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A newly recognized family of the Ascoidea (Acari: Mesostigmata: Gamasina), based on a revised concept of the subgenus *Lasioseius* (*Endopodalius*) Christian and Karg, 2006

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Original research

ABSTRACT

The systematic position of the subgenus *Endopodalius* Christian and Karg, 2006, previously recognized by Lindquist and Evans, 1965, as the *scutalis* species group in *Lasioseius*, is reviewed. Based in part on plesiomorphic structures of the female sperm access system being of a laelapoid type, it is removed as a subgenus of the blattisociid genus *Lasioseius* in the superfamily Phytoseioidea and accomodated as a separate genus within the superfamily Ascoidea. In other respects, adult females of this taxon are so distinctive apomorphically to justify separate family group recognition, Endopodaliidae, **fam. nov.**, tentatively related as a sister-group to the morphologically and behaviorally more derived Antennochelidae Lindquist and Moraza, 2014. Species of this family are tropical, their adult females phoretic on beetles of various families of the infraorder Cucujiformia, suborder Polyphaga. A diagnosis of the family and revised description of *Endopodalius* based on adult females and males are presented, with an updated key to world recognized species of the genus, including the following new binominal combinations, *Endopodalius americanus* (Chant,1963), *Endopodalius mouchei* (Loots, 1980), and a new synonym: *E. scutalis* (Banks, 1914) (= *E. prorsoperitrematus* Abo-Shnaf *et al.*, 2016). A lectotype is designated from type material of *Hypoaspis scutalis* Banks, 1914.

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Introduction

The taxon *Lasioseius (Endopodalius)* was first proposed as a subgenus by Christian and Karg (2006) in their review of the predatory mite genus *Lasioseius* Berlese, 1916. Over forty years previously, the same taxon had been recognized and proposed as the "Scutalis Group» of the genus *Lasioseius* in the unpublished thesis by Lindquist (1964), and thereafter by Lindquist and Evans (1965, p.54) who listed all of the then-named species in that group. The same species group was also referred to as the "*Lasioseius alter* group» by Christian and Karg (2006, p. 135). More recently, the taxon named as *Endopodalius* has continued to be recognized as a subgenus of *Lasioseius* by various authors (Lindquist and Moraza, 2010, 2012; Moraza and Lindquist,

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2011, 2018; Moraes *et al.*, 2016; Abo-Shnaf *et al.*, 2016; Argolo *et al.*, 2018; Quintero-Gutiérrez *et al.*, 2020; Moraza and Balanzategui, 2023). The relationship of *Endopodalius* to *Lasioseius* has been based on various morphological aspects, including the absence versus presence of a phytoseioid sperm access system (Alberti, 2002; Di Palma and Alberti, 2005), which latter is a basic autapomorphic characteristic of the superfamily Phytoseioidea *sensu* Lindquist *et al.* (2009; see below), to which *Lasioseius* (Blattisociidae) formally belongs. Loots (1980) particularly illustrated the spermatheca of *Lasioseius mouchei* Loots, 1980 (herein recognized as belonging in *Endopodalius*), as did Moraza and Balanzategui (2023) for *L. (Endopodalius) ibericus* Moraza & Balanzategui, 2023. However, their descriptions did not describe or distinguish these structures as of the phytoseioid-type, and their illustrations do not show any detailed sclerotized structures definitive of the phytoseioid-type, the latter characterized by a sclerotized calyx and associated embolus (Evans, 1992; Alberti and Coons, 1999; Alberti, 2002) from which a long, fine accessory duct leads to a secondary structure, the spermathecal capsule (Athias-Henriot, 1971), which sometimes is elaborated into species-specific forms (Lindquist, 1964; Walter and Lindquist, 1997). Otherwise, the sperm access system had not been illustrated or described in the female of any of the eight species of *Lasioseius* assigned to *Endopodalius* by Christian and Karg (2006), who overlooked assigning *Lasioseius imitans* (Berlese, 1910), *L. americanus* Chant, 1963, and *L. mouchei* Loots, 1980 to their subgenus. In addition, females of *Lasioseius gabrielae* Santos and Argolo, 2018 (in Argolo *et al.*, 2018), and of a further, five undescribed Neotropical species of *Endopodalius* examined by one of us (E.E.L.) do not present sperm access structures of the phytoseioid-type.

Material and methods

Studied specimens were previously prepared, sometimes over a century ago (e.g., Berlese, 1910; Banks, 1914), mounted on microslides in a variety of media, *e.g.*, either resin-based, permanent Canada balsam or water-miscible Hoyer's or a similar modification of Berlese's gum chloral medium (Singer 1967) and sealed with asphaltum or GLPT insulating varnish.

Morphological observations and illustrations were made using compound microscopes equipped with differential interference contrast (DIC) and phase contrast optical systems, drawing tubes and stage-calibrated eyepiece micrometers. Setal notation for the idiosoma follows that of Lindquist and Evans (1965) as modified slightly by Lindquist (1994). Notation for leg and palpal setation follows that of Evans (1963, 1964, 1969). Distinction of pore-like structures on the idiosomal integument as either poroids (lyrifissures) or glandular openings (solenostomes), as distinguished morphologically by Athias-Henriot (1969) and physiologically by Krantz and Redmond (1987), is applied. Notation for pore-like structures of the peritrematal region follows that of Johnston and Moraza (1991).

Observational notes were made (E.E.L.) from studies of primary type material of each of the following species accorded herein to *Lasioseius (Endopodalius)*: *Lasioseius (Zygoseius) alter* Vitzthum, 1925, Zoologische Sammlung des Bayerischen Staates, Munich; *Lasioseius americanus* Chant, 1963, Canadian National Collection of Insects, Arachnids, and Nematodes (CNCI), Agriculture & Agri-Food Canada, Ottawa; *Lasioseius convexus* Krantz, 1962, Oregon State University, Corvallis; *Lasioseius humberti* Athias-Henriot, 1959, Laboratoire d'Acarologie de l'École Pratique des Hautes Études, Paris and Hochschule für Bodenkultur, Vienna; *Lasioseius (Endopodalius) ibericus* Moraza & Balanzategui, 2023, Universidad de Navarra; *Lasioseius imitans* Berlese, 1910, Research Centre for Plant Protection and Certification (CREA-DC), Florence; *Hypoaspis scutalis* Banks, 1914, Museum of Comparative Zoology, Harvard University, Cambridge; *Lasioseius tectus* Hyatt, 1964, British Museum (Natural History), London.

Background systematics

The systematic placement of *Endopodalius* had been problematical prior and subsequent to the description and illustration of the spermathecal structure of any of its species (*e.g.*, by Loots, 1980, figure 28 for *mouchei*; by Esteca *et al.*, 2020, figure 3F for *prorsoperitrematus* Abo-Shnaf *et al.*, 2016; and by Moraza and Balanzategui, 2023, figure 2D for *ibericus*). What are its sister-group relationships, and in what family of the cohort or infraorder Gamasina should *Endopodalius* be placed? Using the key to families of the order Mesostigmata presented by Lindquist *et al.* (2009), the taxon *Endopodalius* readily reaches couplet 59, where it nearly entirely 'fits' 59b for Blattisociidae, except for one major aspect – the form of the female sperm access system not having any of the apomorphic aspects of the phytoseioid-type, as characterized by Evans (1992; see below). Alternatively, female *Endopodalius* do not share the peculiarities of couplet 59a for Melicharidae, particularly apomorphic aspects of the fixed and movable cheliceral digits (inflated form of pilus dentilis and mucronate midventral process, respectively), and form of the epigynal and opisthogastric shields.

If *Endopodalius* females have a sperm access system that has become degenerated, simplified, reverting as an atavism to a variant of the laelapoid-type form (see figures in Athias-Henriot, 1968), this would follow the contentious notion of Karg (1998, 2003, followed by Christian & Karg, 2006) that at a higher phylogenetic level, sperm access systems are insignificant because both types can be found within various families, and thus allowing for retention of *Endopodalius* in the Blattisociidae. However, Karg's notions regarding evolution of dermanyssine sperm-access systems were evaluated as unfounded by Alberti (2002).

It should be noted that two of the species currently assigned to *Endopodalius*, *Lasioseius (Zygoseius) alter* Vitzthum, 1925 and *L. (Z.) vitzthumi* Westerboer, 1963, were placed by Westerboer (1963) in *Zygoseius* Berlese, 1916, a previously monotypic genus based on *Zygoseius furciger* Berlese, 1916. Westerboer distinguished her placement of *Zygoseius* as a subset of *Lasioseius* on its species having smooth, pointed dorsal body setae; the sternal shield having large extensions between the bases of legs I/II and of legs II/III; very strongly developed endopodal plates extending beneath the metasternal platelets; and shortened hypostomatic setae *C3* and *C4* (hypostomatic setae *hyp 2* and capitular setae *c.s.*, respectively). To these attributes, there can be added that, unlike *Lasioseius* (other than *Endopodalius*), females have a sternal shield with convex posterior margin, and males have a holoventral shield. The systematic placement of *Zygoseius* remains problematical, as reviewed by Halliday (1997). However, *Zygoseius* is currently thought to be placed in the Pachylaelapidae, superfamily Eviphidoidea, not closely related to the families of Ascoidea (Lindquist *et al.*, 2009), in part based on such attributes as a three-tined palptarsal claw, leg I femur with 13 setae (*v4* present), dorsal shield divided in the deutonymph but entire in adults, and other aspects (Halliday, 1997; see Discussion, below).

Recently, Esteca *et al.* (2020, figure 3F) included a micrograph of the spermatheca of *Lasioseius (Endopodalius) prorsoperitrematus*, and Moraza and Balanzategui (2023, figure 2D) drew the spermathecal remnant of *L. (E.) ibericus*. These authors did not identify the type of spermatheca illustrated; however, unlike those of species of *Lasioseius*, the structures are not configured as of the phytoseoid-type spermathecal apparatus.

Furthermore, other distinctive attributes of adult *Endopodalius* are unlike those of *Lasioseius*: (1) dorsal shield humeral setae *r3* are not apomorphically erect or modified in form; (2) nearly all dorsal shield setae are simple, none apomorphically tricarinate, although *Z4* and/or *Z5* may be penicillate; (3) gnathotectum with apomorphically elongate, apically split median branch; (4) female movable chela multidentate, apomorphically with four or more teeth (the movable chela among *Lasioseius* species generally has three teeth, though exceptionally eight teeth in *Lasioseius ruehmi* Hirschmann, 1972; see below); (5) female sternal shield with posterior margin apomorphically convex (other than its general convexity, the posterior margin may be rarely slightly concave medially); (6) tritosternum autapomorphically with small sclerite adjacent to its base; (7) endopodal plates beside coxae III and IV expansive, autapomorphically

underlapping metasternal platelets; (8) male with holoventral shield. Concerning attributes (1) and (2), exceptionally, in adults of *Lasioseius angustus* Evans & Sheals, 1959, *L. frontalis* Evans & Sheals, 1959 and *L. polydesmophilus* Evans & Sheals, 1959, humeral setae *r3* are not erect, and all of the dorsal shield setae are simple in form. These are secondary modifications derived in species that have become closely associated with millipedes — their adults conformed closely to the shapes of the spiracular despressions in which they are found on their hosts (Evans and Sheals, 1959).

In view of the above, the genus *Endopodalius* is so distinctive apomorphically to justify its own family grouping, even lacking information on the attributes of the immature instars except for a drawing of the larval dorsal idiosoma of *E. araucariae* (Hirschmann, 1972, figure 43RL; copied in Christian & Karg, 2006, figure 3.2.2). To be placed among the families and superfamilies of free-living Gamasina as currently recognized, the taxon *Endopodalius* or *scutalis* group of species presents attributes that currently distinguish the superfamily Ascoidea (see below). However, based on current classificatory concepts (Lindquist *et al.*, 2009; Karg, 1993, 2006), distinctions between the superfamilies Ascoidea, Eviphidoidea and Dermanyssoidea are not discrete among the more derivative taxa associated with terrestrial insects and vertebrates, and *Endopodalius* mites associated with coleopterans are another example.

Whether *sensu* Lindquist *et al.* (2009) or Karg (1993, 2006), members of Ascoidea have a usually two-tined palptarsal apotele; adult males have a presternal genital aperture (Karg's concepts accept either a presternal or midsternal genital aperture); the adult male spermatodactyl arises from external face of movable digit, with an open groove, freely projecting distally (Karg's concepts accept presence or absence of a spermatodactyl); adult females have metasternal elements free from the sternal shield; adult males have posterior (caudal) margins of the dorsal and anal or ventrianal shields free from one another (Karg's concepts accept conjoining of those margins as they occur in Zerconidae, in Ascoidea); adults have microtrichia of cribrum confined to the postanal region of anal or ventrianal shield (not extended onto caudal margin of dorsal shield); tibia I maximally has 13 setae, lacking a fourth ventral seta (*pv-2*) (Karg's concepts allow 14 setae, including *pv-2*, as they occur in Zerconidae); genu IV maximally has nine setae, lacking *pv* (Karg's concepts allow ten setae, including *pv*, as they occur in Zerconidae).

The above paragraph leads us to consider an accommodation of the new taxon in the superfamily Ascoidea, based further in part on it having a plesiomorphic "type A» laelapoid-type sperm access system rather than the apomorphically derivative phytoseioid-type system typical of the superfamily Phytoseioidea (see Alberti 2002). Based on cheliceral and leg chaetotactic attributes detailed by Lindquist *et al.* (2009), the new taxon is not readily accommodated among free-living and insecticolous taxa within the superfamilies Eviphidoidea and Dermanyssoidea, while the superfamily Ascoidea is characterized by a series of many attributes, as presented above, which readily accommodate *Endopodalius.*

Within the Ascoidea, however, the new taxon is not readily accommodated in any of the four recognized families as currently defined, Ascidae, Ameroseiidae, Melicharidae, and Antennochelidae, based on the following rationale. Unlike Ascidae, its adult females do not have the third pair of sternal poroids inserted plesiomorphically on the posterior margin of the sternal shield (they are on metasternal platelets), and its males do not have the endopodal strips beside coxae III-IV apomorphically free or at most narrowly connected to the sternitigenital shield (they are fully consolidated with that shield, as well as further consolidated into a holoventral shield).

Unlike Ameroseiidae, *Endopodalius* adults do not have the following apomorphic attributes: absence of the pair of caudal setae *J5* (plesiomorphically present in *Endopodalius*); absence of *R*-series of marginal setae other than *R1* (a full *R*-setal series present in *Endopodalius*); femur II with usually stable seta *al-2* absent (*Endopodalius* femur II retains seta *al-2* basal to the lyrifissure); and the basal row of deutosternal denticles is disrupted medially and widened

laterally to extend beyond insertions of the capitular setae (basal row of deutosternal denticles not disrupted medially and not widened laterally in *Endopodalius*).

Unlike Melicharidae, in *Endopodalius* the corniculus lacks the small, apparently stiff, acuminate apomorphic projection arising paraxially from its base; the pilus dentilis of the fixed cheliceral digit is setiform, not apomorphically modified into a hyaline flap; the movable cheliceral digit lacks a pointed apomorphic projection, the mucro, on its mid-ventral face; the posterior margin of the adult female epigynal shield is strongly truncated, rather than being gently convex; the adult female has a well-developed ventrianal shield bearing at least four pairs of opisthogastric setae, rather than an ovate or elliptical anal shield bearing usually only the anal setae or rarely with the nearest one pair of opisthogastric setae; the adult male has a holoventral shield rather than a typical ventrianal shield abutting or coalesced with, but delineated from, a sternitigenital shield.

Adult *Endopodalius* resemble more those of blattisociids in having the peritrematal shield moderately broadly connected to the exopodal plate beside coxa IV, rather than being free from or narrowly connected to it, as in melicharids. The more plesiomorphic laelapoid form of the female sperm access system of *Endopodalius,* as illustrated by Abo-Shnaf *et al.*, 2016, for *prorsoperitrematus* (their figure 50), by Loots, 1980, for *mouchei* (his figure 28), and herein for *ibericus* Moraza and Balanzategui, 2023 (Figure 2G), resembles that found in Melicharidae (e.g., as shown by Fain *et al.*, 1977 and by Naskrecki and Colwell, 1998) and in Ascidae, but as also found in other families (Athias-Henriot, 1968), so it is not diagnostic in differing from the autapomorphic phytoseioid-type.

Unlike Antennochelidae Lindquist and Moraza, 2014, a taxon based on a single genus characterized mostly by apomorphic gnathosomatic attributes, the cheliceral shafts of adult and nymphal *Endopodalius* are not greatly elongated and projectable, body-length, beyond the gnathosoma; the subcapitulum of *Endopodalius* adults does not have the four pairs of hypostomatic setae aligned longitudinally (*hyp2* and *hyp3* are aligned transversely); the gnathotectum is not modified into an elongated triramous extension (only the mid-tine is elongated); the sternal and peritrematal shields are not broadly fused at the level of endopodal extensions between legs I and II (they are broadly adjacent, contiguous in *Endopodalius*); the intercoxal region of adults lacks a strongly sclerotized pair of invaginations associated with poroids *iv2*; and trochanter I retains seta *ad*, femur II retains *al-2* basal to the lyrifissure, genu III retains *pv-1* (these setae absent in *Antennocheles*).

Linking *Endopodalius* as a sister-group to any of the above families is problematical. However, the following attributes argue for some commonality with the morphologically more highly derived Antennochelidae: (1) Female sternal shield with a somewhat convex posterior margin, more strongly so in *Endopodalius*: other than in the genus *Zygoseius* (see below), this attribute is rarely found among other gamasines of the hyporder or subcohort Dermanyssiae. (2) Adult endopodal sternal anterolateral extensions broadly projecting and fused or contiguous with exopodal-peritrematal plates between legs I and II: these sternal extensions are generally more narrowly projecting and free from or narrowly contiguous with exopodal-peritrematal plates in other gamasines. (3) Adult endopodal plates strongly developed between legs III and IV; in *Antennocheles* (and in *Zygoseius*) these plates are nearly as strongly developed as in *Endopodalius*, although they do not extend under the metapodal platelets. (4) Gnathotectum with elongated tines; in *Endopodalius* only the mid-tine is elongated. (5) Male with holoventral shield: this attribute is not found elsewhere among taxa of Ascidae, although this is characteristic of the genus *Zygoseius*, sometimes having been related with *Lasioseius* (Westerboer, 1963) but provisionally considered generally to be a member of the family Pachylaelapidae (Lindquist and Evans, 1965; Krantz and Ainscough, 1990; Halliday, 1997; Lindquist *et al.*, 2009; see Discussion, below). The placement of *Zygoseius* in Pachylaelapidae was not accepted by Mašán and Halliday, 2014; yet they were unable to argue or opt for its placement in any other family. (6) Dorsal shield with one or two pairs of the *Z*-setal series differentiated in thickened form from adjacent setae; thickened *Z3* are tapered in *Antennocheles*, while *Z4* and/or *Z5* are untapered and penicillate in *Endopodalius*. (7)

Peritremes of adults conspicuously bent or elbowed subapically at level of setae *s1*. (8) Adult mites are closely associated as females phoretic on tropical insects, all coleopterans in families of the infraorder Cucujiformia, suborder Polyphaga: *Antennocheles* with chrysomelid hispine beetles; *Endopodalius* with beetles of various other families, i.e., *E. tectus* with *Hololepra humilis* Payk (sic for *Hololepta humilis* Paykull, 1811) (Histeridae) in Venezuela (Hyatt, 1964) and with *Scyphophorus acupunctatus* Gyllenhaal, 1838 (Dryophthoridae) in southern Spain (Moraza and Balanzategui, 2023)*; E. americanus* with a scarabaeid and with a curculionioid *Metamasius* in Brasil and Costa Rica, respectively (Lindquist, 1964); *E. prorsoperitrematus* Abo-Shnaf *et al.* 2016 with *Sphenophorus levis* Vaurie, 1978 (Curculionidae) in Brasil (Esteca *et al.*, 2020); *E. scutalis* (Banks, 1914) with Scarabaeidae in Brasil; *E. imitans* (Berlese, 1910) with *Oryctes rhynoceros* (Linnaeus, 1758) (Scarabaeidae) in India; and an undescribed species of *Endopodalius* with a curculionid in Costa Rica (E.E.L., personal observation).

The above arguments for a sister relationship between *Antennocheles* and *Endopodalius* are tenuous, but perhaps could be tested by other morphological aspects (apart from eventual molecular analyses). For example, in both the protonymph and deutonymph of *Antennocheles*, the anal shield is expanded, much wider than long, enough so as to bear setae *JV5* in the deutonymph. This poses a test for the nymphs of *Endopodalius*, which as yet remain unknown. A sister relationship may argue for either of two perspectives – either the placement of *Endopodalius* in a separate family, or as a subfamily as a less-derived subset basal to the morphologically and behaviourly more derived *Antennocheles*, whose family group name has seniority over any such name proposed for *Endopodalius*. In this regard, we are persuaded to opt for a separate family, to avoid a revised, expanded concept of Antennochelidae when so little is known about what other taxa phylogenetically related to *Endopodalius* and *Antennocheles* may remain unaccounted for, among the tropical diversity of insect-associated gamasine mites.

Family Endopodaliidae fam. nov.

Type genus: *Endopodalius* Christian and Karg, 2006, **new status**, based on subgenus *Lasioseius* (*Endopodalius*) Christian and Karg, 2006.

Family based on adult females representing 13 described species, keyed below, and a further two undescribed species (E.E.L., both from Costa Rica), and males of two and the larva of one of those species. Quintero-Gutiérrez *et al.* (2020) assigned three other species of *Lasioseius* to *Endopodalius*, *L. frontalis*, *L. polydesmophilus*, and perhaps *L. angustus* (the latter based only on the male), without rationale. Based on arguments presented above, those species are retained in the genus *Lasioseius*, as diagnosed in our other studies (e.g., Moraza and Lindquist, 2018).

(Figures 1–4)

Diagnosis

Adults are apomorphic among members of the superfamily Ascoidea in the females having a sternal shield with (1) posterior margin strongly convex, such that its posteromedial margin reaches same transverse level as laterally adjacent, free metapodal platelets, and (2) anterior margin extending laterally into broadly projecting endopodal extensions between legs I and II where connecting with endopodal-peritrematal plates; (3) females with endopodal plates between legs III and IV uniquely enlarged, extending under metasternal platelets; (4) adults uniquely with a small unpaired platelet at base of tritosternum; (5) female movable cheliceral digit multidentate, with four to nine teeth in addition to apical hook. Other diagnostic attributes include: female sperm access system of laelapoid type, simplified to a short major duct (small section of tubular piece discernibly sclerotized, opening at the base of coxae III), lacking a sclerotized calyx and adjacent atrium with elongated minor duct; fixed cheliceral digit more multidenticulate than movable digit, and with setiform pilus dentilis; movable digit ventral face without a mucronate projection; gnathotectum anterior margin three-tined, with median

tine elongated, fringed apically; dorsal shield setae simple, none tricarinate; humeral setae *r3* of adult not differentiated by perpendicular projection; male with holoventral shield.

Description

Idiosomal dorsum — Adult female (Figure 1A). Dorsal shield entire, without lateral incisions, well sclerotized and well ornamented, sometimes complexly so (Westerboer, 1963, figure 153), without a delineated lateral rim alongside the lateral series of *r-S* setae; surrounding soft cuticle smoothly striate. Dorsal shield holotrichous, with a complement of usually 37 pairs of setae, including usually 22 podonotal (*j1-j6*, *z1-z6*, *s1-s6, r2-r5*) (*r5* sometimes off shield) and 15 opisthonotal (*J1-J5*, *Z1-Z5*, *S1-S5)*; dorsal setae nearly all simple, none tricarinate, though *Z4* and/or *Z5* bushy, penicillate distally and *J5* minute, spiculate basally; humeral setae *r3* not differentiated by more perpendicular projection. Dorsal shield with complement of 23 pairs of discernible pore-like structures (9 podonotal, 14 opisthonotal), of which seven pairs (four podonotal, three opisthonotal) superficially appear secretory (gland pores) and 16 pairs (five podonotal, 11 opisthonotal) non-secretory (poroids). Soft lateral cuticle with seta *r6*, six or seven pairs of marginal *R*-setae, several pairs of submarginal *UR*- setae, and pair of marginal poroids *idRp*. Peritrematal plates broadly uniting with dorsal shield anteriorly at level of setae *z2-s1*; peritremes well developed, reaching to level of, but well laterad, setae *j1*; peritremes conspicuously bent or elbowed subapically at level of setae *s1*.

Adult male. Dorsal shield similar in size, most ornamentation and setation to that of female, except its lateral margins slightly wider to bear setae *r5* and variably some of *R* and *UR* setae; form and relative lengths of shield setae as in female. Extent and form of peritremes as in female.

Idiosomal venter — Adult female (Figure 2A). Tritosternum with laciniae free or fused for at most half their length, without basal elaborations. Presternal region with median sclerotized strip just anterior to base of tritosternum and one pair of relatively large platelets (Figure 2A), these sometimes split in two (Figure 2B) or with several small platelets adjacent to anterior margin of sternal shield (e.g., figure 47 of *Lasioseius prorsoperitrematus* Abo-Shnaf *et al.*, 2016). Sternal shield entire, its anterior margin with a transverse strip of heavier, darker sclerotization behind first pair of sternal setae and poroids which blends into strongly developed, wide endopodal extensions between coxae I and II, contiguous with endopodal-peritrematal plate, and lacking gland pore (*gbv*) in that area; sternal shield with three pairs of setae, two pairs of poroids, strong endopodal extensions between coxae II and III, and with distinctively convex posterior margin, such that its posteromedial margin at same transverse level as laterally adjacent, free metasternal platelets. Poroids *iv3* together with setae *st4* on small metasternal platelets. Endopodal strips between coxae III and IV strongly developed, free, with anterior extremities extending under metasternal platelets and touching sternal shield posterolateral margin, and posterior tips nearly touching parapodal elements which bear gland pores *gv2*. Epigynal shield with rounded hyaline anterior margin nearly abutting posterior edge of sternal shield, with posterior margin truncate; setae *st5* on shield's posteriorly widening lateral margins, paragenital poroids *iv5* on soft cuticle; postgenital furrow with transverse row of four small platelets. Opisthosomatic venter with single pair of freely-standing metapodal platelets. Ventrianal shield well developed, slightly wider than long, with anterior margin abutting posterior edge of epigynal shield where flanked by setae *ZV1* on soft cuticle, and with usually four to sometimes six pairs of opisthogastric setae and two pairs of poroids; paranal setae inserted at mid-level of anus, postanal seta slightly longer than paranal setae; anal opening not enlarged; shield with cribrum formed as a narrow band between pair of prominent gland pores *gv3* along posterior margin; four or five pairs of other opisthogastric setae (*JV4, JV5, ZV3-ZV5*) and two pairs of poroids, flanked by posterior pairs of marginal and submarginal setae, on soft cuticle. Peritrematal shield narrowly separated from exopodal strip from midlevel of coxae II to midlevel of coxae IV, and fused to that strip more anteriorly, and posterior to coxa IV; peritrematal shield with two poroids (*ip3*, *ist*) and one gland pore (*gp3*) in area behind

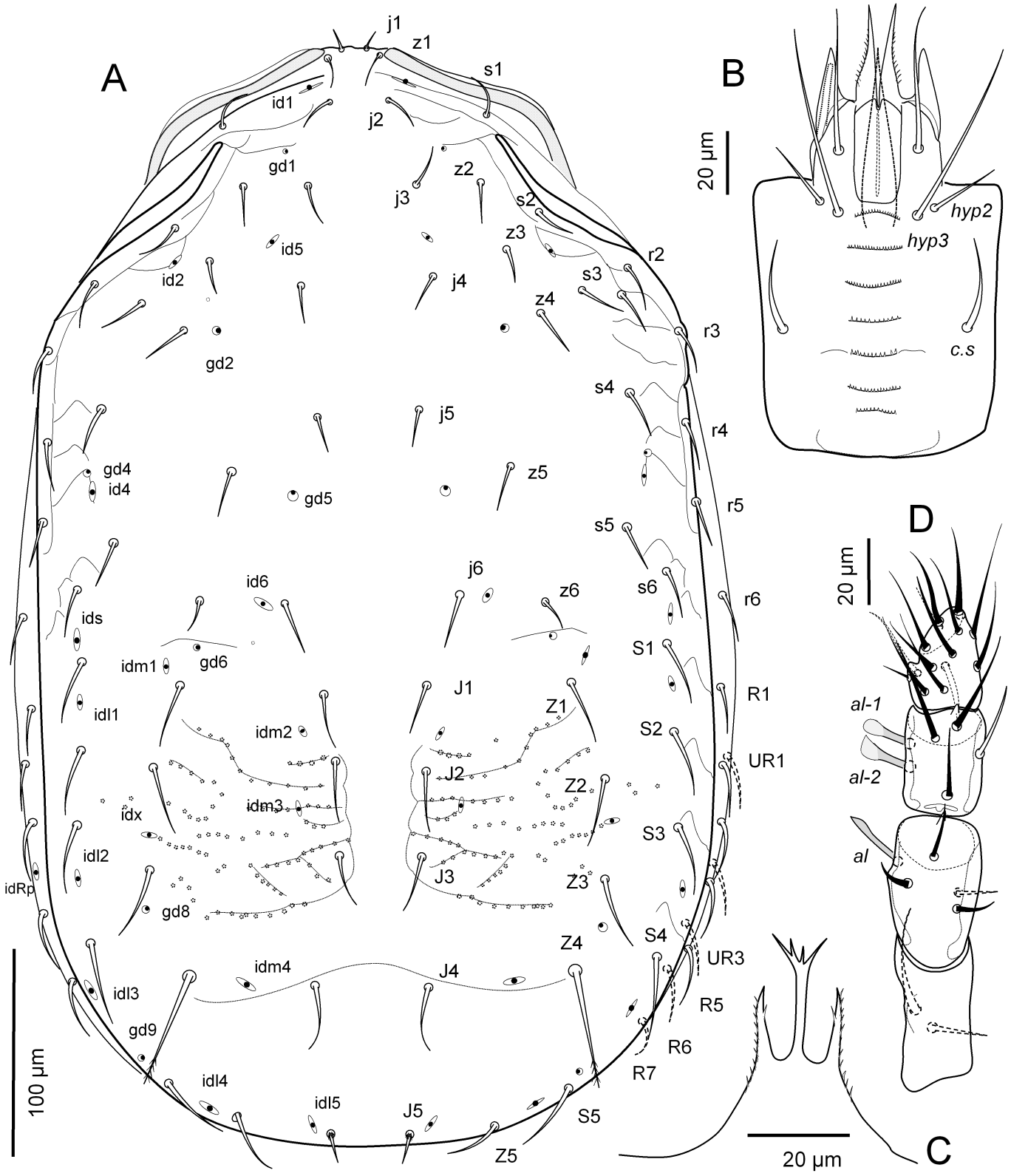

Figure 1 *Endopodalius ibericus* (Moraza and Balanzategui, 2023), adult female: A – idiosoma, dorsal aspect; B – subcapitulum; C – gnathotectum; D – palpus, dorsal view. (All figures after Moraza and Balanzategui, 2023.)

stigma, and with poroid *ip2* and gland pore *gp2* along mid-length of shield; poroid *ip1* and gland pore *gp1* not visible dorsolateral to peritreme at level of coxa II. Spermathecal apparatus weakly developed, of laelapoid type, with tubular piece (major duct) discernibly associated with posterior surface of coxae III (Figure 2G).

Adult male. Form of presternal area, including a median sclerotized strip just anterior to base of tritosternum, as in female. Sternitigenital, ventrianal and podal-peritrematal shields consolidated to form holoventral shield, with transverse line of fusion delineating connection between sternitigenital and ventrianal portions (Westerboer, 1963, figure 158); anterior margin of shield, at level of genital opening, prominent, broadly widened as endopodal extensions between legs I and II as in female but not darkened; shield with five pairs of setae and three pairs of poroids in sternitigenital region, and fully united with endopodal strips between coxae II and III, III and IV; shield ventrianal region with six to eight pairs of opisthogastric setae (usually *JV1*-*JV4*, *ZV1*, *ZV2*, sometimes also *ZV3*, *JV5*) in addition to circumanal setae; metapodal sigilla incorporated in shield; posterior margin of shield broadly rounded, with cribral band as in female; sternitigenital and opisthogastric setae smooth, similar in shape and length as in female. Exopodal and peritrematal shielding and peritremes as in female, except peritrematal union with dorsal shield broader anteriorly.

Gnathosoma — Female and male. Gnathotectum with convex anterior margin bearing three projections, median one longer and split terminally (Figure 1C). Subcapitular platform elongate, narrow (Figure 1B). Chelicerae capable of complete retraction, yet most of length projectable anteriorly free from body; chelicerae elongate, slender (Figure 2C), without any conspicuous process along antiaxial or paraxial lateral surfaces basal to digits, where hyaline rim smooth. Fixed cheliceral digit fully developed, with or without a mucronate process distally, with bifid apical hook (Figures 2D, E), apposed to apical hook of movable digit, with typically short setiform pilus dentilis, and with a continuous ridge of seven to 13 similarly-sized teeth along masticatory surface and few small teeth at base of digit, flanked paraxially by a hyaline multidenticate rim (Figure 2E, from Abo-Shnaf e*t al.*, 2016, figure 52a); movable digit of female with four to nine teeth (Figures 2C, F), that of male with one large tooth, and with spermatodactyl tubular, directed anteriorly, bent or hooked distally (*vide* Westerboer, 1963, p. 285; Abo-Shnaf *et al.*, 2016, figure 59). Corniculi of female moderately long, slender, parallel (Figure 1B), those of adult male slightly more widely spaced, with more conspicuous internal projection from their bases (Westerboer, 1963, figure 157a); internal malae elongate, extending well beyond tips of corniculi. Apex of labrum extending to or slightly beyond tips of corniculi. Salivary styli not reaching tips of corniculi. Subcapitular setae smooth, pair *hp3* nearly transversely aligned with *hp2* and usually longer than pairs *hp1* and *c.s*. Deutosternum with seven moderately wide rows of denticles, similarly multidenticulate, free (Figure 1B) or flanked by lateral margins (Westerboer, 1963, figure 154b). Palpi (Figure 1D) with holotrichous setation as described for Gamasina by Evans (1964); palpfemoral seta *al* slightly lanceolate and palpgenual setae *al-1* and *al-2* clearly spatulate; palptarsal apotele two-tined, with spatulate tips; palptrochanter with inner seta not markedly elongated.

Legs — Female and male. Legs of moderate length, I and IV no longer than dorsal shield. Legs I slightly longest and thinner, and II slightly thicker, than legs III and IV (Figures 4A–D). Distal margins of coxae I–IV without serrated ridges or spur-like processes (Figures 4E–H). Legs I to IV with pretarsi bearing paired claws of moderate size, inconspicuous paradactyli, and rounded pulvilli (Figures 3A, E). Leg I tarsus with 45 setae (Figure 3B) and distinct pedicel bearing pretarsal structures (Figures 3A, C). Tarsus I with sensilla *s* inconspicuous, not noticeably lanceolate distally (Figure 3D). Legs II to IV with tarsus (excluding pretarsus) about twice as long as tibia. Tarsi II–IV with apical setal processes *ad-1*, *pd-1* short, less than half as long as pretarsi (Figures 3E, F), and with rounded triangular apical process ventrally. Setation and their ontogeny on segments of legs I to IV with full complement of Ascidae (as presented by Lindquist and Evans 1965 for Ascini), coxae, 2-2-2-1; trochanters, 6-5-5-5; femora, 12 (2 3/1 2/2 2) –11 (2 3/1 2/2 1) – 6 (1 2/1 1/0 1) – 6 (1 2/1 1/0 1); genua, 13 (2 3/2 3/1 2) – 11 (2 3/1 2/1 2) – 9 (2 2/1 2/1 1) – 9 (2 2/1 3/0 1), genu IV lacking *pv-1*; tibiae, 13 (2 3/2 3/1 2) – 10

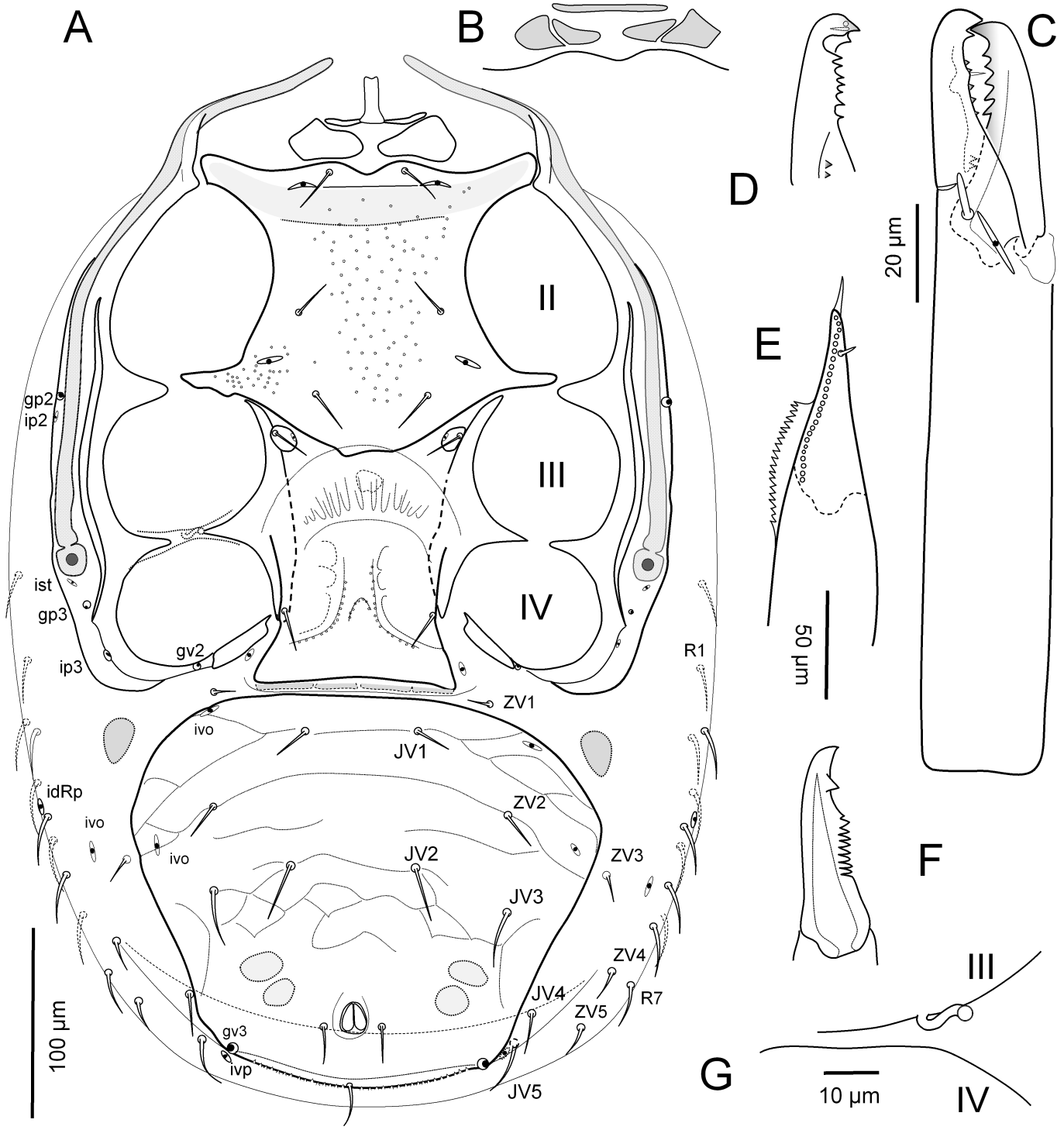

Figure 2 *Endopodalius* species, adult females: A–D, G – *E. ibericus*; E, F – *E. prorsoperitrematus* Abo-Schnaf *et al.*, 2016. A – idiosoma, ventral aspect; B – detail of variant presternal platelets; C – chelicera, lateral adaxial view; D – detail of fixed cheliceral digit, paraxial view; E – fixed cheliceral digit, dorsoventral aspect, showing paraxial denticulate rim and apical mucro (after Abo-Schnaf *et al.* 2016); F – movable cheliceral digit, lateral aspect; G – spermathecal apparatus. Roman numbers indicate acetabulum of legs II, III and IV. (All figures except E, F after Moraza and Balanzategui, 2023.)

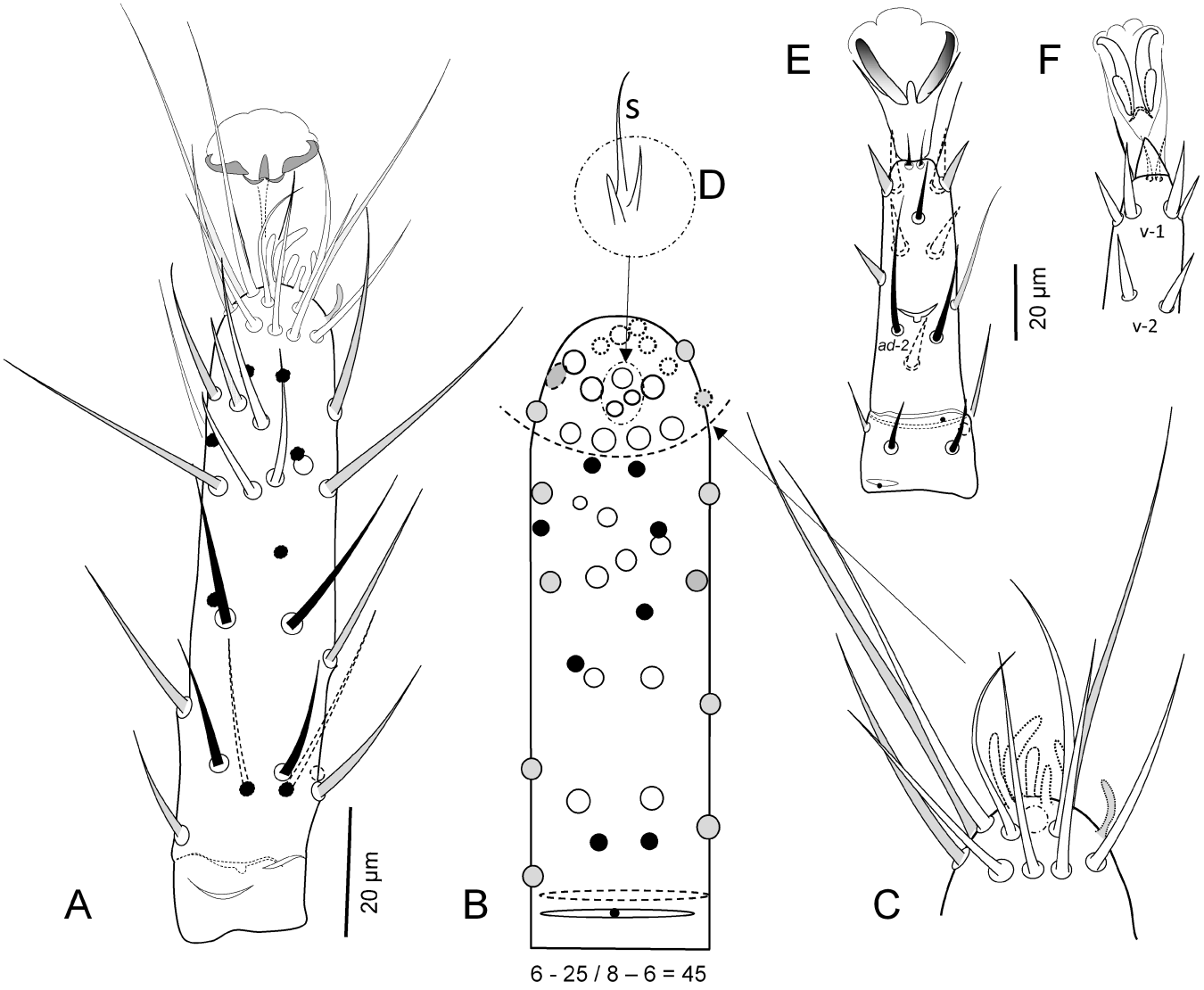

Figure 3 *Endopodalius ibericus*, adult female: A – tarsus I, dorsal view; B – tarsus I, diagrammatic representation; C – detail of dorso-apical region of tarsus I sensorial setae; D – detail of dorso-apical sensorial setae; E – tarsus IV, dorsal view; F – detail of ventral setae on distal region of tarsus IV. Figure A, solid black setae are dorsal basal setae, grey color are lateral setae, black solid circles are ventral setae; figure B, white color are dorsal setae, grey color are lateral setae, black solid circles are ventral setae. (E, F after Moraza and Balanzategui, 2023.)

(2 2/1 2/1 2) – 8 (2 1/1 2/1 1) – 10 (2 1/1 3/1 2). Tarsi II–IV with seta *ad-2* somewhat elongated but not extending to base of pretarsi (Figure 3E); paired ventral setae (*v-1*) and (*v-2*) somewhat spine-like and claws strong (Figure 3F); other leg setae simple, not strongly modified on female. Male leg setal dimorphism not notably developed (Westerboer, 1963).

Genus *Endopodalius* Christian and Karg, 2006

Subgenus *Lasioseius (Endopodalius)* Christian and Karg, 2006

Type species: *Lasioseius (Zygoseius) alter* Vitzthum, 1925, original designation.

Diagnosis — Adults of *Endopodalius* share with other genera included in the superfamily Ascoidea the series of attributes given above for diagnosis of that superfamily. As the only genus of Endopodaliidae, they are distinguished from those of other taxa of Ascoidea by the following characteristics, some of which are apomorphic, as indicated below: Dorsal shield with (1) humeral setae *r3* not erect or differentiated in form from adjacent setae, and with

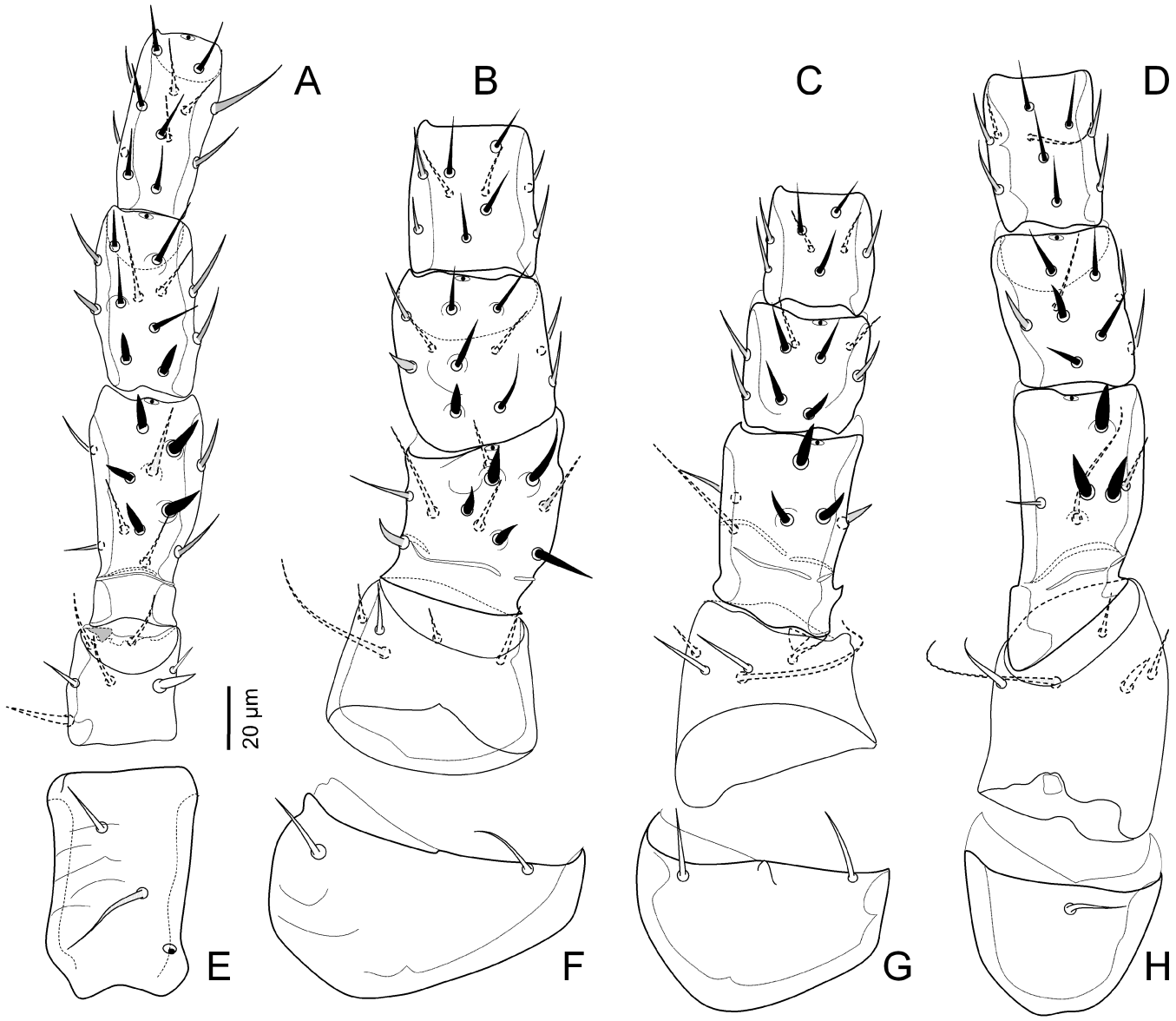

Figure 4 *Endopodalius ibericus*, adult female, legs I-IV, excepting tarsi: A–D, dorsal views of legs I (A), II (B), III (C), IV (D); E–H ventral views of coxae I (E), II (F), III (G), IV (H). (All figures after Moraza and Balanzategui, 2023.)

(2) nearly all setae simple, none tricarinate, but (3) usually with setae *Z4* and/or *Z5* brushy, penicillate distally (apomorphy); (4) adult sternal shield anterior margin with more heavily sclerotized strip continuing as broadly widened extensions to unite with endopodal-peritrematal shield on either side (apomorphy); (5) female sternal shield posterior margin strongly convex, such that its posteromedian margin reaches same transverse level as adjacent, free metasternal plates (autapomorphy); (6) female endopodal plates between legs III-IV enlarged, extending under metasternal platelets (autapomorphy); (7) adult presternal region with small unpaired platelet at base of tritosternum (autapomorphy), and (8) with one to several paired platelets; (9) movable cheliceral digit with usually five or more teeth (apomorphy); (10) gnathotectum with elongated median process, fringed apically (apomorphy); (11) male with holoventral shield. Attributes 1, 2, 5-7 and 9-11 are repeated from the family diagnosis as distinctions from genera in closely related families.

Key to species of *Endopodalius*, adult females

The following key has been elaborated from the original descriptions and illustrations of the previously described species and from our observations of type or reference material of some of them, as noted above. Several of those species are so inadequately described that further studies of type material may indicate other synonymies, especially some of those species among couplets 10 through 12. On the other hand, several other species inadequately described under the genus and subgenus *Lasioseius* may belong to *Endopodalius* (as we have determined for *Lasioseius americanus* Chant, 1963, which was inadvertently placed in the *inguinalis* species complex of the subgenus *Lasioseius* by Christan and Karg, 2006). For example, the adult female of *Lasioseius ruehmi*, Hirschmann, 1972, needs further study, as it has a similarly multidentate (6–7 teeth) movable chela; none of its dorsal shield setae are tricarinate, though *Z5* is penicillate; and its sternal shield posterior margin is partially convex.

1. Dorsal shield with all setae simple, smooth, tapered; sternal shield coarsely ornamented with large, scattered fovea; metapodal plates encompassed into anterolateral corners of ventrianal shield 2
— Dorsal shield with one or two of setae *Z4*, *Z5* untapered, thickened distally; sternal shield more finely ornamented with puncta, striae; metapodal plates free from ventrianal shield 3

2. Ventrianal shield shown with six pairs of opisthogastric setae, *ZV1* and *JV4* on shield; two pairs of presternal platelets . . . . . *alter* (Vitzthum, 1925)
— Ventrianal shield shown with four pairs of opisthogastric setae, *ZV1* and *JV4* off shield; one pair of presternal platelets . . . . . *hirschmanni* Christian and Karg, 2006 (= *alter* sensu Bhattacharyya, 1969)

3. Dorsal shield with both of setae *Z4*, *Z5* untapered, penicillate distally 4
— Dorsal shield with only one of either *Z4* or *Z5* untapered, thickened distally 5

4. Sternal shield anterior margin with wide, rectangular, median notch, posterior margin slightly concave medially (other than its general convexity); dorsal shield setae of *J*-series shorter than intervals between their bases . . . . . *humberti* (Athias-Henriot, 1959)
— Sternal shield anterior margin not notched, posterior margin entirely convex; dorsal shield setae of *J*-series slightly longer than intervals between their bases . . . . . *araucariae* (Hirschmann, 1972)

5. Fixed chela with mucronate process distally (Figure 2E); movable chela with 8–10 teeth . . . . . *scutalis* (Banks, 1914) (=*prorsoperitrematus* Abo-Shnaf *et al.* 2016, **new synonym**)
— Fixed chela without mucronate process distally; movable chela with 4–7 teeth 6

6. Dorsal shield setae *Z4* untapered, stout, blunt-tipped, penicillate distally, *Z5* simple 7
— Dorsal shield setae *Z4* slender, pointed, smooth, but *Z5* untapered, thickened distally 9

7. Ventrianal shield with five or six pairs of opisthogastric setae, including *JV5*, sometimes *JV4*; presternal region with two pairs of well-separated platelets . . . . . *vitzthumi* (Westerboer, 1963)
— Ventrianal shield with four pairs of opisthogastric setae, *JV4*, *JV5* on adjacent soft cuticle; presternal region with one pair of platelets divided into two contiguous pairs (Figure 2B) 8

8. Dorsal shield with prominent, transverse punctated line/groove across entire face behind setae *J4* and *Z4;* fixed cheliceral digit with ca 13 teeth . . . . . *tectus* (Hyatt, 1964)
— Dorsal shield without transverse punctated line across entire face at any level; fixed cheliceral digit with seven to nine teeth . . . . . *ibericus* Moraza and Balanzategui, 2023

9. Distally thickened setae *Z5* abruptly curved distally, about 1.7x longer than setae *Z4* 10
— Distally thickened setae *Z5*, straight, similar in length or longer than setae *Z4* 11

10. Setae *Z5* serrated, penicillate distally; ventrianal shield setae *JV3* over twice as long as other opisthogastric setae; movable cheliceral digit with four teeth ..... *americanus* (Chant, 1963)
— Setae *Z5* knobbed, smooth distally; ventrianal shield setae *JV3* scarcely longer than other opisthogastric setae; movable cheliceral digit with seven teeth ..... *gabrielae* (Santos and Argolo, 2018)

11. Dorsal shield with setae *J1* to *J4* slightly longer than intervals between their bases, *J4* as long as *Z5*; presternal platelets divided but its parts contiguous ..... *convexus* (Krantz, 1962)
— Dorsal shield with setae *J1* to *J4* ca half to nearly as long as intervals between their bases, *J4* ca half to 0.7 as long as *Z5*; presternal platelets entire, subtriangular 12

12. Dorsal shield with only setae *j5*, *z6* shorter (about 0.7 as long) than adjacent setae (E.E.L., personal observation) ..... *imitans* (Berlese, 1910)
— Dorsal shield with setae *j4* and hexagonal area setae *j5, z5, j6* short, about half as long as adjacent *j3*, *z6* ..... *mouchei* (Loots, 1980; possible synonym of *imitans*)

Distribution and habitats

Endopodalius is known at present from species found in Seychelles islands east of Africa (north of Madagascar), India, Sumatra, South and Central America (Brasil, Dominican Republic, and Costa Rica), and new records noted below from Micronesia. Among the thirteen named described species, males of only two species, *E. prorsoperitrematus* (Abo-Shnaf, Sánchez and Moraes, 2016) and *E. vitzthumi* (Westerboer, 1963), and the larva of only *E. araucariae* (Hirschmann, 1972) have been described, while nymphal instars remain unknown so far. Several described species have been reported associated with insects, all coleopterans (see details above).

Discussion

Cheliceral structures — The chelicerae of *Endopodalius* are rather ordinary in various morphological respects, in comparison with many of the gamasine groups of Mesostigmata (Karg, 1965; Evans, 1992; Alberti and Coons, 1999). However, compared with forms of chelicerae within the hyperdiverse genus *Lasioseius*, with which *Endopodalius* has been confused, the multidentate yet not elongate form of the movable digit, with more than three teeth, is relatively unique and perhaps relevant to a more particular feeding behavior, of which nothing is known.

Although occasionally illustrated (e.g., Lindquist, 1971and subsequent papers; Abo-Shnaf *et al.*, 2006) little has been stated about the form and function of the hyaline structure with a denticulated rim on the paraxial surface of the chelicerae at the level of the movable chela's articulation in various blattisociid and melicharid mites (shown in dorsoventral aspect in Figure 2E). This structure is not considered in the major morphological treatises by either Evans (1992) or Alberti and Coons (1999). As a pattern, lateral view drawings of gamasine chelicerae are often from the outer side, showing the antiaxial lyrifissure, i.e., across from the paraxial side where the hyaline structure is located. Evident among various blattisociid and melicharid mites, these structures have not been illustrated or noted among other gamasine taxa such as the ascid subfamilies Ascinae, Arctoseiine and the blattisociid subfamily Platyseiinae (E.E.L. personal observations). These structures may be part of a sieving or straining system when functioning together between the chelicerae.

Sternal shield aspects — Within the highly diverse and speciose genus *Lasioseius* (over 150 species described; Christian and Karg, 2006; Moraes *et al.*, 2016), adult females of the *scutalis* species group now recognized as *Endopodalius* are distinctive in having their sternal shield's anterior margin strongly thickened and darkened as a transverse band. The dark, thickened aspect of this shield was not illustrated in previous species descriptions (other than for *E. ibericus* by Moraza and Balanzategui, 2023); however, personal observations (E.E.L.) of several species suffice to conclude that this thickening is prevalent or ubiquitous in the genus. Interestingly, a similar such sternal shield band (the shield's posterior margin also somewhat convex) was noted and illustrated by Bhattacharyya (1972) for a melicharid, *Proctolaelaps sternalis* Bhattacharyya, found under bark of a dead tree – a habitat similar to those of *Endopodalius*. A somewhat similar but broader transverse band of thickened sternal shield cuticle is evident in deutonymphs of the genus *Poecilochirus* G. & R. Canestrini, 1882, family Parasitidae. Such anterior thickenings of the sternal shield may be correlated with phoretic behavior, which is restricted to the instar and sex for which this thickened structure is found.

The unusually convex form of the female sternal shield's posterior margin, along with strongly developed endopodal plates between legs III and IV in species of *Endopodalius* are also found among those of *Zygoseius*, a taxon confused with *Endopodalius*, in relationships with *Lasioseius* (Westerboer, 1963; Halliday, 1997). Differences among other adjacent coxisternal structures (particularly in *Endopodalius*, incorporation of the metasternal platelets with setae *st4* and poroids *iv3* into the expanded endopodal plates alongside legs III-IV, with those plates extended and connected anteriorly to the sternal shield endopodal extensions between the bases of legs II and III) indicate that these similarities are morphological convergences. In *Endopodalius*, the posteromedial margin of the sternal shield extends to the same transverse level as the small metasternal platelets (bearing setae *st4* and poroids *iv3*), which are freely standing on soft cuticle and underlapped by the endopodal plates which are devoid of other structures. In *Zygoseius*, the sternal shield's posteromedial margin does not extend so far posteriorly as in transverse level between the metasternal setae and poroids; and the latter structures are inserted on even more enlarged endopodal plates which connect with the sternal shield extensions between legs II and III.

Peritrematic aspects — Abo-Shnaf *et al.* (2016) drew attention to the anterior ends of the peritremes being distinctively bent forward at the level of the paravertical setae *z1* in *Lasioseius prorsoperitrematus*, stated to be in distinction to those of *L. americanus* Chant, 1963 and *L. araucariae* Hirschmann, 1972. While this aspect was not noted or illustrated among previous descriptions and illustrations of other species of this genus, our observations (E.E.L.) of type or reference material indicated that the same, anteriorly bent form is present in *L. americanus*, *L. scutalis*, *L. tectus*, but not in material identified as near *L. araucariae* and *L. imitans*, and only slightly so in material of another undescribed species.

Lectotype designation — Observations by one of us (Lindquist, 1964) of Nathan Banks' microslide preparation of *Hypoaspis scutalis* (deposited in the Museum of Comparative Zoology, Harvard University), with the word "type» written on the label, found it to include twelve adult female mites, four of which were identified as *scutalis* and are considered to be syntypes. The specimen most centrally located is here designated as the lectotype: from the orientation of its legs, this specimen is obviously the one upon which Banks based his original illustration, and it can be readily distinguished also by being the only specimen with setae *Z5* and all legs intact. Evans and Hyatt (1960) erroneously anticipated *Hypoaspis scutulis* (sic) Banks, 1914 to belong to the genus *Sejus* Koch, 1843 (subsequently *Cheiroseius* Berlese, 1916, *sensu* Evans and Till, 1979); however, they had not examined Banks' type material of *Hypoaspis scutalis*.

Life history — Although the life cycle instars have not been observed for any species of *Endopodalius*, a presumably free-standing larva of *L. (E.) araucariae* Hirschmann was illustrated by Hirschmann (1972). An adult female identified as *L. (E.) imitans* at hand (E.E.L.) contains an egg with fully formed larval structures, indicating probable larviparity.

Coexistent or polymorphic forms — Further observations (E.E.L. notes, 1964) of Banks' type slide preparation of *Hypoaspis scutalis* determined that among the twelve adult females (of which only four were identifiable as *scutalis*), there are two other closely related forms, both belonging to *Endopodalius*. Of these, two females were at that time identifiable as *Lasioseius americanus* Chant, 1963 (original type material from Guatemala and Ecuador), and three other females as a species closely similar to *Lasioseius tectus* (Hyatt, 1964) (original type material from Venezuela), which was not yet described when those notes were first taken. Other than the *scutalis* females, those of the two other closely related forms were noted (E.E.L. personal observations) as lacking the apical mucronate process on the fixed chela. Three of the specimens were not adequately preserved for more specific identification. The coexistence of three of these forms may indicate a possible adult female polymorphism; however, we are not aware of any other example among gamasine mites where representatives of more than one of a closely related group of species are phoretically coexistent on an arthropod host. The example of *Antennoseius janus* Lindquist and Walter, 1989 exhibiting adult female dimorphism was shown to be phase morphism, involving phoretic and non-phoretic forms (Lindquist and Walter, 1989). Curiously, Hirschmann (1972) described closely similar adult females of two species, *Lasioseius araucariae* and *Lasioseius ruehmi*, which may possibly be another example of polymorphism, or if not, then further studies of material of *L. ruehmi* are needed to confirm its placement in *Endopodalius*. Both forms were collected in association with *Araucaria* trees, *L. araucariae* from phloem infested by numerous insects, and *L. ruehmi* from insect frass galleries in *Araucaria* and phoretic on bark beetles, *Ptelobius valdivianus* (Eggers). While female *L. araucariae* presents all of the attributes typical of *Endopodalius* (form of presternal structures and sternal shield; penicillate dorsal shield setae *Z4*, *Z5*, multidentate five teeth movable chela, median tine of gnathotectum elongate, apically split), female *L. ruehmi* has only setae *Z5* penicillate and a similarly multidentate, six or seven toothed movable chela, median gnathotectal tine less distinctive in form from lateral tines, and lacking presternal platelets and not distinctively convex posterior margin of sternal shield.

Additional collection records of *Endopodalius* species — The Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, has one slide preparation with four females of *Lasioseius (Endopodalius) scutalis* (Banks) from Peru (no locale indicated), ex Brazil nuts; one female of *L. (E.) americanus* (Chant) from Guatemala (no locale) ex *Metamasius sericeus* Kuschel, (Dryophthoridae); one female of *L. (E.) imitans* (Berlese) from Bangalore, India, ex. *Oryctes rhinoceros* (Linnaeus), (Scarabaeideae); one female of *L. (E.)* undescribed sp. 1 from Jokaj Islet, Pohnpei (formerly named Ponape) Island, Micronesia, ex. decaying crown of dead coconut; one slide with two females of *L. (E.)* undescribed sp. 2 from Pohnpei Island, Micronesia, Mt. Nanlaud, elev. 1000 ft. (305 m), ex. dead palm petiole;and four slides each with one female of different described species of *Endopodalius* from La Selva Biological Station, Heredia, Costa Rica: one *L.(E.) tectus*, ex fogged *Vitex* foliage; one *L.(E.) scutalis*, ex fogged unidentified foliage; one, near *L.(E.) araucariae*, ex experimental swamp; one undescribed species, near *L.(E). americanus* ex Curculionidae.

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References

Abo-Shnaf, R.I., Sánchez, L., Moraes, G.J.D. 2016. Plant inhabiting Gamasina mites (Acari: Mesostigmata) from the Dominican Republic, with descriptions of four new species of *Lasioseius* (Blattisociidae) and complementary descriptions of other species. Systematic and Applied Acarology, 21(5): 607-646. https://doi.org/10.11158/saa.21.5.5

Alberti G. 2002. Ultrastructural investigations of sperm and genital systems in Gamasida (Acari: Anactinotrichida): Current state and perspectives for future research. Acarologia, 42: 107-126.

Alberti G., Coons L.B. 1999. Acari: Mites. In: Harrison F.W., Foelix R.F. (Eds.) Microscopic anatomy of invertebrates, Vol. 8C, Chapter 6, Chelicerate Arthropoda. Wiley-Liss, New York, pp. 515-1265.

Argolo P.S., Santos J.C., Oliveira A.R., de Moraes G.J. 2018. Two new species of *Lasioseius* Berlese (Acari: Blattisociidae) from Brazil, and a key for separation of the Brazilian species of the genus. Systematic & Applied Acarology, 23(8): 1567-1577 https://doi.org/10.11158/saa.23.8.7

Athias-Henriot C. 1959. Phytoseiidae et Aceosejidae (Acarina, Gamasina) d'Algérie. III Contribution aux Aceosejinae. Bulletin de la Société d'Histoire Naturelle de L'Afrique du Nord, 50: 158-195.

Athias-Henriot C. 1968. L'appareil d'insémination laelapoïde (Acariens anactinotriches: Laelapoidea). Premières observations. Possibilité d'emploi à des fins taxonomiques. Bulletin Scientifique de Bourgogne, 25: 229-274.

Athias-Henriot C. 1969. Les organes cuticulaires sensoriels et glandulaires des Gamasides. Poroïdotaxie et adénotaxie. Bulletin de la Société Zoologique du France, 94: 485-492.

Athias-Henriot C. 1971. Nouvelles notes sur les Amblyseiini (Gamasides Podospermiques, Phytoseiidae) 1. La dépilation des génuaux et tibias des pattes. Acarologia, 13: 4-15.

Banks N. 1914. The Stanford Expedition to Brazil, 1911. Acarians from Brazil. Psyche 21(5): 160-162. https://doi.org/10.1155/1914/61017

Berlese A. 1910. Brevi diagnosi di generi e specie nuovi di Acari. Redia, 6: 346-388.

Berlese A. 1916. Centuria prima di Acari nuovi. Redia, 12: 19-67.

Bhattacharyya S.K. 1969. Studies on Indian mites (Acarina: Mesostigmata). 7. Six species found under bark in North East Frontier Agency. Zoologische Jahrbuch, Systematische, 96: 69-80.

Bhattacharyya S.K. 1972. Studies on Indian mites (Acarina: Mesostigmata). 9. Additional species found under bark in North East Frontier Agency. Acarologia, 13: 272-279.

Canestrini G., Canestrini R. 1882. Gamasi Italiani. Atti della Societa Veneto-Trentina di Scienze Naturali, 8: 1-80.

Chant D.A. 1963. The subfamily Blattisocinae Garman (=Aceosejinae Evans) (Acarina: Blattisocidae Garman) (=Aceosejidae Baker and Wharton) in North America, with descriptions of new species. Canadian Journal of Zoology, 41: 243-305. https://doi.org/10.1139/z63-025

Christian A., Karg W. 2006. The predatory mite genus *Lasioseius* Berlese, 1916 (Acari, Gamasina). Abhandlungen und Berichten aus den Naturkundemuseum Görlitz, 77: 99-250.

Di Palma A., Alberti G. 2005. Functional morphology of accessory structures involved in reproduction among gamasid mites (Acari, Anactinotrichida): a review. Atti dell'Accademia Nazionale Italiana di Entomologia Rendiconti, 53: 361-378.

Esteca F.C.N., Borges V., Santos J.C., Neves L.S., Moraes G.J. 2020. Report of the mite *Lasioseius prorsoperitrematus* Abo-Shnaf, Sánchez & Moraes, 2016 (Acari: Blattisociidae) in Brazil associated with the insect *Sphenophorus levis* Vaurie, 1978 (Coleoptera: Curculionidae). Entomological Communications, 2, 2020: ec02028 https://doi.org/10.37486/2675-1305.ec02028

Evans G.O. 1963. Observations on the chaetotaxy of the legs in the free-living Gamasina (Acari: Mesostigmata). Bulletin of the British Museum (Natural History) Zoology, 10: 275-303. https://doi.org/10.5962/bhl.part.20528

Evans G.O. 1964. Some observations on the chaetotaxy of the pedipalps in the Mesostigmata (Acari). Annals and Magazine of Natural History, Series 13, 6: 513-527. https://doi.org/10.1080/00222936308651393

Evans G.O. 1969. Observations on the ontogenetic development of the chaetotaxy of the tarsi of legs II-IV in the Mesostigmata (Acari). In: Evans G.O. (Ed.) Proceedings of the 2nd International Congress of Acarology, 1967, Akadémiai Kiadó, Budapest, pp. 195-200.

Evans G.O. 1992. Principles of Acarology. CAB International, Wallingford, xviii+563 pp. https://doi.org/10.1079/9780851988221.0000

Evans G.O., Hyatt K.H. 1960. A revision of the Platyseiinae (Mesostigmata: Aceosejidae) based on material in the collections of the British Museum (Natural History). Bulletin of the British Museum (Natural History), Zoology 6(2): 27-101. https://doi.org/10.5962/bhl.part.26844

Evans G.O., Sheals J.G. 1959. Three new mesostigmatic mites associated with Millepedes in Indonesia. Entomologische Berichten, 19: 107-111.

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

Fain A., Hyland K.E., Aitken T.H.G. 1977. Flower mites of the family Ascidae phoretic in nasal cavities of birds (Acarina: Mesostigmata). Acta Zoologica Pathologica Antverp, 69: 99-154.

Gyllenhaal L. 1838. In: Schönherr C.J., Gyllenhaal L., Boheman C.H. Genera et species Curculionidum, cum synonymia hujus familae species novae. Roret, Paris, Vol. 4, Part 2, pp. 855-859.
Halliday R.B. 1997. Revision of the genus *Zygoseius* Berlese (Acarina: Pachylaelapidae). Acarologia, 38: 3-20.
Hirschmann W. 1972. Von Dr. W. Rühm während seiner Tätigkeit an der Univ. Austral de Chile (Valdevia) gesammelte Araukarien-Milben aus Südchile u. Südbrasilien. Acarologie, Gangsystematik der Parasitiformes, Teil 4, 17: 29-33, 9 plates.
Hyatt K.H. 1964. A collection of Mesostigmata (Acari) associated with Coleoptera and Hemiptera in Venezuela. Bulletin of the British Museum (Natural History), Zoology, 11(7): 465-509. https://doi.org/10.5962/bhl.part.4723
Johnston D.E., Moraza M.L. 1991. The idiosomal adenotaxy and poroidotaxy of Zerconidae (Mesostigmata: Zerconina). In: Dusbábek F., Bukva V.(Eds.) *Modern Acarology*, Academia, Prague, Vol. 2, pp. 349-356.
Karg W. 1965. Larvalsystematische und phylogenetische Untersuchung sowie Revision des Systems der Gamasina Leach, 1915 (Acarina, Parasitiformes). Mitteilungen aus dem Zoologischen Museum in Berlin 41: 193-341. https://doi.org/10.1002/mmnz.19650410207
Karg W. 1993. Acari (Acarina), Milben Parasitiformes (Anactinochaeta) Cohors Gamasina Leach. Raubmilben. Die Tierwelt Deutschlands Teil 59: 523 pp.
Karg W. 1998. Zur Kenntnis der Eugamasides Karg mit neuen Arten aus den Regenwäldern von Ecuador (Acarina, Parasitiformes). Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe, 74: 185- 214. https://doi.org/10.1002/mmnz.4850740204
Karg W. 2003. Neue Raubmilbenarten aus dem tropischen Regenwald von Ecuador mit einem kritischen Beitrag zur Merkmalsevolution bei Gamasina (Acarina, Parasitiformes). Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe, 79: 229 - 251. https://doi.org/10.1002/mmnz.4850790203
Karg W. 2006. The systematics of Parasitiformes, especially of Gamasina Leach (Acarina), with new species from Ecuador. Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe, 82: 140-169. https://doi.org/10.1002/mmnz.200600002
Koch C.L. 1843. Übersicht des Arachnidensystems. Heft 3. C. H. Zeh'schen Buchhandlung, Nürnberg, 131 pp., 13 plates.
Krantz G.W. 1962. Acari. Free-living Mesostigmata. II. The family Aceosejidae. Parc National De La Garamba, Mission H. De Saeger, 34: 3-29.
Krantz G.W., Ainscough B.D. 1990. Acarina: Mesostigmata (Gamasida). In: Dindal, D.L. (Ed.) *Soil Biology Guide*, John Wiley & Sons, New York, pp. 583-665.
Krantz G.W., Redmond B.L. 1987. Identification of glandular and poroidal idiosomal systems in *Macrocheles perglaber* F. & P. (Acari: Macrochelidae). Experimental & Applied Acarology, 3: 243-253. https://doi.org/10.1007/BF01270460
Lindquist E.E. 1964. A revision of mites of the subfamily Blattisocinae (Acarina: Blattisocidae) in America north of Mexico. Ph.D. dissertation, University of California, Berkeley, University Microfilms, Inc., Ann Arbor, Michigan, 64-2093. iii + 413 pp.
Lindquist E.E. 1971. New species of Ascidae (Acarina: Mesostigmata) associated with forest insect pests. Canadian Entomologist, 103: 919-942. https://doi.org/10.4039/Ent103919-7
Lindquist E.E. 1994. Some observations on the chaetotaxy of the caudal body region of gamasine mites (Acari: Mesostigmata), with a modified notation for some ventrolateral body setae. Acarologia, 35: 323-326.
Lindquist E.E., Evans G.O. 1965. Taxonomic concepts in the Ascidae, with a modified setal nomenclature for the idiosoma of the Gamasina (Acarina: Mesostigmata). Memoirs of the Entomological Society of Canada, 47: 1-64. https://doi.org/10.4039/entm9747fv
Lindquist E.E., Moraza M.L. 2010. Revised diagnosis of the family Blattisociidae (Acari: Mesostigmata: Phytoseioidea), with a key to its genera and description of a new fungus-inhabiting genus from Costa Rica. Zootaxa, 2479: 1-21. https://doi.org/10.11646/zootaxa.2479.1.1
Lindquist E.E., Moraza M.L. 2012. A new genus of fungus-inhabiting mites of the family Blattisociidae (Acari Mesostigmata Phytoseioidea) from Costa Rica, with an updated key to genera of the subfamily Blattisociinae. Redia, 95: 9-19.
Lindquist E.E., Moraza M.L. 2014. Mites coexistent with neotropical hispine beetles in unfurled leaves of *Heliconia*: a new genus and family of the Ascoidea (Acari: Mesostigmata: Gamasina). Journal of Natural History, 48(27-28): 1611-1651. https://doi.org/10.1080/00222933.2013.877995
Lindquist E.E., Walter D.E. 1989. *Antennoseius (Vitzthumia) janus* n. sp. (Acari: Ascidae), a mesostigmatic mite exhibiting adult female dimorphism. Canadian Journal of Zoology, 67(11): 2797-2813. https://doi.org/10.1139/z89-184
Lindquist E.E., Walter D.E., Krantz G.W. 2009. *Order Mesostigmata.* In: Krantz G.W, Walter D.E. (Eds.) A Manual of Acarology, Third Edition, Texas Tech University Press, Lubbock, pp. 124-232.
Linnaeus C. 1758. Systema Naturae, 10th ed. L. Salvii, Stockholm.
Loots G.C. 1980. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles (Mission P.L.G.Benoit - J.J. Van Mol 1972). Freeliving Gamasina (Mesostigmata - Acarina) - Revue de zoologie africaine, 94: 745-772.
Mašán P., Halliday B. 2014. Review of the mite family Pachylaelapidae (Acari: Mesostigmata). Zootaxa, 3776(1): 1-66. https://doi.org/10.11646/zootaxa.3776.1.1
Moraes G.J. de, Britto E.P.J., Mineiro J.L. de C., Halliday B. 2016. Catalogue of the mite families Ascidae Voigts & Oudemans, Blattisociidae Garman and Melicharidae Hirschmann (Acarina: Mesostigmata). Zootaxa, 4112(1): 1-299. https://doi.org/10.11646/zootaxa.4112.1.1

Moraza M.L., Balanzategui I. 2023. A new species of *Lasioseius* (*Endopodalius*) (Acari: Mesostigmata: Blattisociidae) coexistent with the invasive agave weevil (Coleoptera: Dryophthoridae) in the southeast of the Iberian Peninsula. Acarologia, 63: 605-614. https://doi.org/10.24349/vfv7-8tut

Moraza M.L., Lindquist E.E. 2018. A new species-group with new species of the genus *Lasioseius* (Acari: Mesostigmata: Blattisociidae) associated with neotropical hispine beetles in furled leaves of *Heliconia*. Acarologia, 58(1): 62-98. https://doi.org/10.24349/acarologia/20184227

Naskreski P., Colwell R.K. 1998. Systematics and host plant affiliations of hummingbird flower mites of the genera *Tropicoseius* Baker & Yunker and *Rhinoseius* Baker & Yunker (Acari: Mesostigmata: Ascidae). Monographs, Thomas Say Publications in Entomology, iii+185 pp. https://doi.org/10.4182/QYFA2793

Paykull G de. 1811. Monographia Histeroidum. Stenhammar & Palmblad, Uppsala. 123 pp + 13 plates.

Quintero-Gutiérrez E.J., Sandmann D., Cómbita-Heredia O., Klarner B., Widyastuti R., Scheu S. 2020. A new species of the genus *Lasioseius* (Acari: Blattisociidae) inhabiting litter of secondary rainforest in Sumatra, Indonesia. Acarologia, 60(2): 338-352. https://doi.org/10.24349/acarologia/20204371

Singer G. 1967. A comparison between different mounting techniques commonly employed in acarology. Acarologia, 9: 475-484.

Vaurie P. 1978. Revision of the genus *Sphenophorus* in South America. Bulletin of the American Museum of Natural History, 2656: 1-30.

Vitzthum H. 1925. Fauna sumatrensis (Beitrag Nr. 5). Acarinae. Supplementa Entomologica Berlin, 11: 1-79.

Walter D.E., Lindquist E.E. 1997. Australian species of *Lasioseius* (Acari: Mesostigmata: Ascidae) the *porulosus* group and other species from rainforest canopies. Invertebrate Taxonomy, 11: 525-547. https://doi.org/10.1071/IT96003

Westerboer I. 1963. Die Familie Podocinidae Berlese, 1916. In: Stammer H.J. (Ed.), Beiträge zur Systematik und Ökologie mitteleuropäischer Acarina, Band II, Mesostigmata 1. Akademie Verlagsgesellschaft, Leipzig, pp.179-450.