

HABITATS

Wooden habitats

Six monophyletic main groups were discovered: *Bonomoia*, (*Myianoetus*, *Pelzneria*), (*Aphodanoetus*, *Glyphanoetus*, *Rhopalanoetus*, *Spinanoetus*, *Wichmannia*), (*Histiostoma phyllophorum* group, “bark inhabiting mites”), the “Pitcher-plant mites and related species” and the *Histiostoma feroniarum*-group (Fig3). Basally branching groups live in animal dung, and compost and other habitats were colonized later. Wooden environments were opened up within a monophyletic group consisting of the *Histiostoma phyllophorum*-group (*H. phyllophorum*, *H. stammeri*) and the “bark inhabiting mites”: the “camouflage-group”, the *H. dryocoeti*-group (*H. dryocoeti*, *H. oudemansi*, *H. pini*) and the *H. piceae*-group (*H. crypturgi*, *H. gordius*, *H. piceae*, *H. trichophorum*, *H. ulmi*, *H. vitzthumi*) (Fig1).

Apomorphies of the *H. piceae*-group concern the deutonymph: Dorsal setae elongated and conspicuously directed to anterior (Fig19A), ventral apodemes bcx2 angled to lateral (Fig19B). It is difficult to differ apodemes r1 (Fig3) and bcx2 (Fig19C) from each other because they form one straight line and apodeme p1 (Fig3) which usually separates r1 from bcx2 is often free ending (Fig19B). The elongated and forwards directed setae seem to be adaptations to carrier-insects which move inside small canals or burrow through compact substrate. During the movement of the insect the deutonymphs are forced to reverse their bodies when their elongated setae point in direction to that movement and offer a resistance to the tunnel walls. The new more stable position with the sucker plate in direction to the insect's movement offers less resistance. It can be expected, that these deutonymphs really are positioned in an identical orientation on the beetles in the field. The elongated setae were lost in the stem species of the *H. dryocoeti*-group and presumably completely reduced several times within the “camouflage group”.

The stem species of the “bark inhabiting mites” evolved in both males and females the following apomorphies: setae d5a-c, setae d6b, d7a and setae d8a on conspicuous cuticula elevations (Figs19D,22E) and a ridge shaped palpmembrane structure running parallel to the cheliceral guiding structure (Fig22H).

The posterior cuticula bulge with setae d8a existent in both female and male runs posteriorly parallel to the ground and was observed to serve for the attachment of legs IV of males during the copulation. Unfortunately all these structures are not understood in correlation to the new habitat in the bark of wood.

As synapomorphy of the *Histiostoma dryocoeti*-group and the *H. piceae*-group bark-beetle

species were chosen as phoretic transporters. Morphological synapomorphies are missing. Species of the “camouflage group” live in duff of trees and in rotting stumps. The transporters are mostly unknown. *H. ruehmi* for example was found on the larva of an elaterid beetle (SCHEUCHER, 1957). Within this group a tactile camouflage by holding substrate on the mite’s back developed. At first an elevated female copulation opening and then derived setae for the substrate fixation evolved.

Camouflage- group (WIRTH, submitted 2004)

The pattern of dorsal setae is homologous between all species within the Histiostomatidae. It was several times transformed into patterns with added new functions. Basically within the Histiostomatidae a pattern developed in which setae d6a changed to anterior whereas d5a and d5b moved to lateral. This pattern with more laterally arranged setae obviously facilitated further modifications within the bark inhabiting-group.

I termed a monophyletic subgroup the „camouflage-group“. It consists of the following species: *Histiostoma* sp. 1, *H.* sp. 2, *H.* sp. 3, *H. ruehmi*, *H. sachsi* and *H. n.* sp. 1. All species were found in wooden environments. Species *H.* sp. 2 and 3 were collected in the USA and come from the collection of B. OCONNOR.

The only character to argue that monophyly is a pattern of dorsal setae which appears to be U-shaped (Fig12B) because all setae are arranged near the lateral and posterior margin of the mite (Fig20G). In the stem species of all members of that subgroup except the basically branching *H.* sp. 1, a conspicuous chimney shaped female copulation opening evolved (Fig20H). In the stem species of *H.* sp 3 and all others the dorsal setae were modified into more tickler and longer ones (termed „claw setae“, Fig20G). In the stem species of *H. ruehmi* and all others these setae were additionally transformed into „hook setae“ (Fig20F). In the stem species of *H. sachsi* and the conspicuous *H. n.* sp. 1 all dorsal setae were arranged on enlarged pedestals. Setae d6b and d7a are shifted closer to each other (Fig20D,H). The hook stae of *H. sachsi* obviously are not clearly distincted.

I interpret these morphological modifications as a series of transformations into structures to fasten substrate as tactile camouflage. The hook setae obviously evolved to adhere the substrate from the surroundings. In that way the whole mite body can be covered with material, but the function of the copulation opening that towers above this substrate is not interfered.

In the stem species of the bark inhabiting group, dorsal cuticula humps in both sexes evolved. Their function is unknown, only the posterior one is assumed to support the male's fixation during the copulation. They were completely retained only in *H. sp. 2* and *H. n. sp. 1* within the bark inhabiting-group (Fig23C). The lateral humps were completely reduced in *H. sp. 3* and *H. ruehmi*, all of them were obviously reduced in *H. sachsi*. These cuticula elevations were observed to support the substrate tecting in *H. n. sp. 1* (Fig20H) by keeping a additional quantity of substrate. But obviously the camouflage species without the full equipment of humps don't need these structures for a successful substrate holding. That's why it is not assumed that the humps which evolved in the stem species of the bark inhabiting-group could be seen as preadaptations into the tactile camouflage, that evolved later in the camouflage-group.

In the stem species of the camouflage group the conspicuously elongated and forward directed dorsal setae of the deutonymphs were reduced to short ones directed to everywhere as usual for histiostomatids of other groups (deutonymphs of *H. n. sp. 1* were never found.).

The camouflage-group is argued to branch basically within the bark inhabiting-group despite of these reductions. Probably the lack of earlier evolved structures enabled the evolution of a new strategy (tactile camouflage). Also the transporters, which are unknown in all species, seem not to live in tunnels, where deutonymphs could get lost when not arranged in the right position (as previously described).

Adaptations of the new species *Histiostoma n. sp. 1* into substrate holding (WIRTH, submitted 2002)

This species is morphologically conspicuous. The propodosoma-shield anteriorly towers above the gnathosoma for the most part (Fig20H). Setae d2 are strongly thickened and are formed like the horns of a billy goat (Fig20C). Both setae d3 and d4 are positioned on common conspicuously enlarged pedestals (Fig20H). Setae d5a, d5b and d5c are arranged on a common sideways flattened cuticula elevation and additionally stay on enlarged pedestals. Setae d6b and d7a are arranged in a similar way (Fig20D). Those dorsal structures seem to form a basket to hold substrate as camouflage. The openings of the opisthosomal glands, located between the setae d6b and d7a, tower like small pillars above this pedestal (Fig20D). The dorsal surface of the tritonymphs is arranged as in the adults. The dorsal cuticula of the larva shapes flat, elevated areas separated by grooves (Figs20E,22C). The dorsal structures of adults and tritonymphs seem to facilitate carrying bigger quantities of substrate as tactile

camouflage, because all important structures are considerably elevated to tower above the substrate. Also the larvae seem to be able to camouflage, but otherwise than the adults. These grooves presumably hold substrate like the sole of a shoe, because similar to the older stages specimens from the field were often loaded with substrate.

Definition of “tactile camouflage”

Caused by the lack of light in the colonized wooden habitats, an optical camouflage would be less adjuvant. That’s why this camouflage is assumed to be a tactile one against predators that fumble for their prey. Because experiments about the impact of carrying substrate to the predators were not performed, the “tactile camouflage” can only be defined by the effect of morphological structures. The ability of claw and hook setae to adhere substrate was proved by my SEM observations. These modified setae seem to be adapted only to that function. That’s why I conclude that the stem species of this group evolved the tactile camouflage.

An unusual quantity of substrate on the dorsum was observed under laboratory conditions only in living specimens of *Histiostoma ruehmi* and *H. n. sp. 1*. The covering with substrate was not observed to happen as an active behavior. The material gets accidentally on the mites, but then becomes fixed in perpetuity.

The other species of the camouflage-group were not observed alive. But the phylogenetic relatedness and the reconstructed row of transformations from normal setae to claw setae and finally to hook setae, and the fact that setae in all observed specimens were contaminated with substrate particles, lead to the conclusion that tactile camouflage is existent in all these species and therefore evolved in their common stem species.

The conical elevated female copulation opening must have evolved earlier, but probably in adaptation to a mite body, that was temporarily covered by substrate. This should not be termed “camouflage”, because special holding structures were still not existent.

Necessity of tactile camouflage

Species of that subgroup live in rotting wooden material (e.g. SCHEUCHER, 1957). The carrier insects are unknown. In case of that conspicuously modified *H. n. sp. 1* I also never found the deutonymphs. I observed the behaviors both of *Histiostoma ruehmi* and *H. n. sp. 1* under laboratory conditions. Both live in habitats with a big biodiversity of arthropod predators, especially Gammasidae. I observed these specimens often to remain nearly motionless and to

move conspicuously slowly. Probably the ability to camouflage allowed them to open up habitats, in which caused by lots of predators other histiostomatid species can't exist.

Watery habitats

The stem species of the “Pitcher Plant mites and related species” and the *Histiostoma feroniarum*-group presumably colonized a watery substrate around fresh waters. Within the *H. feroniarum* group 4 of 8 species: *H. insulare*, *Histiostoma litorale*, *H. maritimum*, *H. palustre* and live in such habitats. Also *H. strenzkei*, branching off basically within the “Pitcher plant mites and related species”, was found near the waterside. Within that group other watery habitats were colonized. Morphological synapomorphies of the *Histiostoma feroniarum*-group and the “Pitcher Plant mites and related species” are the evolution of male dimorphisms and the distinctive elongations of leg setae la and ra of the males (Figs19H,23D,E), which during the copulation are pressed into the female's cuticula for a better fixation. This character is interpreted to be important for colonizing watery habitats.

Histiostoma feroniarum-group (WIRTH, 2003)

The monophyletic group consists of 9 species. Apomorphies are: The digitus fixus is characteristically sawed. Regarded from proximal to distal 3 thicker setae are positioned on part 1 of the digitus fixus. The distal part of the digitus fixus consists of 6 bigger teeth, followed by at first 4 smaller ones and then another 4 setae which are clotted with each other. Apically 1 single seta conspicuously is directed anteriorly. The lobe of the palparmembrane is divided into two half-rounded parts (Fig8B). The apodeme r2 of the deutonymph is existent (Fig14A).

Pitcher plant-group

The taxa *Creutzeria*, *Hormosianoetus*, *Nepenthacarus*, *Sarraceniopus*, *Zwickia* and form a monophyletic group within the Histiostomatidae. It is argued by the following apomorphies: Projection of the idiosoma of the deutonymph bears the gnathosoma, which is laterally punctured (Fig19G), empodial claw of adults distinctly enlarged. *Hormosianoetus* is an inhabitant of plant waterholes (phytotelmata). All other taxa are inhabitants of pitcher-plants, which is an ecological apomorphy of that subgroup, therefore called pitcher plant group. The first branch is *Sarraceniopus* living in the new world pitcher plants of *Sarracenia*. All others

live in the pitchers of the old world *Nepenthes*. The *Nepenthes* group is argued to be monophyletic by morphological arguments (Fig1). The pattern of branches corresponds to the relationships reconstructed by FASHING & OCONNOR (1984), the argumentation is similar.

Arguments for the phylogenetic position of that group within the Histiostomatidae were found. Synapomorphy of *Histiostoma* n. sp. 3 and the monophylum consisting of *Hormosianoetus* and the Pitcher Plant-group is the complete reduction of dorsal sclerotisations of larva (Fig6F), protonymph and tritonymph. Synapomorphy of *H. pulchrum* and the monophylum of *H. n. sp. 3*, *Hormosianoetus* and the Pitcher plant-group is a digitus fixus which is closely toothed with apically downsized cuticula teeth (Fig19F). Synapomorphic of *H. radiferum* and *H. strenzkei* and the remaining monophylum are deutonymphal conoids reduced to small rests (In *H. pulchrum*, they seem to be completely reduced, Fig19E). The whole group is termed “Pitcher-plant mites and related species”.

The phylogenetic reconstruction of that group leads to the following presumption about the colonization of pitcher plants step by step starting from a stem species, which lived in a watery habitat around waters. *H. strenzkei* remained in such a habitat (grasslands around waters). *H. pulchrum* (presumably representing a bigger group of undescribed species) and presumably *H. n. sp. 3* (probably coming from the slime flow of *Aesculus* sp.) inhabit slime flows of trees. That’s why the first step from watery soil habitats to watery plant habitats presumably was the colonization of slime flows. The worldwide distributed *Hormosianoetus* was found in waterfilled treeholes and waterfilled *Bromelia* leafs. Probably out from more unspecific water filled plant habitats life in pitcher plants was opened up. The stem species of the pitcher-plant mites was adapted to a habitat containing acid, digestion enzymes and microorganisms.

As the Pitcher-plant group branches off within “*Histiostoma*”, this taxon is paraphyletic. To name the whole monophyletic group the term *Histiostoma* group is introduced.

Histiostoma-group

In the work of SCHEUCHER (1957) the genus *Histiostoma* is explained by the transverse vulva of the females. But OCONNOR (1981) found, that the vulva of all Histiostomatidae runs in a transverse gap (Fig9A). The clearly visible longitudinal structure in some genera was identified not to be the vulva but the area where the valvulae are connected to each other and presumably form an apodeme (Fig9A). HUGHES and JACKSON (1959) listed some characters of the ventral deutonymph, but I identified all of them to be plesiomorphic.

The following apomorphies of the stem species of the *Histiostoma* group were identified:

Female copulation opening

- consisting of a cuticula fold anterior of a chimney shaped elevated opening of the bursa copulatrix (Fig23F)

Sclerotisations around the vulva

- visible apodeme like fusion of the genital valvulae completely reduced (Fig17B)
- a3 conspicuously elongated medianly (Fig17D)
- anterior osmo-regulatory organs touching apodeme a3 (Figs17D,22D)
- anterior osmo-regulatory organs dorso-ventrally flattened (Fig17D)

Genital suckers of the males (Fig17A)

- completely reduced

Dorsal sclerotisations of the larvae (Fig18B):

- omega shaped indentation at the posterior propodosoma shield
- sclerite 1 on the hysterosoma anteriorly wide, posteriorly rounded.
- sclerite 2 on the hysterosoma compactly rounded
- sclerites 3a and 3b fused to one single sclerite 3
- sclerite 7 present (all characters in Fig18B)

The entirety of these morphological innovations points to ecological changes of the stem species of the *Histiostoma*-group. But such ecological changes could not be demonstrated. Primary groups within the Histiostomatidae live in animal dung and compost. But this is also true for the stem species of the “Bark inhabiting mite group” which is the first branch within the *Histiostoma*-group. Presumably preadaptations to accept new ecological licenses evolved in the stem species of the *Histiostoma* group, but the habitat at first was retained.

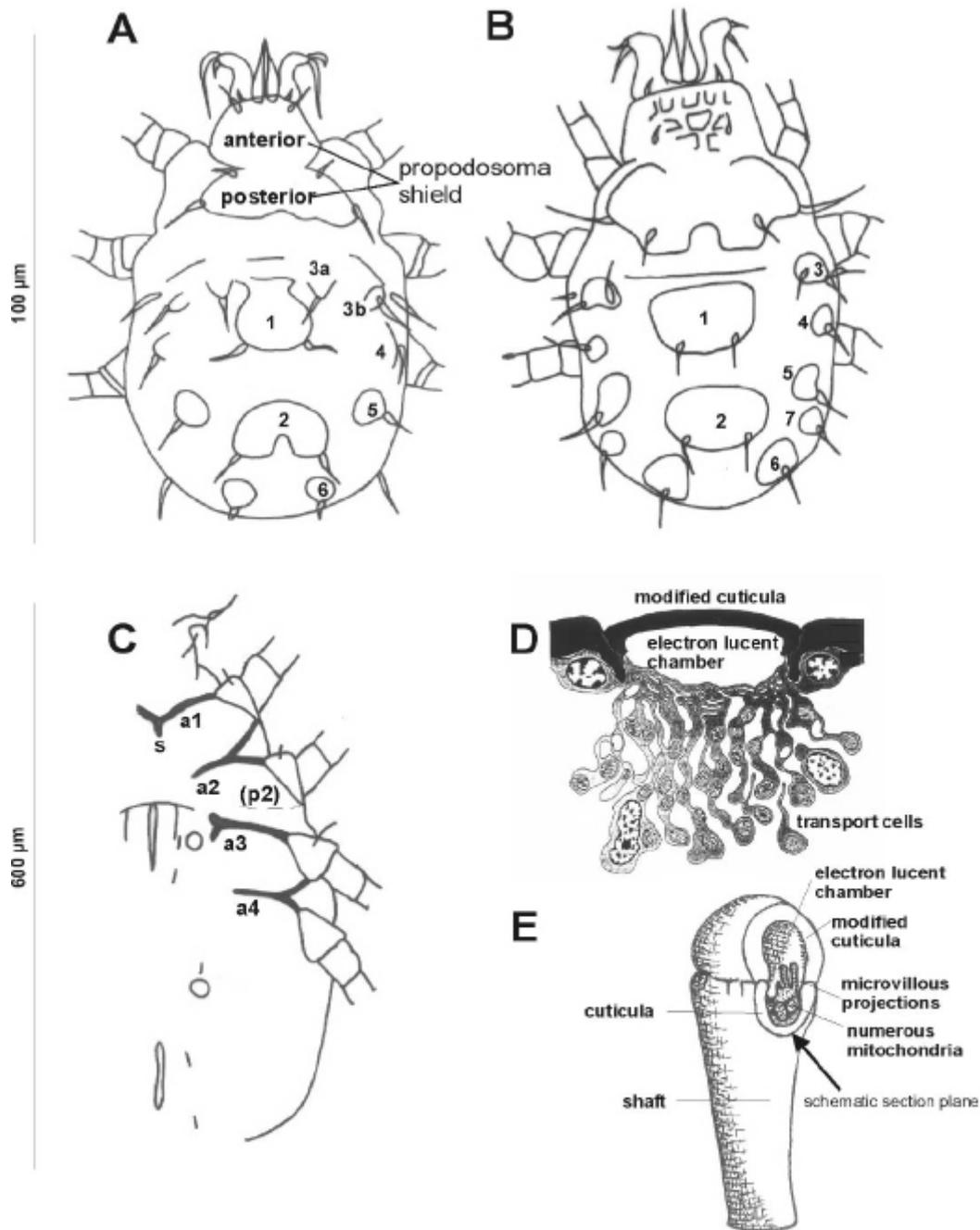


Fig18:
 A: Larva of *Myianoetus simplex* in dorsal view. B: Larva of *Histiostoma* n. sp. (probably from the slime flow of *Aesculus* sp.) in dorsal view. C: Ventral female apodemes of *Spinanoetus weingaertnerae*. D: "Ringorgan" of *Histiostoma feroniarum* in a histological section (WITALINSKI et al., 2002). E: Claparede organ of *Naiadacarus arboricola* (Astigmata). Reconstruction after pictures in FASHING (1988).

figure A after OCONNOR (1985)
 fig. C after SCHEUCHER (1957)
 fig. D after WITALINSKI et al. (2002)

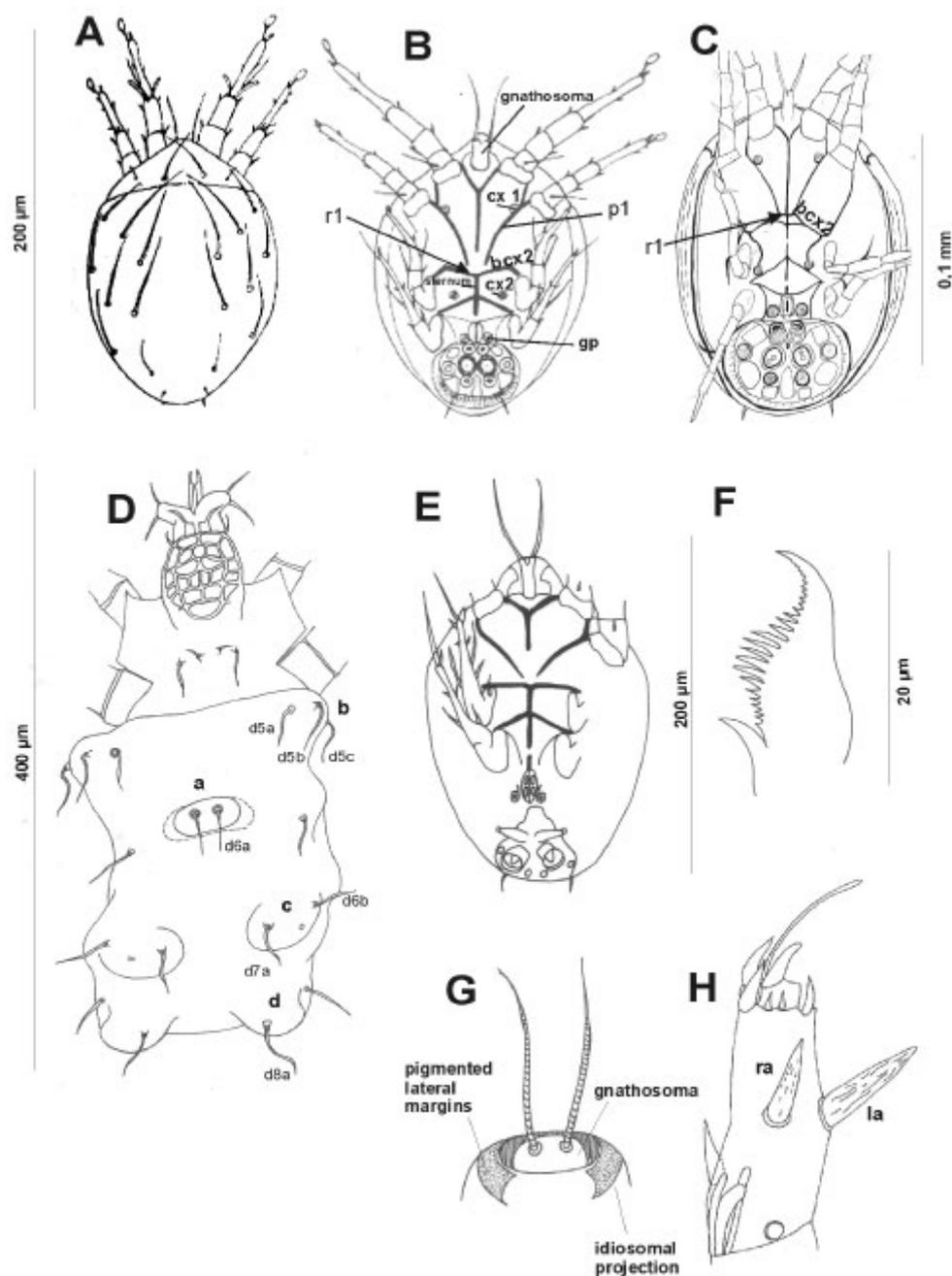


Fig19:
 A: Deutonymph of *Histiotoma piceae* in dorsal view. B: Apodemes r1 and bcx2 of the deutonymph of *H. piceae*. C: Apodemes r1 and bcx2 of *H. palustre*. D: Female of *H. piceae* in dorsal view. E: Deutonymph of *H. pulchrum* in ventral view. F: Digitus fixus of *H. pulchrum* (female). G: Deutonymphal gnathosoma of *S. darlingtoniae* (F,G after FASHING & OCONNOR 1984). H: Setae ra and la on the tarsus of leg II of *Histiotoma pulchrum*.

figure G after FASHING (1981)
 figures A, B, E, F after SCHEUCHER (1957)

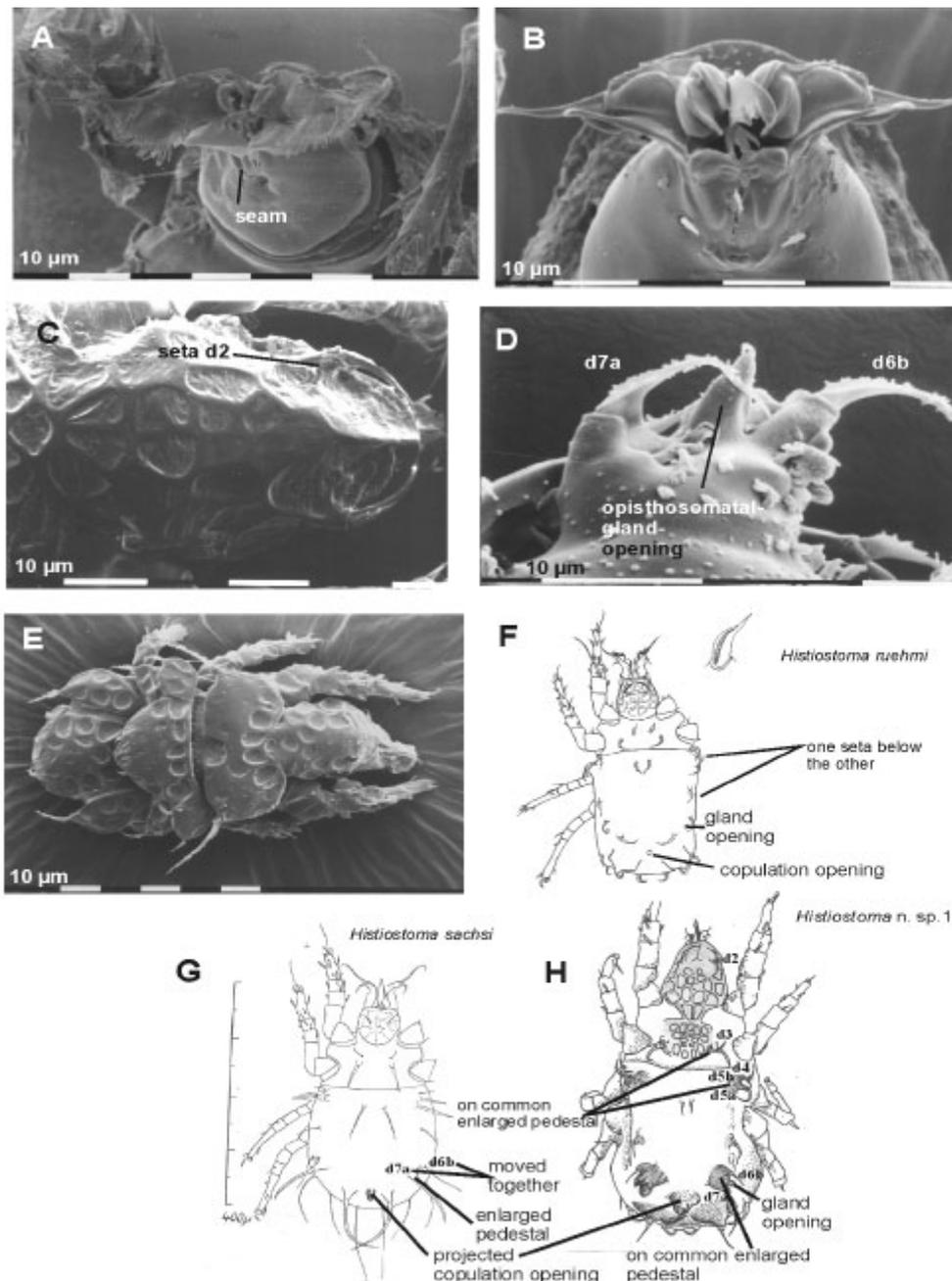


Fig20:

A: Gnathosoma of *Histiostoma ruehmi* in anterior-ventral view. B: Distal gnathosoma of an unknown species, representing characteristics of the stem species of the bark inhabiting mites in ventral view. C: Dorsal view on the propodosoma-shield of *Histiostoma n. sp.*. D: view from median to lateral to the setae d6b and d7a on an enlarged common pedestal of an adult female of *H. n. sp.*. E: Larva of *H. n. sp.* in dorsal view.

F, G, H: dorsal structures of adult females in dorsal view. F: *H. ruehmi*, c.o.= copulation opening, g.o.= opisthosomatal-gland opening (a revised painting of SCHEUCHER, 1957) and clawlike bristle. G: *H. sachsi* (painting of SCHEUCHER, 1957). H: *H. n. sp. 1*.

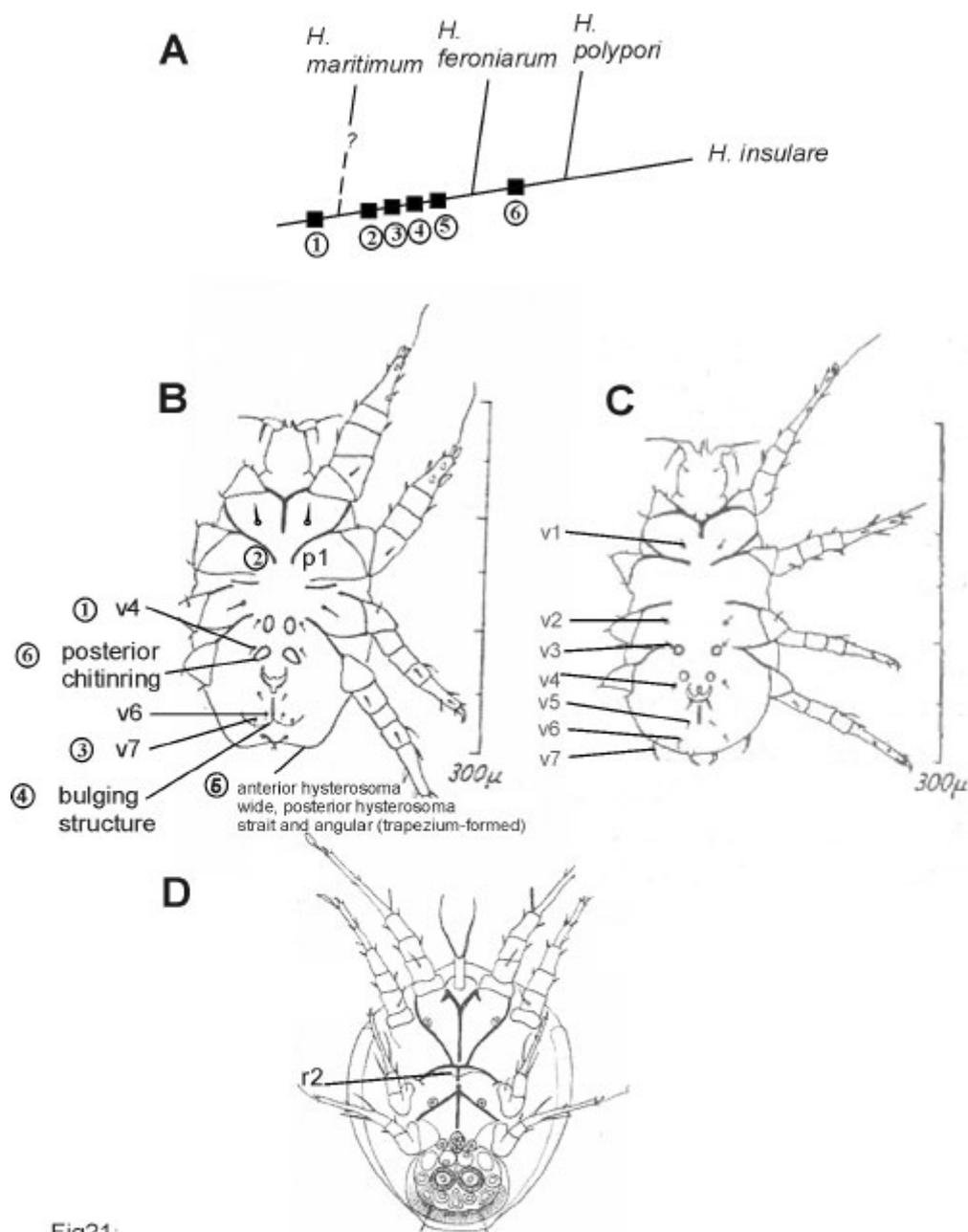


Fig21:

A: Phylogenetic relationships of 4 histiostomatid species. The cladogram is based on the following morphological characteristics of the adult male: 1) seta v4 in front of the posterior chitirring, 2) apodeme p1 bulged to median, 3) seta v7 besides v6, 4) bulging structure behind the anus, 5) anterior hysterosoma clearly wider than its posterior end (trapezium-formed) 6) oval posterior chitirring.

B: *H. polypori* male, C: *H. litorale* = male of an outgroup taxon. Concerning the named characters, this species represents the plesiomorphic state. D: *H. polypori*, deutonymph. The ventral apodeme r2 of the deutonymph is an apomorphy of the higher taxon "*Histiostoma feroniarum*-group". All drawings of mites from SCHEUCHER (1957).

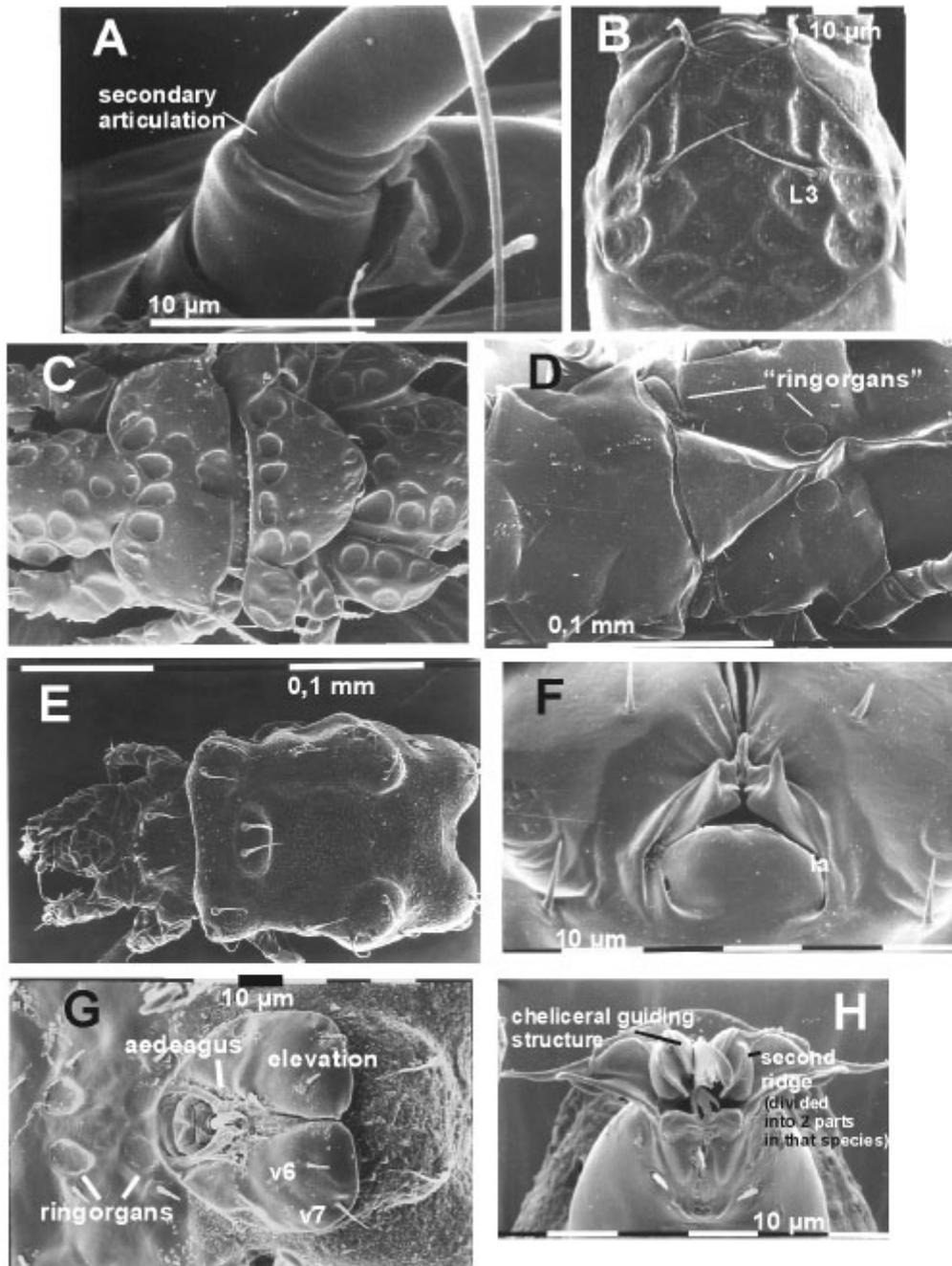


Fig22:

A: Deutonymphal leg IV of *Bonomoia* n. sp.. B: Propodosoma shield of *Histiostoma palustre*. C: Larva of *H. n. sp.* (Camouflage group). D: "Ringorgans" of the female of *H. sp.* (found on *Nicrophorus vespillo*), left side of the picture is anterior. E: *H. piceae* in dorsal view (female). F: Aedeagus of the male of *H. palustre*. G: Aedeagus of *H. feroniarum*, left side of the picture is anterior. H: Ventral view on the gnathosoma of *H. n. sp.* found in a wooden habitat.

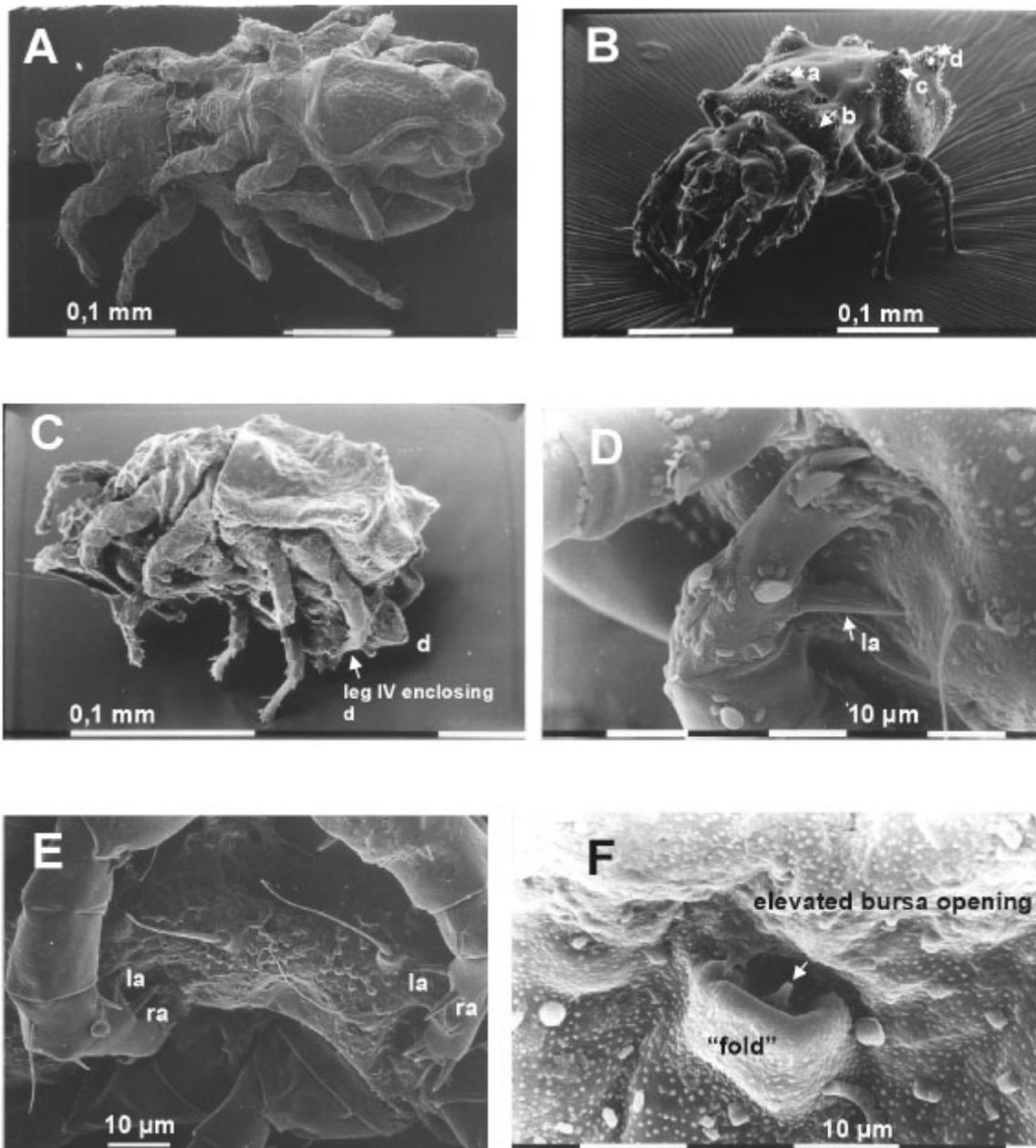


Fig23:

A: Copulation of *Rhopalanoetus lanceocrinus*. B: Female of *Histiostoma piceae* in dorsal view with introduction of the nomenclature (a-d) for the pattern of humps. C: copulation of *H. n. sp.* showing the use of the posterior hump as fixation structure. D: Seta la of the leg of the male of *H. pulchrum* boring into the female's cuticula. E: Copulation of *H. sapromyzarum*. F: Copulation opening of *H. feroniarum* divided into "pocket" and elevated bursa opening. la, ra = leg setae.