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ORIGIN AND CLASSIFICATION OF THE IXODIDES (TICKS) WITHIN THE PARASITIFORMES REUTER 1909 (ACARINA)

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(Accepted August 2008)

PHYLOGENETIC
METHODS
PREDISPOSITIONS
BEHAVIOUR
FOOD
SYSTEMATICS
CLADOGRAM

SUMMARY: Ixodides and Uropodina have a number of synapomorphies in common, which are not present in other groups of the Parasitiformes. Anatomic-morphological trends as well as behavioural peculiarities occurring in the carnivorous Uropodina hint to a transition towards parasitism. In fact, feed deficit can lead to parasitism in Uropodina. Based on synapomorphies, Ixodides and Uropodina are combined as Margotrichina n. cohors, Trigynaspina and Sejides as Antennophorina (n. comb.). Those two taxa form a monophyletic group whose sister group are the Gamasina

PHYLOGENETISCHE
METHODEN
PRAEDISPOSITIONEN
VERHALTEN
NAHRUNG
SYSTEMATIK
KLADOGRAMM

ZUSAMMENFASSUNG : Ixodides und Uropodina haben eine Reihe von Synapomorphien gemeinsam, die sonst in keiner Guppe der Parasitiformes auftreten. Bei den karnivoren Uropodina treten sowohl anatomisch-morphologische Trends als auch Besonderheiten im Verhalten für einen Übergang zum Parasitismus auf. Bei Nahrungsmangel wird Parasitismus beobachtet. Auf der Basis von Synapomorphien werden Ixodides und Uropodina als Margotrichina n. cohors, Trigynaspina und Sejides als Antennophorina n. comb. zusammengefasst. Beide Taxa bilden eine monophyletische Gruppe, dessen Schwestergruppe die Gamasina sind.

INTRODUCTION

The groups of Parasitiformes Reuter were originally carnivorous (EVANS & TILL 1966, KARG 1993). Two groups of the Parasitiformes transitioned to a parasitic blood-sucking nutrition: the Ixodides Latreille and the Dermanyssoidea of Gamasina Leach, subgroup Eviphidides. All subgroups and species of the Ixodides (Ticks) feed in a parasitic manner. However, several subgroups of the Dermanyssoidea are free living in various soil layers and hunt other small edaphic animals. EVANS & TILL (1966) docu-

mented how free-living forms developed into specific parasitic forms. The Hypoaspidae of this group are exclusively carnivorous and live in soil. Laelapidae and Haemogamasidae which transitioned to parasitism, are partially found free-living in soil or in nests of their hosts (KARG 1993). The Dermanyssidae, Macronyssidae, Myonyssidae, Hirstionyssidae and Rhinonyssidae, however, are obligatory haematophagous (EVANS & TILL 1966).

The group of Ixodides takes an isolated position within the Parasitiformes. Even phylogenetic DNA analyses could not demonstrate a closer relationship

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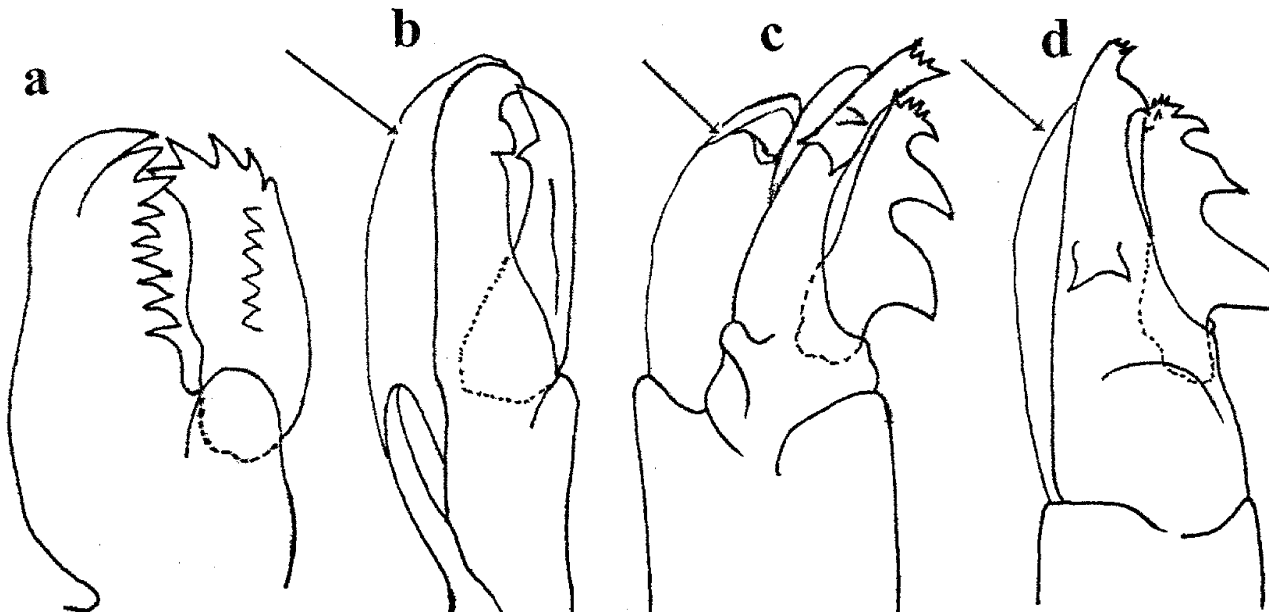


FIG. 1: Chelicerae of Uropodina (a, b) and Ixodidae (c, d). a. — *Trichouropodella* Hirschmann et Zirngiebl-Nicol. b. — *Trachyuropoda* Berlese. c, d. — *Ixodes* Latreille, c. — larva, d. — female.

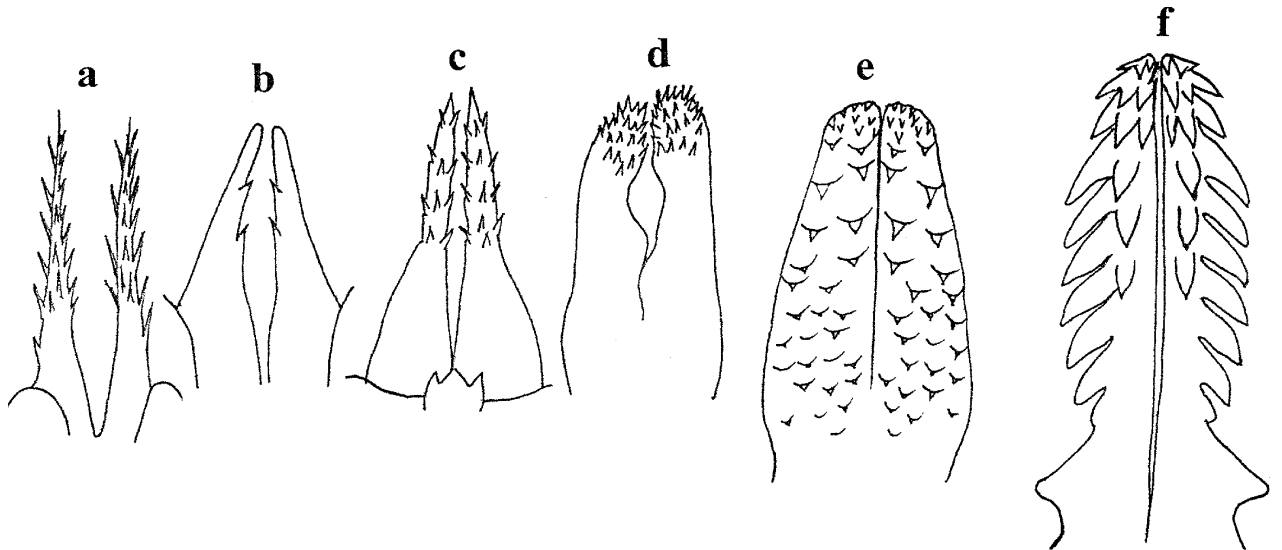


FIG. 2: Processes of the hypostom: laciniae in Uropodina (a-d) and Ixodidae (e, f). a. — *Uroseius* Berlese. b. — *Trichouropoda* Berlese. c. — *Discourella* Berlese. d. — *Trichouropodella* HIRSCHMANN et Zirngiebl-Nicol. e. — *Argas* Latreille. f. — *Ixodes* Latreille.

to another group of the Parasitiformes (KLOMPEN, LEKVEISHVILI & BLACK 2006). However, HIRSCHMANN (1957, 1959) found that the Ixodides might be closely related to the Uropodina Kramer. The aim of the presented work is to investigate whether this hypothesis can be proven and whether, similarly to the Dermanyssoidea, parasites could develop from the free-living Uropodina.

METHODOLOGY

Investigations were divided into three objectives:

First, predispositions in the Uropodina will be identified that already hint to a development towards haematophagy. Trends in anatomic-morphological specialization as well as findings in behavioural characteristics directed towards parasitism will be investigated.

Next, common special homologies (synapomorphies) of Ixodides and Uropodina will be investigated to demonstrate their systematic relationship.

Last, a cladogram will be established based on synapomorphies of subgroups of the Parasitiformes which will show the relationship of the Ixodides and Uropodina. Phylogenetic methods by HENNIG (1950, 1979 & 1994) will serve as methodical basis for these studies.

PREDISPOSITIONS OF PARASITISM IN THE UROPODINA KRAMER

ANATOMIC – MORPHOLOGICAL TRENDS¹

The main mouth parts of ticks are the chelicerae and the denticulated *laciniae* at the hypostom of the gnathosoma (FIG. 1c & 1d, 2e & 2f). Mites penetrate the host's skin with their chelicerae. The originally pair-like *laciniae* form a trunk-like structure (*clava*), which the parasites use to anchor securely into the skin to suck blood. HIRSCHMANN (1957) noticed a hyaline appendix lateral at the *digitus fixus* of the chelicerae in the ticks (FIG. 1d). We could confirm

this in our investigations on larva of Ixodes (FIG. 1c). Such an appendix was also found in a genus of Uropodina (FIG. 1b). Otherwise, it is not present in the Acarina.

The *laciniae* at the hypostom of gnathosoma are in most of the Parasitiformes skin-like with fringes. However, a gradual solidification of the *laciniae* can be noticed in genera of the Uropodina. Only in the genera *Nenteria* and *Trichouropoda*, the *laciniae* take the shape of a scale (KARG 1989). In those group, first tooth formations can be observed (FIG. 2b). A larger number of tooth formations can be found in the genera of *Discourella* and *Trichouropodella* (FIG. 2c & d). We can consider this as the transition to the *laciniae* of the Ixodides. The pair-like *laciniae* closely fused to a *clava* (FIG. 2e & 2f). The denticulation of the Argasidae (FIG. 2e) resembles forms of the Uropodina. Extreme tooth formations developed in the Ixodidae (FIG. 2f).

The chelicerae of ticks are not tools for biting but for piercing. Teeth along the inner edge of the *digitus mobilis* disappeared. Instead, large backwards directed teeth developed on the outer edge, which prevent sliding of the pierced chelicerae out of the wound (FIG. 1c & 1d). Normal tooth formations along the inner chewing edge are conserved in the genus *Trichouropodella* of the Uropodina but at the same time, secondary tooth formations along the outer edge are noticeable, however most likely without function (FIG. 1a).

Ticks show a reduction in shields at the idiosoma compared to the Uropodina. Only a small shield on the prodorsum forms or we generally notice a skin-like shell. The tick body expands abnormally while sucking blood. Restricting shield formations had to disappear. In rare cases, a shield reduction can also be observed in the Uropodina, e.g. in the genus *Uroseius* (FIG. 3).

A special characteristic of shield formation on the dorsum of the Uropodina are marginal shields separated by grooves (arrow, FIG. 4a). Such shields are not developed in the Ixodides but the corresponding grooves are still present (FIG. 4b).

1. Some FIGS. (1 a, b, d, 2 d, 11 b, c) based on partial figures published by HIRSCHMANN (1957), HIRSCHMANN & ZIRNGIEBL-NICOL (1961, 1972), HIRSCHMANN, WISNIEWSKI & KACZMAREK (1991), FIG. 9 after EVANS & TILL (1979) and FIG. 4 b after NUÑEZ, MUÑOZ-COBEÑAS & MOLTEDO (1985), modified, all other figs. based on original drawings.

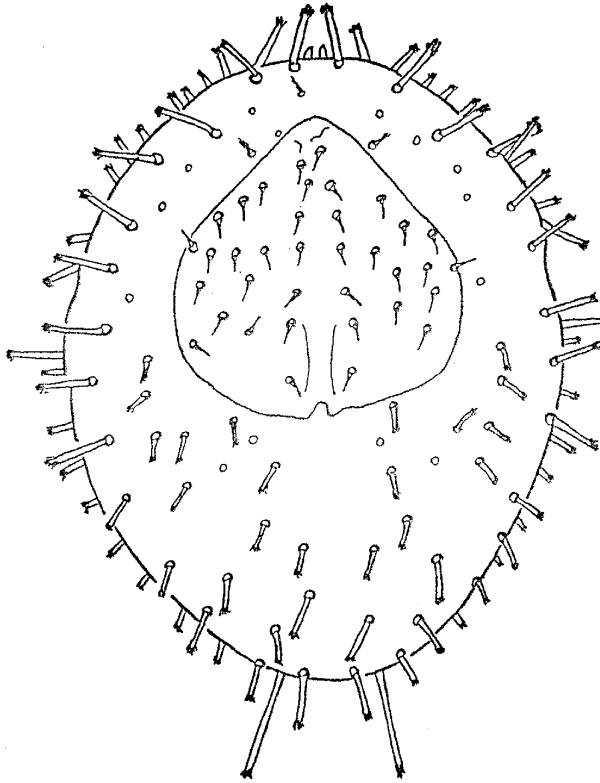


FIG. 3: Dorsum of the female of *Uroseius acuminatus* (C. L. Koch).

BEHAVIOURAL PECULIARITIES

Fully engorged tick females fall off the host and search for protected sites on soil surfaces to lay their eggs. The hatched larvae are able to survive free-living during cooler seasons up to 5 months without feeding (NUÑEZ, MUÑOZ-COBENAS & MOLTEDO 1985). This hints to an origin from soil inhabiting mites.

Soil inhabiting Uropodina were observed on cadavers, sucking body fluids of dead animals (KARG 1989). EICHLER (1977) pointed out that this saprophagous form of nutrition can be considered a precursor of parasitism.

Finally, Uropodina were observed when attacking alive animals which were large relative to the mites: larvae of flies, earth-caterpillars and earthworms. The Uropodids search for soft-skinned parts on the body of the victim to dig their chelicerae into the skin (KARG 1989, FIG. 5). Above mentioned predispositions — stronger, denticulated *laciniae* — should be advantageous for this.

Particularly informative is that Uropodina can temporally change to plant parasitism. Investigations on *Uroobovella marginata* (Koch) in cucumber cultures under glass revealed factors and behavioural characteristics which play a role in the transition to parasitism (KARG 1968): usually, this mite feeds on nematodes and small insect larvae. During feed deficit the mite develops a phoretic appetite. It climbs on cucumber plants to meet a carrier animal. In case of lesions in the cucumber plant stem, the mite changes its behaviour. With its chelicerae, it tears open the tissue cell by cell to suck out its fluids.

These investigations and observations show model-like how a transition from carnivorous to parasitic feeding could have occurred.

Phoresie has to be considered an important precursor to parasitism (ATHIAS-BINCHE 1991). In the Uropodina phoresy is obligatory. The life cycle of the species of the group depends on their host (KARG 1989).

CONCLUSION

The presented overview of predispositions of parasitism in the Uropodina Kramer reveals a mosaic of characteristics in the Uropodina, anatomic-morphological as well as behavioural, which point to a genetic basis that lead to the development of the haematophagous Ixodides.

COMMON SPECIAL HOMOLOGIES (SYNAPOMORPHIES) OF UROPODINA AND IXODIDES

The dorsum of larvae of the Uropodina is covered with two shields, a podonotal shield and a pygidial shield. The podonotal shield is equipped with setae, but the pygidial shield remains without setae. A setation of the postsoma developed, however, the internal setae seem, so to speak, pushed towards the margin by the pygidial shield. In Gamasina, the pygidial shield bears setae (KARG 1993). We see two longitudinal rows in the middle of the postnotum with the setae *I2*, *I3*, *I4* and *I5* (FIG. 6a). In the Uropodina, setae *I3* have changed their position to the margin

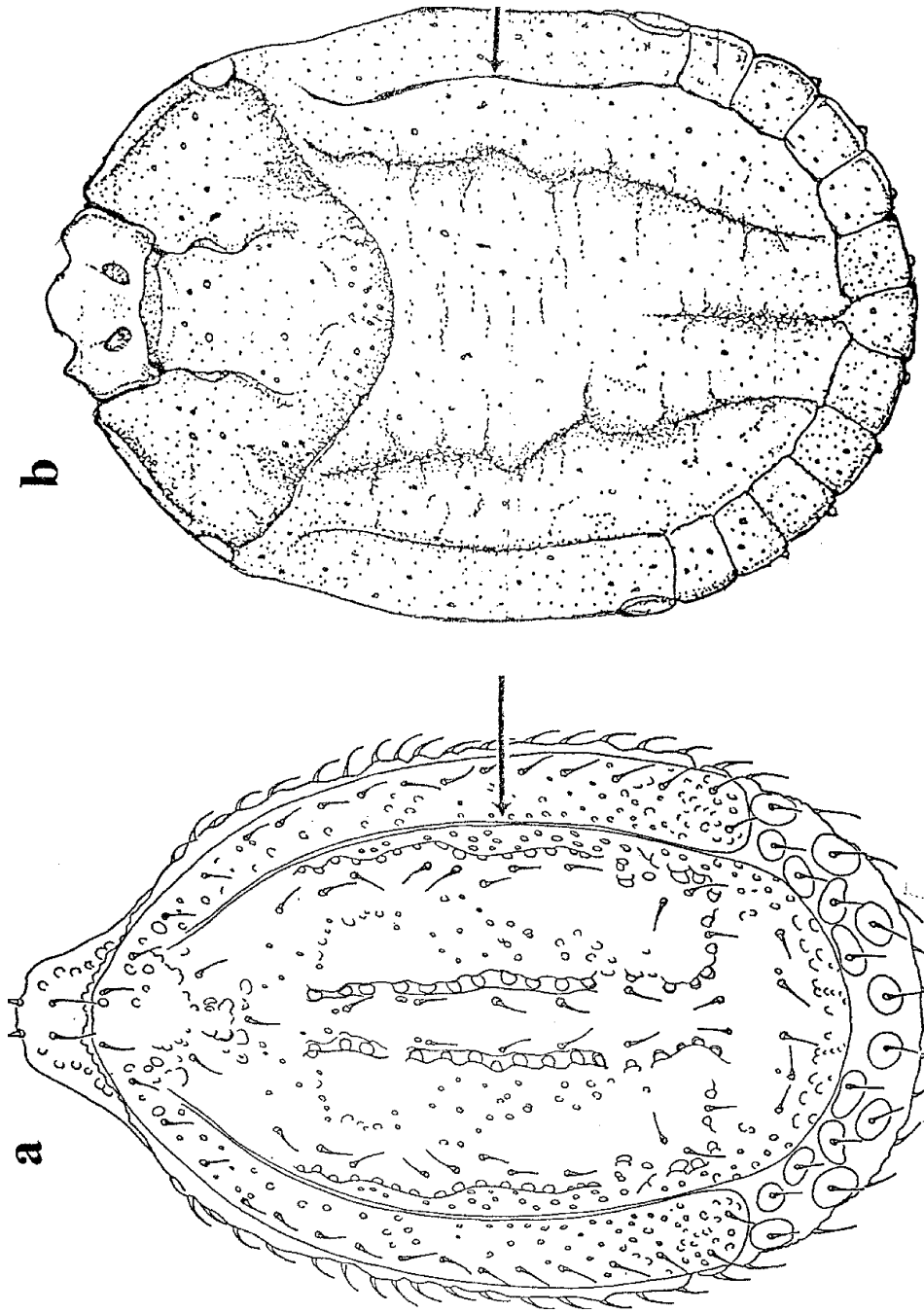


Fig. 4: Dorsum of female in Uropodina (a) and Ixodides (b) with marginal and postmarginal grooves. a. — *Discourella cordieri* (Berlese). b. — *Boophilus microplus* (Canestrini).

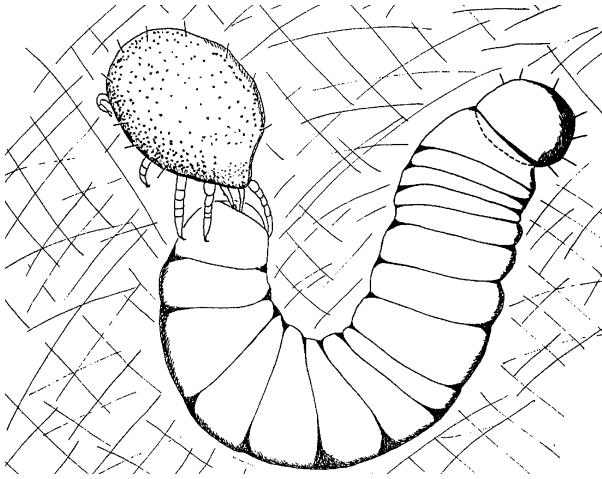


FIG. 5: A specimen of Uropodina attacking a larva of an insect at a soft part of the skin.

(FIG. 6b). This generated space for a pygidial shield without setae between *I3* and *I4*, *I5*. HIRSCHMANN (1975) therefore termed the Uropodina, a group with pygidial shield of the larva without setae, Atrichopygidiina.

This apomorphic formation has so far only been noticed in the Uropodina (KARG 1989). In the frame of the current work, chaetotaxy of larva of the Ixodides was analysed in detail. We show that the same configuration of setae is present as in the Uropodina. Setae *I3* — *I3* are located at the margin (FIG. 6c). Hence, originally, a pygidial shield must have been present. We already pointed out that body shields in ticks were partially or completely reduced. While sucking blood, the opisthosoma of the larvae expands enormously and hence, its skin has to be very elastic. A shield would not allow this process. Adaptation to blood sucking and stretching of the opisthosoma lead secondarily to an elimination of the shield. The figuration of setae of the larvae in Uropodina and Ixodides is synapomorph.

A remarkable apomorphy of the Uropodina are the so called *perigenital* or *endometapodial grooves* at the venter. These grooves run between the coxae of legs and the genital shield (KARG 1989). We came to the conclusion that the Ixodides developed homologous grooves (same position in structural system, FIG. 7a, b & c). With this we found another synapomorphic feature of Uropodina and Ixodides.

Further, characteristic features of the Uropodina are marginal shields separated from the dorsum. They take different shapes in the different genera. Often, separated caudal *postmarginalia* are formed (FIG. 4a). As we already showed, shields are separated by grooves. In the Ixodides, shields are again reduced to a short prodorsum. However, the grooves are conserved and prove the synapomorphy of these formations (FIG. 4b).

In all postembryonal stages of the Ixodides we observed inner anal setae in the anus (FIG. 8b). We observed this characteristic regularly also in the deutonymphs of the Uropodina (FIG. 8a). This synapomorphy again hints to a *relationship* between those two groups, possibly to a common origin from forms with inner anal setae in all stages.

ESTABLISHMENT OF A CLADOGRAM

We documented the close relationship and common origin of the Uropodina and the Ixodida by the above described synapomorphies. These two groups are hence more closely related to each other than to other groups. The group of the Uropodina was divided into three super-families with a total of 10 families by KARG (1989). The Ixodides cannot be directly assigned to any of these groups.

But the Ixodides and Uropodina have to be united in one common group.

WE CLASSIFY UROPODINA AND IXODIDES AS ONE GROUP TERMED:

MARGOTRICHINA N. COHORS.

(margo = margin, trichos = seta, as to the marginal position of the setae *I3* in the larvae)

The Antennophorina Berlese, 1892 form another large group of the Parasitiformes (KARG 1997). EVANS & TILL (1979) revealed the close relationship between the Antennophorina (=Trigynaspida Camin et Gorirossi, 1955) and the Sejides Berlese, 1913 through a synapomorphic characteristic: A small shield bearing a pair of special tactile setae is present at the tarsus IV of nymphs and adults, anterior to the metatarsal fissure (FIG. 9a).

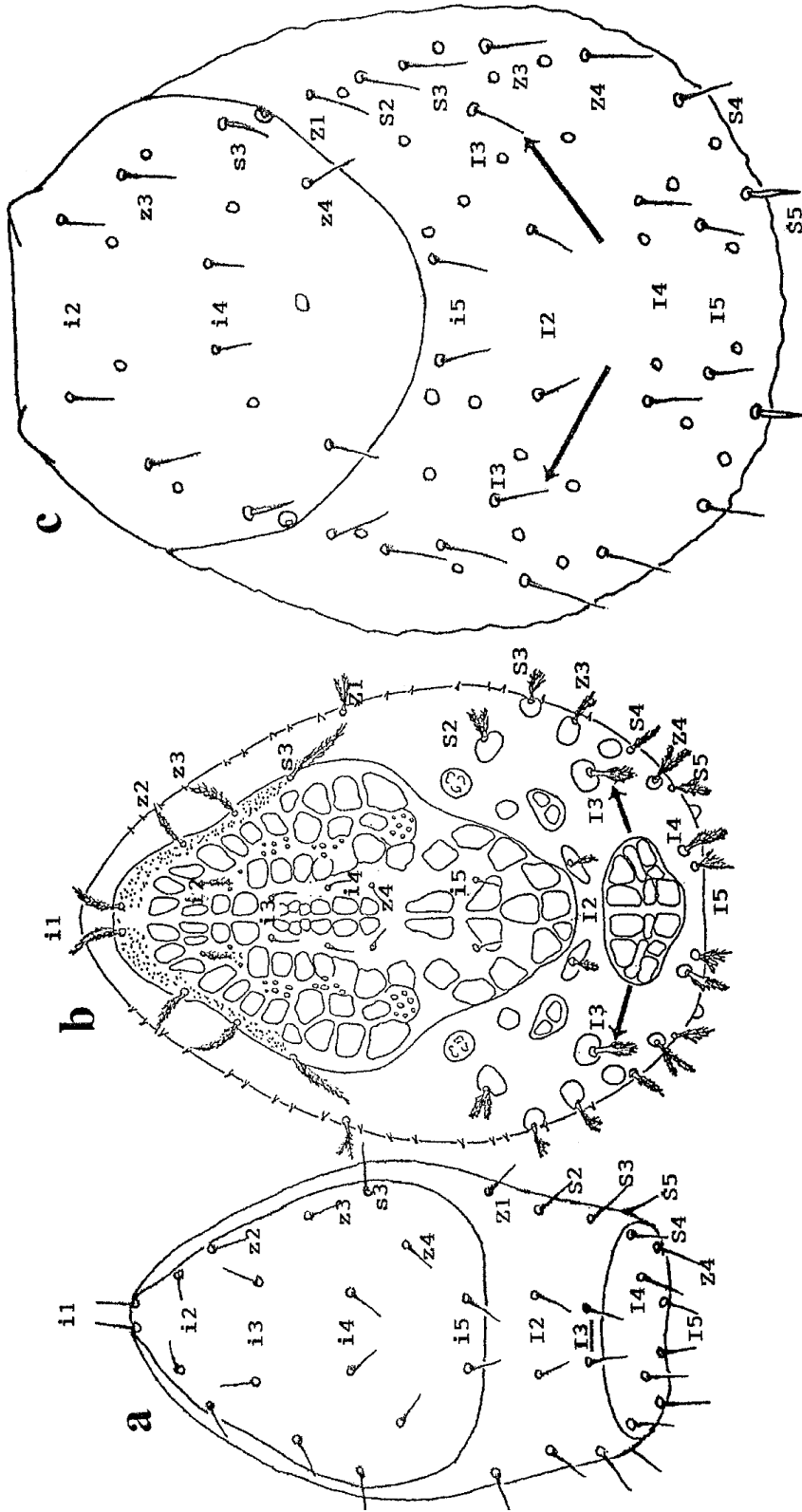


FIG. 6: Dorsum of the larvae showing the shifting of setae *I3* to the margin caused by the pygidial shield of the Uropodina: a. — the Gamasina, b. — the Uropodina, c. — the Ixodides.

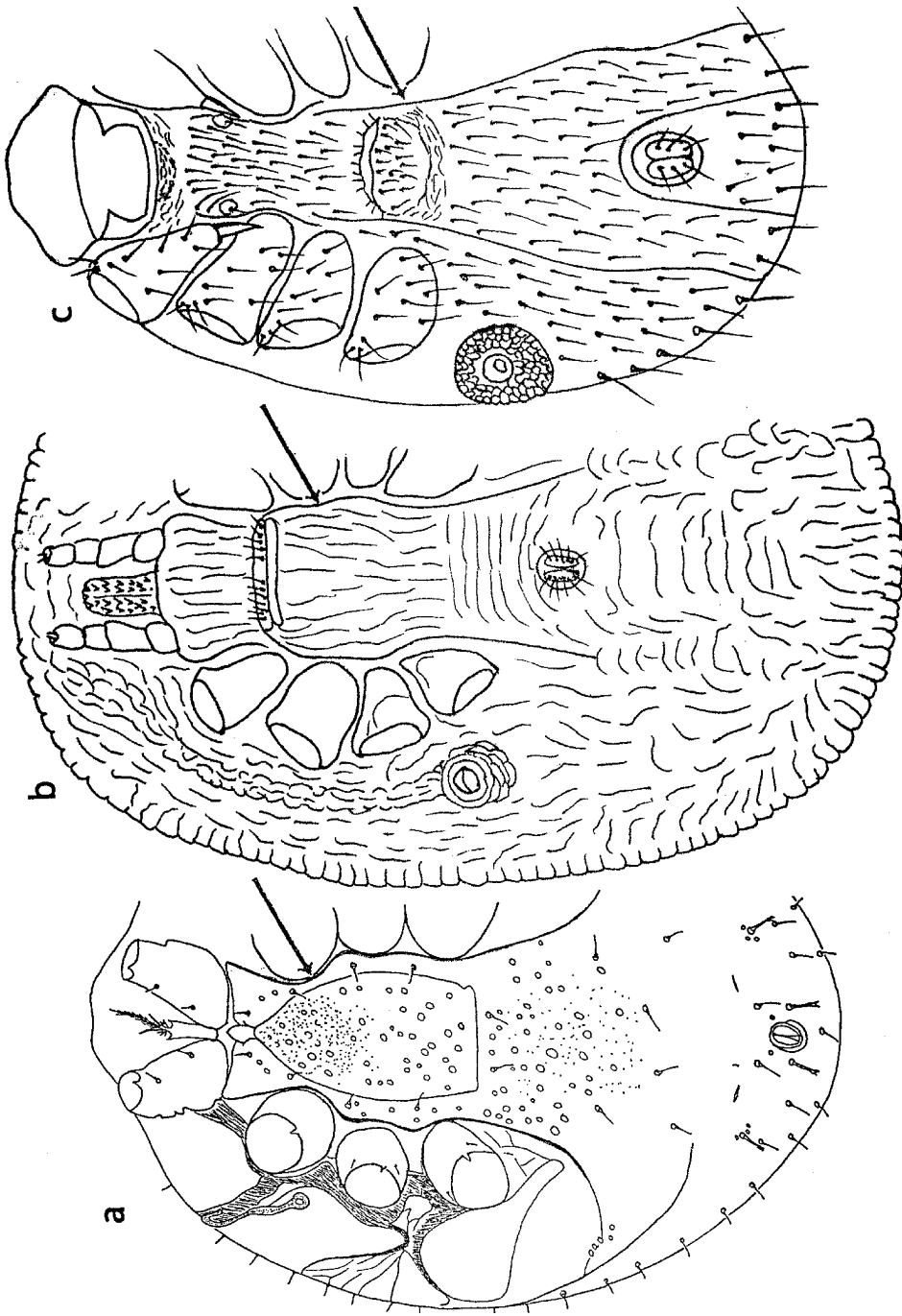


FIG. 7: Venter of females showing the perigenital groove, a synapomorphy developed in Uropodina and Ixodidae. a) Uropodina, b, c) Ixodidae. b) Argasidae., c) Ixodidae.

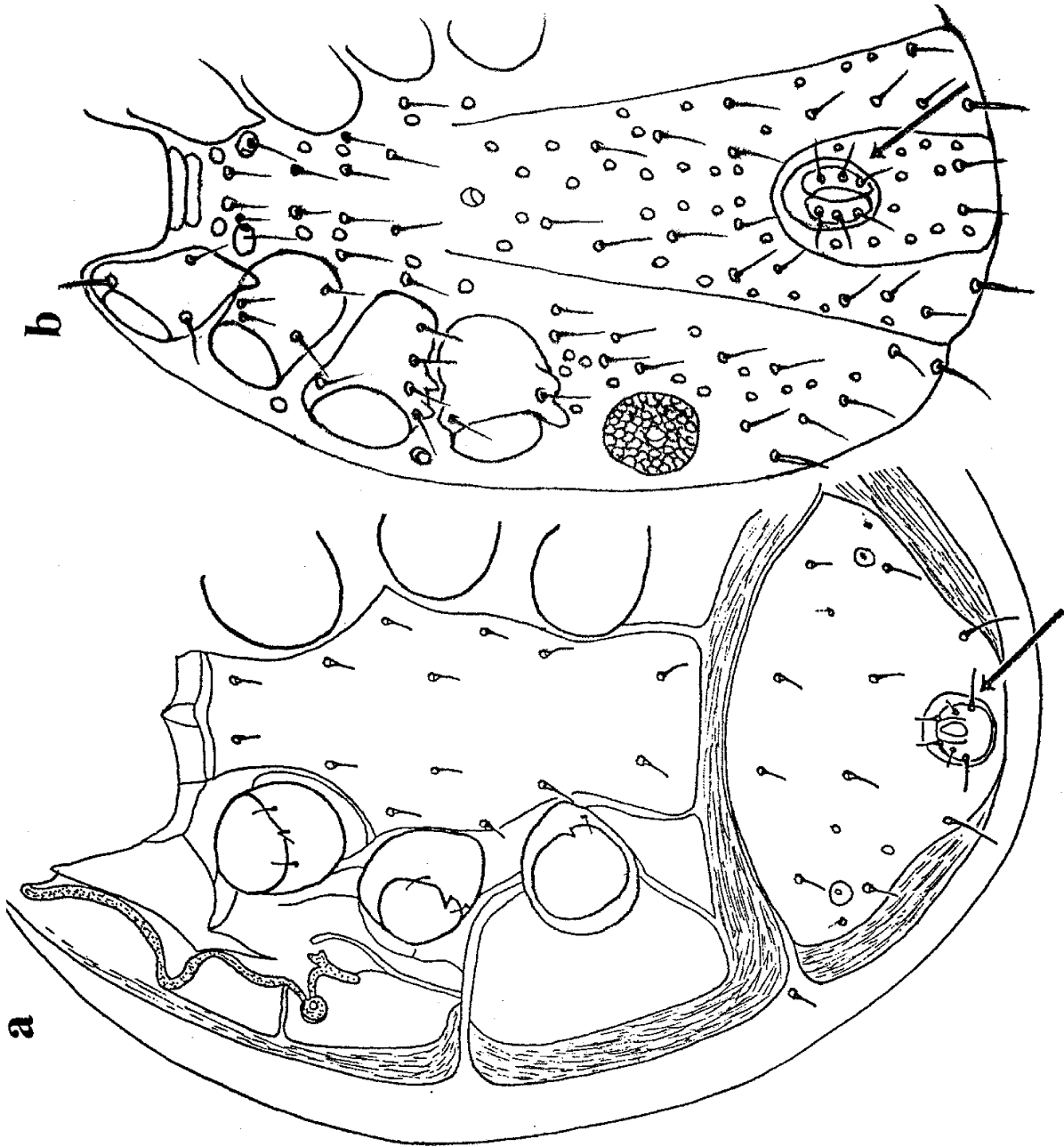


FIG. 8: Venter of deuteronymphs a. — Uropodina. b. — Ixodides showing the inanal setae, a synapomorphy of the two groups.

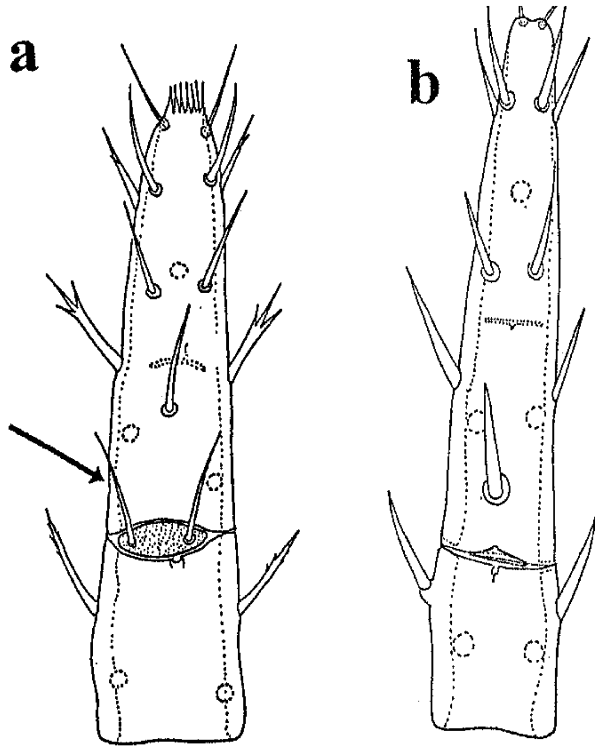


FIG. 9: Tarsus of leg IV in nymphs and adults. a. — a synapomorphy of Trignyaspida and Sejides consisting of a small shield at the metatarsal fissure bearing a pair of special tactile setae. b. — the plesiomorphic stage of development in other groups of Parasitiformes.

**WE HENCE COMBINE THOSE TWO GROUPS
TO ONE TAXON TERMED:
ANTENNOPHORINA BERLESE NOV. COMB.**

These two large groups of the Antennophorina Berlese nov. comb and Margotrichina nov. cohorts can be backtraced to a common origin through a synapomorphy: Special, additional shields developed in the nymph stage (protonymph or deuteronymph): lateral or mesonotal shields (FIG. 11). Those shields are not present in the sister group of the Gamasina Leach.

The Gamasina Leach are characterised such that the males have apomorph chelicerae with a special spermatodactyl for sperm transfer (FIG. 10). There are only few exceptions (KARG 1993). KARG (2006) divided the Gamasina into three taxa: Eviphidides, Eugamasides and Ascides. Eviphidides and Eugama-

sides exhibit a special form of sperm: ribbon sperm (ALBERTI 1995, 2000). This synapomorphic feature proves the close relationship and common origin of the two groups.

The groups Antennophorina-Margotrichina and Gamasina together also exhibit a synapomorphy in the larva stage in the form of a podonotal shield, bearing 8-9 pairs of setae (FIG. 6a & 6b).

1 – Two special tactile setae on a small shield at the metatarsal fissure of tarsus IV of nymphs and adults (FIG. 9)
2 – In the larva, position of setae pair I3 on the dorsum marginal shifted (FIG. 6) – Perigenital grooves developed on the venter of nymphs and adults (FIG. 7) – Dorsum of adults with marginal grooves (FIG. 4) – Inanal setae in the nymphal stage (FIG. 8)
3 – Special form of sperm: ribbon sperm
4 – Chelicerae of males mostly with a spermatodactyl (FIG. 10)
5 – Additional lateral and/or mesonotal shields in protonymph stages (FIG. 11)
6 – Podonotal shield bearing 8 to 9 pairs of setae in larva stage a (FIG. 6 a, b)

Note: As mentioned, body shields are reduced or eliminated in parasitic groups, however, separating grooves are preserved (FIG. 4).

TABLE 1: List of the synapomorphies characterizing the related groups, corresponding to the numbers in the cladogram (FIG. 12)

DISCUSSION

KARG (2006) showed that the **Mesostigmata** Canestrini, 1891 form a rest group of the Parasitiformes because the Ixodides were classified as a higher systematic category than each one of the remaining groups. That means the **Mesostigmata are the “Non-ticks”!** Further, the terms *Metastigmata* for the Ixodides, and *Mesostigmata* for the remaining groups are not correct, as in one family of the Ixodides the ventral stigmata are also localized lateral in the middle of the body: in the Argasidae (FIG. 7). Stigmata are only localized at the opisthosoma in the family of the Ixodidae. This must be regarded as a secondary adaptation to the productive system. In the opisthosoma of the female, 2000 to 5000 eggs (!) develop which have to be supplied with oxygen (NUÑEZ , MUÑOZ-COBENAS& MOLTEDO 1985).

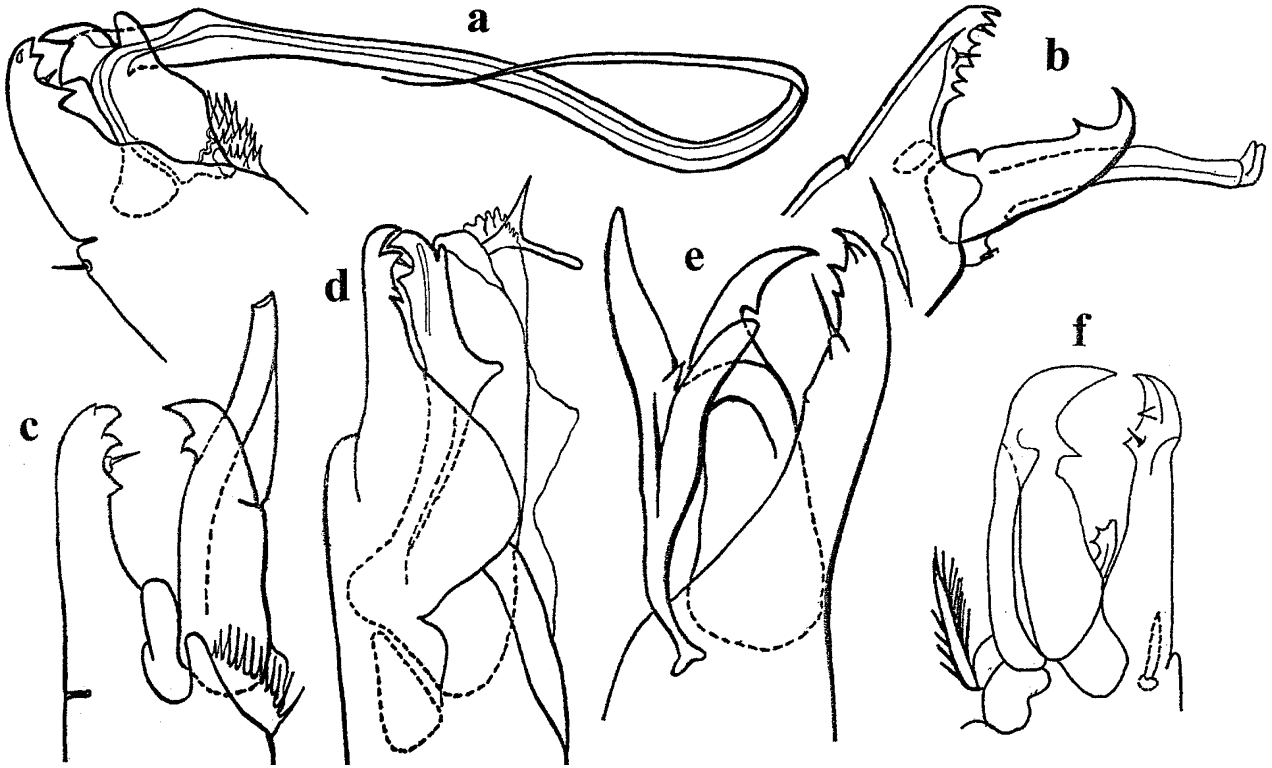


FIG.10: Spermatodactyl in different forms in genera of Gamasina. a. — *Pachylaelaps* Berlese. b. — *Protogamasellus* Karg. c. — *Arctoseius* Sig Thor. d. — *Evirus* Karg. e. — *Amblyseius* Berlese. f. — *Leptogamasus* Trägårdh.

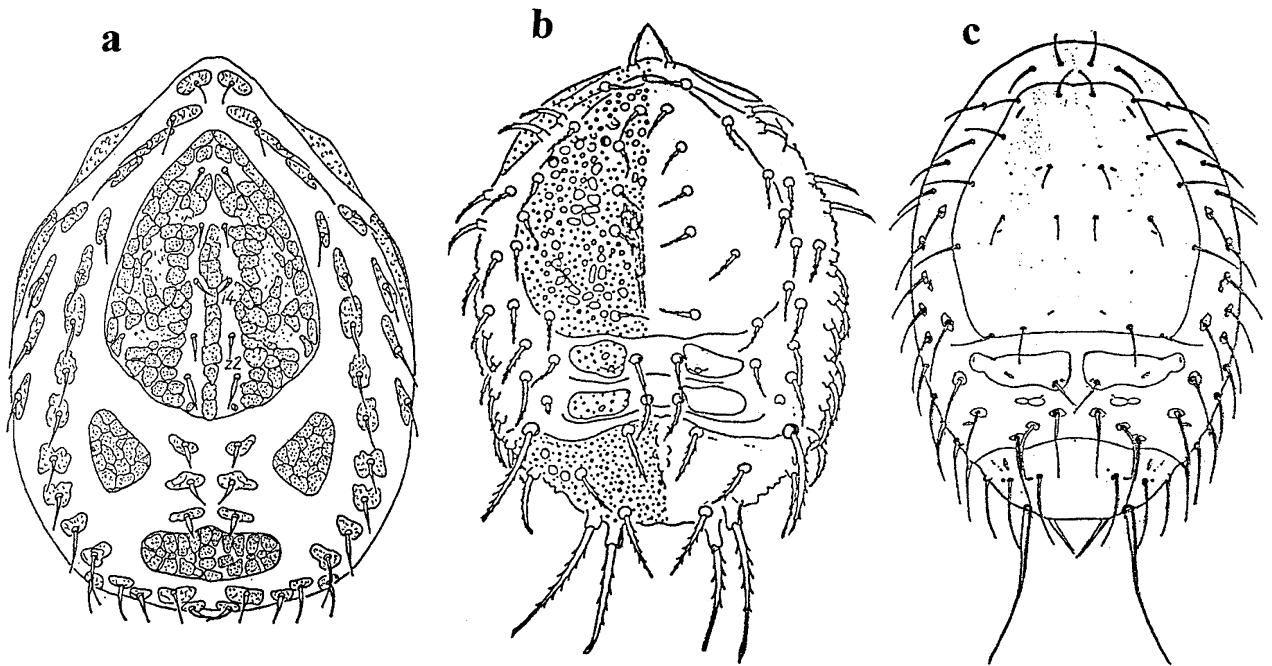


FIG.11: Dorsum of protonymphs showing a synapomorphy of the groups: additional mesonotal respectively lateral shields. a. — Uropodina (*Nenteria* Oudemans). b. — Sejides (*Sejus* C.L.Koch). c. — Trignyaspida (*Celaenopsis* Berlese),

Parasitiformes

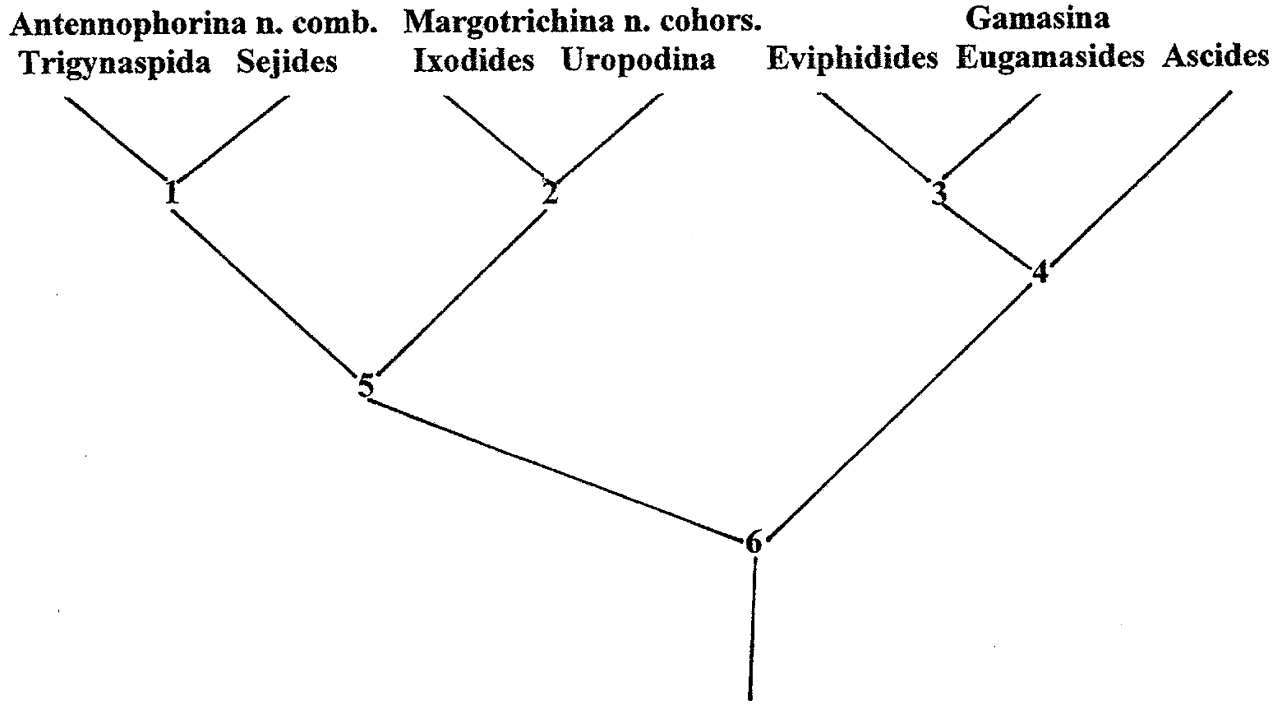


FIG. 12: Cladogram of the groups of the Parasitiformes, based on synapomorphies numbered 1 to 6, corresponding with the details in TABLE 1.

The above mentioned, systematically not justified method was after CANESTRINI also used by other authors: a special group was well established through a special homology, but the remaining groups (rest groups) were summarized as a “super group”, for example:

- Trigynaspida** — rest groups: **Monogynaspida**;
- Atrichopygidiina** — rest groups: **Trichopygidiina**;
- Actinochaeta** — rest groups: **Anactinochaeta**.

EVANS & TILL (1979) made ironic comments about these “super groups”, as these systems contradict each other and cannot be congruent. The “super groups” are based on plesiomorphies. Monophyletic groups can only be based on apomorphy formations of a certain characteristic. Plesiomorphies are preserved in different, but not always related groups. Monophyletic groups cannot be based on plesiomorphies. LINDQUIST (1984) analysed the faulty methodology of several authors and could not understand that taxonomic groups could be based on plesiomorphies.

Two less frequently analysed groups of mites were classified as Parasitiformes based on plesiomorphies by EVANS & TILL (1979): the Notostigmata (=Opilioacaridae) and Tetrastigmata (=Holothyrida). To decide whether one or both of these groups can be classified as Parasitiformes requires further investigations.

The presented work could prove that Ixodides and Uropodina developed from a common origin. The hypothesis by HIRSCHMANN (1957, 1959) could be verified and documented by means of the phylogenetic method by HENNIG (1950, 1979 & 1994).

Application of this method showed the systematic importance of several synapomorphies. However, a functional relevance is not obvious (see No. 2 of synapomorphies TABLE 1 and FIGS. 4, 6, 7, 8).

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