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Comparative and phylogenetic studies of Laelapidae
(Acarii:Mesostigmata)

Casanueva, Maria Eugenia, Ph.D.
The Ohio State University, 1989

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COMPARATIVE AND PHYLOGENETIC STUDIES OF LAELAPIDAE (ACARI: MESOSTIGMATA)

DISSertation

Presented in Partial Fulfillment of the Requirements for the Degree
Doctor of Philosophy in the Graduate School of
The Ohio State University

by

Maria Eugenia Casanueva, B.Sc., M.Sc.

The Ohio State University
1989

Dissertation Committee:

S. W. Fisher
C. A. Triplehorn

Approved by

[Signature]

Department of Entomology
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Maria Eugenia Casanueva
1989
To My Parents
I express sincere appreciation to Dr. Donald E. Johnston for his advice, guidance and insight throughout the research.

I want to thank the acarologists and curators of collections who provided me with the material studied. Special thanks to Dr. Marisa Castagnoli of the Istituto Sperimentale per la Zoologia Agraria for her hospitality and for providing access to the Berlese collection.

Gratitude is expressed to Dr. Calvin Welbourn for his time helping me to get acquainted with the computer programs and systems.

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Finally, my warmest thanks to my family and friends for all their support and unshakable faith in me and their willingness to endure with me the vicissitudes of my endeavors. To all of them, my deepest appreciation and love.
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Studies in Taxonomy of Free-living and Arthropod-associated Mesostigmata (Acari). Laboratory of Acarology, The Ohio State University, Columbus. Dr. Donald E. Johnston (Professor).
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INTRODUCTION

The dermanyssine family Laelapidae is complex, species-rich, very diverse, and very poorly understood. Hypotheses concerning the evolutionary history of this family and its relatives are minimally developed and the classification of the group is consequently inadequate. Early authors (e. g., Canestrini, Berlese) described many genera and species especially from Europe. Subsequent workers have continued with the description of new forms and, at the same time, have attempted to formulate comprehensive classifications. These efforts have failed. These mites have been placed in a single family or in a number of different families. The difficulty in classification might be attributed to the wide range of anatomical forms as a result of diverse adaptation to parasitism and to the consequent concentration of studies on parasites on vertebrates while neglecting the numerous free-living and arthropod-associated species. The Laelapidae exhibits a fascinating range of habitats and associations, mostly not studied in detail.
Among the Laelapidae are many genera that developed ectoparasitic (nest-dwelling or host-dwelling) associations with mammals (35 genera), and also many free-living, soil-dwelling predatory forms (10 genera). Lesser derivative elements are soil inhabiting or nest-associated predators. The greatest anatomical and ecological diversity, however, is seen in the arthropod-associated species (43 genera). Here occur associates of Coleoptera (8 mite genera), Blattaria (2 genera), Isoptera (1 genus), Hymenoptera (21 genera), Araneae (1 genus), Myriapoda (7 genera) and terrestrial Crustacea (2 genera). (Table 1)

The morphological heterogeneity exhibited by the group has encouraged taxonomic and systematic studies by several scientists who have attempted to define it. Berlese (1892) recognized two families: Dermanyssidae Kolenati, 1859, which included the obligatory parasites, and Laelapidae Berlese, 1892 including the free-living forms, paraphages of arthropods and facultative ectoparasites, comprising the genera Laelaps Koch, Hypoaspis Canestrini, Setus Koch, Iphis Koch, Stylochirus Canestrini, Neoberlesia Berlese, Podoctinum Berlese and Iphiopsis Berlese. In 1903 and 1904 Berlese described new species of free-living and ant associated mites. After Berlese's classification of laelapid mites, the subsequent classificatory works have dealt almost exclusively with the "parasitic" forms. Tragardh (1904, 1908) reduced the family
Laelaptidae to subfamily rank and assigned it to the family Parasitidae. Vitzthum (1943) established one of the current approaches to the classification of this family. Vitzthum recognized a single family, Laelaptidae, with thirteen subfamilies: Hypoaspidinae, Hyletastinae, Phytoseiinae, Podocininae, Iphiopsinae, Haemogamasinae, Laelapinae, Raillietiinae, Liponyssinae, Dermanyssinae, Halarachnidae, Entonyssinae and Rhinonyssinae. With some exceptions, the first five given here included free-living mites or associates of invertebrates and the remaining eight parasites of vertebrates. Baker and Strandtman (1948), following Vitzthum classification, described Myrmonyssus chapmantine and included it in the subfamily Hypoaspidinae. Zumpt and Patterson (1951) added a new subfamily, Myonyssoidinae, and tentatively included Dasyponyssinae Fonseca, 1940. However, Zumpt and Till (1958) excluded Myonyssoidinae from Laelapidae and placed it in Ascidae.

A second approach to the interpretation of the Laelapidae was given by Baker and Wharton (1952). They modified Vitzthum's classification and recognized nine families: Laelapidae (Laelapinae, Hypoaspidinae and Hyletastinae), Dermanyssidae (Dermanyssinae and Liponyssinae), Phytoseiidae (Phytoseiinae and Podocininae), Iphiopsidae, Haemogamasidae, Raillietiidae, Rhinonyssidae, Entonyssidae and Halarachnidae. They mentioned that the Laelapinae have strong ventral setae, expanded pilus dentilis, a
fleshy tectum and they are parasitic. On the other hand, Hypoaspidinae have weak ventral setae, seta-like pilus dentills, reduced tectum and they are free-living. The nymphs and adults of Hypoaspidinae mites are all active feeding stages, in many cases they may become phoretically associated with other soil-inhabiting arthropods. Hypoaspids have not developed specialized adaptive structures for phoresy, as in other groups of mites, and they cling to their hosts by means of their chelicerae (Hunter and Mollin, 1964) or clasping the host's hair and curving mainly legs II around it (Rosario, 1981). Evans and Till (1966) considered the Hypoaspidinae mites one of the most primitive mesostigmatid mites because of the absence of specialized structures. The subfamily Hypoaspidinae has been suggested by Radovsky (1969) to have given rise to the parasitic Laelapinae mites from which more specialized parasitic groups (e.g. Dermanyssidae, Spinturnicidae and others) are said to have arisen.

Evans (1955) excluded the Phytoseiinae and Podocininae from Laelapidae. He placed Podocinum near the Macrochelidae and Hypoaspidinae in the Laelapinae, and the Raillietiinae in the Liponyssinae. Evans (1957), working with the British free-living and parasitic members of Laelapidae sensu Vitzthum, recognized the Eviphididae (=Hyletastinae) as a separate family, but included the Spinturnicinae Oudemans as a subfamily of Laelapidae. Several
genera from Laelapinae, Hypoaspidinae and Podocininae were removed and distributed among the Aceosejidae and Neoparasitidae. Evans, Sheals and McFarlane (1961) used the name Macronyssinae rather than Liponyssinae. Laelapidae in this narrow sense then included nine subfamilies: Laelapinae, Haemogamasinae, Iphlopsinae, Macronyssinae, Entonyssinae, Dermanyssinae, Spinturniciniae, Halarachninae and Rhinonyssinae (Radovsky, 1967).

Bregetova's classification (1956) is similar to that of Baker and Wharton (1952). She gave slightly broader limits for the Laelapidae in which Raillietia and Myonyssus were included. Tipton (1960) reviewing the Laelapinae recognized in it only fifteen genera, all of them vertebrate-associated. He also established the subfamily Alphalaelaptinae with the genus Alphalaelaps. Bernhard (1963) mentioned nine subfamilies, but without Spinturniciniae and with Raillietiinae included as a separate subfamily.

In 1965 Karg recognized the superfamily Laelaptoidea Berlese, 1892 sensu Evans, 1957 with the single family Laelaptidae. He included subfamilies: Hypoaspidinae Vitzthum, 1941 with the genera Oloelaeps s. lat. and Hypoaspits s. lat., and the subgenera Cypholaeps, Gymnolaeps, Cosmolaeps and Hypoaspitsella; Laelaptinae Tragardh, 1908 with Laelaps and Haemolaeps; Haemogamasidae Oudemans, 1926 with Eulaeps and

Evans and Till (1966, 1979) adopted Dermanyssidae as the family name with priority over Laelapidae. They restricted their concept of the family and recognize the following subfamilies: Dermanyssinae, Haemogamasesinae, Pseudolaelapinae, Myonyssinae, Melitirphinae, Laelapinae, Hirstionyssinae and Macronyssinae. They defined a basic dermanyssid type as follows: adult chelicerae chelate-dentate; movable digit bidentate in the female, unidentate in the male; pilus dentils short, setiform; spermatodactyl free distally and grooved. Deutosternum with six transverse rows of denticles; corniculi horn-like; pedipalps with two-tined claws; anterior margin of tectum denticulate. Dorsal shield entire with 39 pairs of setae. Metasternal setae free. Genital shield flask-shaped with one pair of
seta. Anal shield with 3 setae, euanal seta absent. Opisthogastric cuticle with 7 pairs of setae, metapodals small, subcircular. Peritrematal shields free posteriorly; peritreme extending beyond coxa I. Male with holoventral shield bearing 10 pairs of setae excluding anals; genital orifice pre-sternal. All legs with developed retractile ambulacra; legs' chaetotaxy normal (as defined by Evans and Till, 1965); without marked sexual dimorphism.

Radovsky (1967) delimited the Laelapidae including the Haemogamasinae. He restored Macronyssidae to family rank, and Hirstonyssus, Echinonyssus, Patrinyssus, Trichosurolaelaps and Australolaelaps are placed in the Laelapidae. He restricted Dermanyssidae to members of the Dermanyssinae and elevated Hystrichonyssidae to family rank. Radovsky (1969) chose the restricted family concept Laelapidae in preference to Dermanyssidae s. lat. based on the long established usage of the former name.

Krantz (1978) also retained the name Laelapidae following Radovsky's ideas but he applied the rules of priority in assigning Dermanyssoloea as the superfamily name. He recognized nine subfamilies in Laelapidae: Hypoaspidinae which includes many free-living species, many associated with arthropods, and a few regularly found in the nest or on the bodies of vertebrates; Haemogamasinae which are facultative parasites of rodents and some
birds, they are polyphagous, feeding on dead arthropods, nematodes or vegetable matter; Laelapinae, facultative parasites of mammals and occasionally with birds; Alphalaelapinae, Myonyssinae and Hirtionyssinae are parasitic on mammals; Iphiopsinae and Melittiphinae are associated with arthropods; and Pseudolaelapinae is free-living. Tenorio and Radovsky (1974) also included the subfamily Mesolaelapinae which is found entirely on mammals. In the sense of Krantz (1978) the Laelapidae can be defined as: adults with chelicerae dentate or edentate, fixed digit present; with three pairs of hypostomal setae in nymphs and adults; peritremes variously produced, typically well developed and elongate, occasionally absent; legs without "metatarsi".

Lindquist (1979) gave the Laelapidae the same status as Dermanyssidae. He included under Dermanyssoloidea Kolenati, 1859 the families Haemogamasidae, Macronyssidae, Rhinonyssidae, Halarachnidae, Spinturnicidae, Ixodorhynchidae, Entonyssidae, Raillietiidae, Dermanyssidae and Laelapidae.

Evans and Till (1979) recognized the family Laelapidae with five subfamilies: Laelapinae, free-living mites or with a range of associations with insects, birds and mammals as inhabitants of nests, scavengers and parasites on the body of the host (Ololaelaps, Androlaelaps, Ondatralaelaps, Laelaps, Hyperlaelaps, Pseudoparasitus,
Stratiolaelaps, Cosmolaelaps, Holostasps, Gymnolaelaps, Pneumolaelaps, Laelaspis and Hypoapsis s. lat.); Haemogamasinae, mites associated with house and field mice and moles (Eulaelaps and Haemogamasus); Myonyssinae, one genus associated with bee-hives (Myonyssus); Pseudolaelapinae, a free-living genus (Pseudolaelaps); and Hirstionyssinae, an obligatory haematophagous ectoparasite of mammals (Hirstionyssus).


Johnston (1982) included the superfamily Dermanyssoidae with seventeen families within the cohort Dermanyssina. He recognized Haemogamasidae and Hirstionyssidae as separate families and not to be included within Laelapidae as Krantz (1978) had done.
From the examples of classifications listed above, it can be clearly seen that there is no precise agreement between any two of these classifications. Furthermore, there are vacillations when it comes to determining the placement of certain taxa. Among these taxa, for example, are: *Urozercon* Berlese, *Myrmonysus* Berlese, *Podolaelaps* Berlese, *Iphiopsis* Berlese, and *Neoberlesia* Berlese.

The placement and definition of the genus *Varroa* Oudemans, 1904 has also been controversial. When first described, the genus was considered to have one species *V. jacobsont*, a parasite of *Apis indica* Fabricius, and was placed into the subfamily Laelapinae. Gunther (1951), based on mites found in the sealed brood cells of honey bees from Singapore, described *Myrmozercon reidii* Baker and Wharton (1952) listed *Varroa* in the subfamily Hypoaspidae within Laelapidae. Delfinado and Baker (1974) studying mites on honey bees considered *M. reidi* as a synonym of *V. jacobsont* and proposed the family Varroidae to accommodate two genera: *Varroa* (*V. jacobsont* Oudemans) and *Euvarroa* (*E. sinhai* Delfinado and Baker); both genera are parasites of domestic and wild honey bees. Unlike some of the Laelapidae, the females of Varroidae completely lack the fixed digit of the chelicerae and have a reduction in the number of gnathosomal setae. These characters are considered as "unique" for Varroidae by Delfinado and Baker, 1974. In 1987 Delfinado-Baker and Aggarwal described a new species of *Varroa*, *V. underwoodi*,
which has also *Apis cerana* (= *A. indica*) as the original host.

From the viewpoint of phylogenetic systematics, this family and included taxa and its relatives are not adequately characterized and understood. Can the Laelapidae be recognized as a monophyletic group (that is, can a unique evolutionary origin be hypothesized) within a monophyletic superfamily Dermanyssoidea? The present study emphasizes the predaceous soil and arthropod-associated genera to discover major patterns of morphological variation in the lesser derivative forms and thus provide a comparative and phylogenetic basis for study of the derivative groups. Finally, comparisons with the eviphidoid family Leptolaelapidae as the hypothesized sister group (nearest evolutionary relative) and with Ologamasidae as the outgroup of Laelapidae have been done. Thus this study provides an improved classification and better understanding of the evolutionary relationships within this diverse group of Mesostigmata mites.

A summary of the major prior classifications of the Laelapidae is presented in Tables 2, 3 and 4.
Table 1.- Ecological Relationships of Genera Previously Assigned to the Family Laelapidae


5.- Associates of Blattaria: *Blaberolaelaps*, *Gromphadorholaelaps*.

6.- Associates of Isoptera: *Urozercorcon*.


8.- Associates of Chilopoda: *Iphiolaelaps*, *Scolopendracaratus*, *Jacobsonta*.

9.- Associates of Araneae: *Ljunghta*.

10.- Associates of Terrestrial Crustacea: *Cyclothorax*, *Gecarctinolaelaps* n. gen.
Table 1.- (continued)

Table 2.- Family Laelaptidae Berlese, 1892 sensu Vitzthum, 1941 and Baker and Wharton, 1952.

I. Subfamily Hyletastinae Vitzthum, 1941

1. *Hyletastea* Gistel, 1848 (= *Iphis* Koch, 1836)  
   type: *Iphis globulus* Koch, 1839

2. *Copriphis* Berlese, 1910
   *Copriphis* (*Copriphis*) type: *Iphis pterophilus* Berlese, 1882
   *Copriphis* (*Peletiphis*) type: *C. (P.) insignis* Berlese, 1911
   *Copriphis* (*Alliphis*) type: *Gamasus halleri* G. and R. Canestrini, 1881

3. *Cosmiphis* Vitzthum, 1926  
   type: *Emaeus bosschat* Oudemans, 1901

4. *Eviphis* Berlese, 1903
   *Eviphis* (*Eviphis*) type: *Eumaeus pyrobolus* Koch, 1839
   *Eviphis* (*Olotphis*) type: *Eviphis magnificent* Berlese, 1916

5. *Iphtidozercon* Berlese, 1918  
   type: *Eviphis gibbus* Berlese, 1903

6. *Melittiphis* Berlese, 1918  
   type: *Laelaps (Iphis) alvearius* Berlese, 1895

7. *Uroiphis* Berlese, 1903  
   type: *Uroiphis scabratus* Berlese, 1903

II. Subfamily Hypoaspidinae Vitzthum, 1941

1. *Hypoaspis* G. Canestrini, 1885  
   *Hypoaspis* (*Hypoaspis*) type: *Laelaps krameri* G. and R. Canestrini, 1881
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<th>Hypoaspis (Androlaelaps) type: Laelaps hermaphroditus Berlese, 1903</th>
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<td>Hypoaspis (Gymnolaelaps) type: Laelaps myrmecophilus Berlese, 1892</td>
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<td>Hypoaspis (Holostaspis) type: Holostaspis isotricha Kolenati, 1858</td>
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<td>Hypoaspis (Laelaspis) type: Iphits astronomicus Berlese, 1889</td>
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<td>Hypoaspis (Leptolaelaps) type: H. (L.) elegans Berlese, 1918</td>
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<td>Hypoaspis (Pneumolaelaps) type: Iphits bombicolens Canestrini, 1885</td>
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<td>Hypoaspis (Stratiolaelaps) type: Laelaps (Iphits) miles Berlese, 1882</td>
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2. Anystipalpus Berlese, 1911
   type: Anystipalpus percicola Berlese, 1911

3. Arctoseius Thor, 1930
   type: Arctoseius lateroincicus Thor, 1930

4. Coleolaelaps Berlese, 1914
   type: Laelaps (Iphits) agrestis Berlese, 1887

5. Dinogamasus Kramer, 1898 (= Greenia Oudemans, 1901; = Greenella Banks, 1904; = Dolaea Oudemans, 1912)
   type: Dinogamasus crassipes Kramer, 1898

6. Iphidosoma Berlese, 1892 (Parasitidae?)
   type: Holostaspis fimetaria Müller, 1859

7. Jordensia Oudemans, 1937
   type: Gamasus cossi Duges, 1834

8. Julolaelaps Berlese, 1916
   type: Julolaelaps dispar Berlese, 1916
Table 2.- (continued)

   type: *Laelantennus lagena* Berlese, 1916

10. *Ljunghia* Oudemans, 1932
    type: *Ljunghia selenocosmiae* Oudemans, 1932

11. *Meliponasptis* Vitzthum, 1930
    type: *Meliponasptis debilipes* Vitzthum, 1930

12. *Myrmeciphtis* Hull, 1923
    type: *Myrmeciphtis crawleianus* Hull, 1923

13. *Myrmolaelaps* Tragardh, 1904
    type: *Myrmolaelaps equitans* Trägardh, 1906

14. *Myrmoleichus* Berlese, 1903
    type: *Myrmoleichus coronatus* Berlese, 1903

15. *Myrmonyssus* Berlese, 1903
    *M. (Myrmonyssus)* type: *M. (Myrmonyssus) diplogenlus* Berlese, 1903
    *M. (Laelaspulus)* type: *M. (Myrmonyssus) acuminatus* Berlese, 1903

16. *Myrmozercon* Berlese, 1902
    type: *Myrmozercon brevipes* Berlese, 1902

17. *Neoberlesia* Berlese, 1892
    type: *Neoberlesia equitans* Berlese, 1892

18. *Neocypholaelaps* Vitzthum, 1941 (= *Cypholaelaps* Berlese)
    type: *Laelaps ampullula* Berlese, 1892

19. *Ololaelaps* Berlese, 1903
    *O. (Ololaelaps)* type: *Laelaps venetus* Berlese, 1903
Table 2.- (continued)

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<td>type: Paradoxiphtis tennibrachatus Berlese, 1910</td>
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<td>Phytojacobsonia Vitzthum, 1925</td>
<td>type: Phytojacobsonia triëgularis Vitzthum, 1925</td>
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<td>22</td>
<td>Podolaelaps Berlese, 1888</td>
<td>type: Podolaelaps ambulacralis Berlese, 1888</td>
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<td>23</td>
<td>Proctolaelaps Berlese, 1914</td>
<td>type: Proctolaelaps productus Berlese, 1923</td>
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<td>24</td>
<td>Stamfordta Trägardh, 1906</td>
<td>type: Stamfordta carabicola Trägardh, 1906</td>
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<td>25</td>
<td>Stylochirus G. and R. Canestrini, 1882</td>
<td>type: Stylochirus rovennensis G. and R Canestrini, 1882</td>
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<td>26</td>
<td>Urozercon Berlese, 1901 (= Termitacarus Trägardh, 1906)</td>
<td>type: Urozercon paradoxus Berlese, 1901</td>
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<td>27</td>
<td>Varroa Oudemans, 1904</td>
<td>type: Varroa jacobsoni Oudemans, 1904</td>
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III. Subfamily Laelaptinae Berlese, 1892

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<tr>
<th>Table Number</th>
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<tr>
<td>1</td>
<td>Laelaps Koch, 1836</td>
<td>type: A. murs Ljungh, 1799 (= Laelaps agilis Koch, 1938)</td>
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<td>1.1</td>
<td>L. (Laelaps)</td>
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<td>1.2</td>
<td>L. (Eugynolaelaps)</td>
<td>type: L.(E.) coriaceus Berlese, 1918</td>
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<td>1.3</td>
<td>L. (Heterolaelaps)</td>
<td>type: L. (H.) antipodianus Hirst, 1926</td>
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<td>Common Name</td>
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<td>L. (Macrolaelaps)</td>
<td>type: <em>Laelaps sanguisugus</em> Vitzthum, 1924</td>
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<td>L. (Mesolaelaps)</td>
<td>type: <em>Mesolaelaps anomalus</em> Hirst, 1926</td>
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<td>L. (Tricholaelaps)</td>
<td>type: <em>L. (T.) comatus</em> Vitzthum, 1926</td>
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<td>3.- Echinolaelaps Ewing, 1929</td>
<td>type: <em>Laelaps echidninus</em> Berlese, 1887</td>
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<td>4. Eubrachylaelaps Ewing, 1929 (= Cyclolaelaps Ewing, 1931)</td>
<td>type: <em>Laelaps hollisteri</em> Ewing, 1925</td>
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<td>5. Eulaelaps Berlese, 1903 (= Hemilaelaps Hull, 1918)</td>
<td>type: <em>Laelaps stabularis</em> Koch, 1839</td>
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<td>E. (Eulaelaps)</td>
<td>type: <em>Laelaps (Hoploelaelaps) doderoi</em> Berlese, 1910</td>
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<td>E. (Pseudolaelaps)</td>
<td>type: <em>Laelaps (Hoptolaelaps) doderoi</em> Berlese, 1910</td>
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<td>8. Longolaelaps Vitzthum, 1926</td>
<td>type: <em>Longolaelaps longulus</em> Vitzthum, 1926</td>
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<td>10. Neolaelaps Hirst, 1926</td>
<td>type: <em>Liponyssus magnistigmatus</em> Vitzthum, 1918</td>
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</table>
Table 2.- (continued)

11. Neoparalaelaps Fonseca, 1935
   type: Neoparalaelaps bispinosus Fonseca, 1935

12. Ophidilaelaps Radford, 1947
   type: Ophidilaelaps imphalensis Radford, 1947

13. Scissuralaelaps Womersley, 1945
   type: Scissuralaelaps nova-guinea Womersley, 1945

14. Ugandolaelaps Radford, 1942
   type: Ugandolaelaps protoxera Radford, 1942

Unassigned genera:
Rad (new name for Banksia Radford, 1942; not Banksia Volgts and
Oudemans, 1905) type: Laelaps longiseta Banks, 1909; Ligilaelaps
Radford, 1942 type: Eulaelaps ewingi Pearse, 1930; Mungosticola
Radford, 1942 type: Mungosticola ugandae Radford, 1942.

Some genera given by Vitzthum (1941) and Baker and Wharton
(1952) as members of the family Laelapidae were not considered in
this study for the following reasons:
- Genera of Hylotastinae (Copriphts, Eviphts, Urolhts) are now
  included in Eviphididae (Eviphidoidea) except for Hylotastes which
  is unrecognizable; Iphidozercon is placed in the Ascidae; Eviphts
  (Olothts) is included in Eviphididae, and Cosmiphts is an unplaced
  genus in Eviphidoidea.

- Genera of Hypoaspidinae are currently included in Laelapidae
  except for:
  Hypoaspis (Leptolaelaps) - now Leptolaelaps (Leptolaelapidae)
Anystipalpus - unknown genus but not Laelapidae
Arctosetus - now Ascidae
Iphidosa - now Ologamasidae (Epiphidinae)
Jordensia - now Proctolaelaps (Ascidae)
Laelantennus - unknown Laelapidae
Meliponasptis - Laelapidae, no specimens available
Neocypholaelaps - now Ameroselidae
Ololaelaps (Cypholaelaps) - now Ologamasidae
Paradoxo - now unplaced genus in Eviphidoidea
Phytojacobsonia - not Laelapidae but otherwise unknown
Podolaelaps - unknown genus, not studied
Proctolaelaps - now in Ascidae
Stamfordia - not studied, unknown
Stylochirus - now Ologamasidae (Epiphidinae)

- Genera of Laelapinae now all in Laelapinae except for:
  Heterolaelaps and Mesolaelaps - now in Mesolaelapinae
  Eulaelaps - now in Haemogamasinae
  Eulaelaps (Pseudolaelaps) - Pseudolaelaps is excluded from Laelapidae
  Ophidiolaelaps - now in Ixodorhynchidae

- The unassigned genera: Banksta is a junior synonym of Poecilochirus
  (Parasitidae); Ligtlaelaps is a synonym of Thinoseius  (Epiphididae);
  and Mungosicola Radford is a synonym of Tympanosptinctus Berlese.
Table 3.- Family Laelaptidae sensu Karg, 1965

Superfamily Laelaptoidea Berlese, 1892 sensu Evans, 1957
Family Laelaptidae Berlese, 1892 sensu Evans, 1957

I. Subfamily Hypoaspidinae v. Vitzthum, 1941

1. **Ololaelaps** Berlese, 1903 s. lat.

   *Ololaelaps (Ololaelaps)* Berlese, 1903 s. str.
   type: *Laelaps venetus* Berlese, 1903

   *Ololaelaps (Cypholaelaps)* Berlese, 1916
   type: *Ololaelaps haemisphaericus* Berlese, 1916

   *Ololaelaps (Gymnolaelaps)* Berlese, 1920
   type: *Laelaps myrmecophilus* Berlese, 1892

2. **Hypoaspis** Canestrini, 1885 s. lat.

   *Hypoaspts (Cosmolaelaps)* Berlese, 1903
   type: *Laelaps claviger* Berlese, 1883

   *Hypoaspis (Hypoaspis)* Canestrini, 1885 s. str.
   type: *Laelaps krameri* Canestrini, 1881

   *Hypoaspis (Hypoaspisella)* (Bernhard, 1955 ) Karg, 1962
   type: *Hypoaspis heyi* Karg, 1962

II. Subfamily Laelaptinae Tragardh, 1908

1. **Laelaps** Koch, 1839
   type: *Acarus muris* Ljungh, 1799

2. **Haemolaelaps** Berlese, 1910
   type: *Laelaps marsupialis* Berlese, 1910
Table 3.- (continued)

III. Subfamily Haemogamasinae Oudemans, 1926

1. *Eulaelaps* Berlese, 1903  
   type: *Laelaps stabularis* Koch, 1839

2. *Haemogamasus* Berlese, 1910  
   type: *Haemogamasus hirsutus* Berlese, 1889
Table 4.- Family Laelapidae sensu Bregetova, 1977

I. Subfamily Myonyssinae Bregetova, 1956

1. *Myonyssus* Tiraboschi, 1904
   type: *Myonyssus decumanus* Tiraboschi, 1904

II. Subfamily Laelapinae Berlese, 1892

   type: *Laelaps* (*Hoplolaelaps*) *doderol* Berlese, 1910

2. *Ololaelaps* Berlese, 1904 (= *Pristolaelaps* Womersley, 1956)
   type: *Hypoaspis venetus* Berlese, 1903

3. *Hypoaspis* (*Euandrolaelaps*) Bregetova, 1977 (= *Androlaelaps*
   Berlese, sensu Bregetova, 1955, 1956)
   type: *Laelaps* (*Androlaelaps*) *sardous* Berlese, 1911

   *Hypoaspis* (*Coleolaelaps*) Berlese, 1914
   type: *Coleolaelaps agrestis* Berlese, 1887

   *Hypoaspis* (*Pneumolaelaps*) Berlese, 1920
   type: *Iphits bombicolens* Canestrini, 1885

   *Hypoaspis* (*Stratiolaelaps*) Berlese, 1916 (= *Davisiella* Zumpt et Patterson, 1951)
   type: *Laelaps* (*Iphits*) *miles* Berlese, 1882

   *Hypoaspis* (*Cosmolaelaps*) Berlese, 1903
   type: *Laelaps claviger* Berlese, 1883

   *Hypoaspis* (*Hypoaspis*) Canestrini, 1884
   type: *Gamasus krameri* Canestrini, 1881

   *Hypoaspis* (*Gymnolaelaps*) Berlese, 1916 (= *Laeliphis* Hull,
   1952; = *Austrogamasus* Womersley, 1942)
   type: *Laelaps myrmecophilus* Berlese, 1892

   *Hypoaspis* (*Geolaelaps*) Tragardh, 1952
   type: *Laelaps aculeifer* Canestrini, 1884
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<th>Species</th>
<th>Type</th>
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<td>4</td>
<td>Androlaelaps Berlese, 1903 (= Haemolaelaps Berlese, 1910)</td>
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<td>Laelaps (Iphis) hermaphroditae Berlese, 1887</td>
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<td>5</td>
<td>Holostasps Kolenati, 1858 (= Oolaelaps Berlese, 1904)</td>
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<td>Holostasps (sotricha) Kolenati, 1858</td>
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<td>6</td>
<td>Reticulolaelaps Costa, 1968</td>
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<td>Reticulolaelaps (faint) Costa, 1968</td>
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<td>Alloparasitus Berlese, 1920 (= Halbertia Hull, in Turk and Turk, 1952)</td>
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<td>Laelaps (Hypoaspis) oblongus Halbert, 1915</td>
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<td>8</td>
<td>Laelaspis Berlese, 1903</td>
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<td>Iphis astronomicus C. L. Koch, 1839</td>
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<td>Eulaelaps Berlese, 1903</td>
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<td>Eulaelaps stahularis C. L. Koch, 1836</td>
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<td>10</td>
<td>Pseudoparasitus Oudemans, 1902 (= Hoploelaep Berlese, 1903; = Laelapsoldtess Willmann, 1952; = AustrogamaseUus Domrow, 1956)</td>
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<td>Laelaps meridionalis Canestrini, 1882</td>
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<td>Laelaps C. L. Koch, 1836</td>
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<td>Laelaps hilaris Koch, 1836</td>
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<td>Hyperlaelaps Zachvatkin, 1948</td>
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<td>Tetragonyssus microt Ewing, 1833</td>
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<td>13</td>
<td>Oryctolaelaps Lange, 1955</td>
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<td>Oryctolaelaps bibikovae Lange, 1955</td>
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MATERIALS AND METHODS

This study was based on specimens in the Acarology Laboratory at The Ohio State University, and in other museums. The total number of genera in this family is ca. 100; of this, one half is available in the collection at Acarology Laboratory. The other half was made available by the following persons and their institutions: Dr. Torbjorn Kronestedt, Swedish Museum of Natural History, Sweden; Dr. Evert E. Lindquist, Biosystematic Research Institute, Canadian National Collection, Ottawa; Dr. David C. Lee, South Australian Museum; Dr. Marisa Castagnoli, Istituto Sperimentale per la Zoologia Agraria, Florence, Italy; Dr. George C. Elckworth, Dept. of Entomology, Cornell University; Dr. John Kethley, Field Museum of Natural History; Dr. R. L. Smiley, Smithsonian Institution, USA and Dr. Mercedes Del-flnado-Baker, Beneficial Insects Laboratory, USDA.

Efforts to borrow specimens from Russia and from the Rijksmuseum van natuurlijke Historie, Leiden, Netherlands, British Museum of Natural History, England and from the Potchefstroom University Collection in South Africa were unsuccessful. As a result, I
was unable to examine the following type species of genera: Angosomaspis multisetosus Costa, 1971; Dynastaspis walhallae Costa, 1971; Holostaspis isotricha Kolenati, 1858; Hypoaspis (Hypohasta) simplexans Womersley, 1956; Iphitolaelaps myrlapoda Womersley, 1956; Iphis astronomicus Koch, 1839; Laelaspisella epyginalis Marals and Loots, 1969; Lucanaspis brachypedes Costa, 1977; Myrmeciphits crawletanus Hull, 1923; Promacrolaelaps hunteri Costa, 1971; Reticulolaelaps faint Costa, 1968; and Zontia melponensts Turk, 1948. For all these, it was necessary to resort literature-based data.

In some taxa a complete account of morphological characters could not be made because the specimens available were poorly mounted and I had no permission to remount them, or broken and body parts were missing. Example of this are the following taxa: Angosomaspis, Cyclothorax, Euandrolaelaps, Laelaspisella, Myrmeciphis, Myrmolaelaps, Myrmoleichus, Promacrolaelaps, Reticulolaelaps, and Zontia.

A total of 50 genera of free-living and arthropod associated lae-lapids was examined; when necessary and permission was granted, some preparations were remounted.

Methods:
Specimens were studied with the aid of a Wild M-20 phase cont-
rast microscope, equipped with camera lucida, 15x wide field oculars and 10x, 20x, 40x bright field, 40x phase contrast, 100x bright field and phase contrast objectives. Measurements were made with a 1 mm scale (divisions of 0.01 mm) using the Wild M-20. Dissecting and mounting were accomplished with an Olympus stereoscopic microscope equipped with 10x oculars and 0.7x - 4x objectives.

The morphological terms used are largely those of Evans and Till (1965) for morphological structures, Lindquist and Evans (1965) for idiosomal chaetotaxy, Evans (1963, 1969) for leg chaetotaxy. Moraza and Johnston (in preparation) for tarsus I chaetotaxy and Athlas-Henriot (1969) for adenotaxy.

The material utilized for outgroup comparisons was extracted from the families Leptolaelapidae Karg, 1978 and Rhodacaridae Oudemans, 1902 (sensu Lee, 1970). Genera like *Leptolaelaps* Berlese, *Ayersacarus* Hunter, *Evansolaelaps* Marais and Loots and *Cerambylaelaps* Costa were originally referred to the family Laelapidae (= Dermanyssidae) on account, for example, of the entire dorsal shield, reduced dorsal chaetotaxy, palp-claw 2-tined, 2 pairs of genital setae and male with an entire holoventral shield. However, the long posteriorly directed spermatodactyl is not a shared character with the males of Laelapidae. Karg, 1978b created the subfamily Leptolaelapinae within Macrochelidae to include *Leptolaelaps*. He
established that *Leptolaelaps* Berl., is an "intermediate form" confirming conception of Eviphidoidea Karg, 1965. The superfamily Eviphidoidea is considered the sister group of Dermanysoidea. Both share the following characters: J4 close to J5, fixed-digit of chelicerae with differentiated dentition and posterior end of dorsum by Z5. Later, in 1983, Karg using phylogenetic methods concluded that Leptolaelapidae is a valid family within Eviphidoidea and the family includes the genera *Leptolaelaps* Berlese, *Ayersacarus* Hunter, *Cerambylaelaps* Costa, *Evansolaelaps* Marais and Loots and *Austrocheles* Karg. These genera are distributed over the southern parts of Africa and South America, over Australia, New Zealand, Malaysia and the subantarctic islands.

Karg, 1983 mentioned that Leptolaelapidae and Laelapidae share the following plesiomorphic characters: slight difference between males and females, dorsal shields with a reticulate pattern, without differences in the shape of dorsal setae, ventral shields not very enlarged and fused, genital shield with one pair of simple setae, anal shield with two paranal and one postanal setae, deutosternum with 7 to 8 rows of denticles and protonymph pygidial shield with 3 internal, 3 medial and 3 lateral setae.

Among the synapomorphies shared by Laelapidae and Leptolaelapidae are: reduction of the dorsal chaetotaxy, a denticulate tectum,
female genital shield flask-shaped, with 1 or 2 pairs of genital setae, metasternal setae off the sternal shield and palp-claw 2-tined.

Analytical methods

One attempt to recover the phylogenetic relationships among the different taxa under study is the Phylogenetic Systematic approach (Felsenstein, 1982; Platnick, 1985).

The major criterion and most reliable method for determination of polarities needed in phylogenetic analysis, is the Outgroup method (Watrous and Wheeler, 1981; Farris, 1982; Maddison et. al., 1984). This method consists of comparing character states in members of a proposed monophyletic taxon with members of a taxon not included in the one under study. Ideally, the comparison is made with the known sister group. A character state present in the monophyletic taxon under study (ingroup) that is not present in the outgroup is considered apomorphic or derived. The character state that is present in the ingroup as well as in the outgroup is considered plesiomorphic or primitive. When the primitive or derived condition of a given character could not be determined by the outgroup method, its polarity was inferred by correlation with the transformation series of other character states previously determined by the outgroup method.
All the data obtained from the study were analyzed using the following computational programs: Q-tree, PAUP and MacClade. These programs are based in the parsimony principle. The parsimony analysis determines which of the phylogenetical hypothesis is most consistent with the pattern of character-state distribution exhibited by the taxa under study. In other words, "economy of assumption in reasoning". i.e. choosing the cladogram postulating the least number of character-states changes.

Q-tree program was written in C-language by Larry E. Watrous, Field Museum of Natural History, for the PDP 11/40 computer, but it is compatible with the AT&T 3B 2/300 (used in this study). This program has several tree construction options which allows a more careful search of best minimal length trees. In general, data with a high number of homoplasies will require a more detailed search and caution in the interpretation of the results.

PAUP was written in Fortran 77 by David Swofford from Illinois. It is based on Wagner's method of parsimony and allows one to work with ordered or unordered data. This program includes two techniques: exact methods for no more than 20 taxa and heuristic method for more than 20 taxa. It requires the use of a IBM or PC compatible computer with, at least 256 KB RAM and a mathematic coprocessor. The operational capacity of Paup for a data matrix is: 30 taxa and 100
characters for computer with 256 KB or 50 taxa and 300 characters, for computers with 512 KB.

MacClade was written by Wayne Madison from the Museum of Comparative Zoology. It is written in compiled Pascal language for Apple Macintosh computers. This program gives the most parsimonious evolution of a given character. It is, mainly, a program of graphics to visualize the character distribution in phylogenetic trees. It accepts a matrix of 80 taxa and 200 characters; missing data are allowed and character weighting is possible.
RESULTS AND DISCUSSION

I.- EXTERNAL MORPHOLOGY

Chelicerae:

The basic type of chelicera found in Rhodacaridae, Leptolaelapidae (Ayersacarus and Leptolaelaps) and in the free-living Laelapidae, like Gaeolaelaps, Ololaelaps and Cosmolaelaps for example, is chelate-dentate, with a short pilus dentilis, a simple dorsal setae, an associated dorsal lyrifissure and an arthrodial process developed as a corona or brush. The major modifications are found in the length or development of the fixed digit, reduction of the arthrodial process and presence or absence of the pilus dentilis and dorsal seta.

Exceptions to the chelate-dentate form of the chelicerae occur in females of the mammals associated Laelapidae Haemogamasus, Myonyssus, Echtnonyssus talpae, and in the arthropod-associated forms Stevelus amicus, Cyclothorax carcinicola, Myrmolaelaps equitans and Neoberlesia equitans, where both digits are edentate. In other cases, like Holostaspis montana, Androlaelaps casalits, some
Laelaspis, Dinogamasus inflatus, Urozercon paradoxus, and Ljunghia selenocosmiae, only the movable digit is edentate. The number of teeth on the movable digit varies; it goes from, normally, two or three on the free-living forms and some phoretic genera like Coleolaelaps, Bistemalis, Hunteria, Jacobsonia, Narceolaelaps, etc., to only one tooth in Iphiolaelaps myriapoda, Gromphadorholaelaps schaeferi, Dyscinetonyssus hystricosus, and more than three teeth in Coleolaelaps gryllotalpae. Ayersacarus and Leptolaelaps present two teeth in the movable digit and more than two teeth in the fixed digit.

The fixed digit of the female is absent in the honeybee-associated laelapids Varroa and Euvarroa. It is reduced, i.e., shorter than the movable digit, in some genera parasitic on arthropods like Scolopendracarus brevipilis, Iphiolaelaps myriapoda, Blaberolaelaps mathiesensis, Dyscinetonyssus hystricosus, Myrmolaelaps equitans as well as in some laelapids parasitic on mammals, Alphalaelaps and Androlaelaps fahrenholzi. In Jacobsonia, associated with millipedes, the fixed digit of the female presents an anterior directed process.

The short and slender pilius dentilis of Leptolaelapidae and the free-living laelapids is enlarged and inflated at the base in Androlaelaps fahrenholzi, long and thin in Androlaelaps casalis and Gromphadorholaelaps schaeferi and absent in Myonyssus, Alphalaelaps, Echinonyssus, Varroa, Euvarroa and Stevelus.
The dorsal seta is relatively short and simple as in all the free-living forms; but it may be absent, as in *Androlaelaps fahrenholzi*, *Stevelus amiculus*, *Melittiptipoides aptarium*, *Hunteria brasiliensis*, *Euvarroa sinhat*, *Neoberlesia equitans* and *Myonyssus*. I have been unable to see a dorsal seta on the female chelicera in *Dinogamasus inflatus*, *Blaberolaelaps mathiesensis*, *Iphitopsis mirabilis*, *Jacobsona*, *Julolaelaps*, *Iphiolaelaps*, *Scolopendracarus brevipilis* and *Cyclothorax carpintcola*; apparently it may be absent. On the other hand, in *Mesolaelaps* and *Haemogamasus* the dorsal seta is greatly enlarged, as long as the fixed digit. The dorsal seta in *Ayersacarus plumapilus* is long and spine-like; in other Leptolaelapidae (*Leptolaelaps*, *Hunteracarus*) and Rhodacaridae the dorsal seta is simple and short.

The arthrodial process may be produced into a conspicuous corona or brush as in the free-living forms, in some arthropod-associated forms as *Coleolaelaps*, *Dyscinetonyssus*, *Gymnolaelaps*, *Bisternalis*, *Laelaspoides*, etc., but in *Androlaelaps*, *Euvarroa*, *Hunteria*, *Dinogamasus*, *Urozercon* and *Jacobsona*, among others, there is a reduction in the number of prongs and length of the arthrodial process.

In the male the chelicera is chelate-dentate; movable digit uni-dentate and with spermadactyl free distally and grooved. Males of *Androlaelaps fahrenholzi* present a non chelate chelicerae, where
the fixed digit is reduced to a small tapering process which bears the enlarged pilus dentilis. An inflated pilus dentilis is also present in males of *Haemogamasus nidi* (Evans and Till, 1965). In males of *Gromphadorholaelaps schaeferi*, a genus associated with Blattaria, the fixed digit is as long as the spermatodactyl. A complex spermatodactyl, with three segments, is found in *Jacobsonia berlesei* and *Jacobsonia audyt* (Evans, 1955). The shape of the spermatodactyl is generally straight throughout its length as in *Cosmolaelaps*, *Gaeolaelsps*, *Euandrolaelaps*, *Pseudoparasitus* and some of the phoretic forms like *Pneumolaelaps*, *Varroa*, *Blaberolaelaps*, *Gromphadorholaelaps*, *Urozercor* and *Julolaelaps*, as well as in some mammals associated genera like *Myonyssus* and some *Echinonyssus*. However, the spermatodactyl could be recurved at the distal level of movable digit as, for example, in *Haemogamasus*, *Ljunghia*, *Gecarcinolaelaps*, *Bisternalis* and *Narceolaelaps*.

In Leptolaelapidae the spermatodactyl is directed posteriorly, and in Rhodacaridae it is straight, free or partially fused to the movable digit.

**Tectum:**

The tectum shows great variation in the form of its anterior margin among the different Laelapidae. Basically, the anterior margin could be denticulate-serrate, smooth, with medial or lateral projections or fimbriate.
In the mammal-associated genera, *Haemogamasus*, *Echinonyssus* and *Alphalaelaps*, the free margin of the tectum is strongly fimbriate. The free-living forms (*Gaeolaelaps*, *Alloparasitus*, *Euandrolaelaps*, *Pseudoparasitus* and *Cosmolaelaps*) and some phoretic forms in arthropods (*Narceolaelaps*, *Jacobsonia*, *Ljunghia*, *Dyscinetonyssus*, *Blaberolaelaps* and *Hypoaspis*) have a multidenticulate tectum. *Pseudolaelaps doderol* present a trispinate tectum, and *Hypohasta* has a smooth lancet-like tectum.

The majority of the arthropod-associated laelapids, for example *Pneumolaelaps*, *Laelasptis*, *Scolopendracarus brevipilis*, *Scissuralaelaps novaguinea*, *Iphiptis mirabilis*, *Gecarcinolaelaps cancer*, *Bisternalis rettenmeyeri*, *Varroa jacobsonii*, etc., presents a smooth anterior margin.

In Leptolaelapidae (*Ayersacarus*, *Leptolaelaps* and *Hunteracarus*) the tectum is multidenticulate, and in Rhodacaridae the anterior margin of the tectum can have many different shapes and may be sexually dimorphic (Lee, 1970)

**Deutosternum:**

In Leptolaelapidae the deutosternum presents 7-8 (*Hunteracarus*), 7-9 (*Ayersacarus*, *Leptolaelaps*) and 10 (*Stevacarus*) rows of denticles with several teeth per row.
This capitular groove presents one, most commonly six or seven to 18 rows of denticles in Laelapidae. The free-living forms (Gaeolaelaps, Ololaelaps, Pseudoparasitus, etc.) have 6, rarely 7, rows of transverse denticles with 1-8 teeth per row.

Members of the parasitic forms, like Dyscinetonyssus, Neohypoaspis, Haemogamasus, Echinonyssus, always have more than 7 rows of denticles, usually between 9 and 18 rows with 1 to 4 denticles per row (Echinonyssus) or 2-6 denticles per row (Haemogamasus). On the other hand, Myonyssus dubini, Melittiphls alvearius and Dinogamasus inflatus present several rows (8-10) of one to a maximum of three teeth per row; Dyscinetonyssus hystricosus has 16 rows with 1-5 teeth per row, and Tropilaelaps clareae presents 5 rows with only 1 or 2 teeth per row.

**Basis Capituli:**

It normally bears a pair of ventral setae, the subcapitular seta (s.c) which first appear at the protonymphal instar (Evans, 1957). The subcapitular seta is normally present in the free-living and phoretic laelapids. However, it is always absent in Scolopendrarcarus brevipilis, an associate of Myriapoda.

**Hypostome:**

The nymphas and adults normally present three pairs of hypos-
tomal setae (hyp 1, hyp 2 and hyp 3). With the exception of Euvarroa sinhai, where hyp 1 is absent, Varroa jacobsoni and Jacobsonia, where hyp 3 is absent, all the other free-living and phoretic Laelapidae present all the hypostomal setae.

The length of these setae presents some variation among the Laelapidae. In some of the free-living forms, such as Alloparasitus oblonga, Cosmolaelaps, Gaeolaelaps and Ololaelaps, hyp 3 is longer than hyp 1; in others, like Euandrolaelaps karawatwiti, Laelaspisella, Pseudoparasitus, Stratiolaelaps miles and Pseudolaelaps doderol, hyp 1 and hyp 3 have the same length. Among the arthropod-associated forms three conditions could be present. First and the most common, seta hyp 3 is longer than hyp 1 (Coleolaelaps, Dysctnetonyssus hystricosus, Hypoasps, Myrmolaelaps equitans, Euvarroa sinhai, Melittiphtis alvearius, Melittiphtsoides apiarium, Urozercon paradoxus, Blaberolaelaps mathiesensis, Scolopendracarus brevipilis and Ljunghia selenocosmiae); second, hyp 3 is shorter than hyp 1, as in Narceolaelaps, Julolaelaps, and Scissurolaelaps; and third, both hypostomal setae have the same length, as in Gromphadorholaelaps schaeferi, Dinogamasus inflatus, Bisternalis, Gecarcinolaelaps cancer and Neoberlesia equitans. In Haemogamasus, Echinonyssus, Myonyssus and Androlaelaps, all associated with mammals, the seta hyp 3 is as long as hyp 1.
Anterolaterally to the hypostome a pair of corniculi is present in all free-living and phoretic laelapids. The length and degree of sclerotization of the corniculi are the features that present more variation within the group. Normally, the corniculi are short, not longer than the palpal femur as in almost all Laelapidae, most Leptolaelapidae and Rhodacaridae. In *Urozercon paradoxus* and *Tropilaelaps clareae* the corniculi are very reduced (shorter than the palpal femur) and, on the other hand, in *Stratiolaelaps miles*, *Sctssuralaelaps novaguinea*, *Jacobsontia*, *Iphiptopsis mirabilis* and *Cyclothorax carcinicola* the corniculi are long, usually longer than the palp-femur. This is extremely obvious in *Stratiolaelaps miles*, where the corniculi are almost twice the length of the palpal femur.

In the free-living and arthropod-associated forms the corniculi are horn-like. However, in the mammal associated forms like *Echinonyssus* and some *Haemogamasus* (*H. hirsutus, H. horridus*) it becomes modified into a broad flat lobe-like structure. On the other hand, *Dysctnetonyssus hystricosus*, *Myrmolaelaps equitans*, *Bisternalis rettenmeyeri*, *Tropilaelaps clareae*, *Urozercon paradoxus*, *Iphiptopsis mirabilis* and *Alphalaelaps* present weak, membranous corniculi. The rest of the Laelapidae have a strong and well sclerotized corniculi.

The hypostomal process is produced into various shaped forms among the Laelapidae. The most common shape of the hypostomal process is two-branched and fringed, as in the free-living and those
forms associated with Coleoptera (Coleolaelaps, Hypoaspis, Dynastasptis, etc.). In Stratiolaelaps miles and Neohypoaspis ampliseta the hypostomal process is trifid and fringed. Some taxa (Cosmolaelaps and Julolaelaps) have one of the branches shorter but wider than the other. Some genera associated with Hymenoptera (Euvarroa sinhat, Melittiphis alvearius, Melittiphisoides apiarium, Varroa Jacobsoni, etc.) and Crustacea (Cyclothorax carcincola and Gecarcinolaelaps cancer), as well as in all forms parasitic on mammals and in Pseudo-laelaps doderoi, the hypostomal process is reduced, with only one branch and sometimes entirely smooth. In Dyscinetonyssus hystricosus the hypostomal process is reduced, short and wider than longer. Some authors (Evans and Till, 1965) have considered these last conditions as "simple"; however, since in Rhodacaridae, as well as in Leptolaelapidae, the hypostomal process is branched and fringed, any other shape has been considered as reduced.

**Labrum:**

Modifications to the forms described by Evans and Till (1965: 259) have not been found. In all taxa studied the labrum presents fimbriate margin and it is usually projected beyond the tip of the hypostome.

In the free-living forms with a well sclerotized corniculi, and some arthropod-associated genera (Jacobsonia, Gecarcinolaelaps cancer and Hypoaspis, among others), the salivary styli lie along the length
of the corniculi, therefore it is hard to see them.

**Pedipalps:**

Evans (1964) has defined the normal chaetotaxy of the pedipalp segments (tr, fe, ge, ti and ta) for all instar as follow: Larva: 0-4-5-12-11, Protonymph: 1-4-5-12-15, Deutonymph and adults: 2-5-6-14-15.

The normal pattern of palp chaetotaxy is found in Leptolaelapidae, Rhodacaridae and in all the free-living, some arthropod-associated and mammal-associated Laelapidae. Deviations from the normal pattern are found in some taxa parasitic on Hymenoptera (Euvarroa sinhai, Varroa jacobsont, Dinogamasus inflatus, Urozercon paradoxus), in Scarabaeidae (Dyscinetonyssus hystricosus), Myriapoda (Scolopendracarus brevibilis, Jacobsonia, Narceolaelaps), Crustacea (Cyclothorax carinicolol) and mammals (Echinonyssus, Alphalaelaps) where they retain the larval complement of setae on the tibia, being unideflcient (2-5-6-13-15) or bideflcient (2-5-6-12-15) in the adult instar. The palpal chaetotaxy of Echinonyssus is 2-5-6-13/12-15, on Varroa is 1-2/3-2-7/8-12, in Euvarroa is 2-2/3-1/2-5-15 and on Dyscinetonyssus is 2-4-3-10/11-14, where there is a neotenic retention of the larval chaetotaxy on femur, genu and tibia of the adult.
Setae antero-laterals (al1, al2) of the femur and al1 of genu may be simple, setiform or spatulated. In Gecarcinolaelaps cancer genual seta al1 is spatulated; palpal femur al1 and al2 are spatulated in Iphitolaelaps myriapoda and palpal femur al2 is spatulated in Dyscinetonyssus hystricosus.

The palp-claw may be two or three-pronged. A three-tined palp-claw is found in Pseudoparasitus, Ololaelaps, Gymnolaelaps and some species of Haemogamasus (H. hirsutus, H. pontiger). The prongs may be large and equal in length as in some Gymnolaelaps or the proximal tine is small and sometimes relatively inconspicuous as in Pseudoparasitus and Ololaelaps (O. veneta). All the other examined genera of Laelapidae have a two-tined palp-claw. In some of the genera phoretic in arthropods like Neoberlesia, Euvarroa, Tropilaelaps, Varroa, Myrmolaelaps, Dinogamasus and Gromphadorholaelaps, the basal tine is reduced.

Antony (1986) reported that in Rhodacaridae a 3-tined palp-claw is the plesiomorphic condition. In Leptolaelapidae the palp-claw is 2-tined, with both tines similar in length as in Ayersacarus or the basal tine shorter than the distal one as in Leptolaelaps.

Dorsal Sclerotization Idiosoma:

The ontogenetic development of the sclerotization of the dor-
sum in the free-living forms and in the facultative ectoparasites of the Laelapidae s. lat. has been well established by Evans and Till, 1965.

The only exceptions to the normal pattern of dorsal sclerotization found in this study are that the deutonymphs of *Dyscinetonyssus hysticosus*, *Gecarcinolaelaps cancer*, *Melittiphils alveartiu*, *Neohypoaspis ampliseta* and *Varroa Jacobsoni* do not present a dorsal shield with lateral incisions. Unfortunately few immature instars were available for study, therefore this finding can not be very conclusive for the entire family.

The dorsal shield in adults shows considerable variation in size and shape. Dorsal surface of the idiosoma is completely covered by an entire shield in Rhodacaridae and in most of the free living laelapids, *Ololaelaps*, *Pseudoparasitus*, *Gaeolaelaps*, *Cosmolaelaps*, *Pseudolaelaps* and in some parasitic form, *Alphalaelaps*.

The dorsal shield is narrow and pointed posteriorly in some *Echinonyssus*, *Narceolaelaps*, *Stratiolaelaps*, *Dinogamasus* and *Ljunghia*. In *Dyscinetonyssus* and *Jacobsonia* the dorsal shield presents its maximum reduction within the Laelapidae; it only covers the anterior half of the idiosoma. In the other Laelapidae, the dorsal shield does not cover the entire dorsum, leaving exposed soft cuticle, as in *Neohypoasps*, *Julolaelaps*, *Blaberolaelaps*, *Stevelus*, *Julolaelaps*,
Coleolaelaps and Urozercon.

Dorsal Chaetotaxy:

Evans and Till, 1965 established that the normal setal complement, the holotrichous condition, is relatively stable through ontogenetic development among the Laelapidae s. lat., and that deviations in the form of hypo- or hypertrichy are common in the specialized facultative and obligatory parasites forms. The holotrichous condition in adults is considered to be 44 pairs of setae, distributed as follow: 11 dorsal (J1-6; J1-5), 11 median (z1-6; Z1-5), 11 lateral (s1-6, S1-5) and 11 marginal (r1-6; R1-5) setae. In the larval instar the dorsal holotrichous condition is formed by 10 pairs of podonotal setae (J1, J3-6, z2, z4-5, s4, s6; with s6 on soft cuticle) and a variable number of opisthonation setae, usually 4 (Holostaspis) to 7 (Hypoaspis) pairs of setae, and it is found commonly in the free-living forms.

Protonymphs normally present 16 pairs of podonotal setae (J1-6, z2, z3-5, s4-5 on the shield, s6 and r2-3, r5 on the soft cuticle) and 14 pairs of opisthonation setae, 8 pairs on the pygidial shield (J3-5, Z3-5, S4-5) and 6 pairs (J1-2, Z1-2, S2-3) on the unsclerotized cuticle. From the few Pn studied a dorsal hypertrichy has been found in Neohypoaspis ampliseta, Varroa Jacobsoni and Gecarcinolaelaps cancer; and Evans and Till (1965) have reported that the
Pn of *Haemogamasus* has a marked hypertrichy of the lateral and marginal series in the podonotum and opisthonotum.

The full complement of 44 pairs of dorsal setae appears at the deutonymph and it is retained in the adults. Evans and Till (1965) also reported that Dn of *Pneumolaelaps marginalis* Willmann shows hypertrichy on the r and R series, with more than 25 setae, and that *Gaeolaelaps praesternalis* Willmann has only one pair of R setae.

The Laelapidae considered in this study present a wide range in the number of dorsal setae. This number goes from marked hypertrichy (more than 47 pairs of setae) to a very reduced dorsal chaetotaxy (14 to 24 pairs). Hypertrichy is common among the arthropod-associated forms *Urozercon, Varroa, Euvarroa, Melittiphis, Troptilaelaps, Dinogamasus, Neohypoaspis, Gecarcinolaelaps*, and in the mammal-associated genus *Haemogamasus*.

The dorsal shields of *Pseudolaelaps* (*P. doderoi* and *P. paulseni*), whose systematic position has been problematical, are markedly hypotrichous with 15 pairs of podonotal and 9 pairs of opisthonotal setae. Other taxa with a very reduced dorsal shield chaetotaxy are: *Jacobsonia* with 14 or 16 pairs of setae (9 pairs in the podonotum and 7-5 pairs in the opisthonotum; setae z1, J2-3 and Z3 absent); *Scolopendracarus brevipilis* with 24 pairs (7 pairs of podonotal and 9
pairs of opisthgonotal; z2, s6, r5-6, J2, J4 absent; *Blaberolaelaps mathiesensis* with 24 pairs of setae on dorsal shields (15 pairs of podonotal and 9 pairs of opisthgonotal setae; j6, z1-3,5-6, s1,6 absent and r6, S2,4,5, R1-5 on soft cuticle); *Dyscinetonyssus hystricosus* with 24 pairs (19 pairs of podonotal and 5 pairs of opisthgonotal setae; z1-2, s1, r2-3, J2, Z2, S5, R1-2,5 are absent; J5, Z4, S1-4 and R3-4 on soft cuticle). Among the free-living laelapids the number of dorsal setae varies from 37 to 44 pairs, 39 pairs being the most common as is *Ololaelaps veneta*, *Euandrolaelaps karawaiensis*, and *Gaeolaelaps aculeifer* which has 22 pairs of podonotal and 17 pairs of opisthgonotal setae; additional setae px1, px2 present. In the other arthropod-associated taxa the number of dorsal setae varies from 44 to 26 pairs. For example, *Scissuralaelaps novagutnea* has 45 pairs (29 pairs podonotal and 17 pairs opisthgonotal setae; R1-2 absent), *Gromphadorholaelaps schaeferi* 47 pairs (21 pairs podonotal and 26 pairs opisthgonotal setae; but setae z2,4,6 and r1 are absent), *Stevelus amicus* 36 pairs (15 pairs podonotal and 21 pairs opisthgonotal setae; z1-2, s1,4 and J5 absent) and *Hypoasps* has 37 pairs (20 pairs in the podonotum and 17 pairs in the opisthgonotum).

Among some of the free-living forms like *Cosmolaelaps claviger*, *Euandrolaelaps karawaiensis*, *Gaeolaelaps aculeifer*, *Laelpisella epigynallis*, *Strattolaelaps miles*, and in the majority of the parasitic forms in arthropods or mammals, there are supernumerary rows of
setae (px1-px3) between the J and Z series of the opisthunotum. Exceptions to this are Stevelus amiculus, Pneumolaelaps, Blaberolaelaps matthiesenst, Gromphadorholaelaps schaeferi, Iphitopsis mirabilis, Jacobsonia berlesei, Narceolaelaps annularis, Scolopendracarus brevipilis, Ljunghia selenocosmiae, Alaphalaelaps, Echionyssus and Mesolaelaps anomalus which do not present the px's setae.

Another important feature is the tendency for addition of unpaired accessory setae between the J series in phoretic forms such as Angosomasptis, Gymnolaelaps, Holostaspis montana, Laelasptis, Myrmolaelaps equitans, Neoberlesia equitans, in almost all forms associated with Hymenoptera (with the exception of Stevelus and some Pneumolaelaps), in Urozercon paradoxus, Dinogamasus inflatus, Gecarcinolaelaps cancer, and Androlaelaps casalis. These unpaired accessory setae show considerable variation in number and position within this group of Laelapidae, as well as in Leptolaelapidae (Leptolaelaps, Ayersacarus).

Within the free-living and phoretic laelapids some hypotrichy of the dorsum is evident. In Ololaelaps setae z1 (O. sellnicket) and z3 (O. veneta) are absent; in Narceolaelaps, Dyscinetonyssus, Stevelus, Jacobsonia, Blaberolaelaps, Neoberlesia, Myrmonyssus, Echionyssus and Alaphalaelaps the podonotal seta z1 is also absent. Hypotrichy of
the J and Z series is especially evident in parasitic taxa. For example, in *Scolopendracarus brevipilis* setae J2, J4 and Z2 are suppressed; in *Blaberolaelaps matthiesensis* J2, J4, Z1 and Z3 are lacking; in *Jacobsonia* J2-3 and Z3 are absent. In *Ljungia selenocosmiae*, *Coleolaelaps*, some *Julolaelaps* (*J. moser*)*, Dyscinetonyssus hystricosus* and *Echinonyssus* seta J2 is absent. J3 is also lacking in *Ljungia selenocosmiae* and *Cyclothorax*; in *Stevelus amiculus*, *Blaberolaelaps matthiesensis*, *Myrmonyssus*, *Echinonyssus*, *Cyclothorax* and *Androlaelaps fahrenholzi* seta J4 is absent. In *Pseudolaelaps doderoti* setae J2, J4 and Z2 are suppressed.

The dorsal setae in the majority of the Laelapidae are smooth and slender or weakly pilose. Exceptions occur in the genera *Cosmolaelaps*, some *Laelasps* and *Stratiolaelaps* where the dorsal setae tend to be scimitar, spatulated or leaf-like, and in some phoretic or parasitic forms where specific setae show different shape or development. For example, in *Stevelus amiculus*, *Dyscinetonyssus hystricosus*, and *Steptolaelaps* setae z4-z6 are spine-like and the other setae are simple. In *Neohypoaspis ampliseta* setae j1-j2 and z1 are spatulated, and in *Scolopendracarus brevipilis* the setae j2-j5, z1-z5 and s1-s5 are short, blunt, spine-like.

Normally seta Z5 is smooth and slender, but in *Laelasподес ordwayae*, *Laelasps*, *Holostaspis montanus*, and *Mesolaelaps* it is in-
conspicuously pilose, and spatulated in *Pseudolaelaps doderoi*. The length of the dorsal setae also show some variation among the free-living and arthropod-associated laelapids. In *Scolopendracarus* and *Narceolaelaps* all dorsal setae are short or minute; in *Blaberolaelaps matthiesenstis* and *Gromphadorholaelaps schaeferi* setae on the S and R series are twice longer than the other dorsal setae, and in *Cyclothorax carcinicola* and *Neohypoaspis ampliseta* seta J1 is the longest.

The majority of the immature instars of the laelapids seen in this study presents simple and thin dorsal setae, with the exception of the protonymph of *Gecarcinolaelaps cancer*, *Eumelittitiphis* (*E. inouei* and *E. philippinensis*, Delfinado-Baker and Baker, 1988) and *Neohypoaspis ampliseta*, where all or some of the dorsal setae are strong and spine-like.

**Dorsal porotaxy:**

Apparently for the Laelapidae s. lat., the basic adult and deutonymphal complement of glands and lyrifissures ("pores") of the dorsum of the idiosoma is 22 pairs (11 pairs on the podonotum and 11 pairs in the opisthonotum) (Evans and Till, 1965). Within the Leptolaelapidae, *Ayersacarus* presents 20 pairs of pores and *Leptolaelaps* 18 pairs of dorsal pores.
For the free-living and arthropod-associated Laelapidae variation in the number of pores is evident. Unfortunately no regular patterns within the different forms of laelapids have been found. For example, among the free-living genera the number of dorsal pores varies from 12 pairs (Cosmolaelaps claviger, Cosmolaelaps vacua), 13-15 pairs (Stratiolaelaps miles), 14 pairs (Ololaelaps veneta), 16 pairs (Pseudoparasitus domrowi and P. centralis), 18 pairs (Euandrolaelaps sardoa), 20 pairs (Holostasps montanus) and 22 pairs (Gaeolaelaps aculeifer). The lowest number of pores determined in this study was 8-11 pairs in some Coleolaelaps, Bisternalis mexicanus and Bisternalis rettenmeyeri. Females of Julolaelaps, Laelasps, Stevelus amiculus, Hunteria brasiliensis and Melittiphis alvearius have 16 pairs of pores; 12 pairs are present in females of Blaberolaelaps matthiesensis and Cosmolaelaps claviger.

Although among the phoretic or parasitic forms the hypoporosity condition is the most common, the males of Gecarcinolaelaps cancer present the basic number of pores (22 pairs). Males of Julolaelaps dispar and Gecarcinolaelaps cancer, present two more pores than the females (22 and 18 pairs respectively). The other males studied in detail (Cosmolaelaps claviger, Gaeolaelaps aculeifer, Ololaelaps veneta, Pseudoparasitus centralis, Dyscinetonysus hystricosus and Narceolaelaps annularis), present the same number of pores as the females. Unfortunately it was impossible to deter-
mine the number of pores in some genera of Laelapidae (i.e., *Cyclothorax*, *Tropilaelaps*, *Gymnolaelaps*, *Melittiphisoides*, *Murmolaelaps*, and *Neoberlesia*) because the specimens were in poor condition or the porotaxy was obscured by hypertrichy of the dorsum.

**Tritosternum:**

In general the tritosternum presents a biramous structure in all Dermanysoidea (Evans and Till, 1965), Leptolaelapidae and Rhodacaridae.

In most of the free-living and arthropod-associated Laelapidae the tritosternum is biramous, with a pilose lacinia and a longer than wide basal portion. Exceptions are *Myrmolaelaps equitans*, *Euvarroa sinhai*, *Scolopendracarus brevipilis* and *Gecarcolaelaps cancer*, where the tritosternum is reduced and with a very short lacinia. In *Stevelus amiculus* the laciniae are long but the pilosity is reduced to the tips.

**Venter of the Idiosoma:**

The sternal shield presents varying degrees of sclerotization among Laelapidae. For example, in *Scolopendracarus brevipilis* the sternal region is occupied by transversely striated cuticle; in *Scsursuralaelaps novaguinea* and *Iphiolaelaps myriapoda* the sternal shield is completely divided longitudinally in females. The sternal shield
normally carries three pairs of setae (st1-3) and two pairs of lyrifissures as in all free-living forms and in the majority of the phoretic laelapids. Exceptions are: *Haemogamasus*, where hypertrichy may be evident; *Varroa jacobsoni* where 5-6 pairs of sternal setae and 4-5 pairs of lyrifissures are present; *Ololaelaps, Neoberlesia* and *Myrmolaelaps* where 4 pairs of sternal setae and 3 pairs of lyrifissures are common.

In *Bisternalis, Melittiphtisoides, Pneumolaelaps, Tropilaelaps, Jacobsonia, Scolopendracarus* and *Cyclothorax*, the sternal setae st1 are placed off the sternal shield, on the presternal region. The metasternal setae (st4) in the outgroup, Rhodacaridae, are present on the sternal shield, and in Leptolaelapidae are present in the metasternal plates. Among the Laelapidae, st4 could be on the sternal shield as in *Ololaelaps, Neoberlesia, Laelaspoides, Melittiphtisoides* and *Varroa*; or off the sternal shield on the soft cuticle or on the metasternal plates as in most of the free-living and phoretic forms; and could be absent as in *Reticulolaelaps faint, Laelaspisella* and *Urozercon*.

The sternal shield is fused laterally with the endopodal shields as in Leptolaelapidae and Rhodacaridae. Its posterior margin may extend as far as the posterior margin of coxae III as in *Gaeolaelaps aculeifer* and *Jacobsonia audyi*. 
The sternal setae are simple, setiform in almost all Laelapidae. An exception is *Dyscinetonyssus hystricosus* where the sternal setae are flattened and blade-like.

The presternal shields are normally present, as a weakly (*G. aculeifer*) or well sclerotized (*O. veneta*) pair in the free-living genera and most of the phoretic forms. In some of the laelapids associated with Coleoptera (*Dyscinetonyssus*), or with Formicidae (*Holostaspis, Laelaspis, Myrmolaelaps, Myrmonyssus* and *Neoberlesia*), as well as in most of the other arthropod-associated forms (with the exceptions of *Bisternalis, Melittiphisoides, Pneumolaelaps, Stevelus, Tropilaelaps* and *Gromphadorholaelaps*) the presternal shields are absent. In Rhodacaridae and Leptolaelapidae the presternal shields are well developed.

The female genital shield extends posteriorly from the level of the fourth coxae and it bears one or more pairs of genital setae. In the least specialized laelapids, the free-living forms, the genital shield is more or less flask-shaped and bears only one pair of genital setae. However, there is a tendency for an increase in the size of the genital shield and in the number of genital setae. This enlarged shield, the genito-ventral shield, is present in *Haemogamasus, Myrmonyssus, Pseudoparasitus, Pseudolaelaps, Alloparasitus, Euandrolaelaps Laelaspis, Gymnolaelaps, Euvarroa, Varroa, Urozer-
con, Bisternalis and Cyclothorax. Hypertrichy of the genital shield is evident in laelapids associate with mammals, Haemogamasus, Myonyssus (with more than 6 pairs of setae) and Alphalaelaps (with 6 pairs of genital setae). The genital shield, on the other hand, shows some reduction in size in some of the arthropod-associated forms. In Jacobsonia, Iphiolaelaps and Scolopendracarus the reduction of the genital shield is very marked.

The posterior margin of the female genital shield may be expanded behind coxae IV as in most of the free-living forms and in some phoretic forms like Gymnolaelaps, Neoberlesia, Bisternalis, Euvarroa, Varroa, Cyclothorax and Gromphadorholaelaps as well as in Pseudo-laelaps doderot, or not expanded as in the majority of the laelapids associated with arthropods or mammals. A slightly longer then wide genital shield is the state most commonly found among the Rhodacaridae and in Leptolaelapidae; therefore, by outgroup comparison, this character state was considered the plesiomorphic condition. In Leptolaelaps the female genital shield presents lateral sclerites where a pair of the genital setae is inserted.

Considerable variation occurs in the chaetotaxy of the opisthogaster in adults of Laelapidae. The normal, holotrichous, condition is seven pairs of setae: Jv1, Jv2, Jv3, Jv4, Jv5, Zv1 and Zv3 (the deutonymphal complement). This occurs in the free-living forms like Pseudoparasitus, Ololaelaps, Gaeolaelaps, Stratiolaelaps and Cosmolaelaps.
However, the opisthogastric region shows some degree of hypertrichy, especially in those forms parasitic on mammals like *Haemogamasus pontiger, Androlaelaps, Echinoonyssus talpae, Myonyssus* and *Mesolaelaps*, and in two taxa associated with arthropods *Tropilaelaps clarae* and *Dinogamasus inflatus*. On the other hand, hypotrichy of the opisthogastr is common in some parasitic forms, such as *Jacobsonia audyi* where only Jv1, Jv2 and Zv3 are present; in *Scolopendracarus brevipilis* Jv1, Jv2, Jv3 and Zv1 are present. *Iphiopsis mirabilis, Iphiolaelaps myriapoda* and *Urozercon paradoxus* also present a reduced chaetotaxy of the opisthogastr.

In *Ololaelaps, Laelaspis* and *Neoberlesia* the female anal shield is fused with the genito-ventral shield. The anal shield most commonly found presents a subtriangular, subcircular or oval shape within the Laelapidae and Leptolaelapidae. However, in *Euvarroa sinhal* it is larger than wide and larger than the ventral shield; in *Bistemalis rettenmeyeri* the anal shield is crescent-shaped, with the median anterior margin convexed above the anal opening; crescent-shaped in females and males of *Neohypoaspis*, and large, truncate anteriorly and posteriorly in *Melittiptis, Neoberlesia, Tropilaelaps, Dinogamasus, Iphiopsts* and *Myonyssus*. In *Urozercon paradoxus* the anal shield is slightly longer than wide with lateral margins almost straight.
The number of anal setae varies from the common 3 (two paranal and one post anal setae), as in Leptolaelapidae, to 2 or 5. In Myrmonyssus, Neoberlesia and Jacobsonia only the paranal setae are present; Urozercon paradoxus presents two extra setae, and some Haemogamasus have secondary unpaired setae on the anal shield. The post anal seta, when present, can be longer, slightly or 1 1/2 times longer than the paranal setae as in Gaeolaelaps, Cosmolaelaps, Euandrolaelaps, Coleolaelaps and Laelasps, or with the same length as the parans as in the mammal associated forms such as Myonysus, Alphalaelaps and Echinonyssus, or it could be shorter than the paranal setae as in most of the forms associate of arthropods (for example: Euvarroa, Melittiphisoides, Pneumolaelaps, Varroa, Narcceolaelpas, Julolaelaps and Scolopendracarus).

The endo and exopodal shields enclose the coxal cavities II-IV in many of the free-living, parasitic and phoretic forms. The podal shields behind coxae IV become greatly enlarged in the free-living forms and some of the parasitic forms like some species of Gymnolaelaps, Holostasps, Hunteria, Gecarcinolaelaps, Dyscistemonyssus and Dynastaspis. Reduction of the exopodal shields occur in Haemogamasus, Alphalaelaps, Echinonyssus and Hypoasps.
The metapodal shields are commonly present as free elements; however, in Ololaelaps the metapodal shields are fused with the genito-ventral shield, and they are absent in Dinogamasus inflatus, Iphitopsis mirabilis, Jacobsonia (J. minor, J. submollis) and Scolopendracarus brevipilis. Generally the metapodal shields are small, oval, elliptical or elongate elements as in the free-living forms; but in some forms associated with arthropods like Neohypoaspis and Varroa they become large subtriangular structures.

The stigmata are situated lateral to the third and fourth coxal interspace as in Rhodacaridae and Leptolaelapidae. The peritreme is normally long, it extends to up or beyond coxae I in the free-living forms and some parasitic forms. However, a short peritreme that extends to coxae II or III is present in forms associated with Euvarroa sinhai, Hunteria brasiliensis, Melittiphithisoides aptarium, Varroa jacobsoni, Stevelus amiculus, Narceolaelaps and Julolaelaps. A higher reduction of the length of the peritreme is present in Iphitopsis mirabilis and Scolopendracarus brevipilis, and it is totally absent in Jacobsonia and Iphitolaelaps.

In the free-living and some phoretic forms (Urozercon paradoxus, Scissuralaelaps novaguinea, Pneumolaelaps, Laelaspoides and Neohypoaspis) a weakly developed peritrematal shield is also present and its posterior margin beyond the stigma bears a conspicuous gland
and lyrifissure openings. The peritrematal shield is fused anteriorly with the dorsal shield, and posteriorly it may be free (most Laelapidae and Leptolaelapidae) or fused (Coleolaelaps, Myrmolaelaps, Neohypoaspis and Jacobsonia) with the podal shield in the area of coxae IV.

The males of Laelapidae normally have a holoventral shield. However, in Ljunghia, Cyclothorax, Gecarcinolaelaps, Neohypoaspis, Tropilaelaps, Blaberolaelaps, some Julolaelaps (J. luctator and J. rotundatus), Iphiolaelaps, Myrmonyssus and Dyscinetonyssus the anal shield is free, not fused to the sterno-genito-ventral shield. The holoventral shield, when present, carries four pairs of sternal setae, the genital seta, the three anal setae and a variable number of opisthogastric setae. Hypertrichy of the ventral surface is evident in males of Tropilaelaps, Cyclothorax, Haemogamasus and Myonyssus.

Legs:

Evans and Till (1965) have defined the normal types of the segmental chaetotaxy of the legs at the deutonymphal and adult stages of the British "Dermanyssidae", which are here considered as the normal pattern for legs chaetotaxy within Laelapidae.
Coxae I - IV:

Almost all the laelapid studied, s with the exception of Narceolaelaps (2-2-2-2) present the normal chaetotaxy of 2-2-2-1 coxal setae in the deutonymphal and adult stages.

The coxal setae are simple in the free-living and phoretic forms. Evans and Till (1965) indicated that in many facultative or obligatory parasites a stout, spine-like structure is present in coxa II. Dyscinetonyssus hystricosus presents two heavy and thorn-like setae on coxae II-III and one on coxae I and IV. Laelaps nutalli presents one peg-like seta and one simple seta on coxae I-III. However, not all Laelaps species present spine-like or peg-like setae on those coxae. For example, L. similimus, L. keegani and L. grenterl have the proximal and distal setae on coxa I, and the anterior setae of coxae II-IV setaceous (Herrin & Tipton, 1976). In Pseudolaelaps doderol the coxal setae are simple, but a rounded anterior protuberance is present in coxa II.

Trochanter I - IV:

The deutonymph and adults of Laelapidae normally have six setae on trochanter I and five setae on trochanters II-IV. An exception occurs in Euvarroa sinhai, Dyscinetonyssus hystricosus and Varroa jacobsoni which have only five (1-0/3-1) setae on trochanter I; Euvarroa sinhai and Varroa jacobsoni with six setae on trochanter IV
and *D. hystricosus* with six setae on trochanter II. *Gecarcinolaelaps cancer* has 6 setae on trochanter I, five on trochanter II-III, and 5-6 on trochanter IV. *Narceolaelaps* (*N. annularis* and *N. gordanus*) has only four setae on trochanter I.

Baker et. al. (1963) reported that *Bisternalis mexicanus* has only five setae on trochanter I; however, after studying specimens of this species it seems that *B. mexicanus*, as well as *B. hunteri*, presents the normal pattern of chaetotaxy on all trochanters.

Femora I - IV:

The normal complement of 2-3/1,2/3-2 setae of femur I has been observed in the free-living and in most of the phoretic forms. As in many obligatory parasitic Dermanyssidoidea (*Dermanyssus* and *Ophionyssus*), in *Dyscinetonyssus hystricosus, Myrmonyssus, Euvarroa, Melittiphisoides, Stevelus, Varroa, Gecarcinolaelaps, Cyclothorax* and *Ljunghia* there is a decrease in the number of ventral setae because one postero-ventral seta (pv3) is missing. A deficiency of two postero-ventral setae (pv2, pv3) is present in taxa associated with Isoptera (*Urozerccon*) and with Myriapoda (*Jacobsonia, Narceolaelaps, Scissuralaelaps, Scolopendracarus* and *Iphiolaelaps*). Only one antero-lateral seta (a1) is present in *Bisternalis* (*B. mexicanus, B. hunteri, B. formosus*) and *Jacobsonia berleset*. Among the Laelapidae with the most reduced leg chaetotaxy are *J. berleset* which has only
six setae on femur I (1-1/1,1/1-1), *Stevelus amiculus* has eight setae (2-1/1,1/2-1) and *Urozercon paradoxus* nine setae (2-2/1,3/1-0). Femur I in *Holostaspis montanus*, as well as in *Laelaspulus flexuosus* (Evans & Till, 1965), shows an addition of one antero-ventral seta to the normal number, giving the formula 2-3/2,2/3-2.

The normal complement of setae (2-3/1,2/2-1) on femur II has been found in *Coleolaelaps, Myrmonyssus, Narceolaelaps gordanus, Pneumolaelaps, Troplaelaps clareae, Julolaelaps, Scissuralaelaps, Cyclothorax carcinicola* and *Gecarcinolaelaps cancer*. Among the studied laelapids the most common number of setae on femur II is 10 (2-1/1,2/2-1) with seta ad3 missing. This condition is present in *Cosmolaelaps claviger, Dyscinetonyssus hystricosus, Holostaspis montanus, Laelaspis, Pseudoparasitus (P. centralis, P. meridionalis), Ololaelaps (O. placentula, O. veneta), Gaeolaelaps aculeifer, Laelaspidides ordwayae* and *Blaberolaelaps mathiesensis*, which have only two antero-dorsal setae. In *Euvarroa sinhai* and *Varroa jacobsoni* two antero-dorsal setae (ad2,ad3) are missing; in *Narceolaelaps burdicki* one antero-lateral seta is lacking; in *Iphitolaelaps myrtrapoda* one antero-lateral (al2) and antero-dorsal (ad3) setae are missing. In *Stevelus amiculus* and *Urozercon paradoxus* setae al2, ad3 and pd2 are lacking. A macroseta (pd1) on femur II is present in *Dyscinetonyssus* and *Hypoaspis*, as well as in *Lucanaspis* and *Promacrolaelaps* (Costa, 1971).
Femur III has six setae (1-2/1,1/0-1) as the basic complement number which, among the Laelapidae, is more or less stable. Exceptions have been observed in *Euvarroa stinha* and *Varroa jacobsoni* which have one additional antero-lateral (al2) and one postero-lateral setae, *Gecarcinolaelaps* with two postero-dorsal setae, *Laelaspoides ordwayae* added one postero-ventral seta (pv1), *Cosmolaelaps vacua* has one postero-dorsal seta, and *Coleolaelaps* with one additional postero-dorsal seta (pd2) and one added postero-ventral seta (pv1). On the other hand, in *D. hystricosus* and *S. amiculus* the antero-lateral seta is missing. The postero-ventral seta on femur III is present in *S. amiculus, D. inflatus, N. annularis* and *L. ordwayae*. Femur III of *Narceolaelaps* has six setae but in a different distribution from the normal pattern; here, the antero-ventral and postero-lateral setae are missing, and two postero-dorsal and one postero-ventral setae are present.

Few exceptions to the remarkably stable number of setae on femur IV (1-2/1,1/0-1) have been found among the studied laelapids. A deficiency of one seta (al) was found in *S. amiculus* and *Myrmonyssus* (0-2/1,1/0-1). In *Narceolaelaps gordanus* an additional antero-ventral (av2) and postero-dorsal (pd2) setae are present, but the postero-lateral seta is missing (1-2/2,2/1-0), and in *N. burdicki* two postero-dorsal setae are present and the postero-lateral seta is missing (1-2/1,2/0-0) (Kethley, 1978). *Cosmolaelaps vacua* presents
seven setae (0-2/1,2/1-1), *Iphtholaelaps myriapoda* has one additional postero-ventral seta (1-2/1,2/1-0), and in *Dyscinetonyssus hystricosus* the antero-lateral and postero-lateral setae are lacking but two postero-dorsal and two postero-ventral setae are present (0-2/1,2/2-0).

A macro, whip-like seta (pd1) is present on femur I) of *Coleolaelaps* and *Dyscinetonyssus*. The antero-dorsal setae could be tri- or bifurcate as in *C. vacua*, or spatulate as in *Stratiolaelaps miles*.

Genua I - IV:

Evans and Till (1965) reported five different chaetotactic patterns on genu I among the British Dermanyssoids, which mainly occur among the obligatory parasites of the genus *Dermanyssus*.

Among the Laelapidae considered in this study the following exceptions to the normal chaetotaxy (2-3/2,3/1-2) of genu I were found:

2-3/1,3/1-2 = 12 in *Varroa jacobsoni, Pseudolaelaps doderoi, Pseudolaelaps paulseni* (av2 missing).

2-2/1,3/1-2 = 11 in *Stevelus amiculus, Dyscinetonyssus hystricosus* (ad3, av2 missing).

1-3/2,2/1-2 = 11 in *Bistemalis mexicanus* and *B. hunteri* (al2, pl3 missing).
2-2/2,2/1-2 = 11 in Gecarctinolaelaps cancer (ad3, pd3 missing).

2-3/1,2/1-2 = 11 in Euvaroa stinhai, Scissuralaelaps novagirnea (av, pd missing).

2-2/1,2/1-1 = 9 in Urozercon paradoxus (ad3, av2, pd3, pl2 missing).

1-2/1,2/1-1 = 8 in Iphiolaelaps myriapoda, Scolopendracarus brevipilis (al2, ad3, av2, pd3, pl2 missing).

1-2/1,2/1-2 = 8 in Narceolaelaps, Myrmonyssus (al2, ad3, av2, pd3, pl2 missing).

1-2/1,2/1-1 = 8 in Iphiolaelaps mirabilis (al2, ad3, av2, pd3, pl2 missing).

1-2/0,2/0-1 = 6 in Cyclotherax carcinicola (al2, ad3, av1-2, pd3, pv1, pl2 missing).

1-1/1,1/1-1 = 6 in Jacobsonia berleset (al2, ad2-3, av2, pd2-3, pl2 missing).

Rhodacaridae and Leptolaelapidae show the normal complement number of 13 setae on genu I.

The normal pattern (2-3/1,2/1-2 = 11) of genu II occurs in Leptolaelapidae, Rhodacaridae and in almost all free-living and phoretic forms within Laelapidae, with the exceptions of:
2-3/0,2/1-2 = 10 in *Pseudolaelaps doderoi*, *P. paulseni* (av1 missing).

2-2/1,2/1-2 = 10 in *Gecarcinolaelaps cancer*, *S. amictulus*, *Hunteria brasilienensis*, *Urozercon paradoxus* and *Narceolaelaps* (ad3 missing).

2-2/1,2/1-1 = 9 in *D. hysticosus* (ad3, pl2 missing).

1-2/1,2/1-1 = 8 in *Iphiopsts mirabilis* (al2, pd3, pl2 missing).

1-2/0,2/0-1 = 6 in *Iphiolaelaps myrtapoda*, which retains the larval complement (al2, ad3, av1, pv1, pl2 missing).

1-1/0,1/0-1 = 5 in *Jacobsonia berlesei* (al2, ad2-3, av1, pd2, pv1, pl2 missing).

Exceptions to the normal pattern (2-2/1,2/1-1 = 9) of genu III has been observed in: *Iphiolaelaps myrtapoda* which retains the larval complement (1-2/0,2/0-1), a condition also present in *Dermanyssus alaudae* (Evans & Till, 1965). *Jacobsonia berlesei* has only four setae (1-1/0,1/0-1); in *Laelaspis astronomica* and *Iphiopsts mirabilis* seta al2 is missing (1-2/1,2/1-1).

The genus *Pseudolaelaps* (*P. doderoi*, *P. paulseni*), as well as *Alphalaelaps*, lacks the postero-ventral seta (2-2/1,2/0-1). In *Euvarroa sinhait* the postero ventral seta may be present or absent (2-2/1,2/0-1-1) (Delfinado and Baker, 1974), and in
Gecarcinolaelaps cancer there is an addition of one postero-lateral seta (2-2/1,2/1-2), a setal condition that is also present in Sauronyssus saurarum (Evans & Till, 1965). Ayersacarus and Leptolaelaps present the normal complement of 9 setae; however, the Rhodacaridae has 10 setae (2-2/1,2/1-2) on genu III.

As in the British" Dermanyssidae" (Evans & Till, 1965), genu IV of laelapid mites shows a great diversity in chaetotaxy. In addition to the normal pattern (2-2/1,3/0-1 = 9), present in Leptolaelapidae, the following chaetotactic patterns have been observed in Laelapidae:

2-2/1,3/1-2 = 11 in Hunterta brasiliensis, Tropilaelaps clarae (pv1, pl2 extra)

2-2/1,3/1-1 = 10 in Bisternalis (B. mexicanus, B. hunteri), Blaberolaelaps, Julolaelaps, Melittiphts alvearius, Myrmolaelaps, Neoberlesta and Gaeolaelaps lubrica (pv2 extra).


2-2/2,2/1-1 = 10 in Dinogamasus, Scissuralaelaps novaguinea (av2, pv extra).

2-2/1,2/0-1 = 8 in Dysctinetonyssus (pd3 missing).

1-2/1,2/0-1 = 7 in Iphiopsis and Alphalaelaps (al2, pd3 missing).
1-2/1,1/0-1 = 6 in *Iphiolaelaps myriapoda*, *Scolopendracarus brevipilis* (al2, pd2-3, pl2 missing).
1-1/0,1/0-1 = 4 in *Jacobsonia* (al2, ad2, av2, pd2-3 missing).

**Tibiae I - IV:**

Eight different chaetotactic patterns have been observed on tibia I, excluding the normal (2-3/2,3/1-2). Thus, *Stevelus amiculus* and *Pseudolaelaps doderoi* have twelve setae (2-3/1,3/1-2), also 12 setae on *Bisternalis mexicanus* and *B. hunteri* (2-3/2,2/1-2); eleven setae on *Scissuralaelaps novaguinea* (2-3/1,2/1-2) and *Geccarinolaelaps cancer* (2-2/2,2/1-2); ten setae on *Dyscinetonyssus hystricosus* (2-2/1,2/1-2); nine setae on *Urozercon paradoxus* (2-2/1,2/1-1). Eight setae are present on *Narceolaelaps*, *Cyclothorax*, *Iphiolaelaps* and *Scolopendracarus* (1-2/1,2/1-1), and the most reduced tibia I chaetotaxy, with only six setae, occurs in *Jacobsonia berleseli* (1-1/1,1/1-1).

The basic adult complement of tibia II of 10 setae (2-2/1,2/1-2) is found in most of the laelapids. Exceptions are *Julolaelaps luctator* with 9 setae (2-2/1,2/1-1), *Narceolaelaps* (*N. gordanus*, *N. burdickii*) and *Geccarinolaelaps cancer* with 9 setae (2-1/1,2/1-2); *Alphalaelaps* has also 9 setae (1-2/1,2/1-2); *D. hystricosus* and *U. paradoxus* with 8 setae (2-1/1,2/1-1), *Iphiopsis mirabilis* with seven setae (1-1/1,2/1-1), *I. myriapoda* with 6 setae (1-2/1,1/1-0) and *Jacob-
sona berlesei with five setae (1-0/1,1/1-1).

Tibia III shows few exceptions to the normal pattern (2-1/1,2/1-1) of eight setae. There is an addition of one postero-lateral seta on Gecarcinolaelaps, Alphalaelaps and Coleolaelaps (2-1/1,2/1-2). On the other hand, Iphiolaelaps myriapoda and Iphiopsis mirabilis have lost one antero-lateral seta (1-1/1,2/1-1), and J. berlesei lost one antero-lateral, the antero-dorsal and one postero-dorsal setae (1-0/1,1/1-1); Bisternalis mexicanus has lost the postero-ventral seta and presents one additional antero-dorsal (ad2) (2-2/1,2/0-1) seta.

Only some of the arthropod-associated laelapids show variants of the normal chaetotaxy of tibia IV (2-1/1,3/1-2). Varroa jacobsoni has eleven setae on this segment (2-2/1,3/1-2) as is Steatonyssus tibialis (Evans & Till, 1965); B. mexicanus presents ten setae (2-2/1,3/1-1); nine setae are present on Narceolaelaps (2-1/1,2/1-2) and G. cancer (1-1/1,3/1-2); eight setae on D. hystricosus and U. paradoxus (2-1/1,2/1-1), seven setae on Iphiopsis and Alphalaelaps (1-1/1,2/1-1) and only five setae on J. berlesei (1-0/1,1/1-1).

Tarsi I - IV:

Tarsus I shows a great diversity in chaetotaxy among the studied Laelapidae. No intention were made to name each seta due to the fact that an unpublished analysis of tarsus I chaetotaxy in the Mesos-
Tigmata mites has been done by Moraza and Johnston (personal communication).

It is impossible to determine any regular basic number of setae on tarsus I; the total number of setae on tarsus I varies from 33 to 52. The following chaetotactic formulas have been found:

- $5-16/8-4 = 33$ in *Bisternalis*
- $5-19/6-4 = 34$ in *Laelaspoides*
- $4-21/6-3 = 34$ in *Jacobsonia*
- $4-28/8-4 = 34$ in *Cyclothorax*
- $5-18/8-5 = 36$ in *Dysctrctonyssus*
- $4-24/6-4 = 38$ in *Melittiphisotides*
- $5-21/8-5 = 39$ in *Dinogamasus*
- $5-23/8-4 = 40$ in *Gecarcinolaelaps*
- $4-24/8-4 = 40$ in *Hunteria* and *Melittiphts*
- $4-26/8-3 = 41$ in *Scissuralaelaps*
- $5-24/8-5 = 42$ in *Myrmolaelaps* and *Tropilaelaps*, also in *Leptolaelaps* and *Ayerscarus*
- $4-26/8-4 = 42$ in *Neohypoasptis*
- $5-25/8-4 = 42$ in *Pneumolaelaps bombicolens* and *G. lubrica*
- $5-27/8-4 = 44$ in *Gymnolaelaps* and *Hypoasptis*
- $5-26/8-5 = 44$ in *Strattolaelaps miles*
- $6-24/8-6 = 44$ in *Coleolaelaps*
- $4-28/8-4 = 46$ in *Blaberolaelaps*
5-30/8-3 = 46 in *Julolaelaps*
5-28/8-5 = 46 in *Gromphadorholaelaps*
5-29/8-4 = 46 in *Alloparasitus*
5-29/8-5 = 47 in *Pseudoparasitus domrowi* and *P. centralis*
5-27/10-5 = 47 in *Holostaspis montanus*
6-28/8-6 = 48 in *Oloaelaps veneta*
6-27/10-5 = 48 in *Laelaspis dubitatus*
6-29/8-5 = 48 in *Cosmolaelaps vacua*
5-28/10-5 = 48 in *Gaeolaelaps aculeifer*
5-28/10-5 = 48 in *Cosmolaelaps claviger*
5-34/8-3 = 50 in *Stevelus amiculus*
5-36/8-3 = 52 in *Pneumolaelaps heyi*

If the tarsus I is divided in five transverse verticils, been section 1 close to the anterior margin of the segment, setae av2 and pv2 could be present (most of the laelapids) or absent (*Coleolaelaps*, *Dyscinetonyssus*, *Julolaelaps luctator*, *Iphitolaelaps*, *Scolopendracarus* and *Urozercon*). In *Myrmolaelaps*, *Pseudoparasitus*, *Oloaelaps*, *Jacobsonia* and *Urozercon* setae av3 and pv3 are absent.

The ventral setae from verticil four (av4, pv4) are lacking in most of the arthropod-associated forms, and av5 is absent in *G. cancer*, *C. carcinicola*, *N. ampliseta* and *E. sinhal*. 
The outgroup complete set of ten ventral setae is present in *Pseudolaelaps, Gaeolaelaps, Laelaspis, Holostasps, Cosmolaelaps claviger* and *Pneumolaelaps heyi*. In *Gecarcinolaelaps cancer* setae pl3, pv4, ad4-5 and av5 are missing.

The basic adult complement of eighteen setae (3-3/2,1/1, 3/2-3) on tarsi II-IV is extremely constant among the Laelapidae. Deviations from the normal pattern have been noted in *D. hystricosus* (2-2/4,1,2/3-2= 16) (Moss and Funk, 1965); *Myrmonyssus, Urozercon paradoxus* and *Melittiphis alvearius* where ad1 and pd1 are absent. Normally the tarsal setae are simple. However, in *G. cancer* tarsi II-IV have two distal blunt, spiniform setae with longitudinal ribs; *C. carctincola* has several short, blunt, spine-like setae on tarsi II-IV, and in *D. hystricosus* setae av1 and av3 of tarsus II are heavy and thorn like. Some other setae on tarsi II-IV are whip-like, for example, setae al1-2, ad1, pd1, pl1-2 in *D. hystricosus*; macrosetae (pd2-3) are present on tarsus IV of *Hypoasps*. On tarsus II of *G. aculeifer* setae al1, pl1, av1-2, pv1-3, md, ad2 are spine-like. On tarsus III-IV setae ad1, pd1, al2, pl2, al3, ad3 and pd3 are simple, others are spine-like.

Most of the Laelapidae present conspicuous leg claws. However, claws are minute or greatly reduced in *Euvarroa sinhal, Stevelus amicus, Tropilaelaps clarae, Varroa jacobsori, Dyscinetonyssus*
paradoxus and in all genera associated with Myriapoda (Iphitopsis, Jacobsonia, Narceolaelaps, Julolaelaps, Scolopendracarus and Iphitolaelaps).
II.- CLADISTIC ANALYSES

Hypotheses about the phylogenetic relationships within the family Laelapidae are shown on Figs. 1 - 9. Numbers on cladograms indicate stems, and the apomorphic characters are listed for each stem.

On the basis of the evidence summarized on the cladograms it appears that the genera of free-living and arthropodo-associated laelapid mites represent 8 main, well defined and probably monophyletic groups. These are referred to as groups I, II, III, IV, V, VI, VII and VIII. Phylogeny within each group is discussed separately followed by a discussion of the relationships among them and with the laelapid associate of vertebrates. In the text character numbers are given in parentheses.

Group I (Fig. 2)

This group includes all the free-living, soil-dwelling, predatory genera: *Ololaelaps, Pseudoparasitus, Gaeolaelaps, Alloparasitus, Cosmolaelaps, Euandrolaelaps* and *Stratiolaelaps*.

The free-living forms show little diversity in morphology, and the genera of this group are plesiomorphic for nearly all of the charac-
ters that have been analyzed. For this reason it can not be defined satisfactorily on the basis of unique derived characters (groups autapomorphies); apomorphies are: one postero-lateral seta (pl2) on genu II absent (53), a state which is also derived independently in Coleolaelaps and Dyscinetonyssus, and seta antero-dorsal two (ad2) on tibia II absent (65), independently derived in Hypoasptis and Coleolaelaps.

The species of Ololaelaps are symplesiomorphic for most of the characters considered here and probably resemble the ancestral laelapid stock in many ways. A peritrematal shield fused to the exopodal shields (36) in the female is the only apomorphy for Ololaelaps, a character state which has also evolved independently in Cosmolaelaps and Coleolaelaps.

The group of genera formed by Pseudoparasitus, Cosmolaelaps, Gaeolaelaps, Stratiolaelaps, Euandmlaelaps and Alloparasitus apomorphically developed additional setae (px) between the J and Z series (31). Pseudoparasitus is an early derived taxon with opisthontonal seta S5 absent (32), which evolved independently at least three times within the laelapids. The Cosmolaelaps - Alloparasitus group of genera present a two-tined palp claw (15); character state which is the predominant one in most of the laelapids with the exception of Ololaelaps, Pseudoparasitus and Gymnolaelaps which retain the
primitive condition of three-tined palp claw.

_Cosmolaelaps_ presents characters 30 and 36 as apomorphies. _Stratiolaelaps_ has evolved four apomorphies: long corniculi, longer than palp femur (13); podonotal seta z2 absent (20); opisthonorotal seta S5 not on the shield (32) and one antero-ventral seta (av2) on genu I absent (49). _Euandrotaelaps_ evolved a short peritreme (34), and in _Alloparasitus_ the podonotal seta z2 is absent (20). _Gaeolaelaps_ is not defined by any apomorphic or autapomorphic characters among the ones analyzed. This problem might be partly resolved by restricting _Gaeolaelaps_ to the _aculeifer_ group.

**Group II (Fig. 3)**

This group includes _Androlaelaps casalis_, a predator, and the paraphages of Coleoptera (_Hypoaspis_, _Coleolaelaps_ and _Dyscinetonys-sus_ and Blattaria (_Blaberolaelaps_ and _Gromphadorholaelaps_). This group of laelapid genera emerged from its sister group, the free-living laelapids, by one autapomorphic character: absence of podonotal seta r6 on the dorsal shield (23).

_Androlaelaps casalis_ has three apomorphies: podonotal seta s6 not on the shield (22), unpaired accessory setae between J series present (30) and additional setae (px) between J and Z series present (31). It is the sister group of the _Hypoaspis_ through _Grom-
**phadorholaelaps** group of genera which are characterized by the loss of the podonotal seta z3 (21).

*Hypoaspis* and *Coleolaelaps* share one character: the absence of one antero-dorsal seta (ad2) on tibia II (65). *Coleolaelaps* is differentiated from its sister genus by characters 28, 32 and 53; *Hypoaspis* cannot be defined with any of the characters used here.

From the *Hypoaspis - Coleolaelaps* group diverged a group of genera formed by *Dyscinetonyssus, Blaberolaelaps* and *Gromphadorholaelaps*, which share three apomorphies: reduced hypostomal process (11), less than two teeth on the movable digit of the female chelicera (18) and a short peritreme, reaching to coxa II-III (34). *Dyscinetonyssus* and *Blaberolaelaps* present two synapomorphies: loss of the opisthontotal setae J2 (24) and Z3 (29), and three apomorphic characters, 20, 22 and 32, which also evolved independently in some predatory laelapids (i.e., *Alloparasitus, Coleolaelaps* and *A. casalis*).

*Gromphadorholaelaps* presents one to three denticles per row on the deutosternum (9), and one autapomorphy: fixed digit of male chelicerae with same length as the spermatodactyl (78).

*Dyscinetonyssus* differentiated from its sister genus by developing fourteen apomorphies: more than 6-7 rows of deutosternal denticles (8), a character state which also is derived independently in
Neohypoaspts and some laelapid associates of mammals (Haemogamasus, Myonyssus and Echinonyssus); a reduced fixed digit on the female chelicera (17), a state also present in Myrmolaelaps, Varroa, Androlaelaps fahrenholzi and Alphalaelaps; podonotal seta z4 spine-like (19); loss of the opisthonomal seta Z2 (28); genital seta off the shield (43); loss of setae ad3 (47) and av2 (49) on genu I; setae ad3 (52) and pl2 (53) on genu II absent; seta pd3 on genu IV absent (56); loss of setae ad3 (60), pd3 (61), av2 (62) and pl2 (63) on tibia I.

On the other hand, Blaberolaelaps is differentiated by losing the opisthonomal seta Z1 (27), and by one unique derived character: trochanter of female palp with one hyaline and flat seta (80).

**Group III (Fig. 4)**

This group includes seven genera associated with Hymenoptera (Formicidae and Apidae): Gymnolaelaps, Holostaspis, Laelaspis, Myrmonyssus, Pneumolaelaps, Hunteria, and Laelaspoides, which share one apomorphic character: loss of seta (ad2) on tibia II.

The Pneumolaelaps - Holostaspis group is defined by one synapomorphic character: sternal seta st4 placed on the endopodals (42). Pneumolaelaps is an early derived taxon with two autapomorphies: sternal seta st1 placed off sternal shield, on the metasternal area (37) and a wide peritreme (82). Its sister group is characterized by having unpaired accessory setae between the J series (30). Holos-
**Laelaspoides** and **Laelaspis** are closely related genera which present one synapomorphic character - podonotal seta z2 absent (20), state which also evolved independently in some free-living laelapids. **Laelaspis** differentiated from its sister group by two progressive apomorphies: loss of seta al2 on genu III (54) and pv1 on genu IV (57). On the other hand, **Laelaspoides** developed three apomorphic characters: loss of podonotal seta s6 (22) and r6 (23) on the dorsal shield, and loss of seta pd3 on genu IV (56), a parallelism with **Myrmonyssus**.

The sister group of **Pneumolaelaps** - **Holostaspis** is **Hunteria** - **Myrmonyssus**, which includes species that have three apomorphic characters: opisthontonal seta S5 not on the shield (32), a short peritreme (34) and seta antero-dorsal three (ad3) on genu II is absent (52). The early derived taxon is **Myrmonyssus** with 28 apomorphies: characters 5, 11, 16, 18, 21, 26, 34, 46-48, 50-56, 59-64, 66, 67, 70 and 72. **Hunteria** evolved less than 6-7 rows of deutosternal denticles (7), opisthontonal seta S5 not on the shield (32) and seta ad3 on genu II absent (52). **Gymnolaelaps** presents one apomorphic characters - podonotal seta z2 absent (20).
Hunteria and Gymnolaelaps present two synapomorphies: less than 6-7 rows of deutosternal denticles (7) and unpaired accessory setae between the J series present (30).

Group IV (Fig. 5)

The Bisternalis - Melittiphisoides group of genera which evolved two synapomorphies: podonotal setae s6 (22) and r6 (23) absent. The distribution of character states summarized in Fig. 5 suggests an early division of this group into four principal lineages. The first lineage represents Bisternalis, taxon defined by three autapomorphic characters at this level: sternal seta st4 on the endopodal shield (42), seta al2 on genu I absent (46), seta av2 on genu I absent (49) and seta pd3 on tibia I absent (61), and a convergent development of three apomorphies: opisthonotal seta S5 not on the shield (32), sternal seta st4 placed off the shield (37) and seta pd3 on genu I absent (48).

A second lineage represents an unnamed taxon defined by two synapomorphies: hypostomal process reduced (11) and the loss of seta ad2 on tibia II (65). The early derived taxa from this lineage are Myrmolaelaps and Neoberlesia which can be tentatively defined by one progressive synapomorphy: a reduced number of teeth (less than two) on movable digit of female chelicera (18). Myrmolaelaps further became differentiated with four apomorphies (10, 16, 34, 37) and one autapomorphetic character: a reduced fixed digit of female
chelicera (17), and legs I twice longer than other legs (75), while *Neoberlesta* achieved two apomorphies: seta hyp 3 of the gnathosoma absent (5), and femur IV with an anterior spur (76).

The third lineage represents *Neohypoaspis* which can be defined by two apomorphies: more than 6-7 rows of deutosternal denticles (8) and female peritrematal shield fused to exopodal IV shield (36) a state also derived independently in *Myrmolaelaps*. *Neohypoaspis* presents spatulated podonotal setae J1 (83).

A fourth lineage represents two nominate genera, *Melittiphis* and *Melittiphisoides*, with two synapomorphies: less than 6-7 rows of deutosternal denticles (7) and seta pv1 on genu IV absent (57). *Melittiphis*, originally placed in the subfamily Melittiphinae by Evans and Till (1966) presents four autapomorphic characters: one denticle per deutosternal row (9), loss of setae pl2 on genu II (53), pl2 on tibia I (63) and pl2 on tibia II (66); and *Melittiphisoides* evolved seven apomorphies (32, 33, 34, 37, 48, 56 and 61).

**Group V (Fig. 6)**

The genera in this group lack the hypostomal setae three (hyp3) or one (hyp1) on the subcapitulum (5). The early derived taxa are the *Tropilaelaps - Urozercon* group, which are closely related genera, sharing three synapomorphies: a reduced hypostomal
process (11), a state which also evolved independently once in the 
*Euvarroa* - *Dinogamasus* group; reduced corniculi (i.e., reaching to 
half palp-femur length) (14) and loss of seta ad3 on genu II (52).
*Urozercon* has five apomorphies: 18, 47, 48, 48 and 62, and four 
autapomorphic characters: sternal seta four (st4) absent (42), loss of 
setae pd3 (61) and pl2 (63) on tibia I, and five setae on the anal 
shield (74).

Its sister group *Stevelus, Euvarroa, Varroa* and *Dinogamasus* is 
defined by a regressive synapomorphy: short peritreme (34). The 
first taxon to differentiate in this lineage is *Stevelus*, with characters 
10, 18, 32, 49, 52 and 57 as apomorphies and five autapomorphies:
seta z4 blunt-like (19), loss of podonotal seta z2 (20), loss of opist­
thonotal seta J4 (26), sternal seta one (st1) placed off the shield (37) 
and loss of seta ad3 on genu I (47).

The lineage which originated the remaining genera on group V 
present one synapomorphic character, which is an autapomorphy for 
the group: palp-claw with basal tine reduced (16); and apomorphic 
character (11), a parallelism with the *Tropilaelaps* - *Urozercon* 
group. *Dinogamasus* has evolved one apomorphy: sternal seta four 
(st4) placed on soft cuticle (43), a state which also has evolved 
independently in some of the free-living forms. From this lineage 
emerged the *Euvarroa* - *Varroa* group with two autapomorphies:
tritosternum short and reduced (10) and fixed digit of female chelicera absent (17). *Varroa* and *Euvarroa* have been originally included in a separate family - Varroidae - by Delfinado and Baker (1974), on the basis of the complete lack of the fixed digit, and the number and arrangement of the gnathosomal setae. However, these regressive apomorphies have evolved independently in several other genera in the family Laelapidae. These authors missed the fact that *Tropilaelaps* and *Stevelus* lack seta hyp3, *Dinogamasus* and *Urozercon* lack setae hyp1 on the gnathosoma, and that *Myrmolaelaps* also presents a very reduced (sometimes regarded as a total absence) fixed digit on the female chelicera.

*Varroa* is differentiated from its sister genus, *Euvarroa*, by regressive autapomorphies: loss of setae av2 on genu I (49), pv1 on genu IV (57) and av2 on tibia I (62). *Euvarroa* presents two autapomorphies: loss of setae pd3 on genu I (48) and ad3 on genu II (52).

**Group VI (Fig. 7)**

This lineage represents one genus, *Scissuralaelaps*, which is differentiated by two apomorphies: smooth tectum (3); corniculi longer than palp femur (12-13), a parallelism with *Stratiolaelaps*; and two regressive characters: loss of setae pd3 (48) and av2 (49) on genu I. This is the sister group of the remaining genera associated with Diplopoda and Chilopoda.
Group VII (fig. 7):

This lineage represents a group of genera formed by *Julolaelaps*, *Iphiolaelps*, *Iphiopsts*, *Jacobsonia*, *Narceolaelaps* and *Scolopendracarus*. It is defined by one regressive synapomorphy: hypostomal seta three (hyp3) absent (5).

*Julolaelaps* is the first taxon to differentiate with only one apomorphy: loss of the opisthontonal seta Z3 (29). Its sister lineage in turn is defined by characters 49, 50 60 and 61 as apomorphies, and by five synapomorphies, which are autapomorphic within the group: loss of setae al2 (46) and ad3 (47) on genu I, loss of setae ad3 on genu II (52), pd3 on genu IV (56) and pd3 on tibia IV (72). *Scolopendracarus* has separated from its sister group of genera by nine apomorphic characters (9, 10, 24, 25, 26, 28, 53, 54 and 57), and by one autapomorphic character: sternal shield not sclerotized (73).

The group *Iphiolaelps - Narceolaelaps* has evolved one autapomorphy: loss of seta al2 on tibia I (59) and three regressive apomorphies: loss of setae pd3 on genu I (48), pl2 on tibia I (63) and pl2 on tibia II (66).

*Narceolaelaps* is the first taxon to emerge from this lineage by evolving one autapomorphic character: loss of the opisthontonal seta
Z1 (27) and two apomorphies: one to three denticles per deutosternal row (9), a state which also evolved independently in *Scolopendracarus*, and loss of seta ad2 on tibia II (65), a parallelism with the *Iphiopsis - Jacobsonia* group. Males of *Narceolaelaps* present a divided dorsal shield (81).

The *Iphiolaelaps - Jacobsonia* group has evolved seven synapomorphic characters (51, 53, 54, 55, 64, 67 and 70); from which four are apomorphies within the group: loss of setae al2 on genu II (51), al2 on genu IV (55), al2 on tibia II (64) and al2 on tibia III (67). *Iphiolaelaps* is an early derived taxon with two apomorphic characters: one tooth on the movable digit of the female chelicera (18), a state which also has evolved independently in *Ljunghia* and *Cyclothorax*, and lack of a peritreme (35), which is a parallelism with *Jacobsonia*.

*Jacobsonia* and *Iphiopsis* present five synapomorphies: corniculi longer than palp-femur (13), opisthonotal seta Z3 absent (29), loss of seta pv1 on genu IV (57) and ad2 on tibia II (65). *Jacobsonia* is differentiated by three apomorphic characters: loss of podonotal seta z3 (21) and opisthonotal seta J2 (24), lack of a peritreme (35), sternal seta one (st1) placed off the shield (37), and one autapomorphic character: fixed digit of females chelicerae with a process directed anteriorly (77).
Group VIII (Fig. 9)

Lineage that represents taxon which includes the genera Ljunghia, Gecarcinolaelaps and Cyclothorax. It is defined by only one apomorphy: less than 6-7 rows of deutosternal denticles (6-7). It seems that Ljunghia is not a well defined taxon (Domrow, 1975) because all the species included are very different from each other. Ljunghia, in the present sense, could be defined by characters 18, 21, 25 and 28, which represent parallelisms with other genera of Laelapidae.

Its sister group, Gecarcinolaelaps - Cyclothorax, evolved four progressive apomorphies: loss of seta pd3 on genu I (48), pv1 on genu IV (57), ad3 on tibia I (60) and seta pd3 on tibia I (61). Cyclothorax is differentiated by ten apomorphies (12, 14, 18, 25, 26, 37, 49, 50, 63, 66), and Gecarcinolaelaps by a short and reduced tritosternum (10), unpaired accessory setae between the J series present (30), sternal seta st4 absent (41), loss of setae ad3 on genu II (52) and al2 on tibia IV (70); and by one autapomorphy: sternal setae of the protonymph hypertrophied (79).

Relationships among groups I - VIII (Fig. 1)

While each of the groups (I - VIII) are reasonably well defined on the basis of synapomorphies and probably monophyletic, the family Laelapidae appears to be weakly characterized.
The Cladogram on Fig. 1 is supported by seven synapomorphies, shared by almost all the members included in this group of genera, and considered results of regressive evolution: a) loss of seta postero-lateral two (pl2) on genu IV, with the exception of Hunteria, Tropilaelaps, Dinogamasus, Gromphadorholaelaps, Narceolaelaps, Scissuralaelaps and Gecarcinolaelaps; b) loss of seta ad2 on tibia III, except in Bisternalis, Euvarroa, Blaberolaelaps, Narceolaelaps; c) loss of seta pl2 on tibia III, except in Dinogamasus, Narceolaelaps, Coleolaelaps, Myrmolaelaps, Euvarroa and Hunteria; d) loss of seta ad2 on tibia IV, with the exception of Tropilaelaps, Gromphadorholaelaps, Iphiolaelaps, Bisternalis and Euvarroa; e) tectum not trispinate (denticulate or smooth); f) sternal seta four (st4) placed off the sternal shield, with the exception of Oloaelaps, Myrmolaelaps, Melittiphisoides, and Neohypoasptis, and g) female anal shield free and triangular except on Oloaelaps and Neoberlestia.

Grandjean (1946) gave several examples on priorities in setal regression and it seems clear that losses usually occur in identical sequences even in different lineages of the same major group. When dealing with presence or absence of body or leg setae as parallelism or convergence, it is common to find high homoplasy. It is my contention that the cladogram on Fig. 1 is the least easily rejected despite the relatively large amount of homoplasy, as shown by the relatively great tree length and the low consistency index.
The results of the analyses indicate that the Hypoaspidae (Groups I to II) is the sister group of the other Laelapidae (Groups III - V).

Groups I and II are supported by one synapomorphic character, which is a regressive autapomorphy: loss of seta pv1 on genu IV (57). Groups I - II share only one synapomorphy with groups III - V, which is also a regressive autapomorphy, the loss of seta pl2 on genu IV (58).

Groups III - V present one synapomorphic character: smooth tectum (3), with Gymnolaelaps and Neohypoaspis as exceptions. Gymnolaelaps has been defined by Evans and Till (1966) as a group of species with a denticulate tectum, and Neohypoaspis also presents a denticulate tectum.

Group III is defined by a regressive apomorphy: loss of seta ad2 on tibia II, state which also evolved independently on group I (free-living laelapids).

Groups IV and V share two synapomorphies: unpaired accessory setae between J series present (30), with the exception of Stevelus and Myrmonyssus; and female anal shield kidney, crescent or bowl shaped (45): exceptions are Myrmolaelaps, Melittiphisoides,
*Stevelus* and *Varroa*. Group IV is defined by two synapomorphies: podonotal setae s6 (22) and r6 (23) not on the dorsal shield, absent or inserted on the lateral soft cuticle. Group V is characterized by lacking seta hyp 3 on the subcapitulum(5).

On the other hand groups VI to VIII, which represent the family Iphiopsididae, are characterized by a regressive autapomorphy: loss of seta av2 on tibia I (62) with the exception of *Julolaelaps*, *Gecarcinolaelaps*, and *Iphiopsis*.

Group VI represents only one genus, *Scissuralaelaps*, defined by four synapomorphies: 3, 12-13, 48-49 and 61.

Groups VII and VIII share two synapomorphies: hypostomal process reduced (11), additional setae (px) between J and Z series present (32); and three apomorphies: setae s6 (22) and r6 (23) not on the shield, and loss of seta pl2 on genu IV (58), a state which also has evolved independently in the Hypoaspidinae.

Group VII is defined by the loss of setae hyp1 or hyp 3 on the gnathosoma (5), which have also evolved independently in group V of the Hypoaspidinae, and a short or absent peritreme (34). Finally, Group VIII is characterized by a deutosternum with less than 6-7 rows of denticles.
When some taxa associate of mammals (*Laelaps, Haemogamasus, Myonyssus, Alphalaelaps, Echinonyssus, Mesolaelaps* and *Androlaelaps fahrenholzi*) were included in the analyses, the tree length went up and the consistency index decreased, indicating a higher number of homoplasies. None of the characters used in this study can be used to define one group of taxa associated with mammals even though they always come together in the tree. This group of laelapids should be recognized as different taxonomic ranks. They have been temporarily included in different subfamilies (i.e., Haemogamasinae, Myonyssinae, Alphalaelapinae, Hirstionyssinae, Laelapinae and Mesolaelapinae) following Evans and Till, 1966, and Radovsky, 1985. The species *Androlaelaps fahrenholzi* should be placed in a separate genus (*Haemolaelaps*), closely related with those laelapines associated with vertebrates and leaving the genus *Androlaelaps* for species which are predators or occasionally associated with nests of vertebrates.

Evans and Till (1966) studying the free-living, paraphagic and ectoparasitic British "Dermanyssidae" recognized eight subfamilies: Dermanyssinae, Haemogamasinae, Pseudolaelapinae (*Pseudolaelaps*), Myonyssinae (*Myonyssus*), Melittiphidinae (*Melittiphits*), Laelapinae, Hirstionyssinae and Macronyssinae. They included within Laelapinae all the free-living laelapids and the species belonging to the following genera: *Laelaps, Androlaelaps, Pneumolaelaps, Gymnolaelaps, Holos-
taspts and Laelaspts. They indicated that Pseudolaelaps and Melittiphts show greater affinities with Laelapinae than with any other subfamily. In this study, Pseudolaelaps always showed greater affinities with the outgroup than with any Laelapidae. It shares more symplesiomorphies than synapomorphic characters with Laelapidae and it presents a trisplnate tectum, and hypotrichy of the idiosoma and appendages. Therefore, it is suggested that Pseudolaelaps should be removed from Laelapidae. Further studies are needed to determine its correct family placement. Melittiphts, as well as other laelapid mites associates of Hymenoptera and Isoptera, has been included in the subfamily Melittiphidinae.

Karg (1979) attempted to give a phylogenetic key for the subgenera Hypoaspts, Cosmolaelaps, Alloparasitus, Gaeolaelaps, Pneumolaelaps, Holostaspts and Laelaspts, including as the most relevant characters: a) tectum with toothed margin or smooth = 0, 1; b) deutosternal rows polydont or oligodont= 0, 1; c) opisthonotal seta Z4 not elongated or elongated= 0, 1; d) female genital shield normal or greatly expanded= 0, 1; and e) genital shield with one pair or more than one pair of seta= 0, 1. An analysis using these characters was done and the results showed that the characters used by Karg vary so much within even each genus that they cannot be used as binary state characters. Some of Karg's characters were used in this study, but they were polarized following the additive method.
III.- CLASSIFICATION.

On the basis of the proposed phylogeny the following classification of the family Laelapidae is suggested.

Family Laelapidae Berlese, 1892

A.- Subfamily Hypoaspilidae Vitzthum, 1940

a) Tribe Pseudoparasitini Vitzthum, 1940

*Oloelaps* Berlese, 1903; type-species: *Hypoaspis venetus* Berlese, 1903

*Pseudoparasitus* Oudemars, 1902; type-species: *Laelaps meridionalis* Canestrini, 1882

*Gaeolaelaps* Tragardh, 1952; type-species: *Laelaps aculeifer* Canestrini, 1884

*Alloparasitus* Berlese, 1920; type-species: *Laelaps (Hypoaspis) oblongus* Halbert, 1915

*Cosmolaelaps* Berlese, 1903; type-species: *Laelaps claviger* Berlese, 1883

*Euandroelaelaps* Bregetova, 1977; type-species: *Laelaps (Androelaelaps) sardous* Berlese, 1911

*Stratiolaelaps* Berlese, 1882; type-species: *Laelaps (Iphits) miles* Berlese, 1892

b) Tribe Hypoaspilini Vitzthum, 1940

*Androelaelaps* Berlese, 1903; *A. casalis* group

*Hypoaspis* Canestrini, 1885; type-species: *Gamarus kramert* G. & R. Canestrini, 1881
Coleolaelaps Berlese, 1903; type-species: Laelaps (Iphis) agrèstis Berlese, 1887

Dysctnetonyssus Moss & Funk, 1965; type-species: Dysctnetonyssus hystricosus Moss & Funk, 1965

Blaberolaelaps Costa, 1980; type-species: Blaberolaelaps matthiesensis Costa, 1980

Gromphadorholaelaps Till, 1969; type-species: Gromphadorholaelaps schaefleri Till, 1969

B.- Subfamily Melittiphidinae Evans and Till, 1966

c) Tribe Laelaspidini, new tribe

Gymnolaelaps Berlese, 1916; type-species: Laelaps myrmecophilus Berlese, 1892

Holostasps Kolenati, 1858; type-species: Holostasps isotricha Kolenati, 1858

Laelasps Berlese, 1903; type-species: Iphis astronomicus Koch, 1889

Myrmonyssus Berlese, 1903; type-species: Myrmonyssus diplogentus Berlese, 1903

Pneumolaelaps Berlese, 1920; type-species: Iphis bombicolens Canestrini, 1885


Laelaspoides Eickwort, 1966; type-species: Laelaspoides ordwayae Eickwort, 1966

d) Tribe Melittiphidini Evans and Till, 1966

Bisternalis Hunter, 1963; type-species: Bisternalis rettenmeyeri Hunter, 1963

Myrmolaelaps Tragardh, 1906; type-species: Myrmolaelaps equittans Tragardh, 1906
Neoberlesta Berlese, 1892; type-species: Neoberlesta equitans Berlese, 1892


Melittiphis Berlese, 1918; type-species: Laelaps (Iphis) alvearius Berlese, 1896


e) Tribe Varroini Delfinado and Baker, 1974

Tropilaelaps Delfinado, 1961; type-species: Tropilaelaps clareae Delfinado, 1961

Urozercon Berlese, 1901; type-species: Urozercon paradoxus Berlese, 1901

Stevelus Hunter, 1963; type-species: Stevelus amiculus Hunter, 1963

Euvarroa Delfinado & Baker, 1974; type-species: Euvarroa sinhali Delfinado & Baker, 1974

Varroa Oudemans, 1904; type-species: Varroa jacobsoni Oudemans, 1904

Dinogamasus Kramer, 1898; type-species: Dinogamasus crassipes Kramer, 1898

C.- Subfamily Haemogamasinae Oudemans, 1926

Euvelaps, Brevisterna, Ischyropoda, Acanthochela, Haemogamasus

D.- Subfamily Alphalaelapinae Tipton, 1960

Alphalaelaps
E.- **Subfamily Laelapinae** Berlese, 1892

*Aetholaelaps, Cavilaelaps, Chrysochlorolaelaps, Domrownyssus, Gigantolaelaps, Gnatholaelaps, Hymenolaelaps, Hyperlaelaps, Laelaps, Liponyssella, Nakhoda, Longolaelaps, Mysolaelaps, Neolaelaps, Neoparalaelaps, Notolaelaps, Ondatralaelaps, Oryctolaelaps, Permelaelaps, Radfordilaelaps, Rhyzolaelaps, Sinolaelaps, Steptolaelaps, Tricholaelaps, Tylolaelaps, Tur*

F.- **Subfamily Myonyssinae** Bregetova, 1956

*Myonyssus*

G.- **Subfamily Ulstonyssinae** Evans and Till, 1960

*Echinonyssus, Ancoranyssus, Patrinyssus, Thadeua, Trichosurolaelaps*

H.- **Subfamily Mesolaelapinae** Tenorio and Radovsky, 1974

*Mesolaelaps, Rhodacantha*

Note: Subfamilies C to H were not analyzed in this study. The list of genera in these subfamilies was taken from Radovsky, 1985.

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**Family Iphiopsididae** Kramer, 1886

A.- **Subfamily Scissuralaelapinae** new subfamily

*Scissuralaelaps Womersley, 1945; type-species: Scissuralaelaps novaguinea Womersley, 1945*
B.- **Subfamily Iphiopsidinae** Kramer, 1886

a) Tribe Iphiopsidini Kramer, 1886

*Julolaelaps* Berlese, 1916; type-species: *Julolaelaps dispar* Berlese, 1916


*Iphiolis* Berlese, 1882; type-species: *Iphis mirabilis* Berlese, 1882

*Jacobsonia* Berlese, 1910; type-species: *Ipthis mirabilis* (Greeniella) submollis Berlese, 1910


*Scolopendracarus* Evans, 1955; type-species: *Scolopendracarus brevipilis* Evans, 1955

b) Tribe Gecarcinolaelapini, new tribe

*Ljunghia* Oudemans, 1932; type-species: *Ljunghia selenocosmatae* Oudemans, 1932

*Cyclothorax* von Frauenfeld, 1868 type-species: *Cyclothorax carcinicola* von Frauenfeld, 1868

*Gecarcinolaelaps* n. gen. Type-species: *Gecarcinolaelaps cancer* (Pearse, 1929) n. comb.

The free-living laelapid mites, Group I, are ranked at the tribe level. These genera are plesiomorphic in many character states relative to the other laelapid-type mites. For example, a denticulate tectum, four pairs of subcapitular setae, normal and bifid tritoster-
num, normal leg chaetotactic pattern, etc., characters which are also present in the Ologamasidae and Leptolaelapidae, and may well represent the plesiomorphic states for the laelapid mites.

The name Hypoaspidinae Vitzthum has priority over other available family group names for the subfamily proposed here to include groups I (Pseudoparasitini) and II (Hypoaspidini). These two groups constitute a well-defined monophyletic lineage representing the sister group of the other laelapid mites.

Since the genera of groups III to V are members of a simple well-defined monophyletic group, they are considered as one subfamily, Melittiphilinae. The name Melittiphilinae has priority over the family name Varroidae for the subfamily proposed here.

Each group (III, IV and V) within the subfamily Melittiphilinae are assigned tribal rank: group III represents the tribe Laelaspidini, new tribe, to include genera associated with Formicidae and Apidae; group IV is tribe Melittiphilini which includes six genera associated with Hymenoptera; and group V represents tribe Varroini which are associates of honey-bees, carpenter bees, bumble-bees and Isoptera.

The species in the subfamilies Haemogamasinae, Alphalaelapidinae, Laelapinae, Myonyssinae, Hirstionyssinae and Mesolaelapinae,
all associates of mammals, were not analyzed in detail here. However, when some of these genera were included in the analyses they always diverged from the Hypoaspidinae. Therefore, their subfamily rank is retained until more analyses are done. The mammal-associated laelapid mites and the Hypoaspidinae are characterized by one synapomorphic character: loss of seta pv1 on genu IV, which is a regressive apomorphy.

The groups VI, VII and VIII represent a new family group: Iphiopsididae. Previous allocation of the genera of these groups was in the subfamily Iphiopsidinae within Laelapidae (Evans, 1955). The iphiopsid mites represent a well-defined and monophyletic group that includes paraphages of Chilopoda, Diplopoda, Araneae and Crustacea.

According to the phylogenetic analyses the family Iphiopsididae Kramer present two subfamilies: Iphiopsidinae, divided into two tribes: Iphiopsidini Kramer, and Gecarcinolaelapini new tribe; and Scissuralaelapinae new subfamily.

Scissuralaelapinae (group VI) represents the sister group of the other two groups of iphiopsid mites. Iphiopsidini is a well-defined and monophyletic group which includes paraphages of Chilopoda and Diplopoda.
Considering the setal losses some members of the family Iphio-
ssididae, *Jacobsonia* and *Iphiopsis*, are among the most regressive
mesostigmatid mites known and this is the result of the retention of
larval character states (paedomorphosis).

The appropriate taxonomic status of the genera (especially *Ljun-
ghta*) temporarily included in the tribe Gecarcinolaelapini, which are
associates of Crustacea and Araneae, will become apparent when new
data are analyzed.

KEY FOR THE TRIBES OF SUBFAMILIES HYPOASPIDINAE AND
MELITTIIPHIDINAE (LAELAPIDAE)

1.- Seta *pvl* on genu IV absent;
tectum denticulate or smooth.................................. Hypoaspidinae....... 2

    Seta *pvl* on genu IV present;
tectum smooth (except on *Gymnolaelaps*
and *Neohypoaspis*)........................................... Melittiphidinae...... 3

2.- Setae *pl2* on genu II and *ad2* on tibia I
absent. Free-living, predaceous .................................. Pseudoparasitini

    Setae *pl2* on genu II and *ad2* on tibia I
present. Podonotal setae *r6* not inserted
on the dorsal shield. Paraphages of Coleop-
tera and Blattaria.............................................. Hypoaspidini
3.- Unpaired accessory setae between the J series absent. Seta ad2 on tibia II absent.  
Associates of Hymenoptera........................................... Laelaspidini

Unpaired accessory setae between the J series present. Hypertrichy common. Seta ad2 on tibia II present ........................................... 4

4.- Setae hyp3 or hyp1 absent. Female chelicera with fixed digit normally reduced (except Uroæron) ................................................................. Varroini

Setae hyp3 or hyp1 present. Female chelicera with digits chelate but weakly dentate ....................... Melittiphidini
Figure 1. Families Laelapidae and Iphiopsididae. Numbers on figure refer to stems. Apomorphic characters are listed for each stem.

STEM 1: 1, 2, 38, 39, 40, 44, 58, 68, 69, 71; STEM 2: 58; STEM 3: 62; STEM 4: 57; STEM 5: 3; STEM 6: 65; STEM 7: 30, 45; STEM 8: 3, 12, 13, 48, 49, 61; STEM 9: 11, 22, 23, 32, 58; STEM 10: 53, 65; STEM 11: 23; STEM 12: 22, 23; STEM 13: 5; STEM 14: 5, 34; STEM 15: 7.
Fig. 1

I - V LAELAPIDAE

VI - VIII IPHIOPSIDIDAE
Figure 2. Group I: Pseudoparasitini. Numbers on figure refer to stems. Apomorphic characters are listed for each stem.

Figure 3. Group II: Hypoaspidini. Numbers on the figure refer to stems. Apomorphic characters are listed for each stem.

STEM 1: 23; STEM 2: 22, 30, 31; STEM 3: 21; STEM 4: 65; STEM 5: 11, 18, 34; STEM 6: 20, 22, 23, 24, 29; STEM 7: 9; STEM 8: --; STEM 9: 28, 32, 53; STEM 10: 8, 17, 19, 28, 43, 47, 49, 52, 53, 56, 60, 61, 62, 63; STEM 11: 27.
Fig. 3

Hypoaspis

Androlaelaps casalis

Coleolaelaps

Dyscinetonyssus

Blaberolaelaps

Gromphadorho - laelaps

HYPOASPIDINI

Group II
Figure 4. Group III: Laelaspidini new tribe: Numbers on figure refer to stems. Apomorphic characters are listed for each stem.

STEM 1: 65; STEM 2: 42; STEM 3: 32; STEM 4: 37; STEM 5: 30; STEM 6: 20; STEM 7: 10, 18; STEM 8: 5, 11, 16, 18, 21, 22, 23, 26, 34, 43, 46, 47, 48, 50, 51, 52, 53, 54, 55, 56, 59, 60, 61, 62, 63, 64, 66, 67, 70, 72; STEM 9: 6, 7, 30; STEM 10: 5, 22, 23, 56; STEM 11: 54, 57; STEM 12: 20; STEM 13: 33, 34, 52.
Fig. 4

LAELASPIDINI

Group III

Pneumolaelaps
Laelaspoides
Laelaspis
Holostaspis
Myrmonyssus
Gymnolaelaps
Hunteria
Figure 5. Group IV: Melittiphidini. Numbers on figure refer to stems. Apomorphic characters are listed for each stem.

STEM 1: 22, 23; STEM 2: 32, 37, 42, 46, 48, 49, 61; STEM 3: 11, 65; STEM 4: 18; STEM 5: --; STEM 6: 8, 36; STEM 7: 7, 57; STEM 8: 16, 17, 33, 34, 36, 49; STEM 9: 5; STEM 10: 9, 53, 63, 66; STEM 11: 32, 33, 34, 37, 48, 56, 61.
Figure 6. Group V: Varroini. Numbers on figure refer to stems.

Apomorphic characters are listed for each stems.

STEM 1: 5; STEM 2: 11, 14, 52; STEM 3: 34; STEM 4: 10, 18, 19, 20, 26, 32, 37, 47, 49, 57; STEM 5: 16, 11; STEM 6: 50; STEM 7: 18, 42, 47, 48, 49, 50, 61, 62, 63; STEM 8: 48, 52; STEM 9: 9, 49, 57, 62; STEM 10: 43; STEM 11: 10, 17.
Figure 7. Groups VI, VII and VIII: Family Iphiopsididae. Group VI: Scissuralaelapinae, new subfamily. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 62; STEM 2: 3, 61; STEM 3: 11, 22, 23, 32; STEM 4: 5; STEM 5: 6, 7.
Figure 8. Group VII: Iphiopsini. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 5; STEM 2: 29; STEM 3: 46, 47, 49, 50, 52, 56, 60, 61, 72; STEM 4: 48, 59, 63, 66; STEM 5: 9, 10, 24, 25, 26, 28, 53, 54, 57; STEM 6: 51, 53, 54, 55, 64, 67, 70; STEM 7: 9, 27, 65; STEM 8: 18, 35; STEM 9: 13, 29, 57, 65; STEM 10: --; STEM 11: 21, 24, 35, 37.
Iphioelaps

Iphiopsis

Jacobsonia

Narceolaelaps

Scolopendracarus
Figure 9. Group VIII: Gecarcinolaelpint, new tribe. Numbers on figure refer to stems. Apomorphic characters are listed for each stems.

STEM 1: 6, 7; STEM 2: 18, 21, 25, 28; STEM 3: 48, 57, 60, 61;
STEM 4: 10, 30, 41, 52, 70; STEM 5: 12, 14, 18, 25, 26, 37, 49, 50, 63, 66.
Fig. 9

Group VIII
GECARCINOLAEELAPINI
CONCLUSIONS

The phylogeny proposed for the free-living and arthropod-associated laelapid mites based on parsimony methods represents a substantial improvement in understanding the evolutionary history of the group, and gives a basis to understand the most derived groups within the cohort Dermanyssina.

Many characters of laelapid mites have yet to be analyzed phylogenetically due to the incompleteness of data and, therefore, the proposed phylogeny must be regarded as preliminary. When data on the immature stages and males, as well as life-history and habitat diversification, become available a more strongly based phylogeny of the family Laelapidae can be achieved.

Concepts of the free-living and arthropod-associated Laelapidae were reviewed in an attempt to determine the internal relationships of the members of the family. Using phylogenetic methods, PAUP and MacClade programs, a comparative study of eighty-three characters
In forty-three generic taxa resulted in the construction of nine consensus cladograms illustrating familial and subfamilial relationships. The Leptolaelapidae Karg, 1978 was used as the sister group and Ologamasidae Ryke, 1962 as the outgroup to the Laelapidae.

In the revision of the taxa included in this study, it is intended that the taxa reflect natural hierarchical groups and to be defined on the basis of synapomorphies where possible. Tree length and consistency index were sometimes sacrificed to obtain the most definable groups of laelapid mites.

The Laelapidae was redefined to include eight subfamilies: Hypoaspidae Vitzthum, 1940; Melittiphinae Evans and Till, 1966; Haemogamasinae Oudemans, 1926; Alphalaelapinae Tipton, 1960; Laelapinae Berlese, 1892; Myonyssinae Bregetova, 1956; Hirstionyssinae Evans and Till, 1960; and Mesolaelapinae Tenorio and Radovsky, 1974. The new arrangement of the free-living and arthropod-associated genera is the following: Family Laelapidae, with two subfamilies: a.- Subfamily Hypoaspidae, which includes the free-living, predatory and phoretic mites on Coleoptera and Blattaria, with: Tribe Pseudoparasitini (Alloparasitus, Cosmolaelaps, Euandrolaelaps, Gaeolaelaps, Ololaelaps, Pseudoparasitus, Stratiolaelaps); Tribe Hypoaspidini (Androlaelaps casalts group, Blaberolaelaps, Coleolaelaps, Dysctnetonyssus, Gromphadorholaelaps,
Hypoasps); b.- Subfamily Melittiphidinae, which includes laelapid mite associates of Hymenoptera (Apidae and Formicidae) and Isoptera, with: Tribe Melittiphidini (Bisternalis, Myrmolaelaps, Neoberlesta, Neohypoasps, Melittiphts, Melitttptisoldes); Tribe Varroini (Dinogamasus, Euvarroa, Stevelus, Tropilaelaps, Urozercon, Varroa).

The family Iphiopsididae, which includes dermanyssoid mite associates of Chilopoda, Diplopoda, Araneae and Crustacea is divided into two subfamilies: a.- Subfamily Scissuralaelapinae, new subfamily, (Scissuralaelaps); b.- Subfamily Iphiopsidinae with: Tribe Iphiopsidini (Iphitolaelaps, Iphipts, Jacobsonia, Julolaelaps, Narceolaelaps, Scolopendracarus); and Tribe Gecarcinolaelapini, new tribe, (Cyclothorax, Gecarcinolaelaps, Ljunghia).

The genus Urozercon is included for the first time in the family Laelapidae; and the new genus Gecarcinolaelaps is established in Iphiopsididae. The prior ranking of Euvarroa and Varroa as the family Varroidae Delfinado and Baker, 1974 is refuted.

The following genera are redescribed: Alloparasitus Berlese, 1920; Cosmolaelaps Berlese, 1903; Gymnolaelaps Berlese, 1916; Iphipts Berlese, 1882; Myrmonyssus Berlese, 1903; Neoberlesta Berlese, 1892; Ololaelaps Berlese, 1903; Pneumolaelaps Berlese, 1921; Stratiolaelaps Berlese, 1916 and Urozercon Berlese, 1906.
LIST OF REFERENCES


APPENDIX A.- SPECIMENS STUDIED

*Alloparasitus oblonga* (Halbert):
2 ♀♀, Berlese collection # 164/49-50, musco, Citta di Castello.

*Alphalaelaps aplodontiae* (Jellison):

*Androlaelaps casalis* (Berl.):
1 ♀, baled hay animal facility 5th floor, Bio.Sci OSU, Columbus, Ohio. 22.VII.76. Ide.
1 ♀, ex. horse manure Rldhaus, Fund, Sweden. DLW, DEJ cols. 18.IX.74.
7 ♀♀, ex. Martin mite colony OSU. Oct. 74. John Davis.
1 ♀, ex: nest of *Passer domesticus* Ypsilanti, Mich. 10.VI.69. W. Phillis.
1 ♀, ex: straw litter Dairy Barn O.S.U. Campus Columbus, Ohio. 4.II.71. D. Parsons 7 J. McGrath.
3 ♀♀, ex: Nest of *Agelatus xanthomus* La Parguera, P. R. Sep. 75. W. Post.
2 ♀♂, Berlese collection # 85/46, nelle case, Padova.

*Androlaelaps centrocarpus* (Berl.):
2 ♀♂, Berlese collection # 189/28, ex Topi, British Somaliland.

*Androlaelaps comatus* Berl.:
1 ♂, Berlese collection # 220/6, Africa orientale, Alluaud et Jeannell.

*Androlaelaps concurrens* (Berl.):
2 ♀♂, Berlese collection # 189/30-31, musco, 1915, Sardegna (Bosa).

*Androlaelaps fahrenholzi* (Berl.):
1 ♀, Berlese collection # 137/13, su *Mus sylvaticus*, Germania (= *Hypoasps* (*Haemolaelaps*) _fahrenholzi*)
4 ♀♂, ex: *Proechlmys guyamensis*. TRVL 4588,7797-10282.
2 ♀♂, ex: strw horse bedding, Reese Valley Chicken Creek Canyon, Utah 19.V.72. Knowlton.
1 ♀, ex: *Scalopus aquaticus*. Stoner's lawn Found alive. 8.X.73. Foryth.

*Androlaelaps glasgowi* (Ewing):

*Androlaelaps inosp* (Berl.):

*Androlaelaps marshalli* Berl.:
1 ♀, 1 ♂, Berlese collection # 193/21, ex *Mus coucha*, Zululand. M’fongosi, 1914.

*Ayersacarus* cf. *plumapilus*:

*Bisternalis hunteri* Baker, Delfinado-Baker & Ordaz:
Bisternalis mexicanus Baker, Delfinado-Baker & Ordaz:

Bisternalis rettenmeyeri Hunter:

Bisternalis trigonarum Baker, Flechtmann & Delfinado-Baker:
1 ♀ patratype, ex: Nest's Tetragona sp. (Geotrigona) nusum, P.A. Col. J. F. Camargo. 24-I-79.

Blaberolaelaps mathiesensis Costa:

Coleolaelaps agrestis (Berl.):
2 ♀♂, Berlese collection # 211/34, tipici, su Polyphylla fullo, Firenze.

Coleolaelaps sp.:

Cosmolaelaps alexandrini (Fox):
5 ♀♂, Guanlca Forest. Puerto Rico #2. June 1975?
1 ♀, Rd. 349 Km 5.3 Las Mesas Mayaguez, P.R. June 1975. J Maldonado.

Cosmolaelaps claviger (Berl.):
1 ♀, Berlese collection # 4/11, humus, Sicilia; 1 ♂ 130/34, detriti cortece pin?i, Firenze.
1 ♀, IA-829 ex litter under shore shrub, Pebble Beach, California. D.L.Wrensch coll. 29.IV.76.
2 ♀♂, 1 ♂, ex: coniferous litter Zoo. Inst. Florence Italy. DLW, colr. 29.X.74-7.
Cosmolaelaps cuneifer Michael (= Laelaps cuneifer Mich.):
1 Q, Berlese collection # 1Myrm./31-35, castiglio; 1 Q, 8Myrm./4, nidi di formiche, Donisthorpe, Inghilterra.

Cosmolaelaps cuneiformis (Berl.):
1 Q, Berlese collection # 220/34, tipico, Glava.

Cosmolaelaps ornata (Berl.):
2 QQ, Berlese collection # 5Myrm./11-12, tipici, formica, Portici.

Cosmolaelaps passali Hunter & Mollin:

Cosmolaelaps vacua (Mich.):
5 QQ, ex: Rd 349 Km 5.3 Las Mesas Mayaguez P.R. June, 1975. J. Maldonado.
23 QQ, ex: coniferous forest Sweden. A. Edler, colr. 15.V.74.
2 QQ, Berlese collection # 4Myrm./15 (= Laelaps scalpriger), nidi formiche, Portici.
1 Q, 1 Q, Berlese collection # 89/33-34 (Cosmolaelaps vacuus var. hastiger Berl.) tipici, nidi formiche, Firenze, Giardino R. Stazione.

Cyclothorax carcinicola von Frauenfeld:

Dinogamasus cf. inflatus LeVeque:

Dyscinetonyssus hystricosus Moss & Funk:
Echinonyssus isabellinus (Oudemans):

Echinonyssus talpae (Zemskaya):

Euandrolaelaps karawalewii (Berl.):
2 QQ, IA-829. ex litter under shore shrub, Pebble Beach, California. D.L. Wrensch coll. 29.IV.76.

Euvarroa sinhat Delfinado & Baker:

Gaeolaelaps aculeifer (Canestrini):
1 Q, ex: coniferous litter. Linkoping, Sweden. A. Edler, colr. 11.VI.74-1.
1 Q, ex: rotting compost Zool. Inst. Florence, Italy. DLW., colr. 28.X.74-1
1 Dn, 1 Pn, ex: soil & Dahlia plant?: at N. Y. Lot. 60-253. 2.IX.59. L. Walder.
1 O, ex: compost, Oslo, Norway. H. P. Leinaas, colr. 5.XI.74-N
Gaeolaelaps queenslandicus (Womersley):
7 QQ, Brazil, Sao Paulo Piracicaba, Pine Plantation at Tupi (14 Km from town) ex: grass piled deep. 2.II.1978. Col. D. E. Johnston. 2.II.78-5.
2 QQ, Brazil, Sao Paulo Eucalyptus Forest at Rio Claro, 35 Km from Piracicaba ex: bamboo litter. 3.II.1978. Col. D. E. Johnston.

Gaeolaelaps lubrica (Voigt & Oudemans):
1 Q, 2.XI.74-1 ex leaf litter; Boboli Gardens; Florence. DLW coll.
1 C', ex: coniferous forest Linkoping, Sweden A. Edler colr. 11.VI.74-1.
1 C', 1 Dn, ex: soil attached to grass roots. Sweden (Sk). A. Edler colr. 15.VI.73.
1 Pn, ex: soil cores. Ecological Station Stensoffa, Sweden. DEJ & DLW. colr. 5.IX.74-3.

Gaeolaelaps nollii Karg:

Gaeolaelaps cf. praesternalis (Willmann):
1 Q, ex: soil cores Ecological Station Stensoff, Sweden. DLW, DEJ, LL colr. 5.IX.1974-3.
3 QQ, Brazil, Sao Paulo Piracicaba, Pine Plantation at Tupi (14 km from town) ex: grass piled deep. 2.II.1978. Col D. E. Johnston.
1 Q, ex: leaf litter, soil mixture; Zoo. Inst. Flo. DLW coll.

Gaeolaelaps sp:
6 QQ, 1 C', ex: Potting material with Lily bulb OARDC Ohio. 17.XI.75 & 21.IV.76. R.Lindquist.
1 QQ, Macdonald College-Ste Anne de Bellevue Quebec. 15.VI.1961. G.D. Sharma coll.
6 QQ, 1 C', 2.XI.74-1 ex leaf litter; Boboli Gardens, Florence.
DLW coll.

Gecarcinolelaps cancer (Pearse) n. comb.:
   6 ♀♀, 20 ♂♂, 1 Dn, 31 Pn, 4 Lv, ex" branchial chamber" of
   eggs, 2 Nymphs, ex: Gecarcinus lateralis Freminville. Tortugas,

Gromphadorholaelaps schaefferi Till:
   10 ♀♀, 1 ♂, 1 nymph, Al 3448. Ohio, Franklin Co. OSU. ex lab

Gymnolaelaps canestrini (Berl.):
   1 ♀, Berlese collection # 221/31, libero nell'humus, spalato;
   4Myrm./45, nidi formichi, Portici.
Gymnolaelaps myrmecophila (Berl.):
   1 ♂, 1 ♀, Berlese collection # 4Myrm./36-40, tipici, nidi
   formica, Portici.

Haemogamasus hirsutus Berl.:
Haemogamasus pontiger (Berl.):
   2 ♀♀, ex: straw Liquor Jacktes. Portugal: at Charleston, S.C. 57-
   7030. G. A. Johnson.
   Walden colr. Lot 59-3193.
   colr. Lot 59-19083.

Holostaspis montana (Berl.):
   1 ♀, ex. ant's nest. Ilstorp Sweden. A. Edler colr. 20.X.74-1.

Hunteria brasiliensis Delfinado-Baker, Baker & Flechtmann:
   1 ♀ holotype, ex: Melipona compressipes fasciculata. S. Luis,
Hypoaspis ptnguts (Berl.):
2 QQ, Berlese collection # 165/19, tiptco, su Coleottero lamellicorne. Rio Quarto, Cordova, Argentina.

Hypoaspis terrestris Leonard:
1 Q, Berlese collection # 106/29, tiptco, ex: Copris hispanus, Rosignano, Pisa.

Hypoaspis spp:
2 QQ, on beetle, Calicoan Isl., Samar. Feb., 1945. Coll. by Malaria unit 75. Lot. 45-16063.
7 QQ, 1 C, Chile Coquimbo Prov., Parque Nac. Fray Jorge ex: relict Valdivian forest; elev. 580 m. 5-1-1985. N. I. Platnick coll.

Iphtopsis mirabilis Berl.:
1 Q, Berlese collection # 4/9-10, su Julus oenologus, Firenze.

Iphitolaelaps myriapoda Womersley:
1 Q holotype, 1 C allotype, on millipede. Mr. Lamnigton. 6 Dec. 1948. Det. H. Womersley

Jacobsonia berlesei n. sp.:
12 Q, 1 C, 2 Dn, 3 Pn, 1 Lv AL 3662. Indonesia: Java. Pangandaran Natural Preserve. ex millipede. D. E. Johnston & D. L. Wrensch colls. 11.IV.88-3

Jacobsonia minor Berl.:
1 Q, 1 C, Berlese collection #130/14, Wonosobo-Giava, Jacobsoni, 2^ spedizione.

Jacobsonia submollis Berl.:
1 Q, Berlese collection # 96/11, su Scolopendra wijnhoopsbai, Giava meridionale.

Julolaelaps dispar Berl.:
1 Q, 1 C, Berlese collection # 160/36,49, su Julide I, Gorici-Som alla italiana, Paoli, 1913.

Julolaelaps luctator Berl.:
1 Q, Berlese collection # 160/39, sul piu grosso Julide, Somalia Italiana, Paoli, 1913.
Julolaelaps sp.:  
2 ♂♂, ex: millipede or centipede Philippines.

Laelaspis astronoma (Koch):  
1 ♀, ex: Crane Hollow. 24.V.75. Chandler coll.  
1 ♀, 1 ♂, ex: Leaf litter & humus, decid. forest. Salt Pte. St. Marysch Parish, LA. DEJ coll.

Laelaspis australis Seltnick:  

Laelaspis brevichelis Hunter:  

Laelaspis dubitatus Hunter:  
1 ♀, 1 ♂, ex: Peromyscus nest. Patuxent Wildlife Refuge.  

Laelaspis heselhausi Oudemans:  

Laelaspis sp:  
1 ♀, Fir & Apen, Logan Canyon, Utah. 15.VIII.75. Knowlton coll.  

Laelaspoides ordwayae Eickwort:  
1 Pn, 1 ♀ paratype, Lawrence, Kansas State Property 26 June 1959. E. Ordway. ex-nest Angochlorella perstilis. 64-0207-2e, 64-0208-2a.  

1 Q paratype, Lawrence, Kansas Nat. Hist. Reserve. 8 June 1962. E. Ordway. ex-nest Angochlorella striata. 64-0215-1d.


Leptolaelaps elegans Berl.:
1 Q, Berlese collection # 189/34, tipico, moss, Transvaal.

Leptolaelaps lawrenceti Evans:

Leptolaelaps sp.:
3 Q,Q, Al 3170. Chile, Malleco Prov. 15 km W. Victoria. ex wet forest; elev. 365 m. 26-I-1985. N. I. Platnick & O. F. Franke colls. original # 1-26-1; litter & moss.

1 Q, 1 O, Chile Osorno Prov. 10 km E. Bahia Mansa, ex: disturbed forest, elev. 15 m. 30-I-1985. N. I. Platnick & O. F. Franke colls.


3 Q,Q, Chile Osorno Prov. 1 km E Termas de Puyehue, ex: wet Forest (305 m). 31-I-1985. N. I. Platnick & O. F. Franke colls.

Ljunghia hoggi Domrow:

2 Q,Q, 1 O, South Australia, ex: Aganippe subtristis
Ijunghia puUeini Womersley:

Ljunghia rainbow Domrow:

Ljunghia solenocosmlae Oudemans:
1 Lv, 3 Nymphs, ex: Selenocosma javanensis Armhemia (Dell). III.1931. Van der Naeer Mohr legit.

Melittiphis alvearius (Berl.):
1 Q, D. Morash 21.VI.85. Furmington Camb. Co. N.S.

Melittiphisoides apiarium Delfinado-Baker, Baker & Flechtmann:

Mesolaelaps anomalus Hirst:

Myonyssus dubini:
2 QQ, Mile 20 Nabesna Rd., Alaska. 27.IX.73. R.L. Rausch, from: Microtus miurus.
Myrmolaelaps equitans Tragard:
1 Q Junction. 28.VI.05. Umfolzi, Zululand.

Myrmonyssus (Laelaspulus) acuminatus Berl.:
1 Q, 1 Q, Berlese collection # 6Myrm./3-4, nidi di formiche, Portici.

Myrmonyssus antennophoroides Berl.:
1 Q, Berlese collection # 1 Myrm./16-17, Camponotus aethiops, Bevagna.

Myrmonyssus brachiatus Berl.:
2 QQ, Berlese collection # 6Myrm./1-2, nidi di formiche, Portici.

Myrmonyssus clarus Hunter & Hunter:

Myrmonyssus diplogenius Berl.:
2 QQ, Berlese collection # 5/47-48, nidi formiche, Portici.

Myrmonyssus spinosus Hunter & Hunter:

Myrmonyssus titan Berl.:
1 Q, Berlese collection # 170/5, Africa Orientale, Alluaud et Jeannel.

Myrmozercon brevipes Berl.:
2 QQ, 1 Q, Berlese collection # 5Myrm./40, 42-43, nidi formiche, Bevagna.

Narceolaelaps annularis Kethley:
1 Q, 1 Q, paratype, ex: Narceus americanus. Ash Cave, Hocking Co. Ohio 30.VI.75.

Narceolaelaps burdicki Kethley:

Narceolaelaps gordanus Kethley:
2 QQ paratype, ex: millipede Narceus gordanus Jacksonville,

*Neoberlesia equitans* Berl.:

1 ♀, Berlese collection # 6Myrm./10, tipico, nidi formica, Portici; 1 ♂, # 1Myrm./37, formiche, Portici.

*Neohypoaspis ampliseta* Delphinado, Baker & Roubik:

4 ♀♀, 1 ♂, 2 Pn, 2 Lv, Barro Colorado Isl. Panama Canal Zone. IX.76. Coll. S. Buchmann, from: *Trigona* nest.

*Neohypoaspis* sp.:

4 ♀♀, 1 ♂, 3 Pn, 1 Lv, Barro Colorado Is., Panama Canal Zone. IX.76. Coll. S. Buchmann, from: *Trigona* nest. det. E. E. Lindquist.

*Ololaelaps formidabilis* (Berl.):

1 ♂, 1 ♀, Berlese collection # 145/30-31, Giava; 1 ♂, 145/29, Giava, Jacobson.

*Ololaelaps hemisphaera* (Berl.):

1 ♀, Berlese collection # 179/2, Columbia, N. A.

*Ololaelaps holaspis* (Oud.):

1 ♀, Berlese collection # 209/8, humus, Maccarese, Roma.

*Ololaelaps placentula* (Berl.):


1 ♀, berlese collection # 17/7 (= *O. confinis*), Norvegia, Thor; 1 ♂, 1 ♀, 43/26, musco Vallombrosa.

*Ololaelaps platenstis* (Berl.):

1 ♀, Berlese collection # 168/20, La Plata, Bruck.

*Ololaelaps stenensis* (Berl.):

1 ♂, 1 ♀, Berlese collection # 170/14, foglie marce, Castions di strada (Udine).

*Ololaelaps veneta* (Berl.):

1 ♂, 1 ♀, Berlese collection # 170/14, foglie marce, Castions di Strada (Udine); 15.16, musco Veneto, tipico del *L. tumidulus*. 
Ololaelaps sp.:  

Pneumolaelaps bombicolens (Can.):  
7 QQ, ex Bombus. Sweden.  
1 Q, Berlese collection # 202/37, Bombus terrestris, Parigi, Michael.

Pneumolaelaps heterosetosa (Hirsch.):  

Pneumolaelaps heyi (Karg):  
8 QQ, ex: leaf compost on farm Fjehle (Sk.) Sweden DEJ, LL collr. 9.X.74-12.  
1 Q, ex: horse manure, Ridhaus,Lund-Sweden. DEJ & DLW. 18.IX. 1974

Pseudolaelaps doderot Berl.:  
1 Q, in soil & Myrtus, etc. Italy: at Boston Sept. 25, 1955. E. C. Hodson coll. det: DEJ.  
1 Q, Robledal, Beunza Navarra, Spain. CA-0218. L. Moraza coll. det: L. Moraza.  
1 Q, 2.XI-74-1. ex leaf litter; Boboli Gardens; Florence. DLW coll. 1 Q, Berlese collection # 83/23, musco, Genova, Dodero.

Pseudolaelaps gamaselloides Berl.:  
2 QQ, Berlese collection # 202/40, cortecce, Boboli, Firenze.

Pseudolaelaps paulseni (Berl.):  
2 QQ, Berlese collection # 99/19, 99/30, musco, Palermo.

Pseudoparasitus centralis (Berl.):  
2 QQ, Prado Biguezal, NA Spain. L. Moraza coll. 27.IV.82. det. L. Moraza.
1 Q, 1 Q, Berlese collection # 202/44, cortecce pini, Firenze. 
Pseudoparasitus (Praeparasitus) collarts Berl.:
2 Q, Q, Berlese collection # 206/11-12, tipico, Africa orientale.
Pseudoparasitus dentatus (Halbert):
Pseudoparasitus domroui Hunter:
1 Q, ex. litter. Rd. 106. Km. 1.4 Mayaguez. P.R. Feb. 77. Maldonado coll. 
Pseudoparasitus major Berl.:
1 Q, Berlese collection # 9Myrm./9, nidi di Acromyrmex lundt, La Plata, Bruck. 
Pseudoparasitus meridionalis (Can.):
1 Q, Berlese collection # 5/49, Bertipaglia (Padova); 1 Q, 5/49 Bertipaglia (Padova); 1 Q, 22/47, serre calde, Cascene, L. meridionalis? 
Pseudoparasitus obsoletus Berl.:
1 Q, Berlese collection # 181/39, Columbia, N. A. 
Pseudoparasitus ovulum Berl.:
1 Q, Berlese collection # 206/5, tipico, Columbia (N.A.); 1 Q, 206/8-9, humus, 1916, Columbia (N.A.). 
Pseudoparasitus (Pseudopachys) parasitzans Berl.:
1 Q, Berlese collection # 181/43, tipico, su Talpa europaea, Padova. 
Pseudoparasitus puellus Berl.:
1 Q, Berlese collection # 181/36, Olavarria, Buenos Aires, Bruck. 
Pseudoparasitus spathulatus Berl.:
1 Q, Berlese collection # 157/31, tipico, Sardegna-moss (1915). 
Pseudoparasitus tenellus Berl.:
1 Q, Berlese collection # 92/17, musco, Palermo; 1 Q, 184/2 musco Sardegna (Iglesias). 
Pseudoparasitus sp.: 
1 Q, Texas, Garza Co. 5 ml E. Justiceburg 2300'elev. 8.IV.78. 
1 Q, Texas, Tom Gree Co. 10.3 ml S. San Angelo. 8.VIII.79. 
1 Q, Brazil Sao Paulo. ESALQ, Piracicaba. ex. pilled grass clipping, Park. 24.III.78. DEJ coll. 
1 Q, ex. nest(s) of Pelecanus occidentalis. Pelican Isl. C. Christi
Scissuralaelaps novaguineae Womersley:
2 QQ, ex: millipede or centipede. Philippines.

Scolopendracarus brevipilis Evans:
3 QQ, ex: centipede. Madam, Davae Prov. Mindanao,

Stevelus amiculus Hunter:
1 Q holotype, Panama Canal Zone, Barro Colorado Is. June 13,
1956. C.W. & M.E. Rettenmeyer. on and in stingless bee cells.

Strattolaelaps cardiophora Berl. (= Hypoaspis (S.) cardiophorus Berl.):
1 Q, Berlese collection # 9Myrm./17, tipico, nidi Acromyrmex
lundl, La Plata, Bruck.

Strattolaelaps egenus (Berl.):
1 Q, Berlese collection # 189/41, tipico, Mus coucha M'fongosi,
Zululand.

Strattolaelaps miles (Berl.):
1 Q, 1 Q, Berlese collection # 176/9, nidi di Arvicola arvalis,
Ferraro, 1916; 85/49 fienlli, Padova.
4 QQ, Brazil Sao Paulo, ESALQ, Piracicaba, second growth
natural forest. ex. litter & humus. 2.III.1978. DEJ coll.
1 Q, 1 Q, on Gladiolus corms. Orizaba, V.C. Mex: at Laredo.
Apr.7, 1945. H. R. Cary col. Laredo 36158. Lot. 45-6541,
45-6542.
1 Q, in nest of Microtus ochrogaster Urbana-III. Apr.13-1939.
P. C. Stone. Lot 40-8270.
1 Dn, IA-208. Ex straw 9and some soll) in pig yard 3 mt. South

Tropilaelaps clareae Delfinado:
2 QQ paratype, Host: field rat. Mataas-na-Kahog Lipa,
Varroa jacobsoni Oudemans:

Urozercon paradoxus Berl.:
  1 ♂, 1 ♀, Berlese collection # 7Myrm./17, tipico, termitofilo, Silvestri.

Urozercon cf. paradoxus Berl.:
APPENDIX B.- LIST OF CHARACTERS

<table>
<thead>
<tr>
<th>Character</th>
<th>Code</th>
<th>Example</th>
<th>Code</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-4. Tectum:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. trifurcate</td>
<td>1000</td>
<td><em>Pseudolaelaps</em></td>
<td>1000</td>
<td><em>Gaeolaelaps</em></td>
</tr>
<tr>
<td>2. denticulate</td>
<td>1100</td>
<td><em>Laelaps</em></td>
<td>1100</td>
<td><em>Haemogamasus</em></td>
</tr>
<tr>
<td>3. smooth</td>
<td>1110</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. fimbriate</td>
<td>1101</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Subcapitular setae hyp 3:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>present</td>
<td>0</td>
<td><em>Gaeolaelaps</em></td>
<td>0</td>
<td><em>Varroa</em></td>
</tr>
<tr>
<td>absent</td>
<td>1</td>
<td><em>Laelaps</em></td>
<td></td>
<td><em>Haemogamasus</em></td>
</tr>
<tr>
<td>6-8. Number of rows of deutosternal denticles:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. 6-7 rows</td>
<td>000</td>
<td><em>Gaeolaelaps</em></td>
<td>000</td>
<td><em>Varroa</em></td>
</tr>
<tr>
<td>7. less than 6 rows</td>
<td>110</td>
<td><em>Laelaps</em></td>
<td>110</td>
<td><em>Haemogamasus</em></td>
</tr>
<tr>
<td>8. more than 7 rows</td>
<td>101</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Number of deutosternal denticles:</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>multidenticulate</td>
<td>0</td>
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<tr>
<td>1-3 denticles</td>
<td>1</td>
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<tr>
<td>10. Tritosternum:</td>
<td></td>
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<tr>
<td>long, bifid</td>
<td>0</td>
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<td></td>
</tr>
<tr>
<td>short, laciniae</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>reduced</td>
<td></td>
<td></td>
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<tr>
<td>11. Hypostomal processes:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>normal, fimbriate</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>reduced</td>
<td>1</td>
<td></td>
<td></td>
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<tr>
<td>12-14. Length of corniculi:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. not longer than palp femur</td>
<td>000</td>
<td><em>Pseudolaelaps</em></td>
<td>000</td>
<td><em>Gaeolaelaps</em></td>
</tr>
<tr>
<td>13. longer than palp femur</td>
<td>110</td>
<td><em>Laelaps</em></td>
<td>110</td>
<td><em>Haemogamasus</em></td>
</tr>
<tr>
<td>14. one-half palp femur</td>
<td>101</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15. Palpal claw:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>with 3 tines</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>with 2 tines</td>
<td>1</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>16. Size of palp claw tines:</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>similar in length</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>basal tine reduced</td>
<td>1</td>
<td></td>
<td></td>
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<tr>
<td>17. Fixed digit female chelicera:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>normally developed</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>reduced or absent</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18. Number of teeth on movable digit female chelicera:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>two teeth</td>
<td>0</td>
<td></td>
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<tr>
<td>one or none</td>
<td>1</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>19. Podonotal seta z4:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>normal, setiform</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>spine-like or blunt-like</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>20. Podonotal seta z2:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>present</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>absent</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21. Podonotal seta z3:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>present</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>absent</td>
<td>1</td>
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147
<table>
<thead>
<tr>
<th></th>
<th>Description</th>
<th>Present</th>
<th>Absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>22. Podonotal seta s6:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
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<tr>
<td></td>
<td>Absent</td>
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<tr>
<td>23. Podonotal seta r6:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
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<td></td>
<td>Absent</td>
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<tr>
<td>24. Opisthonal seta J2:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
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<td>25. Opisthonal seta J3:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
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<tr>
<td></td>
<td>Absent</td>
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<tr>
<td>26. Opisthonal seta J4:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td></td>
<td></td>
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<tr>
<td>27. Opisthonal seta Z1:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td></td>
<td></td>
</tr>
<tr>
<td>28. Opisthonal seta Z2:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td></td>
<td></td>
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<tr>
<td>29. Opisthonal seta Z3:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
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<td></td>
</tr>
<tr>
<td>30. Unpaired accessory setae between J series:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td></td>
<td></td>
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<tr>
<td>31. Additional setae (px's):</td>
<td>Present</td>
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<td>1</td>
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<tr>
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<td>Absent</td>
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</tr>
<tr>
<td>32. Opisthonal seta S5 on the shield:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td></td>
<td></td>
</tr>
<tr>
<td>33-35. Length peritreme:</td>
<td>Present</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td></td>
<td></td>
</tr>
<tr>
<td>33. Long (i.e., reaching coxa I)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>34. Short (i.e., reaching coxae III-II)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35. Absent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>36. Female peritrematal shield:</td>
<td>Not fused to exopodal IV</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Fused to exopodal IV</td>
<td></td>
<td></td>
</tr>
<tr>
<td>37. Sternal seta st1:</td>
<td>Present on sternal shield</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Present off sternal shield</td>
<td></td>
<td></td>
</tr>
<tr>
<td>38-42. Sternal seta st4:</td>
<td>Present on sternal shield</td>
<td>00000</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Present on metasternal shield</td>
<td>10000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Present on soft cuticle</td>
<td>11100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Present on endopodal</td>
<td>11101</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td>11110</td>
<td></td>
</tr>
<tr>
<td>43. Genital seta:</td>
<td>On the shield</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Off the shield</td>
<td></td>
<td></td>
</tr>
<tr>
<td>44. Female anal shield:</td>
<td>Fused with ventral and genital shield</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Free</td>
<td></td>
<td></td>
</tr>
<tr>
<td>45. Shape female anal shield:</td>
<td>Subtriangular, subcircular or suboval</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Other shape (kidney, crescent, bowl shaped)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Seta al2 Ge I:</td>
<td></td>
<td>Seta pv1 Ge IV:</td>
</tr>
<tr>
<td>---</td>
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### APPENDIX C. - DATA MATRIX

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APPENDIX D.- REDESCRIPTION OF THE BERLESE'S GENERA

**ALLOPARASITUS** Berlese

*Hypoaspis (Alloparasitus)* Berlese, 1920  
*Halbertia* Hull in Turk and Turk, 1952

type-species: *Laelaps (Hypoaspis) oblongus* Halbert, 1915

Chelicerae chelate-dentate; movable digit with 2 teeth, fixed-digit with 4 to 6 teeth; corona present. Pilus dentillis and dorsal seta short, setiform. Tectum wide, with a serrate or denticulate anterior margin. Subcapitulum with an elongated base; setae hyp. 3 longer than hyp. 1, hyp. 2 or sc; deutosternum with 6 transverse rows, usually with 3-6 denticles per row Hypostomal process fimbriate. Corniculi short, no longer than palp-femur. Supralabral process present. Palp chaetotaxy normal (2-5-6-14-15); two-tined palp-claw.

Dorsum: Dorsal shield covers the entire body, with 39 pairs of smooth, simple setae and 18 pairs of pores; all setae, with the exception of z1 similar in length; setae z2 and s6 absent; two pairs of accessory (px) setae present.
Venter: Tritosternum normal, bipartite. Presternal shields present. Large sternal shield, straight anterior and posterior margins, with 3 pairs of setae and 2 pairs of pores; st₄ off the shield, inserted on soft cuticle. Genito-ventral shield wide, expanded behind coxae IV, posterior margin almost straight and extends close to the anal shield, with 1 to 3 pairs of setae (the posterior pair may be situated slightly off the shield). Metadodal plates present (A. oblongus, A. pycnosis) or absent (A. tribina). Anal shield triangular, with a straight anterior margin; postanal seta slightly longer than paranal setae. Opisthogastric region with 5 or 6 pairs of setae, one or two pairs between genito-ventral and anal shields. Peritreme extends to coxa II or to middle of coxa I; peritrematal shield free posteriorly and extends beyond level of coxa IV.

Legs robust with well developed claws. Normal leg chaetotaxy, with the exception of genu IV which has 8 setae (al₂ is missing). Tarsus I with 42-46 setae, normally 46 (5-29/8-4).

Male and inmatures stages: unknown.

In this genus there are the following species:

A. eugenitalis (Karg, 1978)  A. femorata (Karg, 1978)
A. oblonga (Halbert, 1915)   A. pycnosis (Karg, 1978)
A. subterranea (Willmann, 1952)  A. tribina (Karg, 1978)
The species of *Alloparasitus* live in moss, under the bark of rotting trees and in rodents' nests. They have been recorded from Europe and South America.

This genus is closely related to *Pseudoparasitus*. It differs from *Pseudoparasitus* in the presence of no more than 3 pairs of genito-ventral setae, presence of at least one pair of setae between the genito-ventral and anal shields, and palp-claw is 2-tined.

**COSMOLAELAPS** Berlese

*Hypoasps (Cosmolaelaps)* Berlese, 1903.

type-species: *Laelaps claviger* Berlese, 1883

Chelicerae chelate-dentate, digits similar in length; movable digit with 2 teeth, fixed-digit with variable number of small teeth, usually 4-5 or 9. Pilus dentilis short. Tectum denticulate or finely serrate. Subcapitulum normal in shape, with 4 pairs of setae; hyp.3 long, at least two times longer than hyp.1; deutosternum with 5 or 6 transverse rows of denticles, with variable number of denticles per row. Hypostomal process fringed. Corniculi short, no longer than palp-femur, parallel. Supralabral process present. Palp chaetotaxy normal (2-5-6-14-15); two-tined palp-claw.
Dorsum: Dorsal shield covers the entire dorsum, with 37 to 39 pairs of setae, 2 to 14 unpaired supplementary setae and 12 pairs of pores. Dorsal setae spatulate, cuneiform, scimitar-like, lanceolate or with bifid tips; dorsal setae similar in length, in some species the marginal setae (r serie) are smaller.

Venter: Presternal plates present or absent. Sternal shield wider than longer, anterior margin deeply notched, straight or weakly concave, with 3 pairs of setae and two pairs of lyrifissures; st4 and associated pore off the shield. Genito-ventral shield large or small, narrow or expanded from the sides, with or without parallel lateral margins and sometimes set very close to the anal shield; with one pair of genital setae, sometimes placed at the lateral margins of the shield (it looks like the seta is off the shield). One or two pairs of metapodal plates present, one pair is smaller than the other. Anal shield subtriangular, with three setae; postanal seta slightly longer than paranal setae. Opisthogastric region with variable number of setae, from 4 to 18 pairs. Peritreme extends to coxa I; peritrematal shield narrow, sometimes evident only around the stigmata, posteriorly fused to endopodal IV.

Legs long and robust or short and stumpy. Sometimes, femora of legs II and IV of female and male with 2 ventral tubercles, or femur II of male with one ventral spine. Femur leg IV with \( C. \ vacua \) or without
(C. acuta) protruding expanded setae. Legs with normal chaetotaxy. Tarsus I on type-species (C. claviger) with 48 setae (5-28/10-5).

Male: With entire holoventral shield or with a free anal shield (C. neocuneifer). Holoventral shield is sometimes drastically narrowed in front of the anal part (C. cuneifer, C. acuta). Spermatodactyl is completely fused with the movable digit (C. acuta) or raised above the movable digit (C. claviger).

Table 5 shows the species included in *Cosmolaelaps*.

Table 5.- List of species included in *Cosmolaelaps*

<table>
<thead>
<tr>
<th>Species</th>
<th>Author and Year</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. alexandrina</em></td>
<td>Fox, 1946</td>
</tr>
<tr>
<td><em>C. acipha</em></td>
<td>Karg, 1987</td>
</tr>
<tr>
<td><em>C. anserina</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. bengalensis</em></td>
<td>Bhattacharya, 1968</td>
</tr>
<tr>
<td><em>C. bicuspisetosa</em></td>
<td>Willman, 1953</td>
</tr>
<tr>
<td><em>C. brevisstilis</em></td>
<td>Karg, 1985</td>
</tr>
<tr>
<td><em>C. canestrini</em></td>
<td>Berlese, 1903</td>
</tr>
<tr>
<td><em>C. cardilophora</em></td>
<td>Berlese, 1917</td>
</tr>
<tr>
<td><em>C. carvalhoi</em></td>
<td>Aswegen &amp; Loots, 1970</td>
</tr>
<tr>
<td><em>C. cassoidea</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. claviger</em></td>
<td>Berlese, 1883</td>
</tr>
<tr>
<td><em>C. cuneifer</em></td>
<td>Michael, 1891</td>
</tr>
<tr>
<td><em>C. cubaensi</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. cuneiformis</em></td>
<td>Berlese</td>
</tr>
<tr>
<td><em>C. digrediens</em></td>
<td>Berlese, 1921</td>
</tr>
<tr>
<td><em>C. furcatoides</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. fusca</em></td>
<td>Berlese, 1917</td>
</tr>
<tr>
<td><em>C. guttulata</em></td>
<td>Karg, 1978</td>
</tr>
<tr>
<td><em>C. laepoauris</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. lawrencei</em></td>
<td>Aswegen &amp; Loots, 1970</td>
</tr>
<tr>
<td><em>C. lingua</em></td>
<td>Karg, 1987</td>
</tr>
<tr>
<td><em>C. longicostalis</em></td>
<td>Karg, 1978</td>
</tr>
<tr>
<td><em>C. longodigit</em></td>
<td>Karg, 1979</td>
</tr>
<tr>
<td><em>C. longogenitalis</em></td>
<td>Karg, 1978</td>
</tr>
<tr>
<td><em>C. machadot</em></td>
<td>Aswegen &amp; Loots, 1970</td>
</tr>
<tr>
<td><em>C. mediocupis</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. multidentata</em></td>
<td>Aswegen &amp; Loots, 1970</td>
</tr>
<tr>
<td><em>C. nanoseta</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. neocuneifer</em></td>
<td>Evans &amp; Till, 1966</td>
</tr>
<tr>
<td><em>C. ornata</em></td>
<td>Berlese, 1903</td>
</tr>
<tr>
<td><em>C. ornatissima</em></td>
<td>Aswegen &amp; Loots, 1970</td>
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<tr>
<td><em>C. pannicula</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. passalis</em></td>
<td>Hunter &amp; Mollin, 1964</td>
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<tr>
<td><em>C. penicillata</em></td>
<td>Karg, 1979</td>
</tr>
<tr>
<td><em>C. pugiocupis</em></td>
<td>Karg, 1981</td>
</tr>
<tr>
<td><em>C. recondita</em></td>
<td>Berlese, 1905</td>
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<tr>
<td><em>C. rectangularis</em></td>
<td>Sheals, 1962</td>
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<tr>
<td><em>C. robusta</em></td>
<td>Berlese, 1905</td>
</tr>
<tr>
<td><em>C. scimitus</em></td>
<td>Womersley, 1956</td>
</tr>
<tr>
<td><em>C. serrata</em></td>
<td>Tragardh, 1952</td>
</tr>
<tr>
<td><em>C. simplex</em></td>
<td>Berlese, 1921</td>
</tr>
<tr>
<td><em>C. transvaalenstis</em></td>
<td>Ryke, 1963</td>
</tr>
<tr>
<td><em>C. ungert</em></td>
<td>Karg, 1985</td>
</tr>
<tr>
<td><em>C. vacua</em></td>
<td>Michael, 1891</td>
</tr>
<tr>
<td><em>C. weeverst</em></td>
<td>Oudemans, 1926</td>
</tr>
</tbody>
</table>
Cosmolaelaps species live in ants' nests, in the soil, in forest litter, mosses, under trees or rodents' nests. The genus shows to be cosmopolitan.

This genus is closely related to Strattolaelaps. They differ, among other characters, in the length of the corniculi and chelae of the chelicerae (shorter in Cosmolaelaps) and in the number of teeth on the movable digit of the female chelicerae (only two in Cosmolaelaps).

GYMNOLAELAPS Berlese

Gynolaelaps Berlese, 1916  
_Laelaps_ Hull, 1952; Bregetova, 1977  
_Austrogamasus_ Womersley, 1942; Bregetova, 1977

type-species: _Laelaps myrmecophilus_ Berlese, 1892.

Hunter and Costa, 1971 and Bregetova, 1977 give descriptions of Gymnolaelaps. The former authors treat Gymnolaelaps as a genus on the basis of host-association and morphological characters. On the other hand Bregetova, 1977 considers it as a subgenus of _Hypoaspts_. This study agrees with Hunter and Costa, 1971 and it treats Gymnolaelaps as a genus of Laelapidae.
The following is added to the description given by Bregetova, 1977: podonotal setae z2 absent; with 3-9 unpaired accessory setae between the J series; setae px’s usually present. Opistthonotal setae Z3 missing; seta Z5 subequal in length to J5. Deustosternum with six transverse rows of 2-5 fine teeth. Post anal seta shorter than paranal setae. Tarsus I with 44 setae (5-27/8-4). Sternal seta four (st4) and associated pore on soft cuticle (G. myrmecophila) or over endopodal shields (G. myrmophila, Evans and Till, 1966). Genital shield large, often extending to the anal shield; usually with 1 (G. myrmecophila), 2, 3 (G. myrmophila) or 4 pairs (G. missouriensis, Hennessey and Farrier, 1988) of setae; the second to third pair of setae inserted on the edge of the shield. One pair of setae between the genital and anal shields, and several pairs (9-13) of opisthogastric setae present. Legs: setae pl2 on genu IV, ad2 on tibia II, ad2 on tibia III and ad2 on tibia IV absent.

The following species have been previously included in Gymnolaelaps:

G. annectans Womersley, 1956
G. australicus Womersley, 1956
G. bisetus Aswegen & Loots, 1970
G. canestrinit Berlese, 1903
G. hospes (Berlese, 1921)
G. krantzi Hunter, 1967
G. laevis (Michael, 1891)
G. longisetus Aswegen & Loots, 1970
G. margopillus (Hunter, 1966)
G. missouriensis (Ewing, 1909)
G. myrmecophila (Berlese, 1892)

G. myrmohila (Michael, 1891)
G. nidicorva (Evans & Till, 1966)

G. pinnae (Karg, 1987)
G. planus Womersley, 1956
G. rentculus (Karg, 1981)
G. shealsi Hunter & Costa, 1971
G. unospinosus (Karg, 1978)
G. victoriensis (Sheals, 1962)
Most of the *Gymnolaelaps* species have been found associated with ants and ant's nests and the genus appears to be cosmopolitan.

**IPHIOPSIS** Berlese

*Iphiopsis* Berlese, 1882

type-species: *Iphits mirabilis* Berlese, 1882

Keegan 1950 briefly describes *Iphiopsis* as mite parasites and commensals of myriapods with tarsus I without claws, tarsi II-IV with claws and stigmata are almost without peritremes. Later, Evans, 1955 mentions that the type-species has not been found since Berlese's description, and he added to Keegan's description that the sternal and genital shields are well developed and the anal shield bears three setae; digits of the chelicerae are dentate and of equal size. Ryke, 1959, reviewing the hypoaspid mites associated with Myriapoda, mentions *Iphiopsis* as mites without claws on legs I, claws on legs II-IV normal and peritreme reduced.

Chelicerae chelate-dentate, digits equals in size; fixed digit bidentate. Tectum smooth. Subcapitulae setae hyp3 absent; deutrosternum with 6-7 rows of irregular and fine teeth. Hypostomal process reduced. Corniculi weakly sclerotized and long. Palp-claws two-tined.
Dorsum: Dorsal shield covers the entire dorsum, with ca. 39 pairs of simple, smooth setae. Podonotal setae s6 and r6 not on the dorsal shield.

Venter: Tritosternum normal, bifid with long lacinia. Presternal shields weakly developed. Sternal shield well sclerotized, bearing three pairs of setae and two pairs of lyrifissures; st4 inserted on soft cuticle. Endopodal shields between coxae fused with sternal shield. Genital shield small, rounded, with one pair of short and thin setae inserted on the edges of the shield. Opisthogastric region with three pairs of setae inserted laterally on soft cuticle. Anal shield elongated; paranal setae inserted at level of the posterior margin of the anal opening; post anal seta equal in length to the paranal setae. Peritreme reduced, it reaches coxae III.

Legs: Legs I with vestigial claws; tarsi II-IV normal. Ventral setae shorter and stronger than dorsal setae. Legs chaetotaxy as follow:

```
I   II   III   IV
Genua 1-2/1,2/1-1 1-2/1,2/1-1 1-2/1,2/1-1 1-2/1,2/1-1
```

Males and immatures: Unknown.

Only one species is known, *Iphtopsts mirabilis* Berlese, from *Julus oenologus*, Firenze and from *Julus vartus*, Padova.
Myrmonyssus Berlese, 1903

type-species: *Myrmonyssus diplogenius* Berlese, 1903; 1904.

Berlese, 1903 and 1904 briefly describe the genus and type-species. Later, Hunter and Hunter, 1963 give a list of the species included in *Myrmonyssus* and they describe two new species from USA.

Chelicerae long, thin and edentate (*M. diplogenius*); fixed digit on female shorter than the movable digit. Pilus dentilis and dorsal setae not seen, probably absent. Tectum smooth. Subcapitulum with hypostomal setae hyp3 missing; deutosternum with 6-7 transverse rows of several fine teeth. Hypostomal process reduced. Corniculi weakly sclerotized. Palps with normal chaetotaxy; two-tined palp-claw.

Dorsum: Dorsal shield covers almost the entire dorsum; with 26 pairs (*M. diplogenius*) to 35 (*M. spinosus*) or 38 (*M. clarus*) pairs of simple setae; some opisthonotal setae are spiny (Hunter and Hunter, 1963). Podonotal setae z1, z3, s6 and r6 missing; opisthonotal setae J4 and J5 absent, and seta S5 not inserted on the shield.
Venter: Tritosternum normal, bipartite. Pre-endopodal shields absent. Sternal shield well sclerotized, bearing three pairs of setae and two pairs of lyrifissures. Sternal setae st4 placed on soft cuticle \((M. \text{ diplobentus})\) or metasternal setae absent \((M. \text{ spinosus}, M. \text{ clarus},\) Hunter and Hunter, 1963). Endopodal plates between coxae III-IV present. Genito-ventral plate present; genital seta not on the shield \((M. \text{ diplobentus})\) or one pair of setae inserted on the edges of the shield \((M. \text{ spinosus}, M. \text{ clarus})\). The paragenital pore \((iv5)\) not seen. Opisthogastric region bearing eight pairs \((M. \text{ diplobentus})\) or 12 pairs \((M. \text{ clarus} \text{ and } M. \text{ spinosus})\) of simple setae. Anal shield subtriangular; postanal seta longer than paranal setae \((M. \text{ diplobentus})\) or off the same length \((M. \text{ clarus})\). Peritrematal shields short, extend to coxae III.

Leg chaetotaxy as follow:

Ge I = 1-2/1,2/1-1 in \(M. \text{ spinosus}\) and \(M. \text{ clarus}\)
Ge II = 1-2/1,2/1-1 in \(M. \text{ spinosus}\) and \(M. \text{ clarus}\)
Ge III = 1-2/1,2/1-1 in \(M. \text{ spinosus}\)
Ge IV = 1-2/1,2/1-1 in \(M. \text{ spinosus}\)

Tl I = 1-2/1,2/1-1 in \(M. \text{ clarus}\) and \(M. \text{ spinosus}\)
Tl II = 1-1/1,2/1-1 in \(M. \text{ clarus}\) and \(M. \text{ spinosus}\)
Tl III = 1-1/1,2/1-1 in \(M. \text{ clarus}\) and \(M. \text{ spinosus}\)
Tl IV = 1-1/1,2/1-1 in \(M. \text{ spinosus}\)

Males of \(M. \text{ acuminatus}\) Berlese are characterized by:
Chelicerae chelate edentate; spermatodactyl free, never completely fused with movable digit. Holoventral shield present; with one pair of
genital setae and six pairs of opisthogastric setae. Metapodal shields elongate. Peritremes extend anteriorly to coxae II; peritrematal shields free anteriorly and posteriorly.

The following species have been included in *Myrmonyssus* (Hunter and Hunter, 1963):

- *M. acuminatus* Berlese, 1903
- *M. brachytus* Berlese, 1903
- *M. chapmani* Baker & Strandtmann, 1948
- *M. diplogenius* Berlese, 1903
- *M. equalis* Banks, 1916
- *M. lingurticus* Vitzthum, 1931
- *M. scutellatus* Hull, 1923
- *M. titan* Berlese, 1916
- *M. antennophoroides* Berlese, 1904
- *M. claus* Hunter & Hunter, 1963
- *M. eidmanni* Sellnick, 1941
- *M. flexuosa* (Michael, 1891)
- *M. minor* Sellnick, 1941
- *M. spinosus* Hunter & Hunter, 1963

Berlese's species, *M. diplogenius*, *M. antennophoroides*, *M. titan*, *M. brachytus*, and *M. acuminatus*, were examined. *M. titan* differs from *M. diplogenius* mainly because the post anal and paranal setae are placed in a "line" at the same level, the anal shield is not obvious, and dorsal shield with fewer and simple setae.

*M. antennophoroides* is characterized by having strong, spine-like anal setae; trochanter and femur with short spine-like setae; it is more setose than *M. diplogenius* and *M. titan*, and tarsus I has 34 setae (4-19/6-5).

*M. brachytus* is the smallest with strong, short legs. The sternal shield is more rectangular than in the other species described by
Berlese: genital shield drop-shaped and narrow. The genital setae are off the shield. Anal shield is wider than long with simple setae.

*M. acuminatus* has narrow and longer peritremes than the other species; peritremes extend to base of coxae I on females and to coxae II on males. All legs with reduced claws. Dorsal setae are barbed.

The species included in *Myrmonyssus* have been found in association with ants and the genus is Cosmopolitan.

**NEOBERLESIA** Berlese

*Neoberlesta* Berlese, 1892.

type-species: *Neoberlesta equitans* Berlese, 1892

Female chelicerae with small digits, apparently edentate. Pilus dentillis and dorsal seta not seen (absent?). Tectum smooth. Gnathosoma elongated. Subcapitulum with normal chaetotaxy; setae short, subequal in length; deutosternum with six transverse rows of irregular and fine teeth. Hypostomal process reduced. Corniculi horn-like. Palp-claw two-tined; basal tine reduced.
Dorsum: Dorsal shield entire, with ca. 37 pairs of simple setae. Podonotal setae r5 not on the shield; additional setae on the opisthpronotum are present.

Venter: Pre-endopodal shields absent. Sternal shield well sclerotized, large, bearing four pairs of setae and three pairs of lyrifissures. Metapodal shield large. Genito-ventro-anal shield present, with seven pairs of ventral setae. Post anal setae absent. Opisthogastric region with several setae inserted on soft cuticle. Peritrematal shields extend anteriorly, close to paravertical setae; posteriorly fused with parapodal element of coxa IV.

Legs: Legs I long, two times longer than legs II. Femur IV of females with an antero-lateral spur, bearing a simple seta. All legs with reduced claws.


One species, Neoberlesia equitans, has been found associated with ants in Portici, Italy.
**OLOLAEAPS** Berlese

*Hypoaspis (Ololaelaps) Berlese, 1903.*


Type-species: *Hypoaspis venetus* Berlese, 1903


The following is added to the description given by Bregetova, 1977:
Dorsum with 14 pairs of pores; podonotum with 2 pairs of glands and 2 pairs of lyrifissures, and opisthonotum with 4 pairs of glands and 6 pairs of lyrifissures. An unpaired seta on the opisthonotum region may be present (*O. veneta, O. sellnickii*) or absent (*O. caucasicus*).

Hypostomal process fringed, bifid and curved in the female and not divided and straight in the male. Supralabral process present. Setae on gnathosoma similar in length.

Leg chaetotaxy normal, as follows:

<table>
<thead>
<tr>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femur</td>
<td>2-3/1,2/3-2</td>
<td>2-2/1,2/2-1</td>
<td>1-2/1,1/0-1</td>
</tr>
</tbody>
</table>
Genu  2-3/2,3/2-2  2-3/2,2/1-2  2-2/1,2/1-1  2-2/1,3/0-1
Tibia  2-3/2,3/1-2  2-2/1,2/1-2  2-1/1,2/1-1  2-1/1,3/1-2
Tarsus  6-28/8-6=48  3-3/3,1,3/2-3=18  18  18

Tarsus II-IV with ventral setae (av1-3, m, pv1-2) and some lateral setae (al1-3, pl1-3 on tarsus IV) thicker and spine-like. Rest of the legs setae are simple.

Karg, 1978 treats Ololaelaps as a subgenus of Pseudoparasitus. However, Bregetova and Koroleva, 1964; Evans and Till, 1966 and Bregetova, 1977 consider it as a valid genus. It is agreed that Ololaelaps is a valid genus within Laelapidae, that includes the following species:

- O. caucasicus Bregetova & Koreva, 1964
- O. hemisphaera (Berlese, 1916)
- O. holaspis (Oudemans, 1902)
- O. formidabilis (Berlese, 1913)
- O. paratasmanicus Ryke, 1962
- O. placentula (Berlese, 1887)
- O. sellnicki Bregetova & Koroleva, 1964
- O. tasmanicus (Womersley, 1956)

It was impossible to examine specimens of O. caucasicus and O. ussuriensis described by Bregetova and Koroleva, 1964 from USSR. However, the descriptions given by the authors show slight differences with O. platensis Berlese and O. placentula (Berlese)
respectively so that they might be junior synonyms of the Berlese's species. Future studies will confirm this hypothesis.

**PNEUMOLAEELAPS** Berlese

*Hypoasps* (*Pneumolaelaps*) Berlese, 1921

type species: *Iphis bombicolens* Canestrini, 1885.

*Pneumolaelaps* was erected as a subgenus of *Hypoasps* by Berlese, 1921. Several other authors (Vitzthum, 1943; Costa, 1966; Evans and Till, 1966; Van Aswegen and Loots, 1970; Karg, 1971, 1979 and Bregetova, 1977) have considered it as a subgenus, others (Willmann, 1953; Hunter, 1966; Hunter and Husband, 1973) as a genus. These authors consider that the host-association is as discriminatory as morphological characters to separate taxa of host-mite related groups. *Species of Pneumolaelaps* have been described, in association with bumble bees, from North America, Greenland, Europa, South America and Asia.

On the basis of morphological characters as well as host association *Pneumolaelaps* is considered as a valid genus with the following features: Dorsal shield often with unpaired accessory setae between J series; dorsum with 12 (*P. heyi*) and 16 (*P. bombicolens*) pairs of
glands and lyrifissures. Deutosternum with 6 rows of 5-8 denticles. Tectum smooth; palp-claw 2-tined; sternal setae (st1-st4) long and approximately equal in length, st1 sometimes off the sternal shield (P. heyi). Genito-ventral shield with one pair of setae and well separate from the anal shield; with one or two pairs of setae on soft cuticle between genito-ventral and anal shields. Peritreme long, extends to coxa I; peritrematal shield broad, extends posteriorly beyond coxa IV. Genu IV with 2 ventral setae. Tarsus I with 42 (5-25/8-4, P. bombicolens) to 52 (5-36/8-3, P. heyi) setae. Associated with bumble bees (except P. heyi)

*P. heyi* presents the following leg chaetotaxy:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femur</td>
<td>2-3/1.2/3-2</td>
<td>2-3/1.2/2-1</td>
<td>1-2/1.1/0-1</td>
<td>1-2/1.1/0-1</td>
</tr>
<tr>
<td>Genu</td>
<td>2-3/2.3/1-2</td>
<td>2-3/1.2/1-2</td>
<td>2-2/1.2/1-1</td>
<td>2-2/1.3/0,1-1</td>
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<tr>
<td>Tibia</td>
<td>2-3/2.3/1-2</td>
<td>2-2/1.2/1-2</td>
<td>2-1/1.2/1-1</td>
<td>2-1/1.3/1-2</td>
</tr>
</tbody>
</table>

Ta II-IV= 3-3/3,1,3/2-3 = 18

Pretarsi= normal with well developed claws

The following species have been included in *Pneumolaelaps*:

*P. aequalipilus* Hunter, 1966
*P. baywangus* Rosario, 1981
*P. brevitseta* (Evans & Till, 1966)
*P. connieae* Hunter & Husband, 1973
*P. antipal* (Solomon, 1968)
*P. bombicolens* (Can., 1885)
*P. colombol* (Evans & Till, 1966)
Stratiolaelaps Berlese, 1916

Davisiella Zumpt et Patterson, 1951; Bregetova, 1977

type-species: *Laelaps (Iphis) miles* Berlese, 1882

Chelicerae chelate-dentate; movable digit bidentate; fixed digit with two or three teeth. Large chelae. Pilus dentillis setiform. Tectum denticulate. Subcapitulum with normal chaetotaxy; deutosternum with six transverse rows of minute and fine teeth. Hypostomal process normal, fringed. Corniculi long, reaching to the tip of the palp-femur. Palp chaetotaxy normal; two-tined palp-claw.

Dorsum: Dorsal shield not covering the entire dorsum. Dorsal shield bears 37 pairs of leaf-like setae; seta px1 present; opisthontotal seta S5 not on the shield. Several additional setae inserted on soft integu-
Dorsal shield with 13-15 pairs of pores.

Venter: Tritosternum normal, bifid, long lacinia. Presternal shield weakly developed. Sternal shield large; anterior margins fused with endopodal shield, bearing three setae and two lyrifissures. Metasternal setae and associated lyrifissure free, inserted on the soft cuticle. Endopodal plates between coxae III and IV present. Genital shield flask-shaped, one pair of genital setae inserted on the edge of the shield. A pair of paragenital pores (iv5) present on the membranous cuticle, close to the insertion of the genital setae. Opisthogastric region bearing 8 - 11 pairs of setae. Anal shield subtriangular; paranal setae longer than post-anal seta. Peritrematal shield free anteriorly and posteriorly.

Leg chaetotaxy normal. *Stratiolaelaps miles* presents the following chaetotactic pattern:

<table>
<thead>
<tr>
<th>Femur</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-3/1,2/3-2</td>
<td>2-3/1,2/2-1</td>
<td>1-2/1,1/0-1</td>
<td>1-2/1,1/0-1</td>
</tr>
<tr>
<td>Genu</td>
<td>2-2/1,3/2-3</td>
<td>2-3/1,2/1-2</td>
<td>2-2/1,2/1-1</td>
</tr>
<tr>
<td>Tibia</td>
<td>2-3/2,3/1-2</td>
<td>2-2/2,2/1-1</td>
<td>2-1/1,2/1-1</td>
</tr>
</tbody>
</table>

On tibia IV setae av1, pv1, al1, al2, pl1 and pl2 spine-like.


Male and inmatures: unknown.
The following species have been described:

_Stratiolaelaps miles_ (Berlese, 1882) with two subspecies, _S. miles miles_ Berlese, 1882 and _S. miles elsi_ Aswegen & Loots, 1970; _S. ornatissima_ Aswegen & Loots. 1970; _S. fuscus_ (Berlese, 1917); _S. cardiophora_ (Berlese, 1917) and _S. egenus_ (Berlese, 1917)

The genus has been found in rotting wood, plant remains, and from a variety of rodents and their nests. In Europe, U.S.S.R., Africa and U.S.A.

**UROZERCON** Berlese

_Urozercon_ Berlese, 1901
_Termitacarus_ Tragardh, 1906; Baker & Wharton, 1952

_type-species: Urozercon paradoxus_ Berlese, 1901

Dorsum: Dorsal shield not covering the entire dorsum; posterior part of the opisthonomotum exposed. Dorsal shield highly hypertrichous, with long and simple setae.

Venter: Tritosternum normal, bipartite. Base of subcapitulum wider than longer. Pre-esternal shields absent. Sternal shield small, bearing three pairs of sternal setae and two pairs of lyrifissures; st4 not on the shield. Genito-ventral shield with one pair of genital setae and three pairs of ventral setae. Opisthogastric region bearing three pairs of simple setae. Metapodal plates elongate. Anal shield large and concave anteriorly, with five pairs of setae. Postanal and paranal setae long, at least two times longer than other anal setae. Peritrematal shields extend anteriorly, close to paravertical setae, posteriorly free and they extend to the level of the posterior margin of coxae IV.

Leg chaetotaxy as follow:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femur</td>
<td>2-2/1,3/1-0</td>
<td>1-2/1,1/1-1</td>
<td>1-2/1,1/0-1</td>
<td>1-2/1,1/0-1</td>
</tr>
<tr>
<td>Genu</td>
<td>2-2/1,2/1-1</td>
<td>2-2/1,2/1-2</td>
<td>2-2/1,2/1-1</td>
<td>2-2/1,2/1-1</td>
</tr>
<tr>
<td>Tibia</td>
<td>2-2/1,2/1-1</td>
<td>2-1/1,2/1-1</td>
<td>2-1/1,2/1-1</td>
<td>2-1/1,2/1-1</td>
</tr>
</tbody>
</table>

Tarsus I apparently with 36 setae (4-22/6-4); tarsi II-IV normal. Legs' claws reduced.
Urozercon paradoxus was found associated with Isoptera (termites). Several species remain undescribed (Delfinado-Baker, 1988, personal communication).

REMARKS: The following Berlese genera were not redescribed because there are detailed descriptions given by the following authors:

Jacobsonia Berlese, 1910: Evans, 1955; Casanueva and Johnston, 1989 (in preparation)

Of the remaining Berlese genera, Laelantennus was not studied because of the poor quality of the type specimen, Anystipalpus is not a genus of Laelapidae and Sphaerosetus was inadvertently omitted.