

MORPHOLOGY AND CHARACTER TRANSFORMATIONS

Morphology of the gnathosoma (WIRTH, submitted 2003)

The modified mouthparts which evolved in the stem species of the Histiostomatidae differ conspicuously from those of other astigmatid mites (SCHEUCHER, 1957). That's why I examined the gnathosoma of *Histiostoma palustre* Wirth, 2003 as representative of all histiostomatids, with help of histological sections. Phylogenetic conclusions are based on my reconstruction of the cladogram of the Histiostomatidae (e.g. WIRTH, submitted 2002). Some terms of mouthpart structures will be newly introduced and are important for comparative studies and the understanding of the derived gnathosoma of *Bonomoia* n. sp..

In both the Guanolichidae and Histiostomatidae, the digitus mobilis of the chelicera is reduced to a vestigial structure. Therefore both groups are argued to be sister taxa (OCONNOR, 1981). Besides, the digitus fixus consists of two different formed parts, a proximal and a distal one (Fig4A).

proximal gnathosoma

In both groups, the Guanolichidae and Histiostomatidae, the proximal gnathosoma is similar. The pedipalps are enlarged in relation to the chelicerae (Fig4B). The preoral cavity is enclosed laterally by the chelicerae, dorsally by the labrum and ventrally by a single lobe shaped by the walls of the preoral channel (Fig5B). This structure is termed the "lateral lips" (GRANDJEAN, 1938c). The coxal endites (AESCHLIMANN, 1984) extend along the entire pedipalps and are laterally connected to them, thereby enclosing the ventral gnathosoma laterally and ventrally (Fig5A).

A median dorsal fold is termed "gnathotecal process" (EVANS & TILL, 1979) and is in *H. palustre* and all Histiostomatidae laterally connected with the pedipalps (Fig5B). The "cheliceral sheath" (EVANS & TILL, 1979) which enable the in- and outwards movements of the mouthparts are clearly visible (Fig5B). In addition the following structures were discovered: Some setiform structures in a small restricted cuticula area at the internal walls of the pedipalps (Fig5A) and more distally longitudinal cuticula elevations on insides of the coxal endites (Fig5B) and around the fused lateral lips.

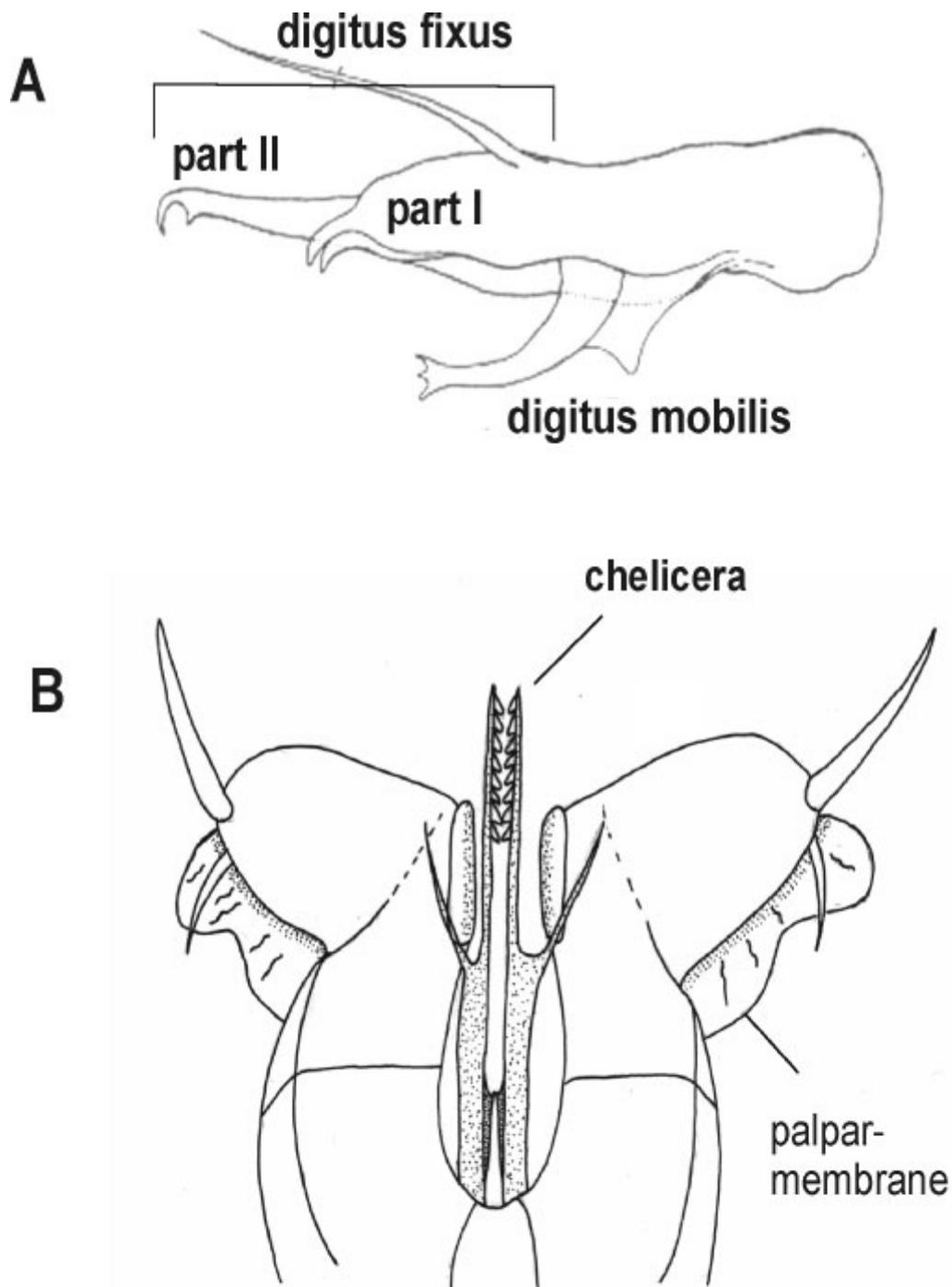


Fig4:
 A: Chelicera of a histiostomatid mite in lateral view. B: Schematic dorsal view on a histiostomatid gnathosoma.

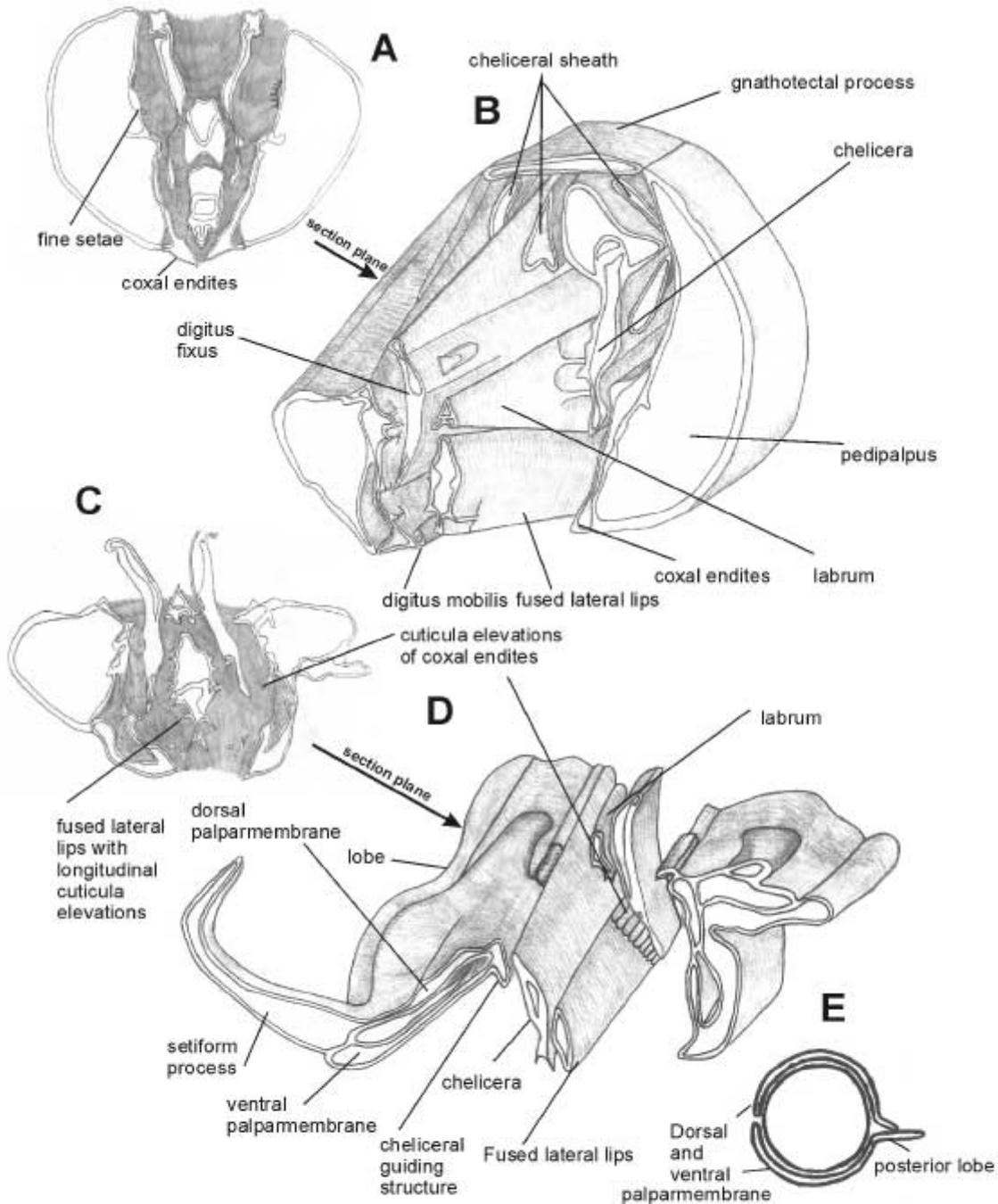


Fig5:

A: Proximal section showing a conspicuous small area with setae on the inside of each pedipalp of unknown function. B: Proximal gnathosoma of *Histiostoma palustre* reconstructed with help of histological sections. It shows two different planes, more proximally and more distally. C: Proximal section of the distal gnathosoma with longitudinal cuticula elevations at the fused lateral lips, star shaped in the transverse section. D: Distal gnathosoma shows the arrangement of the conspicuous palpmembrane, which is part of the coxal endites. E: Schematic section from anterior to posterior of the distal pedipalp article to show the palpmembrane structures and the posterior lobe.

The lateral lips are usually developed as a paired structure in other astigmatid mite groups (for example in *Lepidoglyphus destructor*) or reduced to a single ridge like structure as in *Rhizoglyphus* (EVANS, 1992). In *Histiostoma palustre* it is a distinct single structure, that I termed the “fused lateral lips”. I assume that this character is an apomorphy of the Histiostomatidae. The coxal endites are termed “malapophyses” by some authors (EVANS, 1992). I don’t use this term in the Histiostomatidae because the origin of important distal structures remains easier to follow when the term coxal endites is retained.

The function of the setiform structures on the internal walls of the pedipalps is unknown but they could function as mechanoreceptors. The conspicuous longitudinal cuticula elevations on the coxal endites could interdigitate with similar structures on the lateral lips (Figs5B,C) to prevent unusable big particles to pass the preoral cavity (“filtering structures”). My comparative studies were not suitable to prove the existence of these structures in other histiostomatid species.

distal gnathosoma

As an apomorphy of the Histiostomatidae, the coxal endites distally form conspicuous structures, a cheliceral guiding structure and the palparmembane (Fig5D). Proximally of the distal gnathosoma the coxal endites form a distinct structure with short, parallel running and downward directed components (Fig5D), which I termed “cheliceral guiding structure”.

The distal pedipalp articles are directed laterally (Fig4B). Out from the coxal endites cuticula lobes surround the distal pedipalpal articles ventrally (= ventral palparmembane) and dorsally (= dorsal palparmembane) (Fig5D). There exist three free pedipalp articles, with the second medianly elongated and reaching the anterior margin of the gnathosoma (Fig7A). In this distal area, both the distal part of article two and the total of article three are surrounded by the palparmembane structures (Fig7C). The dorsal and ventral palparmembane touch each other anteriorly and posteriorly (Fig5E). One pair of setiform processes origin on each end of the distal pedipalp articles (Fig5D). In addition, parts of the ventral palparmembane are posteriorly elongated. I term this structure the “posterior lobe”(Fig5E). Contrary to the labrum, the fused lateral lips run to the anterior margin of the gnathosoma (Fig5D). Further proximal they built longitudinal cuticula elevations (Figs1C,D) similar to those of the coxal endites of the proximal gnathosoma.

The strongly shortened coxal endite elements (Figs5D,7C) are interpreted as ventral cheliceral guiding structures. The dorsal cuticula areas of the median parts of the second free pedipalpal articles are folded upwards and function to guide the chelicerae dorsally (Figs7B,C). Distally of the coxal endites of “Oribatida” the rutella are positioned and interpreted to be of setal origin by GRANDJEAN (1957 c). In the same position in the Astigmata a structure with the lack of a basal root and of birefringence is termed pseudorutella (JOHNSTON, 1965). Apparently the morphologically distinctly separated “ventral cheliceral guiding structures” (Fig5D,8i) could be homologous to that structure. It is not of setal origin and is shaped by the coxal endites as in the pseudorutella of non histiostomatid Astigmata. To emphasize its function in the Histiostomatidae it is termed “ventral guiding structure”.

WURST & KOVAC (2003) described the morphology of the gnathosoma of *Tensiostoma veliaphilum* Wurst & Kovac, 2003 with help of a SEM preparation using dorsal and ventral view and a longitudinal section. A terminology for the structures was introduced. But because some structures are distinctly modified and others are missing, that derived gnathosoma does not represent a typical histiostomatid gnathosoma and therefore cannot be used as a model for all Histiostomatidae. The introduced terminology can partly not be adopted, because important structures are missing in that species and some given terms are not suitable for use in comparative studies. The distal pedipalp articles of *T. veliaphilum* are unusually elongated and tube shaped. The posterior lobes are reduced to hardly visible rests. The cheliceral guiding structures are completely missing. The distal cuticula vaultings formed by the coxal endites (Fig8i) are unusually enlarged. That’s why the “rostral funnel” between these vaultings (“distal part of hypostome”) and the distal pedipalp articles “normally” does not exist. I termed the “hypostomal ridge” “fused lateral lips”, because the homology of these structures to those of non histiostomatid mites is obvious. It is unclear whether the longitudinal cuticula elevations proximally of the fused lateral lips of *Histiostoma palustre* are divided into equally sized denticles as in *T. veliaphilum*, where a longitudinal row of such denticles is found in the “hypostomal ridge”.

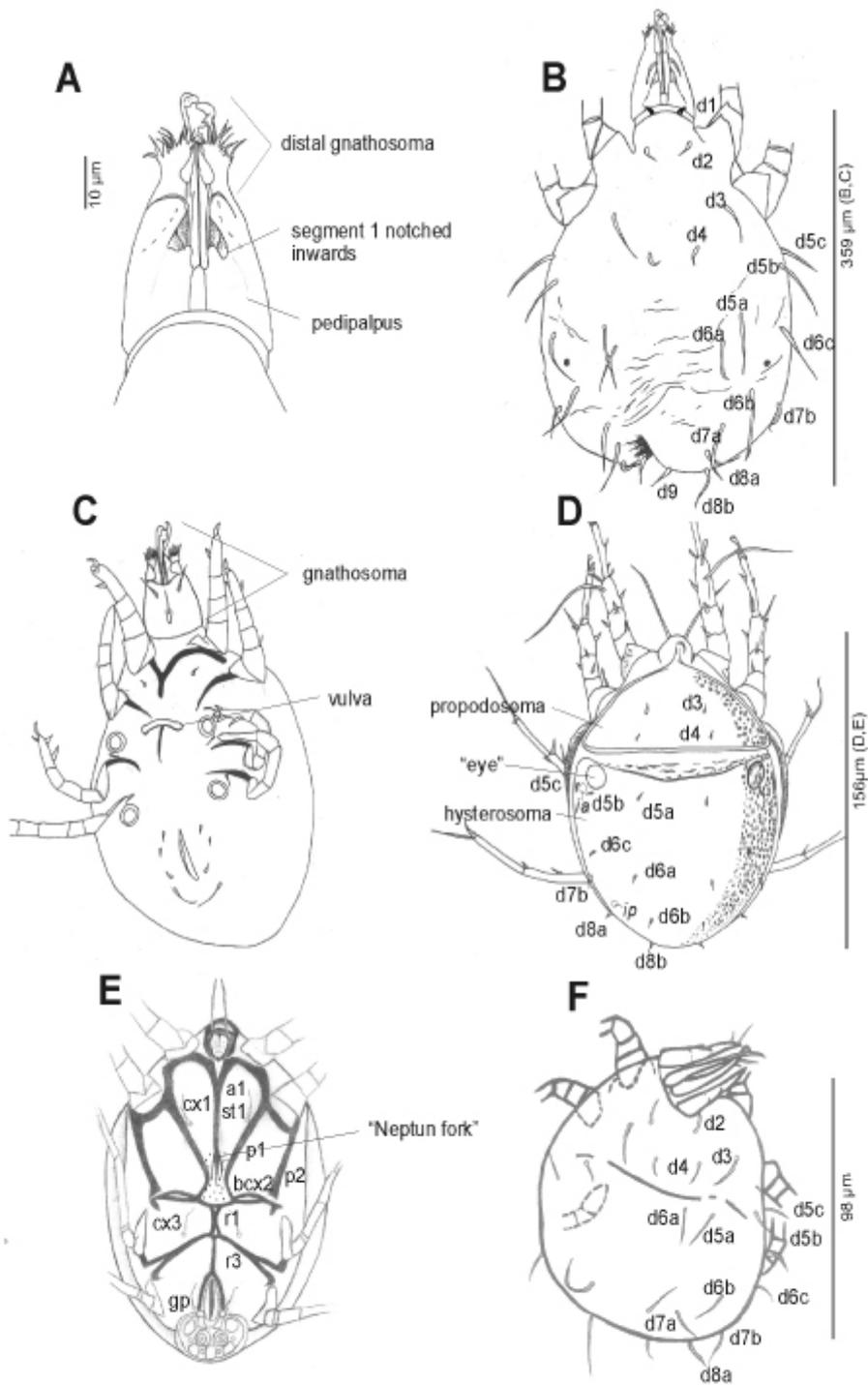


Fig6:

A: Total gnathosoma of *Bonomoia* n. sp. in dorsal view. B: Female in dorsal view. C: Female in ventral view. D: Deutonymph in dorsal view. E: Deutonymph in ventral view. F: Larva in dorsal view. d1-d9= dorsal setae; ia, ip= cupules; a1, st1, p1, p2, bcx2, r1, r3= ventral apodemes of deutonymph; cx1, cx3, gp= ventral setae of the deutonymph, homologous to the conoids.

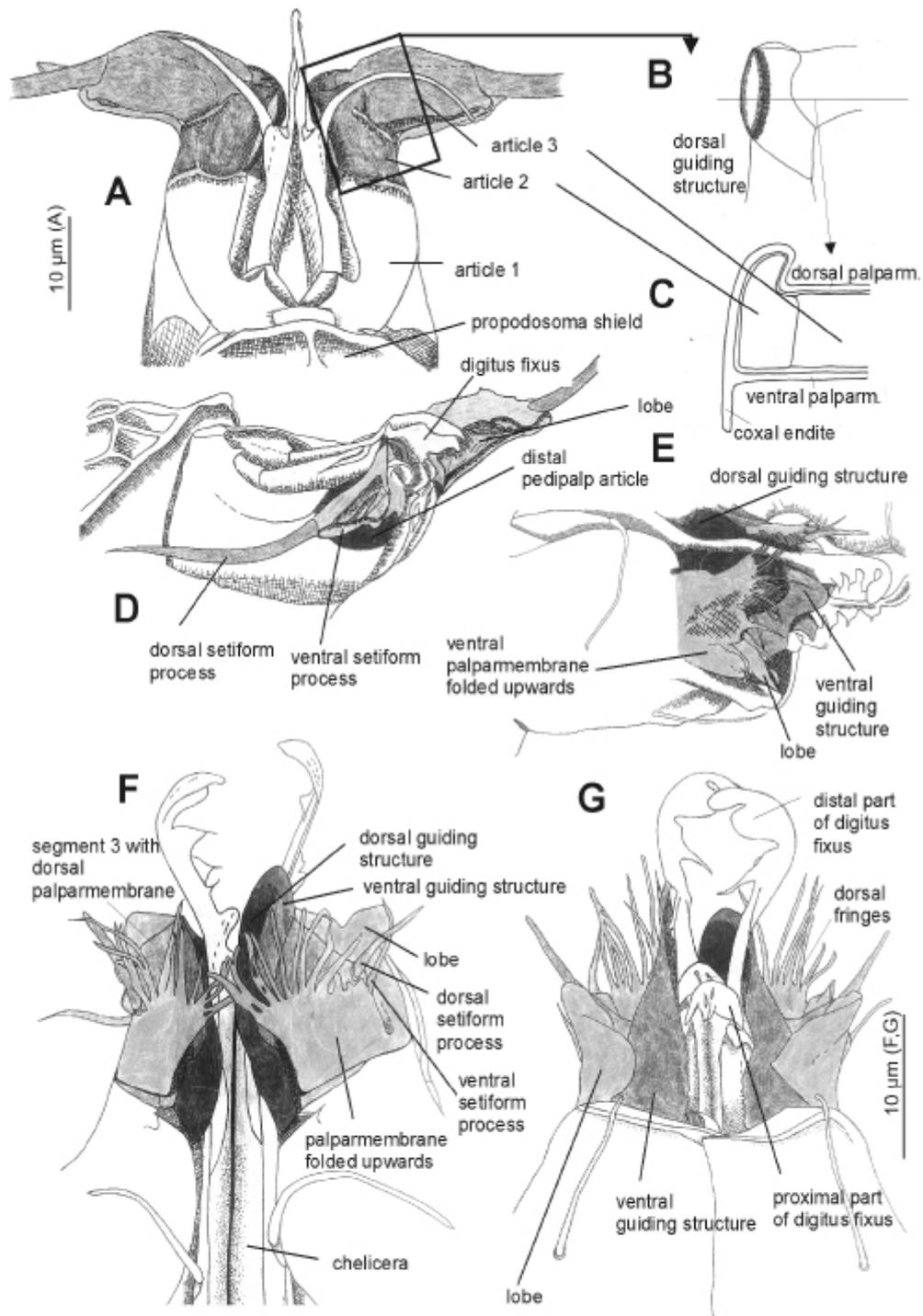


Fig7:

A: Gnathosoma of *Histiostoma* sp. in dorsal view. B: The dorsal guiding structure enlarged in dorsal view. C: Schematic section through the distal right gnathosoma from median to lateral. D: Gnathosoma in lateral view. E-G: Gnathosoma of *Bonomoia* n. sp. (E) in dorsal view, (F) in lateral view, (G) in ventral view.

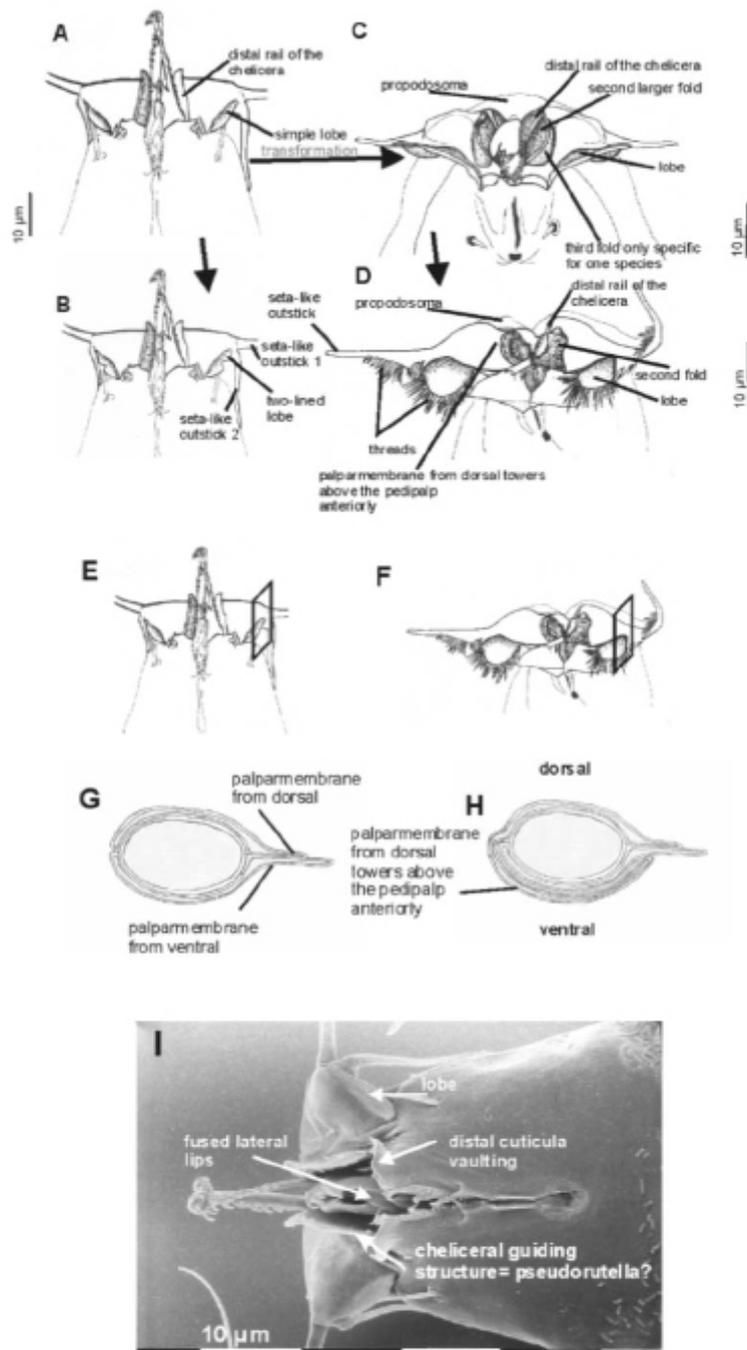


Fig8:
 A: Gnathosoma of *Bonomoia* sp. in schematic ventral view showing a rounded palpmembrane lobe. B: Gnathosoma of a member of the *Histiotoma feroniarum*-group in ventral view showing a divided lobe. C: Gnathosoma of *Histiotoma* sp., a bark inhabiting mite, showing a second ridge besides the ventral cheliceral guiding structure. D: Gnathosoma of *Histiotoma ruehmi* in ventral view. E, F: Gnathosomas of *B. sp* and *H. ruehmi* in ventral view. G, H: Schematic lateral sections from anterior to posterior. I: Ventral view to the gnathosoma of *H. palustre*. Usually the lobe of that species is divided into two parts, but not found in that specimen.

Feeding behavior

Own observations showed that the gnathosoma shoves microorganisms together into mounds in front of the mite's mouth. The posterior lobe that is directed downward (Fig1F) as a result of the gnathosome being distally bent upward aides in mounding the microorganisms in front of the mouthparts, working like an automobile windshield wiper. Probably the distal cuticula vaultings (Fig8i) shaped by the coxal endites support the function of the posterior lobes. I did not observe a mobility of the pedipalps or the setiform processes during feeding. This is confirmed by WURST & KOVAC (2003).

The setiform processes laterally of the distal pedipalp articles are interpreted to be solenidia by some authors (e.g. WURST & KOVAC, 2003) caused by the lack of birefringence. Nevertheless this fuction as chemosensitive structures probably remains doubtful, because it is unproved, and the lack of actinopilin is at most an indirect indication. I assume that they probably support the piling of microorganisms by enlarging the surface of the lobes and other palparambrane structures to lateral. The setiform processes of *Histiostoma ruehmi* for example have conspicuous cuticula fringes on their bases as the other ventral palparambrane structures too. The surface of the whole gnathosoma is additionally enlarged in that way (WIRTH, submitted 2002). The setiform processes of that species are as well modified as the other mouthparts which are important for the piling of microorganisms, what seems to confirm my assumptions concerning the function of these processes.

Important structures for comparative studies

The following structures offered important arguments for my reconstruction of the phylogeny of the Histiostomatidae: dorsal and ventral palparambrane, posterior lobe, cheliceral guiding structure, second and distal free pedipalp article. Concerning these structures *H. palustre* represents character states of the stem species of the Histiostomatidae. The morphological understanding of these structures and the introduction of terms facilitate the description of mouthparts of other species as the conspicuously derived in *Bonomoia* n. sp..

Phylogenetic position of Bonomoia n. sp (WIRTH, submitted 2003)

A morphologically and biologically conspicuous new species was discovered from rotting pieces of *Opuntia* sp. (Fig16B) in Sardinia, Italy, and was named *Bonomoia* n. sp. (WIRTH, submitted 2003). It was argued to belong to the monophyletic taxon *Bonomoia*.

Arguments for the species' status

Bonomoia Oudemans, 1911 is a monophyletic taxon as indicated by the following morphological apomorphies of the deutonymph, which I reconstructed:

- Light sensory organs (“eyes”) on the anterior hysterosoma (Fig6D)
- cx1, cx3 and gp are elongate setae and not conoidal formed (Fig6E)
- Area around the anterior sternum armed with lots of cuticula points (Fig6E)
- Solenidia Phi of legs I conspicuously elongated (Fig6D)

Probably the taxon *Copronomoia* Mahunka, 1976 originates within *Bonomoia* or is its sister group caused by the light sensory organs of the deutonymph, which exist in both groups. Species assigned to the genera *Copronomoia*, *Probonomoia* Fain & Rack, 1987 and *Bonomoia* seem not to differ distinctly enough to substantiate the classification to different genera.

Arguments for the phylogenetic placement of *Bonomoia*

Bonomoia was discovered to be the first basal branch within the Histiostomatidae (Fig3). The larvae (Fig6F) as well as all other instars of *Bonomoia* lack dorsal sclerotisations. The stem species of *Bonomoia* and its sister group consisting of all other histiostomatids developed a symmetric pattern of dorsal sclerites in larval and protonymphal instars. I found only this character to separate *Bonomoia* from all other groups (WIRTH, submitted 2004).

Palpalmembrane transformations of B. opuntiae

The following structures are conspicuously derived in *Bonomoia* n. sp. In the cultures only deutonymphs and females (Figs6B,C) grow up and could be examined: the dorsal guiding

structure is enlarged dorsally (Fig7F); the ventral cheliceral guiding structure is forwardly elongated (Fig7G); the second pedipalpal article is small in relation to other histiostomatid species; the distal pedipalpal articles are strongly shortened, and parts of the ventral palparmembrane are elongated to form dorsal hair-like fringes on their anterior margins (Figs6A, 7E,F). Parts of the propodosoma of the deutonymph bear the gnathosomatal vestigials (Fig25C).

Presumably the uptake of microorganisms occurs in a manner that was derived from the usual mechanism where the laterally directed distal pedipalpal articles with ventral lobes function to sweep microorganisms together into mounds in front of the preoral cavity. In “usual” histiostomatids the function of the laterally arranged pedipalpal articles and their lobes is therefore analogous to that of automobile windshield wipers.

Because this *Bonomoia* species lives submerged in the fluid-like habitat, it cannot funnel the microorganisms into mounds as do many other histiostomatid species. Presumably the ventral lobes and dorsal fringes act together as basket to catch the microorganisms by filtering them out of the fluid as the mite moves about. The food is then transported by the chelicerae to the opening of the pharynx. The transport through the preoral cavity could be supported by the enlarged ventral and dorsal cheliceral guiding structures by preventing the food emulsion from drifting away laterally.

Palparmembrane transformations within the bark inhabiting group (WIRTH, submitted 2002)

The palparmembrane is a morphological adaptation of the histiostomatids to exploit a new food resource, microorganisms. Several times within the Histiostomatidae its structure was transformed in connection with opening up new niches.

Within the paraphyletic “*Histiostoma*” this structure (Fig8A) was transformed into a two-lined lobe (Fig8B) in the stem species of the *Histiostoma feronarium*-group. The stem-species of this monophyletic group probably lived in muddy banks around waters. The structure could be an adaptation to feed microorganisms in these habitats.

Mites of the monophyletic Bark inhabiting-group are adapted to habitats within wood. The stem species of the Bark inhabiting-group consisting of the camouflage-group and the bark beetle-group (including the *H. dryocoeti*-group and the *H. piceae*-group, Fig3) evolved a more complex palparmembrane. The ventral cheliceral guiding structure is enlarged and a second larger fold more laterally on each side (Figs8C,20B, depicted is an unknown species with a

third ridge in addition) is formed. Presumably such a more complex structure is necessary to push together microorganisms in such a drier wooden habitat.

Derived from these palparmembrane modifications, a conspicuous membrane structure divided into lots of fringes evolved in *Histiostoma ruehmi* Scheucher, 1957 (Figs8D,20A).

Laterally of the ventral cheliceral guiding structure of *H. ruehmi* a second ridge is shaped by the palparmembrane as it is usual in members of the bark inhabiting-group. But it is thickened and distally bulged to lateral (Fig8D). Contrary to other histiostomatids (Figs8E,G) and apomorphic for *H. ruehmi*, parts of the dorsal palparmembrane distinctly are elongated to anterior and from there unusually nestle against the posterior lobe (Figs8F,H). Both structures, the anteriorly elongated palparmembrane fold and the posterior lobe are divided into fringes. Additionally the setiform processes formed by the dorsal palparmembrane are basically threaded (Fig8D). There's no indication of the functional necessity of these fringes. Probably feeding in that habitat needs an enlarged shove-area of the palparmembrane to push the microorganism-emulsion together. *H. ruehmi* was found in the mulm of oaks. As transporters of the deutonymph larvae of species of Staphylinidae or Myrmicinae were assumed (SCHEUCHER, 1957).

Propodosoma shield

The propodosoma shield is an area of an eminently thickened cuticula dorsally of the anterior propodosoma in the adults and juvenile stages (except the deutonymph). It is a plesiomorphic character of the Histiostomatidae. As an apomorphy of the Histiostomatidae it is divided into a symmetric pattern of fields (Figs9B,22B). A nomenclature was introduced in WIRTH (2002). According to the conventional nomenclature of the carapace shields of turtles, fields of the propodosoma shield are termed in unpaired Zentralia and paired Lateralialia and Marginalialia. The dorsal setae d2 (Fig9B) are important markers to identify the fields M2, M3, M4 and L3 (it is positioned always midway) between species.

These fields are formed by cuticula areas which are concavely vaulted into the mite's body. Histological sections of an adult female of *Histiostoma palustre* were performed to examine the morphology and the function of these fields.

It became obvious, that a section through the shield resembles to a corrugated iron, that is vaulted up and down, with the cuticula everywhere nearly in the same thickness (Fig9D). The propodosoma shield is the area of origin for muscles moving different parts of the

gnathosoma (Fig9D). Probably caused by the thin cuticula of the Histiostomatidae these longitudinal and transverse pits and elevations evolved to resist the tension of muscles. Histological dorsal sections show more in the depth a pattern of upturning muscles which is similar to the pattern of fields on the shield. That's why it is assumed that the fields are the places where the muscles originate.

Changes of this pattern within the Histiostomatidae therefore could indicate transformations of strongness and position of muscles moving the mouthparts.

Transformations of the propodosoma shield

As an apomorphy the stem species of the group including *Histiostoma feroniarum*, *H. polypori* and *H. insulare* presumably lost the fields Z2, Z3, L2 and L4 completely. Then M6 and M7 were displaced medianly (Fig9C). M6 and M7 are defined to be similar in size to M1 until M5 and are positioned at the posterior edge of the propodosomashield. The homologisation of M6 and M7 is based on these two characteristics. Another not favored possibility would be the complete reduction of M6 and M7 and the enlargement of Z3 and L4, what would be argued by the characteristics of Z3 and L4 to accompany the field L3 (Fig9B,C). The characters of the propodosoma shield would gain in complexity in coherence with the comprehension of the distribution of the musculature thereunder, what is still unobserved.

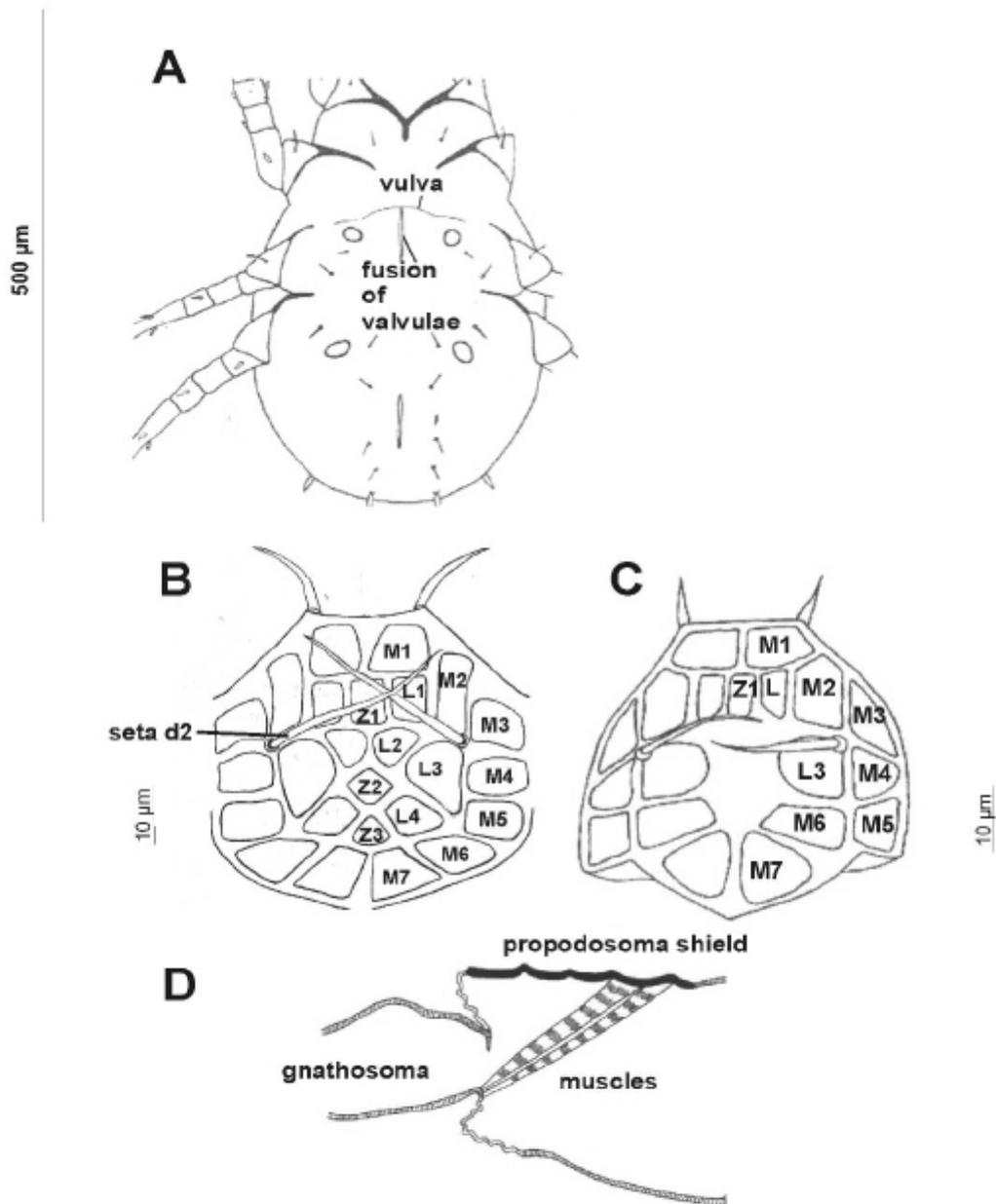


Fig.9:

A: The vulva of *Bonomoia spinifera* and the area where the valvulae fuse with each other and form an apodeme like structure. B: Dorsal view on the propodosoma shield of *Histiotoma palustre*. C: Propodosoma shield of *H. feroniarum*. D: Longitudinal histological section through the propodosoma shield of *H. palustre*.

figures A, C modified after SCHEUCHER (1957)

Pattern of dorsal setae (WIRTH, 2003)

The symmetric pattern of dorsal setae in adults and deutonymphs of the Histiostomatidae is equal in numbers and similar in the arrangement of the setae (Figs10B,C). Setae 1-4 are accommodated in 9 transverse rows. The rows 1-4 consist of two setae, rows 5-6 of six setae and the rest of four setae each. The rows 1-4 are situated dorsally of the propodosoma. I introduced a simple nomenclature in numbers from anterior to posterior (Fig10A) for the pattern of dorsal setae in all stages (WIRTH, 2003) similar to that proposed by SCHEUCHER (1957). My nomenclature follows the arrangement of hysterosomatal setae in rows as it was discovered by GRANDJEAN (1934). I did not adopt the nomenclature of GRANDJEAN (1934) and GRIFFITH et al. (1990) because one pair of setae on the propodosoma (either sce or scx) was lost in the stem species of the Histiostomatidae, therefore the homologisation of the remaining setae with those of the oribatid mites or other Astigmata is complicated. The pattern of setae of taxa which branch off basically within the Histiostomatidae (as for example *Bonomoia*) concerning the formation in rows, quantity and position of the setae (Fig10A) is homologous to the pattern in the Malaconothridae (the assumed sister group of the Astigmata). Because setae of the propodosoma of Malaconothridae and Histiostomatidae differ in number and arrangement the homologiation is complicated.

Transformations of that pattern

Within the Histiostomatidae the position of dorsal setae on the hysterosoma changed in the stem species of the assumed monophyletic group consisting of *Aphodanoetus*, *Glyphanoetus*, *Rhopalanoetus*, *Spinanoetus*, *Wichmannia* and the monophyletic *Histiostoma*-group (Fig3). Setae d5a changed to lateral, d6a to anterior, d6c was displaced to median, only d6b remained at the original place near the openings of the opisthonotal glands (Fig10A,B).

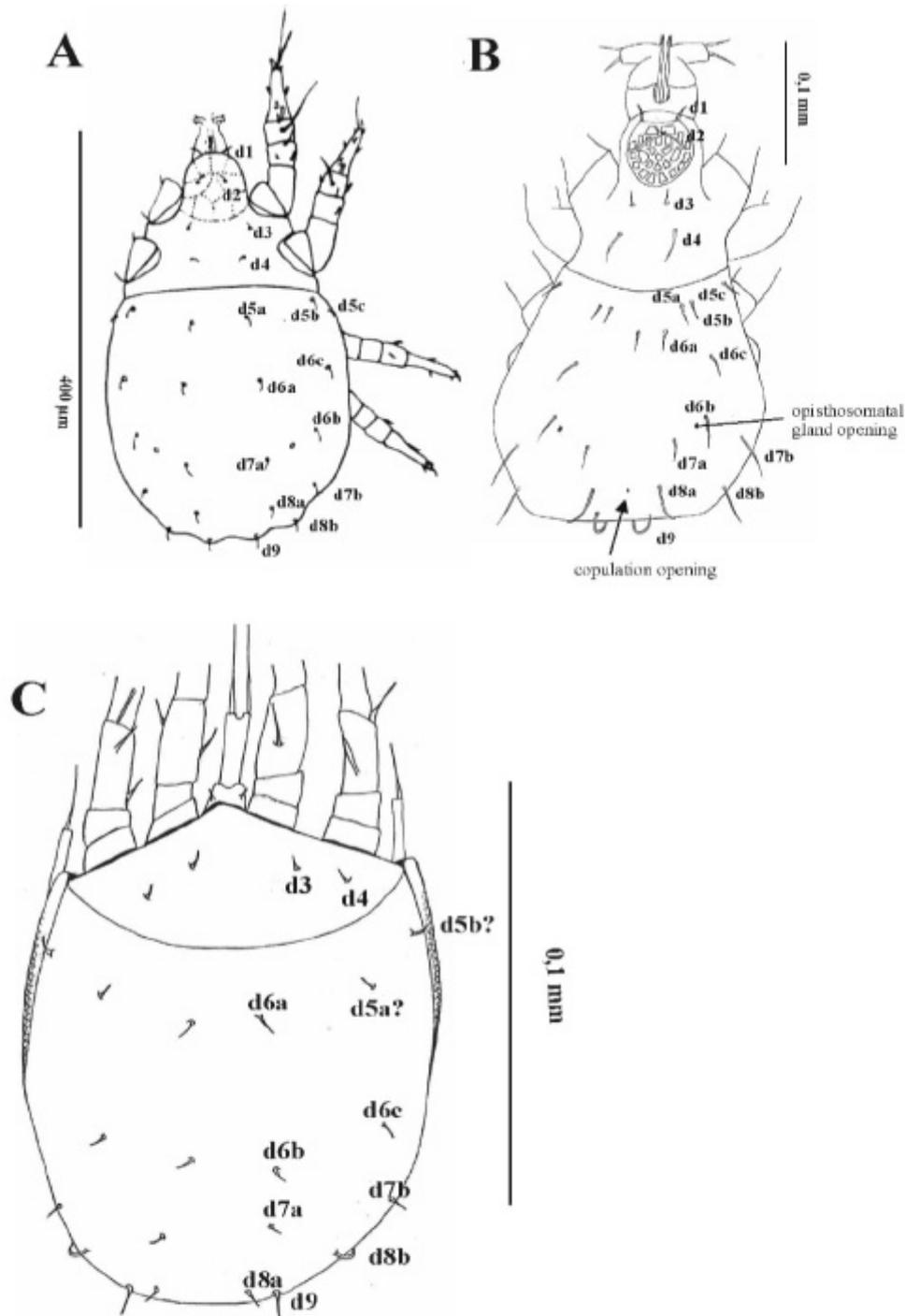


Fig10:
 A: Female of *Bonomoia spinifera* in dorsal view showing the pattern of dorsal setae, that is arranged similar to that of the Malaconothridae. B: Dorsal view on the female of *Histiostoma palustre*, showing a modified pattern of dorsal setae. C: Deutonymph of *H. palustre* showing the typical astigmatid pattern of dorsal setae.

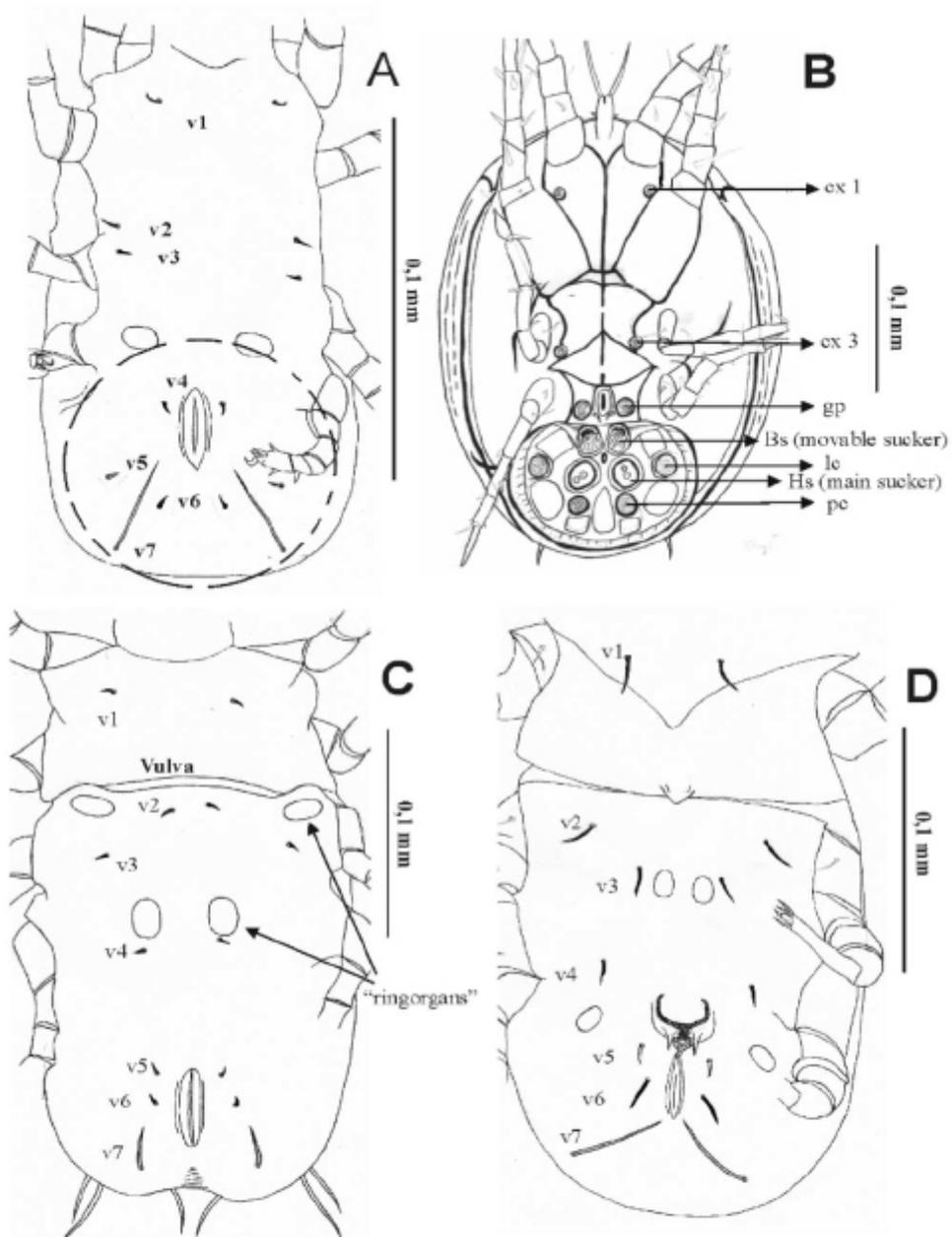


Fig11:
 Stages of *Histiostoma palustre* in ventral view. A: Protonymph. Setae marked with a circle are homologous to the sucker plate structures of the deutonymph. B: Deutonymph. C: Female. D: Male. cx1, 3, gp, lc, pc= conoids, Bs, Hs= suckers, v1-v7= ventral setae.

Pattern of ventral setae (WIRTH, 2003)

Histiostomatid protonymphs possess ventrally 7 pairs of setae (Fig11A). In the *Histiostoma*-group the number of setae in adults corresponds to that in protonymphs (Fig11C,D). The setae of males, females and protonymphs in that group are in numbers and arrangement serial homologous to each other. They are designated as v1 to v7 counting from anterior to posterior (Figs11A,C,D).

Setae v4-v7 in the protonymph are assumed to be homologous to suckers and conoids of the deutonymphal sucker plate (Figs11A,B).

Again the nomenclature of GRANDJEAN (1934) could not be adopted for members of the *Histiostoma*-group, because the few setae in the area around the anus could not be homologized with the many setae of the Malaconothridae.

Basically branching histiostomatids possess 8-10 pairs of ventral setae in the adults. In the development from the protonymphs to the adults some additional setae are added. 7 pairs of ventral setae of the adults in the *Histiostoma*-group is a derived character state within the Histiostomatidae and it is conserved in this group.

Transformations of the copulation opening (WIRTH, submitted 2004)

In basal branches of the Histiostomatidae, the dorsal copulation opening is simple and small (Fig13D, left), as for example in *Bonomoia pini*. In other species, the copulation opening consists of two parts. The opening of the bursa copulatrix towers above the cuticula plane as small conical structure. The area of the posterior cuticula is vaulted partly upwards covering the bursa like a fold and found by me for example in *H. feroniarum* (Fig13D) and other species of the *Histiostoma*-group. It was discovered in *H. cossi* (SCHEUCHER, 1957). By mapping these characters on the reconstructed tree, the copulation opening divided into two parts appears to be derived from the simple type once in the stem species of the *Histiostoma*-group (Fig13A).

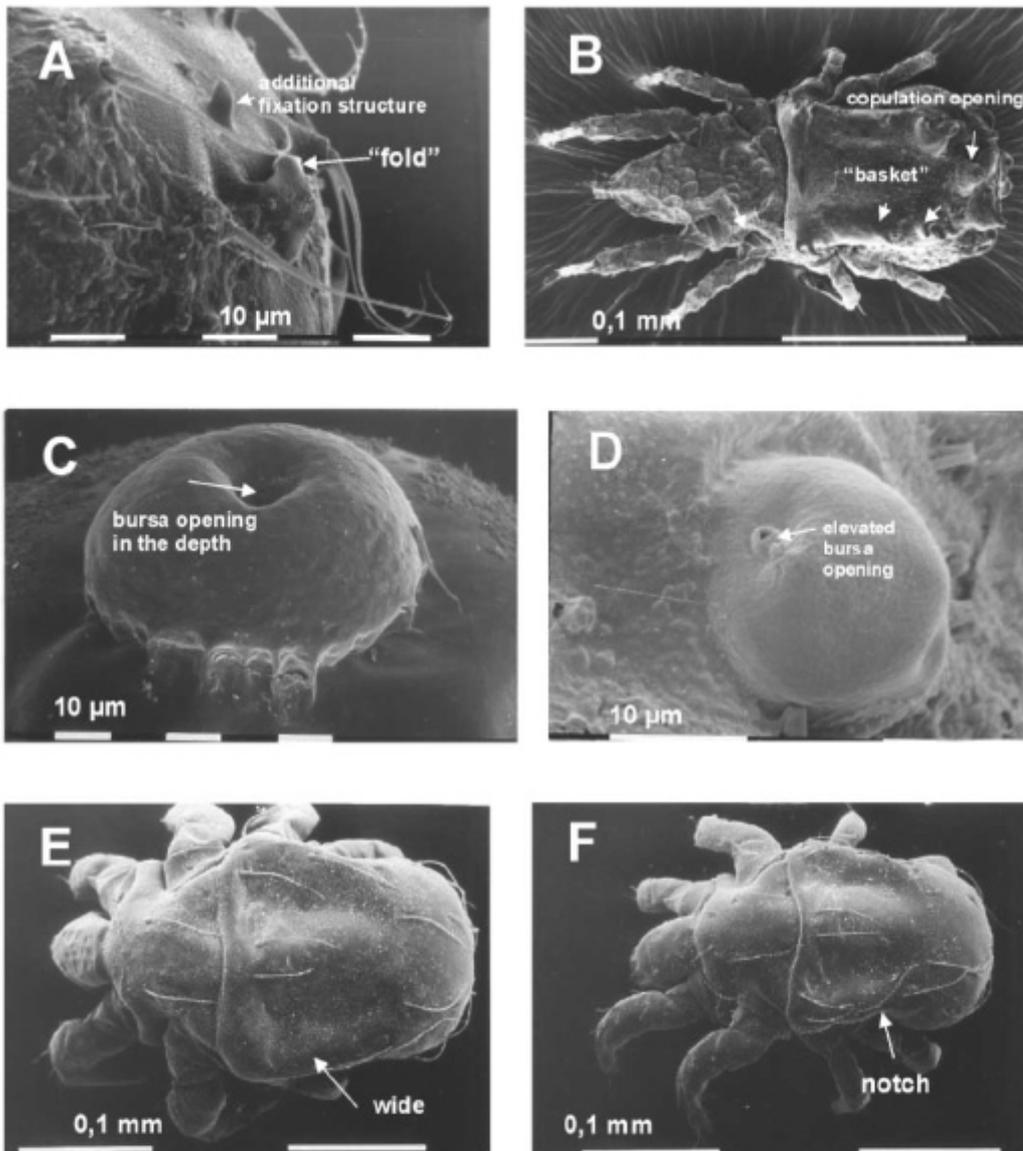


Fig12:

A: Copulation opening of *H. sp. 1* (compost/ Saarland/ Germany) with a small additional fixation structure. B: female of a new *H. n. sp. 1* in dorsal view (tree stump/ Saarland/ Germany). C: Copulation opening of *H.maritimum*. D: copulation opening of *H. sp.* (from *Melolontha melolontha*). E-F: *H. n. sp.* (related to *H. pulchrum*)E: big male morph of in dorsal view. F: small morph in dorsal view.

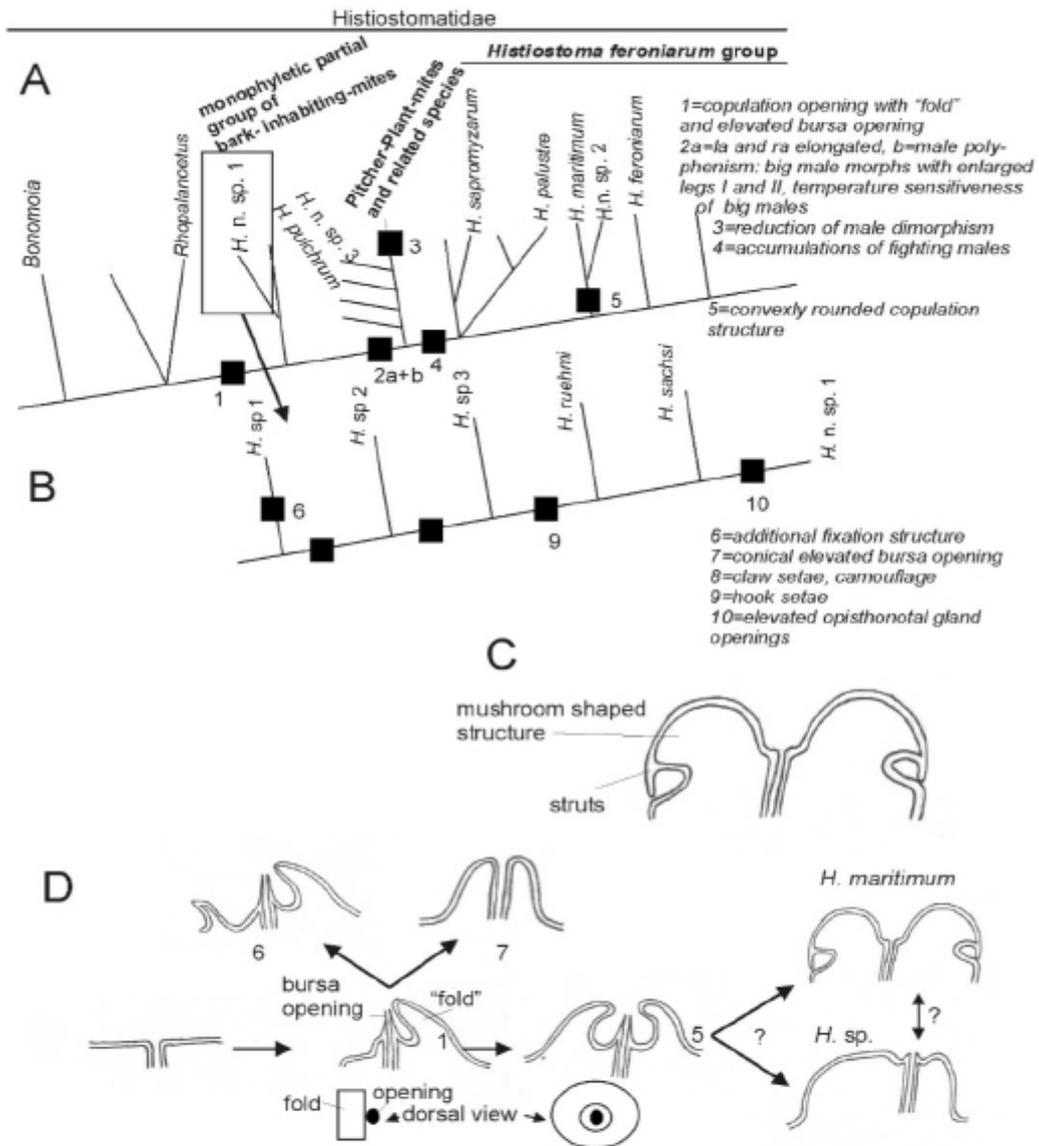


Fig 13:
 A: reconstructed cladogram of the Histiostomatidae. B: phylogenetical relationships of the camouflage-group. C: schematic section through the conspicuous copulation structure of *Histiostoma maritimum*. D: transformations of the female's copulation opening in a schematic section. 1, 5, 6, 7 = apomorphies explained in FigA.

1) Within a monophyletic subgroup of the “Bark-inhabiting-group” (Fig13A), the camouflage group, an elevated chimney-like copulation opening evolved (Fig13B). Before substrate camouflage evolved, the copulation opening was elevated (Fig13B). These mites live in a substrate full of adhesive rotting material. It is assumed that the elevated conical copulation opening evolved as an adaptation to a mite body partly and temporarily covered by substrate. The undetermined species *Histiostoma* sp. 1, found in compost (Saarland/ Germany, Figs12A) presumably represents the first branch within the camouflage-group (Fig13B). Out from the arrangement of setae in both sexes on the hysterosoma in longitudinal rows, the basket-like pattern of further evolved species of that group derived (Fig12B). The copulation opening of *Histiostoma* sp. 1 is of the complex type (conical ending and fold). However the fold is enlarged and the conical bursa ending is not as usual visible under the fold ending. In addition, in front of the opening, there is a thorn shaped structure, which presumably supports the male’s fixation (Fig12A) and which is interpreted to be an apomorphy of that species. Since the described type of copulation opening with conical ending and pocket appeared in the stem species of the *Histiostoma*-group (Fig13A), it is assumed that the chimney shaped opening in the camouflage-group derived from this type (Figs13D,12B). It is thought that the conical elevated bursa became enlarged in evolutionary steps to that structure and the pocket shaped cuticula area was completely lost.

2) The copulation opening of *Histiostoma maritimum* (Figs12C, 13C) is conspicuously shaped. The species lives in tunnels inside the mud around waters in a wet substrate and is adapted to the beetles *Heterocerus fenestratus*, *Heterocerus fuscus* and species of *Bembidion* and *Elaphrus*. The main carriers are the *Heterocerus* species. *H. maritimum* is a necromenic organism: the mites grow up on the cadavers of the former carrier (WIRTH, submitted 2002).

The copulation opening is in a big rounded, elevated and convexly vaulted structure. Basically cuticular struts run downwards from the ventral ridge of this vaulted and mushroom shaped structure (Fig13C). The surface is rough and shows an irregular pattern of notches. The opening is located in the centre, beginning as a wide and funnel-shaped opening, that narrows in depth (Fig12C).

3) A species *Histiostoma* n. sp. 2 was found on cadavers of the beetle *Melolontha melolontha*. Conspicuous characters of that species are the ventral lobes of the palpmembrane which divide into fringes and distinctly small conoids of the deutonymph. The digitus fixus of the

chelicera is divided into teeth-like structures, which are arranged in a pattern that evolved as an apomorphy in the stem species of the *H. feroniarum* group. The most conspicuous apomorphy of *H. n. sp. 2* is a rounded, enlarged cuticula area around the female copulation opening (Figs12D,13D). The distension is similar to the structure around the copulation opening of *H. maritimum*, which I observed additionally, but the cuticula is thinner and the bursa opening surmounts the cuticula plane contrary to *H. maritimum* (Fig13D).

This structure would be the only possible synapomorphic character in favour of a sister group relationship between *H. maritimum* and this unidentified species (Fig13A). Perhaps the enlarged and rounded structure occurred in their stem species as a transformation from the elevated bursa and fold type. The cuticula anterior to the bursa opening vaulted upwards and closed the fold (Fig13D). Nevertheless, it remains open to question which type developed first, with a deep or an elevated opening.

Pattern of apodemes in adult mites

The coxae of all Acariformes in all stages fused with the ventrum (KAESTNER, 1965). The lateral walls of the coxae remained ventrally as apodemes. Muscles origin from there to move the gnathosoma and the legs and besides presumably function to stabilize the whole ventral part. Species of astigmated mites show ventrally a pattern of clearly visible apodemes (Fig11B,14B,18C). The pattern enables the homologization of apodemes between the species of the Histiostomatidae. Caused by its bigger complexity especially the pattern of apodemes of the deutonymph is important for comparative studies in order to reconstruct the phylogeny. For the simple pattern of non deutonymph stages, a nomenclature describes the position of the apodemes related to the legs from anterior to posterior: a1, s (= sternum), a2, p2, a3 and a4 (Fig18C).

In *Myianoetus* and *Pelzneria* the apodemes a1 of the females are not connected to each other, p 2 is elongated in direction to the vulva and apodemes L 4 (Fig.14A) of the deutonymph do not exist or are reduced to vestigial structures.

These characters can be interpreted as synapomorphies, which argue *Myianoetus* and *Pelzneria* to be sister taxa.

Characters of the pattern of apodemes in general are not really complex. But the morphology of muscles within the Histiostomatidae is still unobserved. That's why gradual differences were unaccounted for the phylogenetic reconstruction.

Pattern of deutonymph apodemes (WIRTH, 2003)

In the deutonymphs of the Histiostomatidae these apodemes form a characteristic pattern, which can be homologized between the species. I named the medianly running apodeme, which can be interrupted, “sternum”. From there 4 apodemes branch off in both directions, what reminds of ribs of the Vertebrata. That’s why these apodemes are named r1 until r4. The double-sided apodemes which run to the trochanters of legs I and II shall be named a1 (anterior) and p1-p2 (posterior) according to their positions in the correspondent coxal apodemes. Laterally of legs III and IV the lateral apodemes L3 and L4 are arranged on both sides. The apodeme running underneath of the coxal field 2 is called bcx2 (Fig14A).

The pattern of *Histiostoma palustre* corresponds widely to that of basically off branching groups of the Histiostomatidae like *Bonomoia*, *Glyphanoetus* or *Wichmannia*. The existence of apodeme 2 is an apomorphic character of the stem species of the *Histiostoma feroniarum* group, and the availability of an elongated apodeme l3 a synapomorphy of *H. palustre* and *H. litorale* (Fig14A).

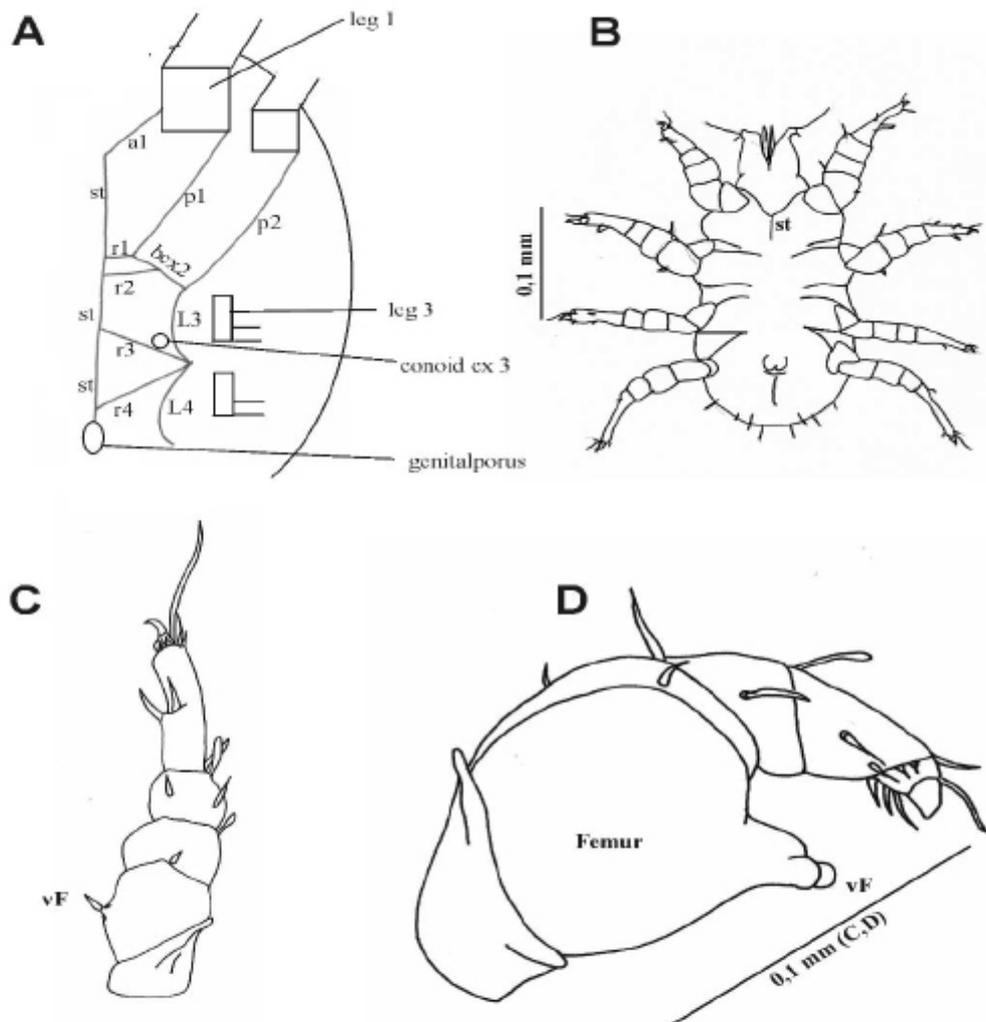


Fig14:
 A: Pattern of ventral deutonymphal apodemes in species of the *Histiostoma feroniarum*-group. B: "Normal" male of *Histiostoma palustre* in ventral view. C: Unmodified leg 2 of a male. D: Modified leg 2 of *H. palustre*. st leg setae = sternum, a1 = anterior leg 1, p1 = post leg 2, L3,4 = parallel to legs 3 and 4, r1-4 = "ribs", bcx2 = basically of coxa 2, vF, ra, la = leg setae.

Problems related to the current serial homologization of leg articles in histiostomatid deutonymphs (WIRTH, submitted 2003)

An apomorphy of the Histiostomatidae is six instead of five free articles on legs III and IV of the deutonymph (Fig15B) contrary to all other stages (Fig15A). One of the articulations is secondary, but it is not easy to decide which of the articulations is secondarily formed. A study of the serial homology of the setal pattern could help to determine where it is located, however such a study is difficult to perform due to the loss of certain setae of legs III and IV in comparison to legs I and II (Fig15B). Usually the last distal visible articulation (Fig25D) is interpreted to be secondary (see, for example, FAIN & ERTELD, 1998). The third visible part of these legs from the proximal end is interpreted to be serially homologous to the genu (Fig15B), but in my observations this “article” seems to be a false one and part of the femur (Fig15B), because it does not look like a real article, but appears to be a partly membranous fold of the femur (Fig22A).

The third visible part of legs III and IV of *Histiostoma palustre* Wirth, 2002, a species not closely related to *B. n. sp.*, was studied by SEM in more detail (Fig25F). After the deutonymph was treated with 90% lactate, this area was folded inwards and nearly invisible. That’s why I assume that the cuticle in this area is thin and membranous.

I therefore interpret this portion of the leg as part of the enlarged articulation membrane basal to the genu and partly of the inwardly folded femur. The fact that the questionable proximal part of legs III and IV does not look like a typical article seems to confirm this interpretation (Fig16A).

Having the femur divided into two parts enables the forward directed position of legs III and IV (an apomorphy of the Histiostomatidae) when the deutonymph is attached to the carrier insect (Fig6E). This leg position is a consequence of another apomorphy of the Histiostomatidae: all legs of the deutonymph are elongated in relation to other body parts. In comparative investigations concerning the function of elongated legs, I observed under laboratory conditions that histiostomatid deutonymphs easily turn around after they have fallen onto their backs. The mobility of these deutonymphs is, for the most part, better developed than in other astigmatic mites. The forward directed position of legs III and IV probably could support the attachment better than to have them sticking out laterally.

The new hypothesis of serial homology of the articles of legs III and IV leads to the assumption that seta d (leg III) and seta r (leg IV) of the old homology hypothesis must be serially homologous to solenidion phi (leg III and IV) (Fig15B).

In case of the distal solenidia on legs III and IV, specific solenidial characteristics were not recognized. These solenidia could have lost their chemosensory function because this function is mainly centered on legs I and II.

“Ringorgans”

As apomorphies of the Histiostomatidae two pairs of rounded structures ventrally on adults and tritonymphs and two pairs on protonymphs (near the anus) and larvae (at legs II, „Clapared’s organ“) were identified to be complex structures, the “ringorgans” (WITALINSKI et al., 2002). The structures are homologous in function and morphology to the genital papillae and to the Clapared organs (Fig18D,E) of other astigmatid mites. For histiostomatids the ringorgans of *Histiostoma feroniarum* (WITALINSKI et al., 2002) were examined to consist of a modified cuticula, an electron lucent chamber and transport cells strongly filled with mitochondria. Presumably they function as osmo-regulatory organs (WITALINSKI et al., 2002). The morphology of these cells, conspicuously riddled with mitochondria, steps up the plausibility that the whole organ functions for ion exchange. This thesis is supported by morphological analogies in other animal groups, for example the osmo-regulatory structures in the ventral tubes of the Collembola (Insecta), in which similar transport cells occur. „Genital papillae“ were termed in regard to their position near the genital opening. But because these structures, the „ringorgans“ and the Clapared’s organ are homologous in morphology and function, I suggest a consistent terminology. The term “osmo-regulatory organ” would comprise the informations „complex structure (organ)“ and „function in ion exchanging“.

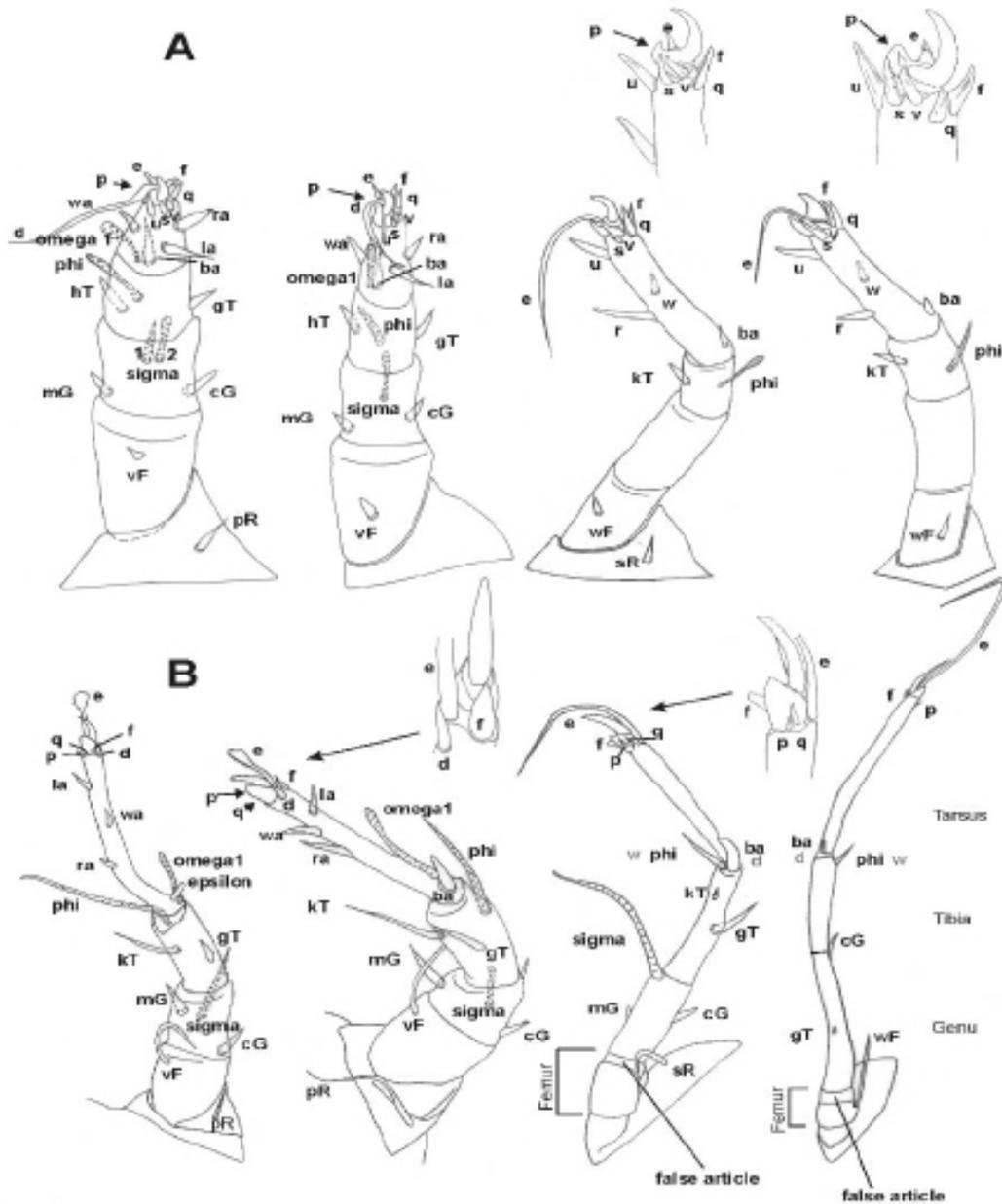


Fig15:
 A: *Bonomoia* n. sp., legs I to IV of the adult female in ventral view. Distal tarsi of legs III and IV depicted enlarged in ventral view. B: Legs I to IV of the deutonymph in ventral view. Distal tarsi of legs II and III depicted enlarged. Tarsus II seen from latero dorsally, Tarsus III from ventrally. Letters in black: new serial homologisation of leg setae, gray letters: old homologisation. Letters and arrows point to setae not visible in the depicted view. Nomenclature of leg setae after for example FAIN and ERTELD (1998).

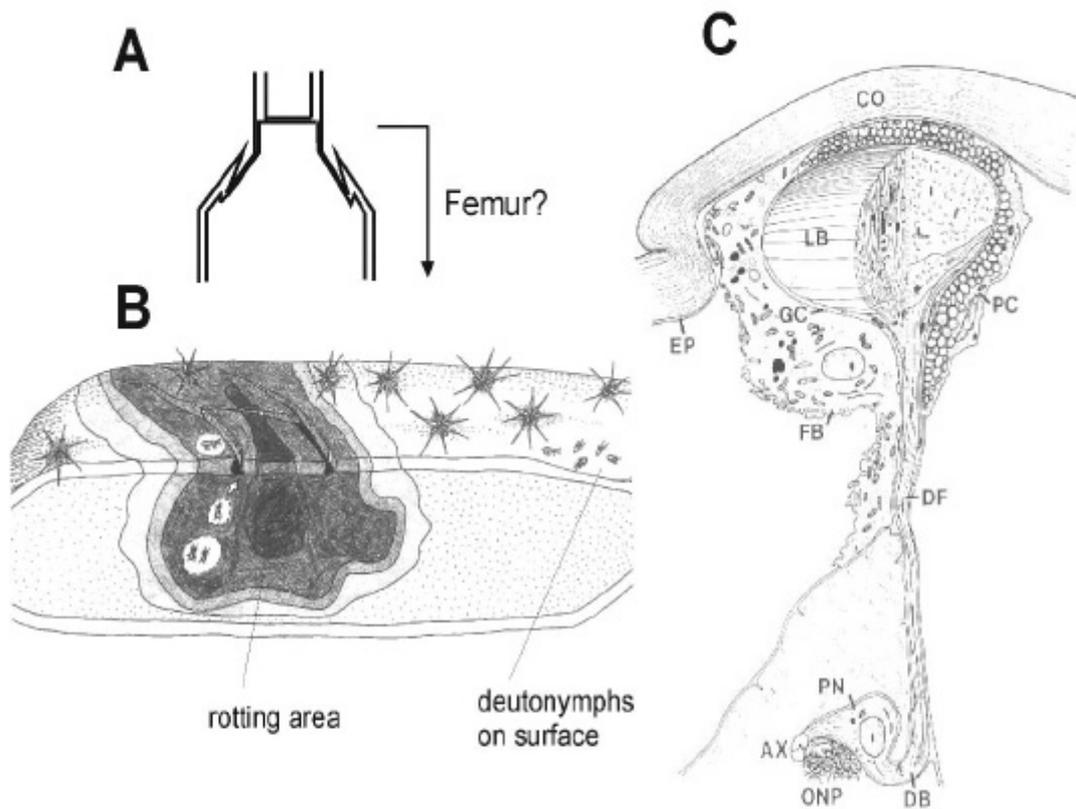


Fig16:

A: Proximal part of leg III of the deutonymph in a schematic longitudinal section. B: Schematic section through a rotting *Opuntia*-piece. C: Reconstruction of the lenticulus (after ALBERTI & FERNANDEZ, 1988): AX = photoneurone axons, CO = cuticular cornea, DB = dendrit base, DF = dendritic fibres, EP = epidermis, FB = fat body cells, LB = lamellated body, ONP = optic neuropile, PC = pigment cell, PN = perikaryon of photoneurone, GC = glial cell.

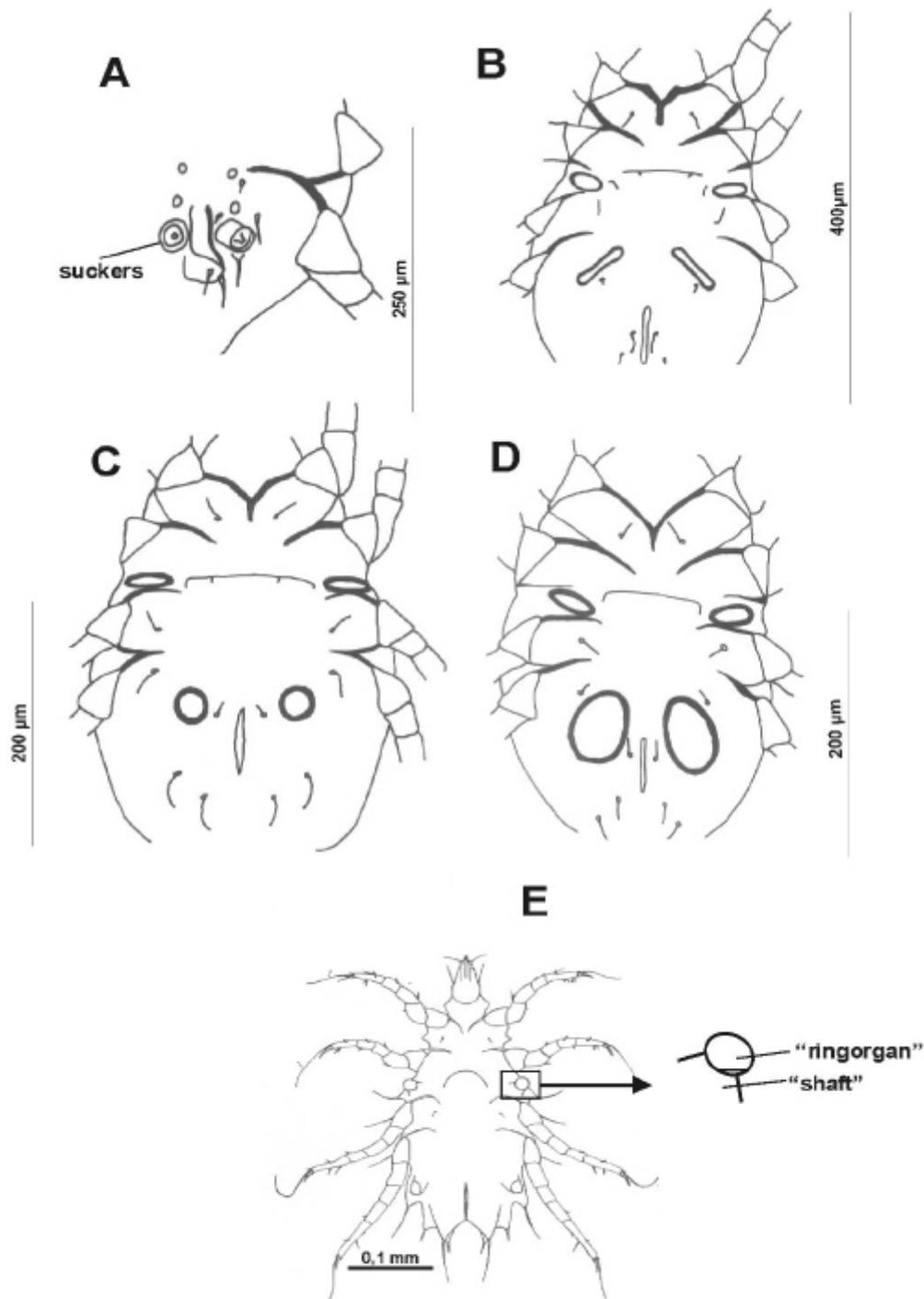


Fig17:
 A: Aedeagus of *Spinanoetus weingaertnerae*. B: Vulva of *Histiostoma myrmicarum*. C: Posterior "ringorgans" of *Histiostoma crypturgi* and (D) of *H. gordius* (A-D after SCHEUCHER, 1957). E: *Zwickia colocasiae* in ventral view (from HUGHES & JACKSON, 1959).

Contour of the „osmo-regulatory organ“

The rounded contour of the osmo-regulatory organ was transformed several times into conspicuously asymmetric or enlarged structures.

Within the monophyletic *Histiostoma piceae* group the posterior osmo regulatory organs of the females of *H. crypturgi* and *H. gordius* are conspicuously enlarged (Fig17C,D) related to the anterior osmo-regulatory organs and the organs of other species. This character is interpreted to be a synapomorphy of these species. The function that necessitates these conspicuous changes is still unexamined.

The posterior osmo-regulatory organs of *H. myrmicarum* (Fig17B) and *H. sapromyzae* are conspicuously elongated with rounded endings and a thinner centrepiece. This character obviously evolved as an apomorphy in the stem species of *H. myrmicarum* and *H. sapromyzae*, which argues them to be sister species.

Similar shaped osmo-regulatory organs occur in *H. bakeri* and *H. humiditatis* which therefore probably are related to *H. myrmicarum* and *H. sapromyzae*.

In non histiostomatid Astigmata the „genital papillae“ and Claparède organs rest inside the body and get extended by hemolymph pressure. In the extended state they are positioned apically of an elongated shaft which enables the contact to the soil (Fig18E). The stem species of the Histiostomatidae evolved osmo-regulatory organs, which are in plane with the surrounding cuticula and ring shaped (Fig18D). It can be assumed, that the stem species of the Histiostomatidae already spent the most time of its life amidst a fluid like substrate to feed. That's why the whole mite body was all along in direct contact with the fluid, in contrast to other astigmatid feeding in more drier areas and therefore apparently keeping in a bigger distance to the low humidity of their subsoil. That's why an elongated organ for the ion exchange in non histiostomatid Astigmata would be important to make the contact to the ground.

In *Zwickia colocasiae* all ringorgans of the female are situated on elevated fixed pedestals (Fig17E). The function of these elevations remains questionable, because the biology of that species is unexamined. Presumably the females of that species temporarily frequent drier areas and need an elongated organ to contact the soil comparable to non histiostomatid Astigmata.

Sclerotisations of the larva

The sister group of *Bonomoia* (including all other groups of the Histiostomatidae) evolved a pattern of dorsal sclerotisations on the larva (Fig18A). A simple nomenclature is introduced: The propodosoma shield is divided into two parts, an anterior and a posterior one. On the hysterosoma, the anterior unpaired cuticula shield is termed with 1, the posterior one with 2. Anterior and more laterally of the hysterosoma, 2 small sclerites 3a and 3b are situated. In a longitudinal row to posterior sclerites 4, 5 and 6 follow (Fig18A).

The propodosoma shield of adult histiostomatids was identified as the area, where muscles originate. A similar function is assumed, but unobserved, for all shields of the larva. Presumably muscles of the legs and the dorso-ventral muscles originate there, because these muscles always originate dorsally in other astigmated mites. The totally thinner cuticula in the stem species of this big subgroup of the Histiostomatidae presumably needed to evolve a modified thick cuticula around the muscle origins, which stabilize these areas during the muscle's contractions.