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Two new species of *Gaeolaelaps* (Acari: Mesostigmata: Laelapidae) from Iran, with a revised generic concept and notes on significant morphological characters in the genus

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Abstract

Two new species of laelapid mites of the genus *Gaeolaelaps* Evans & Till are described based on adult females collected from soil and litter in Kerman Province, southeastern Iran, and Mazandaran Province, northern Iran. *Gaeolaelaps jondishapouri* Nemati & Kavianpour is redescribed based on the holotype and additional specimens collected in southeastern Iran. The concept of the genus is revised to incorporate some atypical characters of recently described species. Finally, some morphological attributes with potential to define natural species groupings as well as hypoaspidine genera are discussed, particularly idiosomal gland pores and poroids.

Key words: Soil mites, Parasitiformes, Iran, gland pores, poroids

Introduction

At present, Laelapidae is the most morphologically and ecologically diverse family of mesostigmatic mites, including obligate and facultative ectoparasites of mammals, soil-dwelling predators, and arthropod symbionts, for many of which the feeding biology is unknown (Evans & Till, 1966; Klimov & OConnor, 2004; Beaulieu, 2009; Lindquist *et al.*, 2009). Since its erection by Berlese (1892), the family has increased dramatically in size with currently *ca.* 90 known genera and over 1300 known species (Beaulieu *et al.*, 2011), and has benefited from several studies that variously tackled its classification (e.g. Berlese, 1903, 1916; Vitzthum, 1940–1943; Evans, 1957; Tipton, 1960; Karg, 1965, 1979; Evans & Till, 1966, 1979; Casanueva, 1993; Radovsky & Gettinger, 1999; Dowling & OConnor, 2010). However, it remains quite unstable overall, with the family being possibly paraphyletic or polyphyletic (Dowling & OConnor, 2010) and many of its inclusive subfamilies and genera have uncertain, tentatively defined boundaries. Radovsky & Gettinger (1999) and Shaw (2012) commented on the difficulty of placing genera in appropriate subfamilies. This incomplete understanding of the family is the result of a dearth of comprehensive systematic studies, as well as the large number of undescribed species from all over the world (Evans & Till, 1966). The limited quality of species descriptions, which often largely ignore key characters such as leg chaetotaxy and gnathosomal attributes, is also a strong impediment to systematic progress, including the elucidation of both taxonomic relationships and species delineation.

Gaeolaelaps, or *Hypoaspis* (*Gaeolaelaps*), is poorly known worldwide, except possibly in some parts of Europe (e.g. Karg, 1993). *Gaeolaelaps* species are typically known from soil and litter, living as opportunistic predators of small invertebrates. The type species of the genus—*Gaeolaelaps aculeifer* (G. Canestrini)—is well known as a predator, and its voracity has been exploited in the biological control of crop pests (Prischmann-Voldseth & Dashiell, 2013). *Gaeolaelaps gillespiei* Beaulieu is another species used in greenhouses, mostly for the control of fungus gnats and thrips (Gillespie & Quiring, 1990; Beaulieu, 2009). On the other hand, an increasing

series of studies show that many *Gaeolaelaps*-like species live in symbiosis with insects and other arthropods inhabiting soil or logs, such as millipedes and mygalomorph spiders (e.g. Strong, 1995; Faraji & Halliday, 2009; Trach, 2012; Kazemi, personal observations). The relationships between these ‘symbiotic’ mites with their hosts is overall little understood, and in some cases may represent relatively intimate, at least phoretic, associations, considering their abundance in the host’s nests, and the degree of host specificity (Strong & Halliday, 1994; Walter & Moser, 2010). Their feeding habits are also poorly known, but based on the strong chelate-dentate chelicerae of these species, horn-like corniculi, and their broad deutosternum, associated with well-developed laciniae, parasitism (at least in an obligate form) can probably be ruled out and predation of small invertebrates in the nests of their arthropod hosts is more likely (Evans & Till, 1965, 1966; Walter & Moser, 2010). It is often difficult to classify these arthropod-associated *Gaeolaelaps*-like species with confidence because they show conspicuous differences from typical *Gaeolaelaps*, exemplified by free-living species such as *G. aculeifer* (this basal plan largely corresponds to the ‘basic dermanyssid type’ of Evans & Till, 1966). For example, the new species described by Faraji & Halliday (2009), Walter & Moser (2012), and Trach (2012) from cockroaches, fire ants, and carabid beetles respectively, all exhibit more or less unique departures from typical *Gaeolaelaps* species (see notes below), which force us, at least provisionally, to adjust the genus concept to accommodate these new species.

In Iran, 16 species have been reported so far, five of which were described from Iran as new for science (Kazemi & Rajaei, 2013; Nemati & Kavianpour, 2013; Nemati & Mohseni, 2013; Kavianpour *et al.*, 2013; Joharchi & Babaeian, 2014; Kavianpour & Nemati, 2014). One of these five species, *G. jondishapouri* Nemati & Kavianpour, 2013, was described from soil and litter taken from Ahvaz region, Khuzestan Province. We have recently collected several specimens of a similar species from soil, litter and cow manure in Kerman Province in southeastern Iran. Comparison of these specimens with the holotype female of *G. jondishapouri* clearly indicated their conspecificity. However, despite their high quality description, we found several discrepancies between Nemati & Kavianpour's original description and the specimens we examined, including the holotype. To address this, we herein redescribe the female of *G. jondishapouri* based on the holotype and additional specimens, and provide a revised species diagnosis of the species. We also describe two new species of *Gaeolaelaps* that were collected from soil and litter in northern (Mazandaran Province) and southeastern Iran (Kerman Province), and revise the diagnosis of the genus by mentioning some additional exceptional characters to facilitate further revisions. We conclude with a discussion on characters that may help define natural species groups and, perhaps, clarify boundaries between genera.

Material and methods

Mites were extracted from soil, litter and manure samples collected in Baft and Jiroft regions, Kerman Province, southeastern Iran, and Tirom-Rud region, Mazandaran Province, northern Iran, using Berlese-Tullgren funnels. Specimens were cleared in lactic acid and then mounted in Hoyer’s medium on microscope slides before examination.

Morphological observations, measurements and illustrations were made using compound microscopes equipped with differential interference contrast and phase contrast optical systems, and a drawing tube. Pencil line drawings were then scanned and traced over using Microsoft Office © Powerpoint 2003. Measurements were made in micrometres. Dorsal shield lengths and widths were respectively taken from the anterior to posterior shield margins along the midline, and from the lateral margins at the level of setae *j6*; the lengths and widths of the idiosoma, including the dorsal shield and the soft marginal cuticle, were also measured at the same levels. The widths of the sternal shields were measured from the lateral margins of the shield at the level of setae *st2*, and their lengths from the anterior to posterior margins along the midline. Lengths of epigynal shields were taken from the anterior margin of the hyaline extension to the posterior margin of the shield along the midline and also from setae *st5* to the posterior tip of the shield; shield width was taken at the level of *st5*. The anal shield lengths were measured along their midline from the anterior to posterior margin, including the cribrum, and their widths at the broadest point. Leg lengths were taken from the base of the coxa to the apex of the tarsus, excluding the ambulacrum (stalk, claws and pulvillus). The length of the second cheliceral segment was measured from the base to the apex of the fixed digit, and its width at the broadest point. The length of the fixed cheliceral digit was taken from the dorsal lyrifissure to the apex, and that of the movable digit from the base to apex. In the case of the

redescription of *G. jondishapouri*, the measurements given first are those taken from specimens collected by us, followed, within square brackets, by: (1) measurements taken on the borrowed holotype specimen (when character was visible), and (2) in parentheses, measurements duplicated from the text of the original species description, when it was provided, in order to facilitate comparison.

The notation for idiosomal setae follows that of Lindquist & Evans (1965) adapted by Evans & Till (1965, 1966) and Lindquist (1994), and that for leg and palp setae follows that of Evans (1963a, 1963b). Distinction of idiosomal pore-like structures as glandular openings (gland pores or solenostomes) versus poroids (proprioceptors or stress receptors, often called ‘lyrifissures’) were distinguished based on previous work by Athias-Henriot (1969b, 1971, 1975) on various Mesostigmata and by Krantz & Redmond (1987) on Macrochelidae, and their notation generally follows that of Athias-Henriot (1975) for the dorsal idiosoma, and Athias-Henriot (1971) for the ventral idiosoma. There are discrepancies in notation of dorsal structures between Athias-Henriot (1975) and Beard (2001) (respectively, homologous setae with different names are *idl1=idl2*, *id5=id1a*) and more substantial ones with Athias-Henriot’s earlier publications (e.g. 1971, 1973). The notation of pore-like structures on the sternal shield and peritrematal shield region also followed modifications and additions by Johnston & Moraza (1991), Lindquist & Makarova (2012; gland opening *gvb*), and Lindquist & Moraza (2014). Because the gland openings on coxae I do not seem to have been given a name in earlier works, we herein use ‘*gc*’ (for ‘gland’ and ‘coxal’) to identify them.

Femur I in *Gaeolaelaps* has three *ad* and two *pd* setae, based on Evans & Till (1965, pp. 283–284). Beaulieu (2009) had erroneously indicated that *G. gillespiei* has two *ad* and three *pd* on femur I, because the most proximal dorsal seta (*ad3*) is more or less aligned with *pd1–2* in the adult stage, as it may appear in other *Gaeolaelaps* species and other Mesostigmata such as *Pergamasus* (Parasitidae; Evans 1963a, p. 281). Setal positions may be interpreted differently due to the elongate or irregular shape of femur I. Since (1) the repression of a seta (e.g. *ad3* of femur I) followed by its replacement by a de novo seta (*pd3*) would represent an unparsimonious hypothesis, and that (2) setae may shift in position through evolutionary time, we suggest to follow Evans & Till’s notation, which was based on Evans’s study (1963a) of leg chaetotaxy of immature and adult stages of several mesostigmatan families.

Notation of the three ventral setae of femur II varies among studies, due to different interpretation of setal positions. Herein, we follow the notation of Strong & Halliday (1994), with seta *av* inserted at a level near the middle of the femur length and more anteriorly than setae *pv1* (distalmost) and *pv2* (proximalmost). Seta *av* was labelled *av2* in Evans & Till (1965, p. 289), Beaulieu (2009) and Walter & Moser (2010). The distalmost seta (herein *pv1*) was labelled *av1* in Evans & Till (1965, also illustration p. 289, consistent with their notes p. 288), therefore considering the presence of two anteroventral setae; however, they also made a contradictory statement (p. 284) that there is one *av* and two *pv* on femur II. Shaw (2012) also considers that there are two anteroventral setae on femur II, labelling the anteriormost seta as *av1* (herein *av*) and the most proximal and posterior seta *av2* (herein *pv2*). Although this variation in notation may appear as a taxonomic impediment, the most important is to homologue setae across taxa, and therefore, an illustration of leg segments or a statement clearly describing the position of any modified seta should suffice.

The revised diagnosis of the genus was modified and expanded from Beaulieu (2009), using descriptions of new species from the literature and specimens of several described and undescribed species of *Gaeolaelaps*, as compared with descriptions and specimens of other related hypoaspidine genera. Species exhibiting characters exceptional for the genus are listed within the detailed diagnosis below. This list of exceptional species is probably not exhaustive (even if also considering those listed in Beaulieu (2009), which are mostly not repeated here), in part because it is essentially based on the literature, which often ignores many characters of interest (leg chaetotaxy, gnathosomal characters, pores and poroids).

Abbreviations are as follows: ACISTE—Acarological Collection, Institute of Science and High Technology and Environmental Sciences, Graduate University of Advanced Technology, Kerman, Iran; ACJAZUT—Acarological Collection, Jalal Afshar Zoological Museum, Faculty of Agriculture, University of Tehran, Karaj, Iran; CNC—Canadian National Collection of Insects, Arachnids and Nematodes, at Agriculture and Agri-Food Canada, Ottawa, Canada.

Genus *Gaeolaelaps* Evans & Till, 1966

Hypoaspis (*Gaeolaelaps*) Evans & Till, 1966: 159.

Type species: *Laelaps aculeifer* G. Canestrini, 1884, by original designation

The short diagnosis below was modified from the genus diagnosis in Beaulieu (2009). The subsequent detailed diagnosis is similar to the genus description in Beaulieu (2009), but excludes several characters of lesser significance at the genus level.

Short diagnosis. Hypoaspidine laelapid mites with the following combination of characters: dorsal shield usually bearing 39 pairs of simple, short to moderately elongate setae, sometimes with 0–3 additional unpaired median setae; adult female sternal shield longer than broad (rarely broader than long), presternal area weakly sclerotised, usually lineate and granulate; epigynal shield tongue-shaped or flask-shaped, not markedly broadened posteriorly, bearing a pair of setae, and usually well separated from, and never touching, the subtriangular or pear-shaped anal shield; opisthogastric cuticle usually with 7–9 pairs of simple setae (rarely more); epistome margin rounded or subtriangular, denticulate; six (rarely five or seven) deutosternal rows with at least five denticles each (rarely 1–4); chelicerae strong, chelate-dentate, pilus dentilis setiform; leg setation normal for Laelapidae, including nine setae on genu IV (*pl2* absent); *av* on femur II, ventral setae on genu and tibia II–IV, and subapical setae of tarsi II–IV usually slightly thickened to spine-like. However, there are numerous exceptions within the genus (see detailed diagnosis below, and genus description in Beaulieu, 2009).

Detailed diagnosis

1. Dorsal shield partly or completely covering dorsal idiosoma, not extending ventrally, suboval to strongly tapered from level of setae *r3–4*, oval in several cockroach, carabid and scarab beetle associates (Strong & Halliday, 1994; Faraji & Halliday, 2009).
2. Dorsal shield usually bearing 39 pairs of simple, short to moderately elongate setae, including *Px2–3* (occasionally absent, including in some arthropod associates), and 0–3 unpaired median setae (*Jx*); *z3* occasionally absent, and rarely a few others; setae, especially *J4–5*, *Z5*, sometimes inconspicuously barbed, rarely other setae, e.g. all dorsal setae except *j1* and *z1* barbed in *G. jondishapouri*.
3. Lateral soft cuticle with 1–8 pairs of marginal (*r–R*) and 0 to few *UR* setae, rarely more, with at least 18 pairs of setae in *G. millipedus* Rosario (1981) and *G. angustiscutatus* (Willmann, 1951), and 32–37 in the carabid associate *G. carabidophilus* Trach (2012).
4. Dorsal shield with 16 pairs of poroids (five podonotal and 11 opisthonotal) and 4–6 gland pores (2–3 podonotal, *gd2* sometimes absent, *gd4* usually absent; 2–3 opisthonotal, *gd6* sometimes absent; see discussion); *gd4* present in some specimens of *G. oreithyiae* (Walter & Oliver, 1989) (Kazemi, personal observation).
5. Presternal region weakly sclerotised and granulate and/or lineate, rarely with a pair of well sclerotised platelets, e.g. in *G. orbiculatus* Nemati & Mohseni (2013).
6. Sternal shield longer than wide; rarely broader than long, mostly in arthropod associates, sternal shield length 0.9 x width in free-living *G. jondishapouri*.
7. Posterior margin of sternal shield straight, or slightly convex or concave; rarely deeply indented, e.g. in the cockroach associate *G. concavus* (Faraji & Halliday, 2009).
8. Sternal shield bearing three pairs of simple setae and two pairs of poroids; rarely setae *st1* off shield, e.g. *G. aculeiferoides* (Teng, 1982), *G. debilis* (Ma, 1996), *G. krantzi* (Arutunian, 1993), or borne on paired anterior extensions of shield in *G. jondishapouri*; rarely poroids *iv3* captured by sternal shield e.g. in *G. carabidophilus*.
9. Setae *st4* on soft cuticle, rarely on separate platelets; in some cases, e.g. *G. minor* (Costa, 1968), *st4* may wrongly appear to be inserted on the endopodal platelet, probably due to the soft cuticle bearing *st4* being folded over the platelet (Kazemi, personal observation).
10. Epigynal shield tongue- or flask-shaped, not markedly broadened posteriorly, bearing one pair of simple setae, and not touching anal shield; ornamented with two slightly curved diagonal lines that typically join medially (as such forming an inversed V, or joined by a transverse line) and enclose posteriorly a reticulated area comprising several cells, posterior area without typical reticulation in the following species: smooth in *G. minor* and *G. negevi* (Costa, 1969) (considered to be a junior synonym of *G. gracilis* (Meledzhava, 1963) by Bregetova, 1977); with eight long narrow cells in *G. schusteri* (Hirschmann, 1966 sensu Costa 1974), and *G.*

theodori (Costa, 1974); with a series of diagonal lines oriented posteromedially (forming a series of Vs) in the ant associate *G. glabrosimilis* (Hirschmann et al., 1969), and *G. franzi* (Van Aswegen & Loots, 1970); with a few similar diagonal to semi-circular lines in *G. ruggi* (Strong & Halliday, 1994) and *G. etiopicus* (Berlese, 1918 sensu Van Aswegen & Loots, 1970); with slightly curved, almost transverse lines in *G. rosei* (Strong & Halliday, 1994); with somewhat longitudinal lines in *G. circularis* (Hyatt, 1964).

11. Anal shield small, inversely pear-shaped or subtriangular, more or less rounded anteriorly, narrowed posteriorly, rarely oval or pentagonal; nearly rounded in *G. orbiculatus*, oval in *G. millipedus* and *G. rosei* (Strong & Halliday, 1994) and pentagonal in *G. brevior* (Faraji & Halliday, 2009) and *G. segregatus* (Faraji & Halliday, 2009); with two 'shoulders' or bulging laterally at position of pore *gv3* (and level of para-anal setae) in *G. farajii* Nemati & Mohseni, 2013.
12. Postanal seta usually slightly longer than para-anal setae, exceptionally absent in the fire-ant associate *G. invictianus* Walter & Moser, 2010.
13. Cribrum typically with 3–4 rows of spicules; anteriormost row sometimes extending anteriorly to level or near level of para-anal setae, e.g. in *G. khajooii* and *G. jondishapouri*.
14. Peritrematal shields narrow, connected to dorsal shield anteriorly, not extending beyond coxae IV posteriorly; nearly always free from exopodals. Parapodal and metapodal elements small, inconspicuously developed.
15. Peritremes narrow, usually reaching anteriorly to the level of coxae I, sometimes shorter, ending near middle of coxae II, exceptionally short in *G. carabidophilus*, reaching only mid-level of coxa III.
16. Soft opisthogastric cuticle usually with 7–9 pairs of simple setae; hypertrichous in *G. carabidophilus*, if considering ventrally inserted *R-UR* setae.
17. Male with holovenral shield, sometimes eroded laterally; rarely with a genitivenral shield eroded in opisthogastric region and a separate anal shield, e.g. in *G. invictianus*.
18. Epistome always denticulate, with rounded or subtriangular anterior margin, sometimes more or less straight e.g. in *G. zhoumanshuae* (Ma, 1997) and *G. dactylifera* (Fouly & Al-Rehiyani, 2011); rarely pronounced and pointed anteriorly e.g. in *G. brevior* and *G. segregatus*.
19. Deutosternal groove with six rows of denticles, rarely five or seven; seven rows in *G. dasypus* (Menzies & Strandtmann, 1952), collected from an armadillo's nest; each row bearing usually at least five denticles; rarely fewer, e.g. 1–5 denticles per row in *G. jondishapouri*.
20. Palp tarsal claw usually two-tined, rarely three-tined; third tine long, or short and basal as in *G. jondishapouri*.
21. Chelicerae well-developed, chelate-dentate; fixed digit often with a serrated row of small teeth proximal to the short, setiform pilus dentilis; movable digit with two teeth, exceptionally separated by a row of smaller teeth (in *G. angustiscutatus*).
22. Leg chaetotaxy normal for Laelapidae; nine setae on genu IV, including only one posterolateral; ventral and/or subapical setae of tarsi II–IV usually slightly thickened or modified into spines; *av* on femur II and ventral setae on genua and tibiae II–IV usually thickened or spine-like; femur IV occasionally with *ad1* elongate, and often with *ad2* and *pd* thickened; tarsus IV occasionally with 1–4 elongate setae (typically *pd2–3*, but also *ad2–3*).

***Gaeolaelaps jondishapouri* Nemati & Kavianpour, 2013**

Gaeolaelaps jondishapouri Nemati & Kavianpour, 2013: 64.

Diagnosis (modified from Nemati & Kavianpour, 2013). Female with dorsal shield abruptly tapering from level of *S4* setae, bearing 39 pairs of moderately long setae, more or less reaching base of next seta in opisthosomal region, each seta with 1–4 small barbs; gland pores *gd2* and *gd6* present; seven marginal (*r-R*) setae, born on soft cuticle, with relatively thick sclerotised rings around alveoli. Sternal shield slightly wider than long, ratio of length/width \approx 0.9; reticulate in its anterior third, smooth posteriorly, slightly concave posteriorly, with setae *st1* on pointed edge of two anterior extensions of shield. Presternal region lightly sclerotised, lineate. Epigynal shield flask-shaped, slightly widened posteriorly, ratio of widths at level of broadest point/level of *st5* \approx 1.2, smooth except for an inversely Y-shaped line. Eight pairs of opisthogastric setae on relatively thick sclerotised rings around alveoli. Peritremes relatively short, anteriorly reaching posterior margin of acetabulum I. Epistome with anterior margin subtriangular. Deutosternum with six rows of 1–5 denticles. Fixed cheliceral digit with 5–7, rarely eight, teeth on its anterior half. Internal malae with long median projections and two additional pairs of lateral projections of

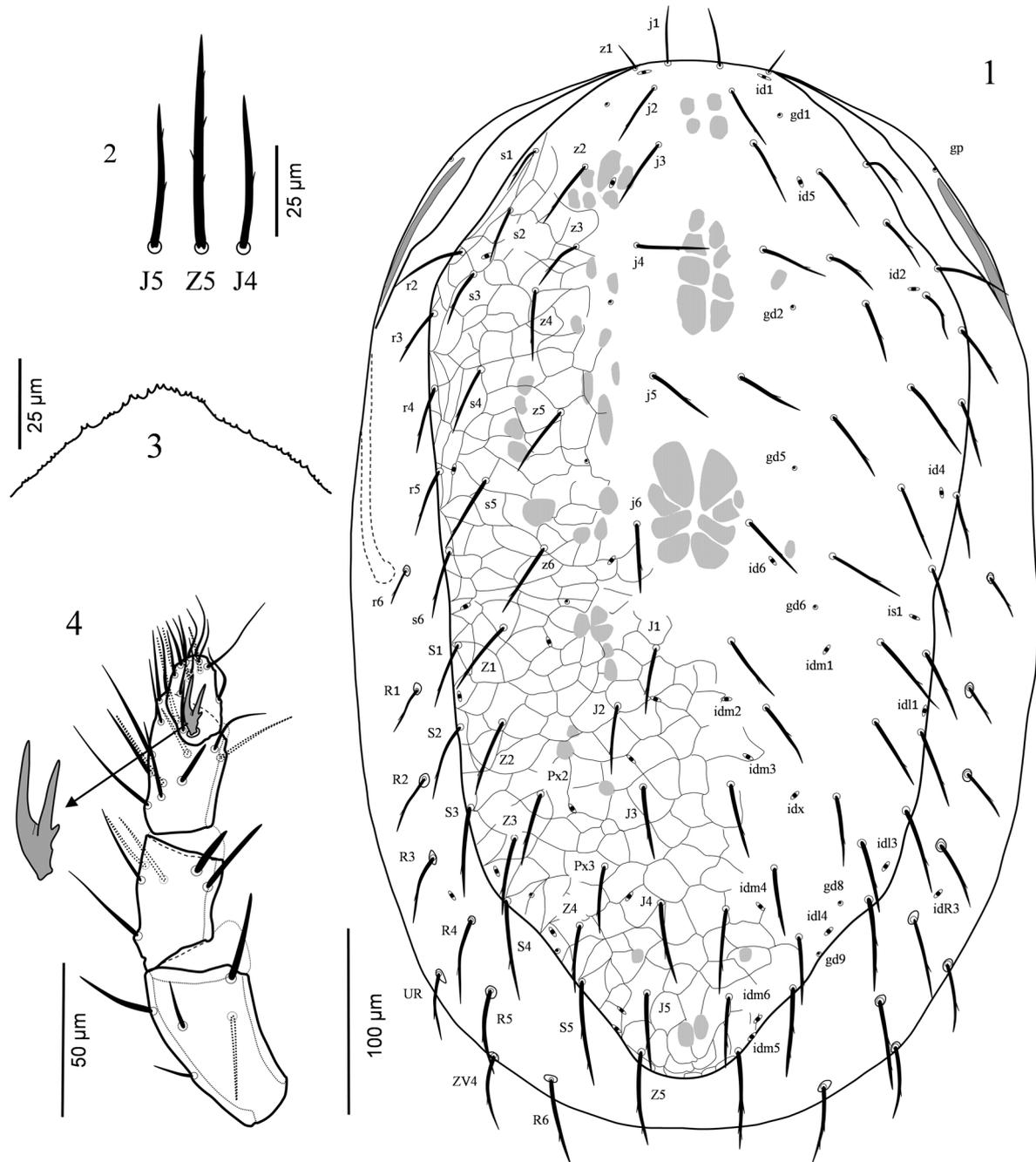
similar length. Palp apotele with three tines, including a minute basal tine. Leg setae simple and mostly slender; ventral setae usually thicker than lateral and dorsal setae; *av* of femur II not spur-like; seta *av* on genu IV, setae *av*, *pv* and *pl2* on tibia IV and setae *md*, *pv2*, *pl2* and *pd2* on tarsus IV thickened; setae *pd2* and *pv2* on tarsus IV inserted well proximal to *ad2* and *av2*, respectively. Male with holovenral shield relatively narrow posteriorly, poorly developed behind coxae IV. Spermatodactyl short, curved and slightly extending beyond movable digit (male characters based on illustrations in Nemati & Kavianpour, 2013).

Redescription (Figs 1–12). **Female** (n=5, excluding holotype). *Dorsal idiosoma* (Figs 1, 11). Idiosoma 545–568 [573] long, 288–311 [291] wide. Dorsal shield 504–526 [562 (543–550)] long, 238–267 [276 (270–340)] wide, reticulate throughout except for smooth anteromedian region extending from behind *j6* setae to anterior shield apex, covering most of dorsal idiosoma but leaving an exposed band of soft lateral cuticle; shield slightly tapering after humeral region from level of *r3* to level of *S4*, where it then sharply tapers into a V-shape, and ends in a rounded posterior apex; shield with 39 pairs of setae of almost uniform length, relatively short and usually not reaching base of following setae. Dorsal shield setae *j1* (39–42) [41] and *z1* (16–18) [16 (17–19)] smooth; *J5* (39–43) [39], *Z4* (44–56) [58 (50–60)], *S4* (48–52) [53], and *S5* (53–59) [54] with 2–3 barbs; *Z5* (57–61) [52] with 3–4 barbs; and all other setae (30–44) [33–47] usually with one small barb on distal half (Fig. 2); without unpaired setae. Shield with 16 pairs of discernible poroids (oval-shaped symbols) and six pairs of gland pores (circular symbols), including *gd2* (posterolaterad of setae *j4*) and *gd6* (posteromedial of *z6*). Setae *r6* (24–27) [24 (34–36)], *R1–6* (26–56) [28–57 (25–70)] and one *UR* (33–34) [34] inserted on soft cuticle laterad of dorsal shield, with relatively thick sclerotised rings around alveoli (Figs 1, 11). Sigillae consistent across individuals, as illustrated in Fig. 1.

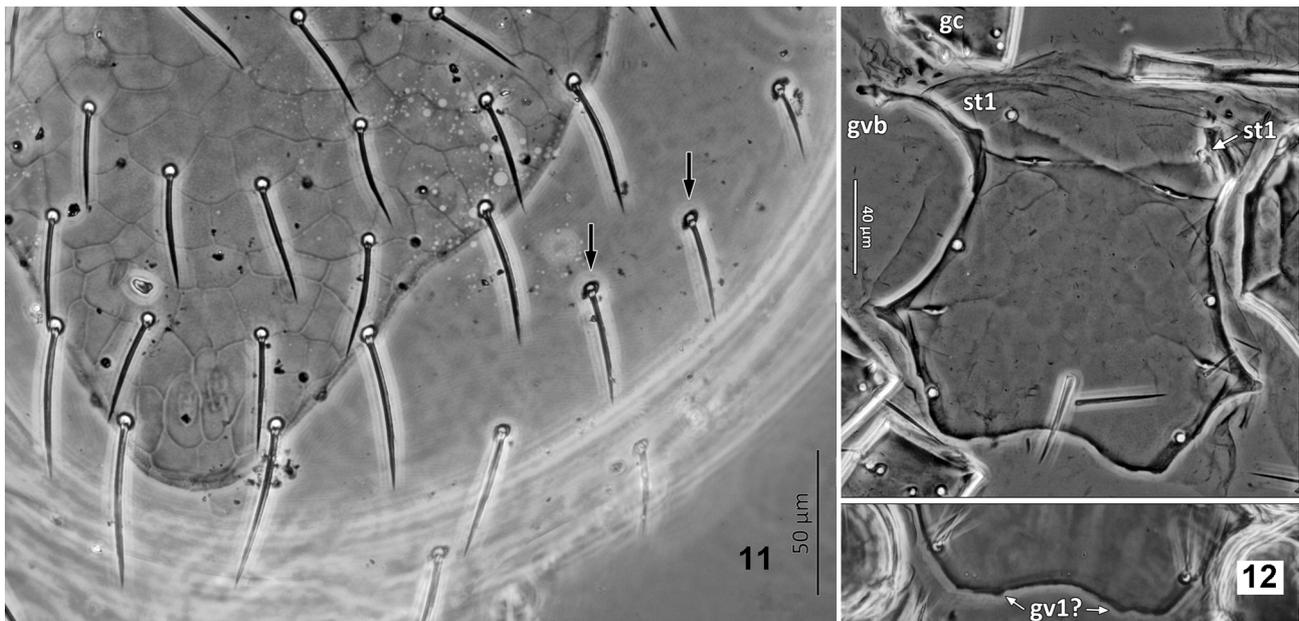
Ventral idiosoma (Fig. 5). Tritosternum with narrow columnar base, 24–34 [34 (44–49)] long, 14–17 [17] wide at base, 7–9 [7] at apex, and two sparsely pilose laciniae 109–114 [111 (119–139)] long, and fused basally for 5–7 [6] μm . Presternal area weakly sclerotised, lineate and very slightly granulate. Soft integument behind coxae I with three pairs of gland openings flanked by two minute valves. Sternal shield 108–114 [115 (120–138)] long, 117–121 [122 (130–145)] wide, finely reticulated anterolaterally, otherwise smooth; anterior and posterior margin of shield moderately concave, anterolateral corners narrowly extending between coxae I–II, distally bearing gland pores *gvb*; endopodal elements between coxae II and III fused with shield; shield bearing three pairs of smooth setae *st1* (37–41) [41], *st2* (38–42) [40] and *st3* (35–38) [38], and two pairs of slit-like poroids, *iv1* and *iv2*, their axes oriented transversely; vestige of gland pores *gv1* apparently present on posterior margin of sternal shield (Fig. 12). Metasternal setae (33–35) [34 (30–34)] and poroids *iv3* on soft cuticle flanked by narrow endopodal elements between coxae III/IV. Epigynal shield flask-shaped, 196–209 [216 (180–213)] long, 99–108 [109] from setae *st5* level to posterior margin, 77–93 [94] wide, slightly broadened past *st5*; anterior hyaline margin of shield irregularly convex and usually slightly covering posterior margin of sternal shield, with an inverse Y-shaped ornamentation, otherwise smooth; epigynal shield separated from anal shield by almost length of anal shield; setae *st5* (31–33) [33 (30–33)] inserted on lateral margins of shield, approximately at level of posterior edge of coxae IV. Poroids *iv5* inserted on soft cuticle, at level of tip of *st5*. A strip-like postgenital sclerite (sometimes divided into 2–4 narrow strips) closely bordering posterior margin of epigynal shield. Anal shield subtriangular, 92–98 [107 (99–103)] long, 87–95 [94 (94–96)] wide, with lineate-reticulate ornamentation, anterior margin of shield slightly convex, circumanal setae smooth, postanal seta (33–39) [38 (33–36)] longer than para-anal setae (26–30) [28 (27–30)]; cribrum well developed, with two single files of denticles each extending from cribrum to near base of para-anal setae; anal opening located at mid-level of shield; pair of glands *gv3* inserted on shield lateral margins, at level between para-anal setae and posterior edge of anus. Peritrematal shields weakly developed posteriorly beyond stigmata, almost reaching level of coxae IV posterior margin, extending anteriorly and fused to dorsal shield at base of seta *z1* level; bearing three gland pores (*gp*) and three poroids (*ip*): two of these poroids and one of these pores located on short, narrow post-stigmatic plate, one pore located near anterior extremity of peritreme (Fig. 6). Peritremes somewhat short (218–228 [221]), extending from stigmata to posterior margin of coxae I (Fig. 6). Exopodal and parapodal platelets narrow, divided into sclerotised strips along coxae II–IV; gland pore *gv2* present anteromedial of parapodal platelet. One pair of minute paragenital platelets anterior to setae *ZV1*. Primary (most lateral) metapodal platelets suboval, with irregular margin, and secondary (more median) pair tiny, oriented more or less transversely. Opisthogaster with five pairs of poroids (four *ivo*; *ivp*) and three pairs of smooth ventral setae *JV1* (30–34) [34 (30–32)], *JV2* (32–36) [32 (30–32)] and *ZV1* (25–29) [28 (30–33)], and five pairs of setae with 1–2 barbs: *JV3* (35–37) [38 (30–32)], *JV4* (40–43) [44 (39–41)], *ZV2* (32–37) [38 (30–33)], *ZV3* (25–29) [31 (30–33)] and *ZV4* (39–42) [42 (30–33)]; *JV5* (58–60) [60 (57–60)] with 3–4 barbs.

Gnathosoma (Figs 3–4, 7–8). Anterior margin of epistome subtriangular and more or less rounded apically,

denticulate, with about 50 small denticles (Fig. 3). Corniculi horn-like, 42–47 [46] long. Salivary stylets narrow and apically pointed. Internal malae fringed, with a pair of thick, contiguous median projections, and two pairs of thinner lateral projections, the inner pair shortest. Labrum considerably longer than corniculi. Hypostomal setae smooth, $h1$ (43–47 [(31–37)] > $h3$ (37–39 [(27–30)]) > $h2$ (27–30 [28 (24–30)]), capitular (pc) setae smooth (39–43 [(36–41)]). Deutosternal groove with six rows of denticles, each row with 2–4 and more rarely 1–5 denticles (holotype has most deutosternal rows with two denticles close to each of lateral margins of deutosternum); lateral margins of deutosternum subparallel (Fig. 7). First (basal) segment of chelicerae 64–76 [67] long, second segment 175–191 [186 (240–245)] long, including fixed digit, 54–56 wide; fixed digit of chelicera 57–63 [63] long, bearing 5–7, rarely eight, teeth on its anterior half, including subapical offset tooth (gabelzhan); pilus dentilis short and setiform (Fig. 8). Movable digit of chelicera 72–77 [79 (75–84)] long, bidentate (Fig. 8). Palp chaetotaxy normal for Laelapidae; all setae smooth, $al1$ and $al2$ of palpgenu and al of palpfemur slightly thickened, palptarsus apotele with two main tines, and an additional, very short basal tine (Fig. 4).



FIGURES 1–4. *Gaeolaelaps jondishapouri*. Female. 1. Dorsal idiosoma; 2. Details of some dorsal shield setae; 3. Epistome; 4. Palp.



FIGURES 11–12. *Gaeolaelaps jondishapouri*. Female. 11. Posterior region of dorsal idiosoma showing the basal platelets around setal sockets of *R* setae. 12. Sternal shield, showing *st1* sockets on its anterior margin.

Legs (Figs 9–10). Leg chaetotaxy normal for Laelapidae (*sensu* Evans and Till, 1965). All legs with ambulacrum, lengths of legs I–IV 549–562 [572 (539–549)], 416–428 [429 (444–452)], 386–405 [424 (418–422)] and 608–634 [621 (623–628)], respectively. Lengths of femora I 94–106 [113 (123–126)], II 78–87 [(80–84)], III 72–76 [76 (71–77)], IV 97–109 [124 (130–135)]; genua I 81–85 [80 (87–95)], II 61–66 [63 (65–70)], III 56–60 [59 (58–62)], IV 78–83 [78 (80–85)]; tibiae I 88–95 [85 (36–39)], II 64–70 [66 (73–77)], III 59–62 [63 (60–65)], IV 90–96 [89 (95–100)]; tarsi I 158–164 [163 (155–161)], II 118–130 [127 (129–136)], III 124–135 [123 (129–136)], IV 194–199 [200 (200–208)]. Leg setae mostly simple, needle-like; tarsi II–IV with *al1*, *pl1*, *av1*, and *pv1* relatively thick; leg I without conspicuously thickened seta; trochanter II with *al* short and thickened; trochanter IV with *ad* slightly thickened; femur IV with *ad2* short and slightly thickened; leg IV with the following setae considerably thickened or spine-like: *av* on genu; *av*, *pv* and *pl2* on tibia; *md*, *av2*, *pv2*, *pl2* and *pd2* on tarsus. Coxa I each bearing two gland pores (*gc*) (Fig. 5).

Remarks. *Gaeolaelaps jondishapouri* can be distinguished from any other *Gaeolaelaps* species by two distinctive, if not exceptional, characters among known members of the genus: (1) a dorsal shield abruptly tapering from the level of setae *S4*; (2) setae *st1* inserted relatively far anteriorly from poroids *iv1*, on the apex of two pointed extensions of the sternal shield (making the anterior margin appear bilobed, see Figs 2, 12). Whereas the original description shows a sternal shield with a straight anterior margin, without extensions, leaving *st1* completely off the shield, the re-illustration of the sternal shield by Kavianpour & Nemati (2014) is similar to ours. Other notable discrepancies that we noticed between the original description and the specimens we examined (including the holotype) are: (1) denticulate rows of deutosternal groove usually with 2–4 denticles [rows appear smooth in the original illustration, and there is no mention of denticles in the text]; (2) palp apotele with a small basal tine, in addition to the two main tines; (3) 16 poroids and six gland pores on the dorsal shield [only 18 pore-like structures in the original description, missing gland pore behind *j4*, and poroids near *s3*, behind *s6*, and laterad of *Z4*; Nemati & Kavianpour had acknowledged in the text that they could have overlooked some pores or poroids]; (4) peritrematal shields anteriorly fused to dorsal shield, each bearing one gland pore [in the original description, peritremes appear without shielding anteriorly and therefore free from the dorsal shield]; (5) coxae I and surrounding soft integument with five gland openings; (6) cribrum with two files of denticles extending anteriorly to near the base of para-anal setae [not illustrated nor mentioned in the original description]; (7) setae *h1* (43–47) and *h3* (37–39) moderately longer [31–37 and 27–30, respectively, in the original description]. A few other measurements do not overlap between the original description and ours (e.g. dorsal shield; see notes in the redescription above), but these differences may at least in part be due to differences among populations; (8) most leg setae are needle-like, i.e. rather straight and with a relatively constant thickness through most of their length

(not finely tapering as many setae in Nemati & Kavianpour, 2013); setae of leg I and of coxa-tibia II are thin and needle-like, except thickened *all* on coxa and ventral setae on tibia (in contrast to the original illustrations showing most setae of legs I-II thickened or spine-like). Although this is a relatively inconspicuous feature, *G. jondishapouri* also has all dorsal setae with one or more barbs, with the exception of *j1* and *z1*.

The specimens of *G. jondishapouri* that we examined also differ from Nemati & Kavianpour's (2013) description by the shape of the posterior region of the dorsal shield. We would rather describe this region as V-shaped, or even subtriangular, with a rounded apex, instead of bell-shaped, as indicated in their species key (examination of the holotype shows a dorsal shield that may appear as 'bell-shaped' because the shield is bent posteriorly on that specimen). With such a distinctive tapering of the dorsal shield, we believe that *G. jondishapouri* is closely related to *G. changlingensis* (Ma, 2000), with the minor difference that the shield of *G. changlingensis* abruptly tapers from the level of *S3* instead of *S4* as in *G. jondishapouri*. Based on its description, *G. changlingensis* also differs from *G. jondishapouri* by its narrower sternal shield (Li-Ming Ma pers. comm.), *st2* inserted more posteriorly, and possibly longer idiosomal setae (however, some of these apparent differences may be due to inaccurate illustrations).

Nemati & Kavianpour (2013) placed *G. jondishapouri* in the *G. angusta* species group (*sensu* Karg, 1979) based on the tapering posterior region of the dorsal shield. However, we do not concur that *G. jondishapouri* can be placed in the *G. angusta* group, because the four species originally placed in this species group have dorsal shields that taper much more anteriorly than that of *G. jondishapouri*, and consequently are quite narrower posteriorly. Based on Karg's hypothesis (1979), the dorsal shield of species in the *angusta* group is wedge-shaped, characterised by 'shoulders' (typically near the level of *r3-4*), from which the shield gradually tapers to a relatively narrow apex (see, for example, the redescription of *G. queenslandicus* (Womersley, 1956) by Costa, 1966). The dorsal shield of *G. jondishapouri* is therefore quite distinct from that of members of the *angusta* species group, and the same applies to the putatively close relative *G. changlingensis*. Such shape of the dorsal shield is strongly reminiscent of that of *Stratiolaelaps scimitus* (Womersley), which differs from congeners by a shield abruptly tapering at level of *S1-2* (Walter & Campbell, 2003).

Very few species of *Gaeolaelaps* have a deutosternum with fewer than five denticles per row. *Gaeolaelaps jondishapouri* is among the exceptions, as is *G. spiniseta*, which has a deutosternum with 3-4 denticles per row (Barilo, 1991). However, *G. jondishapouri* can easily be distinguished from *G. spiniseta* by several characters, including its posteriorly tapered dorsal shield (rounded in *G. spiniseta*), which bears 39 pairs of moderately long setae (38 in *G. spiniseta*, with setae longer, usually reaching the base of next setae), flanked by seven pairs of marginal setae (only one pair in *G. spiniseta*); its sternal shield bearing *st1* on anterior extensions of the sternal shield (*st1* inserted closer to *iv1* and well behind the anterior margin of the shield in *G. spiniseta*); and by its rounded epistome (subtriangular or pointed in *G. spiniseta*, according to the illustration in Barilo, 1991).

Material examined. Holotype female: Southwestern Iran, Ahwaz, Khuzestan Province, 2010, coll. M. Kavianpour. Paratypes: 10 females: southeastern Iran, Kerman Province, Jiroft County (28° 51' 29" N; 57° 71' 92" E), altitude 589 m above sea level, from cow manure in a citrus orchard, 4 Jan 2011, coll. A. Rajaei, deposited in ACISTE. One female with same data, deposited in ACJAZUT. One female with same data, deposited in CNC. Five females: collected from soil and litter, in the same orchard as above, same date and collector, deposited in ACISTE.

***Gaeolaelaps khajooii* Kazemi, Rajaei & Beaulieu sp. nov.**

(Figs 13-28)

Diagnosis (based on adult female). Dorsal shield clearly broadest at level of setae *r3* (ratio of widths at *r3/S3* level ≈ 1.5), progressively tapering until *s6*, subparallel from *s6* to level of *S4*, rounded posteriorly; with 39 pairs of mostly smooth and moderately long setae; an additional, median unpaired seta may be present between *J4-5*; gland pores *gd2* and *gd6* absent; three pairs of marginal setae present on lateral soft cuticle. Sternal shield longer than wide (ratio of length/width ≈ 1.3), reticulate throughout, its anterior margin with or without a small median invagination; posterior margin slightly convex, with two minute projections. Epigynal shield tongue-shaped, very slightly broadened posteriorly. Anal shield subtriangular, with two single files of denticles reaching level of paranal setae; anal shield separated from epigynal by about length of anal shield. Peritremes relatively short, anteriorly reaching mid-level of coxae II. Post-stigmatic area of peritrematal shield narrowly extended to posterior edge of coxae IV. Opisthogastric and dorsolateral soft integument bearing seven and three pairs of setae, respectively.

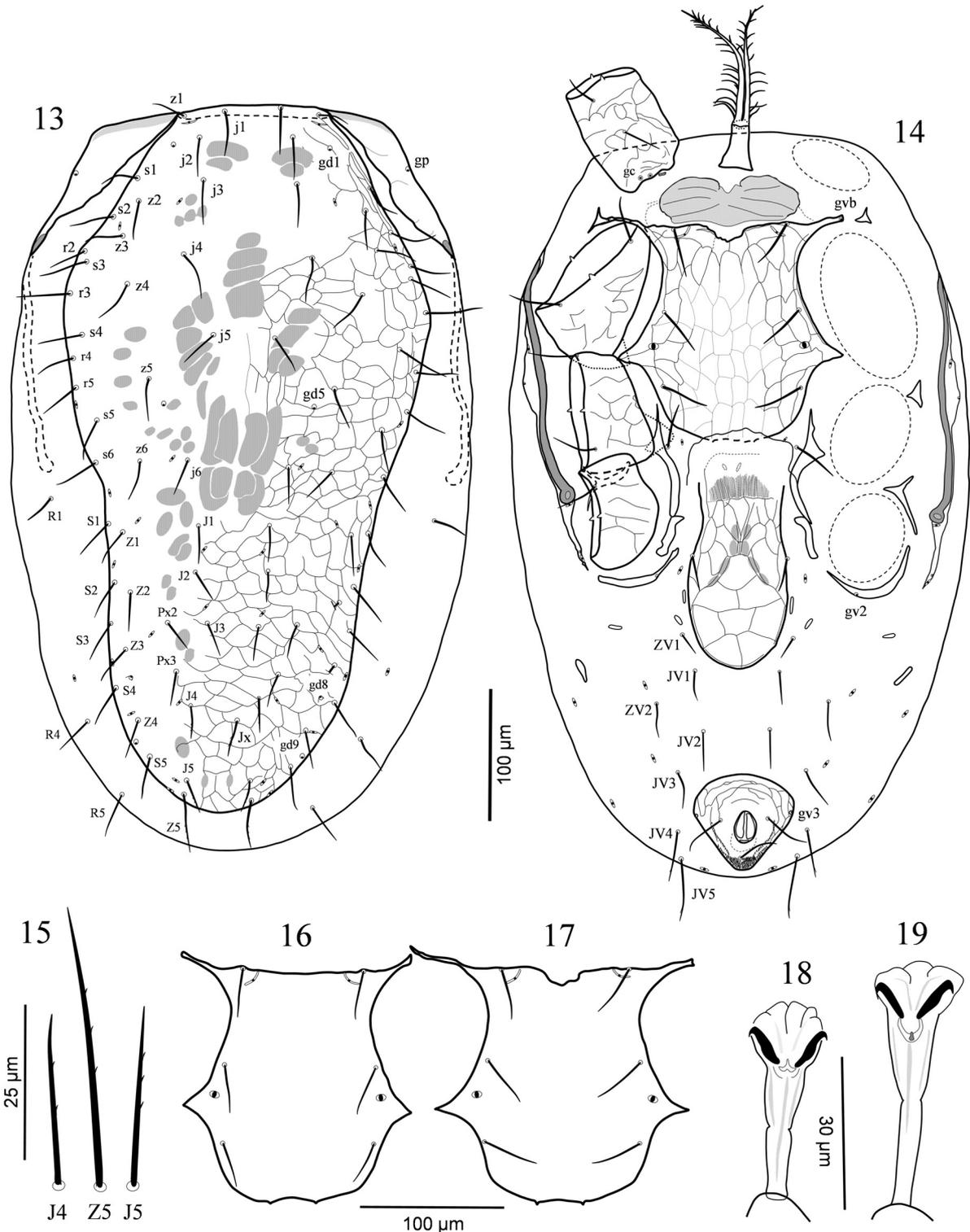
Deutosternal groove with six rows of 10–17 denticles. Internal malae with a pair of long median projections and a pair of shorter lateral projections. Palp apotele 2-tined. Fixed digit of chelicera with 10–13 teeth, including a serrated row of 6–9 small teeth posterior to pilus dentilis. Leg setae simple and slender, except following setae thickened and/or spine-like: *ad3* (only slightly thickened) on femur I; *av* on femur II; *pd* on femur IV; all ventral setae on genua and tibiae II–IV (some only slightly thickened), and *pl1* on tibia IV; *md*, *av1–2*, *mv* and *pv1–pv2* on tarsus II; *all*, *av1–2*, *pv1–2*, *pl1* (slightly thickened), *md* and *mv* on tarsus III; *pl2* (slightly thickened), *av2*, *pv2* and *mv* on tarsus IV; *pd2–3* on tarsus IV slender and elongate.

Description. Female (n=3). *Dorsal idiosoma* (Fig. 13). Idiosoma length 541–552, width 301–307. Dorsal shield 489–522 long, 203–213 wide at *j6* level, covering most of dorsal idiosoma, 248–253 wide at level of *r3* and 163–170 at level of *S3*; reticulate throughout except anteromedially; with 39 pairs of needle-like setae of which some of the most posterior pairs (e.g. *J4–5*, *Z5*, *Jx*) have a few minute barbs; 0–1 unpaired median seta *Jx* between setae *J4–J5*. Dorsal shield setae *j1–5* 32–36, *j6* 28–31, *z1* 23–28, *z2* 31–32, *z3* 33–34, *z4* 34–38, *z5* 34–36, *z6* 28–30, *s1* 22–23, *s2* 24–27, *s3* 35–40, *s4* 29–35, *s5* 28–31, *s6* 29–36, *r2* 31–35, *r3* 38–45, *r4* 31–34, *r5* 29–34, *J1–5* 27–31, *Jx* 28–30, *Z1* 28–31, *Z2–3* 24–29, *Z4* 28–30, *Z5* 38–44, *S1–4* 29–34, *S5* 33–39 long. Setae *R1* (29–31), *R4* (30–33) and *R5* (34–38), and a pair of poroids (*idR3*) on lateral soft integument. Dorsal shield with 16 pairs of poroids and only four pairs of gland pores (*gd2* and *gd6* pores absent).

Ventral idiosoma (Figs 14, 16–17). Tritosternum with a narrow columnar base, 32–36 long, 14–17 wide at base, 7–9 wide at apex, and two sparsely pilose laciniae, length free for 90–95 and fused basally for 2–4 μm . Presternal area lightly sclerotised and punctate, with a few transverse lines. Sternal shield 154–160 long, 114–118 wide, reticulate throughout; anterolateral corners narrowly extending between coxae I–II; anterior margin irregularly straight, with or without a small median invagination; posterior margin slightly convex, with two minute projections near medial axis, which may represent vestiges of gland pore *gv1* (Figs 16–17); shield bearing three pairs of smooth setae *st1* (38–39), *st2* (37–38) and *st3* (34–36), and two pairs of poroids, lyrifissures *iv1* slit-like and oriented obliquely, *iv2* suboval. Metasternal setae (27–30) and poroids *iv3* on soft cuticle. Endopodal elements between coxae III–IV narrow, anteriorly free from sternal shield. Epigynal shield 185–190 long, 92–95 from *st5* level to posterior margin, 69–71 wide, 58–62 wide at narrowest point (near coxae IV level), and 81–83 at broadest point past setae *st5*; anterior hyaline margin irregular, not covering posterior area of sternal shield; surface reticulated with an inverse Y-shaped pattern, with the Y posteriorly embracing eight large cells; setae *st5* (27–29) inserted on lateral margins of shield at level of posterior margin of coxae IV, and poroids *iv5* inserted laterad of *st5*. Anal shield subtriangular, anteriorly rounded, 74–80 long, 74–80 wide, anterior margin gently rounded, and surface lineate-reticulate; circumanal setae smooth, postanal seta (35–38) longer than para-anal setae (29–31), cribrum well developed, narrowly extending laterally to level of adanal setae; anus located slightly posterior to mid-level of shield; pair of glands *gv3* inserted on lateral margins of shield at level of anterior margin of anus. Peritrematal shields well developed anteriorly and fused narrowly to dorsal shield at level of *z1*, with a narrow strip of granular cuticle parallel to anterior edge of shield; between stigmata and coxa II, shield almost limited to a relatively narrow band of cuticle at level between coxae II and III, bearing a poroids and a gland pore; post-stigmatic region of shield narrowly extending to posterior level of coxae IV, bearing two and one gland pore; an additional pore located on peritrematal shield at level of seta *s1*. Peritremes relatively short (178–182) and narrow, extending from stigmata to mid-level of coxae II. Three exopodal platelets between coxae I–II, II–III and III–IV present, anterior two platelets small and subtriangular, those between coxae III–IV slightly extending posteriorly; parapodal platelets strip-like, bearing gland pore *gv2*. Opisthogastric integument with two pairs of small, narrow paragenital platelets between *st5* and *ZV1*, and two pairs of narrow metapodal platelets, the smallest at or above level of *ZV1* and the largest one near level of *JV1*; seven pairs of ventral opisthogastric setae *JV1* (19–23), *JV2* (18–22), *JV3* (24–26), *ZV1* (23–28) and *ZV2* (27–31) smooth; *JV4* (28–32), *JV5* (44–49) with 1–2 minute barbs; and five pairs of poroids.

Gnathosoma (Figs 20–24). Anterior margin of epistome convex and finely denticulate, with about 30 denticles (Fig. 20). Corniculi horn-like (58–64). Internal malae fringed, slightly longer than corniculi, with a pair of long median projections and a pair of shorter lateral projections. Labrum acuminate, considerably longer than internal malae. Hypostomal and capitular setae smooth, *h1* (50–51) > *h3* (35–38) > *h2* (34–35) \approx *pc* (32–35). Deutosternal groove with six rows of denticles, progressively broader from posterior to anterior, each with 9–17 denticles; anteriormost row angled medially. First cheliceral segment 58–67 long, second segment 190–196 long and 54–56 wide; fixed digit 73–75 long, with 10–13 teeth, including (from distal to proximal) a subapical large offset tooth (gabelzhan) followed by two other teeth, one small and one large, anterior to the short, setiform pilus dentilis, and

6–9 smaller, tightly aligned teeth followed posteriorly by a larger tooth; movable digit of chelicera 85–87 long, bidentate; dorsal cheliceral seta short and setiform (Fig. 22). Palp chaetotaxy normal for Laelapidae, all setae smooth; palpgenu setae *al1* and *al2* slightly thick and spatulate, palpfemur *al* slightly thick and spine-like; palp apotele 2-tined (Figs 23–24).



FIGURES 13–19. *Gaeolaelaps khajooii* Female. 13. Dorsal idiosoma; 14. Ventral idiosoma; 15. Details of some dorsal shield setae; 16–17. Sternal shield; 18. Ambulacrum II; 19. Ambulacrum I.

Legs (Figs 25–28). All legs with ambulacrum, that of leg I longer (35–36) than those of legs II–IV (24–26) (Figs 18–19), lengths of legs I–IV as follows: 591–597, 425–451, 384–392, 582–605, respectively. Lengths of femora I 104–111, II 85–96, III 75–77, IV 117–123; genera I 83–87, II 69–70, III 50–53, IV 89–92; tibiae I 95–97, II 66–67, III 51–53, IV 96–98; tarsi I 156–163, II 108–115, III 105–110, IV 156–160. Leg chaetotaxy normal for Laelapidae (*sensu* Evans & Till, 1965) and *Gaeolaelaps* (see Beaulieu, 2009). Most setae simple, needle-like and of similar length, except a few shortened, elongate or thickened setae: trochanter I with *al* short and slightly thickened; trochanter II with *al1* thickened; trochanter IV with *pv1* slightly thickened; femur I with *ad3* slightly thickened, femur II with *av* somewhat spine-like and *al2* very short, slightly thickened; femur IV with *pd* spine-like, *ad2* slightly thickened, and *pl* short and thin; genu II with *av* short and spine-like, and genera III–IV with ventrals slightly thickened; tibia II with *av1* spine-like, *pv1* thickened; tibia III and IV with *pv* spine-like, *av* slightly thickened; *pl* also spine-like on tibia IV; tarsus II with *av1–2*, *md*, *mv*, and *pv1–2* spine-like; tarsus III with *md* and *mv* spine-like, and *av1–2*, *pv1–2* slightly thickened; tarsus IV with *pl2* slightly thickened, *mv*, *av2* and *pv2* thickened, and *pd2* and *pd3* slender and elongate with *pd2* longer than half the length of tarsus. Coxa I bearing two gland pores (*gc*) (Fig. 14).

Material examined. Holotype: female southern Iran, Kerman Province, Baft County (28°39' 46" N; 56°45' 37" E), altitude 1044 m above sea level, from soil and litter at an alfalfa farm, 2 April 2012, coll. A. Rajaei, deposited in ACISTE. One paratype female with same collection data, deposited in ACISTE; another paratype female with same collection data, deposited in CNC.

Etymology. The species is named in honour of the famous Persian poet, Khajooi-e Kermani.

Remarks. The new species can be placed in the *similisetae* species group (*sensu* Karg, 1979) based on its short peritremes reaching only the mid-level of coxae II, and differs from other species of the group by the shape of the dorsal shield, which is clearly widest at the level of setae *r3* and tapers posteriorly. This shape is reminiscent of the *G. angusta* species group, but differs from most members of that group by its dorsal shield with almost parallel sides in the opisthotal region (from *S1* to *S4*). The species most similar to *G. khajooii* is *G. zhoumanshuae* (Ma, 1997), which, justifiably, was classified in the *angusta* species group by Nemati & Kavianpour (2013). In addition to the very similar shape of their dorsal shield, *G. zhoumanshuae* and *G. khajooii* both have peritremes shortened anteriorly, ending before the anterior margin of coxae II, seven opisthogastric setae (six in *G. zhoumanshuae*, but *JV5* may have been illustrated dorsally), three dorsomarginal (*R*) setae (four in *G. zhoumanshuae*, perhaps including *JV5* dorsally), and have a cheliceral fixed digit with a serrated row of small teeth proximally to the pilus dentilis (based on figures in Ma, 1997). *Gaeolaelaps khajooii* differs from it at least by having 39 pairs of setae on the dorsal shield, including *Px2–3*, which are absent in *G. zhoumanshuae*. The new species also resembles *Hypoaspis (sensu lato) atomarius* Berlese, 1917 (*sensu* Van Aswegen & Loots, 1970), which has a similar dorsal shield albeit posteriorly wider, but it can be easily distinguished from *H. atomarius* by having one ventral setae on genu IV (two ventrals in *G. atomarius*) and 39 setae on dorsal shield (38 in *G. atomarius*, with *z3* absent).

The two minute projections on the posterior margin of the sternal shield are unusual, but also occur in other *Gaeolaelaps* species, including *G. jondishapouri*, *G. nolli* (Karg, 1962), *G. praesternalis* (Willmann, 1949) and *G. farajii*, and an undescribed species that have dorsal shield shaped similarly to *G. khajooii*. It is possible that these minute projections represent the vestiges of gland pores *gv1*.

***Gaeolaelaps ahangarani* Kazemi & Beaulieu sp. nov.**

(Figs 29–40)

Diagnosis (based on adult female). Dorsal shield suboval, reticulated throughout, covering almost all dorsal idiosoma, leaving exposed a narrow lateral band of soft cuticle which bears four pairs of marginal setae (*R1–R2*, *R4–5*); shield with 37 pairs of short, needle-like dorsal setae, setae *Px2–3* and unpaired setae *Jx* absent, with 21 pairs of pore-like structures, including six pairs of gland pores (*gd2* and *gd6* present). Sternal shield longer than wide (length/width ratio ≈ 1.35), reticulate throughout except for a narrow smooth area posteriorly; anterolateral arms of shield broadly fused to endopodals between coxae I–II, and posterior margin of shield slightly convex. Epigynal shield tongue-shaped, only slightly widened posteriorly, with eight cells surrounded by a Δ -shaped line, with cell borders sinuous. Post-stigmatic region of peritrematal shield short, extending slightly beyond level of mid-coxa IV. Soft opisthogastric cuticle with ten pairs of short setae, with alveoli surrounded by relatively thick sclerotised rings. Anal shield somewhat pear-shaped, broadly rounded anteriorly; anal opening almost entirely on

anterior half of shield; cribrum spicules not extending significantly anteriorly. Peritremes long, reaching anterior margin of coxae I. Epistome margin rounded, with variously sized denticles. Deutosternum with six rows of 17–20 denticles. Fixed digit of chelicera with seven teeth. Internal malae with two pairs of lateral fringed projections in addition to the pair of long median projections. Palp apotele 2-tined. Femur II with *av* seta thickened, tarsi II–IV with most subapical setae thickened or spine-like; setae *av1*, *pv1* on tarsus II, *pl2–3* on tarsus IV, and *pl1* on tibia IV apically blunt, spur-like; tarsus IV with *pd2* slightly longer than other setae, otherwise without significantly elongate setae, *ad3* and *pd3* very short; most dorsal setae of genu IV and tibia IV short.

Description. Female (n=2). *Dorsal idiosoma* (Fig. 29). Idiosoma 486–494 long, 266–271 wide. Dorsal shield 486–494 long, 247–252 wide, suboval, reticulate throughout, more distinctly on opisthonotal region, and with cells more elongate between setae *j5* and *j6*; shield broadest at level of setae *r3*, ratio of widths at the level of *r3/S3*=1.2; shield covering most of dorsal idiosoma, leaving exposed a narrow marginal band of soft cuticle. Dorsal shield with 37 pairs of short setae, setae *Px2–3* absent, setae *j2–4*, *z4*, *s3*, *r2–3*, *Z5* longest (20–25), *z1* shortest (6–8), other setae 12–17 long; *Z5* usually with 1–2 minute barbs. Setae *R1–R2* (12–14), *R4* (14–15), *R5* (11–12) and one pair of poroids (*idR3*) on soft lateral cuticle. Dorsal shield with 16 pairs of discernible poroids (oval-shaped symbols) and six pairs of gland pores (circular symbols).

Ventral idiosoma (Fig. 30). Tritosternum with a narrow columnar base, 32–33 long, 10–11 wide at base, 7–8 wide at apex, and two free pilose laciniae (68–71). Presternal area weakly sclerotised, granulate-lineate. Sternal shield 146–150 long, 109–111 wide, distinctly reticulate throughout except for a narrow smooth area posteriorly; anterior margin of shield straight, posterior margin slightly convex with a small median depression; anterolateral corners broadly fused to endopodal platelets between coxae I–II, bearing gland pores *gvb*; shield bearing three pairs of smooth setae *st1* (24–25), *st2* (26–27) and *st3* (26–28), and two pairs of poroids, *iv1* slit-like and *iv2* sub-oval. Metasternal setae (26–28) and poroids *iv3* on soft cuticle (*iv3* asymmetrically captured by sternal shield in one specimen). Epigynal shield tongue-shape, very slightly broadened posteriorly, 166–169 long, and 81–83 from *st5* to posterior margin, 70–72 wide; anterior hyaline margin slightly convex, irregular, covering posterior smooth area of sternal shield; epigynal shield with a Λ -shape line delimiting posteriorly eight cells with sinuous borders; setae *st5* (20–21) on lateral margins of shield, almost at level of posterior edge of coxae IV. Paragenital poroids *iv5* on soft cuticle, near level of coxae IV posterior edges. Anal shield somewhat pear-shaped, anterior margin of shield broadly rounded, 67–70 long, 56–58 wide, lineate-reticulate anteriorly and laterally; circumanal setae smooth, postanal seta (20–22) longer than para-anal setae (15–16); cribrum well developed, with three rows of spicules (four medially), the two anteriormost rows only slightly extending anteriorly of postanal seta; anal opening located almost entirely on anterior half of shield; para-anal gland pores *gv3* on lateral shield margins at level of the posterior edge of anal opening. Peritrematal shields relatively well developed throughout, anteriorly fused to dorsal shield behind setae *z1*, bearing one pair of gland pores near external margin of shield at level of anterior edge of coxae III and one pair of poroids at level of posterior edge of coxae II; poststigmatic region with a longitudinal line from stigmata to shield apex, and with two pairs of poroids and one pair of gland pores. Peritremes long (236–243), reaching anterior margin of coxae I. Exopodal platelet between coxae II–III well developed, exopodal between coxae III–IV fused to parapodal. Opisthogastric soft integument with pair of primary metapodal platelets moderately small, narrow, laterad of *ZV1–2*; 2–3 additional pair(s) of minute metapodal platelets anterior to and in-between *ZV1* and primary metapodals; paragenital platelets minute, at level of *ZV1*; five pairs of poroids and 10 pairs of short, needle-like setae *JV1–5*, *ZV1–5*, 14–20 long.

Gnathosoma (Figs 31–34). Anterior margin of epistome somewhat rounded, with about 17 variously sized teeth (Fig. 31). Corniculi horn-like, 45–47 long. Salivary stylets narrow and apically pointed, aligned beneath corniculi. Internal malae fringed, with a pair of adjacent median pilose projections, flanked by two pairs of shorter and thinner lateral projections. Labrum acuminate, pilose, considerably longer than corniculi. Hypostomal and capitular setae smooth, *h3* (46–49) > *h1* (34–37) > *pc* (26–27) > *h2* (19–21). Deutosternal groove with six rows of 17–20 denticles each; lateral margins of deutosternum subparallel (Fig. 32). Basal segment of chelicerae 50–52 long, second segment 140–143 long, 46–48 wide; fixed digit of chelicera 40–42 long, with seven teeth, including subapical offset tooth (gabelzhan), followed by two small teeth, and four larger teeth proximal to the short and setiform pilus dentilis; dorsal seta short and setiform. Movable digit of chelicera 48–50 long, bidentate (Fig. 33). Palp 146–149 long, palp chaetotaxy normal for Laelapidae; all setae smooth, *al1* and *al2* on palpgenu and *al* on palpfemur thick and subspatulate, *ad* on palpfemur slightly thickened, somewhat spine-like; palptarsus apotele 2-tined, anterior tine with spatulate hyaline margin (Fig. 34).

Legs (Figs 35–40). Leg chaetotaxy normal for Laelapidae (*sensu* Evans & Till, 1965). Legs II–III with largest claws and pulvillus, and broadest ambulacral stalk; leg I with narrowest stalk, claws and pulvillus; lengths of legs I–

IV 435–438, 335–341, 289–292 and 432–440, respectively. Lengths of femora I 70–73, II 57–59, III 56–59, IV 89–92; genua I 62–65, II 62–63, III 38, IV 62–67; tibiae I 70–72, II 51–54, III 38, IV 62; tarsi I 116–119, II 73–76, III 83–86, IV 113–121. Leg setae mostly thin and moderately long, except: trochanter I with *al* and *ad* short and slightly thickened; trochanter II with *al* slightly thickened; trochanter IV with *pv1* slightly thickened; femur II with *av* and *pd1* slightly thickened, *ad3* and *al2* short; femur III with *al* and *ad1* thickened, *ad2*, *pd* and *pl* short; femur IV with *ad1* and *av* slightly thickened, *ad2*, *pd* and *pl* short; genu II with *pd2* slightly thickened, and genua III–IV with ventrals slightly thickened; tibiae II–III with *pv* thickened; tibia IV with *av* and *pv* thickened, *pl1* thick, somewhat spur-like, *pd2–3* very short; tarsus II with *al2–3* and *pl2–3* slightly thickened, *av1* and *pv1* stout, spur-like (apically blunt), *al1*, *pl1* and *md* stout and spine-like, *mv*, *av2* and *pv2* thick; tarsus III with *pl2–3* slightly thickened, *ad2*, *pd2*, *pv2* and *al3* thickened, *av1–2*, *pv1–2*, *al1–2*, *mv* and *pl1* thickened, somewhat spine-like, *md* stout, spine-like; tarsus IV with most setae thickened and of moderate length, and *pl2–3* somewhat spur-like, *pl3* half as long as *pl2*, *pd2* slightly longer than other setae, *ad3* and *pd3* short and thin. Coxa I bearing two gland pores (*gc*) (Fig. 30).

Material examined. Holotype: female, northern Iran, Mazandaran Province, Tonekabon County, Tirom Forest (40° 62' 69" N; 47° 11' 26" E), 1465 m above sea level, from decayed wood of Beech trees, 2 June 2010, coll. Y. Ahangaran, deposited in ACISTE. One paratype female with same collection data, deposited in ACISTE.

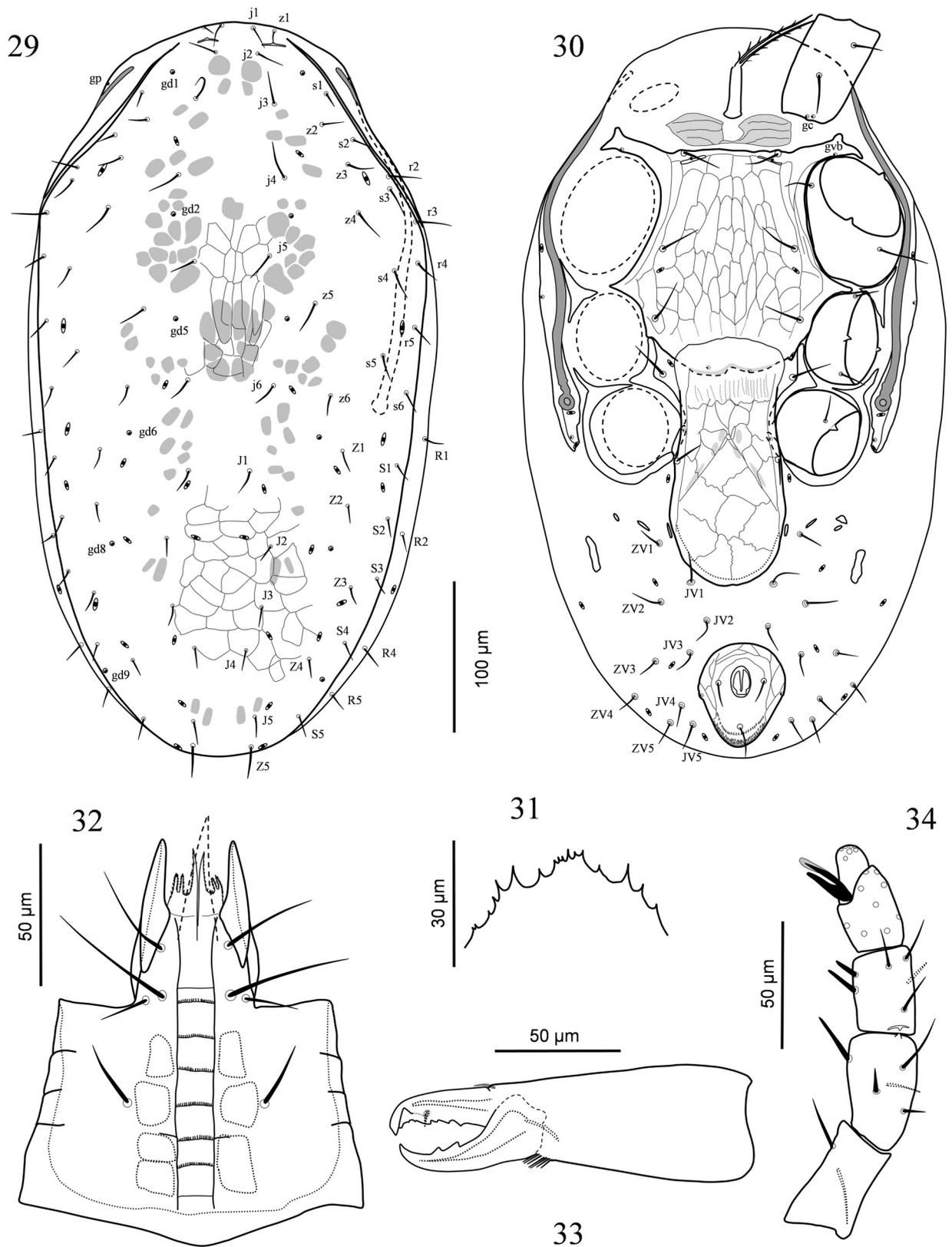
Etymology. The species is named in honour of Yazdanfar Ahangaran (General Office of Natural Resources of Mazandaran Province, Nowshahr, Iran), for his help in collecting these mites.

Remarks. *Gaeolaelaps ahangarani* can most readily be distinguished from all other species in the genus by the following combination of characters: very short dorsal setae, particularly so in the opisthonotal region; the absence of *Px2–3*; only three pairs of marginal setae on soft lateral cuticle; epigynal shield with posterior cells with sinuous borders; an anal shield broadly rounded anteriorly, with the anus almost entirely in the anterior half of shield; and modified leg setae, such as *pl2–3* of tarsus IV and *pl1* of tibia IV spur-like, and *ad3*, *pd3* very short.

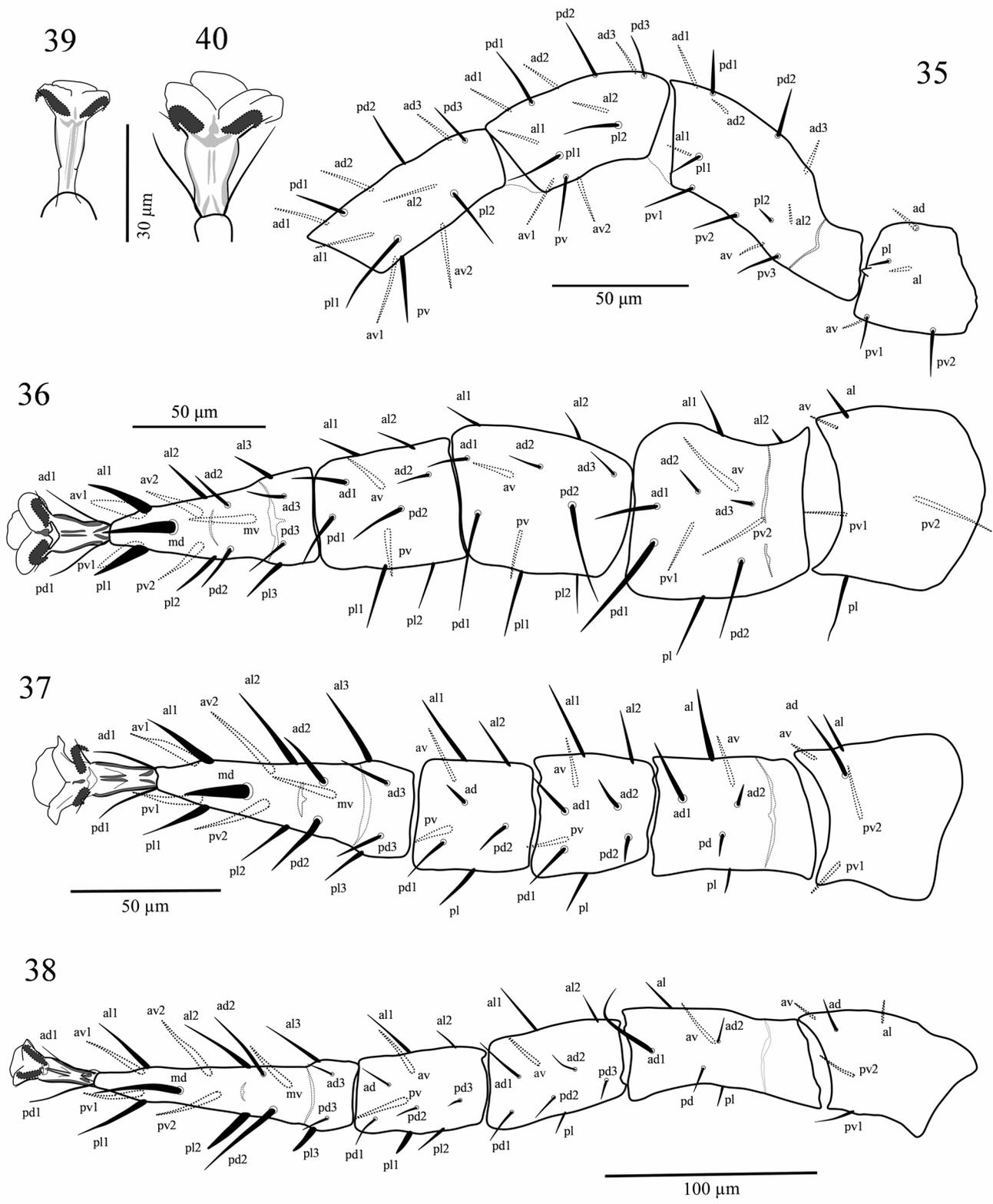
Many other *Gaeolaelaps* have short dorsal setae, but the large majority of them possess *Px2–3* setae, rarely have the anal opening positioned as anteriorly as in the new species (based on species descriptions), and have other distinctive characters. For instance, *G. tenuisetus* Rosario (1981) has short setae, but seems to possess *Px2–3* (at least on one side; the illustration is difficult to interpret), and has an epigynal shield considerably expanded posteriorly (nearly parallel-sided in *G. ahangarani*), and a subtriangular anal shield that is relatively flat anteriorly. *Gaeolaelaps analis* (Karg, 1982) has a broader, more oval dorsal shield, *Px2* present, and a broader anal shield with anus located on its posterior half. *Gaeolaelaps gleba* Karg, 1979 (= *G. glabra* Karg, 1978) has *Px2–3* setae as well as shortened peritremes.

The few *Gaeolaelaps* species lacking *Px2–3* setae that we are aware of are distinguished from *G. ahangarani* by at least a few characters. *Gaeolaelaps queenslandicus* and *G. angustus* (Karg, 1965) have a posteriorly tapered dorsal shield, longer dorsal setae, a three-tined palp apotele, and a deutosternum narrowing posteriorly (based on Costa, 1966). Based on the illustrations, *Gaeolaelaps tengi* (Gu & Bai, 1991) may appear similar to the new species, but it has longer setae, a broader, subtriangular anal shield that is flatter anteriorly, a sternal shield truncate posteriorly, with *st3* setae near the edge, a post-stigmatic region of peritrematal shield almost reaching the posterior margin of coxae IV (shorter in *G. ahangarani*), and a narrower deutosternal groove. *Gaeolaelaps wufengensis* (Liu & Ma, 2003) also has relatively short setae, but possesses an epigynal shield ornamented by circular lines posteriorly, seven rows of deutosternal denticles, and an acuminate epistome. *Gaeolaelaps barbarae* (Strong 1995), associated with funnel-web spiders, has a more oval dorsal shield, and much longer setae, and a subtriangular epistome. Other arthropod associates also lack *Px2–3* (e.g. *G. disjuncta* Hunter & Yeh, 1969, *G. circularis*, *G. ruggi*, and *G. rarosae* Rosario, 1981), but have fewer setae on the dorsal shield (<37), longer setae, and often a more oval dorsal shield, a shorter, more compact sternal shield, and/or an epigynal shield with distinct ornamentation.

Gaeolaelaps ahangarani shares characters with *G. aculeifer* and relatives (see Discussion), such as the spine-like setae on tarsi, especially of legs II–III, the deutosternal groove with numerous denticles per row, and similarly shaped and ornamented dorsal, sternal, and epigynal shields (although these shields are similar in several other *Gaeolaelaps* species). Like *G. aculeifer*, it also has internal malae with two pairs of short lateral projections. However, it differs from *G. aculeifer* and relatives by lacking *Px2–3* setae, and having only three marginal setae laterad of the dorsal shield, a fixed cheliceral digit with fewer teeth proximal to the pilus dentilis, and shortened leg setae (see Diagnosis). At first glance, the sinuous borders of the cells of the epigynal shield appear as a fairly unique character of *G. ahangarani*. However, we suspect that such ornamentation occurs in other species, which we may have overlooked, or that are still undescribed.



FIGURES 29–34. *Gaeolaelaps ahangarani* Female. 29. Dorsal idiosoma; 30. Ventral idiosoma; 31. Epistome; 32. Subcapitulum; 33. Chelicera; 34. Palp.



FIGURES 35–40. *Gaeolaelaps ahangarani* Female. 35. Leg I, posterolateral view; 36–38. Legs II–IV, dorsal view; 39. Ambulacrum I; 40. Ambulacrum II.

Discussion

Worldwide, approximately 100 described species may be considered as *Gaeolaelaps* species. Since Beaulieu's review (2009), several new species of *Gaeolaelaps* or *Hypoaspis* (*Gaeolaelaps*) have been described, and all those that we know of were mentioned in remarks sections above or within the genus diagnosis. However, some species that may belong to *Gaeolaelaps* were omitted from Beaulieu (2009), including the following species: *Hypoaspis arabicus* Hafez, Elbadry & Nasr, 1982, *H. bregetovae* Shereef & Afifi, 1980, *H. cucumerus* Nasr & Nawar, 1989, *H. gergus* Hafez, Elbadry & Nasr, 1982 (a possible junior synonym of *G. aculeifer*), *H. orientalis* Hafez, Elbadry & Nasr, 1982, *Androlaelaps parasingularis* Gu & Wang, 1996, *H. petrovae* Shereef & Afifi, 1980, *A. singularis* Wang & Li, 1965, *A. trifurcatus* Wang & Li, 1965, which appears very close to *G. angustus* and *G. queenslandicus*, and *H. xiningensis* Ma & Lin, 2009. Some of these species may require re-examination or redescription before their taxonomic affinity can be ascertained and an accurate diagnosis can be made. *Hypoaspis koseii* Hafez, Elbadry & Nasr, 1982 may also belong to *Gaeolaelaps*, but this is uncertain given that the authors stated that it is closely related to *H. hermonensis* Costa, 1969, which has a smooth epistomal margin (the epistome of *H. koseii* was not described). In addition, the following species are provisionally excluded from *Gaeolaelaps*. The cockroach associate *Hypoaspis* (*Gaeolaelaps*) *variabilis* Faraji & Halliday, 2009 has a nearly entirely smooth epistomal margin, thicker peritremes, and lacks one or both ventral setae on genu III, suggesting that it does not belong to *Gaeolaelaps*; *H. variabilis* also has a maximum of 35 pairs of setae on the dorsal shield, with *z3* and *z6* always and *Z2* nearly always absent (note that such loss of dorsal setae has unclear significance, and similar losses occur in other species classified as *Gaeolaelaps*, see Beaulieu, 2009). *Gaeolaelaps saboorii* Joharchi & Babaeian, 2014 is also excluded from *Gaeolaelaps* on the basis of its elongate epistome that has an almost entirely smooth margin, its peritrematal shield free anteriorly, and its internal malae characterised by long, blunt fringes (reminiscent of certain *Cosmolaelaps* and *Laelaspis* species; Beaulieu & Kazemi, personal observations). Additional characters that make it more atypical within *Gaeolaelaps* include the ornamentation of its epigynal shield, the presence of *gd4* (rarely seen so far in *Gaeolaelaps*), and a considerably elongate labrum. Although some of these characters might have evolved due to association with insects (as well as the suboval dorsal shield, and the sternal shield being relatively broad and posteriorly concave), we suspect that some of them reflect a taxonomic affiliation of *G. saboorii* with other hypoaspidines distinct from *Gaeolaelaps*. Both *Hypoaspis egenus* Berlese, 1918 and *H. spiculifer* Berlese, 1918 were classified with the *Gaeolaelaps* species group by Van Aswegen & Loots (1970); we exclude them from *Gaeolaelaps* because *H. spiculifer* sensu Van Aswegen & Loots (1970) has an almost entirely smooth epistome (that of *H. egenus* was not described) and because these two names are probably synonyms, given the striking similarity of the two descriptions: both show long dorsal setae, sternal shield smooth in posterior half, *st1* inserted on weak presternal area, para-anals inserted near posterior margin of anal opening, and epigynal shield with two inverted V-shaped lineae. Although *Hypoaspis womersleyi* Domrow, 1957 is *Gaeolaelaps*-like, the apparently edentate chelicerae of the female (as described by Domrow) and the epigynal shield almost touching the anal shield, make its taxonomic affinities uncertain. *Hypoaspis decellei* Van Driel *et al.*, 1977 was classified within the *Gaeolaelaps* species group (sensu Van Aswegen *et al.*, 1970), but some characters, including a smooth epistome margin, genu IV with two posterolateral setae, and highly reduced male cheliceral digits in contrast to a salient spermatodactyl, indicate that it probably belongs to *Androlaelaps* or a related taxon. *Hypoaspis solimani* Nawar, Shereef & Ahmed, 1993, appears not to be a laelapid, considering the well-defined ventrianal shield of the male (female leg chaetotaxy also differs from *Gaeolaelaps*, in lacking one *pl* seta on genu II, and having one extra *ad* on genu III, according to the description).

Genus concept, diagnostic characters, and species groups. *Gaeolaelaps*, as currently defined, may not be monophyletic, since our concept is based on a combination of plesiomorphies and homoplasies that occur in other laelapid genera. This is probably why Evans & Till (1979) refrained from giving generic status to *Gaeolaelaps* (and clumping it with *Hypoaspis* s. str., *Alloparasitus* and *Hypoaspisella*), while giving generic status to most other taxa mentioned as *Hypoaspis* subgenera in Evans & Till, 1966 (see also Till, 1963, pp. 11–12). However, the same way that *Hypoaspis* sensu stricto (Costa, 1971, Joharchi & Halliday, 2011), *Stratiolaelaps* (Walter & Campbell, 2003) and *Laelaspis* (Hunter, 1961; Joharchi *et al.*, 2011) can be clearly and relatively narrowly defined as presumably monophyletic groups, it might be possible to do the same for *Gaeolaelaps*, perhaps in a narrower concept than presented above (e.g. as was done in Walter & Oliver, 1989). It is indeed possible that some species considered herein as *Gaeolaelaps* that depart from the basal morphological plan of *Gaeolaelaps* may best be transferred into

other, new genera; but, this should be done only if reliable, carefully studied characters are identified to define such genera as natural, monophyletic groupings. However, whether the concept of *Gaeolaelaps* is narrowed down or not in the future, using *Gaeolaelaps* at the genus level results in some species being relegated into a probably polyphyletic '*Hypoaspis*' sensu lato, some of which may not be closely related to either *Gaeolaelaps* or *Hypoaspis* (s. str.), such as, for example, species with a smooth epistome. Finding appropriate groupings for those 'orphan' species will be needed, unless we revert to a broader, looser concept of *Hypoaspis* (as done in other works). Describing species as *Hypoaspis* sensu lato may not help taxonomic progress, unless the description is accompanied by a careful diagnosis and a clear taxonomic context that examines characters shared with the species that are most similar morphologically.

Inevitably, steps towards a better understanding of *Gaeolaelaps* will involve sorting species into what we believe to be natural groups of close relatives. Karg's division of *Hypoaspis* subgenera (e.g. *Pneumolaelaps*, *Gaeolaelaps*) into species groups is at least in part artificial—and Karg was aware of this, having created them for their practicality in distinguishing species via more restricted, circumscribed species keys (Karg, 1979, 1989a, 1989b). The defining features of Karg's species groups are at least in part homoplasious, occurring sporadically in unrelated taxa; other times more than one 'diagnostic' character occurs in a single species, qualifying it for more than one species group. *Gaeolaelaps khajooii* is a good example, having 0–1 *Jx* seta, shortened peritremes, and a relatively tapered dorsal shield. These three features individually define three of Karg's species groups. Unpaired median dorsal setae *Jx*, the key character to define members of the *schusteri* species group, occur sporadically in many hypoaspidine genera, and are sometimes present or absent in different individuals of one species (e.g. Evans & Till, 1966; Ishikawa, 1982; Strong & Halliday, 1994; Faraji & Halliday, 2009; also see *G. khajooii*). Besides sharing the presence of one or more *Jx* setae, species considered in the *schusteri* species group (e.g. Karg, 1979, 1982, 1987, 1989a, see also Karg 1989b for two other *Hypoaspis* (s. lat.) species having *Jx* setae) represent a morphologically heterogeneous grouping. However, as stated by Costa (1974), at least two species are related, namely *G. schusteri* and *G. theodori*, because of their general similarity and because they share uncommon characters such as an epigynal shield posteriorly ornamented by eight long narrow cells, sternal poroids *iv4* (*pst4*) medially positioned on the posterior margin of the sternal shield, and males with holovenral shield strongly 'eroded' laterally.

Karg's *angusta* species group (Karg, 1979, 1982; see also Nemati & Kavianpour, 2013) includes some species that are closely related. For instance, *G. angusta* (Karg, 1965), *G. queenslandicus*, and *G. fishtowni* (Ruf & Koehler, 1993) are characterised by a dorsal shield tapering from setae *r3*, soft dorsal cuticle with 6–7 marginal (*r-R*) setae and a few (*UR*) submarginals, deutosternal groove narrowed posteriorly, cheliceral fixed digit with serration of teeth proximal to the pilus dentilis, spine-like setae on tarsi II and IV, femur II with a strong spur-like *av* seta, and the absence of one or both of opisthotal setae *Px2–3* (*Zx1–2* of other authors). *Gaeolaelaps tarsalis* (Bhattacharyya, 1968) appears morphologically similar, although it possesses *Px2–3* and has seven rows of deutosternal denticles. The species *G. angustiscutatus* and *G. elongatus* Hirschmann, *et al.* 1969, may also be related to the species mentioned above based at least on the dorsal shield tapering posteriorly; otherwise, they are clearly more related to each other based particularly on their serrate cheliceral movable digit, but also on their truncate epistome with three short projections, and narrowly rounded epigynal shield (or somewhat flat posteriorly) (these two species names may be synonyms, as suggested by Bregetova, 1977). Given that most *Gaeolaelaps* species and species of many hypoaspidine and laelapine genera possess *Px2–3*, as well as *Mesolaelaps* and *Myonyssus* (e.g. Evans & Till, 1966; Tenorio & Radovsky, 1974), the presence of *Px2–3* is probably plesiomorphic in Laelapidae (Walter & Campbell, 2003), and therefore is not very meaningful; the absence of one or both *Px* setae, might, however, indicate close relationships in some cases, if combined with other shared characters. Tarsal spines on legs II and IV are the main feature defining the *aculeifer* species group (see group concepts and keys in Karg, 1979, 1982; also key in Karg 1989a). However, some species not characterised by key features of other groups were apparently relegated to the *aculeifer* group, despite not having tarsal spines (e.g. *G. kargi* (Costa, 1968); *G. praesternalis*), making the group particularly heterogeneous. Because of poor species descriptions, few of the species in the group can be established as close relatives. *Gaeolaelaps aculeifer*, *G. oreithryae*, and *G. deinos* (Zeman, 1982) are related species, based on their conspicuous tarsal spines, especially on tarsus II (e.g. *all*, *pl1*, and ventral setae) and tarsus IV (most setae), a broad dorsal shield, slightly tapering past level of seta *r3*, a small, pear-shaped anal shield, 7–8 marginal and submarginal setae on soft lateral cuticle, deutosternal rows each with numerous denticles (>10), and fixed cheliceral digits with a serration of about 5–8 small teeth flanked by two larger

teeth, proximally to the pilus dentilis. *Gaeolaelaps concisus* (Womersley, 1956) also seems related to these species, although the original description indicates many fewer setae on the dorsal shield (about 25 pairs), and did not include the chelicerae or the deutosternum. *Gaeolaelaps gillesspiei* also appears similar although its dorsal shield is more parallel-sided, and its fixed cheliceral digit has a more irregular serration with 2–6 teeth. Tarsal spines, especially on leg II, also occur in some species of other genera, including of the morphologically similar genus *Hypoaspis* s. str., as well as other hypoaspidines associated with scarab beetles such as *Mumulaelaps* Clark & Hawke, 2012, and some members of (though not as strong and blunt apically as in some *Gaeolaelaps* and *Hypoaspis* s. str.) *Angosomaspis* Costa, 1971, *Dynastaspis* Costa, 1971, *Lucanaspis* Costa, 1971, and *Coleolaelaps* Berlese, 1914 (Costa & Hunter, 1970). Despite this, tarsal spines, when representing the same setae between species, as well as other modifications of leg setae (see the genus detailed diagnosis above), may indicate species relationships, if in combination with other shared characters.

The presence of peritremes that are shortened anteriorly, exhibited by members of Karg's *similisetae* group (species keys in Karg, 1979, 1982, 2006, Nemati & Mohseni, 2013; see also *G. praesternaloides* (Ma & Yin, 1998) and *G. cucumerus*), is probably meaningful in some cases. Several species (e.g. *G. nolli* (Karg, 1962), *G. similisetae* (Karg, 1965), *G. latopuga* (Karg, 2006), *G. verticis* (Karg, 1978), *G. postreticulatus* (Xu & Liang, 1996), *G. orbiculatus*, *G. khajooii*, *G. zhoumanshuuae*) with short peritremes also have few marginal setae, including *R1* and 1–2 more *R* setae inserted considerably posteriorly, and only 7 or 8 opisthogastric (*Jv*, *Zv*) setae. Some of those species have a relatively elongate dorsal shield, being more or less parallel-sided, whereas others (*khajooii*, *G. zhoumanshuuae*, and undescribed species) have the posterior region of their dorsal shield relatively narrower and similarly shaped. Moreover, among those species, the anal opening is often positioned in the posterior half of the anal shield, and with para-anal setae inserted at the level near that of the anterior margin of anus. These species also tend to have elongate setae on tarsus IV (especially *pd2–3*, secondarily *ad2–3*; a character shared by *G. kargi* and *G. iranicus* Kavianpour & Nemati, 2013). These various combinations of characters may indicate close relationships.

As mentioned above, the shape of the anal shield and the position of the anal opening and circumanal setae could be informative. The cribrum is of particular interest, and it appears to vary among species, with some species characterised by a file of spicules extending considerably forward, as far as reaching (or approaching) the level of the para-anal setae. This is the case for *G. aculeifer*, *G. khajooii*, *G. jondishapouri*, *G. queenslandicus*, and undescribed *Gaeolaelaps* species. Brief examinations of specimens of other undescribed *Gaeolaelaps* species, and of other hypoaspidine genera showed that at least some species do not have such anterior extension of spicules. Similar anterolateral extensions of the cribrum have been noticed in other Mesostigmata, such as macrochelids (Özbek & Bal, 2013). This character is unfortunately largely overlooked in species descriptions of Laelapidae.

We suspect that the epigynal shield ornamentation, in combination with its shape and breadth, will provide additional taxonomic signal, and help decipher species groupings, if not to better define *Gaeolaelaps* and related groups (e.g. see Shaw, 2012 for *Nidilaelaps*). Some species deviate from the more common reticulation of the epigynal shield observed in *G. aculeifer* and other species (see detailed diagnosis of the genus above).

Other unusual characters. The externalmost part of the sockets of setae that are inserted on soft idiosomal cuticle is characterised by various degrees of sclerotisation. At a higher sclerotisation level, they may appear as small platelets, as seen for the dorsomarginal (*r-R*, *UR*) and opisthogastric (*Jv*, *Zv*) setae of *G. jondishapouri*. Such sclerotised rings (sometimes tapering into points at one, or two opposite, ends) surrounding the setal sockets are not often seen in Laelapidae, at least not in species descriptions. A quick survey of the literature and of specimens at hand indicate that similar platelets surrounding dorsomarginal and/or opisthogastric setae occur in other laelapids, such as some *Laelaspis* spp. (e.g. Hunter, 1964), *Bisternalis* (Hunter, 1963), *Laelaps hilaris* Koch (sensu Evans & Till, 1966), *Hyperlaelaps microti* (Ewing) (sensu Evans & Till, 1966), *Nidilaelaps* (Shaw, 2012; mentioned as 'baseplates'), and an undescribed species of *Laelaspisella* (Kazemi, personal observations). Similar sclerotisation occurs in other Mesostigmata, such as some *Lasioseius* species (Blattisociidae), which show cone-like, sclerotised 'protuberances' on which the opisthogastric and *R* setae are sitting on (also similar to protuberances of the dorsal shields on which setae are inserted; Lindquist, 1971). In contrast, more extensive, well-defined platelets bearing individual idiosomal setae, especially on the margins of the dorsum, occur in adults of a number of Mesostigmata, especially in the Sejida, such as *Sejus* (Sejidae) and *Uropodella* (Uropodellidae), and several genera of Uropodina, such as *Polyaspinus* (Trachytidae), *Thinozercon* (Thinozerconidae), *Nothogynus* (Nothogyniidae), Trigynaspida, e.g. *Saltiseius* (Saltiseiidae), and a few, mostly basal Gamasina, such as Heatherellidae and Arctacaridae (*Proarctacarus*), but also in Dermanyssidae, such as *Saprosecans* (Halolaelapidae; although in this case, 2–3 setae are borne on each of four mesonotal platelets (Karg, 1964)). In most Gamasina however, well-sclerotised platelets

bearing dorsal or opisthogastric setae individually are rare, or are limited to expanded sclerotised rims of setal sockets such as those seen in *G. jondishapouri* and *Laelaspis* spp. The function of these more sclerotised rings (as well as more extensive platelets) around setal bases may be to reduce the probability of ripping the surrounding cuticle, in case of severe bending of the setae.

Barbs on setae, as seen on nearly all dorsal and some opisthogastric setae of *G. jondishapouri*, are also unusual for *Gaeolaelaps*. Otherwise, they are rarely considered in descriptions. We have seen inconspicuous barbs on Z5, S4–5 and/or J4–5 of specimens of several *Gaeolaelaps* species, as well as of species of *Hypoaspis* s. str. (Kazemi, personal observations). *Gaeolaelaps* (?) *barbatulae* (Karg, 1989) has several barbs (seven on the illustration) on short, thickened Z5 setae, and at least three species of *Hypoaspis* s. lat. that we know of have most dorsal and some opisthogastric setae pilose or barbed: *H. longichaetus* Ma, 1996, *H. pinnae* Karg, 1987, as well as *H. kassai* Van Aswegen & Loots, 1970, which has feathered or bipectinate setae. Barbs on the posterior dorsomarginal and/or opisthogastric setae are also present in variously distant laelapids such as some *Cosmolaelaps* (Moriera *et al.*, 2014), *Coleolaelaps*, *Pseudoparasitus*, many *Laelaspis* (Kazemi & Beaulieu, personal observations; see also Joharchi *et al.*, 2012), *Androlaelaps* (personal observations; see also Evans & Till, 1966), *Bisternalis* (Baker *et al.*, 1983); *Nidilaelaps*, *Laelapsella* (Shaw, 2012), *Notolaelaps* (Shaw, 2011), *Juxtalaelaps* (Domrow, 1978, Dowling *et al.*, 2007), and more extensively on the idiosoma and legs of at least some *Mesolaelaps* (Tenorio & Radovsky, 1974), haemogamasines and acanthochelins (Radovsky & Gettinger, 1999). Accounting for the presence and the extent of barbs on idiosomal, gnathosomal and leg setae in species description may later help to shed light on the phylogenetic significance of these attributes in laelapids.

The taxonomic potential of gland pores and poroids (lyrifissures). Athias-Henriot (e.g. 1969b, 1969c, 1970, 1975, 1976) studied the external adenotaxy (cuticular glands), poroidotaxy ('poroids'; putatively all cuticular proprioceptors), and sigillotaxy (sigilla, i.e. cuticular imprints of muscle insertions) of various Mesostigmata, including at least some Trignyaspida, Sejida, Epicriidae, Zerconidae, Parasitidae, and many Dermanyssidae. Based on her studies, she developed a system of notation for these cuticular organs (Athias-Henriot, 1970, 1971, 1973), which she further modified (Athias-Henriot, 1975) using representatives of Phytoseiidae (Amblyseini). Whereas poroids have had limited use, the presence, position and shape of gland openings on the dorsal shield has shown some usefulness in distinguishing between species of Mesostigmata, particularly zerconids (e.g., Sellnick, 1958), and phytoseiids, as shown in species keys (e.g. Chant & Yoshida-Shaul, 1987; Chant, *et al.*, 1974; Ragusa & Athias-Henriot, 1983; but see Tixier *et al.*, 2011 for intraspecific variation), and used for defining species groups (Beard, 2001) or delimiting morphologically cryptic species (Beard, 1999). Among ventral pore-like structures (including poroids and gland pores), the pair of 'preanal' pores *gv3*, located on the ventrianal shield (or on or near the anal shield in other groups), is commonly used for species identification of phytoseiids and virtually always included in species descriptions. However, despite the work of Athias-Henriot and of others (particularly Krantz & Redmond, 1987 and Johnston & Moraza, 1991), many (if not most) species descriptions of Phytoseiidae (e.g. see Denmark & Evans, 2011) and of other mesostigmatan families lack any detailed account of the 'pores' (often mentioned as such, without distinguishing true pores and poroids) on the idiosoma other than *gv3* (in the case of phytoseiids), and those are often incompletely illustrated. In other words, Athias-Henriot's notation system (or even alternative systems such as Johnston & Moraza's, 1991) is very infrequently used.

Using the phytoseiid model presented by Athias-Henriot (1975; see Beard 2001 for a modified version of Athias-Henriot's system, and see Method for discrepancies), we attempted to identify all gland pores and poroids on the dorsal shield of several described and undescribed *Gaeolaelaps* spp., with apparent success. These unpublished preliminary data (Beaulieu & Kazemi) show that the dorsal idiosomatic pores and poroids of *Gaeolaelaps* have positions, in relation to setae, similar to those of phytoseiids, suggesting that they are homologous. All *Gaeolaelaps* and other Laelapidae species examined had 16 poroids, just like the basal plan of Phytoseiidae. However, whereas the hypothesised full complement of gland pores is seven (*gd1–2*, *gd4–6*, *gd8–9*), as in some Phytoseiidae, examined *Gaeolaelaps* species had four to six gland pores, nearly always lacking *gd4* (typically located posterad or posterolaterad of *s4* when present), and sometimes also *gd2* (posterolaterad of *j4*) and *gd6* (posteromedial of *z6*). The maximum of six gland pores was seen in specimens of *G. aculeifer*, *G. jondishapouri*, *G. ahangarani*, *G. oreithyiae* (seven pores in some specimens, including *gd4*), *G. angusta*, *G. queenslandicus* and *G. cf. deinos*, and the minimum was observed in *G. khajooii*, as well as *G. praesternalis*, *G. nollii*, *G. kargi*, *G. iranicus* and a few undescribed spp., with both *gd2* and *gd6* absent. *Gaeolaelaps invictianus* Walter & Moser, 2010, possesses gland pore *gd5*, although it was missed and not illustrated by the authors (D.

Walter pers. comm.). In terms of presence/absence, gland pores also appear as the most variable structures in phytoseiids and laelapids, as opposed to the constant 16 poroids. For instance, gland pores *gd2*, *gd4*, *gd5* and *gd8* are present and conspicuous in some *Neoseiulus* species and absent (or not visible) in others (Ragusa & Athias-Henriot, 1983; Beard, 2001; Tixier *et al.*, 2011; Cargnus *et al.*, 2012); *gd2* and *gd5* were also considered absent in various other Gamasina (Athias-Henriot, 1971). Whereas *gd5* was present in nearly all species of *Gaeolaelaps* that we have seen, it was absent (or not visible) in some laelapids examined, including specimens of *Androlaelaps*, *Laelaps*, and *Hyperlaelaps*. Moreover, whereas *gd4* seems rare in *Gaeolaelaps*, it is present in at least some members of several other hypoaspidine genera (e.g. *Cosmolaelaps*, *Holostaspis*, *Hypoaspis* s. str., *Laelaspis*, *Laelaspisella*, *Ololaelaps*, *Pseudoparasitus* spp.; *Euandrolaelaps karawaiewi* (Berlese, 1903); '*Hypoaspis*' *giffordi* Evans & Till, 1966; and '*Hypoaspis*' *lubrica* Voigts & Oudemans, *sensu* Evans & Till, 1966; *Stratiolaelaps* spp., Walter & Campbell, 2003) and laelapine genera (*Androlaelaps* spp., *Hyperlaelaps* sp., *Laelaps* sp.). This leads us to hypothesise that the presence or absence, and the position, of certain gland openings could help define supraspecific laelapid taxa, in addition to providing additional diagnostic characters at species level.

Evans & Till (1965) stated that the basic adult and deutonymphal complement of 'pores' (including poroids) on the dorsal idiosoma was 22 pairs (excluding poroid *Rp*, or *idR3*, on the soft lateral cuticle, at a position between *R3* and *R4*, when these setae are present), exemplified by *Laelaps* species (as shown on their Fig. 9, p. 265). However, *gd5*, typically present posteromesad of seta *z5*, is absent on their figure, and it is also absent in the specimens of *Laelaps* and *Hyperlaelaps* we examined. We have seen 23 pairs of 'pores' on specimens of some laelapid species, for instance *Stratiolaelaps scimitus* (Womersley), *Laelaspis* sp. nr *vitzthumi* (Womersley 1956), and *C. vacua* (Michael, 1891), including 16 poroids and seven gland pores, as seen in some phytoseiids.

Pore-like structures on the dorsal shield of other dermanyssine taxa (Dermanyssiae) appear to be, essentially, compatible with Athias-Henriot's system. For instance, the complement of 23 'pores' (16 poroids, seven gland pores) is also present in at least some members of Eviphididae (*Crassicheles*, Athias-Henriot, 1980), Ascidae (e.g. *Anephiasca*, Athias-Henriot, 1969a; *Antennoseius*, Beaulieu *et al.*, 2008; Moraza & Kazemi, 2009), Blattisociidae (*Orthadenella*, Athias-Henriot, 1973; *Fungiseius clavulisetis* Moraza & Lindquist, 2011), Melicharidae (*Spadiseius*, Lindquist & Moraza, 2008), and Antennochelidae (*Antennocheles*, Lindquist & Moraza, 2014; however, *id6* may have been displaced anteriorly to the *j5*–*z5* region, or represent a de novo poroid). The work by Hirschmann & Wiśniewski (1982) indicates that 16 similarly positioned poroids, and five pores, are present in at least some Digamasellidae, and putatively 16 poroids and at least four pores appear present in *Arctoseius* (Ascidae; Makarova & Lindquist, 2013). The innovative study by Krantz & Redmond (1987) indicates that at least some Macrochelidae have the normal complement of 16 poroids as well as six gland pores (lacking *gd4* or *gd5*). However, although the number of poroids appears to be constant in laelapids (based on those examined) and perhaps in other families (e.g. Phytoseiidae), some deficiencies occur among other Dermanyssiae. For instance, five poroids are apparently missing on the dorsal shield of *Opilioseius grallator* Lindquist & Moraza (2010; Blattisociidae), which bear only 11 poroids (despite having the full complement of seven gland pores). One poroid, *id1*, which is typically elongate and lyriform, is missing in *Mycolaelaps maxinae* Lindquist, 1995 (Melicharidae), with the remaining 15 poroids as well as five pores present in typical positions. Athias-Henriot (1971) noted the absence of poroid *id6* in various Mesostigmata. Interestingly, Lindquist & Evans (1965) illustrated 24 pore-like structures on their schematic representation of idiosomal dorsum (which was based on *Lasioseius allii* Chant, 1958) of holotrichous Gamasina, including an extra pore-like structure posterolaterad of *j5*. An extra poroid, posterad of *s3*, was also illustrated for *Lasioseius corticeus* Lindquist (1971; see also Lindquist & Moraza, 1998); however, examination of *L. allii*, *L. corticeus*, *L. floridensis* Berlese (with the male showing the same extra poroids near *j5* and *s3* in Britto *et al.*, 2011), and other *Lasioseius* spp. suggest that this is erroneous and that there is no poroid in this region in *Lasioseius* (F. Beaulieu personal observations, E. Lindquist pers. comm.).

These observations suggest that these 23 pairs of poroids and gland openings are the general, presumably plesiomorphic, plan for the hyporder (or subcohort) Dermanyssiae. Although considerable effort may be required to extrapolate those observations for the entire Order Mesostigmata, establishing homologies across the infraorder (or cohort) Gamasina could be attempted based on interpretation of Athias-Henriot's research. For instance, the descriptions of some Zerconidae (Athias-Henriot, 1976; Lindquist & Moraza, 1998; Moraza *et al.*, 2009; Díaz-Aguilar & Ujvári, 2010) indicate a relatively similar organisation of gland pores and poroids, if one takes into account poroid *idl2* and gland pore *gd7* (both lacking in Athias-Henriot's 1975 illustration), which appear present in some Zerconidae (*gd7*=*Po2*, Athias-Henriot, 1980, located laterally in the opisthonotal region). These additional

poroid and gland pore are present in an earlier illustration of Athias-Henriot (1971), although *idl2* was not labelled. Gland pore *gd7* appears absent in at least many Dermanyssidae (Athias-Henriot, 1971). Also, the putative duplication of some poroids (Athias-Henriot, 1971) can help interpret the poroidotaxy of zerconids, some of which appear to have two, nearly contiguous, poroids *idl3* (Athias-Henriot, 1980; Johnston & Moraza, 1991). Similar analyses could be made for *Coprozercon* (Coprozerconidae; Moraza & Lindquist, 1998), as well as for *Proarctacarus* (Arctacaridae), although several poroids are evidently lacking on the opisthonotal region of the latter (Makarova, 2003). In contrast, Epicriidae present new difficulties in homologising pore-like structures, with some *Adenoepicrius* species having only nine pairs of poroids (excluding the lateropeltidial or peritrematal region), but as many as 19 pairs of gland pores on the dorsal shield (Moraza 2005).

The position of poroids and gland pores appears to differ only moderately among laelapid species, and if our putative homologies are correct, even among dermanyssine families. Although it is possible that some of them are not homologous between families, the most parsimonious hypothesis is that they are homologous, as opposed to a pore lost and another added instead, which would require two evolutionary steps, instead of a rather simple displacement of the structure. Among laelapids, some variations in position involve, for instance, pore *gd1*, which is usually posterolaterad of seta *j2*, but we have seen it more laterally positioned, very close to the shield margin, in which case it can be more difficult to discern. Pore *gd8*, sometimes the most conspicuous pore-like structure in some laelapids, such as *G. gillespiei* and *G. segregatus*, also varies substantially in position. It is most often located in the region between *Px2–3* and *Z2–3*, but can be as far anterior as the level between *Z1–2* (in *G. aculeifer*), and as far posterior as the area mesad of *S4* (in *G. jondishapouri*, *G. khajooii*). Identifying poroids and gland pores in groups characterised by hypertrichy (e.g. haemogamasines), or by strongly sculptured shields (e.g. some *Antennoseius* and *Lasioseius* species), may represent some difficulties, but we believe they can be resolved (e.g. Beaulieu *et al.*, 2008; Moraza & Kazemi, 2009; Lindquist & Makarova, 2012). In the case of species having strongly sclerotised adults, pore-like structures may be more readily studied on the usually less strongly sclerotised deutonymphs, which would presumably have essentially or nearly the same pores and poroids as their corresponding adults, as it is usually the case for setae (e.g. Lindquist & Moraza, 2008, 2010, 2014).

We have herein used the system of notation developed by Athias-Henriot because of the high similarity between the dorsal pores and poroids of the phytoseiid model (Athias-Henriot, 1975) and those of Laelapidae. On the other hand, the system developed by Johnston & Moraza (1991) for zerconids has some appeal, particularly by giving to each pore-like structure a name that is indicative of the nearest seta. Moraza (e.g. 2005) and her collaborators (e.g. Lindquist and Moraza, 2008; Moraza & Kazemi, 2009) have applied this system to diverse gamasine taxa. The two notation systems could be reconciled in the future, and correspondence in notation established. The system suggested by Hirschmann (1960) and Hirschmann & Wiśniewski (1982) for Digamasellidae may also have its use (and see Evans & Till (1979) for an outline of Hirschman's system; note that Krantz & Redmond (1987) appear to have used the Evans & Till (1979) notation for their own study), but unfortunately does not distinguish between poroids and true (gland) pores. In any case, comparative study of gland pores and proprioceptors (poroids) across mesostigmatan taxa may give us useful insight in their relationships, as implied by Athias-Henriot's research (e.g. 1971). One way to get there faster is to systematically and accurately include idiosomatic pore-like structures in the description and/or illustration of species, and to (at least attempt to) distinguish gland pores from poroids. Although both poroids and gland pores vary considerably in aspect across species, and even within a species (e.g. some poroids are quite distinct from others at different locations on the dorsal shield), gland pores share similarities, and are often more conspicuous, and sometimes brighter in their center (especially *gd8* in laelapids, as well as *gd9*, which sometimes opens more laterad), and extend deeper in the body than poroids, with often their diverticulae, or their calyx, discernible beneath (see Athias-Henriot (1969b), Alberti & Coons (1999, p. 715), and Xu *et al.* (2013)). In some ascids (*Antennoseius* spp.) and blattisociids (*Lasioseius* spp.) that we have studied, dorsal pores are consistently slit-like and flanked by what appears to be two valves (Beaulieu *et al.*, 2008; Athias-Henriot, 1969b, Figs 17–18), in contrast with most other species that we have observed, showing more dot-like or circular gland openings. Coxal gland openings (*gc*) observed in the species described herein are also slit-like, and lead to a calyx, which is the sclerotised distal portion of the gland's vesicle, similar to the calyx of spermathecal apparatus of phytoseioids (see "glandes à calyx" in Athias-Henriot (1969b)). Athias-Henriot (1969a) illustrated very similar coxal glands for *Anephiasca* species. In some cases however, dorsal poroids are more conspicuous (e.g. *Laelaps* and *Hyperlaelaps* spp. examined) while some pores of the podonotal region may be minute and easily overlooked. Confidence in accurately distinguishing poroids from gland pores can

only be gained with experience, through careful comparison of poroids and pores between conspecific specimens and species, and with some literature at hand to guide where to look.

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