

MITES ASSOCIATED WITH NEW WORLD PASSALID BEETLES (COLEOPTERA: PASSALIDAE)

Preston E. Hunter

Department of Entomology

University of Georgia, Athens, Georgia, 30602 U.S.A.

ABSTRACT

Over 200 species of mites have been collected from passalid beetles (Passalidae). This represents collections from only a small portion of the known passalids. The mites are distributed among 21 families and 68 genera. Six of these families occur only in association with passalids. The largest number of mites associated with passalids belong to the taxonomic group Mesostigmata, supercohort Trignyaspida. Species of two mite families live on the beetle in a parasitic or commensal relationship. The remaining families have a phoretic association with the beetles, using the beetles for transportation to new habitats. Species of nine of these mite families are not common on passalids, and are probably opportunistic phoretics on the beetle. Studies suggest that when only the female disperses these mites reproduce parthenogenetically, but when both sexes disperse mating takes place after dispersal. Various methods of holding onto the beetle have evolved among the different mite groups. Mites partition riding space on the beetle and reproductive areas of the beetle tunnel, thus reducing or eliminating competition. Data suggests that mite-beetle host specificity is rarely a 1:1 relationship. Specificity is possibly beetle habitat related, e.g., beetles which live under the bark versus beetles which live deeper in the log. Mites of 17 families have been collected from New World passalids. Taxonomic keys to these families and genera, characters for family recognition, the number of species known from passalids, and comments on these species are included for mites from New World passalid beetles.

Key Words: Passalidae, mites, mite associations, mite phoresy.

RESUMEN

Más de 200 especies de ácaros se han colectado asociadas a escarabajos pasálidos (Passalidae). Estos registros representan colectas de solamente una pequeña porción de los pasálidos conocidos. Los ácaros están distribuidos en 21 familias y 68 géneros. Seis de estas familias ocurren solamente en asociación con pasálidos. El mayor número de ácaros asociados con pasálidos pertenece al grupo taxonómico Mesostigmata, supercohorta Trigynaspida. Las especies de dos familias de ácaros viven con los escarabajos en una relación parásita o comensal. Las familias restantes tienen una asociación forética con los escarabajos, usándolos para transportarse a nuevos habitats. Especies de nueve de estas familias no son comunes en pasálidos y son probablemente pasajeros oportunistas en el escarabajo. Algunos estudios sugieren que cuando solamente la hembra se dispersa estos ácaros pueden reproducirse partenogénicamente, pero cuando ambos sexos se dispersan la cópula se lleva a cabo después de la dispersión. Varios métodos para sujetarse al escarabajo han evolucionado entre los diferentes grupos de ácaros. La selección de sitios de transportación en los escarabajos por los ácaros así como la selección de áreas reproductivas en el tunel del escarabajo, reduce o elimina la competencia entre los ácaros. Los datos sugieren que la especificidad al huésped entre ácaro-escarabajo raramente es 1:1. Posiblemente la especificidad este relacionada con el habitat, e.g., escarabajos que viven bajo la corteza *versus* escarabajos que viven más profundamente en el tronco. Acaros de 17 familias han sido colectadas de pasálidos del Nuevo Mundo. Se incluyen claves para las familias y los géneros de los ácaros asociados con pasálidos del Nuevo Mundo, así como los caracteres para el reconocimiento de las familias, el número de especies conocidas y comentarios sobre ellas.

Palabras Clave: Passalidae, ácaros, asociaciones de ácaros, foresia.

INTRODUCTION

The Acari are divided into seven suborders (Evans, 1992), and species of four suborders (Mesostigmata, Prostigmata, Astigmata and Oribatida) are associated with passalid beetles (Coleoptera: Passalidae). The largest number of passalid associated mites are in the suborder Mesostigmata. The Mesostigmata are divided into two major groups, the supercohort Monogynaspida (one shield covering the genital opening) and the Trigynaspida (three shields covering the genital opening). Most Mesostigmata mites associated with passalid beetles are assigned to the Trigynaspida. The close relationship of the Mesostigmata mites with passalid beetles suggests a long history of

Table 1

Mite families, their taxonomic placement, and geographic areas where species have been collected from passalid beetles (Passalidae).

Mite Taxa	Geographic areas			
	New World	Africa	Australia	Oriental
Mesostigmata				
Cohort Monogynaspida				
Ascidae	x			
* *Diarthrophallidae	x	x	x	x
Digamasellidae	x			
Laelapidae	x			
Macrochelidae	x			
Pachylaelapidae				x
Uropodidae	x			
Cohort Trigynaspida				
Family: *Diplogyniidae	x	x	x	
*Euzerconidae	x	x		
* *Fedrizziidae			x	
* *Hoplomegistidae	x			
* *Klinckowstroemiidae	x			
* *Megisthanidae	x	x	x	
Schizogyniidae		x		
Prostigmata				
* *Heterocheylidae	x	x	x	x
Astigmata				
Acaridae	x			x
Anoetidae	x			x
Canestriniidae				x
Oribatida				
Mesoplorphoridae	x	x		x
Oppiidae	x	x		
Oribatulidae	x			

* Most species of family associated with passalid beetles.

* * Families found only in association with passalid beetles.

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Table 2

Mite families commonly associated with passalid beetles (Passalidae), the total number of genera in each family, the number of genera associated with passalids, and the number of species collected from passalids.

Family	Genera in family		No. species	
	Total	On passalids	On passalids	
Diarthrophallidae	18	18	54	
Diplogyniidae	40	16	39	
Euzerconidae	11	5	22	
Fedrizziidae	3	3	20	
Heterocheylidae	1	1	24	
Hoplomegistidae	1	1	7	
Klinckowstroemiidae	4	4	22	
Megisthanidae	1	1	29	

association. There is no record as to when or how mite-passalid associations developed. Based on the limited information available, it would appear that most of the mite families found exclusively on passalids became associated with their host before the beetles moved from their original point of dispersal. Two families, Klinckowstroemiidae and Hoplomegistidae, are known only from the New World, and a third family, Fedrizziidae, is known only from Australia and the Central Pacific area, suggesting these three families are more recent associates of passalid beetles. Over 200 species of mites have been collected from passalids; however, this represents collections from only a small portion of the approximately 500 described species of passalids (Reyes-Castillo 1970). These mites are distributed in 21 families and 68 genera (Tables 1 and 2).

Six of these families are restricted to passalid beetles. The purpose of this paper is to summarize information on mite-passalid beetle associations and provide keys to the mite families and genera associated with passalid beetles from the New World. This information should provide a starting place for others interested in this little-investigated area.

MATERIAL AND METHODS

The information presented herein is based on publications, unpublished data, and original work for this paper. In the text, the terms passalids and passalid beetles refer to beetle species in the family Passalidae. Illustrations are of mites in the Acarology Collection, Department of Entomology, University of Georgia, Athens, Georgia, U.S.A.

Unless otherwise indicated, all measurement bar scales on illustrations represent 100 micrometers. Abbreviations used in illustrations are:

ap. -----	apotele
a.s. -----	anal shield
d1, d2 -----	dorsal setae of the dorsocentral series
g.s. -----	genital shield
h.h. -----	hyaline hood
la. -----	lamella
lg.s. -----	latigynial shield
m1, m2, m3 -----	dorsal setae of the mediolateral series
m.s. -----	mesogynial shield
per. -----	peritreme
ps.o. -----	pseudostigmatic organ
s.p. -----	sucker plate
sg.s. -----	sternogenital shield
tet.s. -----	tetartosternal shield
tri. -----	tritosternum
va.s. -----	ventroanal shield
vm.s. -----	ventromarginal shield

PHORESY

Phoresy where one animal (the phoretic) seeks out and attaches to another animal (the carrier) for transportation is well documented in mites. Phoresy results in dispersal of the mites from areas unsuitable for further development of the mite or its progeny to areas suitable for population development. It is assumed phoretic mites are r-strategists enabling them to rapidly colonize and exploit temporary habitats.

Phoretic mite dispersal is by the most resistant (e.g., desiccation) life stage, and during dispersal the mite ceases both feeding and ontogenesis. In some cases both the phoretic and the carrier benefit from the relationship, in others only the phoretic benefits. Phoresy may be opportunistic, facultative or obligatory and the types of phoresy involved in mite-passalid associations, and any benefits to the beetles, are speculative at this time (see Hunter and Rosario 1988, Evans 1992, Athias-Binche *et al.* 1993 for discussions of phoresy).

Ecologically a passalid beetle tunnel would be characterized as unstable even though beetles may inhabit large logs for more than one generation. Mites living in these tunnels must rely upon beetles for transportation to new tunnels. In the Monogynaspida mites, females or deutonymphs disperse. In laboratory studies of the monogynaspid mite *Cosmolaelaps trifidus* (Pearse and Wharton), the females reproduced parthenogenetically when males were not present (Hunter and Mollin 1964b), thus new mite colonies could be established by a single phoretic female. Likely this method of reproduction is also true for other monogynaspid mites associated with passalids. Where both males and females disperse, as in the Trigynaspida, parthenogenesis was not noted and mating probably takes place after dispersing, therefore, both sexes must arrive at the new location. These different reproductive strategies probably account for different stages being phoretic in the Monogynaspida and the Trigynaspida.

Nineteen of the 21 families of mites associated with passalid beetles are phoretic, at some level, on the beetles (obligatory in mite families associated exclusively with passalid beetles, opportunistic for groups such as Oribatida). All active life stages of the two remaining mite families (Diarthrophallidae and Heterocheylidae) occur on the beetle, but the relationships of these families to the beetles are unclear. The Diarthrophallids have non-pointed, chelate chelicerae and this, combined with the mite's location on the beetle suggests a commensal relationship (see also Schuster and Summers 1978). In contrast, the Heterocheylidae mites have short, styliform chelicerae, live on the soft integument between the beetle's abdomen and the membranous wings and likely have a parasitic relationship with the beetle. However, the food resource of mites of either family is speculative.

MITE ATTACHMENT

Phoretic mites "attach" to arthropod hosts in areas where they are least likely to be dislodged by the host's activity. Based on studies of the 16 mite species, representing 11 families, associated with the U.S.A. passalid *Odontotaenius disjunctus* (Illiger), specific riding areas on the beetle and methods of mite attachment can be identified (Fig. 1). Based on observations of passalids from other geographic areas, these mite riding locations and methods of attachment represent most, if not all, of the conditions found for mite species on passalids. There are two general areas on the beetle's body where mites ride, on the external surfaces and in protected body niches. Examples of external riders are the Laelapidae (*Cosmolaelaps* and *Geolaelaps*, Fig. 1) which ride in the gular region of the beetle by grasping a seta with the chelicerae. These mites are not found attached to setae on other areas of the beetle's body.

Mites which are found on smooth, sclerotized areas of the frons region of the head, the area around coxae I, and between the pro- and mesothorax cling by large membranous structures (caruncle) located dorsal to claws II-IV. When the pretarsus is pushed down the caruncle

spreads, forming a sucker-like pad which enables the mite to cling to and move rapidly over the smooth body surfaces. Mites with large caruncles do not go to other areas of the beetle's body. Species of Euzerconidae (*Euzercon*), Megisthanidae (*Megisthanus*), and Diplogyniidae (*Passalacarus*) are examples of phoretic mites which cling to the beetle in this manner (Fig. 1). Uropodid deutonymphs produce a secretion (anal pedicel) from a gland opening into the posterior region of the alimentary canal. This pedicel, glued to the beetle's body, hardens upon contact with air and the mites are then suspended from the beetle's body. Uropodids normally attach just posterior to coxae III on the beetle. Deutonymphs (hypopi) of Acaridae and Anoetidae attach to the smooth sclerotized surface of the beetle's body by a sucker plate located at the posterior of the body. The more common area of attachment is on the venter of the beetle's abdomen near coxae III, but under crowded conditions mites may attach to other smooth areas on the beetle's body.

Three families of mites are found in protected niches on the beetle's body. Diarthrophallidae mites are found in the antennal, coxae and maxillary sulci and sometimes where the meso- and prothorax join (Fig. 1). Some diarthrophallids have ultra long body setae, which stand erect, and probably serve to provide information on niche size. Since these niches are in areas where beetle body parts move, niche size changes frequently.

Two families of mites occur under the beetle's elytra. Digamasellidae (*Dendrolaelaps*) occur at the anterolateral corners on the venter of the elytra (Fig. 1). These mites are flattened dorsoventrally, and probably cling to the underside of the elytra by their claws. Heterocheylidae (*Heterocheylus*) are found on the dorsum of the beetle's abdomen, lying in the intersegmental lines. Each walking leg has a pad which extends beyond the single, strong claw, and probably this pad is used in walking as claws would tend to cut the soft integument of the beetle's abdomen.

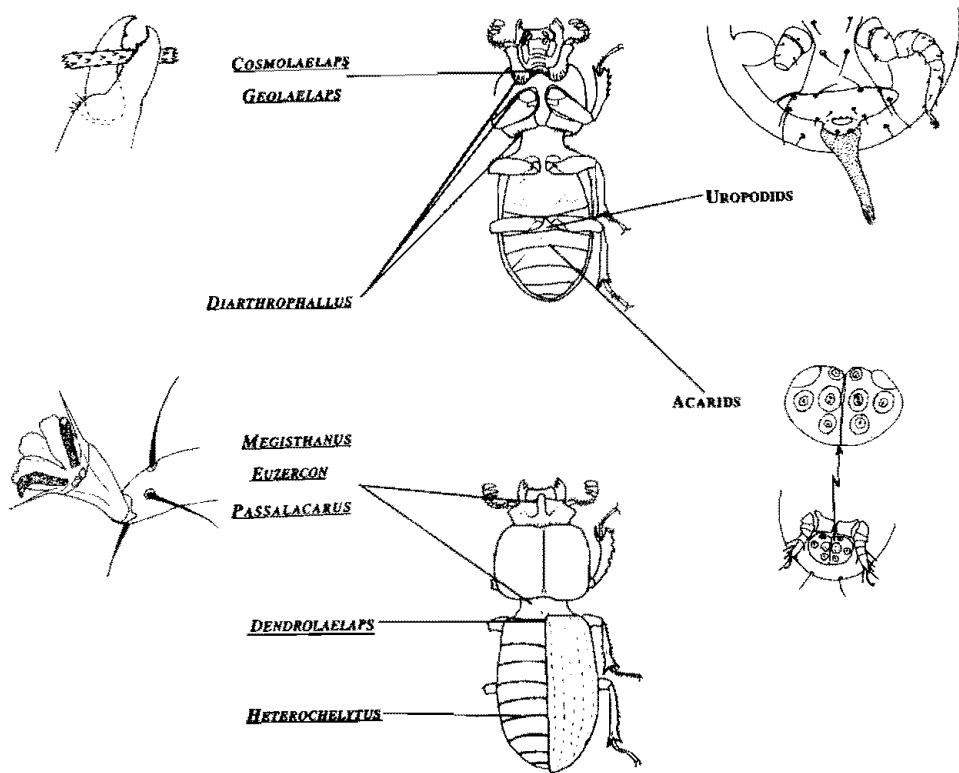


Figure 1
Riding places of some mites associated with the passalid beetle, *Odontotaenius disjunctus* (Illiger).

The Diarthrophallidae and Heterocheylidae mites live on the beetle, but can be found in the tunnel frass from time to time. The other mites reproduce in the tunnel frass and, based on studies of *Cosmolaelaps tridifus* (Pearse and Wharton), go onto and off of beetles. The stimulus which caused mites to leave a beetle is probably chemical cues from the tunnel material and/or beetle.

HOST SPECIFICITY

Host specificity between mites and passalid beetle is probably incorrectly estimated due to limited collecting opportunities for mites to encounter different beetle species. For example 16 mite species are associated exclusively with the beetle *Odontotaenius disjunctus*, the only passalid species occurring north of Mexico, but as reported below at least some of these mites will transfer onto other passalids.

Based on collection data, host specificity can be evaluated for the families Heterocheylidae and Diarthrophallidae. Specimens of both families can be collected from museum beetles. Schuster and Lavoipierre (1970) collected 1,050 specimens of Heterocheylidae from approximately 7,000 museum specimens of passalid beetles. Single species of heterocheylids were commonly found associated with more than one passalid species, especially for the genera *Passalus* and *Popilius*. These authors concluded that host specificity for the Heterocheylidae probably occurs at the beetle generic, but not at the beetle species level. Some beetle genera in the Proculini tribe *sensu* Reyes-Castillo (1970), appeared to have heterocheylid mites to the exclusion of diarthrophallid mites, even though mites of the two families do not occupy the same niche. In an equally detailed study of the Diarthrophallidae, Schuster and Summers (1978) collected mites from approximately 6,000 museum beetle specimens. These authors concluded that host-mite relationships appeared species specific in some cases, but more generally they found one or two diarthrophallid species occurring on one host species.

However, exceptions occurred, e.g., four mite species were recorded from the beetle *Aulacocyclus edentulus* MacLeay, and conversely one mite species, *Tenuiplanta crossi* Hunter and Glover was collected from four beetle hosts. Through the assistance of Pedro Reyes-Castillo, I have carried out preliminary tests of mites from one passalid beetle going onto a different beetle species (unpublished data). The U.S.A. beetle, *O. disjunctus*, with associated mites *Euzercon latus* (Banks) (Euzerconidae), *Passalacarus sylvestris* (Pearse and Wharton) (Diplogyniidae), *Cosmolaelaps trifidus* (Pearse and Wharton) (Laelapidae), *Diarthrophallus querus* (Pearse and Wharton) (Diarthrophallidae), and uropodid deutonymphs, were used. The other beetle, *O. cerastes* Castillo et al., collected from Jalisco, Mexico, had mites of three families Klinckowstroemiidae, Megisthanidae and Diplogyniidae.

Neither this beetle nor the mite species occur in the U.S.A. Six American and four Mexican beetles were used. The beetles were held individually in small dishes, containing decaying wood as food, and the beetle's own frass. Beetles were cleaned of mites and the mites returned to the frass. After cleaning, Mexican beetles were placed in the dishes containing mites from an American beetle and American beetles placed in the dishes containing mites from Mexican beetles. Beetles were checked periodically and counts made of any mites which had moved from the frass onto the non-host beetle. After seven days all mites, beetles and frass were placed in a single container to see if mites would return to their natural hosts.

General conclusions from these tests were: some mites went onto the strange beetles within one hour, and by five hours some individuals of all mite species either were on or had been on the non-host beetles. This was true for both the American and Mexican beetles. After placing all mites, beetles and frass in a single container, mites tended to go back onto their original host by the sixth day, suggesting a preference for their own over the non-host beetles. Although a suggestion of host specificity is indicated, it is not absolute, since in the absence of the

normal host mites would go on and remain on the non-host beetles. Whether these mites would reproduce if confined with a non-host passalid was not investigated.

The presence of different types of mites (large, round, flat, etc.) on different passalid species may be correlated with passalid body size and thickness. This in turn may be correlated with a specific habitat, e.g. under the bark of the log, in the log itself, in the detritus under a log, etc. (see Johki and Kon 1987 for information on beetle size and shape as related to location in logs). Beetle shape and size could limit the amount and type of mite riding space available. For example, large megisthanid mites would have limited space on small, flat passalid beetles, and consequently subject to being rubbed off the beetle.

MITE IDENTIFICATION

A key to the mite families known from New World passalid beetles is given below. Under family comments, critical characters for recognition of the family (compared to other families listed in the key), the number of species known from passalid beetles, and keys to the mite genera currently known from New World passalids are included.

Key to families of mites associated with New World passalid beetles (Males not included)

- 1. Hypopus. Mouth parts absent; sucker plate present on venter of opisthosoma (Figs. 2 and 6) 2
- Mouth parts well developed; chelicerae (Figs. 3, 20a) and palps evident; sucker plate absent 3
- 2. Legs III and IV point posteriorly, legs similar in shape to legs I and II (Fig. 6) **Acaridae**
- Legs III and IV point anteriorly, legs slenderer and of different shape than legs I and II (Fig. 2) **Anoetidae**
- 3. Peritreme present; ventral stigmatal opening clearly visible, located posterolateral of coxae II-IV (Figs. 8, 15) 5
- Peritreme absent; stigmatal opening not apparent, either hidden at base of

- coxae (Oribatida), or on dorsum at anterolateral margins of propodosoma . . .
 (Prostigmata) 4
4. Not heavily sclerotized, off-white or light tan in color; chelicerae short, well
 sclerotized and stylet like (Fig. 3) **Heterocheylidae**
 - Heavily sclerotized, brownish in color; club-shaped pseudostigmatic organs
 present (Figs. 12-14); chelicerae well developed, chelate
 **Oribatida**
5. Deutonymph; without separate sternal or genital shields (Fig. 5, 8a) 6
 - Adult female, with either sternal or sternometasternal and genital shields
 (Megisthanidae has sternal shields fused to posterior shields, Fig. 19) 8
6. Dorsal shield divided (Fig. 7b) **Digamasellidae**
 - Dorsal shield entire 7
7. Idiosoma spherical; base of tritosternum partially covered by coxae I (Fig. 5)
 **Uropodidae**
 - Idiosoma elongate; coxae I well separated, not touching base of tritosternum
 (Fig. 8a) **Laelapidae**
8. Single sclerotized genital shield covering female genital opening (Fig. 8)
 (Monogynaspida) 9
 - Three shields (mesognynial and paired latigynials) covering female genital opening
 (Fig. 17a) (Trigynaspida) 12
9. Idiosomal dorsum with 1-6 pairs of setae, setae often long and barbed; paranal
 setae—arising from anal shield—long, barbed (Fig. 4); legs I terminate in two long
 sensilla (Fig. 4b) **Diarthrophallidae**
 - Dorsum with more than 20 pairs of setae of variable lengths; tarsus I with
 numerous terminal setae, with or without claws 10
10. Peritreme exits stigmata posteriorly then loops anteriorly (Fig. 15); tarsus I
 without claws; palpal apotele 3-tined (Fig. 15a) **Macrochelidae**
 - Peritreme exits stigmata anteriorly (Fig. 8); tarsus I with claws; apotele
 2-tined 11
11. Anal shield triangular in shape (Figs. 8, 9) **Laelapidae**
 - Anal shield large, rounded (Fig. 7a) **Ascidae**
12. Large, heavily sclerotized mites, most over 2,000 μ in length; sternal shield
 fused with ventral shield; genital opening triangular in shape, located in middle
 of fused shields at level of coxae II-III (Fig. 19) **Megisthanidae**
 - Sternal or sternometasternal shields never fused with ventral shield; genital
 shields not forming a circle around genital opening; less than 2,000 μ
 (exception, some Hoplomegisthidae) 13
13. Margin of idiosoma with a hyaline hood forming an anterior crescent (Fig. 17c);
 crescent may extend posteriorly along lateral margins or surround idiosoma (Fig.

17b); sternogynial shield present (Fig. 17a); sternal setae I arise from a separate shield (tetartosternum) (Fig. 17a) **Klinckowstroemiidae**

Idiosoma without a hyaline hood; sternogynial shield absent; sternal setae I arise from sternal shield or from jugular shields. 14

14. Anal shield fused with ventral shield (Fig. 18) **Diplogyniidae**

Anal shield separated from ventral shield by integument 15

15. Latigynial shields fused posteriorly to ventral shield (Fig. 16a); sternal setae I on sternal shield (Fig. 16) **Euzerconidae**

Latigynial shields separated by integument from ventral shield; sternal setae I on fused or separate jugular shields (Fig. 20)

Hoplomegisthidae

Acaridae Ewing and Nesbitt, 1942

A large family of soft bodied mites which includes saprophagous, graminivorous, fungivorous and phytophagous species. Species of Acaridae are often found in decaying organic materials. Many are of economic importance. Only the hypopus (phoretic deutonymph) is found on passalid beetles. Hypopi (Fig. 6) are characterized by: dorsoventral flattening and strong sclerotization; reduced, non-functional mouthparts; ventral opisthosomal sucker plate; legs III-IV directed posterolaterally, similar in shape to legs I-II; and tarsi with a single empodial claw.

The life cycle includes egg, larva, protonymph, deutonymph, tritonymph and adult. Under unfavorable environmental conditions (e.g., deterioration of food quality) some protonymphs molt into the hypopial stage rather than the deutonymph. The hypopus does not feed and is highly resistant to desiccation in contrast to other active life stages. Hypopi attach to insects by suckers, located in the anal area, for transportation to a new habitat. Chemical stimuli in the new habitat induce the hypopi to deattach from the insect host and molt into the tritonymph.

On the passalid beetle these mites attach primarily in the area of the coxae and the abdomen, and occasionally under the elytra. When acarids are present, large numbers of mites may be attached to a beetle. Acarid hypopi have been recorded from passalids of the New World and the Oriental areas, but probably occur throughout the host families' range. It is likely several species are involved, but none have been described.

Anoetidae Oudemans, 1904

Anoetids are soft bodied, and world wide in distribution where organic, wet substrata occur. Species habitats range from the liquor of pitcher plants to decaying organic materials. The mites feed by straining bacteria and other microorganisms from their habitat substrate. Like Acaridae, members of this family go through three nymphal stages, the hypopial stage also being produced under specific environmental conditions. Only hypopi (Fig. 2) attach to arthropods, including passalids; these hypopi are distinct in having legs III and IV directed anteriorly, and these legs are thinner than legs I and II. Some hypopi are able to spring into the air, apparently in response to air movement, and attach to passing hosts (Hall 1959). Hypopi of this family are not common on passalid beetles, but when present, may occur in large numbers primarily around coxae III of the beetle. It is not known where the non-hypopial stages of the mites found on passalids live. Mites could attach to the beetles in the tunnel, or areas outside the tunnel which the beetles might visit in moving from log to log. None of the Anoetidae recovered from passalid beetles have been described.

Heterocheylidae Trägårdh, 1950

Heterocheylids (Fig. 3) are soft bodied mites, off-white or light tan in color, compressed dorsoventrally, and have few body setae. The propodosoma area bears normal setae and a pair of sensory (ampulliform) organs that may be long setae or pits. A long seta arises from the dorsum above each coxa III, and other heavy, long setae arise

from the posterior of the opisthosoma. Legs II-IV have a sucker like caruncle that extends beyond the single strong claw; leg I lacks a claw and caruncle. Ventrally, coxae I and II are well separated from coxae III and IV. Each chelicera consist of a well-sclerotized, pointed stylet.

These mites are known only from passalid beetles, and have been found in all geographical areas where mites have been collected from these beetles. They are found lying in the intersegmental lines on the dorsum of the beetle's abdomen. All active stages occur on the beetle, and this, plus the type of chelicerae, suggests a parasitic relationship with the beetles. Mites are killed when beetles are placed in alcohol or a killing jar, but because of their location mites remain on the beetle and can be collected from museum specimens.

Schuster and Lavoipierre (1970) list 27 species of Heterocheylidae all assigned to a single genus, *Heterocheylus* Trägårdh. These authors gave keys to species from the African, Asian and Australian areas, and North and South America. Five species are listed from the New World.

Diarthrophallidae Trägårdh, 1946

Members of this family (Figs. 4, 4a, 4b) may be recognized by the following characters: leg I palpiform, with two terminal sensilla, one very long; large bi-lobed caruncles on pretarsi II-IV, with poorly developed claws; stigmatal opening present, but peritremes abbreviated or absent; one to six pairs of peripheral, smooth or barbed dorsal body setae, some or all may be ultralong; most dorsomedian setae either absent or microsetae set in pores; female genital shield flap-like, free anteriorly; chelicerae chelate. Male genital opening circular, located in area between coxae II-IV.

Diarthrophallids are known only from passalid beetles and probably occur wherever their hosts occur. These mites are found in the antennal, coxal and maxillary sulci. All active mite stages are found on

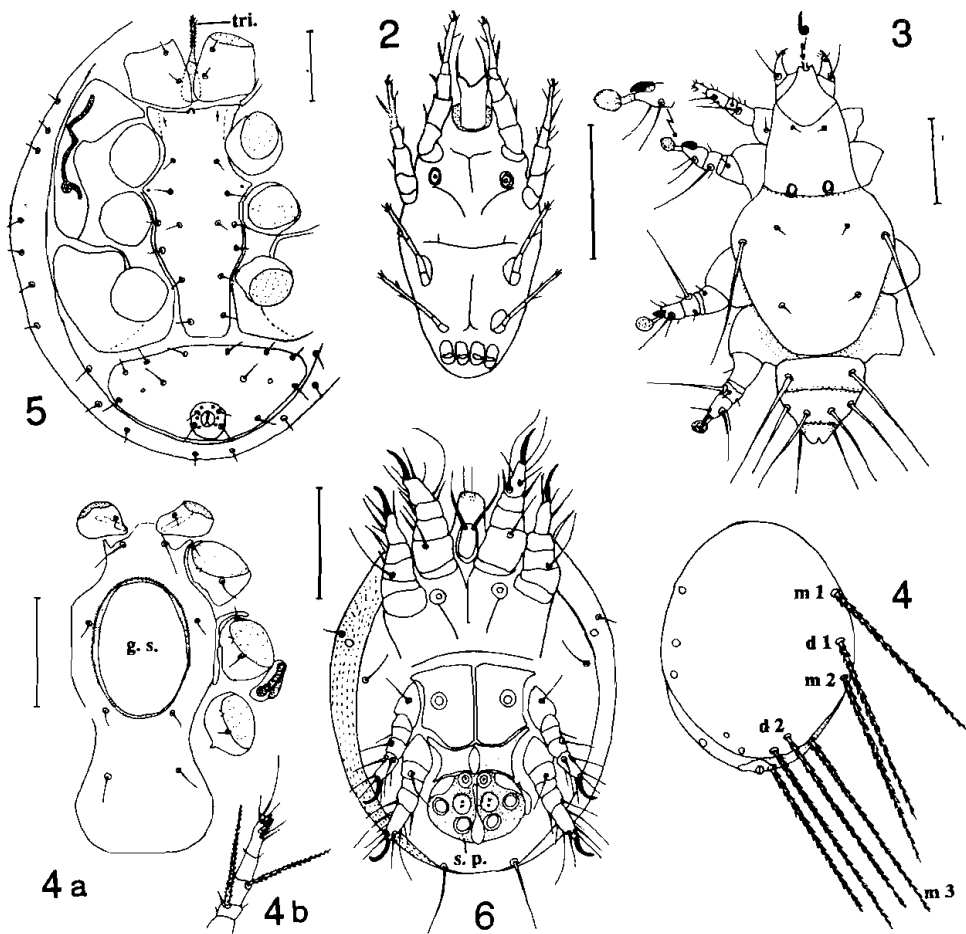
adult beetles; they are not associated with beetle larvae or pupae. Mites move within and between the sulci, and will move from one live beetle to another (based on studies with *Diarthrophallus querus*, Hunter unpublished data). Mites will leave beetles that die, move into the frass and then move onto another beetle.

Schuster and Summers (1978) published a detailed study of the Diarthrophallidae. They list 54 species of diarthrophallids assigned to 18 genera. Eight genera (37 species) were listed from New World passalid beetles. A key to these genera is given below.

Key to New World Genera Of Diarthrophallidae
(Based on females)

1. Coxae I separate (Fig. 4a); suranal seta (small seta dorsal to anal opening) absent (Diarthrophallinae) 2
- Coxae I fused (Fig. 10), suranal seta present (Passalobiinae) 4
2. Femora III (Fig. 10a) and IV each with one macroseta
. *Tenuiplanta* Schuster and Summers
- Femora III and IV each with two macrosetae 3
3. Genua III and IV without macrosetae *Paralana* Schuster and Summers
- Genua III and IV with one macroseta *Diarthrophallus* Trägårdh
4. Perigynial ring closed posteriorly (see Fig. 4a for example of closed ring) . .
. *Abrotarsala* Schuster and Summers
- Perigynial ring open posteriorly 5
5. Anterior margin of genital shield located anterior to coxae IV 6
- Anterior margin of genital shield located between or behind coxae IV . . . 7
6. Idiosoma with abrupt reduction in width; without lateral projections on ventral shield *Passalobia* Lombardini
- Idiosoma without abrupt reduction in width; ventral shield either with lateral projections, or wide and extending into metapodal area
. *Atrema* Schuster and Summers
7. Idiosoma spindle-shaped, of approximately equal width throughout; dorsal shield with a pair of lengthwise deep sutures
. *Liranotus* Schuster and Summers
- idiosoma may appear wider anteriorly; dorsal shield constricts or narrows behind legs IV; dorsal shield without lengthwise sutures
. *Passalobiella* Schuster and Summers

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Figures 2-6

2) *Anoetidae* sp., ex. Costa Rica: hypopus, ventral view. 3) *Heterocheyleus proximus* Schuster and Lavoipierre, ex. U. S. A.: female, dorsal view. 4) *Diarthrophallus* sp., ex. Mexico. Female: dorsal view; a) ventral view; b) leg I, dorsal view. 5) *Uropodidae* sp., ex. Mexico: deutonymph, ventral view. 6) *Acaridae* sp., ex. Costa Rica: hypopus, ventral view.

Uropodidae Berlese, 1917

Uropodids are brown in color and the body is covered by shields which appear smooth, or finely punctuate. Adults may be recognized by: dorsal shield covering the dorsum, or with small separate pygidial shield posteriorly; dorsal marginal shields may be present in some genera; base of tritosternum covered by coxae I; grooves (fovae pedales) for legs; a camerostome, allowing gnathosoma to be retracted, present. In the female the genital shield is hinged posteriorly to the ventral shield. The male genital opening is a circle in the holoventral shield at the level of coxae II-III. Only the deutonymphal stage is found on passalid beetles. This stage does not have a genital shield or a genital opening, and the ventral shields appear as in Fig. 5. Uropodid mites are often referred to as turtle mites because of their ability to withdraw the legs and gnathosoma into the shell-like body covering.

The deutonymph attaches to the passalid beetle by an anal pedicle, discussed above; they commonly attach on the ventral surface (coxal and gular areas) of the beetle. Adult mites live in the tunnel frass, especially in aged, damp frass. The only named species of uropodid are three species associated with *Odontotaenius disjunctus*; however, their taxonomic status may be questionable (Delfinado and Baker 1975).

Digamasellidae Evans, 1957

Adults of this family are characterized by: divided dorsal shield (Fig. 7b); tectum with three anterior projections, median projection arises ventral to lateral projections; chelicerae with many teeth. Female with four pairs of setae arising from sternal shield; genital shield truncate posteriorly, bearing genital setae; ventroanal shield present, bearing the three anal setae plus four or more additional setae (Fig. 7).

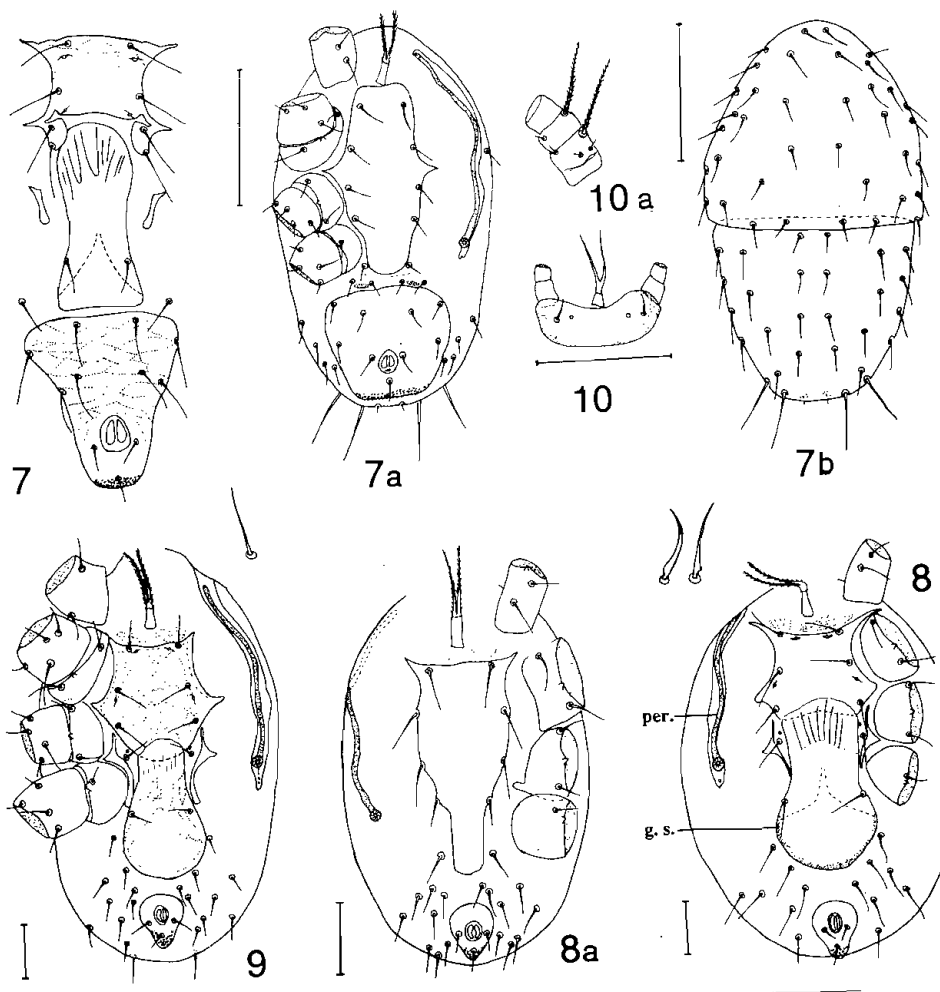
Male with sternogenital and ventroanal shields. Deutonymphs have two ventral shields (Fig. 7a), an anterior shield bearing four pairs of setae, and a posterior shield bearing the three anal setae plus at least

two additional pairs of setae. Approximately 100 species of Digamasellidae have been collected from beetles (Hunter and Rosario 1988). A number of species of the genus *Dendrolaelaps* are associated with wood boring beetles. Collections from Mexico, Brazil and the U. S. A. suggest that species of *Dendrolaelaps* occur on passalid beetles throughout the New World. Only one species, *D. passalorum* (Pearse and Wharton), has been described from a passalid beetle, *Odontotaenius disjunctus*. Deutonymphs of *D. passalorum* are common under the anterolateral corners of the elytra of this beetle. Delfinado and Baker (1975) report adults and deutonymphs of *D. passalorum* taken from the tunnel and under the elytra. It was not clear if the adults were taken from the beetles. Adults are not common on passalid beetles, but I have a few unidentified females from beetles collected in Mexico and Brazil.

Macrochelidae Vitzthum, 1930

Both sexes of macrochelids may be recognized by: dorsal shield entire; legs I without claws; peritreme exits stigmata posteriorly then loops anteriorly (Fig. 15), and palpal apotele three-tined (Fig. 15a). This family includes a large number of species. Many are free-living, but over 250 species are phoretically associated with insects, especially with beetles. The phoretic stage is the adult female. Species of only one genus, *Macrocheles* Latreille, have been collected from passalid beetles.

Three species have been described, all collected from *Odontotaenius disjunctus* in the U. S. A. (see Delfinado and Baker 1975). Although not common on passalid beetles, species of *Macrocheles* have been collected from passalids in Mexico, Trinidad and Brazil, and probably occur in association with many New World passalids. No information is available on the biology of macrochelids associated with passalid.



Figures 7-10

7) *Dendrolaelaps passalorum* (Pearse and Wharton), ex. U. S. A.: female, ventral view; deutonymph a) ventral view, b) dorsal view. 8) *Cosmolaelaps* sp., ex. Brazil: female, ventral view, with dorsal seta; a) deutonymph, ventral view. 9) *Geolaelaps disjuncta* Hunter and Yeh, ex. U. S. A.: female, ventral view, with dorsal seta. 10) *Brachytremelloides* sp., ex. Costa Rica: coxae I, ventral view; a) *Tenuiplanta* sp., ex. Mexico: femora III and IV, dorsal view.

Laelapidae Berlese, 1892

Characterization of this family is difficult. Over 120 genera and/or subgenera have been assigned to the Laelapidae. The family includes vertebrate parasites, free-living species, and associates of arthropods. Over 300 species are associated with Hymenoptera and over 200 species associated with Coleoptera (Hunter and Rosario 1988). Species of two genera (*Cosmolaelaps* Fig. 8 and *Geolaelaps* Fig. 9) are associated with passalid beetles; however, species of these genera are not limited to passalids. Most described species of *Cosmolaelaps* are associated with ants and many species of *Geolaelaps* are free-living. Biological studies of *C. trifidus* and *G. disjuncta* Hunter and Yeh have been reported (Hunter and Mollin 1964a, 1964b; Hunter and Yeh 1969). Reproduction of *C. trifidus* requires contact with beetle frass less than three days old, and these mites are normally found near the beetle. In contrast, *G. disjuncta* reproduces only in aged, dryer frass in the older areas of the tunnel, and contact with the beetle is not required. It is likely this latter species feeds on nematodes which are normally abundant in the beetle tunnel.

In both genera the female is the phoretic stage. With *C. trifidus*, an occasional male (less than 4%) may be found attached to a beetle, but immatures of this species have never been taken from the host. However, in material I have from Brazil both the protonymphal and deutonymphal (Fig. 8a) stages of an undescribed species have been collected from a passalid.

Species of both genera have been collected from both New World and Old World passalid beetles; however, *C. trifidus* and *G. disjuncta*, both from the U. S. A., are the only described species. Species separation for both genera is difficult, especially for *Cosmolaelaps*, the more common genus. The genera *Cosmolaelaps* and *Geolaelaps* may be separated by the following characters.

Key to New World genera of Laelapidae

- 1. Dorsal shield setae lanceolate; female sternal shield concave posteriorly (Fig. 8) *Cosmolaelaps* Berlese
- Dorsal shield setae needle-like; female sternal shield convex posteriorly (Fig. 9) *Geolaelaps* Trägårdh

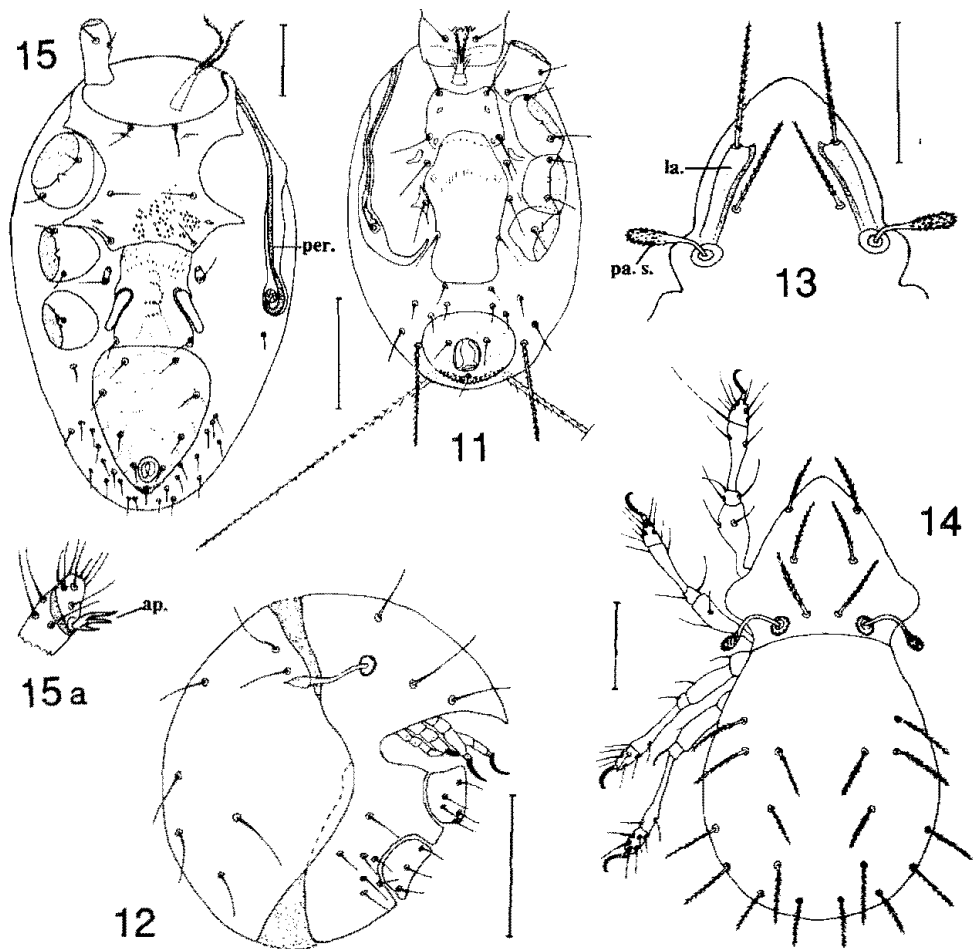
Ascidae Voigts and Oudemans, 1905

Adult female ascids are recognized by: an entire dorsal shield, or shield with distinct notch between the pronotal and opisthonotal areas, and more than 21 pairs of setae on the dorsal shield; sternal shield with three (rarely two) pairs of setae; metasternal setae arise from platelets or from the integument; genital shield truncate posteriorly, one pair of setae on the shield or arising from the integument near the shield; usually one to three small sclerites in the integument behind genital shield; anal shield separate or fused with ventral shield. Male with a sternogenital and a ventroanal shield, rarely with these shields fused to form a holovenral shield.

Many ascids are free-living predators in soil, forest litter, under bark, rotting plant material, etc. Many species of *Proctolaelaps* Berlese are associated with the insect fauna of injured or dying trees (Lindquist and Hunter 1965). Some of these species are commensals and others are predatory upon microorganisms living in the insect galleries. Hunter and Rosario (1988) reported 99 species of ascids associated with insects, over half with Coleoptera; however, none with passalid beetles. I have specimens of two undescribed species of ascids collected from two species of passalid beetles in Mexico (Fig. 11). These species could not be placed in a genus.

Although species of this family have not been reported from passalid beetles previously, future collecting may show some ascid as occasional riders on passalids.

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Figures 11-15

11) *Ascidae* sp., ex. Mexico: female, ventral view. 12) *Mesopliophora* sp., ex. U. S. A.: lateral view. 13) *Oribatulidae* sp., ex. U. S. A.: propodosoma, dorsal view (not collected from passalid beetle). 14) *Oppia* sp., ex. U. S. A.: dorsal view (not collected from passalid beetle). 15) *Macrochelus* sp., ex. Mexico: female, ventral view; a) palpal tarsus, ventral view.

Klinckowstroemiidae Trägårdh, 1950

Both sexes of adult klinckowstroemiid mites are characterized by: hyaline hood (a membranous extension of the dorsal shield) forming a crescent over the gnathosoma (Fig. 17c, h.h.) and extending posteriorly along the lateral margins of the body, or surrounding the entire body (Figs. 17b, h.h.); palpal trochanter seta av1 (anterior seta) strongly pectinate and fan-shaped; corniculi bifid, well developed, inner tooth tapers to a point; legs II-IV with flange-like extension on venter of femur. In the female, a well-developed sternogynial, paired latigynials and a mesogynial shields are present (Figs. 17, 17a). The number of setae on the latigynial shields varies from species to species, within a species and from shield to shield on an individual. The male genital opening is between coxae II and III.

These mites have been collected only from New World passalid beetles. Known distribution is from southern Mexico to northern Brazil. One mite species may occur on several passalid species; however, information is not available to determine if more than one mite species occurs on the same individual beetle at the same time. Twenty two species have been described in four genera. Immature stages have not been described. Genera may be separated by the following key.

Key to genera of Klinckowstroemiidae
(Based on males and females)

- 1. Hyaline hood surrounding body (Fig. 17b, h.h.), metapodal suture absent; male without sternoventral suture; dorsal shield with protuberances posteriorly (Fig. 17b) *Antennurella* Berlese
- Hyaline hood not surrounding body (Fig. 17c), metapodal suture present; male with or without sternoventral suture; dorsal shield with or without protuberances 2
- 2. Anal shield fused to ventral shield; dorsal shield with constriction in region above coxae I, without posterior protuberance (Fig. 17c) *Klinckowstroemilla* Turk
- Anal shield distinct; dorsal shield without constriction in region above coxae I, posterior part of shield with or without protuberances 3

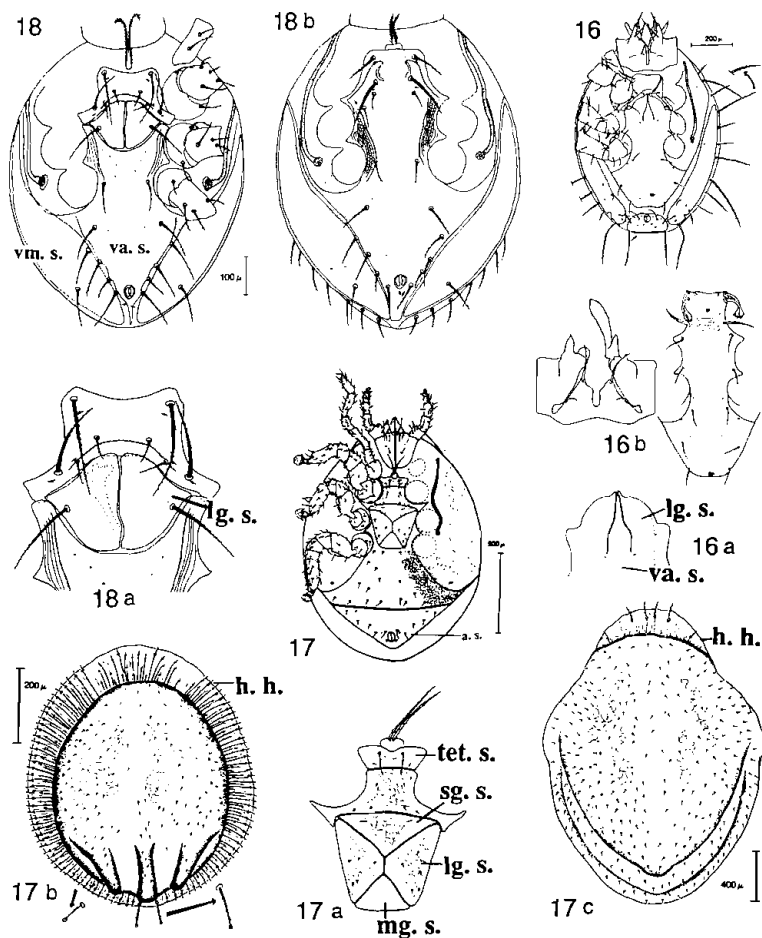
3. Latigynial shield blunt, pointed, straight, or sinuous on median margin; male with sternovenal suture *Klinckowstroemia* Trägårdh
- Latigynial shield L-shaped; mesogynial and sternovenal shields with setae; male without sternovenal suture *Similantennurella* Rosario

Useful references include: Rosario and Hunter 1987, 1988; Rosario 1988.

Diplogyniidae Trägårdh, 1941

Diplogyniidae females are characterized by having the latigynial shields free from adjacent shields (Fig. 18a, lg.s.); anal shield fused with ventral shield (Fig. 18, va.s.) (two genera *Neodiplogynium* Trägårdh and *Paradiplogynium* Womersley have the anal shield outlined by a suture, but the shield is never separated from the ventral shield by integument); ventromarginal shields present, lateral of ventroanal shield (Fig. 18, vm.s.) (exception is *Weiseronyssus* Samsinak from a dynastid beetle, South China, where ventromarginal shields are absent). Variable characters include: number of setae on dorsal shield; number of setae on latigynial shields; presence or absence of metasternal setae; and metasternal shields free, fused to sternal shield, or fused to each other. Although also variable, characteristics of the gnathosoma are useful in generic determinations. The male genital opening is under the anterior margin of the sternal shield and the sternal, metasternal, ventral and anal shields are fused to form a holovenal shield (Fig. 18b). Despite the variations, adults form a morphologically compact group easily recognizable as diplogyniids.

The Diplogyniidae represent a diverse family ecologically. Species have been recorded from the New World and the Old World. Adults appear to be phoretic on arthropods, with the exception of one species recorded from a snake in the Solomon Islands. Species of diplogyniids have been collected from: Passalidae, Scarabaeidae, Histeridae, Tenebrionidae, Dynastidae and undetermined beetles; Hymenoptera; termites; cockroaches; millipedes; and under bark, in soil and on plants.



Figures 16-18

16) *Euzercon anatonon* Hunter and Rosario, ex. Mexico: female, ventral view; a) female genital area, ventral view; b) male, ventral view of sternogenitoventral shield and gnathosoma. 17) *Klinckowstroemia schusteri* Rosario and Hunter, ex. Guatemala: female, ventral view; a) female, sternal and genital shields; b) *Antennurella trousarti* Berlese, ex. Trinidad: female, dorsal view; c) *Klinckowstroemiella blumae* Rosario and Hunter, ex. Costa Rica: female, dorsal view. 18) *Crassoseta fonsceai* Hunter, ex. Brazil: female, ventral view; a) female, genital area; b) *C. starri* Hunter, ex. Brazil: male, ventral view.

Euzerconidae Berlese, 1892

Female Euzerconidae all share the following characteristics: median dorsal shield setal lengths less than length of anal opening; some or all marginal body setae longer than length of anal shield (Fig. 16); sternal shield bears three pairs of setae; latigynial shields fused to ventral shield; anal shield separated by integument from ventral shield; and cornicula of gnathosoma toothed. Males have the genital opening in the anterior margin of the sternogenitoventral shield (anal shield separate); and the hypostoma of the gnathosoma is asymmetrical (Fig. 16b).

Species of Euzerconidae have been collected in both the Old and New World tropics, and one species, *Euzercon latus* Banks from the temperate areas of the U.S.A. Eleven genera, a total of 25 species, have been described. Six of these genera were from passalid beetles, one from millipedes, and the remaining four (from Africa and the Philippines) are listed as "habitat unknown".

In the New World, nine species, representing four genera, have been collected from passalids; however, many species remain to be described. The species *E. latus* has been reared in the laboratory, in frass 3-5 weeks of age taken from *Odontotaenius disjunctus* cultures, in the absence of its host beetle (Hunter and Davis 1965).

Keys to the genera of Euzerconidae are given by Funk (1980), and Hunter and Rosario (1991). A key to the four genera collected from New World passalids is given below.

Key to New World genera of Euzerconidae

- 1. All marginal body setae at least three times as long as anal shield
 *Pseudoeuzercon* Funk
- Some marginal body setae less than three times length of anal shield
 2

Mites associated with new world passalid beetles

- 2. Eight setae on femur III; sternal setae 2 arising lateral of oval sternal pores .
 *Trinizercon* Hunter and Rosario
- Seven setae on femur III; sternal setae 2 arising mesal of oval sternal pores
 3
- 3. Twelve pairs of marginal body setae (the first two pairs of body setae, j1 and
 z1, are not counted as marginal setae); hypostomal seta 1 pilose; continuous
 margins of latigynial shields of female forming an H-shape
 *Etazercon* Hunter and Rosario
- Thirteen pairs of marginal body setae (Fig. 16); hypostomal seta 1 smooth;
 medial margins of latigynial shields of female forming an inverted Y- or
 U-shaped slit (Fig. 16a) *Euzercon* Berlese

Megisthanidae Trägårdh, 1937

These are the largest mites on passalid beetles, many species are over 2,000 μ in length. Megisthanids are heavily sclerotized, dark brown in color and egg-shaped; sternal, metasternal and ventral shields fused and surrounding the triangular shaped genital opening located between coxae II and III; anal shield separate from ventral shield (Fig. 19).

A megisthanid species was the first mite described from a passalid beetle (Thorell 1882). This family contains approximately 30 species, all assigned to the genus *Megisthanus* Thorell. Prior to the mid 1900's the species were poorly described and illustrated, and inclusion of some in *Megisthanus* is questionable. Only the more recently described species can be recognized with certainty.

In the New World species have been collected from passalids in the U.S.A., Mexico, Guatemala and Boliva. In the Old World megisthanids have been collected from passalid and scarabaeid beetles. The latter host is probably a chance associations as megisthanids appear to be specific to passalid beetles. Megisthanid mites appear to be world wide in distribution wherever passalids occur. In addition to the countries listed above, megisthanids have been collected from Africa, Australia,

New Caledonia, New Guinea and Java. Detailed biological studies have been made on *Megisthanus floridanus* Banks (Butler and Hunter 1968). In the laboratory this mite reproduced in the absence of the host beetle, *O. disjunctus*. The larval mite makes a cell of frass particles and subsequent immature stages live in this cell. The young adult mite leaves the cell. Test indicated that the cell is important in controlling the humidity around the mite. Mites in the cell were seen feeding on nematodes. Beetle frass used in these studies was 3-6 weeks of age.

In field logs containing passalid tunnels, cells were commonly found in the older frass away from the area where beetles were actively feeding. Other useful references include Hunter and Costa (1970), Kethley (1977), and Womersley (1937).

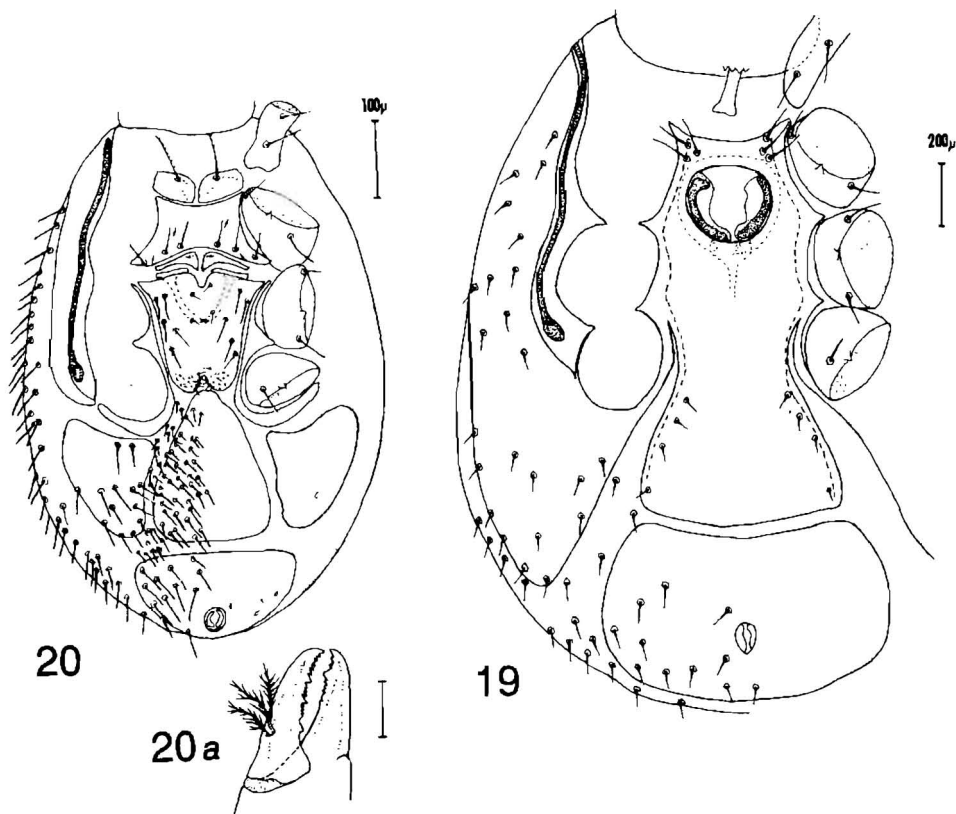
Hoplomegistidae Camin and Gorirossi, 1955

Hoplomegistid mites are large (some over 2,000 μ in length) and may be recognized by the following characters: dorsal shield not covering all of dorsum; sternal setae 1 on jugular shields; and ventral and anal shields separate from each other and from other shields. In the female, the latigynial shields are large (Fig. 20), and separated medially or notched on the midline anteriorly and posteriorly. The male ventral shields are similar to those of the female, and the genital opening is a circle in the posterior area of the sternogenital shield.

The taxonomy of this group is confusing. The family contains seven named species, all assigned to the genus *Stenosternum* Kramer. Six of these species were originally described in the genus *Hoplomegistus* Berlese; however, this genus has been synonymized with *Stenosternum* (Kethley 1977) (Kethley still retained the family name Hoplomegistidae !).

Three species, *S. bicrenius* (Berlese), 1918, *S. trapeziger* (Berlese), 1910 and the type species *S. bipilosum* Kramer, 1898) need to be redescribed and illustrated. The remaining four species are probably

recognizable from published descriptions and illustrations. Camin and Gorirossi (1955) suggested *S. armiger* (Berlese), 1903, and *S. tragardhi* (Berlese), 1910, may be conspecific. Useful references include Butler and Hunter (1966), Kethley (1977) and Turk (1948).



Figures 19-20

19) *Megisthanus* sp., ex. Mexico: female, ventral view. 20) *Stenosternum truittae* (Butler and Hunter), ex. Costa Rica: female, ventral view; a) chelicera, lateral view.

Suborder Oribatida

The family level taxonomy of the Oribatida is in a state of flux, and many general works deal only at the superfamily level. Generic determinations are more stable. Mites from three superfamilies (representing three families) have been collected from passalid beetles.

These superfamilies may be recognized by the following characters: brownish in color; heavily sclerotized; discrete stigmata absent; propodosoma with one pair of sensilla (= pseudostigmata organs or bothridial sensilla) arising from special sensory pits; chelicerae chelate; and strong rutella (analogous to corniculae of Mesostigmata) present on venter of gnathosoma. Sexual dimorphism is absent.

The oribatids are cosmopolitan, occurring primarily in the temperate and tropical areas. Most are fungivorous or saprophagous, but some may feed on algae, bacteria or yeast, and a few species are reported to feed on plants. Oribatid mites commonly inhabit forest humus, ground litter, and the upper soil strata. Norton (1980) lists oribatids collected from insects, and suggests these may fit the classification of phoresy.

Mites were recovered from beetles (passalids, scarabaeids, cerambycids, elaterids and scolytids), a dipteran, and a blattid. Norton had records for a total of 1,154 mites, most from passalid beetles. Mites were collected from 20 passalid species representing nine genera.

Although five genera of oribatids were collected from passalids, three genera-- *Mesoplophora* (Mesoplophoridae), *Metaleius* (Oribatulidae) and *Oppia* (Oppiidae)--represented all but 16 of the mites collected. The most common attachment location on the beetles was in the ventrolateral area between the first and second thoracic segments. The method of attachment is known only for *Mesoplophora*, the most common of the three genera. These mites are capable of closing the anterior part of the body (aspis) ventrally against the posterior body region, much as a jackknife closes. When attached these mites hold a

seta between the aspis and a tooth-like structure on the genital shield. The method of attachment of *Metaleius* and *Oppia* mites is not known, but Norton suggests the mites cling by their claws since the body of neither is closable.

Mesoplophora pulchra is associated with decaying stumps and probably *Mesoplophora* species collected from passalid beetles live in similar habitats. This could bring the mites into contact with passalid beetles. Oribatid mites are rare on passalids. Large numbers (50 or more) were reported by Norton from one beetle, but normally only 1-5 mites were found on a beetle. In years of collecting, I have found only *Mesoplophora* oribatid mites on passalids and these only a few times. These mites were attached to setae in the coxal areas on *Odontotaenius disjunctus*. Oribatid mites are probably opportunist in attaching to passalids and would not represent a true mite-passalid beetle association. The three families of oribatid mites, and thus the three common genera, may be separated by the following key.

Key to Oribatids from passalid beetles

1. Propodosoma closable like blade of jackknife (Fig. 12)
..... **Mesoplophoridae** (*Mesoplophora* Berlese)
- Propodosoma not closable 2
2. With lamella on dorsum of propodosoma (Fig. 13)
..... **Oribatulidae** (*Metaleius* Trave)
- Without lamella (Fig. 14) **Oppiidae** (*Oppia* Koch)

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