Zootaxa 3510: 1–40 (2012)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

urn:lsid:zoobank.org:pub:9FA3E430-E195-4E89-9AAA-7EABEBC494FC

Systematic revision of the genera *Geckobiella* Hirst, 1917 and *Hirstiella* Berlese, 1920 (Acari: Prostigmata: Pterygosomatidae) with description of a new genus for American species parasites on geckos formerly placed in *Hirstiella*

RICARDO PAREDES-LEÓN[1], HANS KLOMPEN[2] & TILA M. PÉREZ[1]

[1]*Colección Nacional de Ácaros, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México. Avenida Universidad 3000, Ciudad Universitaria, C. P. 04510; Distrito Federal, México. E-mail: rparedes@ibiologia.unam.mx*
[2]*Acarology Laboratory, Department of Evolution, Ecology and Organismal Biology, Ohio State University. Columbus, OH 43212, USA*

Table of contents

Accepted by A.V. Bochkov: 4 Sep. 2012; published: 9 Oct. 2012

Abstract

A cladistic analysis based on 274 morphological characters was performed including the 13 previously recognized species of the scale mite genus *Hirstiella*, 2 new species, 5 species in closely related genera, and 3 more distant out-group species. An analysis based on 148 informative characters resulted in one most parsimonious tree (L = 400, CI = 0.57 and RI = 0.79). According to this, the genus *Hirstiella* in its current concept is a polyphyletic taxon whose member species belong to three different clades. The first lineage (Bremer support and jackknife values 2 and 78%) includes the type species *H. trombidiiformis* and seven additional species of *Hirstiella* that are parasites on iguanian lizards. The genus *Geckobiella* is included in this lineage, and the latter taxon name has priority over *Hirstiella*; therefore, the genus *Hirstiella* is considered a synonym of *Geckobiella* and no longer valid. For the second lineage (Bremer support and jackknife values of 2 and 73%) we propose the name *Bertrandiella* **gen. nov**.; it includes *H. tenuipes*, *H. otophila*, *H. jimenezi* and *Bertrandiella chamelaensis* **sp. nov**. The third lineage, and sister taxon of *Bertrandiella*, is a clade comprising *Pimeliaphilus* and the species *H. sharifi* and *H. insignis*. The latter taxa are transferred back to *Pimeliaphilus* (Bremer support and jackknife values >4 and 100%). Updated diagnoses are provided for the genera *Geckobiella* sensu nov. (including a new species *Geckobiella donnae* **sp. nov**.) and *Bertrandiella* **gen. nov.**, and for all their species, as well as for the genera *Pimeliaphilus* sensu nov. and *Tequisistlana*, based on the results of the phylogenetic analyses. The analyses support the hypothesis that lizards are the ancestral hosts for Pterygosomatidae; associations with arthropods (in *Pimeliaphilus*) appear to be secondary, the result of host switching from lizards.

Key words: *Bertrandiella* **gen. nov.**, *Pimeliaphilus*, *Bertrandiella chamelaensis* **sp. nov.**, *Geckobiella donnae* **sp. nov.**, phylogeny, serial homology

Introduction

The family Pterygosomatidae includes 10 genera with approximately 156 described species, most of them (eight genera) are external parasites of lizards, but the species of one genus, *Pimeliaphilus* Trägårdh, 1905 are found on arthropods and another monotypic genus *Bharatoliaphilus* Prasad, 1975 was found on a dove.

Within Pterygosomatidae the genera *Geckobiella* Hirst 1917, *Hirstiella* Berlese 1920 and *Pimeliaphilus*, have been considered less specialized and more "primitive or plesiomorphic, based on their general shape (body longer than wide and with long legs) (Cruz 1984; Bertrand 2002).

The genus *Geckobiella* currently includes two species of mite parasites of iguanian lizards, *G. texana* (Banks, 1904) on Phrynosomatidae in Central and North America and *G. harrisi* Davidson, 1958 on Tropiduridae in South America. This genus was diagnosed by Hirst (1917; 1926), Lawrence (1953), Lane (1954) and Davidson (1958), but of all the characters enumerated, the only valid autapomorphy is the presence of a specific type of idiosomal hypertrichy on the dorsum (different from that seen in *Geckobia* and *Pterygosoma*). Apart from these taxonomic studies, the biology of *Geckobiella* was studied by Goodwing (1954) and additional distributional records for *G. texana* were presented by Jack (1959), Hoffmann (1969) and Paredes-León *et al*. (2008).

The genus *Hirstiella* includes species of mite parasites of iguanian and gekkotan lizards. Thirteen species have been assigned to this genus, which was proposed originally for *Geckobiella* (*Hirstiella*) *trombidiiformis* Berlese from Mexico off an unknown host. Later, Cunliffe (1949a; 1952) described three more species and carried out the first revision of *Hirstiella* and *Pimeliaphilus*, transferring two species to the former genus (*Pimeliaphilus insignis* (Berlese) and *P. tenuipes* (Hirst)). Jack (1961) made the second examination of both genera, described another species, and transferred *Pimeliaphilus sharifi* Abdussalam to *Hirstiella*. Subsequent studies of *Hirstiella* include the description of new species by Newell and Ryckman (1964), Hunter and Loomis (1966), Baker (1998) and Paredes-León and Morales-Malacara (2009). Cruz (1984) described the genus *Cyclurobia* with a single species, *C. javieri* Cruz, an ectoparasite of Cuban iguanas. This genus has been synonymized with *Hirstiella* by Bochkov (2008).

The genus *Pimeliaphilus* was proposed for *P. podapolipophagus* Trägårdh a mite associated with tenebrionid beetles. *Geckobia insignis* Berlese was also included in this genus. *Pimeliaphilus* has been assigned to the family Raphignathidae by Trägårdh (1905), Vitzthum (1942) and Jack (1961; 1964), and to the Pterygosomatidae by Hirst (1917; 1926) and Cunliffe (1952). Further, Vitzthum (1942) proposed the genus *Pimeliaphiloides* Vitzthum for two species of *Pimeliaphilus* parasitic on lizards (*i.e.*, *P. insignis* (Berlese) as type species and *P. tenuipes* Hirst) but Cunliffe (1952) synonymized *Pimeliaphiloides* with *Hirstiella*. Despite these issues, the genus *Pimeliaphilus* has

been considered as very close to *Hirstiella*. As noted above, *Pimeliaphilus* and *Hirstiella* have been revised twice. Cunliffe (1952) mentioned some differences in the number of dorsal body setae and the length of the duplex setae (*i.e.*, companion seta *ft* and solenidion *ω2*) on tarsus I; unfortunately these differences are not satisfactory as diagnostic characters. Jack (1961) proposed a separation between the two genera based on the shape of the chelicerae and considered that the only really valid difference cited by Cunliffe was the host preference, *Hirstiella* on lizards and *Pimeliaphilus* on arthropods. In its current concept the genus *Pimeliaphilus* comprises 18 species parasites of arthropods (triatomine bugs, cockroaches, scorpions and beetles).

Another genus that has been mentioned as very close to *Hirstiella* is the monotypic *Tequisistlana* Hoffmann and Sánchez, 1980. *Tequisistlana oaxacensis* Hoffmann and Sánchez was found associated with the lizard species *Lepidophyma smithii* (Xantusiidae) and the authors suggested that *Hirstiella tenuipes* and *H. otophila* Hunter and Loomis must be transferred to *Tequisistlana* based on the shape of seta *v* on the palpal tibia. This proposal was not considered by subsequent authors.

There are few studies on the biology of mites assigned to the genus *Hirstiella*. We can mention Jack and Girot' s (1965) study on the development of *H. insignis* Berlese, and Werman's (1983) study on population dynamics of *H. pyriformis* Newell and Ryckman. Other studies on pterygosomatid mites have included species of *Hirstiella* (*e. g*., Cruz 1984; Jack 1964; Bertrand *et al*. 2000; Bochkov & OConnor 2006) but a thorough phylogenetic analysis of the genera included in the family Pterygosomatidae has not been carried out. One attempt was made by Cruz (1984) but he included only seven morphological characters without explaining the criteria for developing his hypothesis. Neither did he specify an out-group or another polarization criterion. Cruz (1984) proposed two subfamilies, Pterygosomatinae and Pimeliaphilinae. The proposed "phylogenetic" relationships within the latter subfamily were as follow (*Cyclurobia*, (*Pimeliaphilus*, (*Geckobiella*, *Hirstiella*))) (*Tequisistlana* was not considered).

Our goal is to analyze phylogenetic relationships within the Pimeliaphilinae sensu Cruz, including all the species currently referred to the genera *Geckobiella* and *Hirstiella*. The analyses are based on morphological characters of the adult females, supplemented with a few characters from the males and immatures. Following the results of these analyses, updated diagnoses are provided for the genera *Geckobiella*, *Pimeliaphilus* (both including parts of *Hirstiella*) and *Tequisistlana*. In addition, a new genus is proposed for the American species of *Hirstiella* parasites on gekkotan lizards, two new species are described, and identification keys are presented.

Material and methods

Mite specimens were obtained from field collections and by loans from Acarological Collections: **BM(NH):** The Natural History Museum (formerly British Museum (Natural History)), London, United Kingdom; **CNAC**: Colección Nacional de Ácaros, Instituto de Biología, UNAM, Distrito Federal, Mexico; **IESCA:** Colección Acarológica, Instituto de Ecología y Sistemática, La Habana, Cuba; **OSAL**: Acarology Laboratory, Ohio State University. Columbus, Ohio, USA; **USNMC**: United States National Mite Collection, United States National Museum, Natural History, Smithsonian Institution, Agricultural Research Service, Beltsville, Maryland, USA. In addition, some hosts (Iguanidae) in the Herpetological Collection of Instituto de Ecología y Sistemática (IES), La Habana, Cuba were examined.

The mites were collected by examining hosts under a dissecting microscope Olympus SZ series (Tokyo, Japan); samples were cleared in lactophenol and mounted on microscope slides in the semipermanent Hoyer´s medium. Drawings were prepared using a drawing tube on a Nikon Optiphot Two compound microscope (Tokyo, Japan) with phase contrast and differential interference contrast illumination. All measurements are in micrometers. In the case of leg lengths we measure each leg from coxal plate to tarsus (excluding ambulacra).

The data matrix was assembled including all the 13 valid known species in *Hirstiella*, *Geckobiella texana* and *G. harrisi*, two new species (here named *Geckobiella donnae* and *Bertrandiella chamelaensis*), *Pimeliaphilus ca. podapolipophagus* and *P. trogadermus* (all Pimeliaphilinae sensu Cruz 1984) and *Tequisistlana oaxacensis*. Outgroups include two members of the Pterygosomatinae (sensu Cruz 1984), *Geckobia leonilae* Hoffmann and Morales-Malacara and *Pterygosoma mutabilis* Jack and, as distant outgroup, *Eustigmaeus* sp. (Stigmaeidae). The matrix includes 274 morphological characters (Appendix 1), mostly of adult females (characters 1–267). Seven characters refer to other instars. The specimens analyzed are listed in Table 1 along with voucher numbers.

TABLE 1. Specimens of Pterygosomatidae and outgroups analyzed in this study.

Taxa	Abbreviations	Voucher Numbers
Eustigmaeus sp.	*Eus*. sp.	OSAL0066507, 12
Pterygosoma mutabilis Jack, 1961	*Pte.mut.*	OSAL0067334–35
Geckobia leonilae Hoffmann and Morales-Malacara, 1986	*Geck.leo.*	CNAC000295–96
Tequisistlana oaxacensis Hoffmann and Sánchez, 1980	*Teq.oax*.	CNAC000212–13; CNAC007085
Pimeliaphilus ca. podapolipophagus Trägårdh, 1905	*Pim.pod*.	CNAC007094
Pimeliaphilus trogadermus Cunliffe, 1968	*Pim.tro.*	USNMC
Geckobiella texana (Banks, 1904)	*Gec.tex*.	CNAC006963
Geckobiella harrisi Davidson, 1958	*Gec.har.*	USNMC; OSAL0067352–53
Hirstiella insignis (Berlese, 1892)	*Hir.ins.*	BM(NH)
Hirstiella tenuipes (Hirst, 1917)	*Hir.ten*.	BM(NH)
Hirstiella trombidiiformis (Berlese, 1920)	*Hir.tro.*	CNAC006969
Hirstiella sharifi (Abdussalam, 1941)	*Hir.sha.*	BM(NH)
Hirstiella pelaezi Cunliffe, 1949	*Hir.pel*.	USNMC; CNAC006978
Hirstiella boneti Cunliffe, 1952	*Hir.bon.*	USNMC; CNAC006996
Hirstiella bakeri Cunliffe, 1952	*Hir.bak.*	CNAC007007
Hirstiella stamii Jack, 1961	*Hir.sta.*	BM(NH); OSAL0067360; CNAC007016
Hirstiella pyriformis Newell and Ryckman, 1964	*Hir.pyr.*	USNMC; CNAC007023
Hirstiella otophila Hunter and Loomis, 1966	*Hir.oto.*	CNAC004416–17; BM(NH)
Hirstiella javieri (Cruz, 1984)	*Hir.jav.*	CNAC007046
Hirstiella diolii Baker, 1998	*Hir.dio.*	OSAL0067363–64, 66, 68
Hirstiella jimenezi Paredes-León and Morales-Malacara, 2009	*Hir.jim.*	CNAC005885–99
***Geckobiella donnae* sp. nov.**	*Gec. don.*	OSAL0013661–78; CNAC007050
***Bertrandiella chamelaensis* gen. nov.** and **sp. nov.**	*Ber.cha*.	CNAC007051

In the case of *Hirstiella tenuipes* (Hirst) the only known specimen is a deutonymph, while the only available specimen for *Hirstiella sharifi* (Abdussalam) was also a deutonymph. We included both taxa because most of the characters analyzed are already present in this instar. Those characters that are present only in adult females (*e. g.*, genital setae) were coded as inapplicable (–) for these two taxa. Secondly, characters that could not be observed for various reasons (*e. g.*, specimens poorly preserved or unavailable) are coded as unknown (?). The remaining characters (268–274) correspond to different instars (larvae, deutonymphs and males). States for unavailable instars for certain species are also coded as unknown (?).

We initially coded all structures on the gnathosoma, idiosoma and legs as independent characters. After that we checked on character correlation, especially for serial homology in presence/absence and/or shape of homologous leg setae. In cases with identical state distribution for different legs we analyze the data with the original coding, and by combining potential serial homologues.

The phylogenetic analysis was performed using Winclada-Asado ver. 1.89 (Nixon 1999-2004). The heuristic search mode was used presetting 500 replications (mult*n = 500), 100 starting trees per replication (hold/:100) with 1000 possible trees saved (hold 1000) with "branch swapping" option "multiple Tree Bisection Reconnection" (multiple TBR + TBR). The search was done with all the characters set as nonadditive (unordered character states) to avoid biased results due to the authors' intuitive criteria (Wiley *et al*. 1991). Bremer index and Jackknife analyses were executed in PAUP* 4.0 (Swofford 2002), for the latter using the settings: 37% deletion, emulate "JAC" resampling, 1,000 replications, "random addition sequences" = 1, and "hold trees" = 2 (Freudenstein *et al*. 2004).

The classification of the families of iguanian lizards follows Frost *et al*. (2001) and that for families of gekkotan lizards follows Gamble *et al*. (2008); the host reptile species names were updated in accordance with The

Reptile Database (Uetz 2011; Uetz *et al*. 2007). For the classification and nomenclature of the host of the species of *Pimeliaphilus* we follow Fet *et al*. (2000) for Scorpiones, Beccaloni (2007) for Blattodea, and Lent and Wygodzinsky (1979) for Triatominae (Reduviidae).

Results and discussion

1. Phylogenetic analysis

The analysis of the data matrix (Appendix 2) showed that 148 of 274 characters were parsimony informative. The analysis including only informative characters resulted in 1 most parsimonious tree (Fig. 1). This is 400 steps long and has a consistency index (CI) of 0.57 and retention index (RI) of 0.79. It suggests two main clades, one with the species of *Hirstiella* parasitic on iguanian lizards plus *Geckobiella* (= *Geckobiella* sensu nov.) (Bremer support and jackknife values of respectively 2 and 78%); and the other with the species of *Hirstiella* parasitic on gekkotan lizards, plus *Pimeliaphilus* and *Tequisistlana oaxacensis* (Bremer support and jackknife values of >4 and 99%). The grouping of these two main clades together, that is the Pimeliaphilinae (sensu Cruz 1984) plus *Tequisistlana*, is poorly supported (Fig. 1).

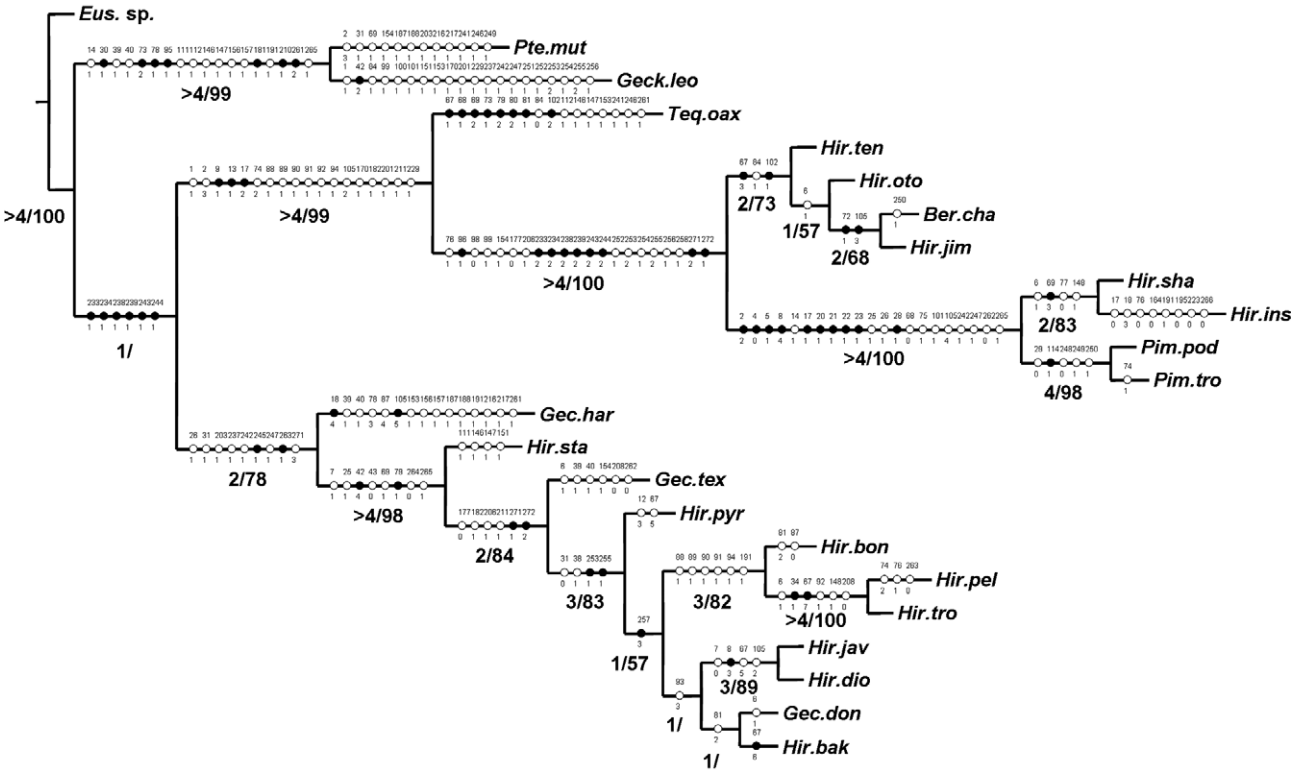

FIGURE 1. The most parsimonious tree (length: 400 steps, CI = 0.57, RI = 0.79) with Bremer support / jackknife values (only if greater than 50%).

We found identical character state distributions for some homologous setae on different legs suggesting serial homology. Most cases involve characters of legs II–IV, especially legs III–IV. Specific characters involve the following setae (numbers refer to listing in Appendix 1): *u"* (characters 199, 227), *tc'* (233, 238, 243), *tc"* (234, 239, 244), *a'* (241, 246) and *a"* (242, 247). Removing potential duplicate characters (227, 238, 243, 239, 244, 246, and 247) results also in a single tree (L = 384, CI = 0.57, RI = 0.79) whose topology is very similar to the most parsimonious tree in the first analysis (see Fig. 1), except for the position of Pterygosomatinae as sister taxon to *Geckobiella* sensu nov. instead of sister taxon to all other Pterygosomatidae included. Notably, jackknife support for the grouping of Pterygosomatinae and *Geckobiella* sensu nov. is quite strong (82%). These results emphasize that support for any arrangement of the three basal lineages, *Geckobiella* sensu nov., *Tequisistlana* / *Pimeliaphilus* / *Bertrandiella*, and Pterygosomatinae is relatively weak, even as support for arrangements within the first two lineages is generally strong.

Based on these results we propose the separation of the known species of the genus *Hirstiella* into three genera. The first (Bremer support and jackknife values 2 and 78%) includes the type species (*H. trombidiiformis* (Berlese, 1920)). But this lineage also includes the type species of *Geckobiella* (*G. texana* (Banks, 1904)), thus the valid name of this clade is *Geckobiella* by principle of priority; therefore, the genus *Hirstiella* is considered a synonym of *Geckobiella* and no longer valid. The second (Bremer support and jackknife values 2 and 73%) includes the American species parasitic on gekkotan lizards for which we propose a new genus, *Bertrandiella* **gen. nov.** Finally, the third lineage (Bremer support and jackknife values >4 and 100%) includes *Pimeliaphilus* and the two Old World species parasitic on gekkotan lizards (*i. e.*, *H. insignis* and *H. sharifi*). These species are transferred back to *Pimeliaphilus*.

2. Discussion of Lineages and Classification

In this section we re-diagnose the genus *Geckobiella* sensu nov. to include the species parasitic on iguanian lizards formerly placed in *Hirstiella*, describe *Bertrandiella* **gen. nov.** for the American species parasites of gekkotan lizards previously placed in *Hirstiella*, and re-diagnose the genus *Pimeliaphilus* sensu. nov. to include the species associated with Old World gekkotan lizards which were formerly included in *Hirstiella*. We also include a re-diagnose for *Tequisistlana*, the sister taxon of *Pimeliaphilus* sensu nov. and *Bertrandiella* **gen. nov.**

Pterygosomatidae Oudemans

Geckobiella Hirst

Geckobiella Hirst, 1917: 138; Hirst 1926: 199; Radford 1943: 71; 1950: 377; Baker and Wharton 1952: 208; Lawrence 1953: 15.
***Geckobiella* (*Hirstiella*)** Berlese, 1920: 194.
Hirstiella (in part): Hirst 1926: 197; Vitzthum 1942: 806; Radford 1943: 71; 1950: 377; Baker and Wharton 1952: 208; Cunliffe 1952: 162; Jack 1961: 305; Cruz, 1984: 2. **New synonymy.**
Cyclurobia Cruz, 1984: 5, syn. Bochkov 2008: 338.
Type species. *Geckobia texana* Banks, 1904, by monotypy.

Diagnosis. Female. Palpal tarsus elongate, narrowly attached to tibia; seta *v* of palpal tibia nude (never ending in thick brush-like structure). Dorsal body setae *c3* present; coxal group I–II separate from coxal group III–IV (distance between groups longer than length of coxal group I–II); genital setae (*g1*) simple, spiniform and slender (sometimes sparsely barbed) and located on the tip of lobes. Tarsi I–IV stout ending blunt; seta *tc'* longer than *tc"* on tarsi II-IV. Addition of setae *ps1–3* delayed to deutonymph.

Description. Female. *Gnathosoma*. Palps slender and long (2–3 times as long as the base of gnathosoma); palpal femur with dorsal seta short (never reaching tip of palp), slightly thick, spiniform or subclavate; palpal genua with dorsal seta short, thin, spiniform or subclavate; seta *v* of palpal tibia nude (never ending in a thick brush-like structure); palpal tarsus slender and narrow. *Idiosoma*. Oligotrichy present (except for *Geckobiella texana* and *G. harrisi* showing hypertrichy). Dorsal setae short, less than 100 µm (except for *G. boneti*, *G. trombidiiformis* and *G. pelaezi*), spinose spatulate (club-like) or peripectinate (in some species setae *f2* and *h1* dimorphic); setal pair *h1* short, half as long as *h2* (subequal in length in *G. harrisi*); setal pair *f2* always barbed; dorsal setae *c3* present; prodorsal shield absent or present, when present with 1 (*vi* or *sci*) or 2 pairs of setae (*vi* and *sci*) (Fig. 2); genital setae located on lobes. *Legs*. Femora I–IV of similar size as genua I–IV; leg setae shorter than length of each podomer (segment); tarsi I–IV blunt distally; seta *ft* of tarsus I acuminate, nude; solenidia $\omega 1$ and $\omega 2$ of tarsus I present ($\omega 1$ absent in *G. harrisi*); setae *a"* of tarsi II–IV barbed; setae *tc* of tarsus I long (longer than pretarsus); seta *v* of genua II absent (present in *G. texana*); seta *vs"* of tarsi II–IV absent (present in *G. texana*); setae *4c* of coxae IV absent; setae *tc* of tarsi II–IV barbed, *tc'* longer than *tc"*; coxal group I–II separate from III–IV (distance longer than length of coxal group I–II), coxal group I–II located on anterior part and III–IV on posterior part of idiosoma, at least coxae IV posterior to midline of the idiosoma body; setae *1b* of coxae I and *2b* of coxae II slender and acuminate, nude; *3c* of coxae III acuminate nude or barbed, and *3d* barbed or bipectinate; femora II and IV without seta *v'* (present in *G. trombidiiformis* and *G. pelaezi*).

Male. *Legs.* Seta *v'* on genua IV large hollow ensiform and seta *v"* on tibia IV solid and spine-like (except in *G. diolii* and *G. stamii*); solenidia $\omega 1$ and $\omega 2$ of tarsus I present. **Setal development.** Addition of setae *ps1–3* delayed to deutonymph.

Hosts. All instars parasitic on the families of iguanian lizards Iguanidae, Phrynosomatidae or Tropiduridae (Table 2).

Included species. *Geckobiella texana* (Banks), *G. trombidiiformis* Berlese, *G. pelaezi* (Cunliffe), *G. boneti* (Cunliffe), *G. bakeri* (Cunliffe), *G. harrisi* Davidson, *G. stamii* (Jack), *G. pyriformis* (Newell et Ryckman), *G. javieri* (Cruz), *G. diolii* (Baker) and *G. donnae* **sp. nov**. Paredes-León, Klompen and Pérez (Table 2).

TABLE 2. Species included in *Geckobiella* with a summary of host and distribution data.

Species	Host		Distribution	Reference
G. texana (Banks, 1904)	Phrynosomatidae	*Sceloporus* spp. (several species), *Phrynosoma* sp.	USA, Mexico, Costa Rica; Mexico	Banks 1906; Jack 1959; Hoffmann 1969
same species	Iguanidae	*Iguana iguana**	Mexico	Hoffmann, 1969
same species	Eublepharidae	*Coleonyx elegans**	Mexico	Paredes-León *et al*, 2008
G. trombidiiformis Berlese, 1920	Phrynosomatidae	*Sceloporus torquatus*	Mexico	Hoffmann and López-Campos 2000
same species	Unknown	Unknown	Mexico	Berlese 1920
G. pelaezi (Cunliffe, 1949)	Phrynosomatidae	*Sceloporus torquatus, S. grammicus, S. palaciosi*	Mexico	Cunliffe 1949a, Gadsden 1988, Hoffmann and López-Campos 2000
same species	Crotaphytidae	*Crotaphytus collaris**	Mexico	Hoffmann 1969
G. boneti (Cunliffe, 1952)	Iguanidae	*Ctenosaura acanthura, C. pectinata*	USA, Mexico	Cunliffe 1952, this study
G. bakeri (Cunliffe, 1952)	Iguanidae	Iguana (undetermined), *Ctenosaura hemilopha, C. pectinata*	USA, Mexico	Cunliffe 1952, Krantz 1978, Paredes-León 2003
same species	Phrynosomatidae	*Sceloporus* sp.*	Mexico	Hoffmann 1969
G. harrisi Davidson, 1958	Tropiduridae	*Plica plica*	Brazil	Davidson, 1958
G. stamii (Jack, 1961)	Iguanidae	*Iguana iguana, I. delicatissima*	Holland (captive), USA, Mexico, Dominica (Island)	Jack 1961, Baker 1998, Corn *et al*. 2011, Knapp *et al*. 2012, this study
G. pyriformis (Newell & Ryckman, 1964)	Iguanidae	*Sauromalus varius, S. hispidus, S. ater, Ctenosaura hemilopha*	Mexico, USA*, Mexico	Newell and Ryckman 1964, this study
G. javieri (Cruz, 1984)	Iguanidae	*Cyclura n. nubila*	Cuba	Cruz 1984
G. diolii (Baker, 1998)	Iguanidae	*Cyclura cornuta, Brachylophus vitiensis, B. fasciatus, Iguana iguana*	England (captive), Australia (captive)	Baker 1998, Walter and Shaw 2002
G. donnae Paredes-León, Klompen & Pérez	Iguanidae	*Iguana iguana, Ctenosaura pectinata*	USA (captive), Mexico	this study

* See remarks in results section for each of these species.

Geckobiella texana (Banks)

Geckobia texana Banks, 1904: 22; 1906: 134.
Pterygosoma texana Banks, 1915: 31.
Geckobiella texana Hirst, 1917: 138; 1926: 199; Radford 1943: 71; 1950: 377; Lawrence 1953: 15; Lane 1954: 94.

Diagnosis. Adults. With many short plumose or peripectinate (club-like) setae present on dorsum and sides; not arranged in transverse rows; prodorsal shield absent; eyes not on platelets associated with setae (Lane 1954; Jack 1964).

Female. Seta *v"* on genua II present; setae *vs"* of tarsi II–IV present.

Type. Depository unknown.

Type locality. Travis Co., Texas, USA.

Type host. *Sceloporus olivaceus* Smith (recorded as *S. floridanus* by Banks 1904).

Material examined. 2 females, 2 males, 2 deutonymphs, 2 larvae ex *Sceloporus* sp., MEXICO, Durango (CNAC006963–68).

Remarks. This species appears to be a specific ectoparasite of Phrynosomatidae lizards (see Table 2). The records on other hosts, such as *Iguana iguana* (Iguanidae) by Hoffmann (1969) or *Coleonyx elegans* (Eublepharidae) by Paredes-León *et al*. (2008) are considered accidental infestations.

Geckobiella trombidiiformis Berlese

Geckobiella (*Hirstiella*) *trombidiiformis* Berlese, 1920: 195.
Hirstiella trombidiformes (sic) Baker and Wharton 1952: 208; Cunliffe 1952: 166; André 1961: 159.
Hirstiella trombidiiformis Hirst, 1926: 197; Radford 1943:71; 1950: 377.

Diagnosis. Female. Prodorsal shield very poorly defined with striae similar to those on body but much lighter; prodorsal shield shaped as inverted isosceles triangle with anterior margin straight and with 1 pair of setae (*vi*) (Fig. 2A). Dorsal body setae of medium length, reaching to bases of next setal row; femora II and IV with seta *v'* (same as in *G. pelaezi*).

Male. Undescribed.

Type. Female HOLOTYPE (Berlese Collection 208/45; Istituto Sperimentale per la Zoologia Agraria, Florence, Italy).

Type locality. Guanajuato, México (Berlese 1920).

Type host. Unknown.

Material examined. 1 female, 2 males, 3 deutonymphs, 3 larvae ex *Sceloporus t. torquatus*, MEXICO, Guanajuato, Cortázar, Cerro del Colorado, 31 January 1976, coll. O. Sánchez (CNAC006969–77).

Remarks. The original description by Berlese (1920) fails to provide clear diagnostic data. Hirst (1926) redescribed the female of *G. trombidiiformis* based on a couple of specimens from Berlese´s material deposited at British Museum (BM(NH)) and mentioned about the scutum that is apparently absent. Cunliffe (1952) provided a drawing based on specimens from Nuevo León, Mexico, which was checked by C. D. Radford against specimens deposited in BM(NH); in this drawing the species is shown without prodorsal shield, but in his diagnosis Cunliffe (1952) mentioned that the species has a poorly defined prodorsal shield with striae similar to those on the body, but much lighter. Baker (1998) mentioned in a key that *G. trombidiiformis* has a triangular prodorsal shield with straight anterior margin and a pair of setae. Neither the type specimen nor the specimens deposited at BM(NH) were available for study but we examined some specimens collected from *Sceloporus t. torquatus* (Phrynosomatidae) of the same state (Guanajuato) as the type collection and can corroborate that *G. trombidiiformis* has a poorly defined triangular prodorsal shield with a pair of setae (*vi*) (Fig. 2A). Additionally, some characters used in this analysis were compared with previous studies provided by Cunliffe (1952), Jack (1961; 1964). Based on the original description and the current analysis *G. pelaezi* is very close to this species.
This species appears to be a specific ectoparasite of Phrynosomatidae lizards (see Table 2).

Geckobiella pelaezi (Cunliffe) new combination

Hirstiella pelaezi Cunliffe, 1949: 25.

Diagnosis. Female. Prodorsal shield shaped like an inverted isosceles triangle (Fig. 2B); differentiated from the rest of the body by having fine striae; anterior central portion with a notch and a seta on each side (*vi*); femora II and IV with seta *v'* (as in *G. trombidiiformis*).

Male. Undescribed.

Type. Female HOLOTYPE (USNMC1850), 1 female, 1 deutonymphal PARATYPES (USNMC).

Type locality. México, Distrito Federal.

Type host. *Sceloporus torquatus* Wiegmann (recorded originally as *Sceloporus ferrari-perezi* by Cunliffe 1952).

Material examined. Female HOLOTYPE and 1 female PARATYPE, ex *Sceloporus torquatus*, MEXICO, Distrito Federal, 14 June 1948 (USNMC); 5 females, 2 males, 3 deutonymphs, 3 larvae, same data as holotype (CNAC006978–86); 1 female, 5 deutonymphs, ex *Sceloporus torquatus*, MEXICO, Distrito Federal, Ciudad Universitaria UNAM, 26 October 2005, coll. R. Paredes-León (CNAC006987–92); 2 larvae, 1 deutonymph ex *Sceloporus* sp., MEXICO, Distrito Federal, Cuautepec, 19.59380° N, -99.12832° W, 2810 m asl, 25 June 2009, coll. R. Paredes-León (CNAC006993–95).

Remarks. The holotype, paratype and topotypes were available for analysis (deutonymph paratype was not requested). According to Cunliffe (1949a) this species was compared at that time (by C. D. Radford) with three deutonymphs of Berlese´s material of *Geckobiella trombidiiformis* deposited in BM(NH), and although they are very close, they differ in body size, type of chelicerae, and size of the rostrum (Cunliffe 1949a). As mentioned above in remarks of *G. trombidiiformis*, females of this species are deposited at BM(NH) and we do not know the reason why deutonymphs were compared rather than females but we consider that is essential to realize a detailed analysis of all the instars to clearly delimit both species (*G. pelaezi* and *G. trombidiiformis*).

This species appears to be a specific ectoparasite of Phrynosomatidae lizards (see Table 2). The record on *Crotaphytus collaris* (Crotaphytidae) could be a misidentification of the host species because according to Ramírez-Bautista *et al*. (2010) this lizard is not distributed in the locality (Hidalgo, Mexico) mentioned by Hoffmann (1969).

Geckobiella boneti (Cunliffe) new combination

Hirstiella boneti Cunliffe, 1952: 166.

Diagnosis. Female. Prodorsal shield pentagonal with 2 pairs of setae (*vi* and *sci*) (Fig. 2C); with long dorsal body setae that extend to bases of next row.

Male. Similar to female but without dorsal shield; palpal femur with short, almost conical seta *d*; genua IV with enlarged, spinelike ventral seta (Cunliffe 1952).

Type. Female HOLOTYPE (USNMC1859), 4 female, 1 male PARATYPES (USNMC).

Type locality. Unknown.

Type host. *Ctenosaura acanthura* (Shaw) (cited as *C. multispinis* by Cunliffe 1952).

Material examined. Female HOLOTYPE and 1 female, 1 male PARATYPES ex *Ctenosaura acanthura* (cited as *C. multispinis*), 22 November 1923, coll. P. Spong (USNMC). 2 females, 1 male, 6 deutonymphs, 2 larvae ex iguana (undetermined but probably *Ctenosaura pectinata* based on geographic distribution), MEXICO, Morelos, Coatetelco, 15 April 1949, coll. W. G. Downs (CNAC006996–007006).

Remarks. This species appears to be a specific ectoparasite of Iguanidae lizards (see Table 2). The host type was a specimen of *Ctenosaura multispinis* in the College Reptile Collection, Wayne, Nebr. The type locality of *C. multispinis* (now *C. acanthura*) is Dondomingovillo (sic), Oaxaca, Mexico (Uetz *et al*. 2007). The specimens from Morelos correspond to the collection of *Geckobiella texana* mentioned by Hoffmann (1969), however the original label says: "ex Iguana". This does not necessarily imply that the host is *Iguana* sp. Based on geographic distribution the host is most likely *Ctenosaura pectinata* instead of *Iguana iguana* (Reynoso pers. comm.).

Geckobiella bakeri (Cunliffe) new combination

Hirstiella bakeri Cunliffe, 1952: 168.

Diagnosis. Female. Prodorsal shield oval possessing only 2 pairs of setae (*vi* and *sci*) (Fig. 2D); dorsal body setae and most leg setae short and club-like.

Male. Gnathosoma not as slender in proportion to body as in female; dorsal shield absent; dorsal body and leg setae short, club-like (as in female); tibia IV with seta *v"* small, short, triangular spine-like and genu IV with seta *v'* large, strong, serrate spine-like.

Type. Female HOLOTYPE (USNMC1860), 2 female, 1 male PARATYPES (USNMC).

Type locality. San Diego, California, USA.

Type host. "Iguana".

Material examined. 1 female, 1 male ex *Sceloporus* sp., MEXICO, Puebla, Izúcar de Matamoros, January 1950, coll. R. Martínez (CNAC007007–08). 2 females, 1 male, 4 larvae ex *Ctenosaura pectinata*, MEXICO, Guerrero, Iguala, April 2003, coll. G. González (CNAC007009–15).

Remarks. The type series of *G. bakeri* was not examined; a loan was requested from USNMC but the specimens could not be located (Ochoa pers. comm.). According to Cunliffe (1952) this type series was collected on an undetermined iguana, and it is not possible to know if the host is any of the two native iguanas of San Diego Co. (*Dipsosaurus dorsalis* or *Sauromalus ater*) or if the host is a captive iguana (not necessarily a native iguana). Based on our observations of material from Mexico this species seems very close to *G. diolii*, *G. javieri* and *Geckobiella donnae* **sp. nov.** in the shape of the dorsal setae.

Hoffmann (1969) recorded specimens of this species from Mexico (which were included in our analysis) supposedly collected on the lizard *Sceloporus* sp. (Phrynosomatidae). After the analysis of several specimens of phrynosomatid lizards (*e. g.*, *Sceloporus* spp., *Phrynosoma* spp., etc.) we consider that *Geckobiella bakeri* is most likely a parasite of Iguanidae instead of Phrynosomatidae (Table 2). A potential host, the iguanid *Ctenosaura pectinata* does occur in the relevant locality (Izúcar de Matamoros) (Reynoso pers. comm.); further, we found specimens of *G. bakeri* on *Ctenosaura pectinata* from another locality. Possibly, the record by Hoffmann (1969) may be based on a misidentification of the host. However, we stress that this comment about the identity of the host is only an assumption.

Geckobiella harrisi Davidson

Geckobiella harrisi Davidson, 1958: 75.

Diagnosis. Female. Idiosoma laterally compressed; dorsal setae short club-like, occurring in patches; short peritremes which do not extend to second palpal segment. Setae *ps1–2* spinose spatulate (club-like) and *ps3* sparsely barbed.

Male. Idiosoma dorso-ventrally flattened; club-like setae present, most abundant anteriorly on margin of dorsum.

Type. Female HOLOTYPE (USNMC 1860) and allotype (USNMC); PARATYPES in OSAL.

Type locality. 12 miles south of Santarem, Para, Brazil.

Type host. *Plica plica* (Linnaeus).

Material examined. Female HOLOTYPE, 1 male ALLOTYPE ex *Plica plica*, BRAZIL, 12 mi South Santarem, Para, 5 September 1955, coll. L. E. Harris Jr. (USNMC); 2 females ex *Plica plica*, BRAZIL, Para, 13 January 1956, coll. L. E. Harris Jr. (OSAL0067352–53).

Remarks. This species appears to be a specific ectoparasite of Tropiduridae lizards (see Table 2). Davidson (1958) mentioned the absence of eyes as a diagnostic character for this species, however we found that *G. harrisi* has a pair of eyes each located anterolaterally as in other pterygosomatids. Apparently without solenidion ω on tarsus III (unlike Jack 1964).

Geckobiella stamii (Jack) new combination

Hirstiella stamii Jack, 1961: 311.

Diagnosis. Adults. Distinct prodorsal shield absent, area striated or ridged over its entire surface.

Female. Dorsal setae short, flattened, expanded and densely spiculate (club-like). Femur II without setae *l'*, *l"* and *v'*; genua II–IV without seta *l'*; femur III–IV without seta *l'*.

Male. Some dorsal setae short and spinous (club-like). Seta *d* of palpal femur very short and stout, forming a "five-pronged fork" (Jack 1961).

Type. Female HOLOTYPE, male and larva PARATYPES (BM(NH)).

Type locality. Origin unknown, mites collected from captive iguanas in the Amsterdam Zoological Gardens, Netherlands.

Type host. *Iguana iguana* (Linnaeus).

Material examined. Female HOLOTYPE ex captive *Iguana iguana*, coll. A. B. Stam (BM(NH)). 6 females, 9 males, 2 deutonymphs, 2 larvae ex *Iguana iguana*, MEXICO, Veracruz, coll. F. Olvera (CNAC007016–32). 1 male ex *Iguana iguana*, MEXICO, Campeche (OSAL0067360).

Remarks. This species appears to be a specific ectoparasite of Iguanidae lizards (see Table 2).

Geckobiella pyriformis (Newell and Ryckman) new combination

Hirstiella pyriformis Newell and Ryckman, 1964: 164.

Diagnosis. Female. Prodorsal shield pyriform (anterior margin not sharply defined) with 1 pair of setae (*sci*) (Fig. 2E). Tarsus III with residual alveolus or minute pore.

Male. Well-defined prodorsal shield absent. Trochanter IV without setae (1 seta present in female); genua IV with a large, hollow ensiform seta (*v'*) and tibia with 1 solid spine-like seta (*v"*), both covered with short, spinose ornamentation (Newell & Ryckman 1964).

Type. HOLOTYPE depositary unknown; female, male and deutonymphal PARATYPES (USNMC and AMNH).

Type locality. San Esteban Island, Gulf of California, Baja California, Mexico.

Type host. *Sauromalus varius* Dickerson.

Material examined. 15 female, 4 male, 1 deutonymphal PARATYPES ex *Sauromalus varius*, MEXICO, Baja California, San Esteban Island, 28° 20' N, -112° 37' W, 23 May 1963, coll. R. E. Ryckman, A. E. Ryckman and C. P. Christianson (USNMC). 5 females, 5 males ex *Ctenosaura hemilopha*, MEXICO, Sonora, Hermosillo, Centro Ecológico de Sonora, 11 March 1986, coll. G. Lara (CNAC007033–42).

Remarks. This species appears to be a specific ectoparasite of Iguanidae lizards (see Table 2). Baker (1998) reports this species from USA based on paratypes deposited at the Natural History Museum, London, but in the original description Newell and Ryckman (1964) mentioned this species only from Baja California, México. This confusion must be due to the fact that the microscope slides are labeled as Loma Linda, California, USA. However, Newell and Ryckman (1964) mentioned that the description was based from mites collected in a laboratory colony of *Sauromalus varius* at Loma Linda University, but that the lizards originated from San Esteban Island.

Geckobiella javieri (Cruz) new combination

Cyclurobia javieri Cruz, 1984: 5.
Hirstiella javieri Bochkov, 2008: 338.

Diagnosis. Female. Prodorsal shield pyriform with 2 pairs of setae (*vi* and *sci*) (Fig. 2F). Dorsal setae spatulate spinose (subclavate to clavate) (except barbed *f2*); *ps1* sparsely pectinate, *ps2* sparsely barbed and *ps3* peripectinate. Solenidion *ω2* on tarsus I as long as companion seta *ft*.

Type. Male HOLOTYPE, male, deutonymphal, protonymphal and larval PARATYPES (IESCA), probably lost.

Type locality. Cabo Cruz, Niquero, Granma, Cuba.

Type host. *Cyclura nubila* Gray.

Material examined. 3 females ex *Cyclura nubila* (IES12729), CUBA, Pinar del Río, Guanahacabibes, 21 February 1985 (CNAC007043–45). 1 female, 1 deutonymph, 2 larvae ex *Cyclura nubila*, CUBA, Pinar del Río, Mpio. Sandino, María La Gorda, 1 km SE from Hotel María La Gorda, 21° 41' 55.34" N, -84° 29' 32.57" W, 10 m asl, 02 November 2011, coll. L. Márquez (CNAC007046–49).

Remarks. This species appears to be a specific ectoparasite of Iguanidae lizards (see Table 2). *Geckobiella javieri* was described originally based on male and immature specimens. One of us (RP-L) visited the Acarological Collection of IES but unfortunately the type series could not be located. However, three females were recovered from a specimen of *Cyclura nubila* collected from Cuba and deposited in the Herpetological Collection of IES (12729). The general morphology of these specimens is consistent with that of females of *Hirstiella* parasitic on Iguanidae (= *Geckobiella* sensu nov. in this study).

Based on the character matrix (Appendix 2), *G. javieri* and *G. diolii* share all character states (except the setal form of dorsal idiosomal setae *h1*). Additional differences between these species are found in the smaller size of *G. javieri*, in particular in the size of some structures such as the prodorsal shield length and width 181 x 189 (versus 198 x 226 in *G. diolii*) (Fig. 2F–G), width between setal pair *sci* on prodorsal shield (WSCI) 112 (versus 125 in *G. diolii*), leg lengths (excluding ambulacrum) from leg I to IV respectively 373, 292, 310 and 362 (versus 463, 360, 369 and 383 in *G. diolii*), and solenidion *ω1* and *ω2* of tarsus I length 27 and 45 respectively (39 and 53 in *G. diolii*).

In one specimen (CNAC007046) one seta *vi* was positioned outside the prodorsal shield.

Geckobiella diolii (Baker) new combination

Hirstiella diolii Baker, 1998: 183.

Diagnosis. Female. Prodorsal shield distinct, pyriform with 2 pairs of setae (*vi* and *sci*) (Fig. 2G). All dorsal setae spatulate spinose (subclavate to clavate), except for *f2* and *h1* which peripectinate or barbed. Solenidion *ω2* on tarsus I as long as companion seta *ft* (as in *G. javieri*).

Male. Characterized by having subclavate median hysterodorsal setae that not overlap and located on smooth plates; dorsal surface largely covered by transverse shields (except posterior end of opisthosoma) (Baker 1998).

Type. Female HOLOTYPE, female, male, deutonymphal and larval PARATYPES (BM(NH)).

Type locality. Origin unknown, mites collected from captive iguanas in Regent´s Park Reptile House of London Zoo, England.

Type host. *Cyclura cornuta* (Bonnaterre).

Material examined. 3 females, 1 male ex *Cyclura cornuta* USA, captive (OSAL0067363–64; 66; 68).

Remarks. *Geckobiella diolii* was described as very close to *Geckobiella javieri* (see remarks). Both species are ectoparasite of *Cyclura* (Iguanidae) species from the Caribbean region.

Geckobiella donnae Paredes-León, Klompen and Pérez, new species
(Figs. 2H; 3–4)

Diagnosis. Female. Prodorsal shield shaped as an inverted pentagon with 2 pairs of short setae (*vi* and *sci*) that not extending to next row of setae (Fig. 2H); anterior sides of shield almost parallel. Dorsal setae short and spinose spatulate (except barbed *f2*); setae *f1* long, subequal to *f2*; setae *ps1–2* sparsely pectinate or barbed; setae *ps3* acuminate, nude.

Description. Female. *Gnathosoma* (Fig. 3A–B). Subcapitulum simple, not expanded at apex, with 1 pair of ventral, slender and smooth setae (*n*) inserted behind palps; palps slender and long (twice length of base of gnathosoma); femoral and genual seta (*d*) spinose and subclavate, that of femur shorter; tibial setae *l'* and *lT* smooth and simple, seta *v* sparsely barbed; tibial claw simple and short (half of length of palpal tarsus); tarsus elongate and narrowly attached to tibia, with basal solenidion *ω* and 6 setae: basal seta proximally sparsely barbed,

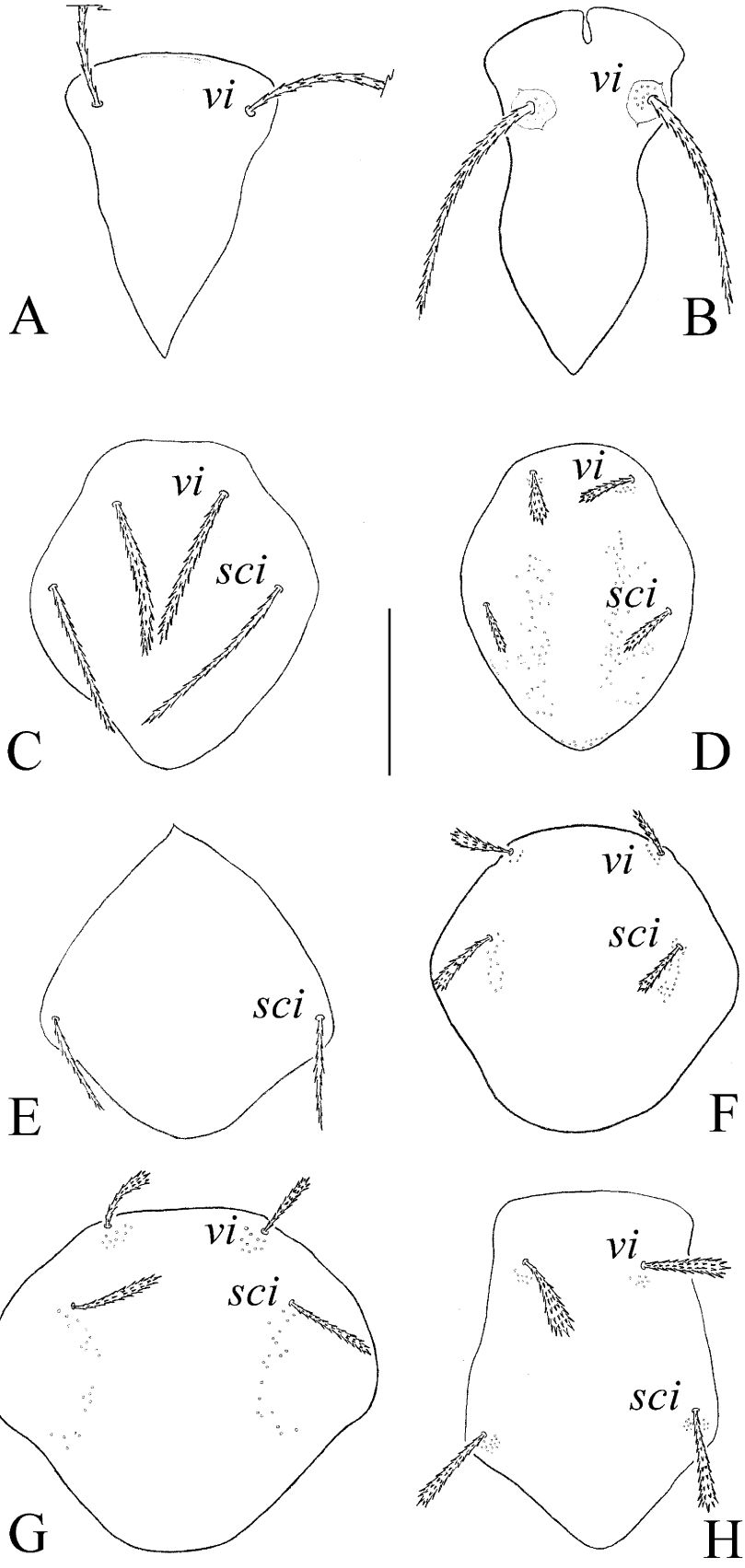

FIGURE 2. Prodorsal shields of the species of *Geckobiella*. **A**, *G. trombidiiformis*; **B**, *G. pelaezi*; **C**, *G. boneti*; **D**, *G. bakeri*; **E**, *G. pyriformis*; **F**, *G. javieri*; **G**, *G. diolii*; **H**, *G. donnae* **sp. nov.** Scale bar 100 μm.

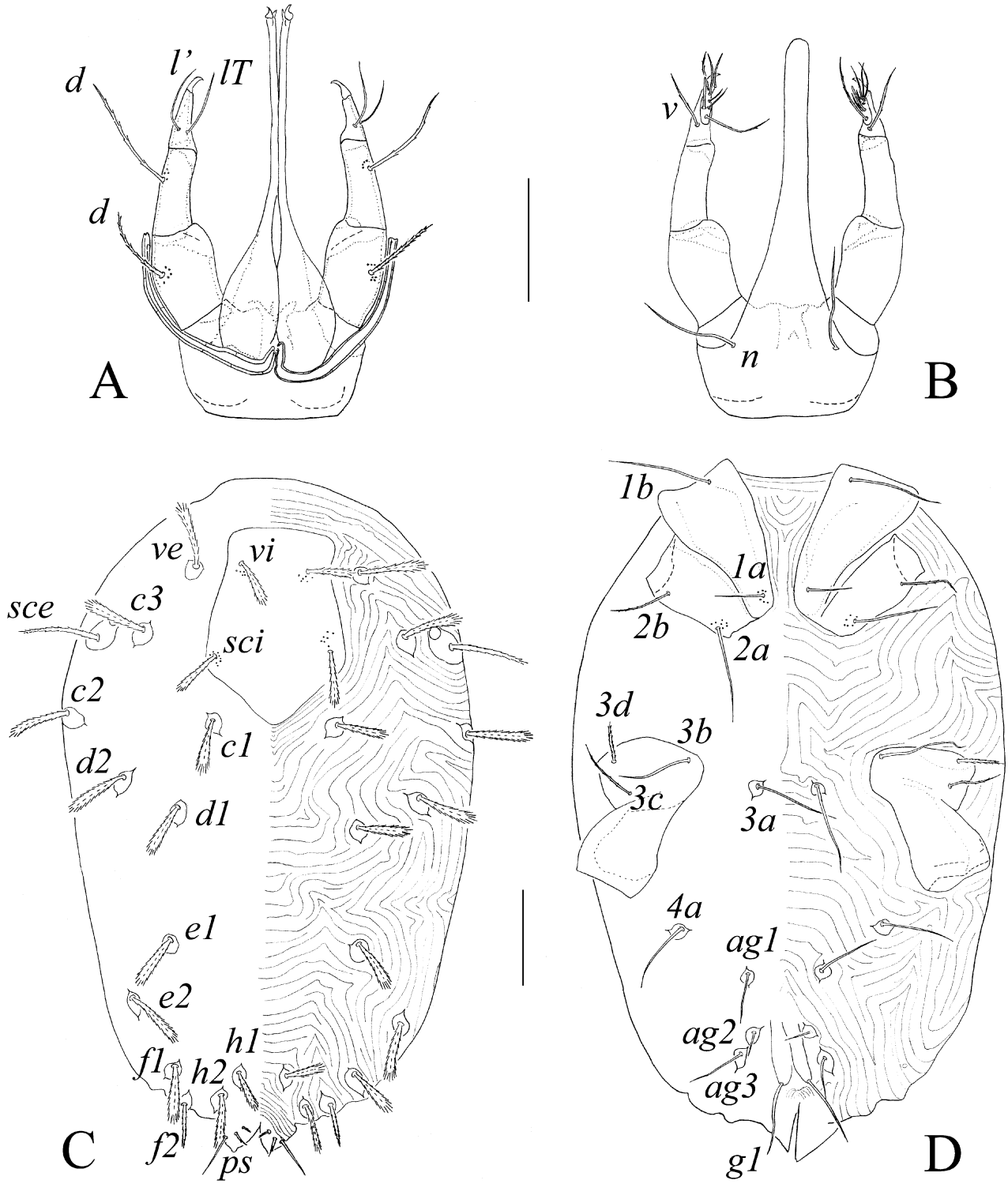

FIGURE 3. *Geckobiella donnae* **sp. nov.**, female. **A**, gnathosoma dorsal view; **B**, gnathosoma ventral view; **C**, Idiosoma dorsum; **D**, Idiosoma venter. Scale bars 100 µm.

2 more distal setae smooth and simple, 2 apical setae smooth and simple and 1 apical seta sparsely barbed. Chelicerae long (anterior end extending beyond tip of palps) and with proximal part of cheliceral base globose and wide (fivefold the width of distal part); fixed digit membranous and spiniform and movable digit robust and curved. Peritreme long, almost reaching palpal tibia.

Idiosoma (Fig. 3C–D). Ovoid, clearly longer than wide; maximum width at level of setae *c2*; cuticle surrounding prodorsal shield, setal platelets, coxae and anogenital area striated; oligotrichous. *Dorsum*. Prodorsal

shield shaped as an inverted pentagon with 2 pairs of short setae (*vi* and *sci*) that not extending to next row of setae (Fig. 2H); anterior sides of shield almost parallel. Dorsal setae short and spinose spatulate (except barbed *f2*); setae *c3* present; anal area located on posterior tip, setae *ps1* and *ps2* sparsely pectinate or barbed and *ps3* acuminate nude. *Venter.* Setae: coxal formula 2–2–4–1, located on coxae I–IV except for *3a* located on intercoxal area and *4a* between posterior coxae IV; *1a*, *1b*, *2a*, *3a*, *3b* and *4a* smooth and slender, *2b* and *3c* barbed, *3d* bipectinate and slightly thicker than the others. Setae *ag1–3* slender and smooth, located between posterior coxae IV and beginning of genital region, setae *ag2* the shortest; 1 of pair smooth genital setae (*g1*) located on lobes and longer than *ag1–3*.

Legs (Fig. 4). Setal formulae (I–IV, microsetae (*κ*) and solenidia in brackets): trochanter 1–1–1–1, femur 5–4–3–2, genu 5(*κ*)–4–3–3, tibia 5–5–5–5, tarsus 14(2)–9(1)–9(1)–9; tarsi I–IV blunt distally, especially tarsus I. All dorsal and lateral setae on trochanter-tibiae I–IV subclavate to clavate and thicker than barbed ventral setae. Tarsi I–IV with setae *p* feather-like; tarsus I with 1 pair of setae *tc* smooth (eupathids) subequal in length, and long (clearly longer than pretarsus); setae *tc* II–IV barbed, shorter than *tc* I; *tc'* II–IV longer than *tc"* II–IV. Tarsus I also with 1 pair of setae *it* (eupathids) at base of pretarsus; seta *vs"* on tarsi II–IV absent; solenidia of tarsus I long, *ω2* longer than *ω1* but shorter than companion seta *ft*. Solenidia on tarsi II–III shorter than solenidia on tarsus I, solenidion on tarsus III shortest. Pretarsi with paired claws bearing tenent hairs.

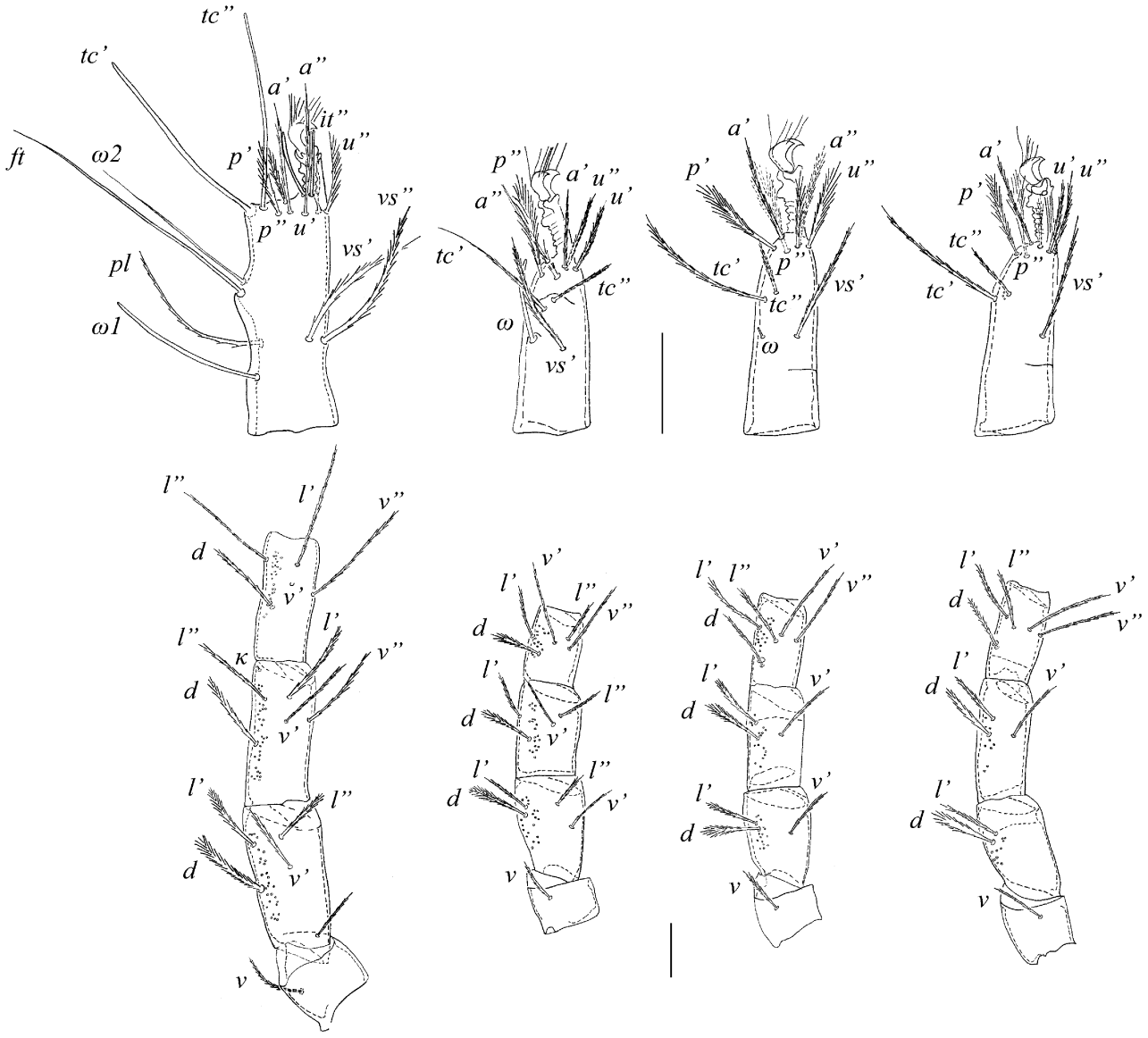

FIGURE 4. *Geckobiella donnae* **sp. nov.**, female, legs I–IV (trochanters-tarsi). Scale bars 50 μm.

Measurements. HOLOTYPE female (followed in parentheses by range and mean of HOLOTYPE and 5 PARATYPE females). Idiosoma length (gnathosoma excluded) 717 (717–992, 815), idiosoma maximum width 448 (448–659, 548), prodorsal shield length 214 (214–247, 232), prodorsal shield width (at anterior margin) 152 (112–170, 140), width between setal pair *vi* on prodorsal shield (WVI) 68 (51–71, 66), width between setal pair *ve* on prodorsal shield (WVE) 174 (174–228, 200), width between setal pair *sci* on prodorsal shield (WSCI) 122 (122–137, 132); setal lengths: *vi* 54 (54–65, 58), *ve* 74 (74–84, 78), *sci* 60 (60–71, 64), *sce* (ocular setae): 70 (70–98, 87); leg lengths (excluding ambulacrum): leg I 749 (723–835, 769), leg II 509 (506–573, 529), leg III 550 (518–608, 559), leg IV 634 (627–717, 659); solenidion *ω1* of tarsus I length 69 (69–77, 74), solenidion *ω2* of tarsus I length 89 (89–197, 96), *ft* (companion seta of solenidion *ω2* of tarsus I) length 126 (126–146, 136), solenidion *ω* of tarsus II length 42 (42–49, 45), solenidion *ω* of tarsus III length 5 (5–7, 6); gnathosoma length 335 (335–352, 339), base of gnathosoma width 146 (146–162, 154), subcapitular setae *n* length 81 (81–99, 89), chelicerae length 294 (294–348, 313), chelicerae width (at base) 46 (46–52, 49), palp length 270 (270–307, 283), palp width 43 (39–52, 46), palp-claw length 20 (13–22, 19), and peritreme length (complete) 335 (335–388, 361).

Type. Female HOLOTYPE (OSAL013670) and 7 female PARATYPES (OSAL0013662–63; 67–69; 71 and CNAC007050).

Type locality. Origin unknown, mites collected from captive iguanas in a pet store of USA.

Type host. *Iguana iguana* (Linnaeus).

Type series. Female HOLOTYPE, 6 female PARATYPES ex *Iguana iguana*, USA, Ohio, Franklin Co., Dublin, pet store, 40° 05' 57" N, -83° 06' 51" W, 4, 15 June 2004, coll. D. Wenzel (OSAL0013670 and OSAL0013662–63; 67–69; 71 respectively). 1 PARATYPE female ex *Ctenosaura pectinata*, MEXICO, Oaxaca, Istmo de Tehuantepec, Reforma de Pineda, 90 m asl, 27–III–2002, coll. G. Köhler and F. Mendoza (CNAC007050).

The holotype and paratypes from USA are deposited in the Ohio State Acarology Laboratory (OSAL013662–63; 67–71). The paratype from Mexico is deposited in Colección Nacional de Ácaros (CNAC007050).

Etymology. This species is named in honor of Donna Wenzel who kindly collected the type series of this species.

Remarks. Very close to *G. bakeri*, sharing, among others, the shape of the dorsal setae and the relative length of solenidion *ω2* on tarsus I (slightly shorter than companion seta *ft*). *Geckobiella donnae* **sp. nov.** differs from *G. bakeri* in the shape of prodorsal shield, by having setae *ps3* nude instead of sparsely barbed, and the branched instead of club-like, shape of seta *d* on femur I.

This species appears to be a specific ectoparasite of Iguanidae lizards (see Table 2).

Key to females of *Geckobiella* Hirst sensu nov.

1.	With hypertrichous idiosoma	2
-.	With oligotrichous idiosoma	3
2.	Setae *ps1–3* sparsely barbed or peripectinate	*G. texana*
-.	Setae *ps1–2* spatulate spinose and club-like and *ps3* sparsely barbed	*G. harrisi*
3.	Prodorsal shield shaped as an inverted isosceles triangle	4
-.	Prodorsal shield shaped as an inverted pentagon, ovoid, inverted pear-shaped or absent	5
4.	Anterior margin of prodorsal shield straight (Fig. 2A)	*G. trombidiiformis*
-.	Anterior margin of prodorsal shield with a notch (Fig. 2B)	*G. pelaezi*
5.	Prodorsal shield shaped as an inverted pentagon	6
-.	Prodorsal shield ovoid, shaped as an inverted pear or absent	7
6.	With anterior sides almost parallel (Fig. 2H)	*Geckobiella donnae* **sp. nov.**
-.	With anterior sides sharply converging anteriorly (Fig. 2C)	*G. boneti*
7.	Prodorsal shield ovoid (Fig. 2D)	*G. bakeri*
-.	Prodorsal shield shaped as inverted pear or absent	8
8.	Prodorsal shield absent	*G. stamii*
-.	Prodorsal shield shaped as an inverted pear	9
9.	Prodorsal shield with one pair of setae (*sci*) (Fig. 2E)	*G. pyriformis*
-.	Prodorsal shield with two pairs of setae (*vi* and *sci*)	10
10.	Dorsal idiosomal setal pair *h1* peripectinate, prodorsal shield clearly wider than long (length ca. 198 µm x width 226 µm) (Fig. 2G), and solenidion *ω1* of tarsus I long (ca. 39 µm).	*G. diolii*
-.	Dorsal idiosomal setal pair *h1* spinose spatulate (club-like), prodorsal shield almost as long as wide (length ca. 181 µm x width 189 µm) (Fig. 2F), and solenidion *ω1* of tarsus I shorter (ca. 27 µm)	*G. javieri*

Bertrandiella Paredes-León, Klompen and Pérez, new genus

Hirstiella (in part): Cunliffe 1952: 162; Jack 1961: 305.
Pimeliaphiloides (in part): Vitzthum, 1942: 806; Baker and Wharton 1952: 208.
Type species**:** *Bertrandiella chamelaensis* sp. nov., designated here

Diagnosis. Female. Palpal tarsus very reduced (distinctly shorter than tibial claw) and round (as long as wide); seta *v* of palpal tibia with nude stalk ending in thick brush-like structure. Idiosoma longer than wide, oligotrichous; dorsal body setae *c3* absent; prodorsal shield shaped as inverted equilateral triangle; setae *vi* located proximal to *ve*, both on prodorsal shield; dorsal setal pair *h1* heavily pectinate; setae *ps1–3* similar in length and arboriform (extensively pectinate), slightly shorter than rest of dorsal setae; genital setae (*g1*) arboriform and not located on lobes; setae *ag1–3* pectinate and long (slightly shorter than *f1*), setae *ag3* longer than subequal *ag1–2*. Tarsi I–IV progressively narrowing from proximal to distal end. Setae *ps1–3* present from larval instar on.

Description. Female. *Gnathosoma.* Palps robust and short; palpal femur with dorsal seta long (sometimes reaching tip of palp), thick and pectinate; palpal tarsus rounded and small; seta *v* of palpal tibia with nude stalk ending in thick brush-like structure; subcapitulum with anterolateral flange. *Idiosoma*. Prodorsal shield always present, shaped as equilateral triangle with anterior margin slightly concave and with 3 pairs of setae: *vi*, *ve* and *sci*. Oligotrichous; dorsal setae long and pectinate; dorsal setae *c3* absent; setae *ps1–3* pectinate; genital setae barbed or pectinate, not located on lobes. *Legs*. Femora I–IV longer than genua I–IV; leg setae long (almost the length of each podomer); tarsal tips I–IV very narrow; setae *v"* of genua II and *vs"* of tarsi II–IV present; setae *4c* of coxae IV present; tarsal setae *tc'* and *tc"* II–IV peripectinate, similar in length; setae *1b* of coxae I, *2b* of coxae II and *3c* and *3d* of coxae III thick, robust and pectinate; seta *ft* of tarsus I peripectinate and at least half as long as *ω2*; solenidion *ω1* of tarsus I absent; setae *a"* of tarsi II–IV nude.

Male. *Idiosoma*. Prodorsal shield always present, trapezoid in shape, clearly wider than long and with 4 pairs of peripectinate setae (*vi*, *ve*, *sci* and *c1*). *Legs.* Setae *v'* on genua IV and *v"* on tibia IV pectinate (neither hollow ensiform on genua IV nor solid spine-like on tibia IV); solenidia *ω1* and *ω2* of tarsus I present.

Setal development. Setae *ps1–3* present from larval instar on.

Hosts. All instars parasitic on lizards of gekkotan families, *i. e.*, Sphaerodactylidae, Phyllodactylidae and Eublepharidae (Table 3).

TABLE 3. Species included in the genus *Bertrandiella* **gen. nov.**, with a summary of host and distribution data.

Species	Host		Distribution	Reference
B. tenuipes (Hirst, 1917)	Sphaerodactylidae	*Gonatodes albogularis*	Colombia	Hirst 1917
B. otophila (Hunter and Loomis, 1966)	Eublepharidae	*Coleonyx variegatus, C. brevis*	Mexico, USA	Hunter and Loomis 1966, Paredes-León *et al*. 2008
same species	Phyllodactylidae	*Tarentola americana*	Cuba	Cruz 1973
B. jimenezi (Paredes-León and Morales-Malacara, 2009)	Phyllodactylidae	*Phyllodactylus bordai, P. tuberculosus*	Mexico	Paredes-León and Morales-Malacara 2009
B. chamelaensis Paredes-León, Klompen and Pérez **sp. nov.**	Phyllodactylidae	*Phyllodactyus lanei rupinus*	Mexico	This study

Etymology. This genus is named in honour of the French acarologist Michel Bertrand for his great contributions to the study of pterygosomatid mites.

Remarks. *Bertrandiella* **gen. nov.** is the sister taxon of *Pimeliaphilus*, both genera have (1) the podomers thin, at least twice as long as wide, (2) tarsi I–IV progressively thinned from proximal to distal end and (3) setae *v'* on genua and *v"* on tibia IV of males peripectinate. However, the shape of the cheliceral digits, the size of the base of gnathosoma and the shape of companion seta (*ft*) of tarsus I, allow us to separate it. In *Bertrandiella* **gen. nov.** (1) seta *ft* is peripectinate and long, (2) the base of the capitulum has an anterolateral flange and is as long as the rest of the palps, (3) the cheliceral digits are typical for Pterygosomatidae (fixed digit as a weakly spinous seta-like or

branched process and movable digit distorted to project laterally and may have one or two teeth), (4) solenidion *ω1* on tarsus I is absent and (5) tibiae I in the larvae are without solenidia; while in *Pimeliaphilus* (1) seta *ft* is nude, spiniform and very reduced, (2) the base of gnathosoma is large and longer than the rest of the palps, (3) the cheliceral digits are long and spine-like, (4) solenidion *ω1* on tarsus I is present and (5) tibiae I in the larvae carry solenidion *φ1*.

The species of *Hirstiella* parasitic on Old World gekkotan lizards share the characters mentioned above (and others) with *Pimeliaphilus*, and for this reason we propose transferring *H. insignis* and *H. sharifi* back to *Pimeliaphilus.*

The monotypic genus *Tequisistlana* is the sister taxon of the clade comprising *Pimeliaphilus* and *Bertrandiella* **gen. nov.** These three genera share some characters such as the presence on the palpal femur and genua of a pectinate and long dorsal seta (almost reaching the tip of palp), emergent peritremes short (at level of subcapitulum), a prodorsal shield with three pairs of setae (*vi*, *ve* and *sci*), dorsal setae *c3* absent and most of the rest of dorsal idiosomal setae peripectinate and long (reaching to the bases of the next setal row).

Tequisistlana and *Bertrandiella* **gen. nov.** also share some characters such as the shape of seta *v* on the palpal tibia (with nude stalk ending in a thick brush-like structure; nude or slightly barbed in *Pimeliaphilus*), the number and type of dorsal setae, etc. However, the bulk of the evidence in the systematic analysis supports a grouping of *Bertrandiella* and *Pimeliaphilus*.

Other included species (all new combinations from *Hirstiella*). *Bertrandiella tenuipes* (Hirst, 1917), *B. otophila* (Hunter & Loomis, 1966) and *B. jimenezi* (Paredes-León & Morales-Malacara, 2009) (Table 3).

The above generic diagnosis is based mainly on characters of adult females. *Hirstiella tenuipes*, for which the female is unknown, was analyzed based on the only available specimen, a deutonymph, which shares all characters listed with the exception of characters pertaining to the genital (*g1*), aggenital setae (*ag3*), dorsal idiosomal setae *f2*, coxal setae *4c* and the length of some setae.

Bertrandiella tenuipes (Hirst) new combination

Pimeliaphilus tenuipes Hirst, 1917: 142; Hirst 1926: 197; Radford 1943: 71.
Pimeliaphiloides tenuipes Vitzthum, 1942: 613.
Hirstiella tenuipes Cunliffe, 1952: 169.

Diagnosis. Adults. Unknown.

Deutonymph. Dorsal propodosomal shield triangular with anterior margin almost straight (slightly concave in middle) and posterior end bluntly pointed; with 3 pairs of long peripectinate setae, 2 anterior (*vi* and *ve*) that form transverse row along anterior margin and third inserted posteriorly (*sci*) (Hirst 1917, 1926). With long seta *sce* adjacent to each eye reaching to base of dorsal setae *e2* and with seta *v* on trochanter I feather-like (Jack 1961).

Type. Deutonymph HOLOTYPE (BM(NH)).

Type locality. Honda, Magdalene River, Colombia.

Type host. *Gonatodes albogularis* (Duméril & Bibrón).

Material examined. Deutonymph HOLOTYPE ex *Gonatodes albogularis*, COLOMBIA, Magdalene River, Honda (BM(NH)).

Remarks. We checked the only known specimen of this species and found that it is a deutonymph. Jack and Girot (1965) mention that *Hirstiella tenuipes* closely resembles the deutonymph of *H. insignis*, differing by its leg setation in the possession of two rather than one seta on femur IV. They concluded that, in the absence of data on the variability in chaetotaxy in these species, it is possible that *H. tenuipes* may (1) be a deutonymph and (2) be synonymous with *H. insignis*. We are confirming their first assumption but we are not agreeing with the latter conclusion and keep both as valid species based on the following evidence: in *H. tenuipes* (1) prodorsal shield shaped as an inverted equilateral triangle, almost as long as wide and with the end bluntly pointed, (2) setae *vi* on the prodorsal shield is located proximal to *ve*, (3) setae *sci* as long as *vi*, (4) palpal seta *v* of tibia with nude stalk ending in a thick brush-like structure, (5) subcapitulum simple, not expanded at apex and (6) cheliceral fixed digit membranous and spiniform, and movable digit robust and curved; while in *H. insignis* (1) prodorsal shield shaped as an inverted pentagon with the posterior sides sharply converging and with a very acute end, (2) setae *vi* on prodorsal shield located anterior to *ve*, (3) setae *sci* longer than *vi* (twice or more), (4) palpal tibia seta *v* simple and

smooth, (5) subcapitulum apex (hypostome) with a rostral flange (the structure stiff, hyaline shelf just proximal to the striated velum) and (6) the cheliceral digits (movable and fixed) are long and spine-like.

According with these and additional characters (noted above in the *Pimeliaphilus* section), all used in our phylogenetic analysis, *H. tenuipes* and *H. insignis* are two valid and unrelated taxa (Fig. 1), the former included in *Bertrandiella* **gen. nov.** and the latter transferred back to *Pimeliaphilus*.

This species appears to be a specific ectoparasite of Sphaerodactylidae (see Table 3).

Bertrandiella otophila (Hunter and Loomis) new combination

Hirstiella otophila Hunter and Loomis, 1966: 683.

Diagnosis. Female. Prodorsal shield triangular bearing 3 pairs of peripectinate setae (*vi*, *ve* and *sci*) and with posterior end as wide as distance between setae *vi* (not acute ending). Tarsus I with long solenidion *ω2* with slightly longer companion seta *ft*.

Male. Prodorsal shield trapezoid in shape with posterior margin wider than anterior and with 4 pairs of long peripectinate setae (*vi*, *ve*, *sci* and *c1*). Companion seta *ft* longer than solenidion *ω2*.

Type. Female HOLOTYPE at Chigger Research Collection at California State University, Long Beach, California, USA (CSULB); female, male, deutonymphal and larval PARATYPES at CSULB, USNMC, OSAL, University of Kansas, University of California at Riverside and Texas Tech University, Lubbock, Texas (Hunter & Loomis 1966); deutonymphal and male PARATYPES (BM(NH)).

Type locality. Barstow, San Bernardino Co., California, USA.

Type host. *Coleonyx variegatus* (Baird).

Material examined. 1 deutonymphal PARATYPE ex *Coleonyx variegatus*, USA, California, San Bernardino Co., Barstow 2 mi S, 1 March 1964, coll. W. L. Hunter (BM(NH)); 1 male PARATYPE ex *Coleonyx variegatus*, USA, California, Riverside Co., 5.8 mi NW Desert Center on New rd to Eagle, J. C. Geest (BM(NH)). 2 females ex *Coleonyx brevis*, MEXICO, Coahuila, San Pedro de las Colonias, Santa Eulalia, 1250 m asl, 19 June 1994, W. Schmidt (CNAC004416–17).

Remarks. This species appears to be a specific ectoparasite of Eublepharidae and Phyllodactylidae (see Table 3).

Bertrandiella jimenezi (Paredes-León and Morales-Malacara) new combination

Hirstiella jimenezi Paredes-León and Morales-Malacara, 2009: 443.

Diagnosis. Adults. Companion seta *ft* shorter than solenidion *ω2* on tarsus I. **Female**. Prodorsal shield triangular in shape, with very acute posterior margin, and 3 pairs of peripectinate setae (*vi*, *ve* and *sci*).

Male. Prodorsal shield trapezoid in shape with anterior margin wider than posterior and with 4 pairs of long peripectinate setae (*vi*, *ve*, *sci* and *c1*) (Paredes-León & Morales-Malacara 2009).

Type. Female HOLOTYPE (CNAC005885); female, male, deutonymphal and larval PARATYPES at CNAC and OSAL.

Type locality. Zapotitlán de las Salinas, Puebla, México

Type host. *Phyllodactylus bordai* Taylor.

Material examined. Female HOLOTYPE, 1 female, 2 male, 2 deutonymphal, 2 larval PARATYPES ex *Phyllodactylus bordai*, MEXICO, Puebla, Zapotitlán de las Salinas, Río Salado cerca del Jardín Botánico, 18° 19’ 33” N, -97° 26’ 59.2” W, 1428 m asl, 30 October 2003, coll. R. Paredes-León (CNAC005885–86; 88–89; 93–94; 98–99).

Remarks. This species appears to be a specific ectoparasite of Phyllodactylidae (see Table 3).

***Bertrandiella chamelaensis* Paredes-León, Klompen and Pérez, new species**
(Figs. 5–6)

Diagnosis. Female. Dorsal idiosomal setae *vi*, *ve*, *sci* and *sce* longer than in *B. otophila* and *B. tenuipes* but shorter than in *B. jimenezi*; femur IV with apparent division into 2 non-articulating segments; companion seta (*ft*) shorter than solenidion *ω2* on tarsus I; subcapitular setae (*n*) longer than length of palpal femur.

Description. Female. *Gnathosoma* (Fig. 5A–B). Subcapitulum simple, not expanded at apex, with a pair of ventral, slender and smooth setae (*n*) inserted behind palps; palps relatively small and stout, mainly at the base; base of gnathosoma almost as long as the rest of palps; femoral and genual setae (*d*) and tibial seta *l'* thick, peripectinate and long (longer than their respective palpal segments); tibial seta *lT* smooth and simple, seta *v* with nude stalk ending in a thick brush-like structure; tibial claw simple and short although longer than reduced palpal tarsus and curved at tip; tarsus short and round, with basal solenidion *ω* and with 5 setae: 2 simple and sparsely barbed (anterior longer); 2 apical, smooth and simple, and 1 (lateral to *ω*) simple and barbed at its tip. Chelicerae short (shorter than palps), and with proximal part of cheliceral base elongate (length five times more than width in distal part); fixed digit membranous and spiniform, and movable digit robust and curved. Peritreme short, never reaching palpal femur.

Idiosoma (Fig. 5C–D). Ovoid, longer than wide; maximum width at level of setae *c2*; cuticle surrounding prodorsal shield, setal platelets, coxae and anogenital area striated; oligotrichy present. *Dorsum*. Prodorsal shield shaped as an inverted equilateral triangle with 3 pairs of long and peripectinate setae (*vi*, *ve* and *sci*). Dorsal setae peripectinate and long, each row of setae reaching next row. Setae *c3* absent; anal area located forward of posterior tip, with *ps1–3* arboriform (extensively pectinate), subequal in length and slightly shorter than rest of dorsal setae. *Venter.* Setae: coxal formula 2–2–4–2, located on coxae I–IV except for *3a* located on intercoxal area and *4a* between coxae IV; *1a*, *2a*, *3a*, *3b* and *4a* slender and sparsely barbed, *1b*, *2b*, *3c*, *3d* and *4c* thick and peripectinate. Setae *ag1–3* longer than coxal setae, thick and heavily pectinate; located between coxae IV and beginning of genital region; *ag3* slightly longer than subequal *ag1–2*; 1 pair of arboriform genital setae (*g1*) not located on lobes, subequal in length to setae *ag1–2*.

Legs (Fig. 6). Setal formulae (I–IV, microsetae (*κ*) and solenidia in brackets): trochanter 1–1–1–1, femur 5–4–3–2, genua 5(*κ*)–5–3–3, tibia 5–5–5–5, tarsus 14(1)–10(1)–10(1)–10; tarsi I–IV progressively thinner from proximal to distal end. All the setae on trochanter-tibia I–IV pectinate and long (some of them as long as each podomer). Tarsi I–IV with setae *p* feather-like; tarsus I with 1 pair of setae *tc* smooth (eupathids), subequal in length and short (as long of pretarsus or shorter); tarsi II–IV with setae *tc* peripectinate and subequal in length (*tc' = tc"*), and longer than setae *tc* of tarsus I. Tarsus I also with 1 pair of setae *it* (eupathids) at base of pretarsus; seta *vs"* on tarsi I–IV present; setae *a* on tarsi I–IV simple and smooth. Solenidion *ω2* on tarsus I longer than its companion seta (*ft*); solenidion *ω1* on tarsus I absent; solenidia on tarsi II–III shorter than solenidia on tarsus I; solenidion on tarsus III shortest. Pretarsi with paired claws bearing tenent hairs.

Measurements. HOLOTYPE female (followed in parentheses by range and mean of HOLOTYPE and nine PARATYPE females). Idiosoma length (gnathosoma excluded) 372 (369–397, 381), idiosoma maximum width 301 (263–301, 292), prodorsal shield length 136 (133–139, 137), prodorsal shield width (at anterior margin) 167 (167–178, 174), width between setal pair *vi* on prodorsal shield (WVI) 53 (50–56, 53), width between setal pair *ve* on prodorsal shield (WVE) 139 (135–146, 141), width between setal pair *sci* on prodorsal shield (WSCI) 56 (43–67, 56); setal lengths: *vi* 132 (132–143, 138), *ve* 146 (144–152, 147), *sci* 143 (135–146, 141), *sce* (ocular setae): 139 (133–139, 138); leg lengths (excluding coxa and ambulacrum): leg I 432 (406–435, 428), leg II 333 (333–406, 385), leg III 422 (352–435, 407), leg IV 467 (429–472, 457); solenidion *ω2* of tarsus I length 52 (51–57, 54), *ft* (companion seta of solenidion *ω2* of tarsus I) length 27 (27–32, 30), solenidion *ω* of tarsus II length 14 (12–14, 13), solenidion *ω* of tarsus III length 10 (9–10, 10); gnathosoma length 158 (153–161, 157), base of gnathosoma width 152 (146–160, 153), subcapitular setae *n* length 47 (42–51, 48), chelicerae length 146 (143–152, 146), chelicerae width (at base) 34 (31–34, 32), palp length 158 (147–160, 152), palp width 46 (43–54, 48), palp-claw length 27 (26–31, 27), and peritreme length (complete) 136 (136–152, 147).

Type. Female HOLOTYPE (CNAC007051), female PARATYPES (CNAC007052–81, OSAL and USNMC).

Type locality. Chamela, Jalisco, México.

Type host. *Phyllodactylus lanei rupinus* Dixon.

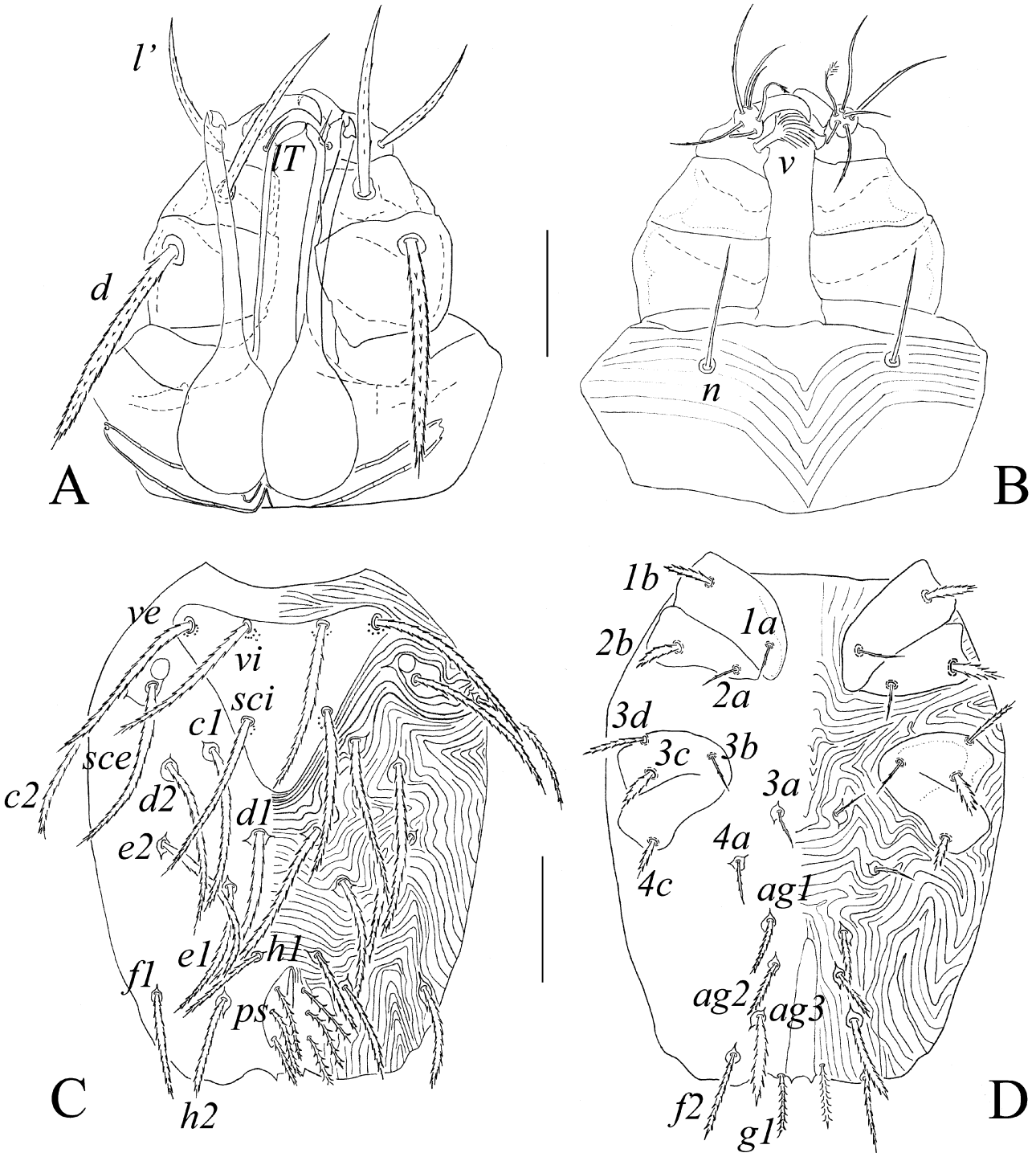

FIGURE 5. *Bertrandiella chamelaensis* **sp. nov.**, female. **A**, gnathosoma dorsal view; **B**, gnathosoma ventral view. Scale bar 50 µm; **C**, Idiosoma dorsum; **D**, Idiosoma venter. Scale bar 100 µm.

Type series. Female HOLOTYPE, 30 female PARATYPES ex *Phyllodactylus lanei rupinus*, MEXICO, Jalisco, Mpio. La Huerta, Chamela, km 54 carr. Manzanillo–Puerto Vallarta, 19.45506° N, -105.03205° W, 15 m asl, 4 October 2010, coll. D. Barrales and R. Paredes-León (CNAC007051–81). 10 female PARATYPES ex *Phyllodactylus lanei rupinus*, same data (OSAL, USNMC).

The holotype and 30 paratype females are deposited at CNAC (007051–81). The remaining paratypes (10 females) are deposited in OSAL and USNMC.

Etymology. The specific name is derived from the collecting locality, the town of Chamela.

Remarks. This species appears to be a specific ectoparasite of Phyllodactylidae (see Table 3).

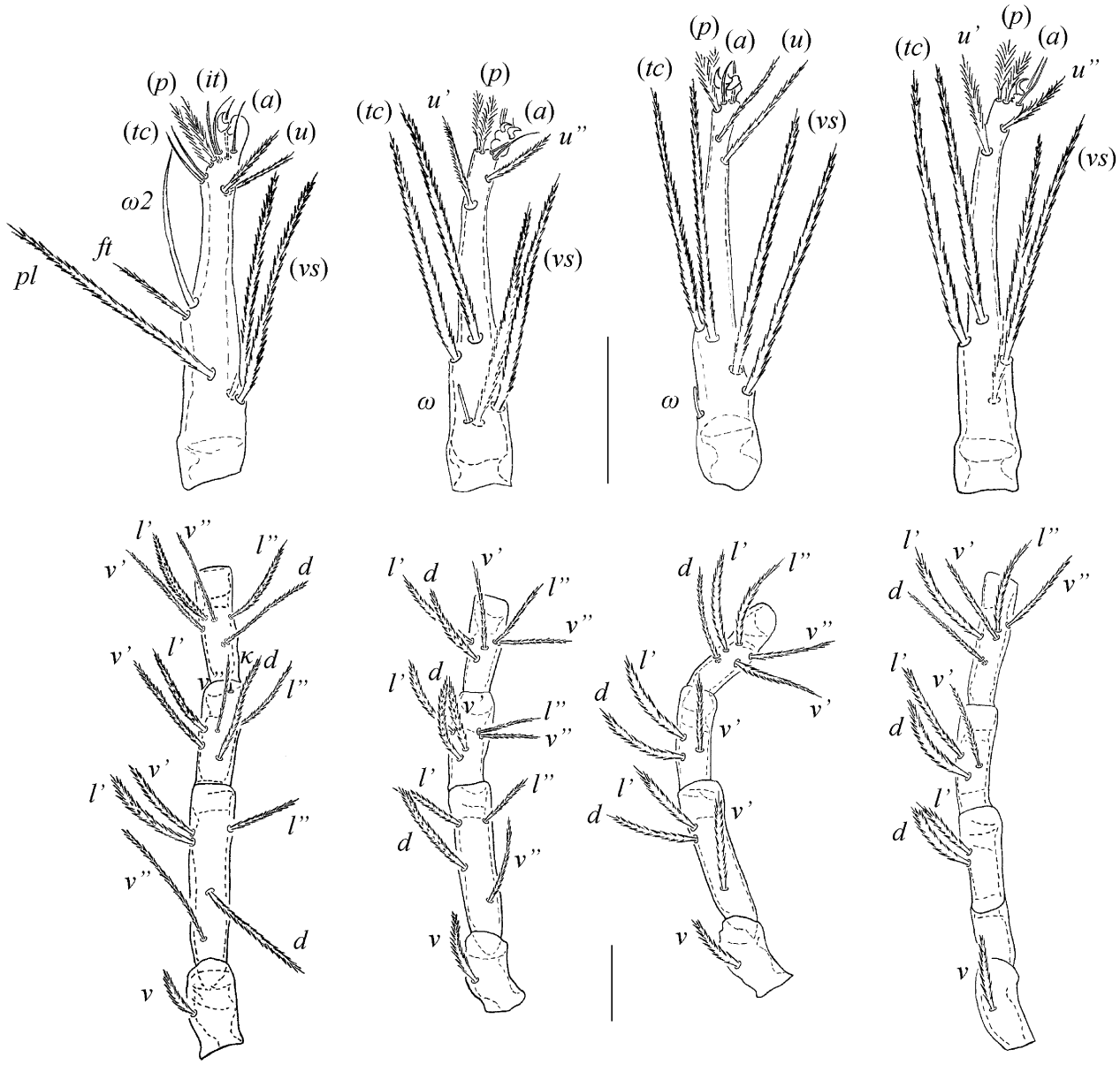

FIGURE 6. *Bertrandiella chamelaensis* **sp. nov.**, female, legs I–IV (trochanters-tarsi). Scale bars 50 µm.

Key to females of *Bertrandiella* Paredes-León, Klompen and Pérez gen. nov.

(female not known for *B. tenuipes*)

1. Solenidion *ω2* on tarsus I slightly shorter than companion seta (*ft*); triangular prodorsal shield with posterior end bluntly pointed . . . . . *B. otophila*
-. Solenidion *ω2* on tarsus I clearly longer than *ft*; triangular prodorsal shield with an acute posterior end 2
2. Femur IV complete, undivided . . . . . *B. jimenezi*
- . Femur IV with an apparent division into two non-articulating segments (Fig. 6) . . . . . *B. chamelaensis* **sp. nov.**

Pimeliaphilus Trägårdh

Pimeliaphilus Trägårdh, 1905: 31; Vitzthum 1942: 612; Radford 1943: 71; Baker and Wharton 1952: 207; Cunliffe 1952: 159; Jack 1961: 305.

Pimeliaphiloides (in part): Vitzthum, 1942: 613; Radford 1950: 377; Baker and Wharton 1952: 208; Cunliffe 1952: 162; Jack 1961: 305.

Type species. *Pimeliaphilus podapolipophagus* Trägårdh, 1905, by original designation.

Diagnosis. Female. *Gnathosoma* (Fig. 7A–B). Base of gnathosoma large and longer than rest of palps; delimitation between subcapitulum and hypostome gradual (inconspicuous); tip of hypostome with distinct membranous velum marked dorsally with prominent, transverse and parallel striae and with rostral flange (structure stiff, hyaline shelf just proximal to striated velum); palpal tibial claw long (2 times longer than palpal tarsus) and curved starting at the middle; cheliceral digits (movable and fixed) long and spine-like; proximal part of cheliceral base thin (3.5 times or less width of distal part). *Idiosoma*. Oligotrichous; setae *c3* absent; prodorsal shield always present. *Legs.* Solenidion *ω1* on tarsus I present; companion seta (*ft*) on tarsus I is nude, spiniform and very reduced; setae *4c* on coxae IV peripectinate.

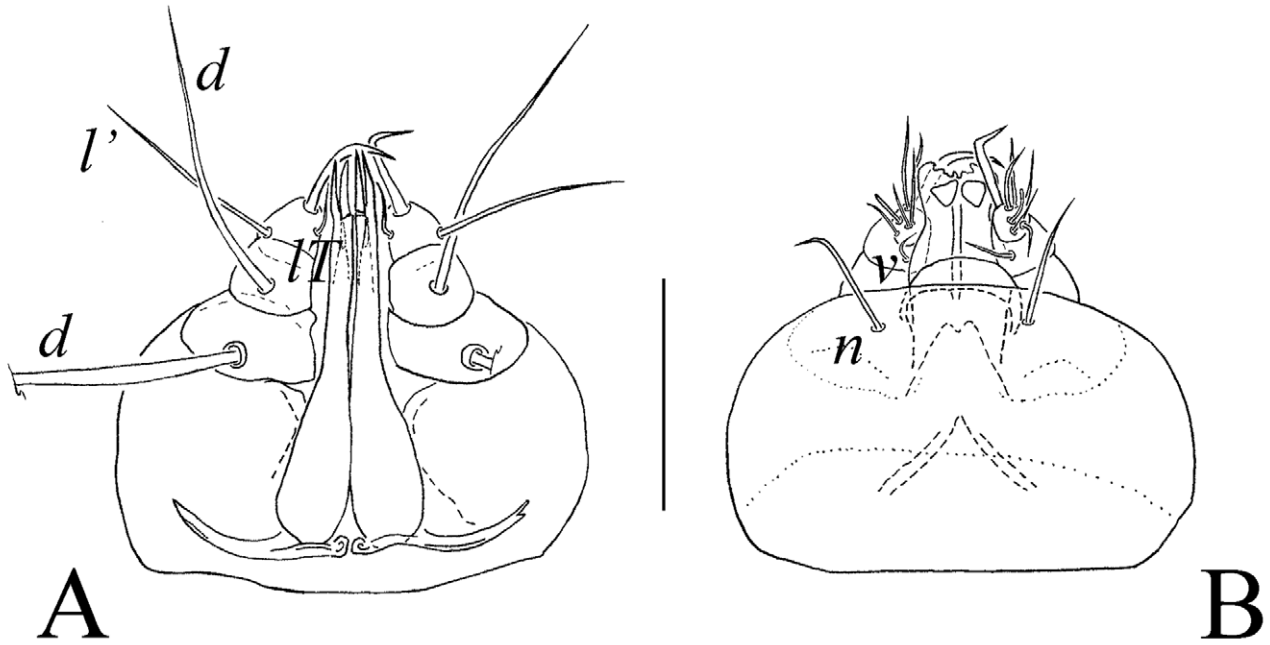

FIGURE 7. *Pimeliaphilus insignis*, female. **A**, gnathosoma dorsal view; **B**, gnathosoma ventral view. Scale bar 100 μm.

Setal development. Larvae with solenidion *φ1* on tibiae I which absent in subsequent instars.

Hosts. Most of the species parasitic on arthropods (*e. g.*, triatomine bugs, scorpions and beetles), and at least two species parasitic on lizards of gekkotan families, *i. e*, Gekkonidae and Phyllodactylidae (Table 4).

Included species (Table 4)**.** *P. insignis* (Berlese, 1892), *P. podapolipophagus* Trägårdh, 1905, *P. sharifi* Abdussalam, 1941, *P. isometri* Cunliffe, 1949, *P. triatomae* Cunliffe, 1952, *P. rapax* Beer, 1960, *P. cunliffei* Jack, 1961, *P. gloriosus* Newell and Ryckman, 1966, *P. sanguisugae* Newell and Ryckman, 1966, *P. plumifer* Newell and Ryckman, 1966, *P. calimesae* Newell and Ryckman, 1966, *P. peninsularis* Newell and Ryckman, 1966, *P. andersoni* Newell and Ryckman, 1966, *P. joshuae* Newell and Ryckman, 1966, *P. trogadermus* Cunliffe, 1968, *P. zeledoni* Newell and Ryckman, 1969, *P. penrithi* Olivier, 1977, *P. sanguicollis* Olivier, 1977, *P. buysi* Olivier, 1977 and *P. desertus* Olivier, 1977.

Remarks. This short diagnosis is based mainly on the four species included in this study (*P. ca. podapolipophagus*, *P. trogadermus*, *P. sharifi* and *P. insignis*). A more detailed review of the genus including all nominal species of *Pimeliaphilus* is clearly needed. For example, the presence of solenidion *φ1* on tibiae I in the larvae should be corroborated in all species (at least all of those where larvae are known).

Contrary to the view of Bochkov and OConnor (2006) who mentioned that setae *c1-3* are present in all active instars, we note that all species in *Pimeliaphilus* lack idiosomal dorsal setae *c3* in all instars.

This genus displays a wide host range, including Old World lizards (Phyllodactylidae and Gekkonidae), Old and New World arachnids (Scorpiones), and insects (Coleoptera, Hemiptera and Blattodea) as well as free living forms (*e. g.*, *P. sanguicollis* Olivier) (Table 4). Their host associations should be also analyzed in more detail because some undetermined specimens of *Pimeliaphilus* were recorded on phlebotomine sandflies *Phlebotomus alexandri* (Diptera: Psychodidae) in Saudi Arabia (Lewis & Macfarlane 1981).

TABLE 4. Species included in the genus *Pimeliaphilus* with a summary of host and distribution data.

Species	Host		Distribution	Reference
P. insignis (Berlese, 1892)	Squamata: Phyllodactylidae	*Tarentola mauritanica*	Italy, Morocco, Algeria, France	Cunliffe 1952, André 1961, Jack and Girot 1965
same species	Gekkonidae	*Hemidactylus turcicus*	Spain	Baker, 1998
same species	Gekkonidae	Gecko (undetermined)	Iraq	This study
P. sharifi Abdussalam, 1941	Squamata: Gekkonidae	*Hemidactylus flaviviridis*	India, Pakistan	Abdussalam 1941, Nagar *et al*. 1978
P. podapolipophagus Trägårdh, 1905	Coleoptera: Tenebrionidae	*Pimelia* sp.	Egypt	Trägårdh, 1905
same species	Blattodea	Cockroaches (undetermined)	Scotland, Portugal, Canada, Venezuela, USA Mexico	Cunliffe 1952, Hoffman and López-Campos 2000
P. isometri Cunliffe, 1949	Scorpiones: Buthidae	*Isometrus* sp.	Philippines	Cunliffe 1949b
P. triatomae Cunliffe, 1952	Hemiptera: Reduviidae	*Triatoma infestans, Triatoma* sp., *Meccus pallidipenis*	Chile, Peru, Argentina, Mexico	Cunliffe 1952, Newell and Ryckman 1966, Hoffmann and López-Campos 2000, Zumaquero *et al*. 2004
P. rapax Beer, 1960	Scorpiones: Vaejovidae	*Vaejovis p. punctatus*, *V. n. nitidulus*, *V. intrepidus cristimanus*	Mexico	Beer 1960, Hoffmann and López-Campos 2000
P. cunliffei Jack, 1961	Unknown	"off an old dog crate"	USA	Jack 1961; Newell and Ryckman 1966
P. gloriosus Newell and Ryckman, 1966	Hemiptera: Reduviidae	*Triatoma barberi*	Mexico	Newell and Ryckman 1966
P. sanguisugae Newell and Ryckman, 1966	Hemiptera: Reduviidae	*Triatoma sanguisuga*	USA	Newell and Ryckman 1966
P. plumifer Newell and Ryckman, 1966	Hemiptera: Reduviidae	*Triatoma rubida, Triatoma protracta* and *Paratriatoma hirsuta* from nest of *Neotoma* sp., *Meccus pallidipennis* from laboratory cultures of *Meccus bassolsae*, *M. longipennis*, *M. picturatus*, *M. pallidipennis*	USA, Mexico	Newell and Ryckman 1966, Martínez-Sánchez *et al*. 2007
P. calimesae Newell and Ryckman, 1966	Hemiptera: Reduviidae	*Triatoma protracta protracta*	USA	Newell and Ryckman 1966
P. peninsularis Newell & Ryckman, 1966	Hemiptera: Reduviidae	*Triatoma peninsularis* from nest of *Neotoma* sp.	Mexico	Newell and Ryckman, 1966
P. andersoni Newell & Ryckman, 1966	Hemiptera: Reduviidae	*Triatoma recurva, T. gerstaeckeri*	USA	Newell and Ryckman 1966

.....continued on the next page

TABLE 4. (Continued)

Species	Host		Distribution	Reference
P. joshuae Newell & Ryckman, 1966	Unknown	In roots of dead *Yucca brevifolia* (Joshua tree)	USA	Newell and Ryckman 1966
same species	Scorpiones: Buthidae	*Androctonus australis*, *A. amoreuxi*, *Leiurus quinquestriatus*	Egypt	Ibrahim and Abdel-Rahman 2011
same species	Scorpiones: Vaejovidae	*Vaejovis confusus*, *V. spinigerus*, S*meringurus mesaensis*, *S. vachoni*	USA	Berkenkamp and Landers 1983
same species	Scorpiones: Caraboctonidae	*Hadrurus arizonensis*	USA	Berkenkamp and Landers 1983
same species	Scorpiones: Buthidae	*Centruroides sculpturatus*	USA	Berkenkamp and Landers 1983
same species	Scorpiones: Superstitioniidae	*Superstitionia donensis*	USA	Berkenkamp and Landers 1983
same species	Hemiptera: Reduviidae	*Triatoma rubida* (artificial infestation in laboratory cultures)	USA	Berkenkamp and Landers 1983
P. trogadermus Cunliffe, 1968	Coleoptera: Dermestidae	*Trogoderma parabile*	USA	Cunliffe 1968
P. zeledoni Newell & Ryckman, 1969	Hemiptera: Reduviidae	*Triatoma dimidiata* (laboratory cultures)	Costa Rica	Newell and Ryckman 1969
P. penrithi Olivier, 1977	Blattodea: Blaberidae	*Derocalymma* sp.	Namibia	Olivier 1977
same species	Unknown	free living under stones and debris beneath *Acacia karroo* trees	Namibia	Oliver 1977
P. sanguicollis Olivier, 1977	Unknown	In soil underneath *Salvadora persica*	Namibia	Olivier 1977
P. buysi Olivier, 1977	Coleoptera: Tenebrionidae	*Physosterna* sp., *Stips dohrni*	Namibia	Olivier 1977
P. desertus Olivier, 1977	Coleoptera: Carabidae	*Anthia thoracica*	Namibia	Olivier 1977
same species	Unknown	free living in soil underneath *Aloe namibiensis*	Namibia	Oliver 1977

Species previously considered in *Hirstiella* and transferred back to the genus *Pimeliaphilus* Trägårdh, 1905

Pimeliaphilus insignis (Berlese)

Geckobia insignis Berlese, 1892: 64.
Pimeliaphilus insignis Trägårdh, 1905: 40; Hirst 1926: 199; Radford 1943: 71.
Pimeliaphiloides insignis Vitzthum, 1942: 613; Radford 1950: 377.
Hirstiella insignis Cunliffe, 1952: 164.

Type. Berlese Collection (42/10–11), Istituto Sperimentale per la Zoologia Agraria, Firenze, Italy (André 1961; Jack & Girot 1965).

Type locality. Portici, Italy.

Type host. *Tarentola mauritanica* (Linnaeus) (cited originally as *Platydactylus muralis*, Cunliffe 1952 and Jack & Girot 1965).

Distribution. ex *Tarentola mauritanica*, ITALY, FRANCE, MOROCCO and ALGERIA (Cunliffe 1952; Andr 1961; Jack & Girot 1965). ex *Hemidactylus turcicus*, SPAIN (Baker 1998) (Table 4).

Material examined. 1 female ex undetermined gecko, IRAQ, south, coll. J. Robson (BM(NH)).

Remarks. According to Jack (1964) this species has all the five setae on femur II however the examined specimen from Iraq lacked seta *l"*. In the latter specimen it is also difficult to see whether both *p'* and *p"* are present. The specimen from Iraq has the same three setae, *d*, *l'* and *v'*, on genua III as mentioned by Jack and Girot (1965) instead of *d*, *l'* and *l"* sensu Jack (1964). It also has solenidion ω on tarsus III (mentioned as absent by Jack 1964 and Jack & Girot 1965). Setae *a'* and *a"* are very difficult to see. Additional data included in the phylogenetic analysis were obtained from André (1961), Jack (1964) and Jack and Girot (1965).

Pimeliaphilus sharifi Abdussalam

Pimeliaphilus sharifi Abdussalam, 1941: 69; Nagar 1978: 107
Hirstiella sharifi Jack, 1961: 310

Type. Unknown, probably at University of Veterinary and Animal Sciences, Lahore, Pakistan (formerly Punjab Veterinary College).

Type locality. Not specified, central and southern Punjab (Hissar (India) and Lahore (now Pakistan)).

Type host. *Hemidactylus flaviviridis* Rüppell.

Distribution. ex *Hemidactylus flaviviridis*, INDIA and PAKISTAN (Abdussalam 1941; Nagar *et al*. 1978) (Table 4).

Material examined. 1 deutonymph LECTOTYPE ex *Hemidactylus flaviviridis*, INDIA, Delhi, 15 April 1976, coll. Nagar (BM(NH)).

Remarks. Most of the data presented for this species were obtained from the literature (Abdussalam 1941; Nagar *et al*. 1978). Some additional information was obtained by examination of a deutonymph (originally misidentified as a female) deposited at BM(NH) and labeled as lectotype by Nagar. Based on the data provided by Nagar *et al*. (1978) we suspect that their redescription of the female of this species was based on deutonymphs instead of females.

Tequisistlana Hoffmann and Sánchez

Tequisistlana Hoffmann and Sánchez, 1980: 99
Type species: *Tequisistlana oaxacensis* Hoffmann and Sánchez, 1980, by original designation.

Diagnosis. Female. Idiosoma almost circular, oligotrichous; prodorsal shield present, rectangular (wider than long) with 3 pairs of setae (*vi*, *ve* and *sci*), *vi* anterior and internal to *ve* (both setal pairs not aligned vertically or horizontally); dorsal setae (except *h1* and *f2*) pectinate and long (reaching the bases of the next setal row); dorsal setal pair *h1* tuft-shaped very reduced (quarter of length of *h2*); dorsal setal pair *f2* tuft-shaped and very reduced (tenth part of length of *f1*); genital region covered with folded fan-shaped cuticular structure; genital setae (*g1*) thick and sparsely serrate and not located on lobes; setae *ag1* long (although shorter than *f1*) and pectinate; setae *ag2–3* short, thick and sparsely serrate (as setae *g1*); setae *ps1–3* tuft shaped, subequal in length and very reduced (quarter of length of *h2*). Seta *v'* on genua IV absent.

Setal development. Setae *ps1–3* present from larval instar on.

Hosts. All instars parasitize lizards of the family Xantusiidae.

Included species. Monotypic genus.

Tequisistlana oaxacensis Hoffmann and Sánchez

Tequisistlana oaxacensis Hoffmann and Sánchez, 1980: 99

Diagnosis. Same as for genus.

Type. Female HOLOTYPE (CNAC000262), 5 female PARATYPES (CNAC000263–67).

Type locality. Magdalena Tequisistlán, Oaxaca, Mexico.

Type host. *Lepidophyma smithii* Bocourt.

Material examined. Female HOLOTYPE, 1 female PARATYPE ex *Lepidophyma smithii*, MEXICO, Oaxaca, Tequisistlán, March 1972, coll. W. López-Forment and O. Sánchez (CNAC000262–63). 3 females ex *Lepidophyma smithii*, same data as type series (CNAC007082–84); 1 female, 1 male, 1 deutonymph, 1 larva ex *Lepidophyma smithii*, MEXICO, Oaxaca, Mpio. San Miguel Chimalapa, Cerro atravesado, 16.67704° N, -94.53239° W, 1190 m asl, 16 April 2003, coll. J. A. Campbell (CNAC007085–88). 5 females ex *Lepidophyma smithii*, Oaxaca, Mpio. Asunción Ixtaltepec, Nizanda, Agua Tibia, 16.65817° N, -95.01057° W, 99 m asl, 15 September 2009, coll. R. Paredes, C. Santibañez and A. Valdez (CNAC007089–93).

Remarks. This species appears to be a specific ectoparasite of lizards of the genus *Lepidophyma* (Xantusiidae). Hoffmann and Sánchez (1980) suggested that *Hirstiella otophila* and *H. tenuipes* should be transferred to *Tequisistlana* based on the shape of seta *v* on the palpal tibia (with nude stalk ending in a thick brush-like structure). However, according to our analysis *H. otophila* and *H. tenuipes* belong to *Bertrandiella* **gen. nov.** (Bremer support and jackknife values 2 and 73%) instead of *Tequisistlana* (see remarks for these species above).

The monotypic genus *Tequisistlana* is the sister taxon of the clade comprising *Pimeliaphilus* and *Bertrandiella* **gen. nov.**

Key to identification of females of the genera of Pterygosomatidae analyzed in this study

1. Companion seta (*ft*) of tarsus I very reduced, simple and spiniform; hypostome with a rostral flange . ***Pimeliaphilus*** Trägårdh
-. Companion seta (*ft*) of tarsus I long, nude, barbed or peripectinate; hypostome simple 2
2. Idiosoma oligotrichous or hypertrichous, dorsal idiosomal setae *c3* present, coxal setae *4c* absent, and genital setae (*g1*) spine-like nude or acuminate nude and slender, located on the tip of lobes . . . . . ***Geckobiella*** Hirst
-. Idiosoma oligotrichous, dorsal idiosomal setae *c3* absent, coxal setae *4c* present, and genital setae (*g1*) arboriform or spine-like serrate, located on the ventral cuticle (not on lobes) 3
3. Solenidion *ω1* on tarsus I absent; dorsal idiosomal setae *h1* peripectinate and long subequal to *h2* . . . . . ***Bertrandiella*** Paredes-León, Klompen and Pérez **gen. nov.**
-. Solenidion *ω1* on tarsus present; dorsal idiosomal setae *h1* tuft-shape and very reduced (a quarter of the length of the pectinate setae *h2*) . . . . . ***Tequisistlana*** Hoffmann and Sánchez

3. Chaetotaxy model propose for Pterygosomatidae

The first model of nomenclature of leg setation for the family Pterygosomatidae was developed by Jack (1964). Bochkov and OConnor (2006) adapted Grandjean's nomenclature for leg, idiosomal and palpal setae (Grandjean 1939; 1944; 1946) to Pterygosomatidae, and proposed homologies with the setal designations of Jack. This model was follow by Bochkov *et al*. (2008).

Chaetotaxy as used in this study shows some differences with the model presented by Bochkov *et al*. (2008). Notably, the Bochkov *et al*. study was aimed at elucidating the position of Myobiidae within the Raphignathae and not with intrafamilial variability in Pterygosomatidae. These authors therefore used only one representative of the Pterygosomatidae, *Hirstiella* spp. The current study allows considerable refinement of this aspect of the model by recognizing a sizable amount of intrafamilial variability (Table 5). Second, one set of setal homologies proposed differs from those proposed by Bochkov *et al*. Those authors note the presence of setae *l"* on genua III–IV and absence of setae *v"* III–IV. In this study we consider the relevant setae on those podomers homologous with *v"* III–IV, not *l"*, for positional reasons.

Further observations on Pterygosomatinae sensu Cruz (1984) will complete the propose chaetotactic pattern in the family.

TABLE 5. Comparison between chaetotaxy models proposed by Bochkov *et al*. (2008) and this study.

Characters	Bochkov *et al.* (2008)	This Study
Gnathosoma		
Setation	*el*, *n*	*n*; *el* not observed
Setation of palp tarsi	ω and 7 setae	ω and 3–7 setae
Idiosoma		
Dorsal setae *c3*	Present	- Absent in *Pimeliaphilus*, *Bertrandiella* and *Tequisistlana*; - Present in *Geckobiella*, *Pterygosoma mutabilis* and *Geckobia leonilae*
Legs		
Number of solenidia on tarsus I	2	- $\omega 1$ absent in *Geckobia leonilae*, *Pterygosoma mutabilis*, *Bertrandiella* and *Geckobiella harrisi*; - $\omega 2$ always present
Setal pair *tc* of tarsi II – IV	Both present	Both present, except in *Pterygosoma mutabilis* (only *tc'* present)
Setal pair *vs* on tarsi II – IV	Only 1 present	- Both present (*vs'* and *vs"*) in *Geckobia leonilae*, *Pimeliaphilus*, *Bertrandiella* and *Tequisistlana*; - Only 1 present (*vs'*) in *Pterygosoma mutabilis* and *Geckobiella*
Setal pair *v* on genu II	Both present (*v'* and *v"*)	- Both present in *Pterygosoma mutabilis*, *Pimeliaphilus*, *Bertrandiella* and *Geckobiella texana*; - Only one present (*v'*) in *Geckobiella* (except *G. texana* and *G. harrisi*); - Both absent in *Geckobia leonilae*, *Tequisistlana* and *Geckobiella harrisi*
Setal pair *l* on genuae III – IV	Present	- *l'* present, except in *Pterygosoma mutabilis*, *Geckobia leonilae*, *Geckobiella stamii* and *G. harrisi* - *l"* always absent
Setal pair *v* on genuae III – IV	Absent	- *v'* present in *Pimeliaphilus*, *Bertrandiella* and *Geckobiella* - *v"* always absent
Setal pair *l* on femur I	Both present (*l'* and *l"*)	Both absent in *G. stamii*; *l'* absent in *Geckobia leonilae* and *Pterygosoma mutabilis*
Setal pair *v* on femur I	Only 1 present	Both present (*v'* and *v"*); *v'* absent in some *Geckobia*, *Pterygosoma* and *Tequisistlana*
"Additional" proximal seta *v*	Absent	Present in some *Pimeliaphilus*
Setal pair *l* on femur II	Both present (*l'* and *l"*)	Both present, except in *G. stamii*, *Tequisistlana*, *Pterygosoma mutabilis* and *Geckobia leonilae*
Setal pair *v* on femur II	Only 1 present	- Both (*v'* and *v"*) present in *Pimeliaphilus insignis*, *P. sharifi*, *Geckobiella trombidiiformis* and *G. pelaezi*; - In most other specimens analyzed only 1 is present (*v"*); - *Pterygosoma mutabilis* lacks both *v'* and *v"*
Setal pair *l* on femur III	Only *l'* present	Only *l'* present; absent in *Pterygosoma mutabilis*, *Geckobia leonilae*, *Geckobiella stamii*, *G. harrisi* and *Tequisistlana*
Setal pair *v* on femur III	Only 1 present	Only *v'* present; absent in *Pterygosoma mutabilis*, *Geckobia leonilae* and *Tequisistlana*; *v"* present only in *Geckobia leonilae*
Setal pair *l* on femur IV	Absent	*l'* present in *Pimeliaphilus*, *Bertrandiella* and *Geckobiella* (except in *G. stamii* and *G. harrisi*)
Setal pair *v* on femur IV	Only 1 present	- *v'* present in *Pimeliaphilus* ca. *podapolipophagus*, *P. trogadermus*, *Bertrandiella* and some *Geckobiella* (*G. trombidiiformis*, *G. pelaezi* y *G. texana*); - *v"* present only in *Geckobia leonilae*
Setae *2a* on coxae II	Present	Always present, except in *Pterygosoma mutabilis*
Setae *3d* on coxae III	Present	Always present, except in *Pterygosoma mutabilis*
Setae *4c*	Present	- Present in *Geckobia leonilae*, *Pimeliaphilus*, *Bertrandiella* and *Tequisistlana*; - Absent in *Pterygosoma mutabilis* and *Geckobiella*

4. Host associations

Most pterygosomatid mites are ectoparasites of lizards worldwide. These mites are not phoretic and transmission is probably from individual to individual; they feed on blood or body fluids taken from their hosts and spend most of their life under the hosts scales, between its toes, or in areas known as mite pockets (Bertrand and Modry 2004). The genera analyzed in this study display different levels of specificity; the species in the genus *Geckobiella* are associated with New World families of iguanian lizards (Iguanidae, Phrynosomatidae and Tropiduridae) whereas the species in *Bertrandiella* **gen. nov.** are restricted to New World lizards in the gekkotan families Phyllodactylidae, Sphaerodactylidae and Eublepharidae (Fig. 8). In contrast, the species of *Pimeliaphilus* display a broad host range including Old World lizards in the gekkotan families Gekkonidae and Phyllodactylidae, but also a wide range of arthropod hosts (see Table 4).

Based on our phylogenetic hypothesis and mapping the main host of each species analyzed (Fig. 8) we propose a possible route of the evolution of parasitism among these genera. Most likely the ancestors of Pterygosomatidae have moved initially from a free living life-style to parasitize lizards and from there moved to modern arthropods. This kind of disjunct pattern of host and mite phylogeny clearly involves host-switching: the mites transferred from their normal hosts, lizards, to an ecologically associated, but phylogenetically distant, one, arthropods. After this transfer, the mites radiated into new species and possible cospeciation with the new hosts (Walter & Proctor 1999). The latter needs to be tested in a detailed analysis of all species of *Pimeliaphilus*. Meanwhile the current study provides strong evidence against the hypothesis by Bochkov and OConnor (2006) that parasitism of arthropods preceded that of lizards.

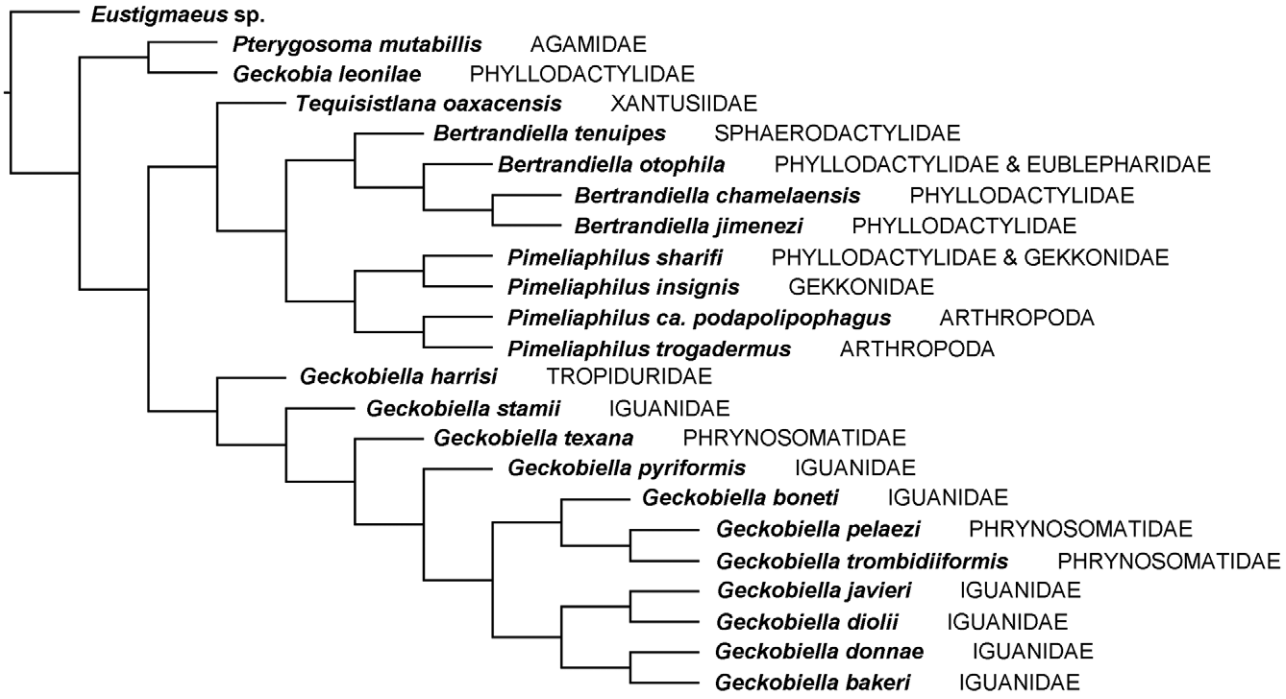

FIGURE 8. Host associations for the taxa of Pterygosomatidae considered (with the taxonomic changes proposed). Phylogeny as in Fig. 1.

Conclusions

In this study, we focus on phylogenetic relationships of the species previously placed in the genera *Geckobiella* and *Hirstiella*. Based on the results of the analyses we conclude that the genus *Hirstiella* is invalid, and should be synonymized with *Geckobiella*. Species previously placed in *Hirstiella* are re-classified in three different genera (Fig. 8), *Geckobiella* sensu nov. (including the species of *Hirstiella* parasitic on iguanian lizards), *Bertrandiella* **gen. nov.** (for the New World species of *Hirstiella* parasitic on gekkotan lizards) and *Pimeliaphilus* (for *Hirstiella insignis* and *H. sharifi*, the species of *Hirstiella* parasitic on Old World gekkotan lizards). These three lineages are

well supported in our analysis. However, relationships of these clades with the other genera of Pterygosomatidae should be analyzed further. Secondly, a systematic revision considering all species of *Pimeliaphilus* and including an analysis of its host relationships, is also indicated. The current analysis suggest that the arthropod associations in *Pimeliaphilus* are secondary, resulting from host switches from lizards.

This study represents the first major attempt at reconstructing phylogenetic relationships in Pterygosomatidae. Clearly some issues remain unclear and require further investigation. These issues include the phylogenetic position of Pterygosomatinae (sensu Cruz 1984) and patterns of host parasite evolution (coevolutionary history of these mites and their hosts). Future analysis including representatives of the rest genera of Pterygosomatidae, the exploration of molecular characters and additional morphological characters in other instars, safely will improve our observations about the evolutionary history of pterygosomatid mites.

Acknowledgements

We thank Griselda Montiel-Parra (Colección Nacional de Ácaros), Ronald Ochoa (United States National Mite Collection) and Janet Beccaloni (The Natural History Museum) for the loan of type and voucher specimens of relevant pterygosomatid mites. Naomi Cuervo and Ariel Rodríguez (Colección Acarológica y Colección Herpetológica, Instituto de Ecología y Sistemática, Ministerio de Ciencias, Tecnología y Medio Ambiente, Cuba) for permission to examine specimens of mites and iguanids in their respective collections. Michel Bertrand (Universit Montpellier, France), Oscar F. Francke (Colección Nacional de Arácnidos, UNAM, Mexico) and Victor H. Reynoso (Colección Nacional de Anfibios y Reptiles, UNAM, Mexico) for their comments during different phases of this study. M. Bertrand, V. H. Reynoso, and Lázaro Márquez Llauger (Parque Nacional Guanahacabibes, Cuba) who kindly donated pterygosomatid mites. The first author thanks CONACyT for a graduate scholarship (42361) and Programa de Posgrado en Ciencias Biológicas, UNAM; this contribution is a qualification to obtain PhD degree. Some of the field collections of mites were supported by a National Science Foundation grant (DEB–0102383) to J. A. Campbell (University of Texas at Arlington) and V. León-Règagnon (Instituto de Biología, UNAM). The authors would like to thank the editor A. Bochkov and anonymous reviewer for their insightful comments that have improved the quality of this manuscript.

References

Abdussalam, M. (1941) Pterygosomid mites from two north Indian lizards. *Indian Journal of Entomology*, 3, 65–72.

Andr, M. (1961) Observations sur *Hirstiella insignis* (Berlese). *Acarologia*, 3, 1959–64.

Baker, A. (1998) A new species of *Hirstiella* Berlese (Acari: Pterygosomatidae) from captive rhinoceros iguanas, *Cyclura cornuta* Bonnaterre (Reptilia: Iguanidae). *Systematic and Applied Acarology*, 3, 183–192.

Banks, N. (1904) A treatise on the Acarina, or mites. *Proceedings of the United States National Museum*, 28, 1–114.

Beccaloni, G.W. (2007) Blattodea species file online. Version 1.0/4.0. Available fromhttp://Blattodea.SpeciesFile.org (accessed 20 December 2011).

Beer, R. (1960) A new species of *Pimeliaphilus* (Acarina: Pterygosomidae) parasitic on scorpions, with a discussion of its postembryonic development. *Journal of Parasitology*, 46, 433–440.

Berkenkamp, S.D. & Landers, E.J. (1983) Observations on the scorpion parasite *Pimeliaphilus joshuae* Newell and Ryckman, 1966 (Acarina: Pterygosomidae). *Journal of the Arizona–Nevada Academy of Science*, 18, 27–31.

Berlese, A. (1892) Ordo Prostigmata (Trombidiidae). *Acari, Myriopoda et Scorpiones hucusque in Italia reperta*, 60: 1–155.

Berlese, A. (1920) Centuria quinta di Acari nuovi. *Redia*, 14, 143–195.

Bertrand, M. (2002) Morphologic adaptations to parasitism on reptiles: Pterygosomatidae (Prostigmata: Raphignathina). *In*: Bernini, F., Nannelli, R., Nuzzaci, G. & de Lillo, E. (Eds.), *Acarid phylogeny and evolution. Adaptations in mites and ticks*. Kluwer Academic Publishers, Netherlands, pp. 233–240.

Bertrand, M. & Modr, D. (2004) The role of mite pocket-like structure on *Agama caudospinosa* (Agamidae) infested by *Pterygosoma livinstonei* sp. n. (Acari: Prostigmata: Pterygosomatidae). *Folia Parasitologica*, 51, 61–66.

Bertrand, M., Paperna, I. & Finkelman, S. (2000) Pterygosomatidae: descriptions et observations sur les genres *Pterygosoma*, *Geckobia*, *Zonurobia* et *Hirstiella* (Acari: Actinedida). *Acarologia*, 40, 275–304.

Bochkov, A.V. (2008) Origin and evolution of parasitism in mites of the infraorder Eleutherengona (Acari: Prostigmata). Report I. Lower Raphignathae. *Parazitologiya (St. Petersburg)*, 42, 337–359.

Bochkov, A.V. & OConnor, B.M. (2006) A review of the external morphology of the family Pterygosomatidae and its position within the Prostigmata (Acari: Acariformes). *Parazitologiya (St. Petersburg)*, 40, 201–214.

Bochkov, A.V., OConnor, B.M. & Wauthy, G. (2008) Phylogenetic position of the mite family Myobiidae within the infraorder Eleutherengona (Acariformes) and origins of parasitism in eleutherengone mites. *Zoologischer Anzeiger*, 247, 15–45.
Corn, J.L., Mertins, J.W., Hanson, B. & Snow, S. (2011) First reports of ectoparasites collected from wild-caught exotic reptiles in Florida. *Journal of Medical Entomology*, 48, 94–100.
Cruz, J.de la. (1973) Nueva especie de ácaro del género *Geckobia* Megnin, 1878 (Acarina; Pterygosomidae) parásito de la *Tarentola americana* (Gray) de Cuba. *Poeyana*, 102, 1–6.
Cruz, J.de la. (1984) Sistemática de la familia Pterygosomidae (Acarina: Prostigmata), con la descripción de un nuevo género y especie. *Poeyana*, 278, 1–22.
Cunliffe, F. (1949a) *Hirstiella pelaezi*, a new lizard parasite from Mexico (Acarina, Pterygosomidae). *Proceedings of the Entomological Society of Washington*, 51, 25–26.
Cunliffe, F. (1949b) *Pimeliaphilus isometri*, a new scorpion parasite from Manila, P. I. *Proceedings of the Entomological Society of Washington*, 51, 123–124.
Cunliffe, F. (1952) Biology of the cockroach parasite, *Pimeliaphilus podapolipophagus* Tragardh; with a discussion of the genera *Pimeliaphilus* and *Hirstiella*. *Proceedings of the Entomological Society of Washington*, 54, 153–169.
Cunliffe, F. (1968) A new species of Pimeliaphilus from California. *Proceedings of the Entomological Society of Washington*, 70, 1–4.
Davidson, J.A. (1958) A new species of lizard mite and a generis key to the family Pterygosomidae (Acarina, Anystoidea). *Proceedings of the Entomological Society of Washington*, 60, 75–79.
Fet, V., Sisson,W.D., Lowe, G. & Braunwalder, M.E. (2000) *Catalog of the scorpions of the World (1758–1998)*. New York Entomological Society. USA. 690 pp.
Freudenstein, J.V., Berg, C., Goldman, D., Kores, P., Molvray, M. & Chase, M. (2004) An expanded plastid DNA phylogeny of Orchidaceae and analysis of jackknife branch support strategy. *American Journal of Botany*, 91, 149–157.
Frost, D.R., Etheridge, R., Janies, D. & Titus, T.A. (2001) Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). *American Museum Novitates*, 3343, 1–39.
Gadsden, H. (1988) Comparación altitudinal de ectoparásitos de lagartijas del complejo *Sceloporus grammicus* (Reptilia, Iguanidae) en la Sierra de Tepoztlán, Morelos, México. *Acta Zoológica Mexicana (Nueva serie)*, 30, 21–31.
Gamble, T., Bauer, A.M., Greenbaum, E. & Jackman, T.R. (2008) Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata). *Zoologica Scripta*, 37, 355–366.
Goloboff, P. (1999) NONA (NO NAME) ver. 2 Published by the author, Tucumán, Argentina.
Goodwing, M. (1954) Observations on the biology of the lizard mite *Geckobiella texana* (Banks) 1904 (Acarina: Pterygosomidae). *Journal of Parasitology*, 40, 54–59.
Grandjean, F. (1939) Les segments postlarvaires de l'hysterosoma chez les oribatides (Acariens). *Bulletin Societe Zoology France*, 64, 273–284.
Grandjean, F. (1944) Observations sure les Acariens de la famille des Stigmaeidae. *Archives des Sciences physiques et naturelles*, 26, 103–131.
Grandjean, F. (1946) Au sujet de l' organe de Claparede, des eupathides multiples et des taenidies mandibulaires chez les Acariens actinochitineux. *Archives des Sciences physiques et naturelles*, 28, 63–87.
Hirst, A.S. (1917) On some new mites living on lizards. *Annals and Magazine of Natural History*, 8, 136–143.
Hirst A.S. (1926) On the parasitic mites of the suborder Prostigmata (Trombidioidea) found on lizards. *Linnean Society Journal (Zoology)*, 36, 173–200.
Hoffmann, A. (1969) Ácaros parásitos de batracios y reptiles en México. *Revista Latino Americana de Microbiología y Parasitología*, 11, 209–216.
Hoffmann, A. & López-Campos, G. (2000) *Biodiversidad de los ácaros en México*. CONABIO y UNAM, México. 230 pp.
Hoffmann, A. & Morales-Malacara, J.B. (1986) Una especie nueva de *Geckobia* (Acárida: Pterygosomatidae) colectada en México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología*, 56, 23–30.
Hoffmann, A. & O. Sánchez. (1980) Género y especie nuevos de un ácaro parásito de lagartijas (Acárida: Pterygosomatidae). *Anales de la Escuela Nacional de Ciencias Biológicas, México*, 23, 97–107.
Hunter, W. & Loomis, R. (1966) A new species of mite, genus *Hirstiella* (Acarina: Pterygosomidae) from the banded gecko, *Coleonyx variegates*, of Western North America. *Journal of the Kansas Entomological Society*, 39, 681–687.
Ibrahim, M.M. & Abdel-Rahman, M.A. (2011) Natural infestation of *Pimeliaphilus joshuae* on scorpion species from Egypt. *Experimental and Applied Acarology*, 55, 77–84.
Jack, K.M. (1959) Additional host and locality records for *Geckobiella texana* (Banks), 1904 (Acarina, Pterygosomidae). *Parasitology*, 49, 462–463.
Jack, K.M. (1961) A re-examination of the genera *Pimeliaphilus* Trägårdh 1905 and *Hirstiella* Berlese 1920 (Acari; Prostigmata). *The Annals and Magazine of Natural History*, 4, 305–314.
Jack, K.M. (1964) Leg-chaetotaxy with special reference to the Pterygosomidae (Acarina). *Annals of the Natal Museum*, 16, 152–171.
Jack, K.M. & Girot, B. (1965) Notes on the development of *Hirstiella insignis* (Berlese) 1892. *Acarologia*, 7, 286–293.
Knapp, C.R., Durden, L.A. & Klompen, H. (2012) Natural History Notes, *Iguana delicatissima* (Lesser Antillean Iguana). *Herpetological Review*, 43, 134.
Krantz, G.W. (1978) *A manual of Acarology.* Second edition. Oregon State University Book Stores, Inc. Oregon, USA. 509 pp.

Lawrence, R. (1953) Two new scale-mite parasites of lizards. *Proceedings of the United States National Museum*, 103, 9–18.
Lane, J.E. (1954) A redescription of the American lizard mite, *Geckobiella texana* (Banks), 1904, with notes on systematics of the species (Acarina: Pterygosomidae). *Journal of Parasitology*, 40, 93–99.
Lent, H. & Wygodzinsky, P. (1979) Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' disease. *Bulletin of the American Museum of Natural History*, 163, 123–520.
Lewis, D.J. & Macfarlane, D. (1981) The mites of Phlebotomine sandflies (Diptera: Psychodidae). *Society of Protozoologists Special Publication*, 1, 177–183
Martínez-Sánchez, A., Camacho, A.D., Quintero-Martínez, M.T. & Alejandre-Aguilar, R. (2007) Effect of ectoparasitic *Pimeliaphilus plumifer* mites (Acari: Pterygosomatidae) on *Meccus pallidipennis* (Hemiptera: Reduviidae) and several other Chagas' disease vectors under laboratory conditions. *Experimental and Applied Acarology*, 42, 139–149.
Nagar, S.K., Kumar, K. & Raizada, R.N. (1978) Redescriptions and certain developmental stages of the pterygosomid mites of the Delhi State. *The Annals of Zoology*, 14, 93–118.
Newell, I.M. & R.E. Ryckman. (1964) *Hirstiella pyriformis* sp. n. (Acari, Pterygosomidae), a new parasite of lizards from Baja California. *Journal of Parasitology*, 50, 163–171.
Newell, I.M. & R.E. Ryckman. (1966) Species of *Pimeliaphilus* (Acari: Pterygosomidae) attacking insects , with particular reference to the species parasitizing Triatominae (Hemiptera: Reduviidae). *Hilgardia*, 37, 403–436.
Newell, I.M. & R.E. Ryckman. (1969) *Pimeliaphilus zeledoni* n. sp. (Acari, Pterygosomidae), a parasite of *Triatoma dimidiata* (Latr.) (Hemiptera, Reduviidae). *Bulletin of the Southern California Academy of Sciences*, 68, 138–144.
Nixon, K.C. (1999–2004) WinClada-Asado ver. 1.89. Published by the author, Ithaca, NY.
Olivier, P.G. (1977) New species of the genus *Pimeliaphilus* (Acari: Pterygosomidae) from South-West Africa. *Phytophylactica*, 9, 29–39.
Paredes-León, R. (2003) Análisis preliminar de los ácaros ectoparásitos de la iguana negra (*Ctenosaura pectinata*) en una población silvestre de Oaxaca. Programa y memorias del VI Taller Nacional Sobre Manejo de Iguanas en Cautiverio, pp. 65–74. (http://www.subcomitedeiguanas.org/). Boca del Río, Veracruz, México.
Paredes-León, R., García-Prieto, L., Guzmán-Cornejo, C., León-Regàgnon, V. & Pérez, T.M. (2008) Metazoan parasites of mexican amphibians and reptiles. *Zootaxa*, 1904, 1–166.
Paredes-León, R. & Morales-Malacara, J.B. (2009) A New Species of the Genus *Hirstiella* (Acari: Prostigmata: Pterygosomatidae) parasitic on *Phyllodactylus bordai* (Reptilia: Squamata: Gekkonidae) in Mexico. *Journal of Medical Entomology*, 46, 442–450.
Paredes-León, R. & Pérez, T.M. (2008) Pterygosomatid mites (Acari: Prostigmata) of Mexico. *In*: Bertrand, M., Kreiter, S., McCoy, K.D., Migeon, A., Navajas, M., Tixier, M.-S. & Vial, L. (Eds.) *Integrative Acarology. Proceedings of the 6th European Congress of Acarology.* European Association of Acarologists, pp. 229–236.
Prasad, V. (1975) A new genus and species of pterygosomatid mite (Acarina: Pterygosomatidae) from India. *International Journal of Acarology*, 1, 14–17.
Ramírez-Bautista, A., Hernández-Salinas, U., Mendoza-Quijano, F., Cruz-Elizalde, R., Stephenson, B.P., Vite-Silva, V.D. & Leyte-Manrique, A. (2010) *Lista anotada de los anfibios y reptiles del estado de Hidalgo, México*. Universidad Autónoma del Estado de Hidalgo y CONABIO. 104 pp.
Swofford, D.L. (2002) PAUP*. *Phylogenetic analysis using parsimony (* and other methods).* Version 4. Sinauer Associates, Sunderland, Massachusetts.
Trägårdh, I. (1905) Acariden aus Ägypten und dem Sudan. *In*: Jägerskiöld, L.A. (Ed.) *Results of the Swedish Zoological Expedition to Egypt and the White Nile. Part II, Expedition.* Upsala. pp. 1–124.
Uetz, P. (2011) The Reptile Database. Available from http://www.reptile-database.org (accessed 20 December 2011).
Uetz, P., Goll, J. & Hallermann, J. (2007) Die TIGR-Reptiliendatenbank. *Elaphe*, 15, 22–25.
Vitzthum, H.G. (1942) Acarina. *In*: Bronns, H. G. (Ed.) *Klassen und Ordungen des Tierreiches*, 5, Sect. 4, Book 5. pp. 1–1011.
Walter, D.E. & Shaw, M. (2002) First record of the mite *Hirstiella diolii* Baker (Prostigmata: Pterygosomatidae) from Australia, with a review of mites found on Australian lizards. *Australian Journal of Entomology*, 41, 30–34.
Werman, S. (1983) Population dynamics of the lizard mite, *Hirstiella pyriformis* (Acari: Pterygosomatidae) on the chuckwalla, *Sauromalus obesus* (Sauria: Iguanidae). *Journal of Parasitology*, 69, 381–386.
Wiley, E.O., Siegel-Causey, D., Brooks, D.R. & Funk, V.A. (1991) The compleat cladistic. *The University of Kansas Museum of Natural History, Special Publications*, 19, 1–158.
Zumaquero, J.L., Alejandre, R., Linares, G., Cedillo, M.L., López, J.F. & Caicedo, R. (2004) *Pimeliaphilus triatomae* (Acari: Pterygosomidae) utilizado como control biológico de *Meccus pallidipennis* (Hemiptera: Reduviidae) en condiciones de laboratorio. *Revista Colombiana de Entomología*, 30, 131–135.

APPENDIX 1. List of morphological characters and character states used in the analysis (based on females only, except characters 268–274).

GNATHOSOMA (Figs. 3 A–B; 5 A–B; 7)

1. Relative size of gnathosoma. 0, thin, clearly narrower than long; 1, thick, as wide as long.
2. Relative length of base of gnathosoma. 0, half of length of palps; 1, a third part of the length of palps; 2, longer than the length of palps; 3, as long as the length of palps.
3. Cheliceral fixed digit. 0, absent; 1, present.
4. Size and shape of cheliceral fixed digit. 0, long spine-like with or without a hook near the tip; 1, reduced to membranous sheath or weakly spinous seta-like (branched process).
5. Shape of cheliceral movable digit. 0, stylet-like; 1, spine-like, with or without small teeth at the apex; 2, curved outward and hook-like with one or more teeth.
6. Length of palpal femur seta *d*. 0, short (less than 65 µm); 1, long (more than 66 µm).
7. Length of palpal genu seta *d*. 0, short (less than 65 µm); 1, long (more than 66 µm).
8. Setal form of palpal genu seta *d*. 0, acuminate nude; 1, peripectinate; 2, barbed throughout; 3, bipectinate; 4, barbed only at base.
9. Thickness of palpal genu seta *d*. 0, thin (slender); 1, thick (stout).
10. Relative size of palpal tarsus. 0, elongate (longer than palpal tibia claw); 1, very reduced (clearly shorter than palpal tibial claw).
11. Shape of palpal tarsus. 0, oval (clearly longer than wide); 1, round (as long as wide).
12. Number of palpal tarsus setae (apart of solenidion ω). 0, eight; 1, seven; 2, six; 3, five; 4, four; 5, three.
13. Relative length of emergent peritreme. 0, without emergent peritreme; 1, short, at level of subcapitulum; 2, long, almost reaching palpal genu.
14. Position of subcapitular ventral setae *n*. 0, proximal to level of insertions of palps; 1, distal to level of insertions of palps.
15. Hypostome (the anterior tubular part of subcapitulum). 0, absent; 1, present.
16. Relative length of hypostome. 0, as long as subcapitulum base or shorter; 1, longer than subcapitulum base.
17. Shape of seta *v* on palpal tibia. 0, nude; 1, sparsely barbed; 2, with nude stalk ending in a thick brush-like structure.
18. Setal form of palpal femur seta *d*. 0, bipectinate; 1, peripectinate; 2, pectinate; 3, nude; 4, barbed throughout.
19. Relative size of tibial claw. 0, subequal to palp tarsus; 1, longer than palp tarsus; 2, shorter than palp tarsus.
20. Shape of palpal tibial claw; 0, curved at tip; 1, curved from the middle.
21. Striated membranous velum on tip of hypostome. 0, absent; 1, present.
22. Rostral flange on tip of hypostome. 0, absent; 1, present.
23. Delimitation between subcapitulum and hypostome. 0, conspicuous; 1, gradual, not evident.
24. Relative size of palpal femur. 0, longer than wide; 1, strongly wider than long.
25. Relative size of palpal genu. 0, strongly wider than long; 1, longer than wide.
26. Relative size of palpal tibia. 0, as long as wide; 1, longer than wide; 2, strongly wider than long.
27. Subcapitulum with an anterolateral flange. 0, absent; 1, present.
28. Size of proximal part of cheliceral base. 0, globose, at least five times the width of distal part; 1, thin, 3.5 times or less the width of distal part.
29. Palpal trochanters. 0, free, distinct of palpal femur; 1, fused, not obvious or invisible.
30. Position of the subcapitulum related to idiosoma. 0, located immediately anterior to the margin of the idiosoma, distinct; 1, inserted ventral.

IDIOSOMA (Figs. 2; 3 C–D; 5 C–D)

31. Prodorsal shield. 0, present; 1, absent.
32. Location of setae *vi*. 0, on the prodorsal shield; 1, not on the prodorsal shield.
33. Location of setae *ve*. 0, on the prodorsal shield; 1, not on the prodorsal shield.
34. Location of setae *sci*. 0, on the prodorsal shield; 1, not on the prodorsal shield.
35. Location of setae *sce*. 0, on the prodorsal shield; 1, not on the prodorsal shield.
36. Location of setae *c3*. 0, not on the prodorsal shield; 1, on the prodorsal shield.
37. Eyes. 0, present; 1, absent.
38. Location of setae *sce* and eyes. 0, separate, not located on a single plate; 1, associated on a small plate.
39. Hypertrichy (more than 15 pairs of dorsal idiosomal setae). 0, absent; 1, present.
40. Arrangement of dorsal idiosomal setae. 0, ordered in transverse rows; 1, unordered, not in transverse rows.
41. Type of hypertrichy. 0, on ventral and dorsal surfaces only (not lateral); 1, on dorsal and lateral surfaces only (not on venter); 2, mainly lateral with patches anterodorsal (not on venter or on complete dorsum).
42. Setal form of genital setae (*g1*). 0, barbed; 1, spine-like nude; 2, peripectinate; 3, arboriform (extensively pectinate); 4, acuminate nude; 5, spine-like serrate.
43. Thickness of genital setae (*g1*). 0, thin (slender); 1, thick (stout).
44. Location of the setae *g1*. 0, inserted directly on the ventral cuticle (not on lobes); 1, inserted on the tip of lobes.
45. Setal pair *vi*. 0, present; 1 absent.

46. Setal pair *ve*. 0, present; 1 absent.
47. Setal pair *sci*. 0, present; 1 absent.
48. Setal pair *sce*. 0, present; 1 absent.
49. Setal pair *c1*. 0, present; 1 absent.
50. Setal pair *c2*. 0, present; 1 absent.
51. Setal pair *c3*. 0, absent; 1 present.
52. Setal pair *d1*. 0, present; 1 absent.
53. Setal pair *d2*. 0, present; 1 absent.
54. Setal pair *e1*. 0, present; 1 absent.
55. Setal pair *e2*. 0, present; 1 absent.
56. Setal pair *f1*. 0, present; 1 absent.
57. Setal pair *f2*. 0, present; 1 absent.
58. Setal pair *h1*. 0, present; 1 absent.
59. Setal pair *h2*. 0, present; 1 absent.
60. Setal pair *ps1*. 0, present; 1 absent.
61. Setal pair *ps2*. 0, present; 1 absent.
62. Setal pair *ps3*. 0, present; 1 absent.
63. Setal pair *ag1*. 0, present; 1 absent.
64. Setal pair *ag2*. 0, present; 1 absent.
65. Setal pair *ag3*. 0, present; 1 absent.
66. Setal pair *g1*. 0, present; 1 absent.
67. Shape of prodorsal shield. 0, half-round; 1, rectangular; 2, trapezoidal; 3, inverted equilateral triangle; 4, pentagonal; 5, inverted pear-shaped; 6, ovoid; 7, inverted isosceles triangle.
68. Relative location of setae *vi*. 0, anterior to *ve*, both setal pair aligned longitudinally; 1 anterior and internal to *ve*, both setal pair not aligned vertically or horizontally; 2, internal to *ve*, both setal pair aligned transversely.
69. Length of setae *ps1–3*. 0, the three pairs long and subequal; 1, increasing in size from *ps1* to *ps3*, with *ps3* clearly the longest; 2, all three pairs highly reduced and subequal in length; 3, decreasing in size from *ps1* to *ps3*, with *ps1* clearly the longest.
70. Sides of the pentagonal prodorsal shield. 0, with anterior sides almost parallel; 1, with anterior sides sharply converging anteriorly.
71. Anterior margin of inverted isosceles triangle prodorsal shield. 0, straight; 1, with a median notch.
72. Posterior margin of inverted equilateral triangle prodorsal shield. 0, end bluntly pointed; 1, with a very acute end.
73. Size of idiosoma. 0, longer than wide; 1, as long as wide (almost circular); 2, wider than long.
74. Relative location of setae *sci*. 0, clearly anterior to *sce*; 1, aligned transversely with *sce*; 2, posterior to *sce*.
75. Position of setae *d1*. 0, each seta *d1* positioned closer to the other seta *d1* than to setae *d2*; 1, each seta *d1* at the same distance, or closer, to setae *d2* than to other seta *d1*.
76. Location of setae *d2*. 0, nearly aligned transversely to *d1*; 1, clearly anterior to *d1*.
77. Location of setae *e1*. 0, at the same distance of the other *e1* as *e2*; 1, clearly closer to *e2* than the other *e1*.
78. Setal form of dorsal pair *h1*. 0, peripectinate; 1, serrate; 2, arboriform (extensively pectinate); 3, spinose spatulate (club-like); 4, tuft-shape.
79. Relative length of dorsal setal pair *h1*. 0, subequal to *h2*;1, half the length of *h2*; 2, a quarter of the length of *h2*..
80. Shape of dorsal setal pair *f2*. 0, peripectinate; 1, barbed; 2, tuft-shape; 3, spinose spatulate (club-like).
81. Relative length of dorsal setal pair *f2*. 0, half or more of the length of *f1*; 1, a tenth of the length of *f1*; 2, subequal to *f1*.
82. Position of setal pair *f2* (in unengorged specimens). 0, lateral, anterior to anal region; 1, ventral, in the anal region; 2, ventral, nearly aligned transversely with genital setae (*g1*), between setae *g1* and *ag3*.
83. Fan-shaped cuticular fold on venter covering genital region up to setal pair *ag1*. 0, absent; 1, present.
84. Position of setal pairs *ps1–3* (in unengorged specimens). 0, ventral; 1, anterior to posterior tip of idiosoma on dorsum; 2, on posterior tip of dorsum.
85. Setal form of setal pair *ps1*. 0, acuminate nude; 1, spine-like serrate; 2, peripectinate; 3, arboriform (extensively pectinate); 4, sparsely barbed; 5, sparsely pectinate; 6, tuft-shape; 7, spinose spatulate (club-like).
86. Setal form of setal pair *ps2*. 0, acuminate nude; 1, spine-like serrate; 2, peripectinate; 3, arboriform (extensively pectinate); 4, sparsely barbed; 5, tuft-shape; 6, spinose spatulate (club-like).
87. Setal form of setal pair *ps3*. 0, acuminate nude; 1, spine-like serrate; 2, peripectinate; 3, arboriform (extensively pectinate); 4, sparsely barbed; 5, tuft-shape.
88. Length of dorsal setal pairs *vi* and *ve*. 0, short (100 µm or less); 1, long (more than 100 µm).
89. Length of dorsal setal pairs *sci* and *sce*. 0, short (100 µm or less); 1, long (more than 100 µm).
90. Length of dorsal setal pairs *e1* and *e2*. 0, short (100 µm or less); 1, long (more than 100 µm).
91. Length of dorsal setal pairs *d1* and *d2*. 0, short (100 µm or less); 1, long (more than 100 µm).
92. Length of dorsal setal pair *f1*. 0, short (less than 75 µm; 1, long (more than 75 µm).
93. Shape of dorsal idiosomal setae (*vi, ve, sci, sce, c1, c2, c3* (if present), *d1, d2, e1, e2* and *f1*). 0, peripectinate; 1, a combination of two types, serrate and flattened pointed cylindrical; 2, serrate; 3, spinose spatulate (club-like)

94. Length of dorsal setal pairs *c1, c2, c3* (if present). 0, short (100 µm or less); 1, long (more than 100 µm).
95. Number of dorsal setal forms. 0, one type of setae (sometimes one to four pairs of setae different from the rest; 1, at least two types of setae (more than ten pairs of different setae).

LEGS (Figs. 4; 6)

96. Thickness of the podomers (trochanters-tibiae I–IV). 0, stout, less than twice as long as wide; 1, thin, at least twice as long as wide.
97. Length of femora I–IV. 0, twice as long as genua I–IV; 1, as long as genua I–IV or only slightly longer (never twice as long).
98. Length of leg setae. 0, some of them as long as each podomer; 1, short, half of the length of each podomer.
99. Shape of seta (*v*) on trochanters I–IV. 0, thin and nude (sometimes with fine barbules); 1, stout and pectinate.
100. Relative length of legs. 0, legs I distinctly longer than legs II–IV; 1, legs IV distinctly longer than I–III.
101. Relative thickness of companion seta (*ft*) on tarsus I. 0, as wide as solenidion *ω2*; 1, thinner than *ω2*.
102. Setal form of companion seta (*ft*) on tarsus I. 0, acuminate nude; 1, peripectinate; 2, barbed.
103. Setal type of pair *p* on tarsi I–IV. 0, nude or slightly barbed; 1, feather-like.
104. Shape of tarsi I–IV. 0, progressively thinned from proximal to distal end; 1, stout ending blunt.
105. Relative length of solenidion *ω2* on tarsus I. 0, slightly shorter than companion seta (*ft*); 1, very reduced, at least a third the length of *ft*; 2, as long as *ft*; 3, long, almost twice the length of *ft*; 4, very long, at least four times the length of *ft*; 5, shorter than *ft* (half of the length of *ft*).
106. Setae *1a* on coxae I. 0, present; 1 absent.
107. Setae *1b* on coxae I. 0, present; 1 absent.
108. Seta *v* on trochanter I. 0, present; 1, absent.
109. Seta *d* on femur I. 0, present; 1, absent.
110. Seta *l'* on femur I. 0, present; 1, absent.
111. Seta *l"* on femur I. 0, present; 1, absent.
112. Seta *v'* on femur I. 0, present; 1, absent.
113. Seta *v"* on femur I. 0, present; 1, absent.
114. Additional proximal seta *v* on femur I. 0, absent; 1, present.
115. Seta *d* on genu I. 0, present; 1, absent.
116. Seta *l'* on genu I. 0, present; 1, absent.
117. Seta *l"* on genu I. 0, present; 1, absent.
118. Seta *v'* on genu I. 0, absent; 1, present.
119. Seta *v"* on genu I. 0, absent; 1, present.
120. Seta *σ* or *κ* (*vestigial*) on genu I. 0, present; 1, absent.
121. Seta *d* on tibia I. 0, present; 1, absent.
122. Seta *l'* on tibia I. 0, present; 1, absent.
123. Seta *l"* on tibia I. 0, present; 1, absent.
124. Seta *v'* on tibia I. 0, present; 1, absent.
125. Seta *v"* on tibia I. 0, present; 1, absent.
126. Solenidion *ω1* on tarsus I. 0, absent; 1, present.
127. Seta *pl* on tarsus I. 0, present; 1, absent.
128. Seta *ft* on tarsus I. 0, present; 1, absent.
129. Solenidion *ω2* on tarsus I. 0, present; 1, absent.
130. Seta *tc'* on tarsus I. 0, present; 1, absent.
131. Seta *tc"* on tarsus I. 0, present; 1, absent.
132. Seta *p'* on tarsus I. 0, present; 1, absent.
133. Seta *p"* on tarsus I. 0, present; 1, absent.
134. Seta *it'* on tarsus I. 0, absent; 1, present.
135. Seta *it"* on tarsus I. 0, absent; 1, present.
136. Seta *a'* on tarsus I. 0, present; 1, absent.
137. Seta *a"* on tarsus I. 0, present; 1, absent.
138. Seta *u'* on tarsus I. 0, present; 1, absent.
139. Seta *u"* on tarsus I. 0, present; 1, absent.
140. Seta *vs'* on tarsus I. 0, present; 1, absent.
141. Seta *vs"* on tarsus I. 0, absent; 1, present.
142. Setae *2a* on coxae II. 0, present; 1, absent.
143. Setae *2b* on coxae II. 0, present; 1 absent.
144. Seta *v* on trochanter II. 0, present; 1, absent.
145. Seta *d* on femur II. 0, present; 1, absent.
146. Seta *l'* on femur II. 0, present; 1, absent.
147. Seta *l"* on femur II. 0, present; 1, absent.

148. Seta *v'* on femur II. 0, absent; 1, present.
149. Seta *v"* on femur II. 0, present; 1, absent.
150. Seta *d* on genu II. 0, present; 1, absent.
151. Seta *l'* on genu II. 0, present; 1, absent.
152. Seta *l"* on genu II. 0, present; 1, absent.
153. Seta *v'* on genu II. 0, present; 1, absent.
154. Seta *v"* on genu II. 0, absent; 1, present.
155. Seta *d* on tibia II. 0, present; 1, absent.
156. Seta *l'* on tibia II. 0, present; 1, absent.
157. Seta *l"* on tibia II. 0, present; 1, absent.
158. Seta *v'* on tibia II. 0, present; 1, absent.
159. Seta *v"* on tibia II. 0, present; 1, absent.
160. Solenidion ω on tarsus II. 0, present; 1, absent.
161. Seta *tc'* on tarsus II. 0, present; 1, absent.
162. Seta *tc"* on tarsus II. 0, present; 1, absent.
163. Seta *p'* on tarsus II. 0, present; 1, absent.
164. Seta *p"* on tarsus II. 0, absent; 1, present.
165. Seta *a'* on tarsus II. 0, present; 1, absent.
166. Seta *a"* on tarsus II. 0, present; 1, absent.
167. Seta *u'* on tarsus II. 0, present; 1, absent.
168. Seta *u"* on tarsus II. 0, present; 1, absent.
169. Seta *vs'* on tarsus II. 0, present; 1, absent.
170. Seta *vs"* on tarsus II. 0, absent; 1, present.
171. Coxal setae *3a*. 0, present; 1 absent.
172. Setae *3b* on coxae III. 0, present; 1 absent.
173. Setae *3c* on coxae III. 0, present; 1 absent.
174. Setae *3d* on coxae III. 0, present; 1, absent.
175. Seta *v* on trochanter III. 0, present; 1 absent.
176. Seta *d* on femur III. 0, present; 1 absent.
177. Seta *l'* on femur III. 0, present; 1 absent.
178. Seta *l"* on femur III. 0, present; 1 absent.
179. Seta *v'* on femur III. 0, absent; 1, present.
180. Seta *v"* on femur III. 0, present; 1 absent.
181. Seta *d* on genua III. 0, present; 1 absent.
182. Seta *l'* on genua III. 0, absent; 1, present.
183. Seta *l"* on genua III. 0, absent; 1, present.
184. Seta *v'* on genua III. 0, absent; 1, present.
185. Seta *v"* on genua III. 0, absent; 1, present.
186. Seta *d* on tibia III. 0, present; 1 absent.
187. Seta *l'* on tibia III. 0, present; 1 absent.
188. Seta *l"* on tibia III. 0, present; 1 absent.
189. Seta *v'* on tibia III. 0, present; 1 absent.
190. Seta *v"* on tibia III. 0, present; 1 absent.
191. Solenidion ω on tarsus III. 0, present; 1 absent.
192. Seta *tc'* on tarsus III. 0, present; 1 absent.
193. Seta *tc"* on tarsus III. 0, present; 1, absent.
194. Seta *p'* on tarsus III. 0, absent; 1, present.
195. Seta *p"* on tarsus III. 0, absent; 1, present.
196. Seta *a'* on tarsus III. 0, present; 1 absent.
197. Seta *a"* on tarsus III. 0, present; 1 absent.
198. Seta *u'* on tarsus III. 0, present; 1 absent.
199. Seta *u"* on tarsus III. 0, present; 1 absent.
200. Seta *vs'* on tarsus III. 0, present; 1 absent.
201. Seta *vs"* on tarsus III. 0, absent; 1, present.
202. Coxal setae *4a*. 0, present; 1 absent.
203. Coxal setae *4c*. 0, present; 1 absent.
204. Seta *v* on trochanter IV. 0, present; 1 absent.
205. Seta *d* on femur IV. 0, present; 1 absent.
206. Seta *l'* on femur IV. 0, absent; 1, present.
207. Seta *l"* on femur IV. 0, absent; 1, present.
208. Seta *v'* on femur IV. 0, present; 1 absent.

209. Seta *v"* on femur IV. 0, absent; 1, present.
210. Seta *d* on genu IV. 0, present; 1 absent.
211. Seta *l'* on genu IV. 0, absent; 1, present.
212. Seta *l"* on genu IV. 0, absent; 1, present.
213. Seta *v'* on genu IV. 0, absent; 1, present.
214. Seta *v"* on genu IV. 0, absent; 1, present.
215. Seta *d* on tibia IV. 0, present; 1 absent.
216. Seta *l'* on tibia IV. 0, present; 1 absent.
217. Seta *l"* on tibia IV. 0, present; 1 absent.
218. Seta *v'* on tibia IV. 0, present; 1 absent.
219. Seta *v"* on tibia IV. 0, present; 1 absent.
220. Seta *tc'* on tarsus IV. 0, present; 1 absent.
221. Seta *tc"* on tarsus IV. 0, present; 1 absent.
222. Seta *p'* on tarsus IV. 0, absent; 1, present.
223. Seta *p"* on tarsus IV. 0, absent; 1, present.
224. Seta *a'* on tarsus IV. 0, present; 1 absent.
225. Seta *a"* on tarsus IV. 0, present; 1 absent.
226. Seta *u'* on tarsus IV. 0, present; 1 absent.
227. Seta *u"* on tarsus IV. 0, present; 1 absent.
228. Seta *vs'* on tarsus IV. 0, present; 1 absent.
229. Seta *vs"* on tarsus IV. 0, absent; 1, present.
230. Setal type of *tc'* on tarsus I. 0, eupathidium; 1, barbed.
231. Setal type of *tc"* on tarsus I. 0, eupathidium; 1, barbed.
232. Length of setal pair *tc* on tarsus I. 0, equal; 1, *tc'* longer than *tc"*.
233. Setal form of *tc'* on tarsus II. 0, acuminate nude; 1, barbed; 2, peripectinate.
234. Setal form of *tc"* on tarsus II. 0, acuminate nude; 1, barbed; 2, peripectinate.
235. Relative length of setal pair *tc* on tarsus II. 0, *tc'* longer than *tc"*; 1, subequal in length.
236. Setal type of *a'* on tarsus II. 0, nude; 1, barbed.
237. Setal type of *a"* on tarsus II. 0, nude; 1, barbed.
238. Setal form of *tc'* on tarsus III. 0, acuminate nude; 1, barbed; 2, peripectinate.
239. Shape of seta *tc"* on tarsus III. 0, acuminate nude; 1, barbed; 2, peripectinate.
240. Relative length of setal pair *tc* on tarsus III. 0, subequal in length; 1, *tc'* longer than *tc"*.
241. Setal type of *a'* on tarsus III. 0, barbed; 1, nude.
242. Setal type of *a"* on tarsus III. 0, nude; 1, barbed.
243. Setal form of *tc'* on tarsus IV. 0, acuminate nude; 1, barbed; 2, peripectinate.
244. Setal form of *tc"* on tarsus IV. 0, acuminate nude; 1, barbed; 2, peripectinate.
245. Relative length of setal pair *tc* on tarsus IV. 0, subequal in length; 1, *tc'* longer than *tc"*.
246. Setal type of *a'* on tarsus IV. 0, barbed; 1, nude.
247. Setal type of *a"* on tarsus IV. 0, nude; 1, barbed.
248. Length of setal pair *tc* on tarsus I in relation to pretarsus. 0, long, longer than pretarsus; 1, short, as long as pretarsus or shorter.
249. Apparent division on femur I into two non-articulating segments. 0, absent; 1, present.
250. Apparent division on femur IV into two non-articulating segments. 0, absent; 1, present.
251. Setal form of *1b* on coxae I. 0, acuminate nude; 1, barbed; 2, peripectinate.
252. Thickness of setae *1b*. 0, thin (spiniform); 1, thick (stout).
253. Setal form of *2b* on coxae II. 0, acuminate nude; 1, barbed; 2, peripectinate.
254. Thickness of setae *2b*. 0, thin (spiniform); 1, thick (stout).
255. Setal form of *3c* on coxae III. 0, acuminate nude; 1, barbed; 2, peripectinate.
256. Thickness of setae *3c*. 0, thin (spiniform); 1, thick (stout).
257. Setal form of *3d* on coxae III. 0, acuminate nude; 1, barbed; 2, peripectinate; 3, bipectinate.
258. Thickness of setae *3d*. 0, thin (spiniform); 1, thick (stout).
259. Setal form of *4c* on coxae IV. 0, acuminate nude; 1, barbed; 2, peripectinate.
260. Thickness of setae *4c*. 0, thin (slender); 1, thick (stout).
261. Ensemble of coxae I–II. 0, grouped but not fused, with a complete thick line of separation between coxae I and II; 1, fused although with an incomplete fine line division (only on distal part); 2, completely fused.
262. Ensemble of coxae III–IV. 0, grouped but not fused, with a complete thick line of separation between coxae III and IV; 1, fused although with an incomplete fine line division (only on distal part); 2, completely fused.
263. Proximity of coxal group I–II with coxal group III–IV. 0, very close with a small distance not longer than length of coxal group I–II; 1, away with great distance (longer than length of coxal group I–II).
264. Location of coxal groups. 0, I–II on anterior part and III–IV on posterior part (at least coxae IV beyond of middle body); 1, I–II and III–IV on anterior part of idiosoma.

265. Location of setal pair *4a*. 0, very close together, between coxae IV (almost aligned longitudinally to setal pair *3a*); 1, separate, posterior to coxae IV (longitudinally more external than *3a*).
266. Relative length of coxae I. 0, subequal to coxae II; 1, longer than coxae II.
267. Relative length of coxae III. 0, shorter than coxae IV; 1, longer than coxae IV.

MALES

268. Solenidion *ω1* on tarsus I. 0, absent; 1, present.
269. Trochanter IV seta *v.* 0, present; 1, absent.
270. Seta *v'* on genua IV. 0, present; 1, absent.
271. Setal form of *v'* on genua IV. 0, nude; 1, hollow ensiform; 2, pectinate; 3, barbed.
272. Setal form of *v"* on tibia IV. 0, barbed; 1, pectinate; 2, solid and spine-like.

SETAL DEVELOPMENT

273. Solenidion *φ1* on tibia I of larva. 0, absent; 1, present.
274. Addition of setae *ps1–3*. 0, present in larvae; 1, delayed to the deutonymph.

APPENDIX 2. Matrix of morphological characters (Abbreviations as in Table 1).

	20 40 60
Eus.sp.	000–00000000000–0000–––000000000000–0000–00000000000000000000000
Pte.mut	0311200001152111032000000200111–––––1–11211100000010000000000000
Geck.leo	1011200001142110022000010200110000110111021100000010000000000000
Teq.oax	13112001111210102100000102101000001–0100–51000000000000000000000
Pim.pod	12101004111111101111111011010000001–0100–31000000000000000000000
Pim.tro	12101004111?11101111111011010000001–0100–31000000000000000000000
Gec.tex	0011211201122011012000001100101–––––0011140100000010000000000000
Gec.har	00112002011?2011042000010100101–––––0011111100000010000000000000
Hir.ins	12101114111111100311111111011000001–0100–10000000000000000000000
Hir.ten	131120–1111310112110000102101000001–0100––––00000000000–0000000–
Hir.tro	0011211200022011012000001100100011100100–40100000?10000000000000
Hir.sha	121011–4111311101111111011011000001–0100––––00000000000–0000000?
Hir.pel	0011211200022011012000001100100011100100–40100000010000000000000
Hir.bon	0111201200022011012000001100100010100100–40100000010000000000000
Hir.bak	0111201200022011012000001100100010100100–40100000010000000000000
Hir.sta	0011201000022011012000001100101–––––0000–40100000010000000000000
Hir.pyr	0011201200032011012000001100100110100100–40100000010000000000000
Hir.oto	13112111111310112110000102101000001–0100–31000000000000000000000
Hir.jav	0111200300022011012000001100100010100100–40100000010000000000000
Hir.dio	0111200300022011012000001100100010100100–40100000010000000000000
Hir.jim	13112111111310112110000102101000001–0100–31000000000000000000000
Gec.don	0111211200022011012000001100100010100100–40100000010000000000000
Ber.cha	13112111111310112110000102101000001–0100–31000000000000000000000

	80 100 120
Eus.sp.	0000–––000000000000000000000000000000000000000000000000000000000
Pte.mut	0–21–––21–0–1000002111000000101011000011100000110000000000001000
Geck.leo	0220–––21–0–1000001222000002010011110114000001100101000000000000
Teq.oax	0112–––120014221110655111110100110002102000000100000000000010000
Pim.pod	04000––021112000202333111110101001110104000000010001100000010000
Pim.tro	04000––011112000202333111110101001010104000000010001100000010000
Gec.tex	0–21–––01–0–0110002542000000000110000110000000000001100000010000
Gec.har	0–20–––01–0–3030002764000003000110000115000000000001100000000000
Hir.ins	04030––021000000202444111110101001110104000000000001100000010000
Hir.ten	0320––00201120–––0133311111010100100110?000000000001100000000000
Hir.tro	0721–0–0110101100025421111101001100001100000000000011?0000010000
Hir.sha	04030––0211000–––02122111110101001110104000000000001100000010000
Hir.pel	0721–1–0211101100025421111101001100001100000000000011000000 10000
Hir.bon	04211––0110131120025401111001001100001100000000000011000000 10000
Hir.bak	0621–––0110131120025440000030001100001100000000000011000000 10000
Hir.sta	0–21–––0110101100025400000030001100001100000110000011000000 10000
Hir.pyr	0521–––0110101100025420000000001100001100000000000011000000 10000
Hir.oto	0320––0020112000201333111110101001101102000000000001100000000000
Hir.jav	0521–––0110131100025420000030001100001120000000000011000000 10000
Hir.dio	0521–––0110101100025420000030001100001120000000000011000000 10000
Hir.jim	0320––1020112000201333111110101001101103000000000001100000000000
Gec.don	04210––0110131120025400000030001100001100000000000011000000 10000
Ber.cha	0320––1020112000201333111110101001101103000000000001100000000000

	140 160 180
Eus.sp.	00000000000000000000000000000000000000000000000000000000000000000
Pte.mut	00011000001100011010000101100001010000000001001101100000110010111
Geck.leo	00011000001000011001111011111000010000010000001100100000000010011
Teq.oax	00011000001000011000001000000000010000010000001101010000000000011
Pim.pod	00011000001000000000000100000000010000010000000111010100000000011
Pim.tro	00011000001000000000000100000000010000010000000111010100000000011
Gec.tex	00011000001000000000000100000000010000000000000111010100000000011
Gec.har	00011000001000000000001001100000010000000000001111000100110010011
Hir.ins	00111000001000000100000100000000000000010000000111010100000010010
Hir.ten	00011000001000000000000100000000010000010000000111010100000000011
Hir.tro	00011000001000000100000000000000010000000000000111010100000010011
Hir.sha	00011000001000000100001000000000010000010000000111010100000000011
Hir.pel	00011000001000000100000000000000010000000000000111010100000010011
Hir.bon	00011000001000000000000000000000010000000000000111010100000010011
Hir.bak	00011000001000000000000000000000010000000000000111010100000000011
Hir.sta	00011000001000011000100000000000010000000000001111000100000000011
Hir.pyr	00011000001000000000000000000000010000000000000111010100000000011
Hir.oto	00011000001000000000000100000000010000010000000111010100000000011
Hir.jav	00011000001000000000000000000000010000000000000111010100000000011
Hir.dio	00011000001000000000000000000000010000000000000111010100000000011
Hir.jim	00011000001000000000000100000000010000010000000111010100000000011
Gec.don	00011000001000000000000000000000010000000000000111010100000000011
Ber.cha	00011000001000000000000100000000010000010000000111010100000000011

APPENDIX 2. (continued)

	200 220 240 260
Eus.sp.	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Pte.mut	0 0 0 0 0 0 0 1 0 0 0 0 1 0 1 0 0 1 0 0 1 1 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 – – 0 0 0 – – 1 0 0 – – 1 0 1 1 0 0 0 0 0 0 0 – – – –
Geck.leo	0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 1 1 1 0 0 1 0 1 0 0 0 0 1 1 0 0 1 1 2 1 2 1 2 1 2 1
Teq.oax	0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 1 1 1 0 0 1 1 0 1 0 1 1 0 1 0 1 0 0 1 0 0 0 0 0 1 0 2 0
Pim.pod	0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 2 2 1 1 1 2 2 0 0 1 2 2 0 0 1 0 1 1 2 1 2 1 2 1 2 1 2 0
Pim.tro	0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 2 2 1 1 1 2 2 0 0 1 2 2 0 0 1 0 1 1 2 1 2 1 2 1 2 1 2 0
Gec.tex	0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 1 0 – –
Gec.har	0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 1 0 – –
Hir.ins	0 0 0 0 0 1 0 0 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 0 2 2 1 1 0 2 2 0 0 1 2 2 0 0 1 1 0 0 2 1 2 1 2 1 2 1 1 0
Hir.ten	0 0 0 0 0 1 0 – – 0 1 0 – 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 2 2 1 1 0 2 2 0 0 0 2 2 0 0 0 1 0 0 2 1 2 1 2 1 2 1 – –
Hir.tro	0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 3 0 – –
Hir.sha	0 0 0 0 0 1 0 – 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 2 2 1 1 1 2 2 0 0 1 2 2 0 0 1 1 0 0 2 1 2 1 2 1 2 1 – 0
Hir.pel	0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 3 0 – –
Hir.bon	0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 3 0 – –
Hir.bak	0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 3 0 – –
Hir.sta	0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 1 0 – –
Hir.pyr	0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 1 0 – –
Hir.oto	0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 0 2 2 1 1 0 2 2 0 0 0 2 2 0 0 0 1 0 0 2 1 2 1 2 1 2 1 2 1
Hir.jav	0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 3 0 – –
Hir.dio	0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 3 0 – –
Hir.jim	0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 2 2 1 1 0 2 2 0 0 0 2 2 0 0 0 1 0 0 2 1 2 1 2 1 2 1 2 1
Gec.don	0 0 0 0 0 0 0 1 0 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 0 1 1 1 1 0 1 0 0 0 0 0 1 0 1 0 3 0 – –
Ber.cha	0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 2 2 1 1 0 2 2 0 0 0 2 2 0 0 0 1 0 1 2 1 2 1 2 1 2 1 2 1

Eus.sp.	0 0 0 0 0 0 0 ? ? ? ? ? ? ?
Pte.mut	2 2 0 1 1 1 1 0 ? 0 0 0 0 0
Geck.leo	2 2 0 1 1 0 0 0 0 1 – 0 0 0
Teq.oax	1 1 0 1 0 1 0 1 1 0 0 0 0 0
Pim.pod	0 0 0 1 1 1 0 1 1 0 2 1 ? ?
Pim.tro	0 0 0 1 1 1 0 ? ? ? ? ? ? ?
Gec.tex	0 0 1 0 1 1 0 1 1 0 1 2 0 1
Gec.har	1 1 1 1 0 1 0 0 0 0 3 0 ? ?
Hir.ins	0 0 0 1 1 0 0 ? ? ? ? ? ? ?
Hir.ten	0 1 0 1 0 1 0 ? ? ? ? ? 0 ?
Hir.tro	0 1 1 0 1 1 0 1 1 0 1 2 0 1
Hir.sha	0 0 0 1 1 1 0 ? ? ? ? ? 1 ?
Hir.pel	0 1 0 0 1 1 0 1 1 0 1 2 0 1
Hir.bon	0 1 1 0 1 1 0 1 1 0 1 2 0 1
Hir.bak	0 1 1 0 1 1 0 1 1 0 1 2 0 1
Hir.sta	0 1 1 0 1 1 0 1 1 0 3 0 0 1
Hir.pyr	0 1 1 0 1 1 0 1 1 0 1 2 0 1
Hir.oto	0 1 0 1 0 1 0 1 1 0 2 1 0 0
Hir.jav	0 1 1 0 1 1 0 ? ? ? ? ? 0 1
Hir.dio	0 1 1 0 1 1 0 1 1 0 3 0 0 1
Hir.jim	0 1 0 1 0 1 0 1 1 0 2 1 0 0
Gec.don	0 1 1 0 1 1 0 1 1 0 1 2 0 1
Ber.cha	0 1 0 1 0 1 0 1 1 0 2 1 0 0