

## INTRODUCTION

### *Reconstruction of the phylogeny*

The Acari are phylogenetically not well studied. In his doctor thesis OCONNOR (1981) reconstructed the phylogenetic relationships within the astigmatid mites by using morphological characters of the deutonymphs. It is one of the few existing phylogenetic trees within the Acari. I reconstructed a phylogenetic cladogram of the Histiostomatidae by using the method developed by Willi HENNIG in 1950 as explained in (SUDHAUS & REHFELD, 1992). The reconstruction consists of the search and determination of the sister group of a certain taxon. A founded cladogram is a phylogenetic diagram of relatedness (AX 1984), in which each sister taxon relationship is argued by synapomorphies. Such trees are not implicitly “correct”, but they are hypotheses, in which the particular argumentation is exposed and therefore criticizable. They fulfill an essential supposition for science. The polarity decision, whether a character state is apomorphic or plesiomorphic, is the essential step in the phylogenetic reconstruction. Monophyletic groups must be argued by apomorphies, characters which do not exist in the outgroup.

### *Phylogenetic position of the Histiostomatidae*

The Histiostomatidae is a subgroup of the monophyletic astigmatid mites. The Astigmata branch off within the paraphyletic “Oribatida”. The Malaconothridae are considered to be the sister group of the Astigmata (NORTON, 1998). Some apomorphies of the Astigmata concerning the deutonymph are: absence of the chelicera and of the mouth opening, cuticula well-sclerotized. Some adult apomorphies are the loss of the ovipositor of the female and the existence of a dorsal copulation opening in the female and a sclerotized aedeagus in the male (OCONNOR, 1981).

The Astigmata consist of 27 main taxa. Supported by morphological characters of the deutonymph, the Histiostomatidae were seen to branch off basically within that group (Fig1). One synapomorphy of Guanolichidae/Histiostomatidae (Histiostomatoidea) and its sister group is the existence of conoids ventrally of the deutonymph. An apomorphy of the sister group of the Histiostomatoidea is the existence of Grandjean’s organ (OCONNOR, 1981).

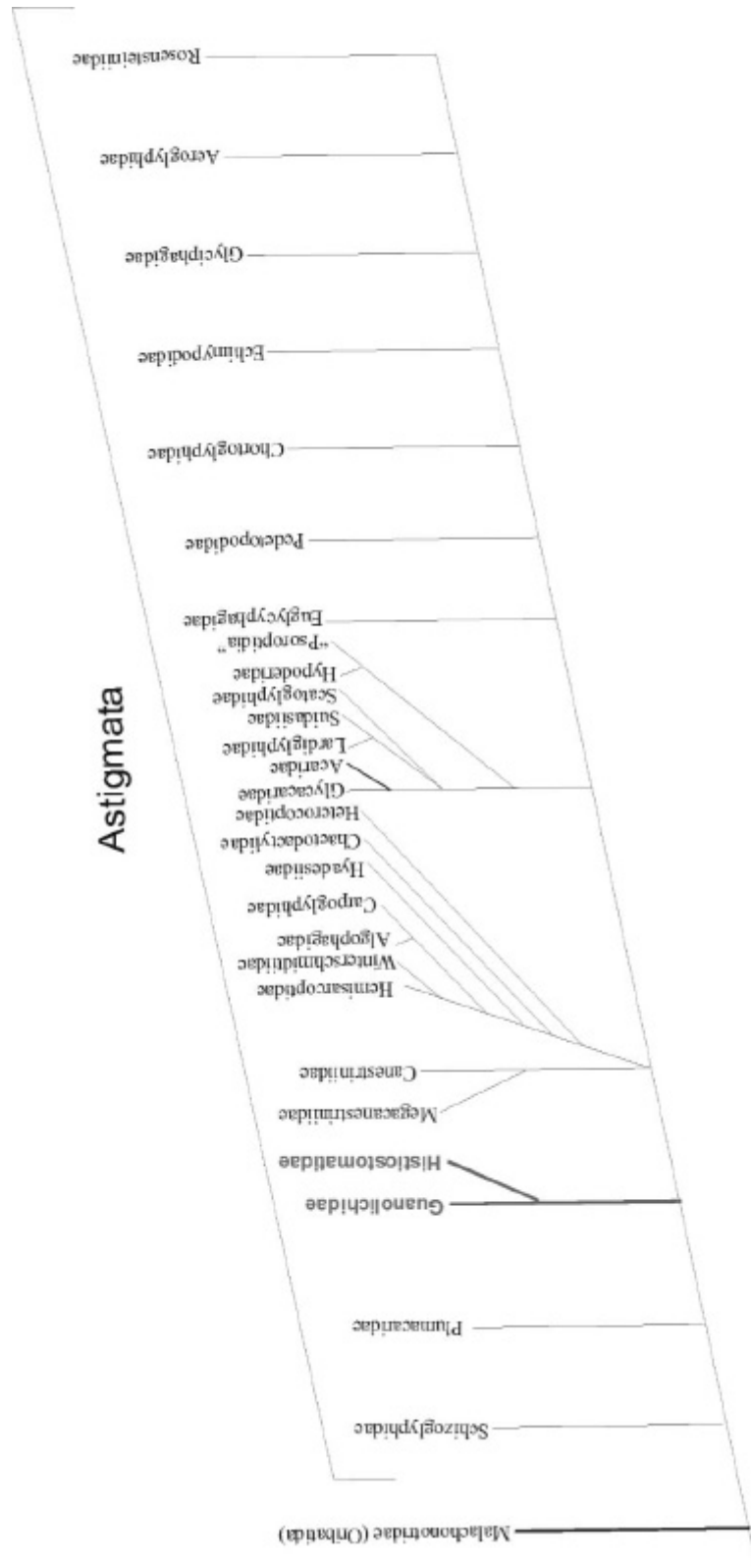


Fig 1 :  
Cladogram of the astigmatid mites, mainly reconstructed with help of deutonymphal characters (OCONNOR, 1981)

### *Plesiomorphic characters of the Astigmata*

Some plesiomorphic characters of the Histiostomatidae evolved in the stem species of the Actinotrichida which consist of the Prostigmata, the “Oribatida” and the Astigmata. Important apomorphies of the Actinotrichida are the fusion of the coxae of all legs with the venter and the nearly complete reductions of genital and anal shields. Further apomorphies concern the displacement of body segments: a downward dislocation of the opisthosoma brings the anus into a ventral position, the appendages of the first two segments (cheliceral and pedipalpal segments) were dislocated forwards and leg bearing segments reduced into small remnants and displaced to ventral (BERNINI, 1986).

### *Sense organs*

The sense organs of mites consist of mechanoreceptors, chemoreceptors, thermoreceptors and photoreceptors. The most important sense organs in the astigmatid mites are setiform and are both positioned on the propodosoma and the hysterosoma and in large numbers on the distal legs. EVANS (1992) differentiates between sensilli without a pore system, sensilli with terminal pore system and sensilli with wall pores. Sensilli without a pore system don't have a simple innervation of the shaft and function as mechanoreceptors. Another type has a complex innervation of the shaft by some more dendritic branches and has terminal pores. It can function as mechanoreceptor or chemoreceptor (contact chemoreceptor). Sense organs with wall pores have numbers of pores around the whole shaft of the seta. These setae function as olfactory receptors. Examples are solenidia. Another system of the terminology of setae was introduced by GRANDJEAN (1935a and 1970 a). It depends on the existence or the absence of an anisotropic material which is termed actinopilin. Ordinary setae only have an axis of actinopilin and a thin isotropic layer. Eupathidia and famuli consist of actinopilin and a protoplasmic core. Solenidia lack actinopilin and have distinct lumina: They are transversely striated on their inner surface. During the ontogenetic development ordinary setae can become eupathidia but (as far as known) not solenidia.

In a comparative study I observed how deutonymphs of astigmatid mites orientate under laboratory conditions and how they behave to find phoretic transporters. For the phoretic dispersion in the astigmatid mites mechano receptive and chemo receptive organs of the deutonymph are important to recognize suitable transport insects and the right habitats for later development. Special movements of legs I and II were observed, which have the biggest

quantity of solenidia, which therefore seem to play an important role. Unfortunately up to now the way the solenidia function is unknown.

Observations about the optical orientation were performed with deutonymphs of *Bonomoia opuntiae* (Histiostomatidae) which have conspicuous light sensitive organs.

Photoreceptors are common within the Acari. In most groups eyes consist of retinula cells and rhabdomeres and presumably derived from arthropod ocelli (EVANS, 1992). Within the oribatid mites a new type of light sensory organs evolved and presumably retained in deriving astigmatid groups (WITALINSKI et al., 2002).

#### *Chemotactic behavior and light receptor sense in the Histiostomatidae*

Biological and behavioral observations of *Bonomoia* as well as of histiostomatid species in general do not exist. Therefore I observed the interesting chemotactic behavior in comparative studies.

Deutonymphs of the taxon *Bonomoia* possess what appear to be light sensitive structures (eyes) on the lateral margins of the idiosoma (EVANS, 1992). Up to now light sensitive organs of astigmatid mites are morphologically and functionally not investigated. In contrary eyes, termed "lenticuli", of the related and paraphyletic "Oribatida" are well analyzed. They newly evolved within the oribatids and differ morphologically from that complex type with retinula cells in more basically branching mite groups (ALBERTI & FERNANDEZ 1988). Experiments should help to find ideas about the function of the eyes in *Bonomoia*.

#### *Phoresy*

Besides antagonistic relationships between organisms such as parasitism and competition, the more neutral phoresy exists. It appears in some animal groups, for example within the Hexapoda. Larvae of oil beetles (Meloidae) get for example transported by some Hymenoptera. But phoresy appears especially frequently within the Nematoda and the Acari. Phoresy evolved several times convergently within the Acari: within the Gammasida, the Uropodina and once within the Astigmata. Phoresy clearly represents an ancestral characteristic of the Astigmata (OCONNOR, 1991). Because all histiostomatids produce phoretic deutonymphs, that phenomenon is the most important part of their biology. I observed some examples of relations between mites and their carriers, that life strategy shall be closer explained in the following and some astigmatid examples will be given.

The following definition for the phoresy was given by (KIONTKE, 1997):

Phoresy is a phenomenon in which one individual of a species ascends an individual of another species at a given time of its ontogenesis. It is carried for a limited while to get to a new habitat. Usually they don't feed during that time.

Terms for the partners of such a phoretic relation are “phoret” for the ascending animal and “transporteur” for the carrier (KIONTKE 1997).

Phoresy is commonly found in habitats which change their conditions rapidly and elapse after a short time. Such habitats are called ephemer biochoria. Biochoria are defined by TISCHLER (1994) to be parts of ecological systems which are distributed like islands and have a characteristic inventory of species. Examples for biochoria are animal dung, carrion and compost. These habitats arise at uncertain locations to uncertain times. They differ from biochoria as for example puddles or formicaries, which regularly arise at certain locations.

In some nematode and mite groups a behavior of the juvenile phorets appears to find their transporters. This behavior is termed “waving” for nematodes (VÖLK, 1950). I adopted this term for the behavior of the deutonymphs of astigmatid mites.

Phoresy is a common phenomenon in the life cycle of free-living Astigmata. The Astigmata is a diverse and widely distributed monophyletic group. Some of them are permanent parasites of birds and mammals. But ancestrally astigmatid mites are free living and fungivorous. From there the group has colonized many habitats. Astigmatid deutonymphs most commonly occur in association with coleopterans and hymenopterans in arboreal and soil habitats.

Deutonymphs can respond to both genders of the carrier or respond only to females or to males. *Naiadacarus arboricola* for example responds only to syrphid female carriers which visit water-filled treeholes to oviposit. *Rhizoglyphus echinopus* collected from the scarab beetle *Osmoderma eremicola* for example responds mainly to males (OCONNOR, 1991).

Interesting is the life cycle of *Kennethiella trisetosa*, which only matures on male larvae of the wasp *Ancistrocerus antilope* (OCONNOR, 1991). The mites propagate in the brood chambers of the wasp. Then all mite stages except the deutonymphs feed on the hemolymph of wasps in the stage immediately before the pupa phase without damaging them. The deutonymphs can only ascend the adult male wasps, because female wasp larvae kill the mites before growing up. During the wasp's copulation the mites change actively into the genital chambers of the female wasps. From there they leave that female during the egg deposition.

During the transport the deutonymphs are always positioned on the propodeum of the males on small polished cuticula areas. Because up to now no other function could be assigned to that structure, it is assumed that it evolved for the transportation of the mite deutonymphs.

Such a structure is called Acarinarium. A satisfying evolutionary explication is missing. It is assumed that a mutualistic relationship between phoret and transporteur exists. It cannot be ruled out that this relationship between mite and wasp for example bears advantages for the transporteur. But this is still unproved. Alternatively the acarinarium could be evolved in a parasitic or in a “neutral” relationship. It could be beneficial for the transporteur to have the mites restricted to areas where they are as possible less hindering (KIONTKE, 1997). Up to now acarinarium are unknown for the histiostomatids. But because I assume that some histiostomatids bear advantages for their carriers probably acarinarium will be found in future times on some carriers. The preference of one carrier gender is unknown for species of the Histiostomatidae and not mentioned in SCHEUCHER (1957) or HUGHES & JACKSON (1959) but could probably exist.

The act to ascend the carrier in astigmatid mites in general as in the histiostomatids too can occur spontaneously or can be provoked by a tactile stimulation of gnathosomal setae or solenidia (OCONNOR, 1991).

The deutonymphs of the non histiostomatid *Carpoglyphus lactis* for example show a conspicuous behavior and wait in a position with the body anchored to the substrate by the caudoventral suckers. Jumping to a height of 2.5-5.0 cm allows the mite to spring onto a passing drosophilid carrier (OCONNOR, 1991).

Deutonymphs of *Sancassania* species remain on the carrier when it dies and subsequent stages exploit the carriers as saprophages of necrotic host tissues (OCONNOR, 1991). Such a strategy is called necromeny and derived from the phoresy (SCHULTE, 1989). It appeared at least twice within the Histiostomatidae, and therefore to understand of necromenic relations was an important part of my researchs.

Sometimes deutonymphs are positioned in similar numbers on both sides of the carrier to minimize interference with the carrier flight. An example is *Glyphanoetus nomiensis* (Histiostomatidae) which is attached to the alkali bee *Nomia melanderi* (Hymenoptera: Halictidae) (OCONNOR, 1991).

It is less known concerning the detachment stimuli in the Astigmata. It could correlate with the oviposition of the carrier as observed for non astigmatid mites. Deutonymphs of *Histiostoma polypori* (Histiostomatidae) which change from one earwig stage to the following of the same individual may respond to chemical changes in the transporters cuticle (OCONNOR, 1991).

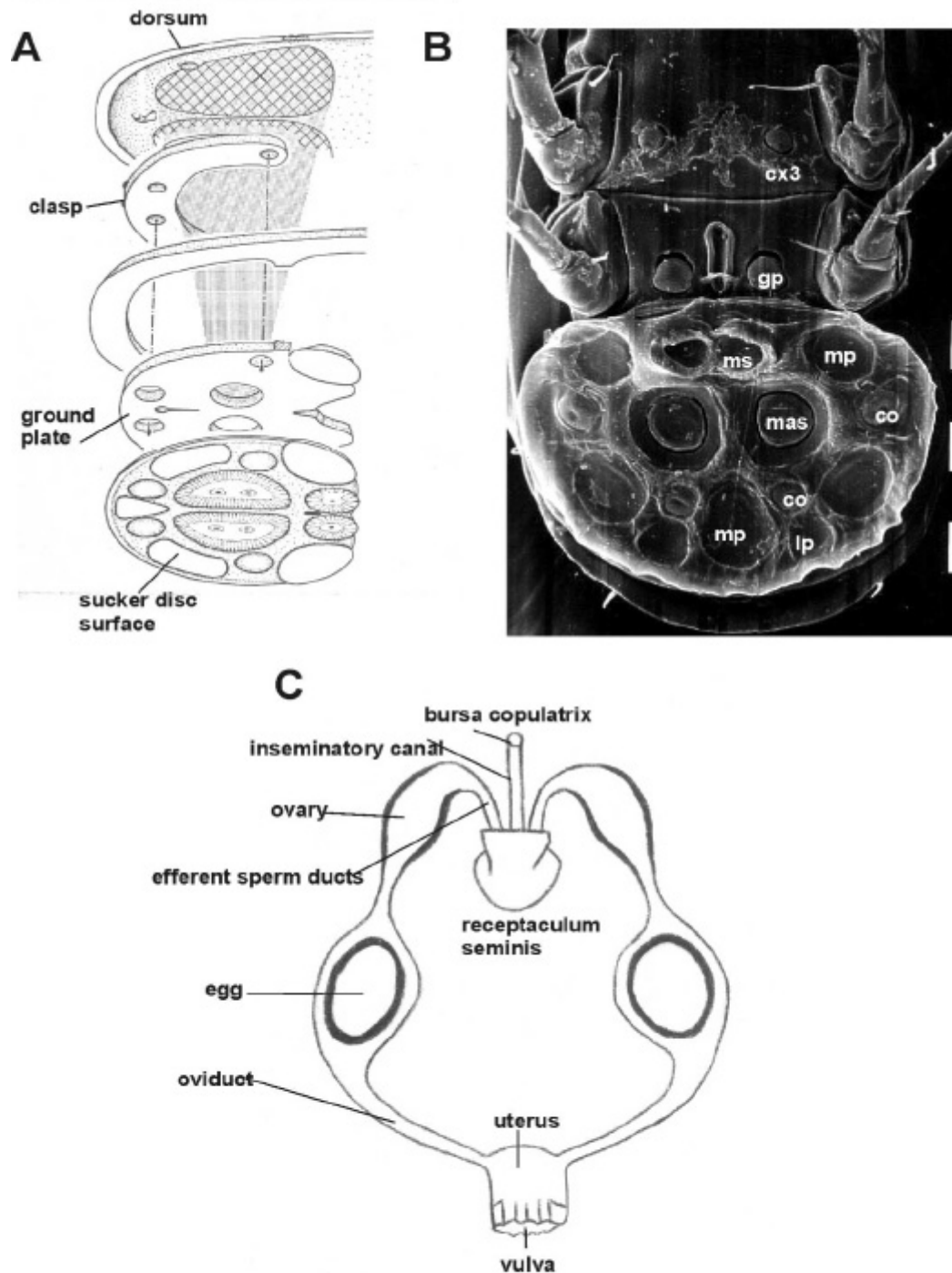


Fig2:

A: Schematic picture of the deutonymphal sucker plate, showing all cuticular components (SPIETH, 1977). B: Sucker plate of *Histiostoma palustre*. cx3, gp= conoids of the anterior mite body. ms= movable sucker, mp= movable plate, mas= main sucker, mp= median plate, lp= lateral plate, co= conoids. C= Schematic section through the female reproductive system of an astigmatid mite (EVANS, 1992).

### *Sucker plate of the deutonymph*

In my research about orientation behavior of the deutonymphs, the phoretic attachment and detachment, a conspicuous flexibility of the suckerplate became obvious. That's why some information about its composition and its ultrastructure shall be given. In the anterior row the suckerplate of an astigmatid deutonymph consists of one pair of “movable suckers” and laterally a pair of “movable plates” (SPIETH 1977). In the median row one pair of main suckers with laterally a pair of conoids is arranged. Posteriorly another pair of conoids is positioned with a lateral and a median pair of plates. The small anus is located anteriorly between the two movable suckers (Fig2B). The deutonymph possesses on its resting ventral body another 3 pairs of conoids. Conoids and suckers can be homologized with the ventral setae v1-v2 of the protonymph caused by their setiform ultrastructure and the similar arrangement.

The pattern of conoids and suckers in non histiostomatid mites corresponds to that in the Histiostomatidae. The nomenclature of conoids was adopted from FAIN and ERTELD (1998). The conoids are termed from anterior to posterior cx 1, cx 3 and gp (Fig2B), those of the sucker plate as lc (lateral conoid) and pc (posterior conoid) corresponding to their arrangement.

The sucker plate is a complex organ which enables the mite to attach and to leave the carrier precisely at the right time. It consists of several chitin elements (Fig2A), which became visible in the TEM observations of SPIETH (1977): the clasp, the groundplate and the sucker disc. The clasp, the innermost element, is horseshoe-shaped and is ventrally connected to the conoids and dorsally fixed at the endocuticula of the back shield. It functions as buffer of the conoids. The ground plate functions as support of the sucker disc surface and is a guiding structure for the conoids. The flexibility of the groundplate enables the adhesion structures to attach at a vaulted base, for example legs of carrier insects (SPIETH 1977).

The elements of the sucker disc differ morphologically and functionally. The movable suckers get extended by hemolymph pressure and retracted by muscles, which begin as four sinews at the sucker. The innervation indicates that one movable sucker is of one setal origin. In contradiction to that, one main sucker derived ontogenetically from two setae, what is among other things verifiable by two tubular bodies on each sucker. The conoids are modified setae with all typical characters of a mite seta. The shaft is filled with actinopilin which appears birefringent in a polarized beam. The basis of the conoids are innervated. As receptive structures bundles of microtubuli were identified by SPIETH (1977). These



characteristic receptors point to their function to receive mechanical stimuli. The movable plates mainly consist of chitinous cones which underlay the whole surface of these structures. The concave inside of the plate is attachment for the dorso lateral musculature and origin of muscles running to the anus. The movable suckers make the first contact to the surface of the carrier insect and bring the whole sucker plate in a suitable contact. In addition the main suckers probably function to attract the suckerplate powerfully to the base with help of their massive muscles. The conoids were interpreted to be pressure receptors while the suckerplate is coming in contact to the insect cuticula. The movable plates presumably support the detachment of the suckerplate from the insect cuticula (SPIETH 1977).

### *Female reproductive system of the Astigmata*

Cuticula modifications around the dorsal female copulation opening in the Histiostomatidae were an interesting topic of my research. Because these cuticula areas are only substructures of a complex organ, the functional anatomy of the whole female reproductive system shall be explained (Fig2C). The female reproductive system of mites consists of the ovary, genital ducts, accessory glands and the seminal receptacles.

The ovary of some derived „Oribatida“ is an unpaired structure. In the Astigmata it is paired with each ovary connected by a narrow duct to the median sac-like seminal receptaculum of the sperm access system.

The oviducts in all major mite taxa are paired. Secretions of the epithelial cells are assumed to be responsible for the formation of eggshell in the „Oribatida“ (MICHAEL, 1884) and the Astigmata (MICHAEL, 1901). The oviducts lead directly to the vulva by way of the uterus. In contrast to the „Oribatida“ the uterus is clearly developed in the Astigmata.

The vulva is of ectodermal origin. In the Acaroidea (subgroup of the Astigmata consisting of: Acaridae, Glycacaridae, Lardoglyphidae, Scatoglyphidae and Suidasiidae, OCONNOR, 1981) it was observed to be a large organ with flexible walls and lack of musculature (PRASSE, 1970). Up to now these details were obviously closer observed only in this subgroup of the Astigmata, and I assume a similar anatomy of those reproductive structures within the Histiostomatidae. Setae of the ovipositor are interpreted to be eupathidia with a mechanochemosensory function (WOODRING & COOK, 1962 a). Accessory glands are absent in most Oribatida and Astigmata (EVANS, 1992). In the Astigmata (MICHAEL, 1901) sperm is introduced through a special copulatory pore (bursa copulatrix, sperm induction pore) which leads to the sperm access system. Sperm storage and maturation happen in the sperm access system. The bursa copulatrix is located dorsally at the posterior region of the hysterosoma. A

short cuticular inseminatory canal leads to a saccular organ, the receptaculum seminis, with a wall of an epithelial layer. From there short efferent sperm ducts lead to the ovaries. In *Acarus siro* for example the receptaculum seminis is unusually and conspicuously formed with numerous cuticular lamellae dividing the organ into three regions. The sperms seem to remain in close contact with these lamellae (WITALINSKI et al., 1990).

### *Polymorphisms/ Polyphenisms*

Within the Astigmata several examples for species with morphologically differing male types in the same population exist. This phenomenon is also known for histiostomatid species SCHEUCHER (1957). Male dimorphisms of *Histiostoma feroniarum* and *H. pulchrum* within the Histiostomatidae were mentioned by SCHEUCHER, 1957. But the function and the determination of these different male types were not examined. For that reason I studied these aspects more closer.

Exclusively genetic or genetic and inductive factors are observed to be responsible for such significant differences between specimens of the same species (KNÜLLE, 2003). Male polymorphisms (here the term is used for both genetic heterogeneity and polyphenism or ecological plasticity) are not uncommon within the Actinotrichida, mostly influenced by environmental conditions. It is very common in the Astigmata and besides two subgroups of the Prostigmata, the Anystidae and the Cheyletidae. In species of the Rhizogylyphinae (Astigmata, Acaridae) four types of males are known (TÜRK & TÜRK, 1957). The homomorphic type looks similar to the female, the heteromorphic one has modified legs. Both are termed homotypes (EVANS, 1992), because they are similar in shape of the body to the ungravid female. The bimorphic males differ in the body shape from other morphs. The pleomorphic males are similar, but have additionally modified legs III. These two types are termed the bimotypes.

All four male morphs were found in *Sancassania anomalus* (EVANS, 1992). But heteromorphic and bimorphic males appeared only rarely. Pleomorphic males use their enlarged legs to fight among themselves and to kill and feed on homomorphic males. The highest ratio of pleomorphic/ homomorphic males was found at 20°C and with a diet of animal tissues. The development of these morphs therefore was observed to be dependent on environmental conditions (polyphenism), namely temperature and food supply (EVANS, 1992). Such environmental conditions were also responsible for the ratio of male types in *S. berlesei* (TIMMS et al., 1982). TIMMS et al. (1980) found that females mated with pleomorphs had a selective advantage and produced more offspring earlier than females mated with

bimorphs. Additionally a distinctive longevity of this offspring was observed. In that way a rapid increase of population numbers can happen, what could be advantageous for the survival of that species.

WOODRING (1969) observed the polymorphic male types of *Rhizoglyphus echinopus* and *Sancassania boharti* under laboratory conditions. In *R. echinopus* the heteromorphic males only appeared rarely under normal conditions. In *S. boharti* the bimorphic males predominate. In culture the suppression of morphs in both species seems to be caused by a non specific volatile pheromone. In the absence of other stages the larvae developed to both morphs in equal numbers.

Also the deutonymph stage can be affected by dimorphisms. KNÜLLE (2003) found dimorphic deutonymphs in *Glycyphagus privatus* and *G. ornatus*, one morph with attachment structures for the phoretic dispersal and another one without a sucker plate to survive inimical life conditions. The development of the morphs is influenced by environmental conditions: Poor trophic conditions lead to sedentary morphs, favorable trophic conditions to phoretic morphs (polyphenism).

*Morphology of the histiostomatid structures: gnathosoma, female copulation opening and "ringorgans"*

In the usual mite taxonomy the arrangement of ventral apodemes and of leg- and body setae offer important characters (TÜRK & TÜRK, 1957). SCHEUCHER (1957) already recognized the importance of mouthpart structures for the taxonomy of the Histiostomatidae. WURST & KOVAC (2003) tried for the first time to understand the morphology of a histiostomatid gnathosoma with help of SEM observations. I examined the structure and transformations of the palpmembrane in detail with help of histological sections (WIRTH, submitted 2002 and 2003) and explained the functional correlation with a new food supply, microorganisms in emulsion, which get shoved together by palpmembrane structures in front of the mouth.

The anterior propodosoma shield of histiostomatids and the sclerotisations dorsally on the hysterosoma of larvae and protonymphs were depicted several times (e.g. OCONNOR, 1985) but never used as arguments in systematics.

Cuticula modifications around the female copulation opening were already mentioned for some distinctive species by SCHEUCHER (1957). But series of transformations could only be reconstructed in connection with a phylogenetic tree.

The ultrastructures of “genital papillae”, “claparede organs” (Fig.3E) and “ringorgans” (WITALINSKI et al., 2002) are well documented. A similar function of all these structures is well argued (WITALINSKI et al., 2002). Though these structures are homologous the different traditional terms were retained.

#### *Habitats of the Histiostomatidae*

The biology and morphology of histiostomatid taxa, which inhabit phytotelmata as waterfilled treeholes and the pitchers of *Sarracenia* and *Nepenthes* were studied by FASHING & OCONNOR (1984) and FASHING (2002). Phylogenetic relationships of these taxa were reconstructed by the same authors.

SCHEUCHER (1957) explained the genus *Histiostoma* by the possession of a transverse vulva, HUGHES & JACKSON (1959) used some deutonymphal characters instead. However non *Histiostoma* species possess a transverse vulva and the structure, which SCHEUCHER (1957) interpreted to be a longitudinal vulva was identified as the area, where the valvulae are connected to each other (OCONNOR, 1981).

The habitats and the carrier insects of european histiostomatids were mostly precisely described by SCHEUCHER (1957). She explained some relationships of some histiostomatid species and recognized for example mites from bark beetles to be closely related to each other.

#### *Necromeny within the histiostomatids*

The histiostomatid mites *Histiostoma polypori* Oudemans, 1914, and *H. maritimum* Oudemans, 1914, were examined to be difficult to culture (SCHEUCHER, 1957). In contrast, other histiostomatids such as *H. feroniarum* develop well under laboratory conditions on microbial growth on pieces of potatoes or meat (SCHEUCHER, 1957). The former species, however have a special life strategy derived from phoretic transport and propagate only on the carrier's cadavers by feeding on microorganisms. This strategy is called necromeny. Necromenic organisms ascend a carrier organism when it is alive and complete their life-cycles on the cadaver of the former carrier (SCHULTE, 1989). Some examples from nematodes are the occurrence of dauer juveniles of *Rhabditis maupasi* Seurat, *R. marionis* Maupas and *R. pelloi* Schneider in earthworms (Lumbricidae) (VÖLK, 1950; POINAR & THOMAS, 1975). *R. papillosa* Schneider and *R. neopapillosa* Mengert are necromenic nematodes from slugs

(Limacidae and Arionidae) (MENGERT, 1953). Another example is *R. myriophila* Poinar from the garden millipede, *Oxidis gracilis* Koch (POINAR, 1986). In the case of the histiostomatid mite *H. polypori* I am extending this definition to an organism which occupies a female insect with brooding-behavior in order to later develop on cadavers of this insect's offspring. Necromenic mite species were known from other astigmatic mite groups (SAMSINAK, 1970), but the existence of necromeny within the Histiostomatidae was not fully recognised until now. In a previous study BEHURA (1956), described a bimodal strategy in the relationship between *H. polypori* and the earwig *Forficula auricularia*. That is, "the hypopi usually remained attached to the earwig until it died", and then developed on liquified material of the cadaver. But he observed the mites not only growing up on cadavers, but also, when there is the "availability of freshly decayed vegetable and animal matter". He assumed that mites developing on the cadavers of the earwig males (that usually died near the nest) and on females (that usually died in the nest) would have the possibility to attach to earwig-nymphs. as in my own observations he recognised, that a mite-deutonymph would attach to earwig-nymphs and then stay on the same individual without developing, switching from one earwig stage to the next one through the earwig's exuvial suture. The necromenic life-cycles of these two histiostomatid species and the biology of the carrier insects are described below.