specific name is a Latinized adjectival combination of 'serra', meaning saw or toothed like a saw, and 'pes', meaning foot, and refers to the unusual apically serrated form of the ventral apical tarsal process of legs II to IV.

Remarks — One female is asymmetrical in having seta *r6* on edge of dorsal shield on one side,

rather than on soft cuticle. As noted under morphological remarks following description of the *cassidini* species-group, the rudimentary presence of seta *av-1* on femur IV and full presence of seta *pl-1* on genu IV are ontogenetic accelerations of setae that are typically first expressed in the deutonymph (Evans 1963).

Although far from definite, collection records of *Lasioseius serripes* indicate a frequent association with *Cephaloleia ornatrix*, which perhaps is the preferred companion. Tentatively, subject to further studies, we conclude that, at La Selva, *Lasioseius serripes* is associated regularly with the host specialist *C. ornatrix* and to some extent with a form of *Chelobasis* and the host generalist *C. belti* on *H. pogonantha*.

### ***Lasioseius fuscina* n. sp. (Figures 8, 9, 11C, 12D, 13E-F, 14D)**

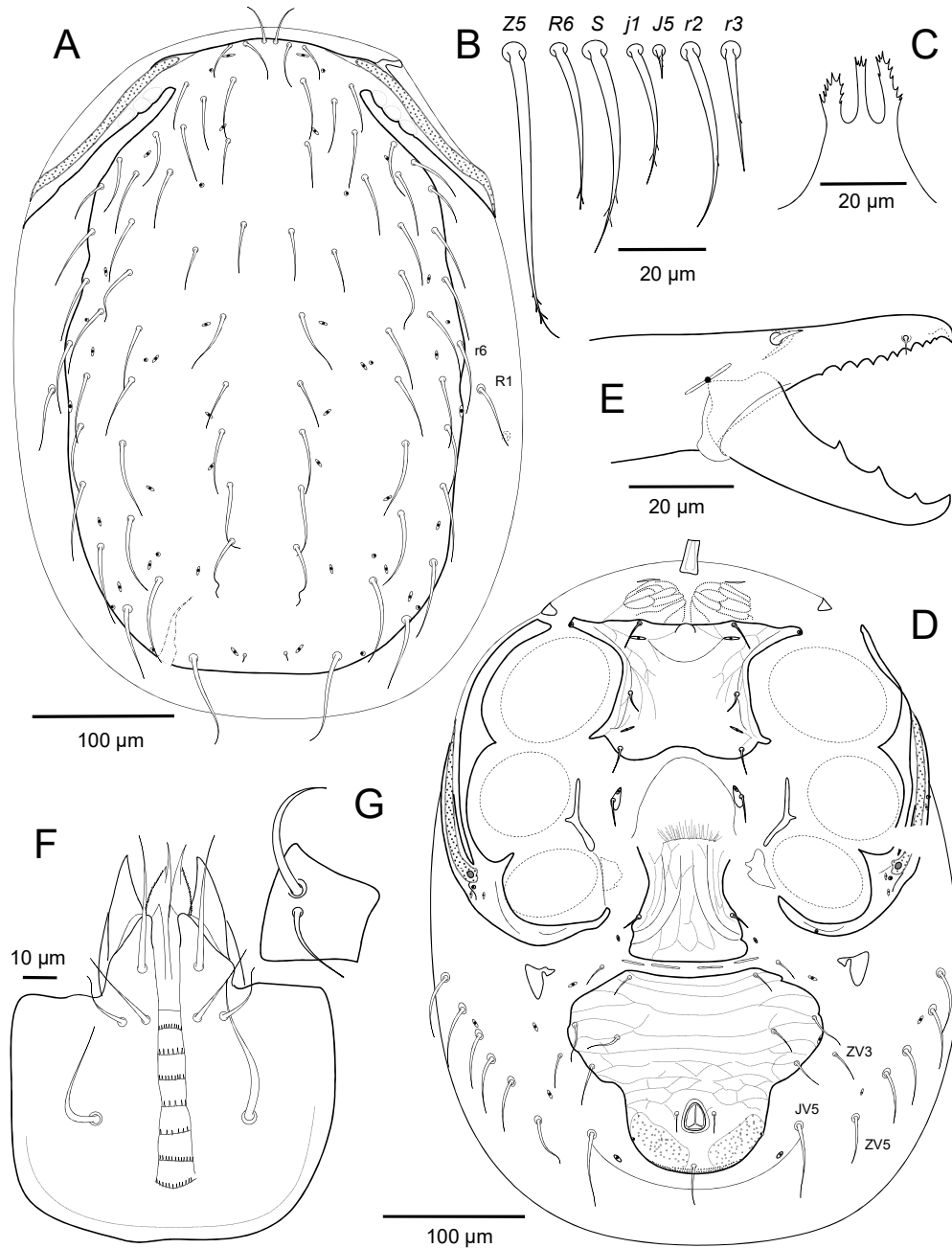
Zoobank: [F088E970-F8B8-4E76-8382-87DA2EF12B7F](https://doi.org/10.21203/rs.3.rs-1212121/v1)

Diagnosis — Adult female: Sternal shield lineated laterally and anteromedially, its anterior margin with blunt medial projection, its posterolateral corners not emarginated; poroids *iv3* and setae *st4* on slender metasternal platelets; epigynal shield reticulated over nearly entire surface, its lateral margins concave, narrowed anterior to setae *st5*; ventrianal shield with posterolateral margins on either side of anus nearly parallel, and with four pairs of opisthogastric setae, *JV1* on shield; metapodal plates nearly connected or coalesced on each side. Dorsal setae *r6* on edge of dorsal shield; *Z5*, *S5* attenuated like adjacent setae. Adult male: Sternitigenital shield incompletely reticulated, nearly smooth medially. Dimorphic leg setal structures minimal. Adult attributes: Gnathotectum anterior margin with 3 elongated, denticulated tines. Fixed chela with file of 8-9 teeth in female, ca 4 in male. Sternal setae *st1* inserted on anterior edge of sternal shield. Tarsi II-IV with ventral apical process bluntly pointed, smooth apically; tarsi II-III with setae (*l-1*) shorter, more spinelike than (*v-1*); tarsus IV with distal seta *pv-1* longer, more attenuate than *av-1*, (*l-1*); pretarsus with anterior paradactylus slightly longer than posterior one.

### **Description**

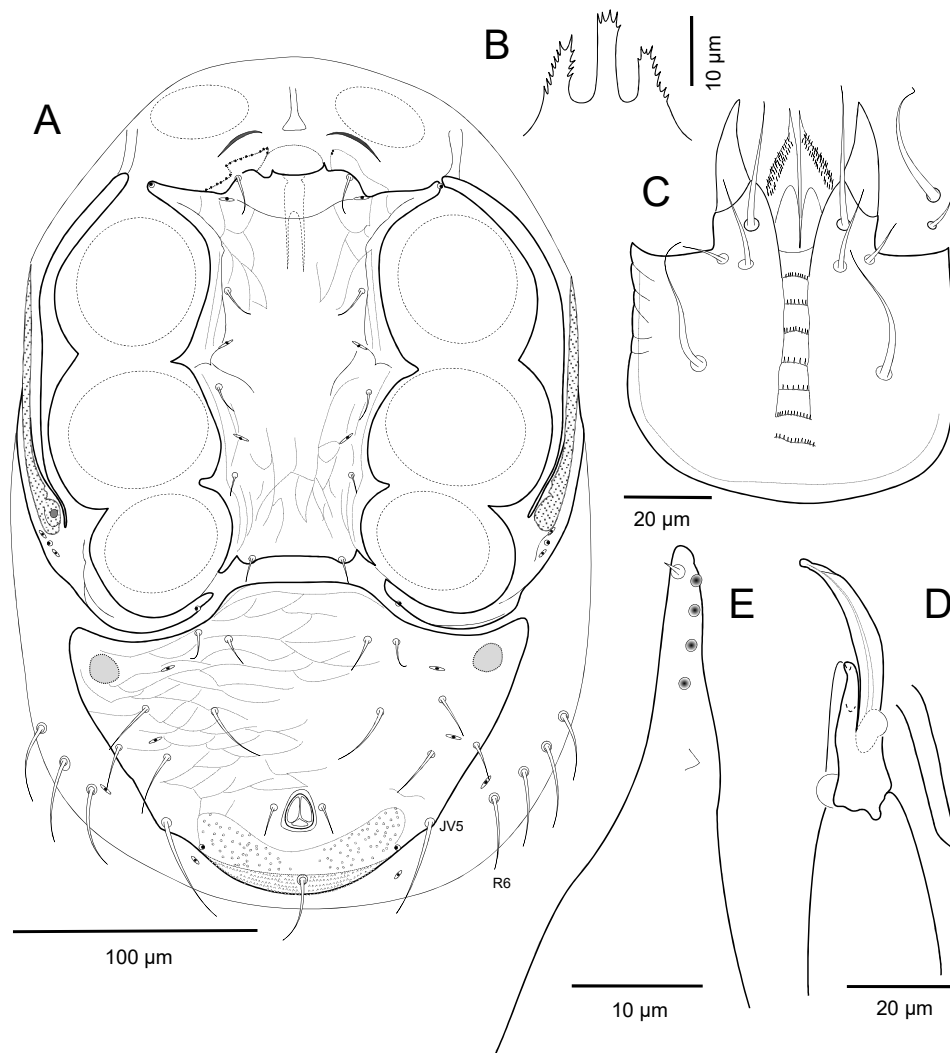
Idiosomatic dorsum — Adult female. Dorsal shield 424 – 450 long, 201 – 245 wide at level of *r3*, 267 – 296 wide at level of *r6* (n=7), lightly reticulate-lineate on lateral surfaces but nearly smooth medially between bases of setae *j4* to *J4*, and sparsely punctate behind level of setae *Z4*; shield with 38 pairs of setae generally similar in size and acutely pointed form, with few apical barbs, more so on *Z4*, *Z5*, *S4*, *S5* (Figs 8A, B); *J1-J3* and *Z1-Z4* slightly longer than longitudinal intervals between their bases, *S2-S4* clearly so; *J5* minute, barbed (4 – 6): *j1* (28 – 31), *j2* (26 – 32), *j3* (41 – 44), *j4* (26 – 32), *j5* (32 – 35), *j6* (45 – 47), *z1* (19 – 24), *z2* (30 – 35), *z3* (37 – 42), *z4* (41 – 45), *z5* (32 – 37), *z6* (41 – 46); *s1* (32 – 38), *s2* (34 – 43), *s3* (40 – 45), *s4* (43 – 48), *s5* (45 – 50), *s6* (47 – 52), *r2* (35 – 42), *r3* erect (21 – 30), *r4* (32 – 48), *r5* (32 – 50), *r6* (32 – 48), *J1* (32 – 42), *J2* (40 – 50), *J3* (43 – 52), *J4* (43 – 52), *Z1* (48 – 51), *Z2* (51 – 54), *Z3* (54 – 58), *Z4* (58 – 62), *Z5* (63 – 70), *S1* (43 – 50), *S2* (44 – 53), *S3* (46 – 58), *S4* (46 – 58), *S5* (43 – 52). Lateral soft cuticle with seven pairs of smooth setae, including *R1* (40 – 48), *R2-R6* (35 – 42) and *ZV5* posteriorly (30 – 33) (Fig. 8D). Peritrematal shield fused to dorsal shield at level of *s1*.

Adult male. Dorsal shield 338 – 340 long, 185 – 200 wide at level of setae *r3*, 200 – 215 wide at level of *r6* (n = 2); shield ornamentation, complement of pore-like structures and setation as in female except slightly more expanded laterally so as to become united with peritrematal shields at level of setae *s2* and bear setae *R1*. Dorsal shield with 39 pairs of setae, their attenuated form and relative lengths as in female. Setae *j1* (21 – 23), *j2* (16 – 26), *j3* (35 – 36), *j4* (21 – 25), *j5* (24 – 25), *j6* (32 – 33), *z1* (14 – 16), *z2* (22), *z3* (32), *z4* (34 – 35), *z5* (27 – 28), *z6* (32 – 36), *s1* (29 – 30), *s2* (30 – 31), *s3* (34 – 38), *s4* (36), *s5* (42), *s6* (35 – 36), *r2*, *r4*, *r5* (33 – 37), *r3* erect, shorter (23 – 27), *r6* (36 – 38), *J1-J3* (27 – 32), *J4* (25 – 27), *J5* (3 – 4), *Z1-Z2* (40 – 43), *Z3* (44 – 45), *Z4*, *Z5* longest (48 – 54), *S1*, *S2* (35 – 41), *S3* (41 – 45), *S4* (40



**Figure 8** *Lasioseius fuscina* n. sp., adult female: A – Idiosoma, dorsal view; B – Detail of denoted dorsal setae; C – Gnathotectum; D – Idiosoma, ventral view; E – Cheliceral digits, paraxial view; F – Subcapitulum; G – Detail of ventral setae of palptrochanter.





**Figure 9** *Lasioseius fuscina* n. sp., adult male: A – Idiosoma, ventral view; B – Gnathotectum; C – Subcapitulum and ventral setae of palptrochanter; D – Chelicera and spermatodactyl, ventral view; E – Detail of cheliceral fixed digit, ventral view.

– 43), *S5* (32 – 35). Lateral soft cuticle with six pairs of setae, *R2-R6* (27 – 37) followed by *ZV5*.

Idiosomatic venter — Adult female. Tritosternum base 26 – 28 long and 10 – 14 wide at its base, with paired laciniae fused for about 33 – 37 of entire length (96 – 100). Presternal region with circumscribed pair of jagged-lineate, granulated areas adhered to anterior margin of sternal shield, sometimes flanked anteriorly by a pair of narrow slightly sclerotized strips on either side of tritosternum base. Sternal shield 87 – 93 long from slight, blunt medial projection of anterior margin to gently concave posterior margin, 85 – 95 wide, weakly reticulate-lineate over much of surface or nearly smooth medially, with arcuate transverse line between poroids *iv1* (Fig. 8D); sternal shield setae of similar lengths, *st1* (15 – 20), *st2*, *st3* (11 – 16). Sternal poroids *iv3* and setae *st4* (6 – 14) inserted together on small metasternal platelets (15 – 20). Endopodal strips narrow between coxae III and IV. Epigynal shield lightly reticulate over entire surface, its narrowly rounded hyaline margin nearly reaching or slightly overlapping posterior edge of sternal shield, its lateral margins concave, narrowed anterior to setae *st5* (11 – 15), and its posterolateral corners slightly emarginated behind *st5*; shield 140 – 147 long,

78 – 87 at widest level at posterior rounded corners, 66 – 71 at level of *st5*, and 49 – 54 at narrowest width between legs IV. Opisthosomatic venter with two pairs of metapodal platelets touching or coalesced on each side, primary pair ovoid to subtriangular, 20 – 25 long, 10 – 12 wide, secondary pair smaller, greatest transverse dimension 8 – 12. Ventrianal shield inversely subtriangular with irregularly rounded anterior corners, with posterolateral margins on either side of anus nearly parallel; surface entirely lightly sculptured, with primarily transverse lineation changing to reticulation behind setae *JV2-ZV2*, except anal region sparsely punctate on either side of postanal seta; shield wider (160 – 183) than long including cribrum (136 – 147), width at anal level (95 – 104); gland pore *gv3* on shield edge posterior to anal opening; shield with four pairs of ventral setae: *JV1* (12 – 17), *JV2* (22 – 27), *JV3* (24 – 31), *ZV2* (22 – 27); with paranal setae (11 – 14) shorter than postanal seta (28 – 35). Soft cuticle with four pairs of simple opisthogastric setae, *ZV1* (11 – 15) anterior to ventrianal shield, *ZV3* (17 – 22), *JV5* attenuated, barbed (48 – 55) flanking the shield, and *ZV5* (30 – 33) somewhat aligned behind *R6*; three pairs of poroids (including *ivp*) on soft opisthogastric cuticle, *ivo2* sometimes captured on anterolateral edge of ventrianal shield. Peritrematal-exopodal shield with lines extending from stigma into rounded posterior margin (Fig. 8D); peritreme extending to level between setae *s1* and *z1* (Fig. 8A). Spermathecal apparatus with cup-like calyx (12 – 15 long including embolus).

Adult male. Tritosternum much as in female, but with base biarticulate, wider (6 – 11) than long (5 – 10), and laciniae (37 – 40) fused (8) for only about 1/5 of total length. Presternal region weakly ornamented, sometimes with pair of narrow strips on either side of tritosternum base. Sternitigenital shield length 158 – 162 from genital opening, widths 65 – 72 at level between coxae II, 50 between coxae IV; shield with a concave arcuate line between poroids *iv1*, lightly lineate-reticulate along lateral margins and posteriorly between coxae IV, unornamented medially between *st2* and *iv3*, with endopodal apices freely acuminate beside coxae IV; setae *st1-st5* of dissimilar lengths as in female, *st1* (14 – 16), *st2* (11 – 12), *st3* (8 – 11), *st4* shorter (4 – 8), *st5* (7 – 8). Ventrianal shield reticulate as in female, its convex anterolateral margins entire behind apices of exopodal strips behind coxae IV, and posterolateral margins not constricted in anal region, its greatest width (173 – 189) larger than its length (123 – 141, including cribrum ca. 3 – 8 long, 73 – 80 wide); shield with seven pairs of opisthogastric setae, *JV1*, *ZV1* (10 – 12), *JV2*, *JV3* (25 – 29), *ZV2* (20 – 26), *ZV3* (17 – 20), and longest *JV5* (40 – 43); postanal seta smooth (26 – 28), about three times as long as paranal setae (8 – 12) (Fig. 9A). Soft opisthogastric cuticle with two pairs of lyrifissures including *ivp*.

Gnathosoma — Adult female. Gnathotectum anterior margin with three denticulate prongs of similar moderately elongate length or medial prong longer than laterals (Fig. 8C). Cheliceral shaft, excluding basal section, 139 – 155 long, with slender digits; dorsal seta simple (10 – 11); fixed digit with tiny subapical tooth and row of 7-10 fine teeth, pilus dentilis minute, at level of 3<sup>rd</sup> apical tooth; movable digit (48 – 51) tridentate (Fig. 8E). Subcapitulum with deutosternal rows differing little in width, most anterior row with 9-10 teeth, 2<sup>nd</sup> to 5<sup>th</sup> rows with 8-15 teeth, basalmost two rows slightly wider, with ca 15-20 teeth (Fig. 8F); subcapitular setae *hp1* (40 – 50) about as long as capitular setae *pc* (40 – 46), longer than *hp3* (27 – 29), and *hp2* (20 – 22). Palp length (113 – 122), apical margin of palptrochanter with two or usually three spines anterolaterally; palptrochanter with internal seta *v1* sickle-shaped, longer (35 – 44) and thicker than *v2* (24 – 30) (Fig. 8G).

Adult male. Gnathotectum anterior margin with elongated prongs as in female (Fig. 9B). Cheliceral shaft, excluding short basal section 91 – 98 long; fixed digit with offset subapical tooth followed by pilus dentilis and sparse row of 4-5 small teeth (Fig. 9E); movable digit (27 – 28) unidentate; spermatodactyl 30 – 40 long, 3 – 6 wide at base, extending anteriorly ca 23 – 30 beyond apex of digit, with narrowed neck and small head apically (Fig. 9D). Corniculi slightly more widely spaced but not more arched than in female, 24 – 26 long, their bases flanked medially by pair of short (5 – 7) spiculate processes (Figs 9C, 11C); internal malae and labrum as in female. Subcapitulum with rows of deutosternal denticles much as in female,

anterior five rows with ca 8-15 teeth, 6<sup>th</sup> and 7<sup>th</sup> rows with ca 15-20 teeth; hypostomatic setae *hp1* (28 – 30) slightly attenuated, about as long as *pc* (24 – 31), longer than *hp3* (20 – 21), and *hp2* shortest (10 – 12) (Fig. 9D). Palpi (length 96 – 101) similar in structure, form of setae as in female; apical margin of palptrochanter with three spines anterolaterally; palptrochanter with inner seta (26 – 30) longer than outer seta (8 – 11) (Fig. 9D).

Legs — Adult female. Legs I (357 – 385) subequally as long as legs IV (360 – 380), and shorter than dorsal shield; other leg lengths (excluding pretarsi): II 286 – 319, III 288 – 303. Leg I pretarsus with biarticulated shaft (16 – 21 to base of claws), claws 10 – 12 long; tarsus (107 – 112) about 1.9-2.1 longer than tibia; other length ratios, femur (70 – 77): genu (50 – 52): tibia (52 – 60), about 1.3: 0.9: 1.0. Legs II, III with tarsus/tibia length ratio about 1.8-2.0, leg IV with that ratio about 1.9-2.0. Chaetotactic formulae of leg segments as given for species-group. Tarsi II-IV with ventroapical process (7 – 9) bluntly pointed, smooth apically (Fig. 14D), and with setae (*d-1*) (15 – 20) nearly as long as pretarsus to base of claws (17 – 20). Tarsi II-III with paradactyli reaching tips of tarsal claws, but tarsus IV with anterior paradactylus extending about 3-5 beyond claw (Fig. 14D). Tarsi II (Fig. 13F), III with setae (*l-1*) shorter (16 – 19), more spinelike than (*v-1*) (28 – 34); dorsal seta *md* (34 – 37) no longer than *pd-2*, *pl-3*, *mv* (34 – 35); setae *al-2*, *ad-2* (36 – 41), *pl-2* (43 – 44), *al-3*, (*pd-3*) (28 – 32); all tarsal setae smooth. Tarsus IV with distal setae (*v-1*) symmetrical in size (26 – 31), slenderer than somewhat spinelike (*l-1*) (15 – 22).

Adult male. Relative leg thicknesses and lengths, excluding pretarsi, similar to those of female, I 305 – 310, II 255 – 260, III 242 – 250, IV 302 – 305. Legs with segment length ratios as in female. Tarsus I pretarsus 10 – 15 to base of claws, claws 5 – 9 long. Tarsi II-IV with dorsoapical setal processes (*d-1*), ventroapical process and pretarsal structures formed as in female, pretarsus lengths 12 – 17 excluding claws (10) (Fig. 13E). Apical setal processes (*d-1*) (11 – 13) shorter than pretarsi to bases of claws (14 – 17). Dimorphic leg setal structures not apparent.

Type material — All specimens collected at the La Selva Biological Station, Heredia Province, Costa Rica (10°26'N, 84°01'W, elevation 50-150 m): HOLOTYPE: adult female, 12 June 1997, ex *Heliconia* sp. leaves, successional plots, coll. ALAS. PARATYPES: 1 adult female, 1 adult male, with same data as holotype; 1 adult female, 12 June 1997, ex coexistent adults of *Cephaloleia belti* Baly and *C. ornatrix* Donckier from *Heliconia* leaves, coll. ALAS; 3 adult females, 15 April 1994, ex adult Chrysomelidae, no host plant data, coll. M. Paniagua; 2 adult females, 18 February 1994, ex adult Chrysomelidae, no host plant data, coll. ALAS; 3 adult females, 1 adult male, date not indicated, ex adult *Cephaloleia belti* on *Calathea* leaf, coll. not indicated.

Host identifications — As noted for the records of *Lasioseius serripes*, the identities of the associated beetles given above are in accord with current molecular studies, which indicate that records of *Cephaloleia belti* and *C. ornatrix* on *Heliconia pogonantha* are in accord with field diet records. While *C. belti* is a host generalist, *C. ornatrix* is a host specialist of *Heliconia pogonantha* (Staines & Garcia-Robledo 2014, Garcia-Robledo *et al.* 2017).

Etymology — The specific name is based on the Latin noun, 'fuscina', indicating a three-pronged fork or trident, and refers to the elongated three-pronged gnathotectum characteristic of this species.

Remarks — Limited collection data indicate a possible host association preference for *Cephaloleia belti*, a plant host generalist. If so, the mite/host size would correlate, as adults of *L. fuscina* are the smallest of the described mites of this species-group, and among species of *Cephaloleia*, beetles of *C. belti* are relatively small-sized as well, although those of *C. ornatrix* are mid-sized. However, collection data uncertainties must be kept in mind, as two of the collection samples for this species also included many adults of *Lasioseius serripes*, one

of them as well with a few adults of *L. cassidini* which also co-occurred with *fuscina* in two other samples (Table 1). Tentatively, subject to further studies, we conclude that, at La Selva, *Lasioseius fuscina* may be associated regularly with the host generalist *Cephaloleia belti* and to some extent with the host specialist *C. ornatrix* on *Heliconia pogonantha*.

### ***Lasioseius duobtusetis* n. sp. (Figures 10, 12E-F, 13I, 14C)**

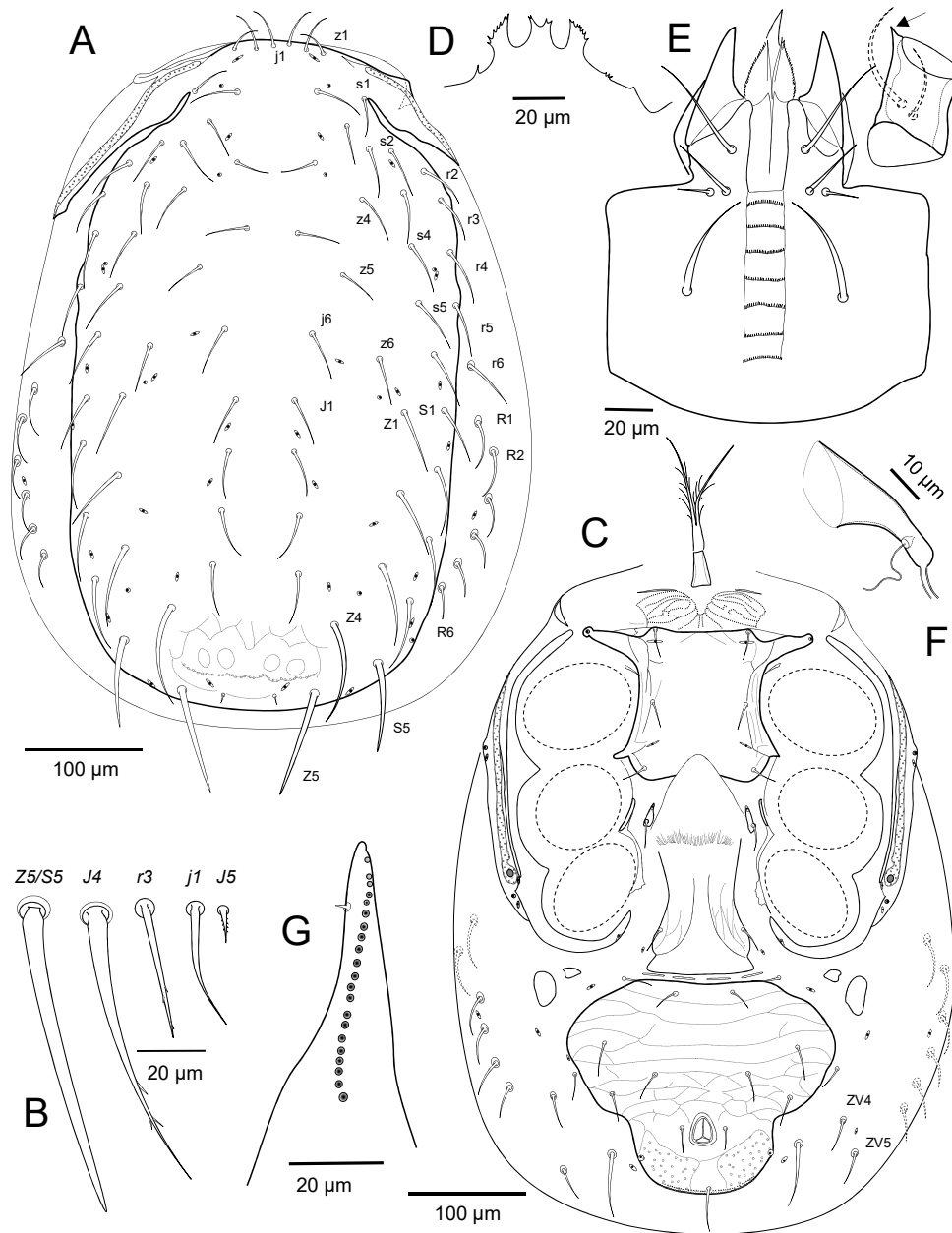
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**Diagnosis.** Adult female: Sternal shield weakly lineate along lateral margins, smooth medially, its posterolateral corners not emarginated; poroids *iv3* and setae *st4* together on slender metasternal platelets; epigynal shield partially reticulated laterally, its lateral margins gently concave, narrowed anterior to setae *st5*; ventrianal shield with posterolateral margins on either side of anus nearly parallel, and with four pairs of opisthogastric setae, *JV1* on shield; metapodal plates well separated on each side. Dorsal setae *r6* on soft cuticle; setae *Z5*, *S5* thickened, spinelike with blunt tips, *Z4*, *S4* somewhat thickened but attenuated. Adult attributes: Gnathotectum anterior margin triramous, denticulate. Fixed chela with file of ca 20 teeth in female. Sternal setae *st1* inserted on anterior edge of sternal shield. Tarsi II-IV with ventral apical process bluntly pointed, smooth apically; tarsi II-III with setae (*v-1*), (*l-1*) symmetrically stout; tarsus IV with apical seta *av-1* longer, stouter than *pv-1*, (*l-1*), and pretarsus with anterior paradactylus longer than posterior one.

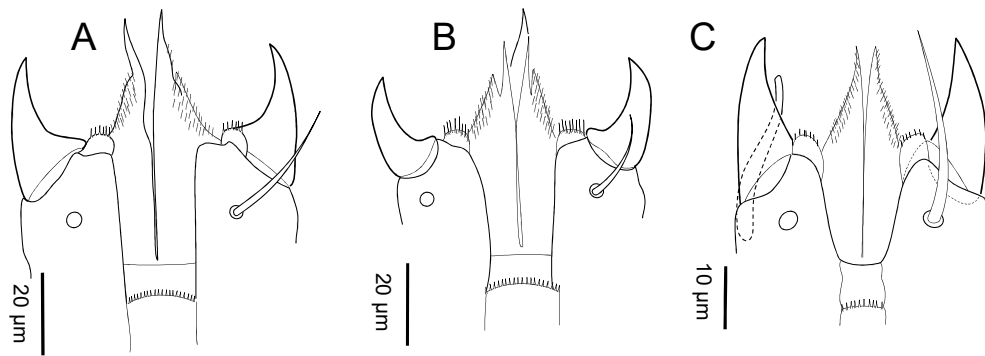
### **Description**

Idiosomatic dorsum — Adult female. Dorsal shield 540 – 595 long, 293 – 319 wide at level of *r3*, 320 – 345 at level of *r5* (n=4), lightly reticulated over most of surface, but nearly smooth in dorsal hexagonal area (delimited by setae *j5-z5-j6*), not punctate behind level of setae *Z4*, but finely transversely striate between *Z5* behind *J5*; shield with 37 pairs of setae, with lengths of most podonotal setae and *J1-J3* not reaching bases of following setae; *Z5*, *S5* thickened, spinelike with blunt tips, *Z4*, *S4* somewhat thickened but attenuated (Figs. 10A, B): *j1* (34 – 42), *j2* (31 – 40), *j3* (39 – 43), *j4* (28 – 34), *j5* (30 – 37), *j6* (38 – 50), *z1* (24 – 27), *z2* (33 – 40), *z3* (40 – 43), *z4* (40 – 50), *z5* (30 – 38), *z6* (37 – 40), *s1* (29 – 35), *s2* (38 – 50), *s3* (43 – 50), *s4* (40 – 51), *s5* (45 – 52), *s6* (50 – 57), *r2* (40 – 50), *r3* erect (38 – 42), *r4* (44 – 57), *r5* (47 – 57), *J1* (33 – 38), *J2* (33 – 42), *J3* (43 – 52), *J4* (40 – 57), *J5* minute and barbed (7 – 9), *Z1* (53 – 62), *Z2* (58 – 62), *Z3* (62 – 70), *Z4* (80 – 87), *Z5* blunt (85 – 103), *S1* (48 – 59), *S2* (55 – 67), *S3* (58 – 69), *S4* (63 – 75), *S5* blunt (75 – 90). Lateral soft cuticle with eight pairs of smooth setae, including *r6* (45 – 60), *R1* (35 – 52), *R2-R6* shorter (28 – 42) and *ZV5* posteriorly (40) (Fig. 10C).

Idiosomatic venter — Adult female. Tritosternum base 26 – 35 long, 15 – 16 wide at its base, with paired laciniae fused for about 10 – 17 of their total length (112 – 118). Presternal region with circumscribed pair of weakly granulated areas with jigsawed lineation, sometimes flanked anteriorly by a pair of narrow slightly sclerotized strips. Sternal shield 115 – 127 long, with slightly concave posterior margin, 98 – 109 wide, its surface nearly smooth medially, weakly lineate along lateral margins; sternal setae *st1-st3* attenuate, of similar length (21 – 25) (Fig. 10C). Sternal poroids *iv3* and setae *st4* (20 – 22) inserted together on small metasternal platelets (21 – 26 long). Endopodal strips narrow between coxae III and IV. Epigynal shield with lightly reticulated lateral areas separated by smooth area medially, its narrowly rounded hyaline anterior margin reaching or slightly overlapping posterior edge of sternal shield, its lateral margins slightly concave, narrowed anterior to setae *st5* (20 – 24), and its posterolateral corners slightly emarginated behind *st5*: shield 178 – 197 long, 82 – 102 at widest level at posterior angulate corners, 70 – 75 at level of *st5*, and 54 – 62 at narrowest width between legs IV. Opisthosomatic venter with two pairs of well separated metapodal platelets, primary pair oval, 30 – 40 long, 15 – 19 wide, secondary pair small, greatest dimension transverse, 18 – 25. Ventrianal shield inversely subtriangular with rounded anterior corners, with posterolateral



**Figure 10** *Lasioseius duobtusisetis* n. sp., adult female: A – Idiosoma, dorsal view; B – Detail of denoted dorsal setae; C. Idiosoma, ventral view; D – Gnathotectum; E – Subcapitulum and ventral setae of palptrochanter; F – Spermathecal structures; G – Detail of cheliceral fixed digit, ventral view.

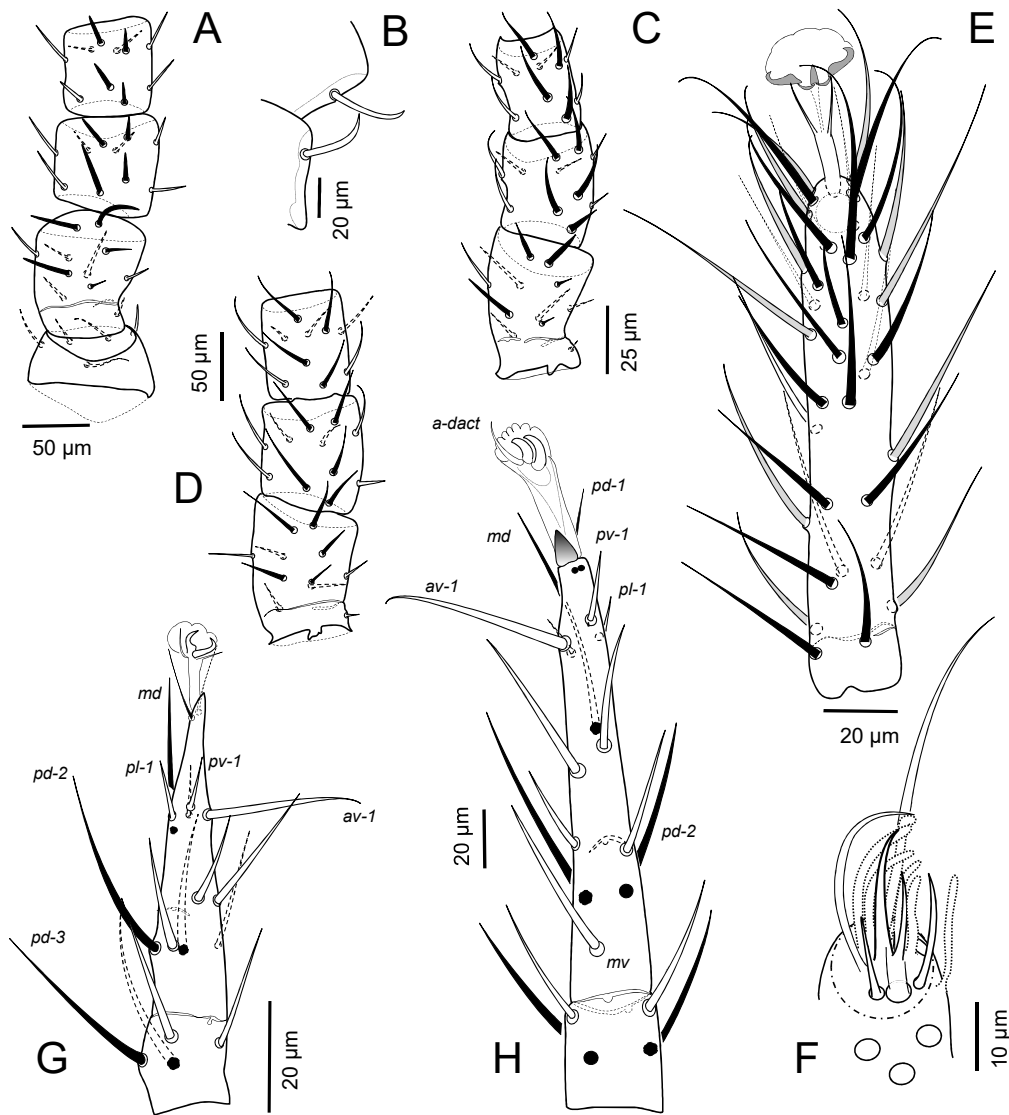


**Figure 11** Distal subcapitular region, adult males: A – *L. cassidini*; B – *L. serripes*; C. — *L. fuscina*

margins on either side of anus nearly parallel; surface entirely sculptured, with primarily transverse lineation changing to reticulation behind setae *JV2-ZV2*, except anal region conspicuously punctate on either side of postanal seta; shield wider (216 – 235) than long, including cribrum (176 – 197), 113 – 132 wide at anal region; shield with four pairs of ventral setae and glandular pores *gv3*: *JV1*(19 – 22), *JV2* (22 – 25), *JV3* (23 – 27), *ZV2* (23 – 29); with paranal setae (17 – 20) shorter than postanal seta (36 – 45). Soft cuticle with five pairs of simple opisthogastric setae, *ZV1* (22 – 24) anterior to ventrianal shield, *ZV3* (22 – 26), *ZV4* (25 – 33), *JV5* markedly thicker (53 – 57) flanking the shield, and *ZV5* somewhat aligned behind *R6*; four pairs of poroids (including *ivp*). Peritrematal-exopodal shield lineate posteriorly behind leg IV; peritreme extending to level between insertions of setae *s1* and *z1* (Fig. 10C). Spermathecal apparatus with cup-like calyx 40 long including embolus and 22 wide at distal margin (Fig. 10F).

**Gnathosoma** — Gnathotectum anterior margin triramous, with three short denticulate prongs, lateral margin slightly serrate (Fig. 10D). Cheliceral shaft, excluding basal section, 161 – 182 long, with slender digits; dorsal seta blunt (10); fixed digit with tiny, slightly offset subapical tooth and row of 20-28 very fine teeth (Fig. 10G), pilus dentilus minute (3) at level of 4<sup>th</sup> or 5<sup>th</sup> apical tooth; movable digit (70 – 80) tridentate. Subcapitulum rows of deutosternal denticles each with numerous (ca 20-30) fine denticles, 6<sup>th</sup> and sometimes 7<sup>th</sup> slightly widest and with ca 35 and 30 teeth, respectively; subcapitular setae *hp1* (41 – 45) nearly as long as capitular setae *pc* (48 – 50), *hp3* shorter (30 – 32), but longer than *hp2* (13 – 17) (Fig. 10E). Palp length (160 – 165); apical margin of palptrochanter with a single spine anterolaterally; palptrochanter setae dissimilar in length, *v1* 42 – 45 and *v2* 27 – 36 (Fig. 10E).

**Legs** — Legs I (503 – 562) slightly longer than legs IV (488 – 546), and shorter than dorsal shield; other leg lengths (excluding pretarsi): II 390 – 445, III 380 – 442. Leg I pretarsus with biarticulated shaft (25 – 27 to base of claws), claws 15 long; tarsus (142 – 167) about 1.8 longer than tibia; other length ratios, femur (88 – 105): genu (73 – 82): tibia (80 – 95), about 1.1: 0.9: 1.0. Legs II-III with tarsus/tibia length ratio about 1.8-2.2, leg IV with that ratio about 1.8-1.9. Chaetotactic formulae of leg segments as given for species-group. Tarsi II-IV with ventroapical process (8 – 10) bluntly pointed, smooth apically (Figs 13I, 14C), and with setae (*d-1*) (13 – 18) nearly as long as pretarsus to base of claws (15 – 18). Tarsi II-III with paradactyli reaching tips of tarsal claws, but tarsus IV with anterior paradactylus about 1.5 longer (Fig. 14C). Tarsi II and III with setae (*l-1*) and (*v-1*) symmetrically stout, *pl-1* (18) and *pv-1* (18 – 25) slightly longer than *al-1* (15) and *av-1* (17 – 20), respectively; *md* (43 – 50) reaching bases of claws; setae (*d-2*) symmetrically attenuate (45 – 53). Tarsus IV with apical

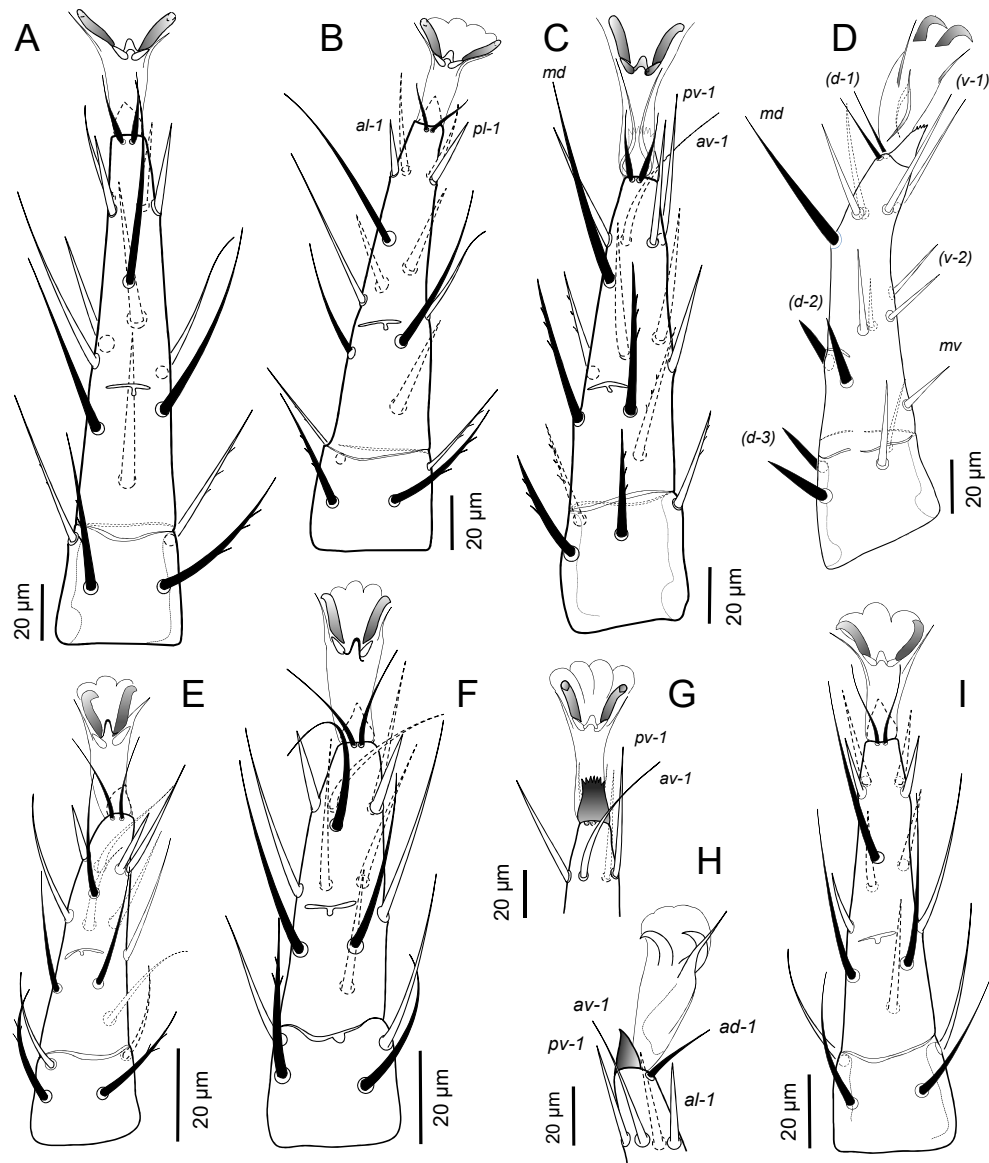


**Figure 12** A-D – Leg II, dorsal view (right leg, excluding tarsus, coxa and trochanter), adult males: A— *Lasioseius serripes* n. sp.; B – *L. serripes*, detail of ventral setae on genu and tibia III; C – *Lasioseius cassidini* n. sp.; D – *Lasioseius fuscina* n. sp. E, F – *Lasioseius duobtussetis*, adult female, tarsus I right leg, dorsal view; E – General aspect without detail of dorsodistal sensorial area; F – Detail of dorsodistal sensorial area. G – *Lasioseius serripes*, protonymph, tarsus IV left leg; H – *Lasioseius* sp. undescribed, adult female, tarsus IV right leg, ventral view. (Solid black setae in figures A-G and solid black circles in figures G and H indicate dorsal setae).

seta *av-1* longer (28 – 45), stouter than *pv-1* (16 – 23); setae (*l-1*) symmetrically similar in length (13 – 15), *md* (55 – 61) and (*d-2*) (60 – 72) attenuate (Fig. 14C).

ADULT MALE. Unknown.

Type material — All specimens collected at the La Selva Biological Station, Heredia Province, Costa Rica (10°26'N, 84°01'W, elevation 50-150 m): HOLOTYPE: adult female, (CRI 002, 739028), 8 July 1997, ex adult *Chelobasis perplexa* Baly, no host plant data, coll. M. Paniagua. PARATYPES: 1 adult female, February 1994, associated with adult *Chelobasis* sp. on leaf of *Heliconia pogonantha*, coll. E.E. Lindquist & ALAS; 1 adult female, 15 April 1994, ex adult *Chrysomelidae*, no host plant data, coll. M. Paniagua; 1 adult female, 12 June 1997, ex adult

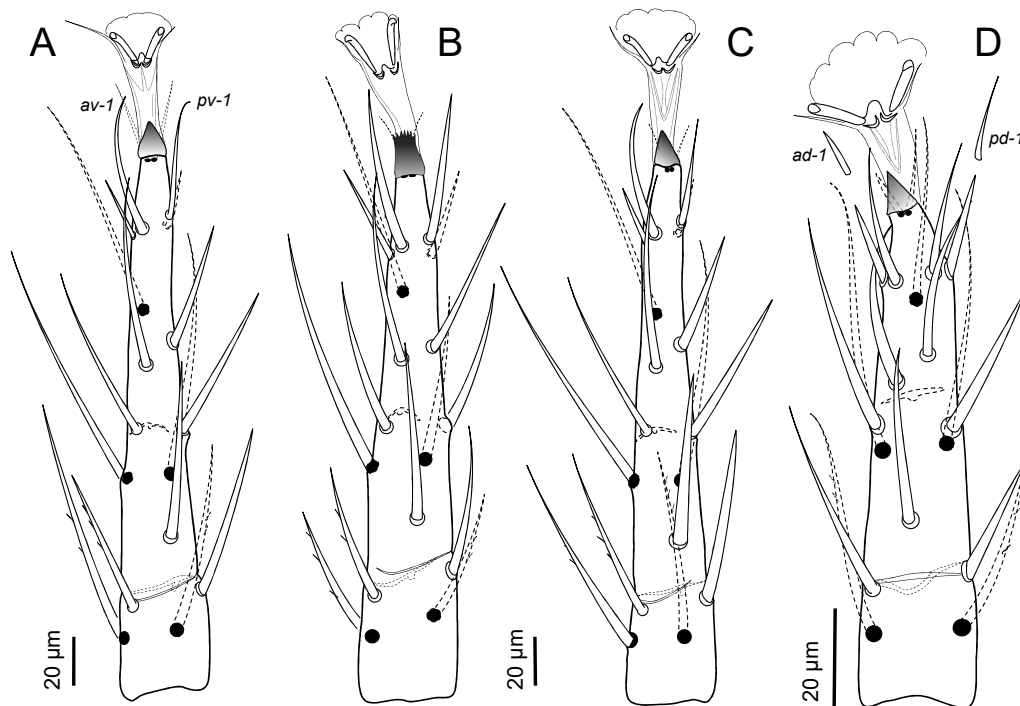


**Figure 13** Tarsus II, right leg. A, B, H. *Lasioseius cassidini* n. sp.: A – Adult female, dorsal view; B – Adult male, dorsal view; H — Detail of distal region, lateroventral view. C, D, G. *Lasioseius serripes* n. sp.: C – Adult female, dorsal view; D – Adult male, anterolateral view; G. Detail of distal region, ventral view. E, F. *Lasioseius fuscina* n. sp.: E – Adult male, dorsal view; F – Adult female, dorsal view. I — *Lasioseius duobtusisetis* n. sp., adult female, dorsal view. (Solid black color indicates dorsal setae on segment).

*Cephaloleia aequilata* Uhmman (misidentification, see below) on leaf of *Calathea*, coll. ALAS; 1 adult female, 12 June 1997, ex adult *Cephaloleia erichsonii* Baly on leaf of *Calathea*, coll. ALAS.

Host identifications — With one exception, the identities of the associated beetles given above are in accord with current molecular studies of their field diet records, which indicate that one haplotype of *Chelobasis perplexa* sensu stricto is on *Heliconia pogonantha*. *Cephaloleia erichsonii* is a host generalist. *Cephaloleia aequilata* does not occur at La Selva, and specimens identified as such from there are, in all cases checked by DNA barcodes, *C. dilaticollis* Baly, which is a host generalist, often on *Heliconia*, *Calathea* and other host plants (Carlos Garcia-Robledo, personal communications 2017; Garcia-Robledo *et al.* 2017).





**Figure 14** Tarsus IV, adult females, right leg, ventral view: A – *Lasioseius cassidini* n. sp.; B – *Lasioseius serripes* n. sp.; C – *Lasioseius duobtusisetis* n. sp.; D – *Lasioseius fuscina* n. sp. (solid black circles indicate dorsal setae insertions).

**Etymology** — The specific name is a Latinized adjectival combination of ‘duo-obtusi-setis’, referring to two pairs of characteristically blunt-tipped setae Z5 and S5 on the dorsal shield.

**Remarks** — One female asymmetrically lacks one of setae s2. One female asymmetrically has seta JV4 inserted on the ventrianal shield; otherwise, this setal pair is symmetrically absent, characteristically in all species described of this group.

One female at hand, from under elytra of *Cephaloleia erichsonii*, Corcovado National Park, May 1997, coll. D. Johnson, has been tentatively identified as *Lasioseius duobtusisetis*, but is excluded from the type material. It differs primarily from other females by having lengths of most podonotal setae and J1–J3 longer, reaching beyond bases of following setae; yet setae Z5, S5 are thickened, spinelike with blunt tips, and Z4, S4 somewhat thickened but attenuated, which are distinctive of this species.

Two aspects of the sparse collection data are notable, with two records of association with beetles of the genus *Chelobasis*, and two other records with beetles of two species of *Cephaloleia* from leaves of a different genus of host plant, *Calathea*. Tentatively, subject to further studies, we conclude that, at La Selva, *Lasioseius duobtusisetis* is associated regularly with generalist forms of *Chelobasis perplexa* and *Cephaloleia erichsonii* on leaves of various species of *Heliconia* (and *C. erichsonii* also on various species of *Calathea* and *Goepertia*), and also to some extent with another generalist form, *Cephaloleia dilaticollis* on a similar variety of host plant genera (Staines & Garcia-Robledo 2014, Garcia-Robledo *et al.* 2017).

**Table 1** Co-occurrence of species of *Lasioseius* with beetles in host plant leaves, La Selva, Costa Rica. Abbreviations: coex, coexistent; *H.*, *Heliconia*; n/c, no data; ALAS, Arthropods of La Selva paratonomist collectors; DJ, Derek Johnson, collector; EEL, Evert E. Lindquist, collector; MP, Maylin Paniagua, collector.

Collection Records				<i>Lasioseius</i> new species			
Coll. date	host beetle	host plant	collector	<i>cassid.</i>	<i>serripes</i>	<i>fuscina</i>	<i>duobtu.</i>
Feb '94	<i>Chelobasis</i> sp.	<i>H. pogonantha</i>	EEL/ALAS	+			+
Feb '94	<i>Cephaloleia vicina</i> (=bella)	<i>H. pogonantha</i>	EEL/ALAS	+			
18 Feb '94	Chrysomelidae	n/c	ALAS	+		+	
15 Apr '94	Chrysomelidae	n/c	MP	+		+	+
June '97	<i>Cephaloleia vicina</i> (=bella)	<i>H. pogonantha</i>	n/c	+			
June '97	<i>Cephaloleia bella</i>	n/c	DJ	+			
June '97	<i>Cephaloleia belti</i>	n/c	DJ	+			
June '97	<i>Cephaloleia ornatrix</i>	n/c	DJ		+		
2 June '97	hispidines	Heliconiaceae leaves	EEL	+			
12 June '97	n/c	<i>Heliconia</i> leaves	ALAS		+	+	
12 June '97	coex <i>Ceph. belti/ornatrix</i>	<i>Heliconia</i> leaves	ALAS	+	+	+	
12 June '97	<i>Ceph. aequilata</i> (=dilatocollis)	<i>Calathea</i>	ALAS				+
12 June '97	<i>Cephaloleia erichsonii</i>	<i>Calathea</i>	ALAS				+
8 July '97	<i>Chelobasis perplexa</i>	n/c	MP (739027,8)		+		+
8 July '97	<i>Cephaloleia bella</i>	<i>H. pogonantha</i>	MP	+			
97?	<i>Cephaloleia belti</i>	<i>Calathea</i>	ALAS			+	
May '97	<i>Chelobasis bicolor</i>	n/c	DJ -Corcovado NP	+			

## Discussion

### Life history aspects

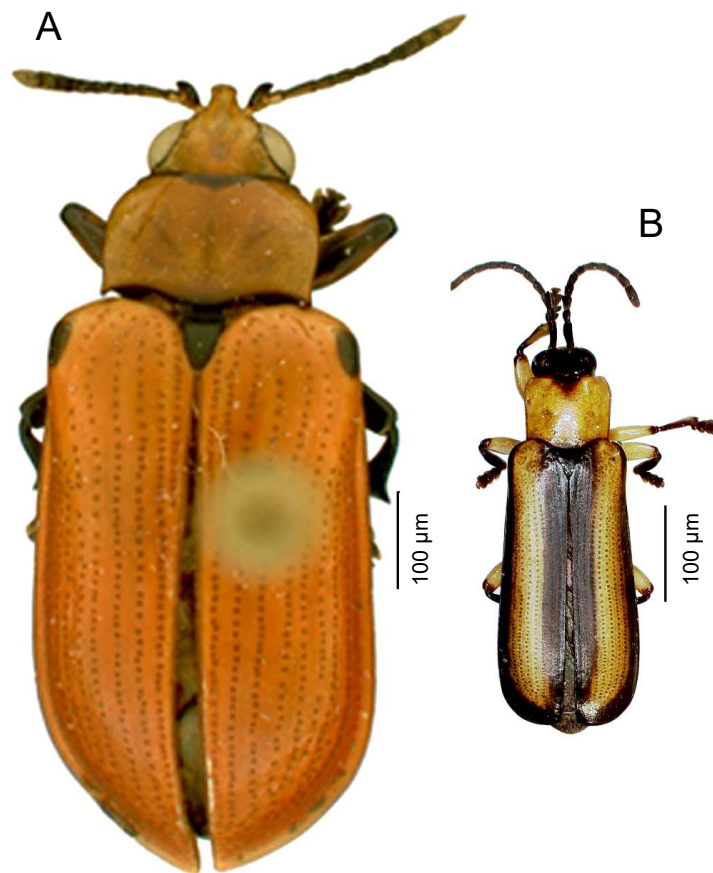
When furred leaves of *Heliconia* were opened for observation of their arthropodan occupants, mites of the *Lasioseius cassidini* species-group were among several different taxa of mesostigmatans found associated with hispine beetles on the moist inner leaf surfaces (Lindquist & Moraza 2014). Quite active, adult females and males ran around on and with the beetles as the latter were removed from the leaves. Beetles observed subsequently under a stereomicroscope in the lab were found to harbor mesostigmatans of other taxa under their elytra (Moraza & Lindquist 2015), but these did not include the *Lasioseius* mites.

Based on viewing a few adult females each with a fully formed larva in its opisthosoma, species of the *cassidini*-group are larviparous. Gravid females presented no indications of nymphiparity, such as occurs rarely among insect-parasitic forms of gamasine mites (Lindquist *et al.* 2016).

Although species of *Lasioseius* generally disperse as adult females phoretic on arthropodan associates, this was not determined for members of the *cassidini*-group, as the behavior of adults of both sexes running off and on the beetles may differ from a phoretic behavior of remaining on the beetles upon their departure for other plant host resources.

### Two or three species of mites of the same species-group in particular collection samples

The collection data for each species of the *cassidini*-group show some overlap with others, indicating their coexistence to a considerable extent (Table 1). Thus, *L. cassidini* was found with *L. fuscina* in three collection instances, along with *L. serripes* in one of those three, and with *L. duobtusisetis* in another, and with *L. duobotusisetis* alone in yet another; separately, *L. serripes* was found with *L. fuscina* in another collection, and with *L. duobtusisetis* in yet another. This may be largely due to coexistence of their hispine beetle associates. Because of



**Figure 15** Dorsal habitus photos of hispine beetle hosts, shown at same size scale: A – *Chelobasis perplexa* Baly; B – *Cephaloleia bella* Baly.

different diet breadths and overlapping host ranges, several species of these beetles (as many as five of *Cephaloleia* and two of *Chelobasis*) may coexist within the scrolls formed by the young rolled leaves of just one plant (Garcia-Robledo *et al.* 2010, Staines 2011, Schmitt & Frank 2013, Garcia-Robledo *et al.* 2017).

### Sizes of mites relative to their beetle hosts

Adult body sizes clearly differ among the four species described, those of *L. cassidini* and *L. fuscina* clearly larger and smaller, respectively, than those of *L. serripes* and *L. duobtusetis*. Strikingly, those of *L. fuscina* are hardly half the size of those of *L. cassidini*. Under the remarks for some species, we have speculated about possible correlation between sizes of these mites and sizes of possibly preferred ‘companions’ or host associates. Previously, in dealing with other taxa of gamasine mites that undergo development under the elytra of these same beetles, we referred to Harrison’s rule (Harrison 1915), as the sizes of those closely symbiotic mites are roughly proportional to the sizes of their hosts (Moraza & Lindquist 2015). However, the adaptive basis for that pattern is poorly understood (Johnson *et al.* 2005), and mites of the *cassidini* species-group of *Lasioseius* present no morphological or behavioral indications of a parasitic way of life. Their cheliceral dentition and other gnathosomatic structures are typical of many species of the genus, whose members are mostly thought to be predators, often of collembolans and other mites (Karg 1993), but also of nematodes (Walter & Lindquist 1989).

For the *Lasioseius cassidini* species-group the data available are inadequate to test whether such mite/beetle size correlations exist. If such a correlation were found to exist, we would anticipate that the two mite species with clearly larger adults are associated primarily with the two species of *Chelobasis*, whose adults are clearly larger than those of the species of *Cephaloleia* (Figs. 15A, B).

## Fungal associations

A fungal ‘foot’ was noted on the dorsal shield of one adult female *Lasioseius serripes* associated with *Cephaloleia ornatrix*, and one was noted on the epigynal shield and another on coxa IV on each of two other adult female *Lasioseius serripes* associated with *Cephaloleia ornatrix* and *C. belti*. This may be the same entity as an undescribed species of the laboulbeniaceae fungus *Rickia*, noted abundantly on adult gamasine mites of *Makarovaia ornata* Moraza & Lindquist, which are sometimes coexistent with those of *Lasioseius* (Moraza & Lindquist 2015). The rarity of such findings among specimens of *Lasioseius* gives further evidence of preferential association between these fungi and *Makarovaia* mites. As the findings of this fungus among members of the *cassidini*-group are restricted to *L. serripes*, perhaps mites of this species more frequently encounter those of *Makarovaia* when the latter’s *Chelobasis* beetle hosts coexist with *Cephaloleia ornatrix* or *C. belti*. Collection records for *L. serripes* accord with this speculation.

## Identification issues

The remarks under each mite species have touched upon how morphologically closely similar some of their hispine beetle associates are, to the extent that some beetles may have been misidentified, and some readily distinguished primarily by molecular analysis (Garcia-Robledo *et al.* 2016, 2017). Similarly, then, we are concerned whether our newly-proposed species-group may consist of a complex of multiple cryptic species with similar morphology. We hope that the details of our descriptions and illustrations may guard against misidentifications, anticipating the level of current research being done by Garcia-Robledo and collaborators on these hispine beetles, which combines traditional taxonomy, ecological observations and molecular markers to uncover the cryptic diversity in complex plant/insect herbivore/mite symbiont networks.

## Host preferences and species diversity

Available collection data do not clarify whether preferred host associations exist among mites of the *cassidini* species-group. However, the fact that five morphologically readily-discriminated forms occur among several commonly coexisting beetle species (five of *Cephaloleia* and two of *Chelobasis*) indicates host preference patterns, as yet unclarified. If these limited records of the *cassidini* species-group mite diversity and hispine-beetle host preferences represent some degree of reality, there may be a bewildering array of these mites associated with the hundreds of species of rolled-leaf hispine beetles occurring throughout the Neotropical Region, *i.e.*, ca 200 species of *Cephaloleia* (Staines & Garcia-Robledo 2014), 4 of *Chelobasis* (Staines 2009), and perhaps other genera as yet not determined to be associates.

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