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Article

Glandular and non-glandular cuticular organs on the idiosoma of Gamasina mites (Acari: Mesostigmata)

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ABSTRACT
The idiosoma of orthoadenic Gamasina (Mesostigmata) bears a maximum complement of 47 pairs of discernible cuticular organs that are distinct from setae. Superficially, 15 pairs appear secretory (gland pores) (four podonotal, four opisthonotal, one peritrematal, and six ventral) and 32 pairs (five podonotal, 13 opisthonotal, three on the peritrematal shield, 12 ventral) non-secretory (poroids); five pairs of gland openings and 18 pairs of poroids appearing at the larval instar, eight pairs of glands and 10 pairs of poroids are added at the protonymph, and two pairs of glands and two more pairs of poroids appear at the deutonymphal instar. The neoadenic condition observed in monogynaspid Gamasines (Zerconidae, Epicriidae, Heatherellidae, and other families of Dermanyssina mites), some Uropodina and Trigynaspina mites is due to the duplication or multiplication of several dorsal, peritrematal, and ventral glands forming glandular areas or groups, as well as the apparition of new glands, which complement the existing orthoadenic provision. The neoadeny begins in the protonymphal instar through the duplication of certain larval glands and continues with other duplications of larval and postlarval glands along with the appearance of new ones in the deutonymph. The addition of several newly identified pore-like structures to the complement given by Athias-Henriot (1969, 1975) is given and several changes in notation for idiosomal organs following Athias-Henriot are proposed. The homologies of cuticular organs are based on the topographic position of each on the idiosomal surface and on their ontogenies. Ontogeny appears to be useful in identifying glands, poroids and setae, although some organs can accelerate or delay their ontogeny.

KEYWORDS: Adenotaxy, idionomic system, ontogeny, organotaxy, poroidotaxy.

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INTRODUCTION

Some morphological characters of Mesostigmata mites need to be studied in more detail since they may have important physiological and ecological significance and could form part of the basis for the understanding of the relationships of these mites with other organisms and the environment.

Idiosomatic gland openings and poroids are distinctive cuticular organs which may be easily observed by trained researchers using appropriate microscopic techniques. However, the presence of such organs can be masked by certain advanced techniques such as those involving the scanning electron microscope (SEM) due to the preparation required for the material to be examined. Distinctions between individual homologous cuticular organs such as in setae, gland openings and poroids, are important for the comparative and ontogenetic study of mites. At the same time, having systems of idionomy for the designation of homologous structures is essential for identification purposes and for systematic and phylogenetic studies.

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The development of idionomic systems for mesostigmatic mites began with comparative- and ontogenetic-based systems for designation of idionotal setae (Hirschmann 1957; Athias-Henriot 1957). In 1965, Lindquist and Evans presented a modified system for the designation of idiosomatic setae that has achieved global acceptance among taxonomists who study these mites. There have also been attempts to describe and designate other idiosomatic cuticular organs, often referred to as "pores"; these were denoted in combination with the signatures of adjacent setae (Hirschmann 1960, Hirschmann and Wisniewski 1982; Johnston and Moraza 1991). A more comprehensive approach to the study of cuticular organs was carried out by Athias-Henriot (1969a, b, c, 1970, 1971, 1972, 1973, 1975a, b, 1976, 1980), who distinguished and designated gland pores with the abbreviation "*gd*" and poroids with the abbreviation "*id*". However, this system was developed only for Dermanyssina mites exhibiting the orthoadenic condition (Athias-Henriot 1971, 1975b), a condition understood as a full complement of glands present in the ancestor of a group, therefore excluding any additional glands that were more recently derived. This full complement included nine dorsal "*gd*" and three ventral "*gv*" glandular openings (designated as *gd1- gd9, gv1-gv3*) and 18 dorsal (*id1-id6, ids, idx1, idm1-idm6, idl1-idl4*) and nine ventral pairs of poroids (*iv1-iv3, iv5, ivo1-ivo4,* and *ivp*).

The same author studied neoadenic Mesostigmata (Athias-Henriot 1970), such as Celaenopsoidea, Antenophorina and *Heterozercon*. The term neoadenic refers to any newly added (derived) gland, including duplication of a long-present nearby gland, as well as the apparition of a gland independently from other glands present in that species and its ancestor shared with other species. Athias-Henriot did not propose designations for the added glands.

Progress in understanding the distribution of cuticular organs was made by Krantz and Redmond (1987) who distinguished dorsal idiosomatic glands from poroids based on silver nitrate reductions and designated the glands with "p" followed by the name of the most proximate seta. Subsequently, based on light microscopy alone, Johnston and Moraza (1991) made the same distinctions and created a notation system adding to the designation of these organs by describing them as either glandular openings (*gd*) or poroids (*id*), following Athias-Henriot, with the signatures related to the closest pair of setae. The last two mentioned systems implicitly provide information about the spatial distribution of these structures on the idiosomal surfaces in relation to the position of setae.

The system created by Johnston and Moraza (1991) was an attempt to homologize glands and poroids of Zerconidae with those of previously studied Mesostigmata, and at the same time to offer a unified idionymic system for designating these organs. Currently, the use of this system has been almost reduced to the Epicriina mites (Zerconidae, Epicriina and Arctacaridae), while the Athias-Henriot's system is regaining popularity.

The complete ontogeny of these organs in mesostigmatic mites was described for the families Zerconidae (Moraza 1991; Johnston and Moraza 1991; Lindquist and Moraza 1998), Uropodina (Moraza 1989a; Moraza *et al*. 2016), Trigynaspida (Pyrosejidae) (Lindquist and Moraza 1993), and more recently in several Dermanyssina families: *Spadiseius* (Lindquist and Moraza 2008), *Makarovaia* (Moraza and Lindquist 2015), and *Hispiniphis* (Moraza and Lindquist 2016) as members of the family Melicharidae, and *Lasioseius* (Moraza and Lindquist 2018) of the family Blattisociidae. Partial ontogeny of pore-like organs has been described for *Arrhenoseius gloriosus* (Ascidae) larva (Walter and Lindquist 2001); for Epicriidae (Moraza 2005a), for *Neopodocinum* (Macrochelidae) by Moraza (2004a); for *Metacryptoseius* (Eviphididae) by Kazemi *et al.* (2008); for *Antennocheles* (Antennochelidae) by Lindquist and Moraza (2014); for *Calyptoseius* (Blattisociidae) by Lindquist and Moraza (2016) and most recently for the uropodine genus *Uroseius* (Moraza 2019). Adult adenotaxy and porotaxy of Zerconidae have also been described by Moraza (1989b, 1991, 2006b), Moraza *et al*. (2009), of Heatherellidae (Seeman *et al*. 2018) and for several members of Dermanyssina: Ascidae (Lindquist and Moraza 2009; Moraza and Kazemi 2009; Kazemi *et al.* 2013), Blattisociidae (Lindquist and Moraza 2010; Moraza and Lindquist 2011, 2012, 2018), Halolaelapidae (Evans and Fain 1995); Laelapidae (Moraza 1993; Moraza and Johnston 1993; Moraza & Peña 2004; Moraza *et al.* 2009; Moraza and Kazemi 2012; Kazemi *et al.* 2014) Macronyssidae (Moraza *et al.*

2009), Parholaspidae (Moraza and Peña, 2006b), Phytoseiidae (Moraza *et al*. 2005c; Moraza & Peña, 2006b), and Rhodacaridae (Moraza 2004).

This work aims to (1) summarize the full complement of idiosomatic glandular and poroid organs (organotaxy) described in Mesostigmata Gamasina mites, (2) determine the ontogeny of each of these organs, and finally to (3) propose some changes in the notations of poroids and gland openings from the idionomic systems created by Athias-Henriot (1975b), in order to have a more functional, comprehensive system.

MATERIAL AND METHODS

This study is based on material deposited primarily in the Museum of Zoology of the University of Navarra as well as in the Canadian National Collection of Insects and Arachnids in Ottawa, and on the most recently published works in which specific reference is made to these cuticular organs. Observations were made of complete (larva, protonymph, deutonymph and adult) or partial (larva associated to adult, or protonymph associated to adult) ontogenetic series of previously described species of Zerconidae (Johnston aand Moraza 1991), Epicriidae (Moraza 2005), and several families of Dermanyssina mentioned above.

In this work, the system used by Athias-Henriot to designate these cuticular organs is followed except when designating several other organs of the peritrematal region, where the new abbreviation “p” refers to that region, “s” to the stigmata, and organs of the podal region where “a” refers to the axillary region (exopodal region between legs I and II). Other previously used abbreviations referring to the location of pore-like structures in the idiosoma have been retained: “i” refers to inguinal region, on the margin of the parapodal sclerite surrounding the posterior margin of coxa IV (Johnston and Moraza 1991); “t” refers to temporal peritreme region (Makarova 2003); “b” refers to “brachium”, at the intercoxal extension of the sternal shield between coxae I-II (Makarova 2003); “an” refers to anal valves (Makarova 2003). Several other organs on the dorsal shield have new sigla. These abbreviation changes are followed by an asterisk (*). The sigla used for the sternigenital and opisthogastric glands and poroids are those of Athias-Henriot (e.g. 1969, 1970, 1971) and I see no reason to change them.

In the figures, red color refers to glands and green color to poroids (gland openings and poroids that want to be highlighted; other pore-like structures remain in black color); red circles refer to glandular neoadenic groups. In the “Remarks and Discussion” section only newly proposed notations are used.

Glands resulting from the replication of others present in the orthoadenic complement are designated by adding an "x" to the name of the original gland.

The homologies of cuticular structures are based on the topographic position of each structure on the body surface and on the ontogeny of those structures.

Organotaxy associated with the peritreme will be treated separately. Coxal gland openings on coxae I or on soft cuticle adjacent to coxae I have not been taken into consideration. Only idiosomal gland openings have been studied.

RESULTS

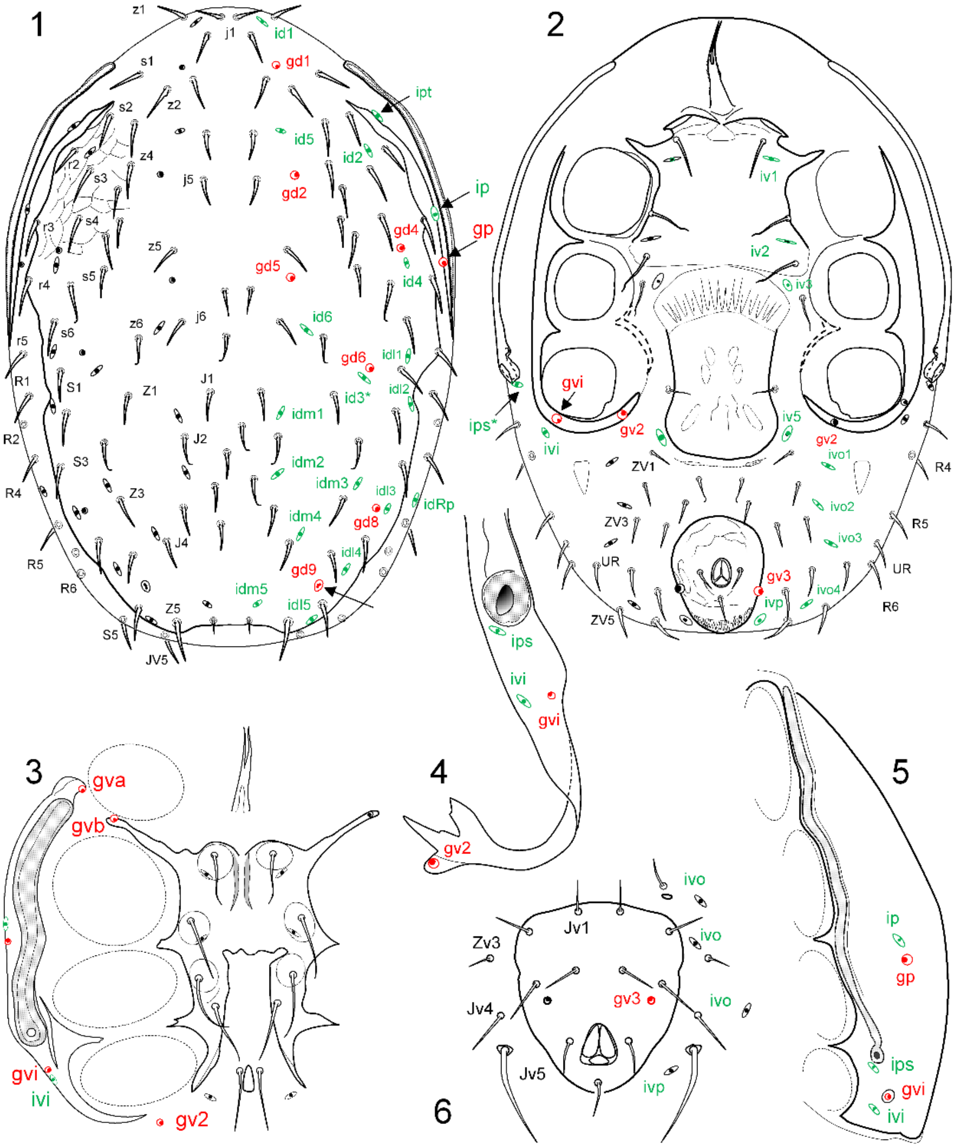
The idiosoma of orthoadenic Dermanyssina bears a maximum complement of 47 pairs of discernible cuticular organs (excluding setae), of which 33 pairs are dorsal (nine podonotal, 16 opisthonotal, three peritrematal) and 14 pairs are ventral. Superficially, 10 pairs appear secretory (gland pores) (four podonotal, three opisthonotal, one peritrematal, and five ventral) and 29 pairs (five podonotal, 13 opisthonotal, two on the peritremal shield, and nine ventral) non-secretory (poroids). Several of these organs may be on the shields or on the soft cuticle (Table 1, Figs. 1–6).

Table 1. Idionomy of idiosomal glands and lyrifissures and their ontogeny. New sigla in bold. “*” Athias-Henriot's sigla that are modified in the proposed system. Lateral glands gdl present in Heatherellidae. Lv = larva; Pn = protonymph; Dn = deutonymph; ontogenetic delays in brackets); “+” = present and common in a group; “–” absent in a group; ““present or absent in a group; “x2” duplicated in the group; “x4” quadrupled in the group.

Proposed sigla	Athias-Henriot	Ontogeny	Dermanyssina	Zerconidae	Epicriidae
PODONOTAL ADENOTAXY					
gd1	gd1	Pn	+	+	+; (x2/x4)
gd2	gd2	Lv	+	+	+; (x2)
gd3	–	Pn	-	-	+
gd4	gd4	Lv	+	+	+; (x2/x4)
gd5	gd5	Pn	+	-	+
OPISTHONTAL ADENOTAXY					
gd6	gd6	Lv	+	+	+; (x2)
gd7	gd7	Pn	-	+	+
gd8	gd8	Lv	+	+	+ (Dn?)
gd9	gd9	Pn	+	+	+
gdm2, 5	–	Dn	-	-	+
PERITREMATAL ADENOTAXY					
gp	gd3*	Pn	+	+ (Dn)	+ (Dn)
VENTRAL ADENOTAXY					
gv1	gv1	Dn	+/-	+	-
gv2	gv2	Pn	+	+	`+; (x2)
gv3	gv3	Lv	+	+	+; (x2)
gvb	–	Pn	+/-	-	-
gvi	gdp*	Pn	+	+ (Dn)	+; (x2)
gva	–	Pn	+/-	-/+	+ Dn?
PODONOTAL POROIDOTAXY					
id1	id1	Pn	+	+	+ (Dn?)
id2	id2	Lv	+	+	+ (Dn?)
id3	idm1*	Lv	+	+	+ (Dn?)
id4	id4	Lv	+	+	-
id5	id5	Lv	+	+	+ (Dn?)
id6	id6	Lv	+	+	-
-	id7*	Lv			
OPISTHONOTAL POROIDOTAXY					
idm1	idm2	Pn	+	+	-
idm2	idm3	Lv	+	+ (Pn)	-
idm3	idx*	Lv	+	+	+ (Dn?)
idm4	idm4	Pn	+	+ (Pn)	-
idm5	idm6*	Lv	+	+ (Pn)	-
idl1	is1*	Lv	+	+	+ (Dn?)
idl2	idl1*	Lv	+	+ (Pn)	+ (Dn?)
idl3	idl2*	Lv	+	+ (Pn)	+ (Dn?)
idl4	idl3*	Pn	+	+	+
idl5	Idl4*	Pn	+	+	+
idRp	idRp	Pn	+	+	-
PERITREMATAL POROIDOTAXY					
ipt	-	Pn	-	-	+ (Dn?)
ip	id3*	Lv	+	+	+
ips	id7*	Pn	+	+	+

Table 1. Continued.

Proposed sigla	Athias-Henriot	Ontogeny	Dermanyssina	Zerconidae	Epicriidae
VENTRAL POROIDOTAXY					
iv1	iv1	Lv	+	+ (Pn)	-
iv2	iv2	Lv	+	+ (Pn)	-
iv3	iv3	Dn	+	+	+
iv5	iv5	Dn	+	+	+
ivo1	ivo1	Lv	+	+	+ (Dn?)
ivo-2-ivo4	ivo2-ivo4	Pn	+	+	+
ivp	ivp	Lv	+	+	+ (Dn?)
ivi	-	Pn	+	+	+ (Dn?)
ian	-	Pn	-	+	+ (Dn?)



Figures 1–6. Organotaxy of Dermanyssina (Mesostigmata) – *Spadiseius calyptrogynae* Moraza & Lindquist, 2008, adult female: 1. Dorsal idiosoma; 2. Ventral idiosoma. 3. Detail of sternal and peritrematal shield of *Makarovia* (male); 4. Detail of peritrematal region of *Calyptoseius longinoi* Lindquist & Moraza, 2016 (female); 5. Detail of peritrematal shield of *Zercoseius*; 6. Detail of ventrianal shield of a phytoseid mite. Modified after Moraza and Lindquist (2008) and Lindquist and Moraza (2016), respectively.

Addition and changes to notations for idiosomal pore-like organs from Athias-Henriot's system (1975)

Since the observations of Athias-Henriot, several new cuticular organs have been described for monogynaspid Gamasina: newly proposed axillary gland *gva*, previously nominated ”*gd10*” by Evans and Fain (1994) and by Beaulieu and Beard (2018), as “*gp1*” by Moraza (2005a,) and Moraza and Lindquist (2015, 2016…); peritrematal *ipt*, first time designated as “*it*” by Makarova (2003); *gvb* at the intercoxal extension of the sternal shield between coxae I-II, first designated by Makarova (2003); on the inguinal region, *ivi*, first time described and nominated by Johnston and Moraza (1991), and recently designated as “*ip3”*, “*gp3”* by several authors.

For Epicriina mites, two new cuticular organs have been described: the herein proposed *gd3* in the dorsal podonotal region in Epicriidae (Fig. 20); and *ian*, first time designated as “ia” by Johnston and Moraza 1991) on the anal valves (Figs. 14, 16) and nominated as “*ian*” by Makarova (2003). The gland *gd7* in the opisthonotal shield was previously nominate by Athias-Henriot (1970).

Organs on the peritrematal shield *gd3*, *id3*, *id7* and *gdp* following Athias-Henriot (1975) have been renamed herein as *gp, ip, ips* and *gvi*, respectively (Figs. 1, 4); organs on the opisthonotal region of the dorsal shield *is1*, *idm1*, *idm5*, *idm6* and *idx* herein renamed as *idl1*, *id3, idl5*, *idm5* and *idm3*, respectively (Table 1, Fig. 1).

Ontogeny of cuticular organs in Dermanyssina

The complement of cuticular organs and their ontogeny is summarized in Table 1. The larva of orthoadenic Dermanyssina (Figs. 7, 8) bears 17 pairs of dorsal organs, including six podonotal pairs (*gd2*, *gd4*, *id2*, *id4*, *id5*, *id6*), 10 opisthonotal pairs (*gd6*, *gd8*, *id3*, *idm2*, *idm3*, *idm5*, *idl1*, *idl2*, *idl3*, *idl4*), two pairs (*ipt*, *ip*) in the peritrematal region, and five pairs of organs on the ventral region (*gv3*, *iv1*, *iv2*, *ivo1*, *ivp*).

In the protonymphal instar (Figs. 9, 10) three pairs of dorsal glandular organs (*gd1*, *gd5*, *gd9*), three pairs of dorsal poroids (*idm1*, *idl5*, *idRp*), two pairs in the peritremal region (*gp*, *ips*), and six pairs on the ventral region (*gva*, *gvi*, *gv2*, *ivi*, *ivo2*, *ivo3*, *ivo4*), are added to the larval complement.

The deutonymph adds *iv3*, *iv5* and *gvb*, completing the orthoadenic condition of adult Dermanyssina mites (Figs. 1–6). Usually, the deutonymphs and adult males and females bear the same dotation of organs as their deutonymphal instars.

Organotaxy of Epicriina

Comparing the above complement of organs with the condition found in epicriine mites of families Zerconiidae, Coprozerconidae, Arctacaridae, Epicriidae, and Heatherellidae, we found that they exhibit singular patterns.

Zerconiidae – The ontogeny of the organotaxy of this group of mites was previously described by Moraza (1989b, 1991), Johnston and Moraza (1991), and by Lindquist and Moraza (1998). This ontogeny follows the same pattern as in Dermanyssina mites, with several peculiarities.

The larva of *Zercon* (Figs. 11, 12) has the same glandular complement as other monogynaspid Gamasines, however poroids *idm1*, *idm5*, *idl2-idl5*, *iv1*, *iv2* delay their appearance to the protonymphal instar. The protonymphal instar lacks *gd5*, and *gva*; *gvi* and *ivi* delay their appearance to the deutonymphal instar (Figs. 13, 14); the deutonymph adds organs *gd7*, ventral *gv1*, and apparently lacks deutonymphal *ipt* (Table 1) (Figs. 15, 16).

In the opisthonotal region, the nine genera of the family previously studied by Lindquist and Moraza (1998) have the four pairs of glands mentioned above (*gd6*–*gd9*), but with *gd7* and *gd8* occupying different positions on the dorsal surface and, therefore, interacting with different opisthonotal setae; the 12 pairs of poroids are in the same positions as in Dermanyssina mites except for pair *idRp* (*idR3* in Johnston and Moraza 1991), which is included on the dorsal shield (Fig. 15) (see Lindquist and Moraza 1998). The idiosomatic venter bears sternal deutonymphal *gv1*, and *gv2* may be simple or with plicate openings such as in other tocospermic Mesostigmata such as Veigaiidae

(Fig. 16); *gvi* and *iv1* are on the margin of the parapodal sclerite surrounding the posterior margin of coxa IV (the inguinal region) (Fig. 30); and the pair of poroids *ivp* may be double.

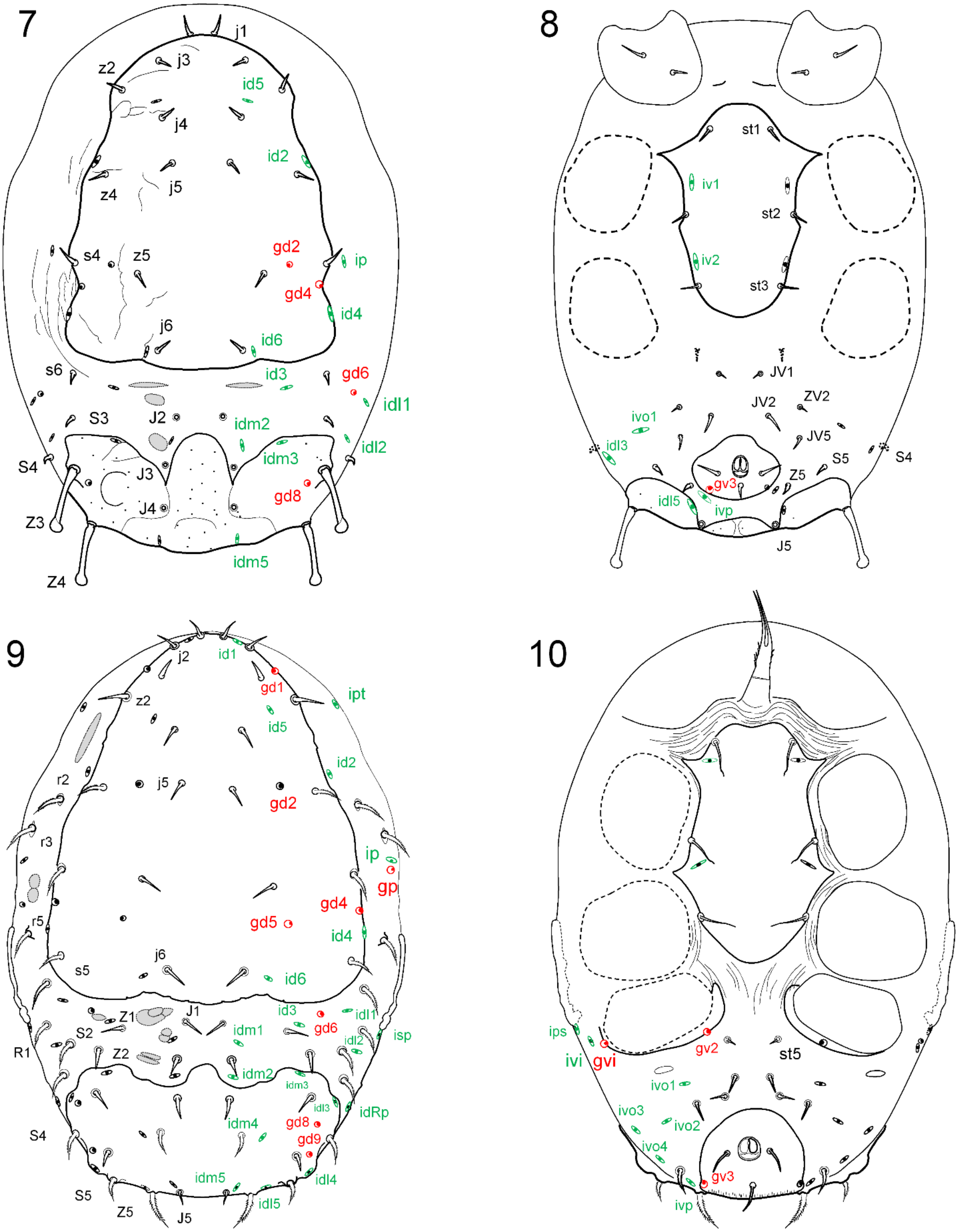
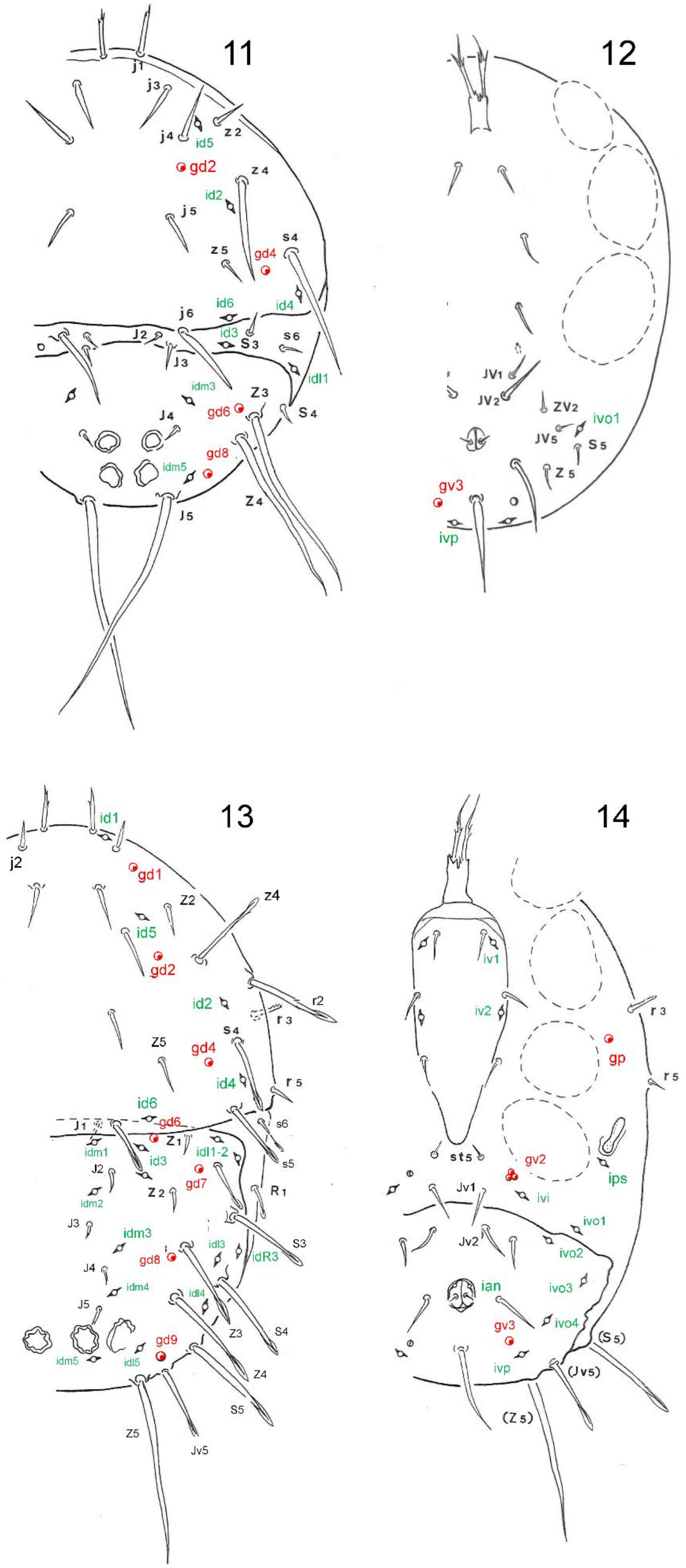


Figure 7–10. *Spadiseius calyptrogynae*, cuticular organs – 7. Dorsal idiosoma (larva); 8. Ventral idiosoma (larva); 9., Dorsal idiosoma (protonymph); 10. Ventral idiosoma (protonymph).



Figures 11–14. *Zercon parivus* Moraza – 1. Dorsal idiosoma (larva); 12. Ventral idiosoma (larva); 13. Dorsal idiosoma (protonymph); 14. Ventral idiosoma (protonymph). Modified of Moraza and Lindquist (1998).

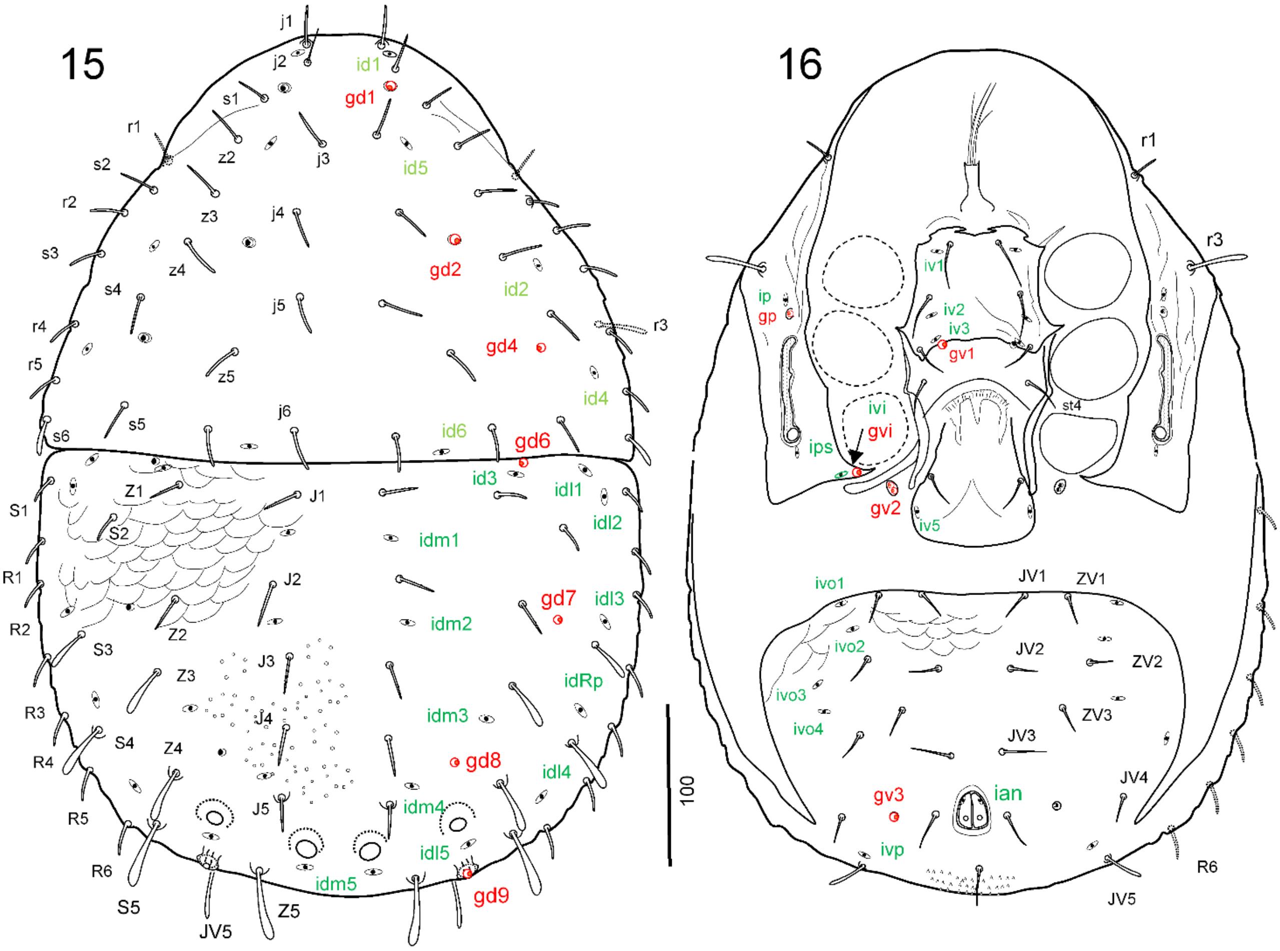
The genus *Syskenoercon* Athias-Henriot, 1976, an earlier derivative genus which exhibits extensive neotrichy on both shields, bears six setae (*r1* and *r6* double) and three glands in the peritrematal shield (Fig. 31), probably *gva*, and two *gp* (*gp*, *gpx*) associated with *ip*.

Coproцerconidae – In the family Coprozerconidae, considered a zerconid mite by Lindquist and Moraza (1998), *gd2*, *gd5*, *gv1*, *ian* are present, and *gd7*, *ipt*, *gva*, *gvi*, *ivi* absent (see Figures 1–5 in Moraza and Lindquist 1998).

Epicriidae – In the family Epicriidae, which exhibits a reduced dorsal chaetome (several deutonymphal setae are absent), gland openings are in cup-like cuticular structures such as in Zerconidae, whereas their poroids are usually not ornate and are sometimes associated with glandular structures, as was described for *Berlesiana* and other genera of the family (Fig. 27) (Moraza 2004, 2005a, b, 2006a).

Only one larval specimen of Epicriidae was described by Evans (1955) and a complement of glands and poroids was neither mentioned nor illustrated. Based on the described immature instars given by Moraza (2005a) for the genus *Epicrius* and on the adult neotenic *Neoepicrius*, we may assume that such larva may have at least the same complement of podonotal structures as the larva of the related family Zerconidae previously described.

The protonymph of *Epicrius* has a discernible podonotal complement of seven pairs of glands (*gd1*, *gd2*, *gd2x*, *gd3*, *gd4*, *gd5*, *gd6*), and one pair of poroids (*id1*) (Fig. 17). There are no other discernible opisthonotal glands nor poroids (probably due to the deteriorated state of the specimen).

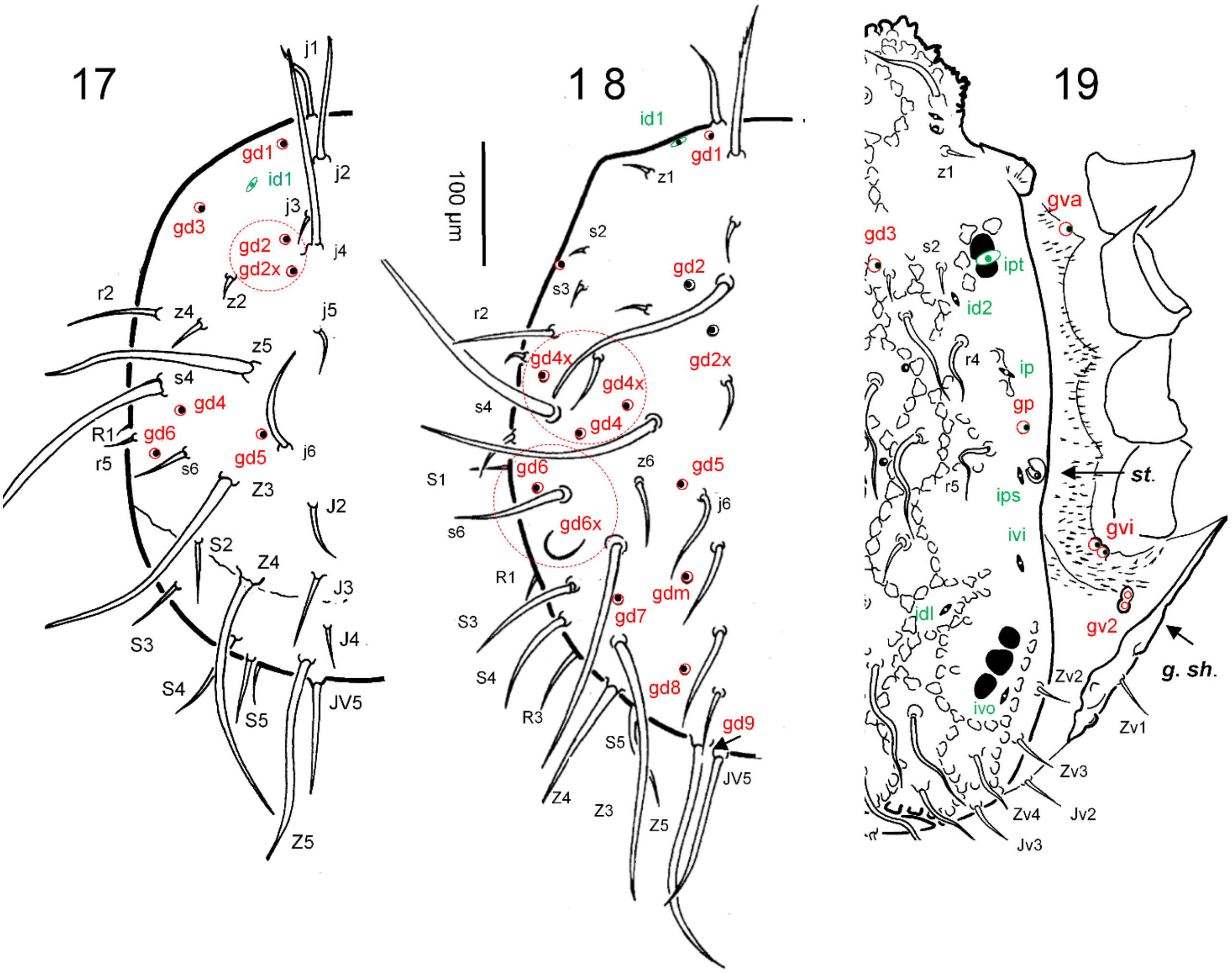


Figures 15–16. *Zercon curryi* Moraza (adult female), cuticular organs – 15. Dorsal idiosoma; 16. Ventral idiosoma.

The deutonymphal instar of *Epicrius* (Fig. 18) adds four more pairs of glands to the protonymphal complement: two pairs of *gd4x*, the pustular gland "*gd6x*" and four discernible pairs of glands (*gd7*, *gd8*, *gdm2*, *gdm5*).

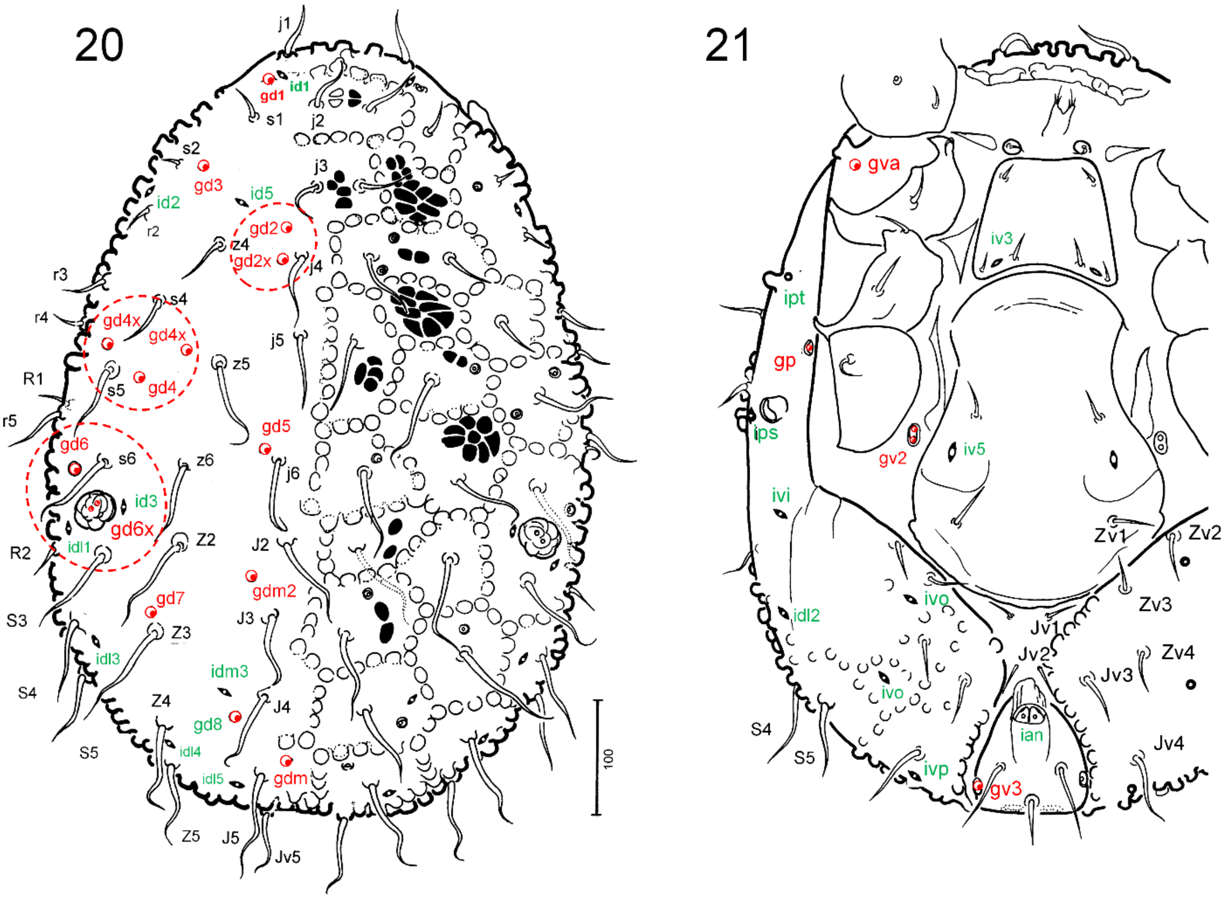
In adults, the lateral region of the idiosoma (dorsal, peritrematal and part of ventral shields fused) includes *ipt*, *gp*, *ip*, *ips*, *ivi*; *gva* on the soft axillar exopododal cuticle between legs I and II, and *gvi* in the unsclerotized inguinal parapodal region (Figs 19, 21), organs which are all present in at least some Dermanyssina.

The ventral idiosoma in the family lacks *iv1*, *iv2* and *gv1*; *gv2* on the soft cuticle (may be simple or double), *gv3* on the margin of the anal shield, *iv5* on the genital shield, *ian*, *ivp*, and at least three pairs of *ivo* (Fig. 21).



Figures 17–19. *Epicrius johnstoni* Moraza, cuticular organs – 17. Dorsal idiosoma (protonymph); 18. Dorsal idiosoma (deutonymph); 19. Idiosoma, lateral view with detail of the peritrematal region (adult). Captions g. sh. = genital shield; st. = stigmata.

The neoadenic condition of *Epicrius* and adults of other genera of Epicriidae exhibit complex glandular regions, the consequence of replication of certain glands, all of them present in the orthoadenic state in Dermanyssina and Zerconidae mites (replicate glands *gd1*, *gd2*, *gd4*, *gd6, gvi*, and *gv2*).

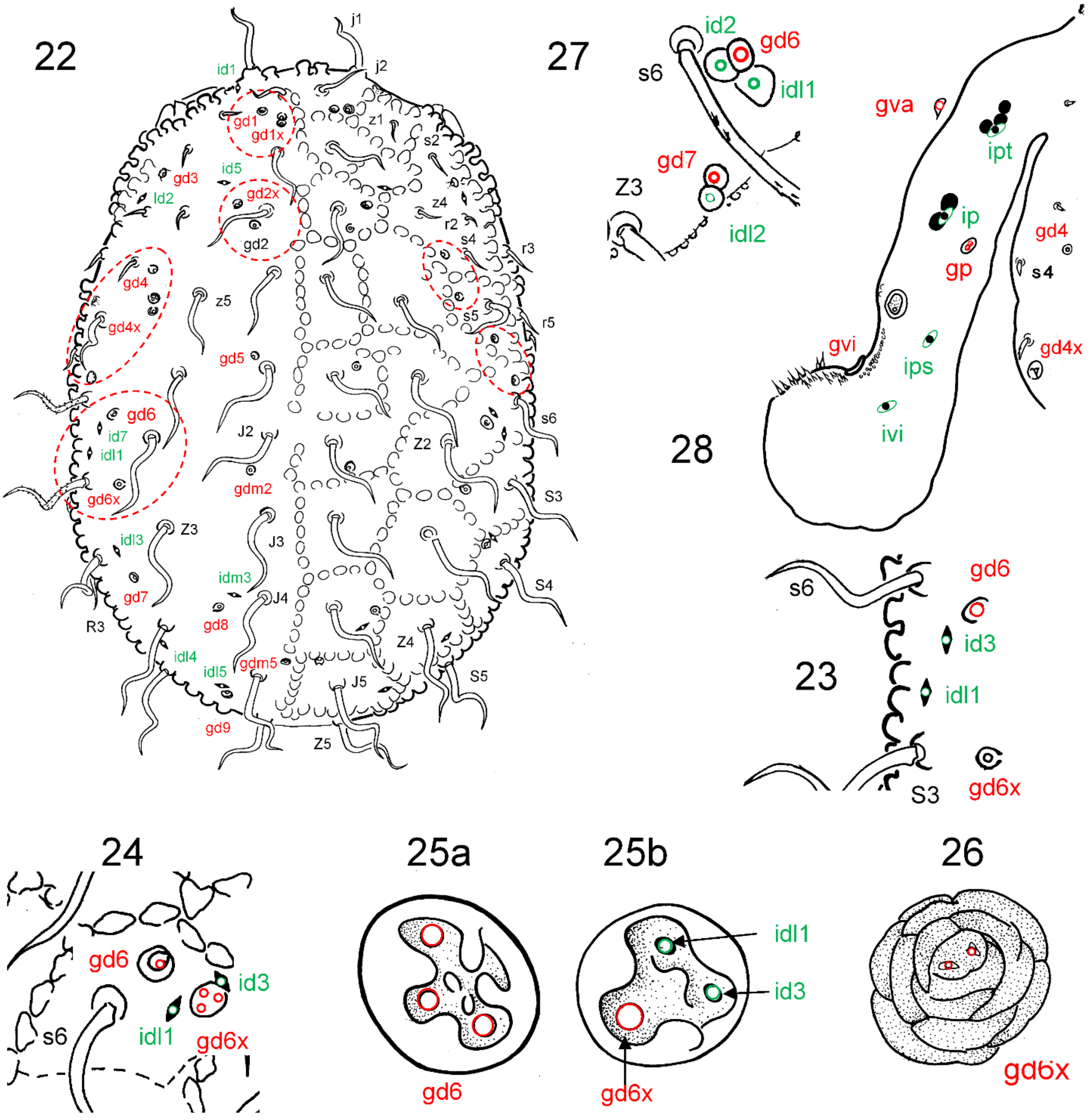


Figures 20–21. *Epicrius johnstoni* Moraza, cuticular organs (adult female) – 20. Dorsal idiosoma; 21. Ventral idiosoma.

The maximum number of glandular cuticular organs for the family Epicriidae is observed in the genus *Adenoepicrius* Moraza (2005) (Fig. 22). The adult instar of this genus bears at least 28 pairs of dorsal cuticular organs. In the podonotal region: *gd1* associated with poroids *id1* and setae *j1* and *gd2* associated with *j4* duplicated; glandular complex *gd4* (four pairs of glands) in association with setae *s4* and *s5*, and *gd5*, simple. In the opisthonotal region, glandular complex *gd6* duplicated (*gd6* + *gd6x*) associated with *idl1* and *id3*; gland *gd9*, and two pairs of *gdm* associated with setae *J2* and *J5*. Podonotal discernible poroids are *id1*, *id2*, *id5* and seven opisthonotal pairs *id3*, *idl1*- *idl5*. In the peritrematal region, *ipt*, *gp* and *ip*; *gva* and *gvi* on soft exopodal region, ventral *gv2* is simple and *ian* present.

The adult instar of *Berlesiana* (see Figures 8 and 9 in Moraza (2006a) lacks three pairs of dorsal glands (*gd3*, *gd4x*, *gdm5*), and bears a pustule-like glands in the position of glands that are putatively *gd6* and *gd6x*. The neotenic genus *Neoepicrius* lacks *gd1x*, *gd3*, *gd6x* and the two *gdm* [see Figures 13 and 14 in Moraza and Johnston (2004)]; the peritrematal region exhibits the orthoadenic condition of dermanyssine mites with *ipt*, *ip*, *gp*, *ips*, clearly on the dorso-peritrematal region, and *ivi*, *gvi* on the sclerotized parapodal region fused with peritrematal shield (Fig. 29); *gv3* duplicated and *ivp* on the anal shield.

Heatherellidae – The family Heatherellidae Walter, 1997, considered a superfamily of gamasine mites within the subcohort Epicriiae (Seeman *et al.* 2018), shows a neoadenic condition. Based on the topographic position, glands on the podonotal-mesonotal shield are: duplicated *gd2*, *gd4*, *gd6*, *gdm2*, *gdm4*, and simple *gd1*, *gd3*, *gdm* (no included in Table 1) associated with setae *j5*, *gd5*, *gd7*, *gdm1*, and *gdm3*; on the latinotal shields: duplicated *gd8*; and on pygidial shields, duplicated *gd9* on the lateral and *gdm5* on the central shield; on the marginal shield, numerous glands "*gdl*" (some of them spout-like protuberances), attribute shared with at least the genus *Uroseius* (Trachytidae). Ventrally, simple *gv1*, *gv3*, *gva*, and duplicated glands *gv2* (on opisthogastric region), *gp*, and *gvi*. This pattern remarkably resembles that found in some uropodine mites (see Moraza, 2019).

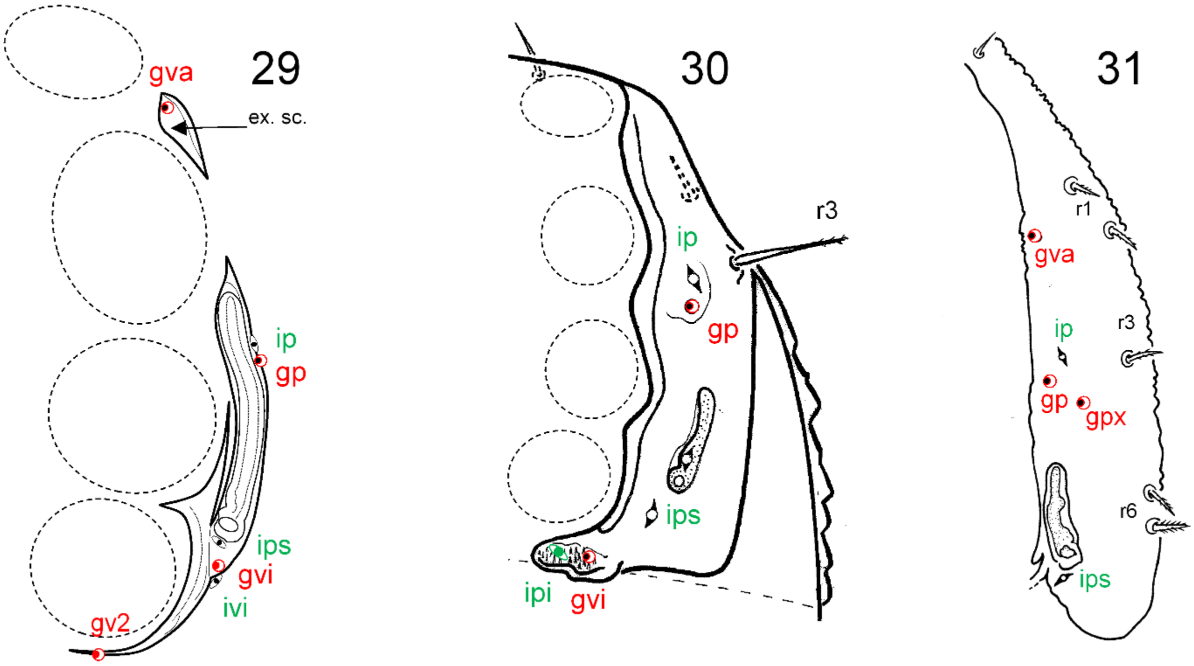


Figures 22–28. Cuticular organs – 22. *Adenoepicrius magnus* Moraza, dorsal idiosoma (adult female). 23–27. Detail of glandular complex “gd6”: 23. *Adenoepicrius magnus*; 24. *Adenoepicrius oconori* Moraza; 25a, b. *Berlesiana beunzana* Moraza; 26 *Epicrius* Moraza; 27. *Neoepicrius* Moraza. 28. *Neoepicrius* Moraza, detail of peritrematal region. Figures modified from Moraza (2004, 2005, 2006).

Glandular (pustule-like) structure

In Epicriidae, gland *gd6* is usually duplicated (*gd6* + *gd6x*) and putative *gd6x* may form a pustular, ornate structure. This pustular structure appears at the deutonymphal instar (Figs. 23–27). Glands *gd6* in *Neoepicrius* exhibit the primitive simple condition, *gd6* with an ornate/inflated cuticle, with a unique opening, similar to other dorsal gland openings (Fig. 27) and associated with two poroids (*idl1*, *id7*). In *Adenoepicrius*, *gd6* is duplicated and both glandular openings are simple, in a cuticular cup (Fig. 23) or, at best, *gd6x* is slightly modified, revealing up to three pores (Fig. 24). In *Berlesiana*, both glands (*gd6* and *gd6x*), and separately, form a pustular structure: putative *gd6* with three glandular openings (Fig. 25a), and posterior putative *gd6x* with one glandular opening and what looks like two poroids incorporated into the pustule (*idl1*, *id7*) (Fig. 25b). In *Epicrius*, the pair *gd6* is simple and *gd6x* is a well-developed pustule including two gland openings not associated with poroids (Fig. 26). Other enlarged complexes of two pores can be found in this family (e.g. gland opening *gp* in Figure 28).

Glandular structures of a pustular or simpler type have been found in other families. Modified pores in the Heatherellidae (enlarge pores, pustules and protuberances) are associated with podonotal and opisthonotal setae on the dorsomarginal plates. Enlarged glands openings have also been observed in some Dermanyssina, such as a complex of three pore-like structures -*gd9*- in *Spadiseius* (Moraza and Lindquist 2008) (Fig. 1), and a complex of two pore-like structures posterolaterad of the metapodal-peritrematal shield in *Zygoseius* (Ahadiyat and Beaulieu 2016).



Figures 29–31. Dertail of peritrematal and podal region – 29. *Hispiniphis* Moraza & Lindquist, 2016; 30. *Zercon* sp.; 31. *Syskenozercon* Athias-Henriot, 1976. Figures 29 and 30 modified from Moraza and Lindquist (2016); Figure 31 modified from Athias-Henriot (1976). Caption ex. sc. = exapodal sclerite.

REMARKS AND DISCUSSION

Regarding gland opening positions and homologies

The homologies of most idiosomal glandular and porelike organs described for the above-mentioned families of Epiciina mites and other Dermanyssina families can be determined. However, the homologies of some pore-like structures are questionable or simply impossible to determine. This is the case of podonotal *gd2* as compared with *gd5*. In Zerconidae, the larval gland designated "gd2" is on the line j4-j5 (Fig. 11); in Dermanyssina, a larval gland is usually in the area j5-z5-s4 (Fig. 7). Based on its ontogeny, the gland on position "gd2" and the gland on position "gd5" are the same larval gland and, given their final position on the shield, are identified as *gd2*, and as a conclusion the loss of *gd5* in zerconids. Here and in other cases, the ontogeny is the priority tool in establishing the identity of a gland or other cuticular organ.

Adults of Epicriina and Dermanyssina mites have the relative position of most glands in common. The gland opening *gd4* is usually associated with *id4*, in the area between setae *s4* and *s5*; *gd8* is usually associated with *idm3*; and *gd5* is usually found in the pentagonal central region j5-j6-z5. Opisthonotal glands *gd8*, *gd9*, and *gd6*, *gd7* in zerconids, occupy a lateral position close to the edge of the dorsal shield.

The gland *gd6* opening is usually associated with setae *Z1* and *S1* on the anterior margin of the opisthonotal shield and associated with the same poroids (*id3* and sometimes with *idl1*). However, the pair of glands *gd6* is found in different positions in the opisthonotal region of the mite's body depending on the development of the dorsal shields at each of the ontogenetic instars. In the larva of Zerconidae, *gd6* is on the opisthonotal shield away from the edge of the plate and poroids *id3* and *idl1* (Fig. 11); in the nymphal and adult instars of Zerconidae (Fig. 13) this gland is on the opisthonotal shield, such as in deutonymphs and adults of Dermanyssina when this shield is present. In the poorly known and poorly sclerotized protonymph of Epicriidae, *gd6* is clearly in the opisthonotal region of the body (Fig. 17). In the larva and protonymph of Dermanyssina, *gd6* is usually on the soft cuticle (Figs. 7, 9) when the opisthonotal shield is reduced.

In zerconid mites, glands *gd7* and *gd8*, "gdZ1" and "gdZ3", respectively, in Johnston and Moraza (1991), are found in various positions on the opisthonotal surface, moving away from their usual lateral positions. In *Aspar*, glands *gd8* move to a *gdm* position associated with seta *J4*; in *Krantzas* and *Macrozercon*, Johnston and Moraza (1991) described extra glands "gdJ2" and "gdJ4", positions denoted as *gdm* in Epicriidae. These two pairs of glands are now identified as *gd7* and *gd8*.

Dorsomedial glands "gdm" have been notated as *gdm2* and *gdm5* due to their correspondence with the positions of the poroids *idm2*, *idm5*.

The poroid *ipt* is located in the humeral region of the dorsal plate, paraxial to the peritreme and associated with sigillary area sl1 (L1) (see Athias-Henriot 1975a). This poroid aligns with *gp* and *ip* (Figs. 1, 19, 32).

Axillary glands *gva* is located in the non-sclerotized exopodal region between legs I-II (Figs. 19, 32), or in the exopodal sclerite I-II (Fig. 29), or in the peritrematal plate when it is fused with the exopodal element (Fig. 3). Although this gland could be designated as a coxal gland "gc", its constant position in the exopodal region, even in the exopodal sclerite, suggests that it belongs to the idiosoma. Same argument could be made about *gvb*.

Inguinal gland *gvi* is found in the parapodal region (Fig. 19 and Figure 1 in Makarova 2003), on the margin of the parapodal sclerite surrounding the posterior margin of coxa IV (Figs. 2, 30), or the gland moves, together with *ivi*, towards the posterior margin of the peritreme (Figs. 3, 5, 29). The latter position is what led to name these organs as *gp3*, *ip3* belonging to the peritrematal region (e.g. Moraza and Lindquist, 2015, 2018; Kazemi *et al*. 2014).

Lacks, losses, delays, and neoadeny

Some ontogenetic delays have been detected compared with the ontogeny of organs in Dermanyssina mites that deserve to be mentioned. Those delays are displayed in Table 1.

In epicriid mites, the protonymph seems to lack the opisthonothal glands and poroids that characterize that instar in dermanyssine (*gd7*-*gd9*, *id4*, *idm1*-*idm5*, *iv1*, *iv2*) (Fig. 17, Table 1). Just as these glands delay their ontogeny to the deutonymphal instar, the same does not occur with the poroids, which are apparently lost in the adult. In zerconid mites, we find similar delays for some dorsal and ventral larval poroids. However, in this case, these poroids delay their ontogeny to the postlarval instars and, finally, are present in adults (Table 1). Both groups present, to a greater or lesser degree (only *gv2*, *ivp* and *gp* may be multiplied in Zerconidae), duplications of glands and so we could theorize that the neoadenic processes involve the loss of some poroids such as in epicriids, or at least the delay in their ontogeny as in zerconids.

Cases of neoadeny in the herein studied Gamasina are restricted to the idiosomal glands *gd1*, *gd2*, *gd4*, *gd6*, *gvi*, *gv2* and *gv3*, in Epicriina. This condition seems to be due to the duplication or multiplication of glands forming glandular areas or groups, such as dorsal groups *gd1* + *gd1x*, *gd2* + *gd2x*, *gd4* + *gd4x*, and *gd6* + *dg6x* in the family Epicriidae (Figs. 20, 22), and *gvi* + *gv1x* + *gv2* + *gv2x* in Arctacaridae (see Figure 1 in Makarova 2003). In other cases, both glands (or glands openings) resulting from duplication/multiplication are grouped together, as is the case of *gvi*, *gv2* in Epicriidae, *gv2* in Zerconidae, and multiplied dorsal gland (Po3) in Arctacaridae. In addition, other glands are present, such as *gd3*, *gd7*, *gdm*, and marginal glands "gdx", glands absent in orthoadenic Dermanyssina.

The presence of pairs of dorso-medial glands *gdm*, in addition to *gd1–gd9*, is an attribute present in Epicriidae and Heatherellidae. The same glands are present in some uropodine members, such as in the family Trachytidae (see Moraza 1989a, 2019), Eutrachytidae (see Moraza *et al*. 2016), and in some Trigynaspida mites (see Lindquist and Moraza 1993). Epicriidae, and some trigynaspids mites, have lost podonotal glands *gdm*, although the latter present unpaired medial podo- and opisthonotal glands. The presence of glands *gdm* could be considered as an ancestral attribute.

The gland *gv1*, is present in Zerconidae and *Heatherella* but not in the more early-derived sejine and in epicriids, it is also present in Arctacaridae, some Parasitina, in some Rhodacaroidea, and as a vestige in some Dermanyssoidea [in *Gaeolaelaps* see Fig. 2 in Beaulieu 2009, and in *Persicolaelaps* Kazemi and Beaulieu 2016). Some Trigynaspida (in *Pirosejus*, see Fig. 18 in Lindquist and Moraza 1993, and in *Weiseronyssus persicus*, see Fig. 5 in Kazemi *et al*. 2008)], a sternal gland associated with *iv2* is present. The homology of this larval gland with *gv1* is uncertain, not only because of its position but also because of its ontogeny.

In view of the results presented here, we can characterize the studied families. Attributes for the family Epicriidae are: (1) putative apormiphc duplication of dorsal idiosomal glands *gd1*, *gd2*, *gd4*, *gd6*, and even *gv3* in *Neoepicrius*; (2) putative glands *gd6x* and sometimes *gd6* forming a pustular structure; (3) *gd3* present; (4) ancestral podonotal glands *gdm* present; (5) lack of poroids *id4*, *id6*, *idm1*, *idm2*, *idm4*, *idm5*, *iv1*, *iv2*, and may be *id2*. Zerconidae are diagnosed by the loss of podonotal *gd3*, *gd5* (shared with some Dermanyssina families), *ipt* and retention of *ivi*, *gvi* together at the inguinal position.

Dermanyssine families lack *ian*, *gd3*, *gd7*, *gdm*, and marginal glands present in *Heatherella*. Other glands and/or poroids can be lost in different families, such as the loss of *gvi* and *ivi* in *Antennoseius* and *Anystipalpus* (see Moraza and Kazemi 2009; Lindquist and Moraza 2009, Kazemi and Moraza 2013), *gd5* in Rhodacaridae (see Moraza 2004b), in Eviphididae (see Kazemi *et al*. 2008), and apparently several glands in the unsclerotized cuticle in parasitic Macronyssidae (see Moraza *et al*. 2009). Athias-Henriot (1975b) pointed out the weakness of *gd5* and that the absence of this gland was usually accompanied by epineoadenic duplication of *gd2* and *gd4*. The same author includes the duplication of *gd6* in the phytoseiid mites.

The studied uropodine mites regarding glands ontogeny by Moraza (1989a, 2016, 2019), could have the same larval adenotaxy than monogynaspid Gamasina. In these mites, duplication of dorsal and ventral glands begins in the protonymphal instar, and the adult has three pairs of sternal glands, including *gv1*. Although ontogenetic studies of many other taxa of uropodine and sejine mites are necessary to complete information of all tocospermic Monogynaspida, it appears that these mites have the same orthoadenic glandular complement than other Gamasina mites, complement on which to add new glands through multiplications of the present ones and the appearance of new marginal and none marginal ones.

At least in mites of the monogynaspid Gamasina families, the designation of glands and poroids using the names of the associated setae nearest to these structures implicitly provides information about the spatial distribution of these organs on the idiosoma. However, idionomy of pore-like structures based on the use of the names of the associated setae may mask some homologies of these organs. These organs can migrate on the dorsal and ventral surface of the body, occupying different relative positions as sometimes happens in the family Zerconidae. Besides, the loss of certain glands involves the positional reorganization on the idiosomal surface of those that remain, which could mask their identity.

For this reason, in order to establish the identity of a gland, poroid and seta, ontogeny is a reliable and useful tool, although not the only one, given the existence of ontogenetic loss, accelerations and delays. Johnston and Moraza' system may be more useful when it is important to differentiate the position of an organ within a higher taxonomic group once the specific organ has been identified. It is said that the relative positions of glands and the lack/loss of organs can be used as diagnostic characteristics in future taxonomic work and support future molecular results of this mites.

The system created by Athias-Henriot for orthoadenic Gamasina can be applied to neoadenic Epicriina (Zerconidae, Epicriidae, and Heatherellidae), Dermanyssina, and even to some uropodine, sejine and trigynaspds mites, which duplicate/multiplicate several podonotal, peritrematal and ventral glands notated as “x”, while adding other new dorsal glands such as *gd3*, *gd7*, *gdm*, and marginal “*gdx*” of Heatherellidae. Based on the ontogeny of the distinct organs, together with their relative position on the idiosomal surface of Epicriina mites, we may conclude that Dermanyssina and Epicriina mites share the same larval adenotaxy, and the neoadenic condition begins in the protonymphal instar through the duplication of certain larval glands (*gd2* in Epicriidae) and continues with other duplications of larval and postlaval glands (*gd1*, *gd4*, *gd6* in Epicriidae, *gd8*, *gd9*, *gdm* in Heatherellidae) along with the appearance of new ones in the deutonymph (e.g. *gdm*, and lateral *“gdl”*).

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REFERENCES

Ahadiyat, A. & Beaulieu, F. (2016) Two new mite species of the genus *Zygoseius* Berlese from Mexico (Acari, Mesostigmata). *ZooKeys*, 629, 11–49. DOI: 10.3897/zookeys.629.10121

Athias-Henriot, C. (1957) Phytoseiidae et Aceosejidae (Acarinas, Gamasina) d’Algérie. I. Genres *Blatisocius* Keegan, *Iphiseius* Berlese, *Amblyseius* Berlese, *Phytoseius* Ribaga, *Phytoseiulus* Evans. *Bulletin de la Société d'histoire naturelle de l'Afrique du Nord*, 48: 319–352.

Athias-Henriot, C. (1969a) Gamasides chiliens (Acariens Anactinotriches). I – Genre *Anephiasca* n. g. (Ascidae). *Revista de Biologia*, 7: 123–149.

Athias-Henriot, C. (1969b) Les organes cuticulaires sensoriels et glandulaires des Gamasides. Poroidotaxie et adenotaxie. *Bulletin de la Société zoologique de France*, 94: 485–492.

Athias-Henriot, C. (l969c) Notes sur la morphologie externe des Gamasides (Acariens anactinotriches). *Acarologia*, 11(4): 609–629.

Athias-Henriot, C. (1970) Un progrès dans la connaissance de la composition métamérique des Gamasides leur sigillotaxie idiosomale (Arachnida). *Bulletin de la Société zoologique de France*, 96(1): 73–85.

Athias-Henriot, C. (1971) La divergence neotaxique des Gamasides (Arachnides). Deuxième partie. *Bulletin scientifique de Bourgogne*, 28: 93–106.

Athias-Henriot, C. (1972) Gamasides chilens (Arachnides). II. Revision de la famille *Ichthyostomatogasteridae* Sellnick, 1953 (= Uropodellidae) Camin, 1955). *Arquivos de Zoologia*, 22: 113–191. DOI: 10.11606/issn.2176-7793.v22i3p113-191

Athias-Henriot, C. (1973) Un cas de déviation structurale (Catégorie Particuliere des anomalies de descleritisation idisomale) chez une femelle de Gamasides (Arachnides, Parasitina). description et commntaires. *Bulletin de la Société zoologique de France*, 98: 105–113.

Athias-Henriot, C. (1975a) Nouvelles notes sur les Amblyseiini. II - Le Relevé Organotaxique de la face Dorsle adulte (Gamasida Protoadeniques, Phytoseiidae). *Acarologia*, 17: 20–29.

Athias-Henriot, C. (1975b) The idiosomatic euneotaxy and epineotaxy in gamasids (Arachnida, Parasitiformes). *Journal of Zoological Systematics and Evolutionary Research*, 13(2): 97–109. DOI: 10.1111/j.1439-0469.1975.tb00503.x

Athias-Henriot, C. (1976) *Syskenozercon kosiri* n. g., n. sp., Zerconidae dorsoneotriche des alpes et de l'Himalaya (Arachnides, Gamasides). Bulletin de la Société Zoologique de France. *Bulletin de la Société zoologique de France*, 101: 433–444.

Athias-Henriot, C. (1980) Terrestrial Parasitiformes Gamasida I. The families Phytoseiidae, Pergamasidae, Eviphididae, and Zerconidae. *The Zoology of Iceland*, 3(57d): 1–38.

Beaulieu, F. (2009) Review of the mite genus *Gaeolaelaps* Evans &Till (Acari: Laelapidae) and description of a new species from North America, *G. gillespiei*. *Zootaxa*, 2158: 33–49.

Beaulieu, F. & Beard, J.J. (2018) Acarine biocontrol agents *Neoseiulus californicus* sensu Athias-Henriot (1977) and *N. barkeri* Hughes (Mesostigmata: Phytoseiidae) redescribed, their synonymies assessed, and the identity of *N. californicus* (McGregor) clarified based on examination of types. *Zootaxa*, 4500(4): 451–507. DOI: 10.11646/zootaxa.4500.4.1

Evans, G.O. (1955) A revision of the family Epicriidae (Acarina Mesostigmata). *Bulletin of the British Museum (Natural History) Zoology*, 3: 169–200, Pl. 1, 2. DOI: 10.5962/bhl.part.4122

Evans, G.O. & Fain, A. (1995) A new phoretic deuteronymph of *Halodarcia* Karg (Acari: Mesostigmata: Halolaelapidae) associated with carabid beetles in Belgium with a review of the genus. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* (Entomologie), 65: 63–71.

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

Hirschmann, W. (1957) Acarologie. Gangsystematik der Parasitiformes. Teil 1. Rumpfbehaarung und Rückenflächen. *Acalogogie. Gangsystematik der Parasitiformes*, 1: 1–20, I–V, Tafel 1–26.

Hirschmann, W. (1960) Gangsystematik der Parasitiformes. Teil 3. Die Gattung *Dendrolaelaps* Halbert, 1915. *Acarologie*, 22: 1–27, Tafel 1 –28.

Hirschmann, W. & Wisniewski, J. (1982) Weltweite Revision der Gattungen *Dendrolaelaps* Halbert, 1915 und *Longoseius* Chant, 1961 (Parasitiformes). Band 1. Beschreibung der Untergattungen und Arten, Bestimmungstabellen, Chätotaxie, Porotaxie. *Acarologie Schriftenreihe für Vergleichende Milbenkunde*, 29, 1–190.

Johnston, D.E. & Moraza, M.L. (1991) The idiosomal adenotaxy and poroidotaxy of Zerconidae (Mesostigmata: Zerconina). *In*: Dusbábek F., Bukva V. (Eds.), *Modern Acarology*, Vol. 2. Prague, Academia and The Hague, SPB Academic Publishing bv., pp. 349–356.

Kazemi, S. & Beaulieu, F. (2016) A new genus and species of Laelapidae (Acari: Mesostigmata) from Iran. *Zootaxa*, 4200(4): 487–500. DOI: 10.11646/zootaxa.4200.4.2

Kazemi, S., Klompen, H., Moraza, M.L., Kamali, K. & Saboori, A. (2008) A new species of *Weiseronyssus* Samsinak 1962 (Acari: Mesostigmata: Diplogyniidae) from Iran, with a key for genera. *Zootaxa* 1824: 17–27. DOI: 10.5281/zenodo.183078

Kazemi, Z., Moraza, M.L. & Kamali, K. (2013) Mites of the genus *Antennoseius* Berlese (Acari: Mesostigmata: Ascidae) from Iran. *Persian Journal of Acarology*, 2(2): 217–234. DOI: 10.22073/pja.v2i2.9956

Kazemi, Z., Moraza, M.L., Kamali, K. & Saboori, A. (2008) A new genus and three new species of the family Eviphididae (Acari: Mesostigmata) associated with scarab beetles in Iran. *Zootaxa* 1852: 1–20. DOI: 10.11646/zootaxa.1852.1.1

Kazemi, S., Rajaei, A. & Beaulieu, F. (2014) Two new species of *Gaeolaelaps* (Acari: Mesostigmata: Laelapidae) from Iran, with a revised generic concept and notes on significant morphological characters in the genus. *Zootaxa*, 3861: 501–530.

Krantz, G.W. & Redmond, B.L. (1987) Identification of glandular and poroidal idionotal systems in *Macrocheles perglaber* F. & P. (Acari: Macrochelidae). *Experimental and. Applied Acarology*, 3: 243–253.

Lindquist, E.E. & Evans, G.O. (1965) Taxonomic concepts in the Ascidae, with a modified setal nomenclature for the idiosoma of the Gamasina (Acarina: Mesostigrnata). *Memoirs of the Entomological Society of Canada*, 47: 1–64. DOI: 10.4039/entm9747fv

Lindquist, E. & Moraza, M.L. (1993) Pyrosejidae, a new family of trigynaspid mites (Acari: Mesostigmata: Cercomegistina) from Middle America. *Acarologia*, 34(4): 283–307.

Lindquist, E. & Moraza, M.L. (1998) Observations on homologies of idiosomal setae in Zerconidae (Acari: Mesostigmata), with modified notation for some posterior body setae. *Acarologia*, 39(3): 203–226.

Lindquist, E. & Moraza, M.L. (2008) A new genus of flower-dwelling melicharid mites (Acari: Mesostigmata: Ascoidea) phoretic on bats and insects in Costa Rica and Brasil. *Zootaxa*, 1685: 1–37. DOI: 10.11646/zootaxa.1685.1.1

Lindquist, E. & Moraza, M.L. (2009) *Anystipalpus*, *Antennoseius* and *Vitzthumia*: a taxonomic and nomenclatural conundrum of genera (Acari: Mesostigmata: Dermanyssina), with description of four species of *Anystipalpus*. *Zootaxa*, 2243: 1–39. DOI: 10.5281/zenodo.190657

Lindquist, E. & Moraza, M.L. (2010) Revised diagnosis of the family Blattisociidae (Acari: Mesostigmata: Phytoseioidea), with a key to its genera and description of a new fungus- inhabiting genus from Costa Rica. *Zootaxa*, 2479: 1–21. DOI: 10.11646/zootaxa.2479.1.1

Lindquist, E. & Moraza, M.L. (2014) Mites coexistent with neotropical hispine beetles in unfurled leaves of *Heliconia*: a new genus and family of the Ascoidea (Acari: Mesostigmata: Gamasina). *Journal of Natural History*, 27–28: 1611–1651. DOI: 10.1080/00222933.2013.877995

Lindquist, E. & Moraza, M.L. (2016) A new genus of mites of the subfamily Platyseiinae associated with *Azteca* ant galleries in *Cecropia* trees in Costa Rica (Acari: Mesostigmata: Blattisociidae). *Acarologia*, 56(1): 3–29. DOI: 10.1051/acarologia/20162242

Lindquist, E. & Moraza, M.L. (2018) Review of the genus *Leioseius* Berlese, 1916 in North America, with description of two new species (Acari: Mesostigmata: Ascidae). *Systematic & Applied Acarology*, 23(10): 1986–2021. DOI: 10.11158/saa.23.10.10

Makarova, O.L. (2003) A new genus and three new species of the family Arctacaridae (Parasitiformes, Mesostigmata) from North America. *Entomological Reviews*, 83: 868–886.

Moraza, M.L. (1989a) El género *Trachytes* Michael, 1894 en Navarra (Norte de España) y descripción de la especie *Trachytes welbourni* sp. n. (Acari, Mesostigmata: Uropodides). *Redia*, 72(1): 225–239.

Moraza, M.L. (1989b) Descripcion de *Zercon navarrensis* sp. n. encontrada en Navarra (Norte de Espana). (Acari, Mesostigmata: Zerconidae). *Eos*, 65(2): 57–64.

Moraza, M.L. (1991) *Zercon parivus* sp. n., una nueva especie de Acari (Mesostigmata: Zerconidae). *Boletín de la Asociación española de Entomología*, 15: 79–90.

Moraza, M.L. (1993) Two new species of *Pachyseius* Berlese, 1910 from Spain (Acari, Mesostigmata: Pachylaelapidae). *Acarologia*, 34 (2): 89–94.

Moraza, M.L. (2004a) The phoretic genus *Neopodocinum* (Oudemans, 1902) in the Iberian Peninsula (Acari: Mesostigmata: Macrochelidae). *Revista Ibérica de Aracnología*, 10: 261−269.

Moraza, M.L. (2004b) *Rhodacarella*, a new genus of Rhodacaridae mites from North America (Acari: Mesostigmata: Rhodacaridae). *Zootaxa*, 470: 1–10. DOI: 10.11646/zootaxa.470.1.1

Moraza, M.L. (2005a) Revised diagnosis of *Epicrius* Canestrini and Fanzago, 1877 and description of four new species (Acari: Mesostigmata: Epicriidae). *International Journal of Acarology*, 31(4): 341–354. DOI: 10.1080/01647950508683674

Moraza, M.L (2005b) A new genus and species of Epicriidae (Acari, Mesostigmata) from eastern North America (Acari, Mesostigmata, Epicriidae). *Canadian Entomologist*, 137(5): 539–550. DOI: 10.4039/N04-101

Moraza, M.L. (2006a) Characterization of *Berlesiana* Turk, 1943 and description of *Berlesiana beunzana* sp. n. from Spain (Acari, Mesostigmata, Epicriidae). *Acarologia*, 66(3–4): 181–187.

Moraza, M.L. (2006b) New species of zerconid mites from southern Europe and the Macaronesian region (Acari: Mesostigmata: Zerconidae). *Zootaxa* 1255: 1–15. DOI: 10.5281/zenodo.173074

Moraza, M.L. (2019) New data on the genus *Uroseius* Berlese (Acari: Mesostigmata: Uropodina: Trachytidae) with a redescription of *U. sorrentinus* (Lombardini, 1952). *Zootaxa*, 4717(1): 7–29. DOI: 10.11646/zootaxa.4717.1.4

Moraza, M.L., Arroyo, J. & Bolger, T. (2009) Three new species of mites (Acari: Zerconidae) from canopy habitats in Irish forests. *Zootaxa*, 2019: 29–39. DOI: 10.11646/zootaxa.2019.1.2

Moraza, M.L., Iraola, V. & Alemani, C. (2009) A new species of *Ljunghia* Oudemans, 1932 (Arachnida, Acari, Laelapidae) from a mygalomorph spider. *Zoosystema*, 31(1): 117–126. DOI: 10.5252/z2009n1a6

Moraza, M.L., Irwin, N., Godinho, R., Baird, S.J.E. & de Bellocq, J.G. (2009) A new species of *Ophionyssus* Mégnin (Acari: Mesostigmata: Macronyssidae) parasitic on *Lacerta schreiberi* Bedriaga (Reptilia: Lacertidae) from the Iberian Peninsula, and a world key to species. *Zootaxa*, 2007: 58–68. DOI: 10.5281/zenodo.185725

Moraza, M.L. & Johnston, D.E. (1993) *Pseudopachyseiulus ignacii* n. gen., n. sp., from Navarra (Northern Spain) (Acari: Mesostigmata: Pachylaelapidae). *Redia*, LXXVI (2): 263–271.

Moraza, M.L. & Johnston, D.E. (2004) *Neoepicrius*, gen. n., from Western North America (Acari: Mesostigmata: Epicriidae). *Acarologia*, 44: 195–207.

Moraza, M.L. & Kazemi, S. (2009) A new species of *Antennoseius* (*Vitzthumia*) Thor (Acari: Mesostigmata, Ascidae), associated with carabid beetles in Iran and a key to species. *International Journal of Acarology*, 35(1): 59–65. DOI: 10.1080/01647950902884538

Moraza, M.L. & Kazemi, S. (2012) Description of a new millipede-associated species (Acari: Mesostigmata: Laelapidae) from Iran and a key to species of *Julolaelaps* Berlese. *International Journal of Acarology*, 38(1): 6–17. DOI: 10.1080/01647954.2011.583273

Moraza, M.L., Kontschán, J., Sahoo, G. & Ansari, Z.A. (2016) A new species of *Eutrachytes* (Acari: Uropodina: Eutrachytidae) associated with the Indian mangrove (*Avicennia officinalis*). *Acarologia*, 56(1): 73–89. DOI: 10.1051/acarologia/20162189

Moraza, M.L. & Lindquist, E.E. (1998) Coprozerconidae, a new family of zerconoid mites from North America (Acari: Mesostigmata: Zerconoidea). *Acarologia*, 39(4): 291–313.

Moraza, M.L. & Lindquist E.E. (2011) A new genus of fungus-inhabiting blattisociid mites (Acari: Mesostigmata: Phytoseioidea) from Middle America, with a key to genera and subgenera of the subfamily Blattisociinae. *Zootaxa*, 2758: 1–25. DOI: 10.11646/zootaxa.2758.1.1

Moraza, M.L. & Lindquist, E.E. (2015) Systematics and biology of mites associated with neotropical hispine beetles in unfurled leaves of *Heliconia*, with descriptions of two new genera of the family Melicharidae (Acari: Mesostigmata: Gamasina: Ascoidea). *Zootaxa*, 3931(3): 301–351. DOI: 10.11646/zootaxa.3931.3.1

Moraza, M.L. & Lindquist, E.E. (2016) New species and biological data for the neotropical genus *Hispiniphis* (Acari: Mesostigmata: Melicharidae) associated with hispine beetles, genus *Cephaloleia*, in unfurled leaves of *Heliconia*. *Systematic and Applied Acarology*, 21(1): 85–118. DOI: 10.11158/saa.21.1.7

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

Moraza, M.L. & Peña, M.A. (2004) [2005] The family Pachylaelapidae Vitzthum, 1931on Tenerife Island (Canary Islands), with description of seven new species of the genus *Pachylaelaps* (Acari, Mesostigmata: Pachylaelapidae). *Acarologia*, 45(2–3): 103–129.

Moraza, M.L. & Peña, M.A. (2006a) Two new taxa of Parholaspidae Evans, 1956 (Acari, Mesostigmata) from Tenerife (Canary Islands). *Graellsia*, 62(1): 75–86. DOI: 10.3989/graellsia.2006.v62.i1.27

Moraza, M.L. & Peña, M.A. (2006b) A new species of *Neoseiulella* (Acari: Phytoseiidae) from the Macaronesian Region, Canary Islands. *Zootaxa*, 1366: 55–59. DOI: 10.5281/zenodo.174812

Moraza, M.L., Pena-Estevez, M.A. & Ferragut, F. (2005c) Two new species of *Neoseiulella* Muma of the Canary Islands (Acari: Phytoseiidae). *International Journal of Acarology*, 31(2): 107–112. DOI: 10.1080/01647950508683659

Seeman, O., Minor, M., Baker, M. & Walter, D.E. (2018) A revision of the Heatherellidae (Parasitiformes: Mesostigmata) with a new genus and two new species from Australasia. *Zootaxa*, 4434 (3): 441–465.

Walter, D.E. (1997) Heatherellidae - a new family of Mesostigmata (Acari: Parasitiformes) based on two new species from rainforest litter in Australia. *International Journal of Acarology*, 23: 167–175.

Walter, D.E. & Lindquist, E.E. (2001) *Arrhenoseius gloriosus* n.g., n.sp. (Acari: Mesostigmata: Ascidae), an arrhenotokous mite from rainforests in Queensland, Australia. *Acarologia*, 41: 53–68.

اندام‌های کوتیکولی غده‌ای و غیر غده‌ای روی ایدیوزومای هرناهای Gamasina (Acari: Mesostigmata)

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چکیده

ایدیوزومای گاماسینای ارتوآدنیک (Mesostigmata) دارای حداکثر مجموعه‌ای از ٤٧ جفت اندام کوتیکولی قابل تشخیص است که متمایز از موها هستند. در ظاهر، ١٥ جفت ترشحی (منافذ غدد) (چهار جفت پُدونوتال، چهار جفت اپیستونوتال، یک جفت پری‌ترمی، و شش جفت شکمی) و ٣٢ جفت (پنج جفت پُدونوتال، ١٣ جفت اپیستونوتال، سه جفت روی صفحهٔ پری‌ترمی، ١٢ جفت شکمی) غیر ترشحی به نظر می‌رسند. پنج جفت دهانه غده و ١٨ جفت شبه‌روزنه در سن لاروی ظاهر می‌شوند، هشت جفت غده و ١٠ جفت شبه‌روزنه در پورهٔ سن نخست اضافه می‌شوند و دو جفت غده و دو جفت شبه‌روزنه دیگر در پورهٔ سن دوم ظاهر می‌شوند. وضعیت نئوآدنیک مشاهده شده در گاماسین‌های مونوجیناسپید (Zerconidae، Epicriidae، Heatherellidae و سایر خانواده‌های هرناهای Dermanyssina)، برخی هرناهای Uropodina و Trigynaspina به دلیل دوبرابر شدن یا چند برابر شدن چندین غدد پشتی، پری‌ترمی و شکمی است که ناحیه یا گروه‌های غددی تشکیل می‌دهند، همچنین ظهور غدد جدید، مکمل مقررات ارتوآدنیک موجود است. نئوآدنی در پورهٔ سن نخست از طریق دو برابر شدن برخی از غدد لاروی شروع می شود و با دو برابر شدن‌های دیگر غدد لاروی و پس‌لاروی همراه با ظهور غدد جدید در پورهٔ سن دوم ادامه می‌یابد. چندین ساختار منفذ مانند تازه شناسایی شده به مجموعهٔ ارایه شده توسط آتیاس–هنریوت (١٩٦٩، ١٩٧٥) اضافه شده است و چندین تغییر در نمادگذاری اندام‌های ایدیوزوما با پیروی از آتیاس–هنریوت پیشنهاد شده است. همسانی اندام های کوتیکولی بر اساس موقعیت توپوگرافی هر یک از آنها در سطح ایدیوزوما و بر اساس نموشناسی آنها است. به نظر می‌رسد نموشناسی در شناسایی غدد، شبه روزنه‌ها و موها مفید باشد، اگرچه برخی از اندام ها می‌توانند نمو خود را تسریع یا به تاخیر بیندازند.

کلمات کلیدی: غده‌آذین، سامانه اصطلاحی، نموشناسی، اندام‌آذین، منفذآذین.

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