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Morphological description, DNA barcodes and phylogenetic placement of a new mite species: *Dinogamasus saengdaoae* sp. nov. (Mesostigmata: Laelapidae) found in the acarinarium of carpenter bees in Thailand

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Abstract

Dinogamasus saengdaoae Attasopa & Ferrari **sp. nov.** is described based on adult females from the abdominal pouch of females of *Xylocopa tenuiscapa* (Westwood) in Chiang Mai Province, Northern Thailand. The new species belongs to the *D. perkinsi* (Oudemans) group (*sensu* LeVeque) and can be distinguished from its congeners by the combination of the following characters: (1) dorsal shield covering opisthosoma neither laterally nor posteriorly; (2) opisthonotal soft cuticle with a pair of relatively long setae posteriorly; (3) setae *pd1*, *pd2* on genu I and *ad3*, *pd3*, *pl1*, *pl2* on both genu and tibia I conical. Maximum likelihood-based analysis of newly-generated DNA barcodes shows that the sequenced specimens of *D. saengdaoae* **sp. nov.** form a monophyletic cluster, and parsimony analysis of a previously available morphological dataset indicates that the species comprises a strongly-supported clade with *D. perkinsi* and *D. piperi* LeVeque. We provide an additional couplet for Lundqvist's key for the species of *Dinogamasus* Kramer to facilitate identification of *D. saengdaoae* **sp. nov.**.

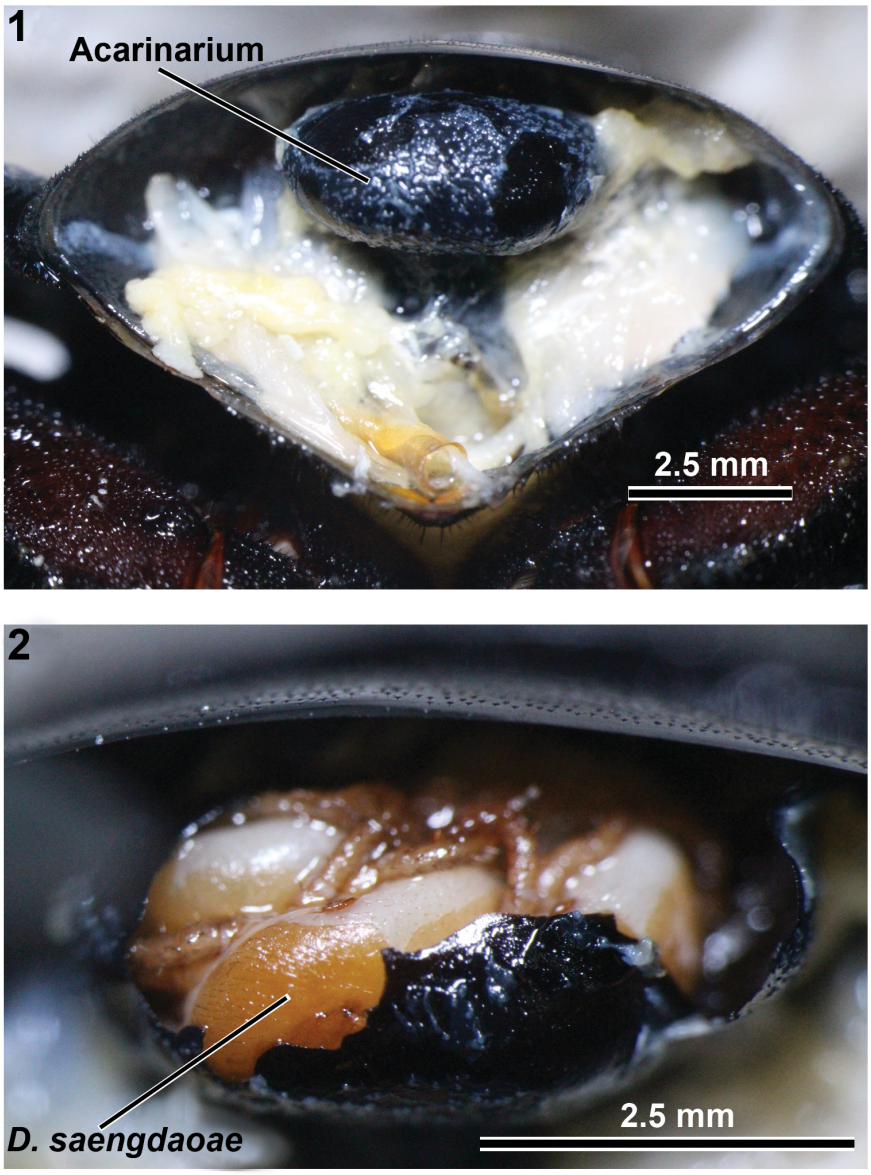
Keywords: Acari, COI, key, Oriental region, phoretic mites, *Xylocopa*

Introduction

Dinogamasus Kramer (Acari: Mesostigmata: Laelapidae) is known as a symbiotic genus of mites that includes 46 named species currently (Lundqvist 1999; Joharchi *et al.* 2016). They are strictly associated with African and Asian carpenter bees of the genus *Xylocopa* Latreille (Hymenoptera: Apidae: Xylocopini) (Lundqvist 1999). The adult females of *Dinogamasus* are transported by female carpenter bees in a metasomal chitinous pouch—a specialized acarinarium located inside the first metasomal segment (LeVeque 1930ab; Lundqvist 1999; Michener 2007; Makino *et al.* 2018) (see also Figures 1, 2).

LeVeque (1930a) proposed the *perkinsi* species group to accommodate three species—*D. perkinsi*, *D. piperi* LeVeque, and *D. philippinensis* LeVeque—based on the following shared characteristics: dorsal shield with lateral notch (LeVeque 1930a: figures 1a, 2a); anal shield with parallel lateral margins basally (LeVeque 1930a: figure 2d); peritrematral shield rudimentary or produced and fused with a projection from the dorsal shield anteriorly; fixed digit of chelicerae with

prominent tooth (LeVeque 1930a: figure 2e); trochanter–genu I with unmodified setae ventrally (Lundqvist 1999: figures 83c, e); leg I with conical setae, although its chaetotaxy usually varies among species (LeVeque 1930a: figures 1a, 2a, 3a); and tarsus II with three blunt conical setae (Lundqvist 1999: figure 83g). A strongly-supported morphological phylogeny of the genus, however, indicated that the *D. perkinsi* group, as proposed by LeVeque (1930a), is not monophyletic: *D. perkinsi* and *D. piperi* formed the sister clade to all other species of the genus (except *D. villosior* (Berlese)), while *D. philippinensis* was placed within a relatively-derived clade (Lundqvist 1999). All three species are found exclusively in the Indo-Malay ecoregion (*sensu* Olson *et al*. 2001), which encompasses India and Southeast Asia (the latter including most of the Malay Archipelago; see Figure 3).



FIGURES 1–2. Posterodorsal view of the internal cavity of T1 of female *Xylocopa tenuiscapa* showing metasomal acarinarium (chitinous pouch). 1. Undissected acarinarium; 2. Acarinarium with most of its posterodorsal part removed to show individuals of *Dinogamasus saengdaoae* **sp. nov.**

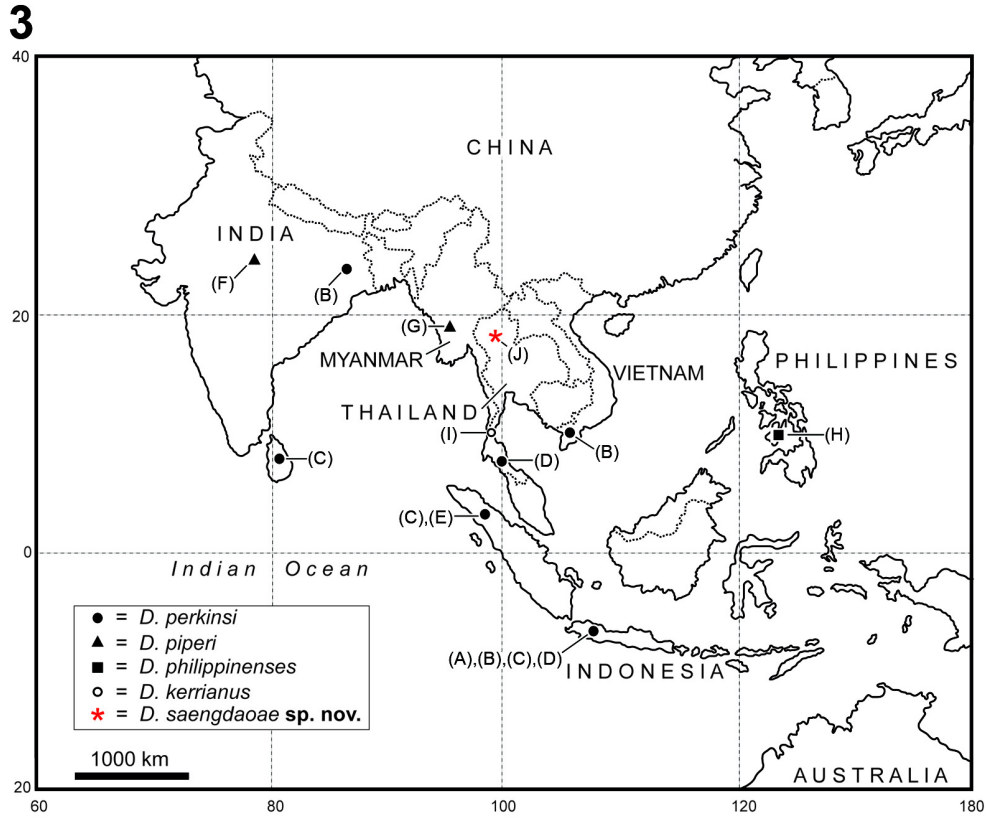


FIGURE 3. Distribution map of the species in the *Dinogamasus perkinsi* group based on published records of their respective hosts. *D. perkinsi*: (A) Oudemans (1901): *X. tenuiscapa* (Indonesia); (B) Vitzthum (1919): *Xylocopa latipes* and *X. tenuiscapa* (India, Indonesia, Vitenam); (C) Vitzthum (1930): *X. tenuiscapa* (Sri Lanka); *X. latipes* (Indonesia, Sri Lanka); *X. auripennis* (Indonesia); (D) LeVeque (1930a): *X. latipes* (Indonesia, South Thailand); (E) OConnor (1993): *X. latipes* (Indonesia). *D. piperi*: (F) LeVeque (1930a): *X. tenuiscapa* (India); (G) Lundqvist (1999): *Xylocopa* sp. (Myanmar). *D. philippinensis*: (H) LeVeque (1930a): *X. latipes* (Philippines). *D. kerrianus*: (I) Lundqvist (1999): *X. kerri* (South Thailand). *D. saengdaoae* **sp. nov.**, (J) this study: *X. tenuiscapa* (Chiang Mai Prov., North Thailand.

Overall, the Indo-Malayan species of *Dinogamasus* are fairly distinct from their Afrotropical and middle-eastern congeners in morphology: tibia II of the Indo-Malayan species does not have any hook-shaped *pv* setae (Lundqvist 1999: figure 6), while such setae are present in most of the African and middle-eastern species; in addition, the *av* seta of femur II is setiform in the Indo-Malayan species, but modified in the African species (Joharchi *et al.* 2016). Both character states exhibited by African species are apomorphic within *Dinogamasus* (Lundqvist 1999). Species of the two regional groups of *Dinogamasus* are also known to use different geographically-restricted groups of *Xylocopa* as hosts (LeVeque 1930a).

The most comprehensive taxonomic treatment of *Dinogamasus* currently available is that of Lundqvist (1999), in which 38 species were recognized (including eight newly described). Of these, 21 species are known to occur in Asia, including a species recently described from the Middle East (Lundqvist 1999; Joharchi *et al*. 2016). Only two species of *Dinogamasus* have so far been recorded in Thailand—*D. kerrianus* LeVeque and *D. perkinsi*—which were found in Ranong and Trang Provinces (southern Thailand), respectively (see Figure 3).

The main goals of this paper are to describe a new species of *Dinogamasus* based on ten adult females found inside the metasomal pouch of six female *X. tenuiscapa* (Westwood), and to propose a phylogenetic hypothesis for its placement within the *Dinogamasus*' tree of life. To determine that the species described herein is indeed new, we proceeded though an integrative approach to taxonomy, combining standard morphological procedures and DNA barcodes (*i.e.* the 658-bp Folmer fragment of the cytochrome *c* oxidase subunit 1 (COI); see Hebert *et al*. 2003), a practice that has proven very successful when it comes to species delimitation within Acari (*e.g.* Beaulieu *et al*. 2009; Negm & Gotoh 2019; Young *et al*. 2019a). *Dinogamasus saengdaoae* **sp. nov.** is most similar to *D. piperi* and *D. perkinsi*, but it can be easily distinguished from both through the illustrated diagnosis and modified version of Lundqvist's key given below. We also provide DNA barcodes for *X. tenuiscapa* to confirm its identification (as in Sheffield *et al*. 2009; Packer & Ruz 2017) and to compare its intraspecific genetic variation with that of *D. saengdaoae* **sp. nov.**

Materials and Methods

***Morphological methods*.** All specimens of the new *Dinogamasus* species described herein were obtained from six females of *X. tenuiscapa*, which were collected at two different localities in Chiang Mai Province, northern Thailand: the agricultural field of the Faculty of Agriculture of Chiang Mai University (18º 47′ 41.3″ N, 98º 57′ 34.3″ E) (Figure 4) and a private farm in Nong Chom Sub-district, San Sai District (18º 50′ 27.8″ N, 99º 01′ 31.0″ E). The mite holotype and bee specimens are deposited in the Queen Sirikit Botanical Garden, Thailand (QSBG), and the mite paratypes will be deposited in the following repositories: Attasopa Collection at Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Thailand (BCMU); Chulalongkorn University Museum of Natural History, Thailand (CUMZ); Natural History Museum, United Kingdom (NHMUK); Packer Collection at York University, Canada (PCYU).

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FIGURE 4. Type locality of *Dinogamasus saengdaoae* **sp. nov.**: the agricultural field of the Faculty of Agriculture of Chiang Mai University, Chiang Mai Prov., Thailand.

The mites were dissected from the metasomal acarinarium of the bees (Figures 1, 2) with extra fine forceps and then transferred to a container with 70% ethanol until they were further processed. Next, they were immersed in a 10% NaOH solution for 1–2 minutes at 90ºC for clearing and washed with distilled water. The mites were then mounted on microscopy slides with Hoyer's medium under

a Nikon SMZ800 stereomicroscope to facilitate comparative morphological study. All slide-mounted mites were carefully examined under an Olympus CX31 compound microscope and measured with a calibrated ocular micrometer. All measurements are given in micrometers (μm); those of the holotype are shown in bold, followed by ranges (average±SD) calculated from the paratypes (n=9).

The terminology for mite morphology used in this paper is essentially that of Evans (1992), except that we followed Evans (1963a,b) for leg and palp chaetotaxy and Lindquist & Evans (1965) for dorsal and ventral chaetotaxy. Line drawings and maps were prepared using Adobe Illustrator CS6 and then mounted onto plates using Adobe Photoshop CS6.

Molecular procedures and tree estimation. Genomic DNA of mites and bees was extracted using the DNeasy Blood & Tissue Kit (Qiagen, USA) and then stored at -20°C until further processing. DNA concentration of each sample was estimated using a Nanodrop spectrophotometer at 260 nm (ThermoScientific, USA). PCR amplifications of COI were performed in 25 μl reactions using the forward primer LCO1490 (5′ GGTCAACAAATCATAAAGATATTGG-3′) and the reverse primer HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer *et al.* 1994). Thermal cycling conditions were as follows: 94°C for 5 min; 40 cycles of 94°C for 30 sec, 55°C for 30 sec and 72°C for 45 sec; followed by a final extension of 72°C for 7 min. Five μl of PCR products previously mixed with 6× loading dye (New England BioLabs, USA) were loaded onto a 2% agarose gel and then electrophoresed for 40 min at 100 V in TBE buffer. Sequencing of high-quality PCR products was performed by Macrogen Inc. (South Korea).

The resulting COI sequences were compared with their respective trace files and edited manually in BioEdit v.7.2.5 (Hall 1999). They were then checked for stop codons and gaps and trimmed to equal size using MEGA v.7.0.26 (Kumar *et al.* 2016). Then, all sequences were uploaded into GenBank, where they were aligned using the algorithm MUSCLE v.3.6 (Edgar 2004). A maximum likelihood-based analysis of the aligned dataset was performed in PhyML v.3.0 (Guindon *et al.* 2010) through 10,000 bootstrap replicates. This analysis was carried out under a GTR+G model, which was previously suggested as the best one with the program SMS (Lefort *et al*. 2017). *Androlaelaps* sp. and *Varroa destructor* Anderson & Trueman were chosen as outgroups for the ML analysis of the mite dataset, whereas *X. appendiculata* Smith and *X. violacea* (Linnaeus) were chosen as outgroups for the ML analysis of the carpenter-bee dataset (see Table 1 for GenBank accession numbers). The resulting phylogenetic trees were visualized with FigTree v.1.4.3 (Rambaut 2012) and then redrawn using Adobe Illustrator CS6. Pairwise distances within the COI datasets of mites and bees were estimated through the Kimura 2-parameter model (Kimura 1980) with a gamma distribution in MEGA. COI haplotype networks of mites and bees (outgroups excluded) were constructed using TCS network methods (Clement *et al.* 2002) in the program PopArt (Leigh & Bryant 2015).

Parsimony analysis. We added *D. saengdaoae* **sp. nov.**, as well as the recently described *D. kazerunensis* Joharchi, Khodaparast & Moghadam, to the morphological dataset matrix (Table 3) provided by Lundqvist (1999) and then conducted a parsimony analysis in the program TNT v.1.5 (Goloboff *et al*. 2003, 2008; Goloboff & Catalano 2016). Trees were estimated through 'New Technology search' using the Ratchet, Drift and Tree fusing. We performed 1,000 replications with 'driven search' with the option 'find minimum length' set to 100. Consistency and retention indexes (CI and RI, respectively) were calculated with the 'stats' script (available at http://tnt.insectmuseum.org/index.php/scripts). As in Lundqvist (1999), all characters were treated as non-additive (except characters 1, 9 and 12) and group support was estimated by the percentage of times that a given clade was found among the most parsimonious trees. Final cladogram was edited in WinClada v.1.0.8 (Nixon 2002) and Adobe Photoshop v.13.0.1.

TABLE 1. Voucher and GenBank accession numbers of the taxa included in our ML analyses of COI data.

Taxa	Specimen no.	GenBank accession no.	Reference
Mite sequences			
Dinogamasus saengdaoae **sp. nov.**	CMUD_B01	MW070023	this study
Dinogamasus saengdaoae **sp. nov.**	OKJD_B01	MW070024	this study
Dinogamasus saengdaoae **sp. nov.**	OKJD_B02	MW070025	this study
Dinogamasus saengdaoae **sp. nov.**	OKJD_B03	MW070026	this study
Dinogamasus saengdaoae **sp. nov.**	OKJD_B04	MW070027	this study
Dinogamasus saengdaoae **sp. nov.**	OKJD_B05	MW070028	this study
Dinogamasus saengdaoae **sp. nov.**	OKJD_B06	MW070029	this study
Androlaelaps sp. (outgroup)	n/a	MH983812.1	Young *et al*. (2019a)
Varroa destructor (outgroup)	n/a	MN360198.1	Young *et al*. (2019b)
Bee sequences			
Xylocopa tenuiscapa	CMUX_01	MW065795	this study
Xylocopa tenuiscapa	OKJX_01	MW065796	this study
Xylocopa tenuiscapa	OKJX_02	MW065797	this study
Xylocopa tenuiscapa	OKJX_03	MW065798	this study
Xylocopa tenuiscapa	OKJX_04	MW065799	this study
Xylocopa tenuiscapa	OKJX_05	MW065800	this study
Xylocopa tenuiscapa	OKJX_06	MW065801	this study
Xylocopa appendiculata (outgroup)	n/a	KX494104.1	Zheng *et al*. (2018)
Xylocopa violacea (outgroup)	n/a	HM401101.1	Schmidt *et al*. (2015)

Results

Dinogamasus saengdaoae **Attasopa & Ferrari, sp. nov.**

(Figures 5–21)

Diagnosis (female)

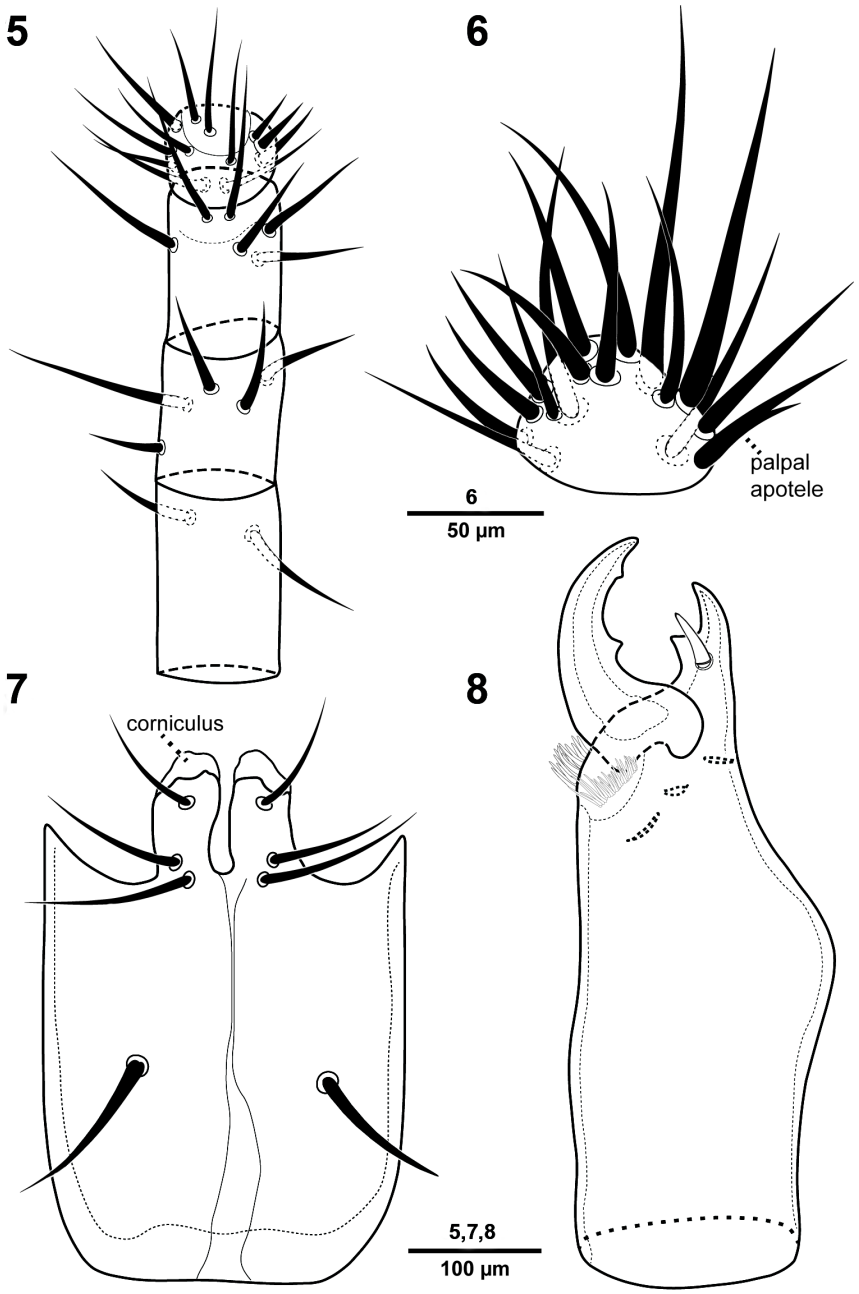
Setae *h1* usually shorter than palpcoxal setae. Dorsal schizodorsal with a pair of deep notches laterally, shield not covering posterior and lateral margins of opisthosoma. Opisthonotal soft cuticle with one pair of distinct setae posteriorly. Sternal shield U-shaped posteriorly, setae *st2* off the shield. Peritrematral shield fused with a projection of dorsal shield. Opisthogastric cuticle hypertrichous with 5–8 pairs of relatively long setae between genital and anal shields. Anal shield narrowing posteriorly. Genu I with six conical setae (*ad3*, *pd1–pd3*, *pl1*, *pl2*); tibia I with four conical setae (*ad3*, *pd2*, *pl1*, *pl2*).

Description

Female

Gnathosoma (Figures 5–8). Movable digit of chelicerae curved and bearing two teeth, larger tooth located medially, smaller tooth near apex; fixed digit of chelicerae with a large tooth adjacent to pilus dentilis; fixed digit ~0.75x as long as movable digit; seta *h1* shorter than palpcoxal seta, seta *h1* length **125**/113–132 (122±7); palpcoxal seta **137**/132–149 (138±6); corniculus short, apex slightly crenelate; palpal setal formula 2-5-6-12-15; palptibia with narrow setiform setae.

Dorsal idiosoma (Figure 9). Dorsal shield length **2587**/2646–2989 (2871±115) and maximum width **1813**/1764–1940 (1862±62); dorsal shield with deep lateral notches behind podonotal region, not covering posterior and lateral margins of opisthosoma, podonotal region of shield slightly extending ventrally, with reticulate ornamentation throughout and hypertrichous (except podonotal area with less setae medially), seta *j1* longest, length **196**/167–245 (199±21), other setae shorter overall, length 60–180. Opisthonotal soft cuticle with **26**/20–26 (23±2) pairs of setae, **78**/59–83 (74±9) long, and bearing one pair of long setae, 127/137–176 (148±13) long.



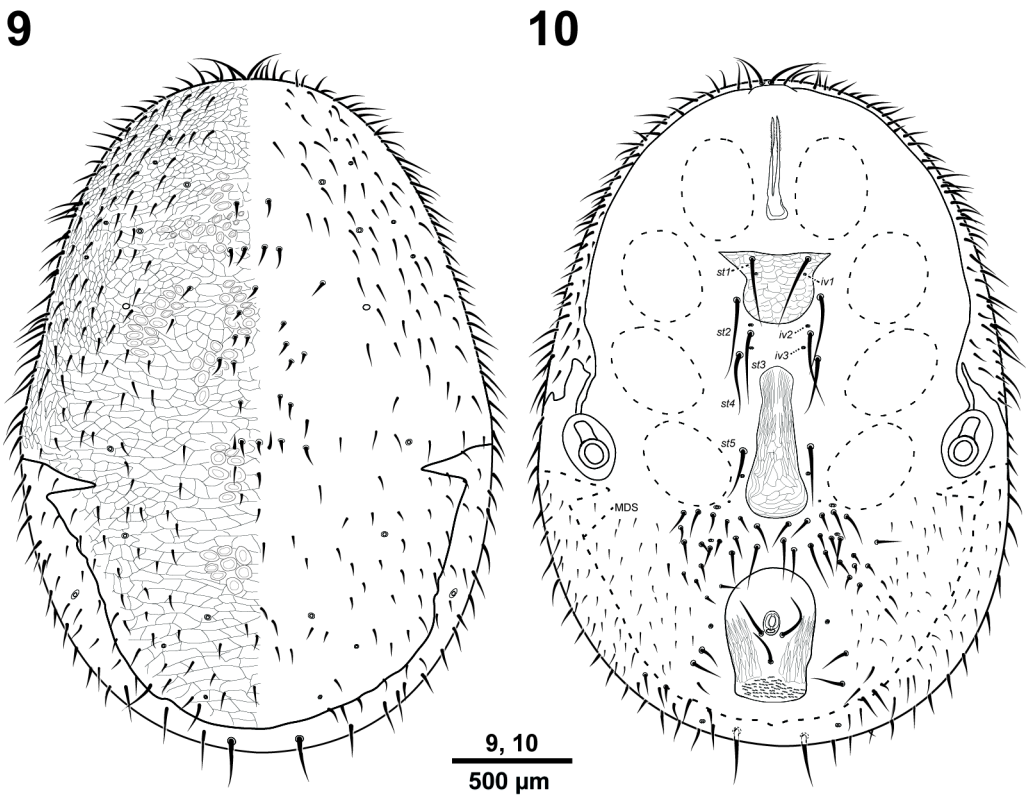
FIGURES 5–8. *Dinogamasus saengdaoae* **sp. nov.**, gnathosoma of the female holotype. 5. Palp trochanter—tibia, dorsal view; 6. Palp tarsus, dorsal view; 7. Subcapitulum; 8. Chelicerae, lateral view.

Ventral idiosoma (Figure 10). Tritosternum well developed with a broad base, **110**/102–113 (108±4) long, **85**/83–105 (92±0.7) wide at base, having a pair of long pilose laciniae, length free for **314**/294–353 (309±19). Presternal platelets absent. Sternal shield with areolate ornamentation, length **284**/255–353 (287±28), anterior margin slightly emarginate and **431**/382–441 (409±18) in length, lateral margin strongly emarginate on its anterior 2/5, area below emargination almost U-shaped, poroid *iv1* minute and rounded, located below base of seta *st1*. Seta *st1* shorter than setae *st2–st4*, **240**/235–314 (265±25) long; seta *st2* located in soft cuticle, **265**/265–392 (311±39) long [small part of sternal shield protruded laterally and attaining to setae *st2* in paratypes OKJD_02, OKJD_06, and OKJD_08]; seta *st3* **294**/255–363 (301±30) long, *st4* **225**/225–294 (250±19) long; poroids *iv2* and *iv3* subellipsoidal and horizontally oriented, both slightly larger than *iv1*, poroid *iv2* located on soft cuticle between base of setae *st2* and *st3*, *iv3* located between base of *st3* and *st4*; distance between setae *st1* **216**/196–235 (219±14), distance between setae *st2* **323**/304–353 (331±17); distance between setae *st3* **245**/216–274 (242±19); distance between setae *st4* **323**/265–373 (313±31); distance between setae *st1* and *st2* **137**/132–171 (153±12). Metasternal platelets absent. Genital shield broader posteriorly, **637**/627–676 (647±18) long, and maximum width **274**/265–304 (281±14), genital seta (*st5*) length **245**/216–284 (242±22) [one side of genital shield with 2x more setae than other side in paratypes CMUD_02 and OKJD_02 (additional setae more anteriad than others in relation to the shield)]; paragenital poroids subellipsoidal and horizontally oriented, located below base of seta *st5*. Opisthogastric soft cuticle between genital and anal shields with **5**/5–8 (6±2) pairs of setae. Peritrematral shield narrowly connected with dorsal shield at level of coxa III; peritrematral atrium length **314**/299–343 (326±16) and width **216**/206–245 (232±11). Anal shield longer than wide, length **490**/421–519 (474±29) and maximum width **323**/294–353 (326±21), and posterior margin of the shield **250**/235–294 (263±18) in length, shield slightly narrowing posteriorly, anal opening ellipsoidal and vertically oriented located just above midlength of shield, adenal setae inserted at posterior level of anal opening, **147**/142–206 (172±22) long, almost as long as postanal seta **142**/147–216 (182±25).

Legs (Figures 11–21). Coxae I–III, 0 0/1 0/1 0, with pointed bulbiform setae; coxa IV 0 0/1 0/0 0, with a single pointed bulbiform seta (Figure 11). Trochanter I, 1 1/1 0/2 1, with setiform setae, *al*, *av*, *pv1*, *pl* short, *al* shortest, *pv2* longest (Figure 11); trochanters II–IV with setiform and slightly thickened setae, trochanters II–III, 1 0/1 0/2 1, trochanter IV, 1 1/1 0/2 0 (Figure 11). Femur I, 2 3/1 3/3 1, with setiform setae, *ad1–ad3*, *pd1–pd3* moderately long and slightly thickened setae (Figure 12); femur II, 0 3/1 2/2 1, with setiform setae (short setiform seta: *ad2*, *ad3*; moderately long and slightly thickened setae: *ad1*, *av*, *pd1*, *pd2*, *pv1*, *pv2*) (Figure 13); femur III, 1 2/1 1/1 1, with moderately long and thickened setae (except *ad2*, short) (Figure 14); femur IV, 1 2/1 1/1 1, with thick setiform setae, *ad2* short. Genu I, 2 3/2 3/1 2, with six modified setae (blunt conical setae: *ad3*, *pd1–pd3*, *pl1*, *pl2*; *pl1* longer than the other conical setae), remaining setae setiform (Figure 15) [setae *ad1* and *ad2* of genu I in paratypes OKJD_07 and OKJD_08 shorter and thicker than those of holotype]; genu II, 2 3/1 2/1 2, with setiform setae (*ad1–ad3* shorter than others), *av* and *pv* thick and apically pointed (Figure 16); genu III, 2 2/1 2/1 2, with moderately long and thickened setae, setae *pd1* and *pd2* shorter than others (Figure 17); genu IV, 2 2/1 3/1 2, setiform, moderately long and thickened setae. Tibia I, 2 3/2 3/1 2, with four modified setae (conical setae: *ad3*, *pd3*, *pl1*, *pl2*; *ad3* slightly pointed, the latter three blunt), seta *pl1* the longest among modified setae, remaining setae setiform, seta *pd2* the shortest among setiform setae (Figure 18); tibia II, 2 2/1 2/1 2, with setiform setae (moderately long and thickened setae: *av* and *pv*), seta *ad2* the shortest (Figure 19); tibia III, 2 1/1 2/1 2, with setiform setae (moderately long and thickened setae: *al1*, *al2*, *av*, *pl1*, *pl2*, *pv*), *pd1* and *pd2* subequal in length and shorter than others (Figure 20); tibia IV, 2 2/1 3/1 2, setiform moderately long and thickened setae, *pd1* the shortest. Tarsi II–IV, 3/2 3/2 3 + mv and md; tarsus II with three blunt conical setae (1st near apex posterolaterally, 2nd just below 1st midlength ventrally,

3rd on half laterally), and a seta with broad base located just above 3rd conical seta medioventrally (Figure 21); tarsi III–IV with long thin setiform setae. Pre-tarsi I–IV bearing ambulacrum and pair of claws.

Male. Unknown.

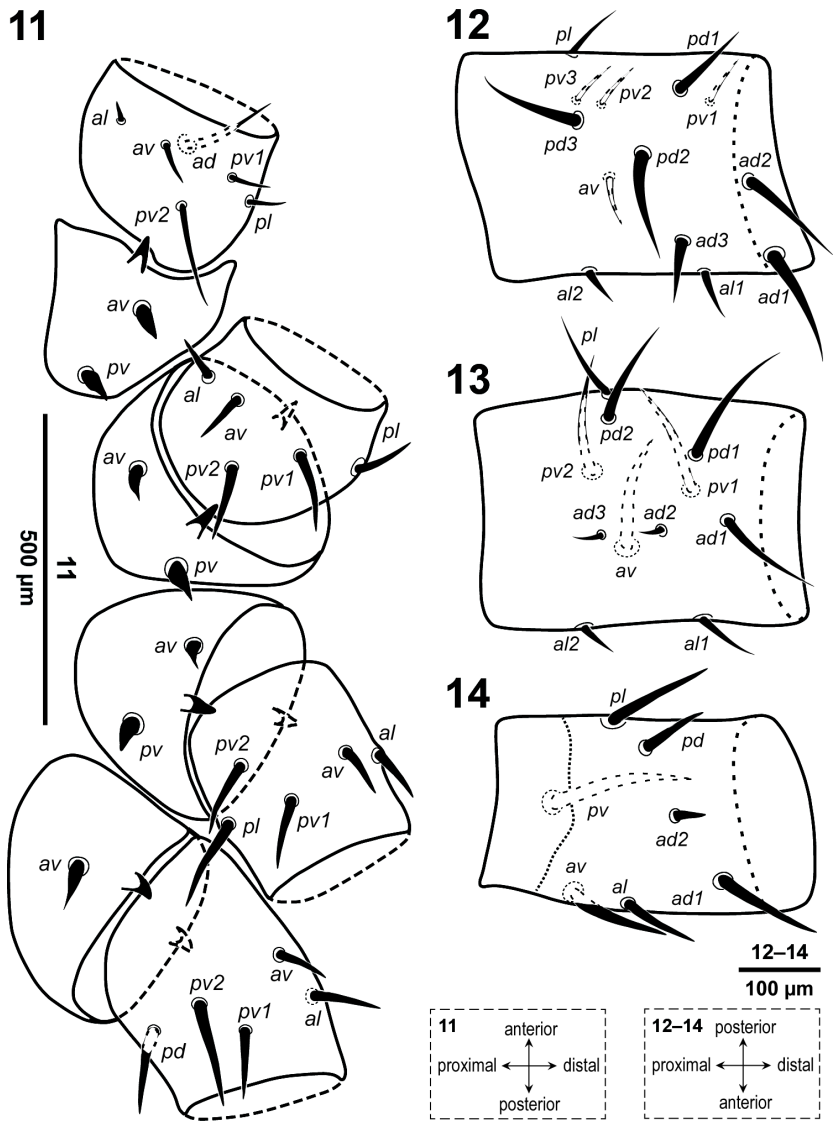


FIGURES 9–10. *Dinogamasus saengdaoae* **sp. nov.**, holotype female. 9. Dorsal view of idiosoma; 10. Ventral view of idiosoma. MDS: margin of dorsal shield.

Type material

Holotype ♀ (specimen no. CMUD_01): Agricultural field of Faculty of Agriculture (18º 47′ 41.3″ N, 98º 57′ 34.3″ E), Chiang Mai University, Chiang Mai Prov., THAILAND; 13 Feb. 2020, Namthip Leksingto coll.; K. Attasopa prep. det. [QSBG]; bee host: *X. tenuiscapa* (specimen no. CMUX_01) [QSBG].

Paratypes: 3♀♀ (specimens no. CMUD_02, CMUD_03 and CMUD_04) with the same labels as the holotype [BCMU]. 5 ♀♀ (specimens no. OKJD_01, OKJD_05, OKJD_06, OKJD_07 and OKJD_08), Ohkajhu farm (18º 50′ 27.8″ N, 99º 01′ 31.0″ E), Nong Chom Sub-district, San Sai District, Chiang Mai Prov., THAILAND; 30 May 2020, N. Hankeereerat & K. Attasopa coll., K. Attasopa prep. det.; bee host: *X. tenuiscapa* (specimens no. OKJX_01, OKJX_05, OKJX_06, OKJX_07 and OKJX_08, respectively) [BCMU]. All remaining paratypes with the same labels as the previous specimens, except as follows: 1 ♀ (specimen no. OKJD_02); bee host: *X. tenuiscapa* (specimen no. OKJX_02) [CMUZ]. 1 ♀ (specimen no. OKJD_03); bee host: *X. tenuiscapa* (specimen no. OKJX_03) [PCYU]. 1 ♀ (specimen no. OKJD_04); bee host: *X. tenuiscapa* (specimen no. OKJX_04) [NMNH].



FIGURES 11–14. *Dinogamasus saengdaoae* **sp. nov.**, female holotype. 11. Coxae I–IV and trochanters I–IV, ventral view; 12–14. Femora I–III, dorsal view.

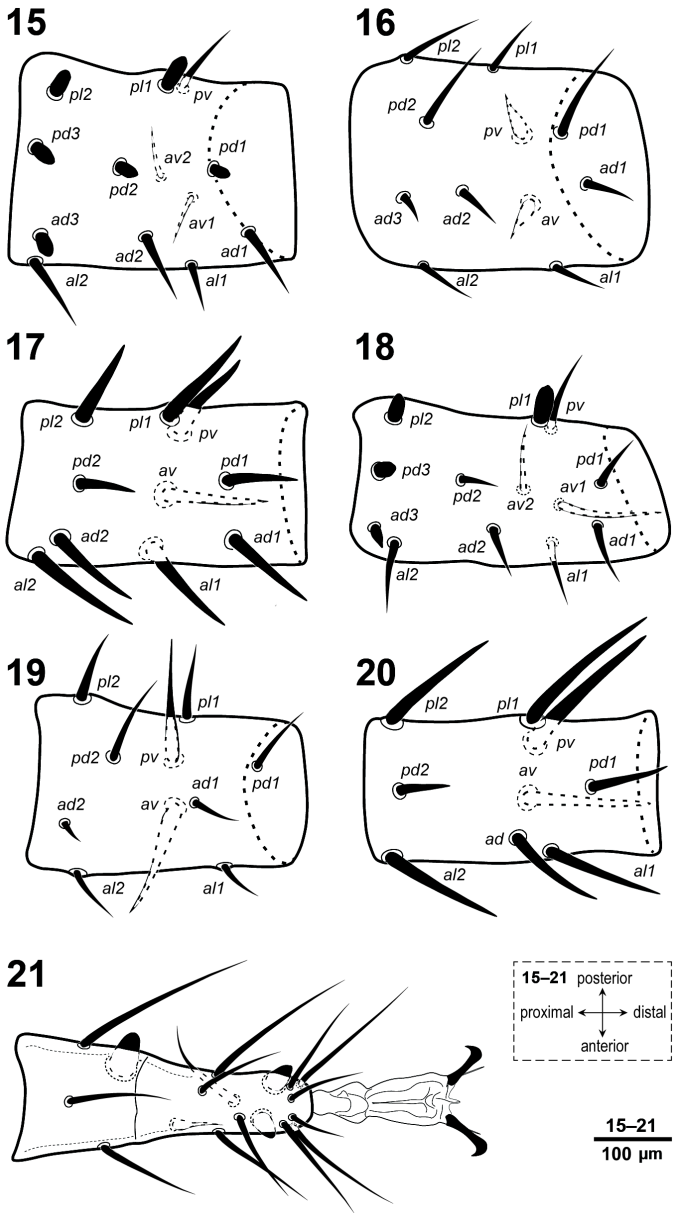
Barcoded material

Mites: 1♀ (specimen no. CMUD_B01) obtained from CMUX_01's acarinarium (the same host of the holotype). 6♀♀ (specimens no. OKJD_B01, OKJD_B02, OKJD_B03, OKJD_B04, OKJD_B05 and OKJD_B06) obtained from acarinaria of OKJX_01, OKJX_02, OKJX_03, OKJX_04, OKJX_05, OKJX_06, respectively.

Bees: 7♀♀ (specimens no. CMUX_01, OKJX_01, OKJX_02, OKJX_03, OKJX_04, OKJX_05 and OKJX_06).

Etymology

The species is named after H.B.'s wife, Saengdao Bänziger, in recognition of her long-time professional collaboration with him, especially in computational matters.



FIGURES 15–21. *Dinogamasus saengdaoae* **sp. nov.**, female holotype, left legs. 15–17. Genua I–III, dorsal view; 18–20. Tibae I–III, dorsal view; 21. Tarsus II, ventral view.

Differential diagnosis

The adult female *D. saengdaoae* **sp. nov.** (the male remains unknown) can be differentiated from the other species of the genus, except *D. perkinsi* and *D. piperi*, by its unique sternal shield, which is U-shaped posteriorly and bears only setae *st1*, setae *st2* off the shield (Figure 10). However, it can also be easily distinguished from both *D. perkinsi* and *D. piperi* by opisthonotal soft cuticle bearing one pair of long and distinct setae posteriorly (Figures 9, 10) (opisthonotal soft cuticle without these setae in the other two species). *Dinogamasus saengdaoae* **sp. nov.** is also distinct from *D. kerrianus*, *D. perkinsi*, and *D. philippinensis* by the different number of the modified setae on genu and tibia I, as the new species have six conical setae (*ad3*, *pd1–pd3*, *pl1*, *pl2*) on genu I (Figure

15) and four conical setae (*ad3*, *pd2*, *pl1*, *pl2*) on tibia I (Figure 18) vs. genu I and tibia I with three conical setae (*ad3*, *pd3*, *pl2*) in *D. kerrianus* and *D. perkinsi*, and with 4–5 (*ad3*, *pd3*, *pl1*, *pl2*, (*pd2*)) and three (*pd2*, *pl1*, *pl2*) conical setae, respectively, in *D. philippinensis*. The new species can be further differentiated from both *D. piperi* and *D. philippinensis* by the dorsal shield not covering dorsal opisthosoma neither laterally nor posteriorly (the dorsal shield covering dorsal opisthosoma entirely in *D. piperi*, with a pair of short lateral notches, and covering its posterior margin in *D. philippinensis*). The new species also differs from *D. perkinsi* by having setae *h1* (113–132) shorter than palpcoxal setae (132–149) (Figure 7); according to Lundqvist (1999), setae *h1* (96–128) are longer than those on palpcoxa (76–102) in *D. perkinsi*.

Notes

In this study, most *X. tenuiscapa* bees were collected while visiting flowers of sunn hemp (*Crotalaria juncea* L.). Although the bees had several individuals of *D. saengdaoae* **sp. nov.** in their acarinarium, none of them seemed to be being harmed by the presence of the mites, at least as far as their foraging behavior is concerned.

Modification of Lundqvist's (1999) key to permit identification of *D. saengdaoae* sp. nov.
Note: Couplet 23 is herein modified as follows:

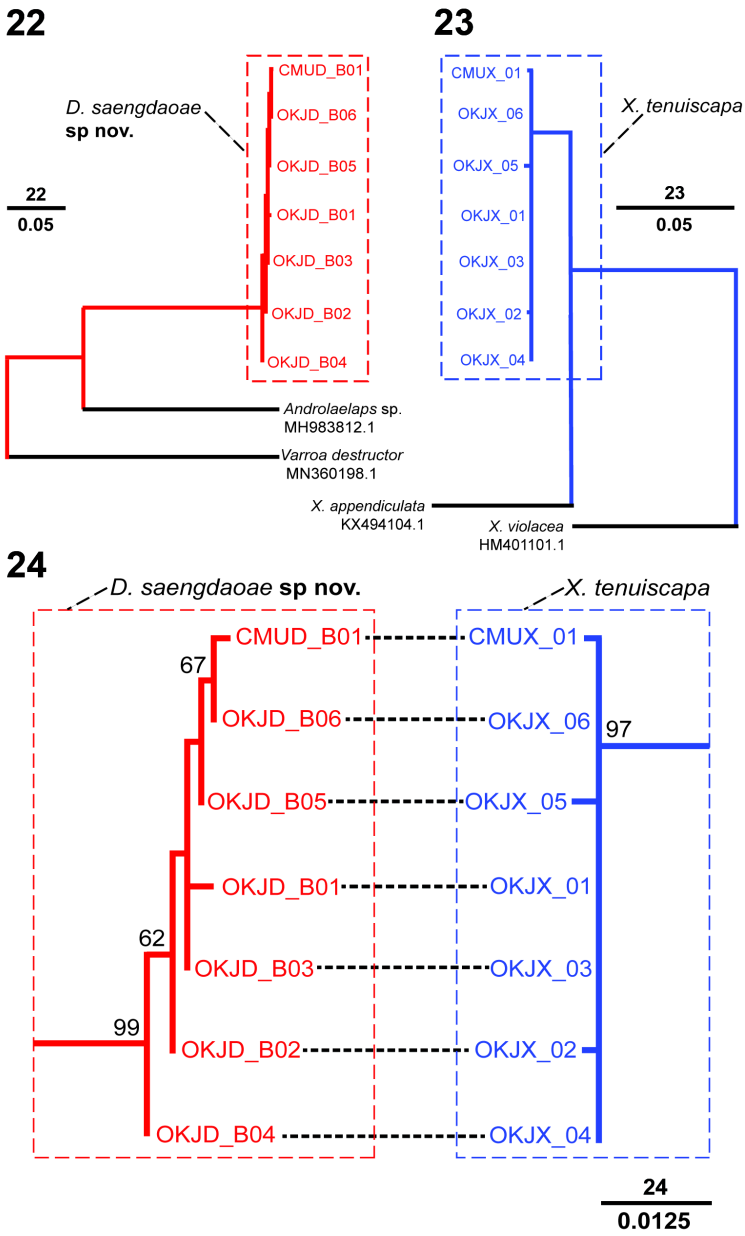
23A(21) Anal shield evenly broad throughout (Lundqvist 1999: figure 83f); genu & tibia I each with three conical setae (*ad3*, *pd3*, *pl2*) (Lundqvist 1999: figure 83c) . . . . . .*D. perkinsi* (Oudemans)
- Anal shield narrowing posteriorly (Figure 10); genu I with six (*ad3*, *pd1–pd3*, *pl1*, *pl2*; Figure 15) and tibia I with four conical setae (*ad3*, *pd2*, *pl1*, *pl2*; Figure 18) 23B

23B(23A) Dorsal shield covering idiosoma entirely; opisthonotal area without long setae posteriorly (LeVeque 1930a: figure 3a) . . . . . *D. piperi* LeVeque
- Dorsal shield covering idiosoma neither laterally nor posteriorly; opisthonotal area with long setae posteriorly (Figure 9) . . . . . *D. saengdaoae* **sp. nov.**

***Molecular results*.** In total, we successfully amplified and sequenced the COI of seven *D. saengdaoae* **sp. nov.** as well as seven *X. tenuiscapa* hosts. After alignment and trimming of the sequences, we generated a DNA dataset with a final length of 658 aligned base pairs for both species.

The results revealed that each sequenced individual of *D. saengdaoae* **sp. nov.** belongs to a different haplotype. They nonetheless formed a strongly-supported monophyletic group (99% bootstrap value) in our ML analysis (Figures 22–24). In turn, the sequenced individuals of *X. tenuiscapa* were shown to belong to four different haplotypes (Figure 25). The calculated pairwise distances in COI within the two species are tabulated in Table 2. Overall, the intraspecific variation of *D. saengdaoae* **sp. nov.** (0.2–0.9%) was greater than that of its bee host (0–0.5%).

***Parsimony results*.** Our parsimony analysis in TNT yielded 264 equally most parsimonious trees with 164 steps each (CI = 0.274 and RI = 0.593). The calculated majority-rule consensus tree is shown in Figure 26. According to our phylogenetic results, *D. saengdaoae* **sp. nov.** constitutes a strongly-supported clade alongside *D. perkinsi* and *D. piperi*, even though the relationships among the three species could not be resolved (Figure 26). The monophyly of the clade, which is sister to the remaining species of the genus, is supported by four homoplastic characters: (1) dorsal shield 1800–2200 µm in length (character 1, state 1 > 3); (2) palptibia with one or more modified setae (character 8, state 0 > 1, Figure 5); (3) sternal shield with a single pair of sternal setae (character 10, state 1 > 2, Figure 9); and (4) seta *st1* relatively long, reaching the insertion of seta *st3* (character 13, state 0 > 1, Figure 9). Our analysis placed *D. phillipinensis* as sister to *D. tonkinensis* Lundqvist plus *D. assimiensis* Lundqvist, thus rending the *D. perkinsi* group (*sensu* LeVeque) paraphyletic.



FIGURES 22–24. Resulting trees from ML analyses of the COI datasets of *Dinogamasus saengdaoae* sp. nov.(red line) and *Xylocopa tenuiscapa* (blue line). 22. *D. saengdaoae* sp. nov. 23. *X. tenuiscapa*. 24. Tangled plot constructed from the clades within the dashed line rectangles of Figures 22, 23. Numbers above internodes are bootstrap values (values < 50% not shown).

Discussion

In this paper, we resorted to traditional methods in alpha-taxonomy and a ML analysis of newly-generated COI sequence data to describe a new species of *Dinogamasus* from northern Thailand. *Dinogamasus saengdaoae* **sp. nov.** was unequivocally an undescribed species as shown by a unique set of morphological features exhibited by the female (regrettably, no males were available for study; see 'Diagnosis' above). Moreover, the sequenced specimens of *D. saengdaoae* **sp. nov.** were

recovered as a well-supported monophyletic group in our ML analysis (Figures 22–24). On the other hand, we must emphasize that the outgroups (*Varroa* and *Androlaelaps*) used in the analysis are both relatively distant allies of *Dinogamasus*, and therefore the monophyly of *D. saengdaoae* **sp. nov.** in the resulting ML tree is but an obvious outcome and thus should be interpreted with caution. A rigorous assessment of whether this new species comprises a monophyletic taxonomic unit or not would necessarily need to include a more comprehensive sampling of *Dinogamasus*, with special attention to the *D. perkinsi* group (as understood herein). However, there unfortunately is no COI sequence of *Dinogamasus* available on GenBank currently, which renders the dataset provided herein an important step towards the construction of a more comprehensive genetic library for the genus.

TABLE 2. Pairwise-distance estimations based on COI data. 1–7: *Dinogamasus saengdaoae* **sp. nov.**; a–g: *Xylocopa tenuiscapa*; 8–9 and h–i: outgroups. Distances and standard errors are shown below and above the blank diagonals, respectively.

Mite sequences	**1)**	**2)**	**3)**	**4)**	**5)**	**6)**	**7)**	**8)**	**9)**
1) CMUD_B01		0.003	0.003	0.003	0.004	0.002	0.001	0.026	0.032
2) OKJD_B01	0.008		0.003	0.002	0.003	0.003	0.003	0.026	0.032
3) OKJD_B02	0.006	0.005		0.001	0.002	0.002	0.003	0.026	0.033
4) OKJD_B03	0.005	0.003	0.002		0.003	0.002	0.002	0.026	0.032
5) OKJD_B04	0.009	0.008	0.003	0.005		0.003	0.003	0.026	0.032
6) OKJD_B05	0.003	0.005	0.003	0.002	0.006		0.001	0.026	0.032
7) OKJD_B06	0.002	0.006	0.005	0.003	0.008	0.002		0.026	0.032
8) MH983812.1	0.254	0.254	0.252	0.254	0.249	0.254	0.257		0.033
9) MN360198.1	0.322	0.322	0.329	0.326	0.322	0.322	0.325	0.322	
Bee sequences	**a)**	**b)**	**c)**	**d)**	**e)**	**f)**	**g)**	**h)**	**i)**
a) CMUX_01		0.002	0.002	0.002	0.002	0.003	0.002	0.011	0.017
b) OKJX_01	0.002		0.001	0.000	0.000	0.002	0.000	0.011	0.017
c) OKJX_02	0.003	0.002		0.001	0.001	0.003	0.001	0.011	0.017
d) OKJX_03	0.002	0.000	0.002		0.000	0.002	0.000	0.011	0.017
e) OKJX_04	0.002	0.000	0.002	0.000		0.002	0.000	0.011	0.017
f) OKJX_05	0.005	0.003	0.005	0.003	0.003		0.002	0.012	0.017
g) OKJX_06	0.002	0.000	0.002	0.000	0.000	0.003		0.011	0.017
h) KX494104.1	0.066	0.066	0.068	0.066	0.066	0.070	0.066		0.019
i) HM401101.1	0.131	0.131	0.133	0.131	0.131	0.133	0.131	0.150	

The re-analysis of Lundqvist's (1999) dataset with the inclusion of *D. saengdaoae* **sp. nov.** allowed us to conclude that this new species is phylogenetically closely related to both *D. perkinsi* and *D. piperi*, although this is not surprising, given the notable morphological similarities shared by the three species. Nor it is surprising the fact that they herein formed a clade without the fourth member of the *D. perkinsi* group, *D. phillipinensis*, which was placed in a clade of relatively late divergence, as previously found by Lundqvist (1999). This result implies that the *D. perkinsi* group, as originally proposed by LeVeque (1930a), is paraphyletic as far as Lundqvist's data are concerned. Although LeVeque provided the morphological basis for the establishment of the group, the author was also able to find a series of characteristics that clearly differentiates *D. phillipinensis* from both *D. perkinsi* and *D. piperi* (*e.g.* dorsal shield covered with moderately long hairs in the former but

covered with short hairs in the two latter; see also LeVeque 1930a: 3), which are herein shown to also apply to *D. saengdaoae* **sp. nov.**

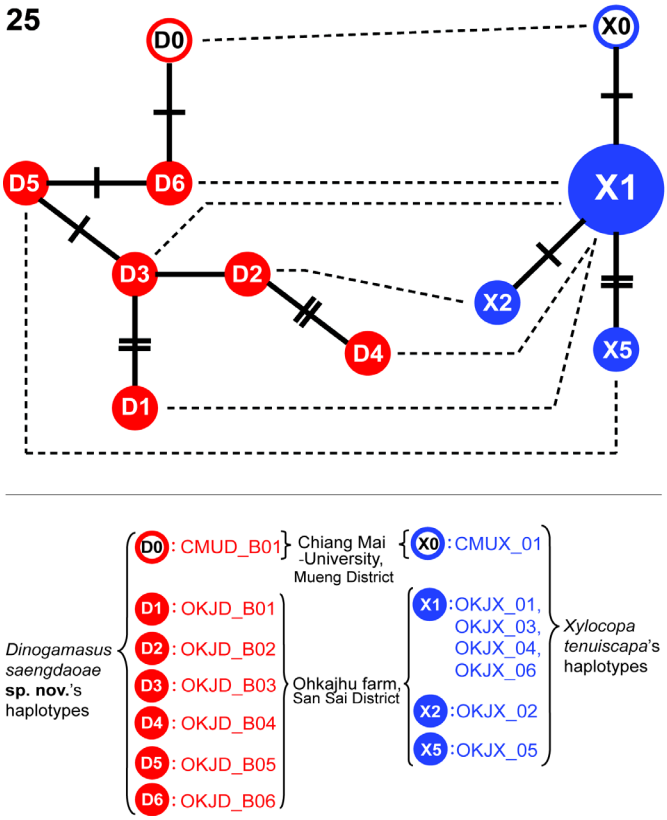


FIGURE 25. COI haplotype networks of *Dinogamasus saengdaoae* **sp. nov.** (red circles) and their hosts of *Xylocopa tenuiscapa* (blue circles).

Although the peculiar metasomal acarinarium found in some species of *Xylocopa* was firstly noted almost two centuries ago (Brilman in 1839; see LeVeque 1930b), the relationships between mites and their carpenter bee hosts remain little understood. Various authors have suggested commensalism, mutualism, or even parasitism (see below). Whereas this may be partly due to a lack of consensus regarding the terminology commonly used in the field, the main reason seems to rest in the complexity of the associations and the difficulty in studying them. LeVeque (1930b) assumed that *Dinogamasus* mites feed upon excess pollen in the nest galleries of *Xylocopa* in South Africa, thus implying they are commensals. Skaife (1952) showed that larvae of *D. braunsi* Vitzthum feed off the exudations of pupae of the carpenter bee *X. caffra* (Linnaeus) and concluded that the host bees are neither harmed nor benefit from such association. However, it has been shown that *Dinogamasus* may also be mildly parasitic on the immature bees (Watmough 1974; Madel 1975; Gerling *et al.* 1989). It appears safe to assume that the development of such a specialized structure, as the acarinarium, must be advantageous for the hosts, hence some form of mutualism should be expected. In a notable case involving *Allodynerus delphinalis* (Giraud), a wasp that also has an acarinarium, it was demonstrated that the mites *Ensliniella parasitica* (Vitzthum) protect their hosts' immature forms by attacking the parasitoid wasp *Melittobia acasta* (Walker) (Okabe & Makino 2008). In another study, laelapid mites were shown to keep nests of halictid bees clean by controlling fungal contamination (Biani *et al.* 2009), although in this case the host bees do not have an acarinarium.

Interestingly, it has long been known (*e.g.* Lundström 1887) that plants also developed analogous structures to bee acarinaria to shelter mites, termed acarodomatia. They consist of depressions partly covered with hairs, which are found on the vein axils located on the abaxial side of leaves. For example, predatory mites have been found in acarodomatia of *Viburnum tinus* L. (Parolin *et al*. 2011). A review of positive, neutral and negative associations between vertebrate and invertebrates, plants, fungi and microorganisms in Central European ecosystems has been recently published (Gigon 2020).

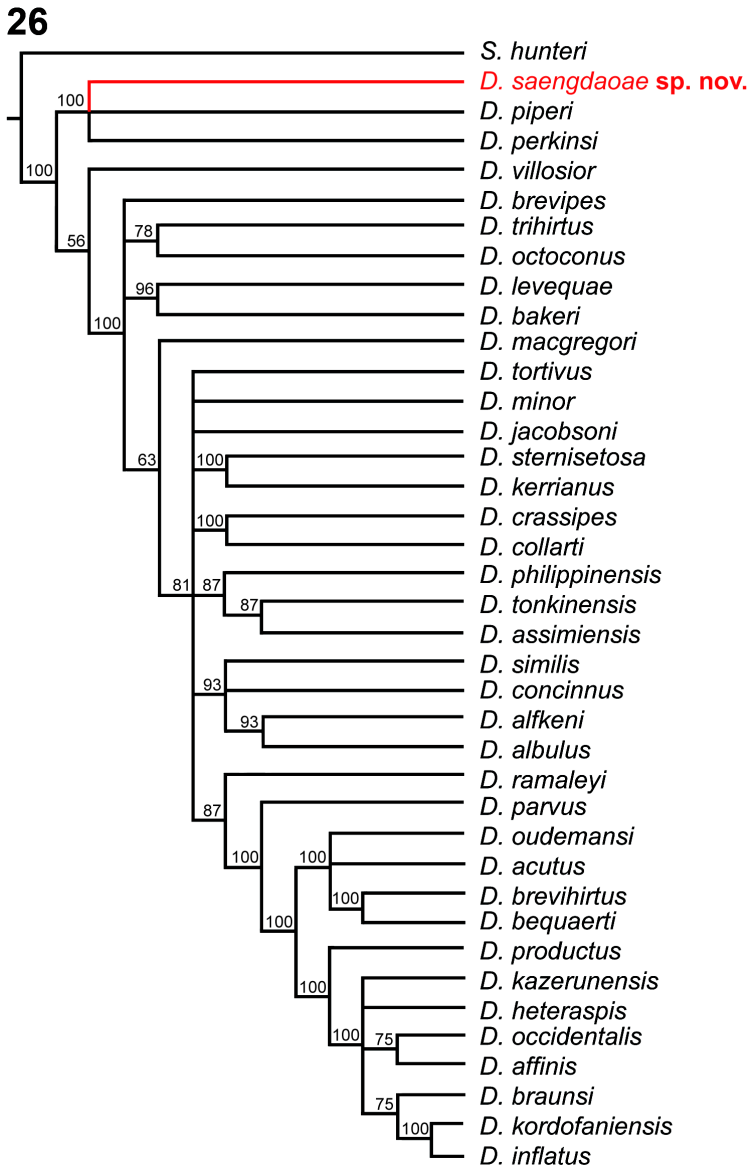


FIGURE 26. Majority-rule consensus tree obtained from the parsimony analysis of Lundqvist's (1999) morphological dataset with the inclusion of *Dinogamasus saengdaoae* **sp. nov.** (red branch). and *D. kazerunensis*. Numbers above internodes represent the percentage of times that corresponding clades were found among the most parsimonious trees.

TABLE 3. Character matrix used in our parsimony analysis of *Dinogamasus*. ? = missing data.

Species	Characters																			
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
S. hunteri	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1
D. acutus	1	1	1	0	0	0	1	1	2	1	0	1	1	1	0	1	0	1	0	0
D. affinis	1	0	1	0	0	0	0	0	2	1	1	1	1	1	0	0	0	0	0	0
D. albulus	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1	0	0
D. alfkeni	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
D. assimiensis	2	1	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	1	1	0
D. bakeri	1	1	1	1	0	1	0	1	1	1	0	01	1	0	1	1	0	1	0	0
D. bequaerti	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	1	0	0
D. braunsi	1	1	1	1	0	1	1	1	2	1	1	1	1	1	0	0	1	0	0	0
D. brevihirtus	1	1	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	1	0	0
D. brevipes	1	0	0	0	0	1	0	0	1	1	0	01	0	1	0	0	0	0	0	0
D. collarti	3	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0
D. concinnus	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
D. crassipes	4	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0
D. heteraspis	2	1	0	0	0	0	0	1	2	1	0	1	1	1	0	1	1	0	0	0
D. inflatus	1	1	0	0	1	1	0	0	2	1	0	1	1	1	0	0	1	0	0	0
D. jacobsoni	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
D. kazerunensis	2	0	1	0	0	0	0	1	2	1	0	1	1	1	0	1	1	0	1	0
D. kerrianus	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0
D. kordofaniensis	1	1	0	1	1	1	0	1	2	1	0	01	1	0	0	0	1	0	0	0
D. levequae	2	1	0	0	0	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0
D. macgregori	1	1	0	0	0	0	0	0	0	1	0	12	0	0	1	0	0	1	0	0
D. minor	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0
D. occidentalis	1	1	1	1	0	0	0	1	2	1	1	1	1	1	0	1	0	0	0	0
D. octoconus	1	1	1	1	1	1	0	0	0	1	0	12	0	0	1	0	0	1	0	1
D. oudemansi	0	1	1	0	0	0	1	1	1	1	0	1	1	1	0	1	0	1	0	0
D. parvus	0	1	1	0	0	0	0	0	1	1	0	01	1	1	0	1	0	1	0	0
D. perkinsi	3	1	0	0	1	1	0	1	0	2	0	012	1	0	0	0	0	1	1	0
D. philippinensis	2	1	1	0	0	0	0	1	1	1	0	01	1	1	0	1	0	1	1	0
D. piperi	3	1	0	0	1	1	0	1	1	2	0	2	1	0	0	0	0	1	0	0
D. productus	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0
D. ramaleyi	1	1	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	0
D. saengdaoae **sp.nov.**	4	1	0	0	1	1	0	1	0	2	0	12	1	0	0	2	0	1	0	0
D. similis	1	1	1	0	0	0	0	0	0	1	0	012	1	0	0	0	0	1	0	0
D. sternisetosa	2	1	0	0	0	0	0	0	0	1	1	01	1	1	0	0	0	1	0	0
D. tonkinensis	2	1	1	0	0	0	1	1	0	1	0	01	1	1	0	1	0	1	1	0
D. tortivus	1	1	1	1	0	0	0	0	0	2	1	01	1	1	0	1	0	1	0	0
D. trihirtus	0	1	1	1	1	1	0	0	1	1	0	1	0	0	1	0	0	1	0	0
D. villosior	1	1	1	0	1	1	0	0	2	1	0	1	0	0	0	1	0	1	0	0

.....continued on the next page

TABLE 3. (Continued)

Species	Characters															
	21	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**
S. hunteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D. acutus	1	1	2	1	0	0	0	1	1	1	1	1	0	0	2	0
D. affinis	1	1	2	0	1	1	0	1	1	1	1	1	0	0	2	0
D. albulus	0	0	1	0	0	0	0	1	1	1	1	0	0	0	2	0
D. alfkeni	0	0	1	0	0	0	0	1	1	1	1	0	0	0	2	0
D. assimiensis	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0
D. bakeri	0	0	1	0	0	0	1	1	1	1	1	0	0	0	2	0
D. bequaerti	1	1	2	1	0	1	0	1	1	1	1	1	1	1	2	0
D. braunsi	1	1	2	1	1	1	0	1	1	1	1	1	0	0	2	0
D. brevihirtus	1	1	2	1	1	1	0	1	1	1	1	1	1	1	2	0
D. brevipes	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0
D. collarti	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2	1
D. concinnus	0	0	1	0	0	0	0	1	1	1	1	0	0	0	2	0
D. crassipes	0	0	0	0	0	0	?	1	1	1	0	0	0	0	2	1
D. heteraspis	1	1	0	1	0	0	0	1	1	1	1	1	0	0	2	0
D. inflatus	1	1	2	1	1	1	0	1	1	1	1	1	0	0	1	0
D. jacobsoni	0	0	0	0	0	0	0	1	1	1	1	0	0	?	2	0
D. kazerunensis	1	1	1	1	1	1	0	1	1	1	1	0	0	0	3	0
D. kerrianus	1	1	1	1	1	1	0	1	1	1	1	0	0	0	3	0
D. kordofaniensis	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
D. levequae	1	1	2	1	1	1	0	1	1	1	1	1	0	0	2	0
D. macgregori	0	0	1	0	0	0	1	1	1	1	1	0	0	0	2	0
D. minor	0	0	0	0	0	0	0	1	1	1	1	0	0	0	2	0
D. occidentalis	0	0	0	0	0	0	0	1	1	1	1	0	0	0	2	0
D. octoconus	1	1	0	0	1	1	0	1	1	1	1	1	0	0	2	0
D. oudemansi	0	0	0	0	0	0	1	1	1	1	1	0	0	1	2	0
D. parvus	1	1	2	1	0	0	0	1	1	1	1	1	0	0	2	0
D. perkinsi	0	1	2	0	0	0	0	1	1	1	1	1	1	0	2	0
D. philippinensis	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
D. piperi	0	0	0	0	0	0	0	0	1	1	1	0	0	0	?	0
D. productus	0	0	0	0	0	0	01	1	1	1	1	0	0	0	1	0
D. ramaleyi	1	1	2	1	0	0	0	1	1	1	1	1	0	0	1	0
D. saengdaoae **sp.nov.**	0	0	2	0	0	0	0	1	1	1	1	0	0	1	1	0
D. similis	0	0	0	0	0	0	1	1	1	2	2	0	0	0	0	0
D. sternisetosa	0	0	1	0	0	0	0	1	1	1	1	0	0	0	2	0
D. tonkinensis	0	0	1	0	0	0	0	1	1	0	?	0	0	0	3	0
D. tortivus	0	0	0	0	0	0	1	1	1	1	1	0	0	0	2	0
D. trihirtus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0
D. villosior	0	0	2	0	0	0	0	1	1	1	1	0	0	0	2	0

It has been demonstrated that the same carpenter bee species may host multiple species of *Dinogamasus* over its geographical range (Vitzthum 1919; LaVeque 1930a; see also Figure 3). Actually, today we know that synhospitality (*i.e.* the association of two or more parasites with one host species; Eichler 1966) is a relatively common phenomenon in the relationship between *Dinogamasus* and *Xylocopa*. For instance, *X. latipes* is a known host of both *D. perkinsi* and *D. philippinensis*, while *X. tenuiscapa*, which was previously found in association with both *D. piperi* and *D. perkinsi* (Vitzthum 1919, 1930; LeVeque 1930a), is herein shown to also host *D. saengdaoae* **sp. nov.** (Figure 3). In particular, the relationship between *X. tenuiscapa* and its associated mite complex represents a clear case of phylogenetic synhospitality (*sensu* Bochkov & Mironov 2008), since the three *Dinogamasus* species comprise a monophyletic group (Figures 22, 24). Phylogenetic synhospitality occurs because mites typically evolve faster than their hosts, mainly due to shorter generation times (Kaltz & Shykoff 1998; Paterson & Banks 2001). In fact, we showed herein that the intraspecific variation in COI is greater in *D. saengdaoae* **sp. nov.** than in *X. tenuiscapa*, as shown by overall higher pairwise distances (Table 2) and greater number of haplotypes (Figures 22, 24, 25), which in turn point to a faster evolution rate. Phylogenetic synhospitality could in theory have occurred as a result of a disjunct distribution of *X. tenuiscapa*, which would have allowed for allopatric speciation within the *D. perkinsi* group; however, the distribution of the three mite species overlap with each other (Figure 3), rendering this hypothesis inapplicable to the case. It thus seems more likely that speciation may have taken place in sympatry in response to different evolutionary adaptations to the host body (Bochkov & Mironov 2008).

Surprisingly, males of only two *Dinogamasus* species (both from Africa) have so far been found and described. One of them is *D. amaniensis* Vitzthum whose two known deutonymph males were re-examined by Lundqvist (1999). The same author also described a single adult male of *D. occidentalis* Lundqvist, and noted that in males of both *D. amaniensis* and *D. occidentalis* the genu and tibia of leg I lack modified *ad3* and setae *pd3*, a remarkable sexual dimorphism as such setae are found in females of the two species (Lundqvist 1999). Given the specialized morphology of setae *ad3* and *pd3*, it is possible that they are used by females of *Dinogamasus* to keep themselves more firmly attached to female carpenter bees. This would also explain, at least to some extent, the reason why males of the genus are almost never found in association with the bees.

It would be most desirable that research on *Dinogamasus* be expanded to include, besides taxonomy, also study of the biology of the nest inquilines of *Xylocopa* bees. Results may offer important insights into a wide range of roles that might be played by mites in hymenopterans, with possible applications to beekeeping and wild bee conservation.

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