BIOLOGY

Wave behavior (of Bonomoia *n. sp.)*
(WIRTH, submitted 2003)

For histiostomatic mites in general, “leg-waving” was observed in a characteristic pattern. Legs I are alternately moved with the right leg being raised and lowered twice followed by the left leg being raised and lowered twice. During this “waving” of legs I, which happens very rapidly, the deutonymph walks on three pairs of legs, or stops walking for a brief moment (Fig24C).

the “waving” behavior

Deutonymphs of *Bonomoia* n. sp. demonstrate conspicuous behavioral attributes while moving around. Important structures for chemotactic orientation in all instars are the leg solenidia, with those on legs I and II being the most important (Fig25E). A comparative study of „waving behavior“ involving the deutonymphs of several species was performed utilizing two experimental designs.

1. A pattern of fields was arranged on the surface of a piece of dry cardboard, and deutonymphs released at a standardized location. Observations were made for nine minutes, and the distance covered was described by a painted line.
2. A pattern of fields was arranged under a transparent Petri-dish (diagonal 5 cm) filled with 1,5 % agar media, thereby creating a wet surface. The procedure given above was followed.

Then the same experiments were performed for a comparative study with the following histiostomatids: *H. feroniarum* Dufour, 1839, *H. maritimum* Oudemans, 1914, *H. sapromyzarum* Dufour, 1839, *Histiostoma* sp. (related to *H. piceae*), *H. pulchrum* Kramer, 1886 and *Rhopalanoetus* sp.. Three species of *Acarus* sp. were observed as outgroup members.

Experiment 1. Deutonymphs left the starting-point quickly, with both rapid and slow walking alternating in a conspicuous manner. The up and down movement of legs I or II for

chemosensory reception while walking ("waving") was missing in *Bonomoia* n. sp. contrary to other histiostomatid genus taxa or outgroup members of *Acarus*. Deutonymphs regularly stopped walking and attached to the cardboard surface with their suckerplates, positioning the entire body flat on the surface. In this position they used their legs to rotate their bodies around the attached suckerplate in either direction. Only legs I were used for "waving" (Fig24D).
2: Deutonymphs walked slowly and didn't change their speed. After each 2-3 steps they straightened their bodies, being fixed on the agar surface by the sucker plates. In this position they "waved" (Fig24E).

Transformations of the "waving" behavior within the Histiostomatidae

On a dry cardboard and on agar *Rhopalanoetus* sp. left the release point quickly, "waving" regularly after each step. *Histiostoma* species remained for some time near the starting place where they walked around in a zig-zag manner before leaving. The "waving" behavior was similar to *Rhopalanoetus* sp.. Occasionally deutonymphs of *Histiostoma* straightened up while being fixed on the ground by their sucker-plates. In this position they used all legs to move the whole body alternating to the right and to the left. Meanwhile legs I and sometimes legs II were used to "wave" (Fig24B). This behavior is somewhat different from the straightening up of *B.* n. sp., because *Histiostoma* deutonymphs remained longer in the described positions in a behavior reminiscent of a dance.
Deutonymphs of *Acarus* immediately left the release point, and "waving" with legs I occurred often but not in a regular rhythm. Sometimes instead, both legs were stretched upwards at the same time.

Possible reasons for this behavior

I observed „waving" legs I also in the non histiostomatid outgroup members. Therefore it is a plesiomorphic character for the histiostomatid stem species. *Bonomoia* n.sp., however, inhabits a fluid like-habitat. Distance chemoreception via the solenidia of legs I or II is only possible if the deutonymph can elevate its body above the fluid surface. This is one possible explanation for the perpendicular orientation of the body on wet agar under laboratory-conditions. In addition, a light-sensitive function of this behavior was observed.
In the field deutonymphs require a carrier arthropod for dispersal. It is assumed that deutonymphs must leave the rotting area of *Opuntia* and wait on its dry surface for such a

transporter. Rotting *Opuntia* pieces were primarily found on the ground near the living plant, so the position of a deutonymph on the *Opuntia* surface would provide maximal exposure to air currents. Pieces in which the mites were found were collected from a flattened plane. In such a location it is probably easy to perceive all scents from the surrounding area with minimal movement. It is probably sufficient to remain in a fixed position and occasionally rotate and wave (Fig16B).

Phylogenetic conclusions

The cladogram of the Histiostomatidae was reconstructed using morphological characters (WIRTH, submitted2002) (Fig24A), and the behavioral characters mapped on this tree. The bahavior of deutonymphs to leave the release point immediately is considered a plesiomorphy of the stem species of the Histiostomatidae (Fig24A, no. 1). “Released” in the experiment probably could be that point in the field where protonymphs molted into deutonymphs. As an apomorphy of the stem species of the Histiostomatidae, deutonymphs wave after each step (?) (Fig24A, no. 2). As apomorphies of *Histiostoma* (Fig. 24A, no. 4), deutonymphs remain for a period of time at the release point, and sometimes straighten up their bodies while moving alternatingly both to the right and to the left (Fig24B).
It could not be determined whether the conspicuous behaviors of *B.* n. sp. to rotate the body on the dry cardboard and regularly to straighten up on the agar surface are apomorphies of that species or apomorphies of the stem species of *Bonomoia* (Fig24A, no. 3).

The light sensitive organs of Bonomoia *(WIRTH, submitted 2003)*

Light sensory organs frequently occur in the Acari, and except for the “Oribatida” and Astigmata, are presumably homologous and commonly located in the propodosomatic region of the prosoma. Propodosomatic eyes are divided into retinula cells and rhabdomers, and presumably were lost within the “Oribatida” (ALBERTI & FERNANDEZ, 1990). A completely different kind of light sensitive organs, the lenticulus (Fig16C), developed within the “Oribatida” and is located in the hysterosomatic region (ALBERTI & FERNANDEZ, 1990). The "clear spots" in “Oribatida” species is interpreted to be homologous to the lenticulus of *Hydrozetes lemnae*, whose “eyes” were investigated by the authors (ALBERTI & FERNANDEZ, 1988) more precisely (Fig16C). The lenticulus is a paired organ with two parts being located in close contact (ALBERTI & FERNANDEZ, 1990). The eye structure of *H. lemnae* probably

developed from the clear spot type on the basis of a specialisation of distinct neurones in the synganglion whose dendrites moved to the surface of the central nervous system and finally came to lie close to the dorsal surface of the body (ALBERTI & FERNANDEZ, 1988).

The “eye’s” surface of *Bonomoia* n. sp. forms a pattern of small and parallel running grooves (Fig25B). I have not yet conclusively demonstrated that the “eyes” of *Bonomoia* are derived from this oribatid eye type. In a SEM view of a section made with a razorblade, a cuticular lens is recognizable as is a conspicuous rounded structure that appears to be the photosensitive area and could be homologous to the lamellated body of the lenticulus (Fig25B). Then within the Astigmata, the parts of this organ must have migrated away from each other to be located laterally on the hysterosoma as in *Bonomoia*.

Light sensitive behavior of Bonomoia n.sp. *in comparison to other histiostomatids*

To understand the function of the eyes of *B.* n. sp., comparative experiments using deutonymphs of the following mite species were performed: *Acarus* sp. (outgroup taxon), *Bonomoia* n. sp., *H. feroniarum*, *H. maritimum*, *Histiostoma* sp. (related to *H. piceae*) and *Rhopalanoetus* sp.. These species represent the main groups of the Histiostomatidae.

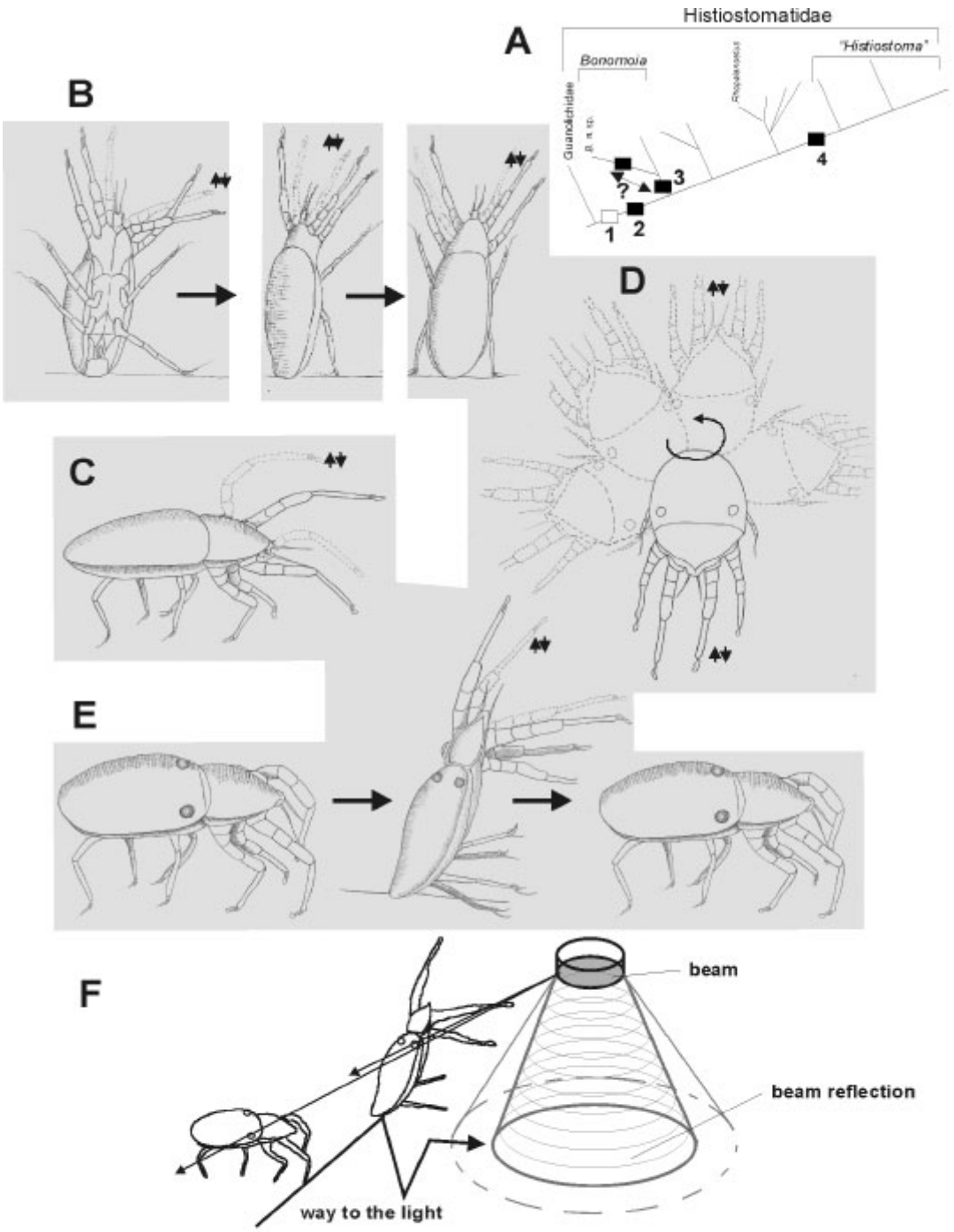


Fig24:
A: Reconstructed cladogram of the Histiostomatidae; 1, 2, 3, 4: behavioral characters (see text). B: Deutonymph of "*Histiostoma*" straightened up and moving its body alternating to the right and to the left ("wave" and wait for the carrier organism). C: Deutonymph of "*Histiostoma*" waving with legs I during the walk. D-F: Deutonymph of *Bonomoia* n. sp.:(D) fixed on the ground and moving its body around ("wave" and wait for the carrier organism), (E) while straightening up its body during the walk ("wave" and visual orientation), (F) while receiving small spots of a beam from a distance.

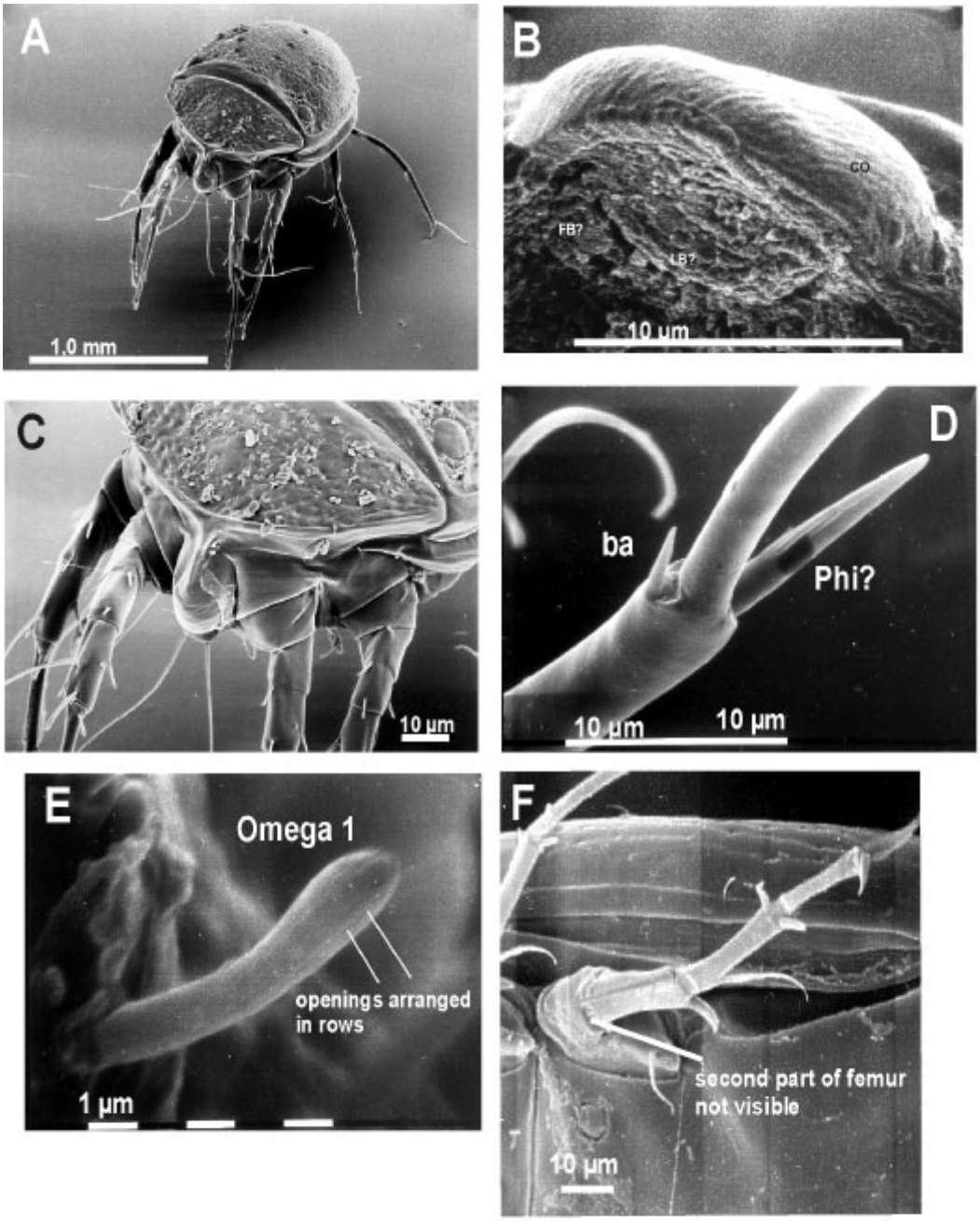


Fig25:
A: Deutonymph of *Bonomoia* n. sp. in dorsal view. B: "Eye" enlarged. C: Dorsal anterior propodosoma bearing the gnathosoma of the deutonymph. . D: Distal secondary articulation. E: An enlarged typical solenidium with pattern of small openings for receiving scent particles. F: Leg III of the deutonymph of *Histiostoma palustre* treated with lactat during preparation. H: Gnathosoma of *Histiostoma palustre* in ventral view. LB = lamellated body, FB = Fat body cells, CO = cornea, ba/ phi = leg setae.

Experiment 1

In the first experiment an agar dish (5 cm) was subdivided into a pattern of quadratic fields (0,5x0,5 cm) arranged under the transparent dish. The middle field was illuminated by a beam that lighted its entirety. To avoid warmth that could influence the mite's behaviour, a cold-light-beam for illumination of stereomicroscopes was used. Four different intensities of light could be distinguished. Deutonymphs were released singly at different distances away from the illuminated field and their phototactic behaviour recorded.

Regardless of the release distance, deutonymphs of *Bonomoia* n.sp. always moved into the lighted field where they remained for the duration of the experiment. Deutonymphs of *Histiostoma* sp. (related to *H. piceae*) did not respond either positively or negatively to the light stimulus, and dispersed in all directions regardless of the release distance. Deutonymphs of *H. maritimum* always avoided the light. Deutonymphs of *Acarus* sp., *Rhopalanoetus* sp. and *Histiostoma feroniarum* were photopositive only when released close to the illuminated field. When released at a distance greater than 1 cm, they moved in all directions, only accidentally reaching the beam.

Experiment 2

In a second experiment to determine whether deutonymphs would follow a moved light beam, the position of the beam on the agar plate was changed after five minutes and the mites observed for a 20 minute duration. The new beam position was always 1.5 cm away from the deutonymph. At the beginning of the experiment deutonymphs were released near the first beam position. The experiments were repeated 10 times for deutonymphs of the following photopositive species: *Bonomoia* n. sp, *Histiostoma feroniarum* and *Rhopalanoetus* sp..

Deutonymphs of all three species always went into the illuminated field at the beginning of the experiment, but only *Bonomoia* n. sp. followed the beam to its new locations. The other histiostomatids walked in random directions after the position of the beam was changed. When a deutonymph of *B.* n. sp. was placed at a greater distance from the light source, it walked slowly around in a zig-zag pattern. After about 2 seconds of walking, it straightened its body as described previously. When the deutonymph encountered some diffuse light, it remained in the upright position for a short time and then oriented to the beam. It was

observed that the line of walking was corrected at intervals as the deutonymph was illuminated by light rays. They obviously were received by the deutonymph's "eyes" (Fig24F). In this way the mite always found the light source after each change.

Conclusions

Deutonymphs of the Histiostomatidae and the observed outgroup members behaved photopositive, even if only released close to the illuminated field. That’s why the photopositive behavior in general is interpreted to be a plesiomorphic character of the histiostomatid stem species. It is therefore assumed that all species are capable of orienting to light, even those without visible "eyes". It is possible that such histiostomatids have rudimentary light sensory organs beneath the body cuticle.

The behavior of *Bonomoia* n. sp. to regularly upright its body during walking is assumed to be an adaptation that not only maximizes its ability to receive chemical stimuli ("waving") but also to bring the "eyes" in a position to maximize the reception of incidence of light. But because the "waving" behavior of this species is generally reduced (they do not "wink" during the walk as other histiostomatids do), this behavior mainly could have been evolved in correlation with phototactic orientation. Such behavior would enable this species to differentiate gradients of light much better than other histiostomatid mites.

Within the *Opuntia* pieces *Bonomoia* n. sp. prefers the area with optimal growth of microorganisms, an area which is usually dark-brown in color (Fig16B). It is possible that deutonymphs must leave this area and move to the *Opuntia* surface in order to locate the organisms used for phoresy. The transporter is unknown, and in the rotting tissue below the *Opuntia* surface I never found adult or juvenile insects that seemed to be attractive carriers for the deutonymphs. In the field the *Opuntia* surface over the rotting area was always damaged and there were some small splits in the external wall. Deutonymphs presumably need to find these small openings in order to ascend to the outside surface, a probable reason why the light sensory system is so well developed in this *Bonomoia* species. The second conspicuous behavior of the deutonymph, attaching to the surface and turning around while "waving", cannot be explained in the context of visual orientation because it occurs only on the *Opuntia* surface. It cannot be determined whether this behavior already existed in the stem species of *Bonomoia*. Other *Bonomoia* species were not examined. Comparative studies of deutonymphal behavior are needed. The visible “eyes” (Fig25A) are apomorphic in the stem species of *Bonomoia*.

I often observed deutonymphs of other histiostomatid species (and astigmated mites in general) developing in insect tunnels that exist inside the dung of mammals or inside rotten wood. That's why I assume that they only need to orient to a close light source, and/or that the organism used for dispersal shares the habitat.
Deutonymphs of *Histiostoma maritimum* in my experiments were not attracted by light and even seemed to avoid it. This can be explained in regard of their biology. Carrier organisms are the beetles *Heterocerus fenestratus* and *H. fusculus* (WIRTH, submitted 2002), and both the adult beetles and mites spend most of their life inside tunnels in mud around fresh waters. Deutonymphs can therefore easily find new carriers without being forced to leave the tunnels.

The mode of reproduction (WIRTH, submitted 2003)

In laboratory cultures, *Bonomoia* n. sp. was observed to undergo thelytoky (diploid parthenogenesis) (WITALINSKI, personal communication). Thelytoky is not uncommon in the Histiostomatidae, and HUGHES and JACKSON (1958) observed four of twenty species to be thelytokous. They found two species, *Histiostoma humiditatis* and *H. feroniarum*, to be capable of thelytoky as well as arrhenotoky, with both modes of reproduction appearing in the same habitats and populations. *H. feroniarum* is also able to reproduce only by thelytoky (FASHING, personal communication). The cultures of *Bonomoia* n. sp. were reared from only a few specimens found in Sardinia, and it cannot be ruled out that both modes also exist in *B.* n. sp. in the field.

Copulation position (WIRTH, submitted 2004)

Apomorphic for the stem species of the Histiostomatidae is that males are positioned dorsally on the female during copulation. Both gnathosomas are orientated in the same direction. Legs I, II and III of the male clasp between legs I, II and III of the female for a better fixation during copulation. Legs IV of the male are directed posteriorly and clutch the end of the female's hysterosoma (Fig23A). Legs I and II of the male are directed anteriorly, but the tarsi are turned posteriorly, which is why setae la and ra are directed backwards. Legs III and IV are arranged exactly the other way round. Setae la and ra are directed anteriorly (Fig23E). Within the Histiostomatidae, this method of holding on to the female was transformed several times in adaptation to environmental conditions.

1) Females and males of the stem species of the monophyletic “Bark-inhabiting group” (Fig3) were reconstructed to have a characteristic pattern of humps, formed by the cuticula of the dorsal hysterosoma. A simple nomenclature is introduced (Fig23B). One unpaired hump (a) surrounds setae d5a and is located centrally anteriorly. Three pairs of humps (b-d) directed upwards are arranged from anterior to posterior, each bearing pairs of dorsal setae. The posterior hump (d) is directed to the backside in all males and females of the mite. In addition, males of species within that group were observed to fix the copulation position by embracing the posterior humps of the female.

The original function of the anterior and lateral humps is unknown. They can be seen as a first step in the evolution of structures, which are adapted to a tactile camouflage in the monophyletic camouflage-group, that is a subgroup of the bark inhabiting mites. By forming a basket shaped dorsal surface to hold substrate from the surroundings, these cuticula elevations could support the distinctly modified setae, that are able to adhere substrate particles. In the females the posterior humps are assumed to have been evolved in order to support the male’s fixation during the copulation, because they are conspicuously directed backwards and the function as a holding structure was shown (Fig23C). The function of psterior humps in the males is still not examined.

2) The monophyletic taxon comprising, *H. radiferum*, *H. pulchrum*, *H. strenzkei*, *H.* n. sp., *Hormosianoetus* and the taxa of the “Pitcher plant group”, which inhabit the pitcher fluids of *Sarracenia* and *Nepenthes*, was hypothesized to be the sister taxon of the *H. feroniarum* group (WIRTH, submitted 2002). The stem species of these taxa developed conspicuously enlarged setae la and ra at legs I and II of the males (Fig23D). *H. pulchrum* was regularly found in the slime flow of different tree species (often oaks). SEM observations show that the enlarged and elongated setae ra of legs II are distinctly pressed into the cuticula of the female during the copulation (Fig23D).

The possession of these derived setae obviously supports the fixation of the male on the female for a while inside a more or less liquid substrate, which moves down the tree. To resist the strength of this fluid flow, it is obvious that a selection pressure promoted the evolution of these additional fastening structures.

The habitats of *H. strenzkei* and *H. radiferum* are not exactly known (SCHEUCHER, 1957). So a similar function of these enlarged setae only can be assumed. Pitcher plant inhabiting mites live swimming in a water-like liquid, which complicates restful copulation. Therefore the

function of the enlarged setae la and ra as fastening structures is assumed, but still unobserved.

Most species of the *H. feroniarum* group (Fig3) live around water: *H. litorale, H. maritimum*, *H. palustre* and *H. insulare*. Species of the pitcher plant group live inside water-like habitats, related and basically branching species in slime flows of trees. This could be the reason why the stem species of the "Pitcher plant mites and related species" and the "*H. feroniarum* group" was adapted to live in a wet substrate, an apomorphic ecological character, derived from inhabiting slightly damped habitats.

The main arguments for the sister group relationship are the elongation of leg setae ra and la, the copulation behavior as described for *H. pulchrum* and the development of a male dimorphism (Fig13A). This copulation behavior to claw into the female's cuticula obviously developed in adaptation to a wet habitat in their stem species. A copulation behavior similar to *H. pulchrum* was observed in species of the *H. feroniarum* group: *H. feroniarum* ("normal" male type), *H. litorale, H. palustre,* ("normal"male type) and *H. sapromyzarum* (Fig23E).

Histiostoma palustre *Wirth, 2003 (WIRTH, 2003)*

The deutonymphs of the biologically conspicuous *Histiostoma palustre* (Fig26C,D) only were found only once in May 2000 in the mud around waters (gravel-pit of the "Teufelssee", Berlin) attached to the hydrophilid beetle *Coelostoma orbiculare*. Then the species could be cultured for nearly 2 years. Random samples in the mud and at other specimens of the Hydrophilidae later remained unsuccessfully to find further specimens, despite of the fact that the mite grew up very successfully under laboratory conditions.

Choice tests with the beetles *Cercyon litoralis* (Hydrophilidae), *Hygrotus inaequalis* (Dytiscidae) and *Coelostoma orbiculare*, which live in the same habitat, showed, that *Cercyon litoralis* was more frequently occupied than *Coelostoma orbiculare*. *H. inaequalis* was only ascended by an unsignificant small number of deutonymphs. That's why it is assumed, that *H. palustre* in the field associated with both hydrophilid beetles. The mud around these waters consists of a distinctive relief of small puddles. In their surrounding exists the dampness which the mites need to survive. There the hydrophilids *Cercyon. litoralis* and *Coelostoma. orbiculare* were found. The puddles in that area dry up regularly and newly arise somewhere else. That's why the mites depend on the phoretic transport.

The laboratory observations show, that the deutonymphs prefer to ascend the insect's head. The preference of a special place for the attachment is common within the Histiostomatidae.

Under laboratory conditions at room temperature one life cycle of *H. palustre* needs 8,6 days on average for those individuals which skip the deutonymph stage, which happens very seldom in this species. Most individuals molt to deutonymphs and remain in that stage for some days. Then the life cycle needs 9,3 days in average.

The females are able to reproduce parthenogenetically. Inseminated eggs develop into males as common within the Histiostomatidae (KRIVOLUCKIJ, 1975). A conspicuous male diphenism occurs: legs two of the derived male type changed into clasp organs. Contrary to the normally formed legs (Fig14C), the modified seta vF of the enlarged femur is movable against the enlarged empodial claw of the tarsus (Fig14D,28C)

The phylogenetic position

Histiostoma litorale Oudemans, 1914 is assumed to be the sister species of *H. palustre* within the *Histiostoma feroniarum*-group. Synapomorphies are (Fig. 27): The outline of the deutonymph is oval shaped. The setae sigma and eG of the third pair of legs and sigma of the fourth legs are conspicuously elongated. Apodemes p1 converse in a pointed angle to the sternum. Apodeme l3 is elongated. The sucker plate is oval shaped and covers the whole posterior ventrum. Whereas *H. palustre* is adapted to the beetle *Coelostoma orbiculare* and probably also to *Cercyon litoralis*, *H. litorale* is phoretically associated with carabid beetles (*Bembidion, Pterostichus*) and Diplopoda near the waterside (SCHEUCHER, 1957).

Both species live in the mud around waters. It is therefore assumed, that this habitat was colonized by their stem species. Similar habitats were opened up by *H. insulare* Oudemans, 1914 and *H. maritimum* Oudemans, 1914. But both are caused by morphological arguments not closer related to *H. insulare* and *H. palustre*. That's why this habitat must have been colonized three times convergently.

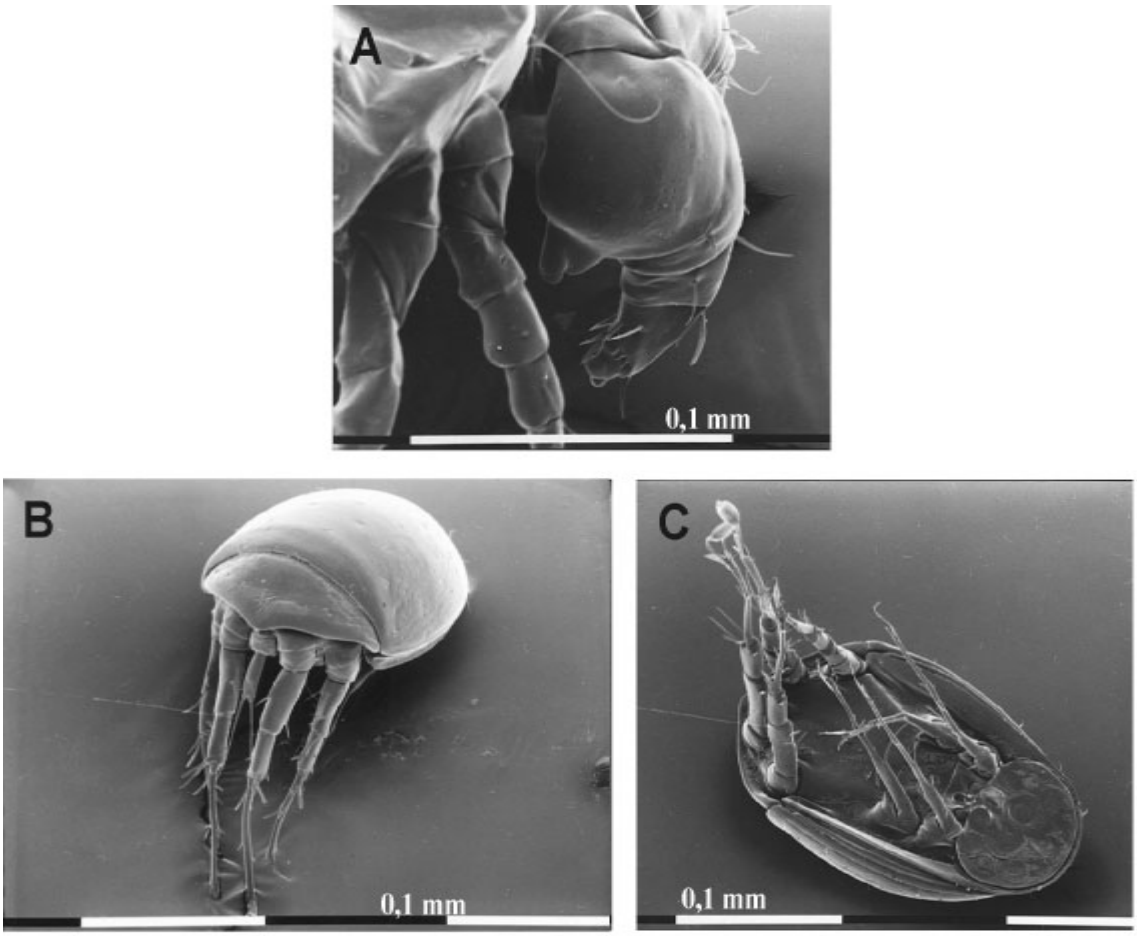


Fig26:
Histiostoma palustre: A: Leg II of the male modified into a clasp organ in a posterior view. B: Deutonymph in anterior view, C: in ventral view.

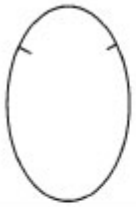
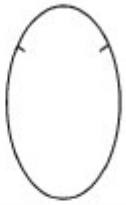
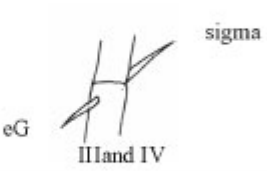
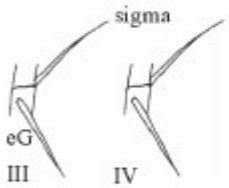
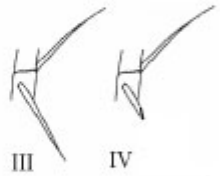
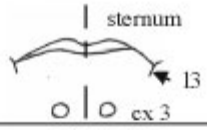
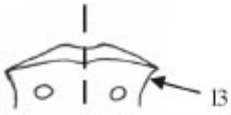
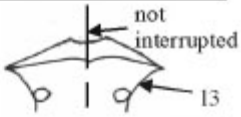
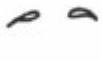
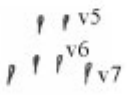
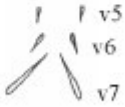
Characters	*Histiostoma feroniarum*	*Histiostoma litorale*	*Histiostoma palustre*
outline of the deuto-nymph dorsally			
deutonymphal leg-setae Genu, Tibia			
deutonymph in ventral view with sucker plate			
deutonymphal apodemes p1			
deutonymph ventral view, sternalapodeme and apodeme p3			
adulti in dorsal view; lengh of setae d3			
adulti in dorsal distance of setae to each other			
females in ventral view, distance of setae			
adulti in ventral view, setae v5-v7 and lengh of v7			

Fig27:
Depicted are synapomorphies of *Histiostoma palustre* and *H. litorale*. They are compared with corresponding characters of *H. feroniarum* as outgroup member.

Evolution of male polyphenisms within the Histiostomatidae (WIRTH, submitted 2004)

Within the Histiostomatidae different male morphs are known e.g. from *Sancassania*. In *S. anomalus* pleomorphic males with enlarged legs and homomorphic males exist. The pleomorphic ones were observed to kill and feed on the homomorphic types and to fight among themselves (EVANS, 1992). Females of *S. berlesei* mated with pleomorphs produced more offspring and therefore had a selective advantage (TIMMS et al., 1982). Male dimorphisms were also mentioned for histiostomatid mites (e.g. different sizes of males in *Histiostoma pulchrum* and in *H. feroniarum*, SCHEUCHER, 1957). I observed male dimorphisms of the following three species under laboratory conditions: *H*. n. sp. 3, *H. palustre*, *H. feroniarum*. The morphological differences of the male morphs were described and the inductive factors for the development of each morph were tried to discover. The terms homomorphs/heteromorphs and bimorphs/pleomorphs were introduced for species of *Sancassania* in which usually all four types appear. As only two different types were found in those histiostomatid species the necessity to adopt these terms was not given. Instead "normal" males were differed from the modified ones with simple descriptive terms.

Two male types of *Histiostoma* n. sp. 3 (closely related to *H. pulchrum*) were observed, which exist in conspicuously different sizes within the same population. In dorsal view, the outline of the big morph is wider than in the small morph (Fig12E), where it is distinctly notched inwards at the level of legs IV (Fig12F). In lateral view, the posterior hysterosoma of the big morph bulges ventrally (Fig28A), the hysterosoma of the small morph is shorter and not bulged (Fig28B). Different from the big morph, in the small morph a propodosoma shield divided into a pattern of clearly visible cuticula fields is missing. The legs of the big morph are longer in relation to the rest of the body and legs I and II are distinctly thicker in contrast to the small morph.

Conspicuous behavioral male characters were not observed. It could not be decided which factors cause the different male morphs in this species, but the temperature seemed to be an important factor.

The males in populations of *H. palustre* differ in a conspicuous way. There exist males with legs II transformed into clasp organs (Fig28C), which can be developed on both sides or only on the right or on the left. The other morph of similar size has no clasp organs.

An experiment was performed to find out the factors which are responsible for this male dimorphism.

Inseminated females were separated into small dishes (diameter 1,0 cm). The second following generation was observed and numbers of different male morphs and numbers of males altogether and females were controlled.

This experiment was performed both at room temperature (30 -32°C) and at 20°C. Significant differences were found in the relation between both males with and those without clasp organs. At lower temperatures the derived type (18 %) existed statistically in smaller numbers than the "normal" (82 %) morph (10 experiments, 237 males). At higher temperatures numbers of derived males (45 %) increased significantly in relation to the "normal" (55 %) morph (10 experiments= 10, 729 males) . Males with clasp organs on both sides and those with these modified legs on the left or on the right hand side only, always stayed in similar numbers. In all experiments, numbers of females were significantly similar to the male numbers (63 % of all mite individuals at low temperatures, 412 females; 61 % of all mite individuals at high temperatures, 1173 females).

Conspicuous behavioral characters of the males were observed. Males of all existing morphs took part in accumulations, which were identified as large numbers of males fighting for one single female tritonymph (Fig28G). Males with clasp organs used them to take hold of legs of competitors. Males without clasp organs were involved in similar numbers in these fights. They were observed mainly to use legs II (as the derived morph) to hook onto the legs of competitors. It was observed that the numbers of successfully copulating males, both with and without clasp organs, stayed statistically similar.

It was expected that derived males with clasp organs would be more successful in these fights and would copulate more often, but this could not be proved under laboratory conditions. Nevertheless, it is thought that a selective pressure must be responsible for these morphological transformations, which is why, in the field, advantages during the fights with respect to "normal" males are assumed. It was expected that females would be a minority in all experiments. This minority of unmated females or female tritonymphs in the field is presumed to have caused a selection pressure for transformations of males.

In *H. feroniarum* two different male morphs were found in the same populations. They were clearly different from each other in both size and other details.

Legs I and II of the big morph are distinctly thicker than in the small one. From the dorsal view, the posterior outline of the hysterosoma of the small morph is trapeze shaped (Fig28E) contrary to the rounded posterior end of the big morph (Fig28D). During copulaton with female tritonymphs, small males assume a position as previously described. Big males embrace the whole female body with their legs (Fig28F).

Experiments as described for *H. palustre* were performed at 16°C, 20°C and room temperature. Contrary to *H. palustre*, at low temperatures (16°C, 20°C), numbers of "normal" males were similar related to the derived ones. At higher temperatures (30 -32°C) there are significantly more big males than small ones. As in *H. palustre* the number of derived big males increased significantly at higher temperatures(Table 1).

As in *H. palustre* males of *H. feroniarum* fight against each other in bigger accumulations. While fighting and afterwards successfully copulating, both types were represented in similar numbers. Like in *H. palustre*, this was unexpected and probably a consequence of the artificial culture conditions or probably of the unexpected high numbers of females.The fights of modified males against the normal ones remind of the observations of *Sancassania anomalus* (EVANS, 1992), but contrary to them, killing and feeding on the normal morphs were not found in these histiostomatid species.

The male dimorphism is an additional character aside from the distinctly enlarged leg setae la and ra (connected with a more stable copulation position) to argue for the sister group relationship between the *H. feroniarum*-group and the "Pitcher Plant group with related species" (Fig3). For their stem species, the existence of two male morphs significantly different in size can be hypothesized. The big morph had enlarged legs I and II. Probably this male dimorphism was caused by a temperature sensitivity as described above (polyphenism). Presumably, the big male morph had advantages during the copulation, because a special fighting behavior could not be reconstructed for that stem species. The development of thicker legs I and II in the derived male morphs probably took place in context with a more secure copulation position. All male morphs were able to claw into the female's cuticula with enlarged leg setae for better fixation. Obviously, this fixation was additionally supported in the derived male morphs by their enlarged legs.

The stem species of the *H. feroniarum* group developed males fighting in bigger accumulations (Fig28G). The benefits of the derived male morphs presumably concern the fights against competitors and a better stability during copulation. It is still unkonown whether in addition a selective advantage of females mated with modified males exists as was observed in *S. berlesei* (TIMMS et al., 1982), where such females produced more offspring.

The dimorphism of *H. palustre* is different from that observed in other species. The morphs are similar in size, but differ in the form of legs II. The dimorphism in size must have been completely reduced and instead enlarged legs II transformed into a more complex structure.

In several species within the "Pitcher Plant group and related species" and the *H. feroniarum* group male dimorphisms could not be observed. Presumably within the Pitcher Plant group

this character was completely reduced once (Fig3). The following species probably completely reduced the dimorphism convergently: *H. radiferum*, *H. strenzkei* and species of the *H. feroniarum* group: *H. insulare, H. maritimum, H. myrmicarum, H. polypori* and *H. sapromyzarum*. It is expected that male dimorphisms exist at least in some of these species' populations, but have not been discovered until now, because dimorphism does probably not always appear in all populations of a species.

TABLE1:
Numbers of big and small males related to each other under different culture temperatures and numbers of males related to females of *Histiostoma feroniarum*.

mb = big males, ms = small males, f = females, nm = number of all male specimens, nf = number of all female specimens, nexp. = number of performed experiments.

16°C			20°C			30°C		
mb	ms	f	mb	ms	f	mb	ms	f
62%	38%	69%	53%	47%	58%	88%	12%	53%
of all males		of all individ.						
nm= 461 nf= 1018 nexp.=14			nm= 423 nf= 587 nexp.= 10			nm= 942 nf= 1072 nexp.= 20		

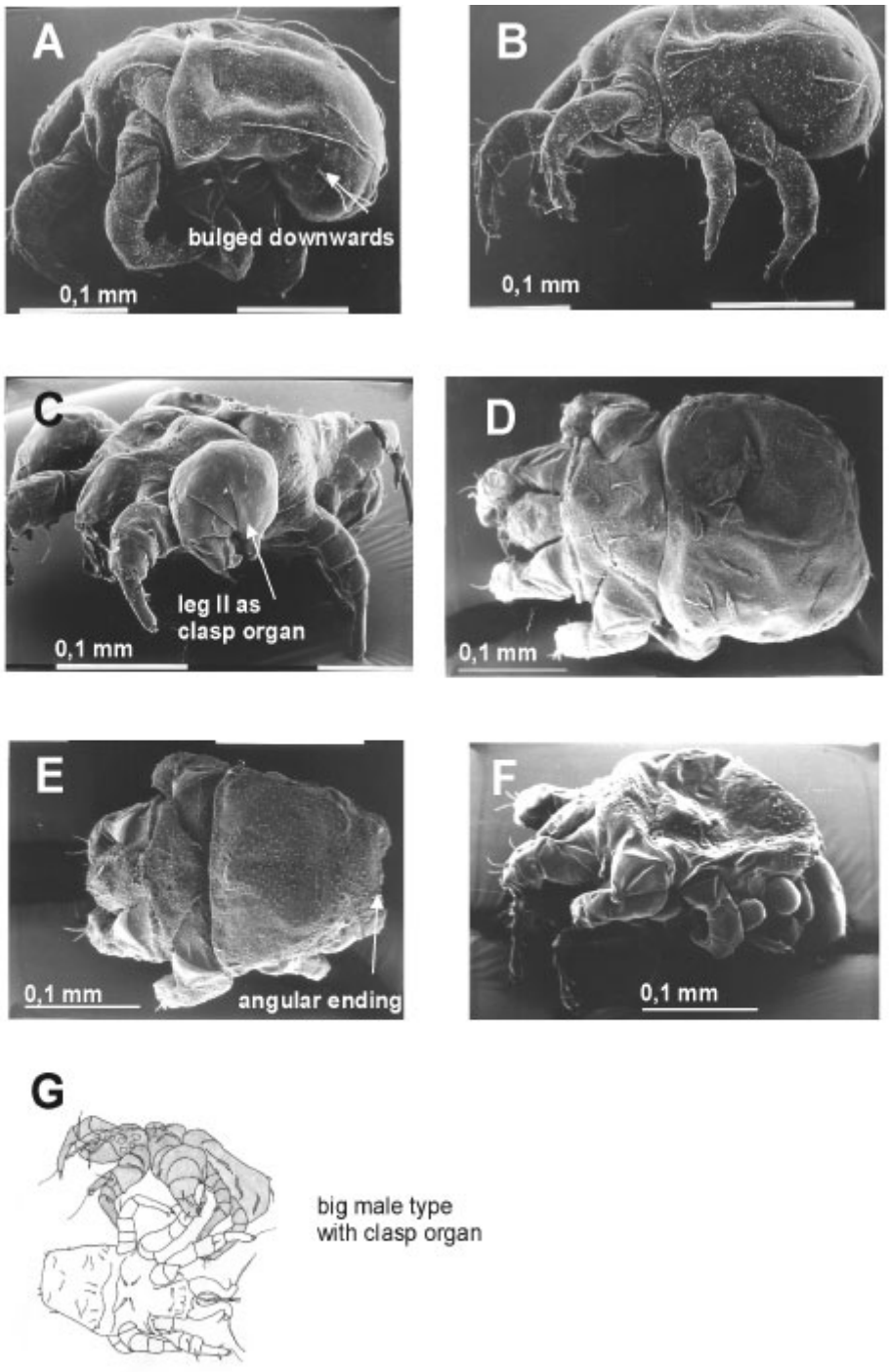


Fig28:
A-B: *H.* n. sp (related to *H. pulchrum*): A: Big type in lateral view, B: small type in lateral view. C: Male of *H. palustre* in latero anterior view. D-F: *H. feroniarum:* D: Big male in dorsal view, E: small type in dorsal view, F: big type in copula with a female tritonymph. G: Males of *H. palustre* fighting against each other.

The carrier-species of H. polypori

SCHEUCHER (1957) writes that *Histiostoma polypori* is specific for earwigs, and that the deutonymphs mainly can be found on *Forficula auricularia* (Dermaptera, Fig29A) always sitting between cephalon and prothorax. 90 % of this *Forficula* -species are occupied by the mites (SCHEUCHER, 1957). The female of *Forficula* takes care of the eggs and worries about the nymphs (HERTER, 1965). I observed this brooding-behavior to be very important for the propagation of the mite. But such brooding-behavior occurs in nearly all earwig species. Thus, I investigated the behavior of the mite deutonymphs in response to other earwig species that live sympatrically with *F. auricularia*. I investigated individuals of the following species: *Apterygida media* Hagenbach, 1822 (n= 19 individuals, different stages from Berlin and the Saarland, Germany), *Chelidurella acanthopygia* Gené, 1832 (n= 16 adults, from the Saarland), *Forficula decipiens* Gené, 1837 (n= 15 adults, from Sardinia, Italy), *Labia minor* Linnaeus, 1758 (n= 1 adult, Sardinia) and *Nala lividipes* Dufour, 1828 (n= 3 individuals, different stages from Sardinia). None of these earwig-individuals was occupied by histiostomatid deutonymphs**.** *F. auricularia* is obviously the only carrier of *H. polypori* in the field.

Choice tests with different carrier species

To test the attractiveness of other earwig species to the deutonymphs (Fig29D) of *H. polypori* under laboratory conditions, I put one earwig-individual of *F. auricularia* with one earwig of another species together in mite-culture-dishes for 24 hours. The results show that *Apterygida media* and *Chelidurelle acanthopygia* were occupied by significantly less deutonymphs than *F. auricularia* (Table 2). Deutonymphs never ascended either *Labia minor* or *Nala lividipes*, despite repeated experiments. This is probably due to the fact that those earwig species are quite hairy. Their body surfaces offer few of the smooth surfaces necessary for good purchase. It was observed that deutonymphs try to attach, but cannot find a suitable position on the earwig.

These experiments show that *Forficula decipiens* (Fig29B) is as attractive for the deutonymphs as *F. auricularia* (Table 2). In further experiments, every developmental stage of *F. decipiens*, including the adult stage, was ascended. Nevertheless, the 15 observed adult individuals of *F. decipiens* from the field had no histiostomatid deutonymphs. *F. decipiens*

was often found to live syntopically with *F. auricularia*, which is always occupied with deutonymphs of *Histiostoma polypori*. But obviously a deutonymph transfer cannot occur in the field.

The biology of *F. decipiens* is similar to that of *F. auricularia*, but *F. decipiens* broods close to the coast in a hardwood environment in Sardinia, a habitat in which *F. auricularia* was not found (Fig29C). Therefore, the transfer of the mite from *F. auricularia* to *F. decipiens* does not take place, because the preferred brooding zones of these species are separated.

Brooding-biology of Forficula decipiens

Though HERTER (1965) and earlier authors collected a great body of information about the brooding-behavior of *Forficula auricularia*, the biology of earwigs is not yet well examined. Special information important for the understanding of the mite's development is missing. Because the brooding *F. auricularia* individuals that I examined under laboratory conditions built no nests which were visible on the surface, I examined brooding *F. decipiens* as a model-organism instead. I discovered that *F. decipiens* was easy to culture, and the brooding-behavior is similar to that of *F. auricularia* (HERTER, 1965), including similar periods of development. *F. decipiens* was therefore a suitable model for examining the mite's behavior during the development of the "carrier earwig".

I examined the broods of two female individuals, both occupied by at least 50 deutonymphs. The earwigs were held in small bowls (10 cm x 5 cm) with wet earth and humid air and some flat stones (by room-temperature, but at different places). They were fed with pieces of apple. The nests were hollows under objects such as flat stones. Both females produced about 50 eggs and behaved similarly. The numbers used in my calculations are averages of these two broods. The females licked their eggs regularly and controlled the structure of the egg-heap by repositioning single eggs that had fallen down (Fig30A).

The female earwigs defended the eggs against attackers with help of their cerci. They stayed in body-contact with the eggs at all times, but sometimes they left to feed on an apple piece nearby. This was proved by the excrements found on the apple. After 12 days, about 50 N2-nymphs had developed (Fig30B). Females and nymphs stayed together in the nest. For several days, the females continued to defend the nymphs, after which that behavior ceased. However, the females and the offspring continued to group together in the nest, with occasional forays by the females to feed on the apple. The nymphs fed on micro-organisms and on fungus hyphae present in the nest, both at night and during the day. By night some of

them left the nest, but returned during the daytime. The mortality of N2-nymphs in the last 4-5 days of this stage was about 40 % (30 and 32 of 50). The development to the N3-stage took 19 days. The N3-nymphs and the females stayed together in the nest around the original brooding-place. These movements appear to depend on the location of the food-supply. Sometimes a few nymph individuals aggregated in smaller groups outside the nest, but a day later they had returned and were all found inside the nest. After 5-6 days, only 2-4 individuals remained alive. The surviving nymphs stayed together with the females. Around 15 days after molting from N2 to N3, the nest ceased to exist, and aggregations with or without the females began to take place in different areas every day. Three days later, the nymphs molted to N4. The females survived.

Though only two broods of *F. decipiens* were closely observed, it can be assumed, that the results confirm the earwig's behavior in the wild, because both broods followed exactly the same course. In fact the broods developed under comparable conditions but at different places (my home, University). That reduces the possibility of a culture-artefact (apart from the unbelievable high mortality-rate). Besides the results were in agreement with the partly observed brood of *F. auricularia*.

Only one brood of *F. auricularia* could be examined, which was not easily to observe, because the nest wasn't visible on the surface in the culture-vessel. Nymphs fed on microorganisms. Many N2 nymphs died. The female did not die in the nest.
Both *F. auricularia* and *F. decipiens* brood in nests which can be located both inside the soil or are visible on its surface. Mechanical damages of the nest always provoke the female to leave its brood, that's why nests not visible on the surface are impossible to observe in detail.

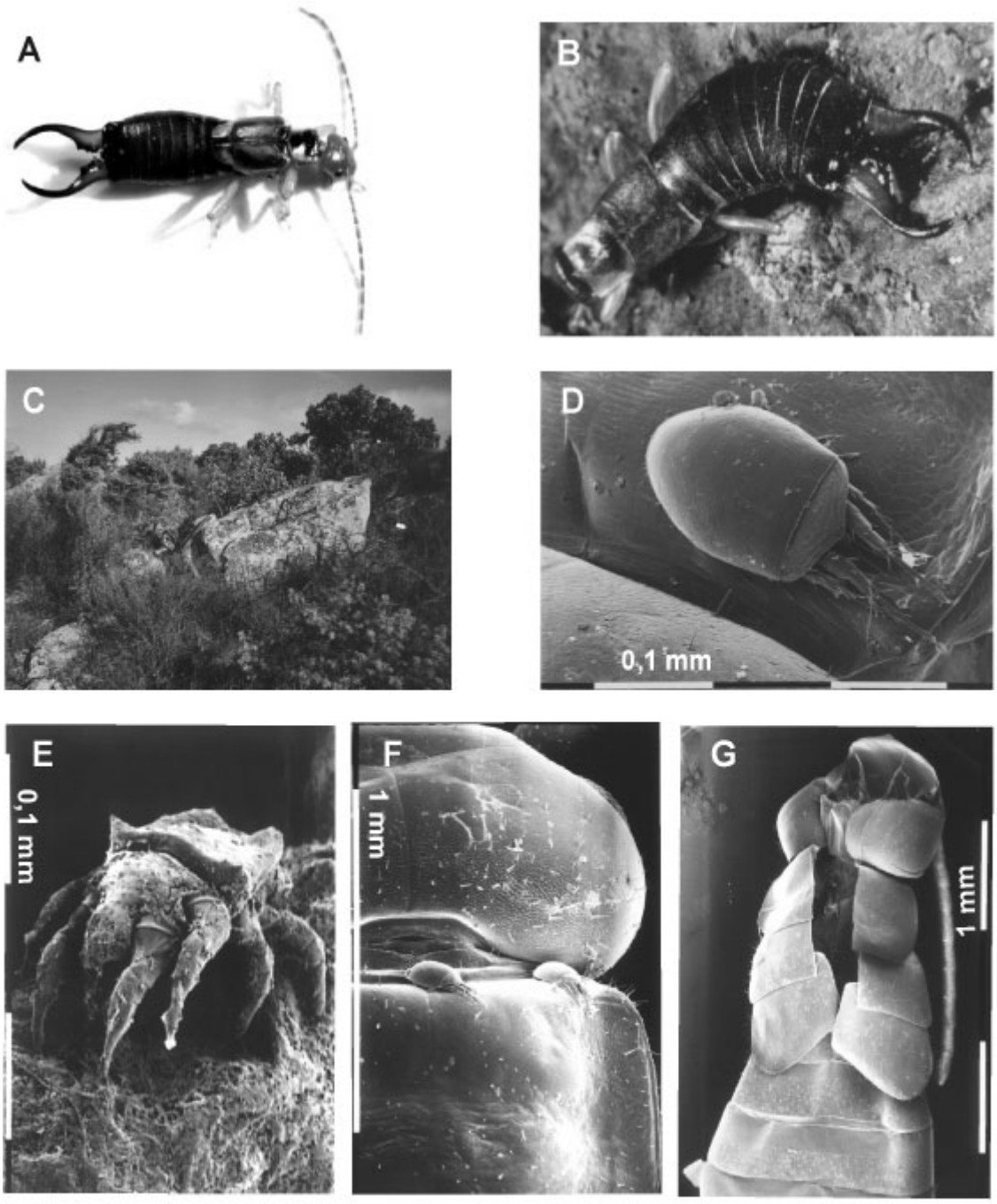


Fig29:
A: Male of *Forficula auricularia* in dorsal view. B: Male of *F. decipiens* in dorsal-posterior view. C: Hardwood environment in Sardinia close to the coast, where only broods of *F. decipiens* were found. D: Deutonymph of *Histiostoma polypori*, sitting on the posterior parts of the head of a N4-nymph of *F. auricularia*. E: Adult male of *H. polypori* moving on the surface of an earwig-cadaver. F: Deutonymphs sitting on the anterior prothorax of a N4-nymph of *F. auricularia*. This area is adjacent to the exuvial-sutur .G: Exuvie of a N4 stage.

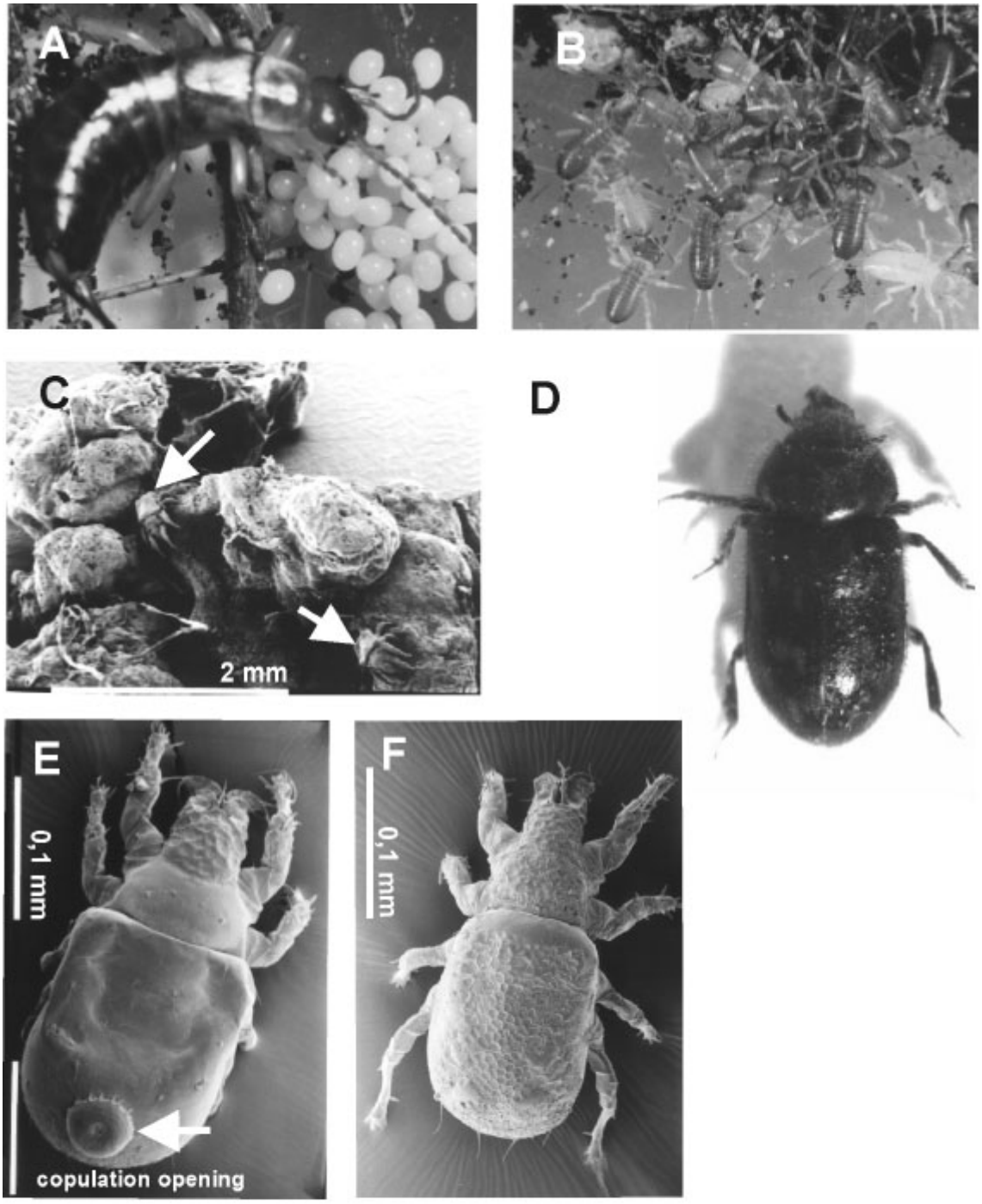


Fig30:
A:. Female of *Forficula decipiens* worries about its eggs. B: Aggregation of just molted N2-nymphs. The female remains nearby. C: Two males of *Histiostoma polypori* on a N2-cadaver of *F. decipiens*. D: Individual of *Heterocerus fenestratus*. E: Female, F: male of *Histiostoma maritimum* in dorsal view.

WEYRAUCH (1929) reports that in *F. auricularia* many of the eggs cared for by the female did not develop. In the observed broods of *F. decipiens*, however, nearly as many N2-nymphs as eggs were found. The female sometimes left its eggs and offspring to feed. HERTER (1965) found the same behavior in *F. auricularia*. My results showing that the female remained in aggregation also with the N3-nymphs confirm the observations of BEIER (1959). HERTER (1965), however, did not observe the female staying with the juveniles for such a long time. Both authors didn't mention details about the composition of the nest after the eggs had developed. WEYRAUCH (1929) assumed that females regularly die in the nest, but my results and those of HERTER (1965) suggest that the females survive and that BEHURA (1956) was wrong in assuming that the mites develop on the female's cadaver in the field.

Mite development in the earwig-nest

The deutonymphs waiting on the female earwig do not leave it to develop on dead eggs or on female or nymphal excrements. But they develop well on the cadavers of the dead N2 and N3 earwig stages (Fig30C). Old N3 nymphs were ascended after about 14 days and were more (5-10 deutonymphs) or less (1 deutonymph) occupied by deutonymphs.
Just before and after the earwigs molted to N3, the mortality of earwig-nymphs in culture was high. It cannot be assumed that such a high mortality occurs in the field, and this might be an artefact caused by the laboratory conditions. But it does show that molting from N2 to N3 may be a time of high mortality, in contrast to molting from N1 to N2. Thus, the N2-N3 molt may regularly result in earwig cadavers available for mite development. Because the living nymphs aggregate near those that die in the nest, newly developed deutonymphs are able to ascend living earwig nymphs.

The mites probably prevent a dangerous microorganism growth on the juvenile cadavers in the nest, which could be destructive for the earwigs. Then the mites would be useful organisms supporting the earwig's development. It is not assumed that the mite affects the earwig nymph mortality in any way, because at first earwig-cadavers were found and a few days later, mite-development on the cadavers appeared.

Concerning *F. auricularia*, the following statements can be made: Mites did not develop on the earwigs eggs or their excrements. Living N2-nymphs were not occupied by deutonymphs.

Deutonymphs (≥20) descended to develop on N2-cadavers. Such a life-strategy is called necromeny (Fig31). It has evolved from a phoretic strategy within the Histiostomatidae.

Development requirements of the mite

This mite could not be cultured on pieces of potatoe and hardly on pieces of meat. My observations of the mite's behavior in the earwig's nest showed that *Histiostoma polypori* requires a special substrate for development: the cadavers of *F. auricularia* nymphs. To determine if earwig cadavers were the only place of development, I kept 34 living adult earwigs for 7 days under favorable conditions. Deutonymphs on living earwigs did not leave the carriers or initiated development, but on 8 out of 31 adult earwig cadavers they continued their development. This experiment was repeated with 8 earwig nymphs for 18-21 days during which they molted into the subsequent stages. Again the mites did not develop, neither on potato-pieces nor on apple-pieces, or on the excrements of *Forficula*. This indicates that the cadavers of the earwigs are the appropriate resource of the mite (Fig29E). BEHURA (1956) assumed that deutonymphs sometimes leave the earwig to develop on vegetable food. But I did not observe them feeding on plant material. The mites seem to be adapted into feeding on microorganisms from an earwig cadaver.

Position of the deutonymphs on earwigs collected in the field

The deutonymphs are attached on earwigs from the field dorsally and laterally in the region between head and prothorax (Fig29F). Using a SEM I could show that the earwig's exuvial suture is located dorsal median of the pro- and mesothorax (Fig29G).
I observed 13 individuals (12x N5 to adults, 1x N3 to N4) of *Forficula auricularia* molting under laboratory conditions. The number of deutonymphs on earwig individuals before and after molting remained nearly the same, suggesting that deutonymphs change over to the new stage after a molt.

Molting and cleaning behavior of earwigs

The thesis was that deutonymphs sitting in regions far away from the exuvial suture could not change to a new earwig stage during molting. To test this I observed the moltings of one N2 nymph and one N3 nymph (*Forficula decipiens*) being occupied by deutonymphs of

Histiostoma polypori. When deutonymphs ascend an earwig, they take positions on its whole body. That's why the juveniles had been occupied all over their bodies before their moltings. Nearly all deutonymphs of the N2-earwig changed during the molting to the following earwig stage, being afterwards located on the posterior head and the anterior prothorax. The N2-stage is short and thick. There is only a small distance between head and abdomen. That's why all deutonymphs could change to the next earwig stage ascending the head which is the first part of the body to exit the exuvial suture. During the earwig's molting from N3 to N4, deutonymphs being located around the head completely changed to the new earwig stage. The majority of those deutonymphs on other body-parts got lost during molting. Only a few from the abdomen could change after molting from the exuvie to the near by resting new earwig stage, ascending its abdomen again. The fresh molted earwig cleaned its body more often and more intensely than older N4 stages did. That's why all of them on the abdomen were pushed away within about 10 hours. Caused by the adult-like body proportion of the N3 stage, the distance between abdomen and prothorax can not be surmounted by deutonymphs during the earwig's molting.

These mites near the exuvial suture shift completely to the next earwig stage and there also take up positions in the head-prothorax region. Mites positioned on the earwig's abdomen get lost during the molting process or are removed shortly thereafter. Deutonymphs between head and prothorax can always make the change during the following moltings of the earwig.

The behavior of 4 adult earwig individuals was observed to find out how deutonymphs come to the region between head and prothorax. Therefore the earwigs were put in mite-culture-dishes crowded with lots of deutonymphs of *H. polypori*. They took positions on different earwig-parts: the head (dorsal anterior), the legs I-III, the ventral abdomen, and the cerci. Only on rare occasions a few deutonymphs did take positions between the earwigs' head and prothorax. 3 days later, the number of deutonymphs spread out over the earwig's bodies was still the same, but their positions around the head had changed conspicuously. All deutonymphs from the anterior head were now positioned on posterior head and anterior prothorax. These are the areas where deutonymphs always sit on earwig individuals in the wild. It was assumed that the earwig's cleaning behavior is responsible for this deutonymph-displacement, which therefore was closer examined. *F. auricularia* uses the tarsi of legs I to clean the head dorsally by moving them from median to lateral posterior (sometimes also from posterior to anterior). The head is cleaned more often than other parts of the body. The legs are cleaned by using the mouthparts. The ventral tarsi of legs III clean the dorsal

abdomen and the dorsal tarsi the ventral abdomen. The cerci are polished by the claws of legs III.

The position of deutonymphs in the region between earwig's head and prothorax could be a consequence of the head-cleaning behavior. Deutonymphs sitting on the anterior head were pushed by the earwig's legs I to that posterior position, what was supported by the polished head's surface. Some of these deutonymphs sometimes migrated to the anterior prothorax. It happened when earwig head and prothorax came into contact.

However, other parts of the body get cleaned too, yet the deutonymphs there at first remain in place. Only after the next molting of the occupied earwig juvenile, they get lost. That's why N4 and older earwig-stages are occupied by mite deutonymphs only around the exuvial suture.

Deutonymphs from the wild always sit between head and prothorax of the earwig, which is another argument for the thesis, that deutonymphs ascend earwigs once in the nest. If deutonymphs developed outside the nest and ascended older earwig stages, they should also be found on the abdomen and the cerci. But they only sit adjacent to the exuvial suture. This confirms my laboratory observations. BEHURA (1956) describes that the deutonymphs move from all body-parts to the exuvial suture before the earwig's molting in order to change to the next earwig stage. "After each fresh moult", they would be "aggregated in the groove between the head and the thorax". In my observations, the head-cleaning-behavior of the earwig was responsible for the mite's positions between head and prothorax. I observed them to be located in this area also before the earwig molts. I agree with BEHURA, that they continue to rest in that region in all subsequent earwig stages.

Earwig-stages bear an invariable number of mite deutonymphs

It is expected that deutonymphs of *H. polypori* regularly complete their life-cycle only on the earwig-nymph-cadavers in the nest. To examine whether the numbers of deutonymphs on all earwig-stages outside the nest (N4, N5, adults) remains statistically similar, the following survey was made.

I counted the deutonymphs on different earwig-stages from different regions in Germany (Berlin, Brandenburg, Neunkirchen-Saar) and adults from Sardinia (Porto San Paolo). There's no significant difference between the numbers of deutonymphs on N4, N5 and Adults (Table 2). In Saarland and Sardinia the deutonymph-number of individuals compared to those of the Berlin-region are somewhat (not statistically) greater. Obviously the bigger quantity is caused

by higher temperatures in Saarland and Sardinia. My results show that deutonymphs don't develop outside the nest, because the number of deutonymphs of all older earwig stages always stays the same (table 3). The generalistic *Forficula auricularia* which is not closely associated with specific environments, is the only known carrier of this mite. It could be possible that any insect-cadavers including other earwig cadavers outside the nest, the earwig occupied with deutonymphs accidentally passes by, were also suitable for the mite to develop on it. But those cadavers wouldn't offer the mite a secure way of afterwards finding the living earwigs necessary to their further dispersal. It is therefore not surprising that deutonymphs outside the nest don't develop anywhere and don't ascend older earwig stages.

Life cycle duration of H. polypori

Observations of earwig brooding behavior show that the largest numbers of juvenile earwigs die (leaving cadavers) just before and after they molt to the N3 stage. Living juvenile earwigs are ascended by deutonymphs after about two weeks. This must therefore be the period of the mite's development. By controlling 6 mite-cultures each for one generation, it was tested whether this period remains constant. Because individuals separated from the culture were not able to survive, the duration of development was determined by controlling an entire culture. This was only possible because all of the mites in the culture molted nearly simultaneously; moltings within a generation usually took place within a 24-hour period. They fed on micro-organisms which grew on the earwig-cadavers.

The development-cycle from an adult to the one of the next generation takes (average of 6 cultures) 11,1 days (Fig31). The deutonymph stage can also be skipped, and the protonymphs then directly molt to tritonymphs. The whole cycle then takes one day less.

Because the development of the earwig's N3-nymphs requires 18 days until they molt to the N4-stage (*Forficula decipiens*, own observations) or 17 days (*F. auricularia*, after HERTER, 1965), there is enough time for the mite to complete the life cycle and then to ascend the earwig's older N3-nymphs.

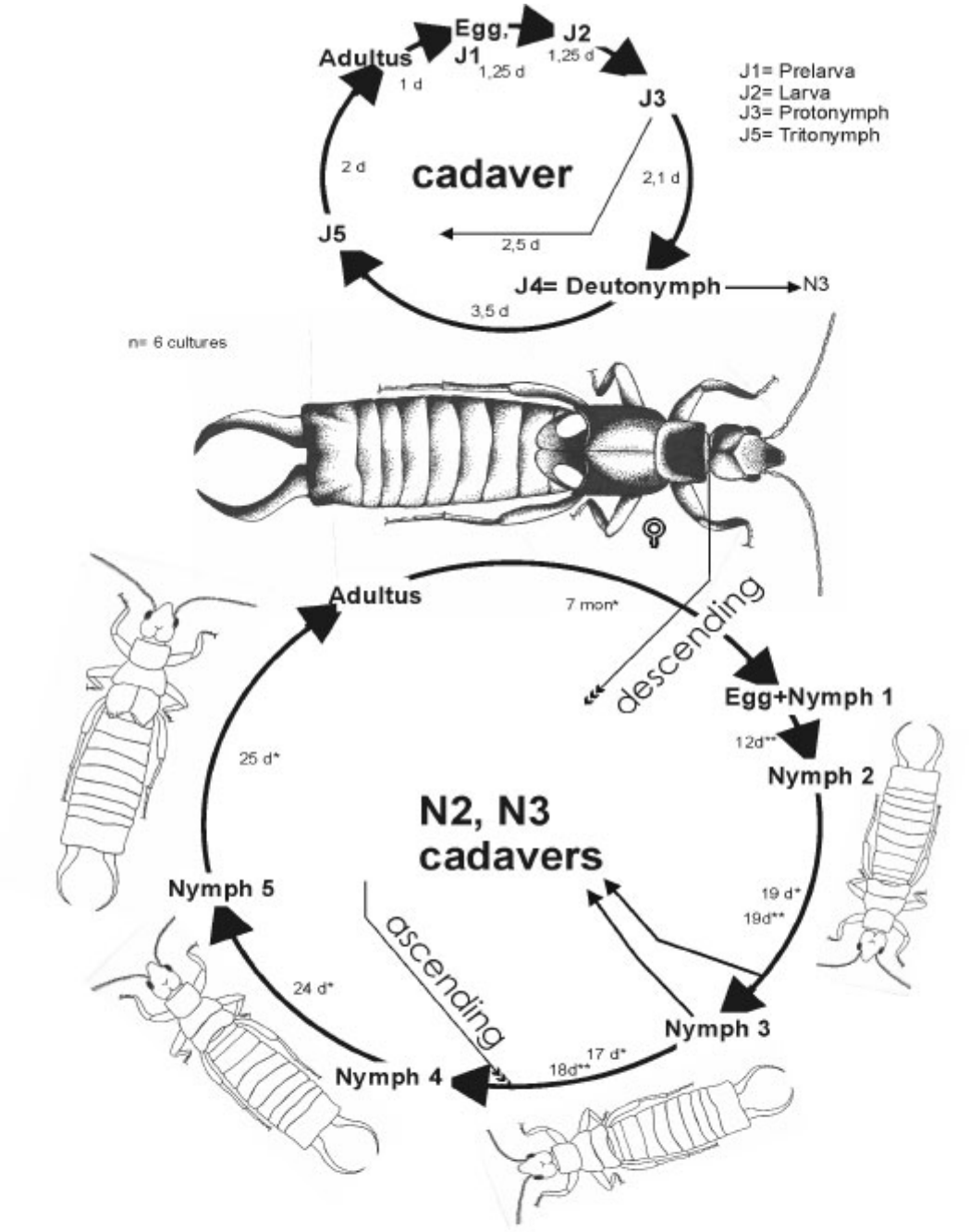


Fig31:
Life-cycle of *Histiostoma polypori*, which is associated to the life cycle of the earwig *F. auricularia*. Development-period of stages in days (=d) or month (=mon). The deutonymphs descend the adult earwig female to develop on the N2- and N3-cadavers, that died just before and after the molting from N2 to N3. The newly developed deutonymphs ascend the old N3-nymphs. These deutonymphs switch from stage to stage until the earwig reaches adulthood. J= Juvenile.

*HERTER, 1964
** *F. decipiens*, n = 2 cultures

Possibilities of deutonymph-transfer outside the earwig-nest

There are also other possibilities for an earwig individual without deutonymphs from the nest to get ascended at a later time. For the mite, this would also guarantee that it would be spread. Earwig N3 nymphs, which are ascended by mite-deutonymphs, often molt to N4 in presence of other nymphs, because all nymph stages continue to aggregate by day at different places, even though the nest no longer exists. Deutonymphs that were not able to switch from one earwig instar to another (caused by their position on the abdomen) are undoubtedly able to ascend unoccupied earwig individuals nearby.

Another possible deutonymph-transfer could occur as a result of the earwig's mating behavior. Couples of *F. auricularia* copulate repeatedly. In between they keep close contact (HERTER, 1965). This could be confirmed. These contacts could stimulate the deutonymphs to descend the male and switch to an unoccupied female and vice versa. Comparable close contacts leading to deutonymph-transfer were not observed for earwig-individuals of similar sexes or nymphs under laboratory conditions.

Summary of H. polypori *life-strategy*

The information concerning the life-strategy of *Histiostoma polypori* can be summarized as follows: the deutonymphs leave the female earwig to develop on the cadavers of the N2 and N3 nymphs. After the cycle, the new deutonymphs occupy the whole body surface of the living N3-earwig-nymphs. The earwig's head-cleaning behavior brings deutonymphs on the head in a position adjacent to the exuvial suture. Deutonymphs in this region are able to change from one earwig stage to another until the earwig reaches adulthood. The transfer from earwig stage to another was already observed by BEHURA (1956).The deutonymphs sitting on other body parts are partially "lost" or are brushed away by the especially intensive cleaning behavior within the first 10 hours of the new earwig stage. These deutonymphs in the region between head and prothorax remain from stage to stage until the earwig reaches adulthood. Then the deutonymphs leave the female earwig in presence of earwig-nymph-cadavers to grow up by feeding on the cadaver-microorganisms.

Place of development

The most frequent carriers of *Histiostoma maritimum* are the beetles *Heterocerus fenestratus* (Fig30D) and *H. fusculus*, more rarely some beetle-species of *Bembidion* and *Elaphrus* living in the borderline of freshwater. The deutonymphs are attached to the ventral areas, mainly around the coxae. This mite, like *Histiostoma polypori*, is difficult to culture. It became obvious, that *H. maritimum* (Fig30E,F) must develop in a specific place. This place appeared to be the cadavers of related beetles, because many mite individuals developed there. To test this, I killed some beetles occupied with deutonymphs to see what happened with the mites. In another test I put some living beetle individuals with deutonymphs in dishes (∅3 cm) with agar and mud from the place where they were captured, each individual separately. 4 individuals of *Heterocerus fenestratus* (with 10, 4, 14 and 3 deutonymphs), 4 *Heterocerus fusculus* (with 1 deutonymphe each) and 3 *Elaphrus cupreus* (with 3, 2 and 19 deutonymphs) were controlled. They lived in the Petri-dishes under good conditions for one month.
The deutonymphs developed and propagated on the cadavers. As exceptions 1 of the 10, 1 of the 4 and 1 of the 14 deutonymphs from the living *Heterocerus fenestratus* developed to adults and died without reproduction.
That shows that possible food resources in the substrate of *Heterocerus* -- such as microorganisms in the mud, dead plants, cadavers of other animals, or excrements of some other animal species -- are not suitable for the development of the mite. Under culture conditions the deutonymphs require the beetles' death in order to develop on their cadavers. So the species is necromenic.

The biology of Heterocerus fenestratus

Histiostoma maritimum is associated with the beetle *Heterocerus fenestratus*. Its biology was insufficiently known. These beetles burrow tunnels in muddy banks, where they spend most of their life. The females build brood-chambers. The young develop through five larval stages. The final larval stage forms a conspicuous pupae chamber (HIRSCHMANN, 1952).
The biology of *Heterocerus fenestratus* was observed under laboratory conditions. Beetles were examined in small Petri-dishes filled with mud from the field. *Heterocerus fenestratus* feed on microorganisms. The observed beetles from Berlin always live together in

communities containing large numbers of individuals, and the tunnel of each individual is connected to those of other individuals. They move both in their own burrows and in those of neighboring beetles.

Larger numbers of individuals from two species of Hydrophilidae, *Coelostoma orbiculare* and *Hygrotus inaequalis*, have often been found living syntopically together with *Heterocerus fenestratus*. These species are also able to build tunnels, and *Heterocerus fenestratus* can be found in those tunnels as well, although I never found Hydrophilids together with the deutonymphs of *H. maritimum*. Some individuals from the species *Bembidion dentellum* were also often found in the same muddy areas, but they are not able to burrow and were never found inside the tunnels of other beetles; they apparently live only on the surface.

Elaphrus cupreus individuals were both sometimes found nearby the *Heterocerus*-aggregations on the surface and sometimes far away in the area about the edge of the muddy banks. However, both *Elaphrus* and *Bembidion* are occupied with deutonymphs of *Histiostoma maritimum*.

Heterocerus fusculus lives syntopically with *Heterocerus fenestratus*, but its niche is associated with damper areas. Its biology is very similar to that of *Heterocerus fenestratus*, and it is also occupied by *Histiostoma maritimum* deutonymphs.

Deutonymphs which develop on the cadavers of *Heterocerus fenestratus* and *Heterocerus fusculus* also need to have later access to living carriers. Because many *Heterocerus* individuals always live in close proximity to each other in a connected system of tunnels, living beetles often meet with beetle cadavers. That's why deutonymphs easily can ascend new carriers.

Relationship between season and frequency of occupation with deutonymphs

Dispersion of *Histiostoma maritimum* is dependent on large numbers of beetles living in close proximity to each other, because deutonymphs which developed on cadavers need to have a chance regularly to find living beetles to ascend. Most matings in both *Heterocerus fenestratus* and *H. fusculus* occur in the early summer-months, which is why muddy banks are so densely populated with the offspring of those beetles in summer (HIRSCHMANN, 1952). The frequency of occupation with deutonymphs in spring and sommer was observed

In May and June of 2000, only 17.3 % of the collected *H. fenestratus* individuals (n=29) and none of the *H. fusculus* individuals (n=5) were occupied by deutonymphs. In August of 2000, 100% of all captured *H. fenestratus* individuals (n=7) and 100% of the *H. fusculus* (n=8)

individuals carried deutonymphs. In August *H. fenestratus* carried significantly more deutonymphs than in May and June. The individuals of *H. fusculus* were occupied by significant less deutonymphs than *H. fenestratus* (Table 4).

Because *H. maritimum* needs beetle-cadavers to develop, a high quantity of beetles, which die and let lots of cadavers lead to a high quantity of mites. That's why the results confirm the expectation, that there is a low frequency of occupation by deutonymphs in spring and a high frequency in summer.

Crossing experiments

In addition to the two *Heterocerus*-species, *Histiostoma maritimum* was also found on carabids of the genera *Bembidion* and *Elaphrus*. I examined individuals of *Bembidion dentellum* and *Elaphrus cupreus* that were occupied by deutonymphs being morphologically identical to *H. maritimum* from *Heterocerus*. These deutonymphs only develop on beetle's cadavers too. Because it is expected that a necromenic organism is highly specialized concerning behavior, food-supply and carrier species, the discovery of this mite on carabids is difficult to explain. It was therefore important to determine whether these mites belong to *H. maritimum*. Crossing-experiments could be easily and unequivocally attempted because, in contrast to most histiostomatid-species, *H. maritimum* is not able to reproduce parthenogenetically.

Mite individuals (one female, grown to adult in isolation; several males) were placed together in small dishes (∅ 1 cm) filled with 1.5 % agar and small pieces of beetle-cadaver. The experiments were observed for at least one week.

One out of six control-experiments with the *Elaphrus*-mite (males and females from *Elaphrus*) had a positive result.

The control-experiments show, that isolated individuals of *H. maritimum* don't find suitable conditions to reproduce regularly. Five negative controls make the interpretation of crossing-experiments difficult.

The following experiments were performed nevertheless: Females of the *Heterocerus*-mite were placed together with males from the *Bembidion*-mite and males of the *Elaphrus*-mite (Table 5).

Caused by the positive results of the crossing-experiments with mites from *Heterocerus* and *Elaphrus* I have in spite of the 5 of 6 negative controls no doubts that these carabids also carry *H. maritimum*. However, the question which remains unanswered is how the deutonymphs

reach the carabids. *Bembidion* and *Elaphrus* don't aggregate as *Heterocerus* does. My assumption is that deutonymphs which developed on *Heterocerus*-cadavers ascended the carabids. *Elaphrus cupreus* was identified to be a predator of *Heterocerus* pupae and larvae, and therefore was often found near *Heterocerus*-aggregations. The same is supposed for *Bembidion dentellum* as predator for *Heterocerus*-larvae. That's why my assumption is a change of the mite from the prey to the predator.

Necromeny

Results about the life-strategy of *Histiostoma maritimum* (laboratory conditions) show that it is a necromenic species similar to *H. polypori*.
The deutonymphs of *H. maritimum* ascend living adult individuals of *Heterocerus fenestratus* and *H. fusculus* and stay attached on them until the beetle's death. Then the mite develops on the cadavers. Mite-development duration was determined under conditions as explained for *H. polypori* and took 8,75 days (average over 6 mite generations). Under laboratory conditions, the deutonymph stage was only very rarely skipped. The deutonymphs of the next generation can easily ascend living beetles because *Heterocerus*-individuals live aggregated nearby and will eventually pass the cadaver (Fig32).

Phylogenetic relationship of Histiostoma maritimum *and* H. polypori *based on morphological characters*

Histiostoma maritimum and *H. polypori* belong to the *Histiostoma*-f*eroniarum*-group. Based on the following apomorphies, this group can be viewed as a monophylum (WIRTH, submitted):
- the digitus fixus has a sawlike form with a special number and form of teeth,
- the lobe of the palparmembrane is divided into two parts,
- apodeme r2 present (Fig21D).

8 central European species belong to the *Histiostoma-feroniarum*-group. *H. polypori* belongs to a small monophylum of 3 species (*H. feroniarum*, *H. insulare*, *H. polypori*) within this group that is well-founded by the following morphological characters of adult males (Fig21B,C):
- The ventral seta v7 lies beside v6, and apodem 2 is vaulted to the median side,

- posterior of the anus is a bulging cuticula elevation which is U-shaped from median to each side with the anus located medianly (the structure is probably an apodeme, Fig22G),
- the posterior outline is trapezium-shaped (anterior hysterosoma wide, posterior one strait and angular).

H. insulare can be argued to be the sister species of *H. polypori* (Fig21A). Their synapomorphy is the oval posterior chitin-ring in males. *Histiostoma maritimum* (and *H*. n. sp. 2) probably is the sister taxon of this monophylum of 3 species. As a synapomorphy the position of the male's v4 is posterior to the posterior osmo-regulatory organ. The posterior osmo-regulatory organs are located anterior of the genital opening. The position of *H. maritimum* nevertheless remains very doubtful, because palparmembrane and digitus fixus don't look like those of all other species within the *H. feroniarum*-group. If it originates outside this group, then the presence of the deutonymph's apodeme r2 and the position of the male's v4 would be convergencies to the similar features of *H. feroniarum*, *H. polypori* and *H. insulare*. But it is undoubted that several apomorphies separate *H. maritimum* from *H. feroniarum*, *H. polypori* and *H. insulare*. Therefore, necromeny was evolved independently in *H. maritimum* and *H. polypori*. The most parsimonious assumption is that the development of necromeny in the *Histiostoma feroniarum*-group derived twice convergently from the phoretic transport. It can't be assumed that the stem-species of *H. maritimum*, *H. feroniarum*, *H. insulare* and *H. polypori* already was necromenic, because *H. feroniarum* and *H. insulare* are phoretic species. The phoresy of *H. feroniarum* and its carrier *Lithobius* sp.could be examined under laboratory conditions and SCHEUCHER (1957) observed *H. insulare* to develop well on potatoe pieces, what is unusual for necromenic histiostomatids. A possible reversion from a highly specialized strategy as necromeny back to phoresy would be difficult to explain. Necromeny requires several special adaptations such into new food (microorganisms of an insect cadaver) and the new deutonymph behavior, not to descend the living carrier but to develop on its cadaver.

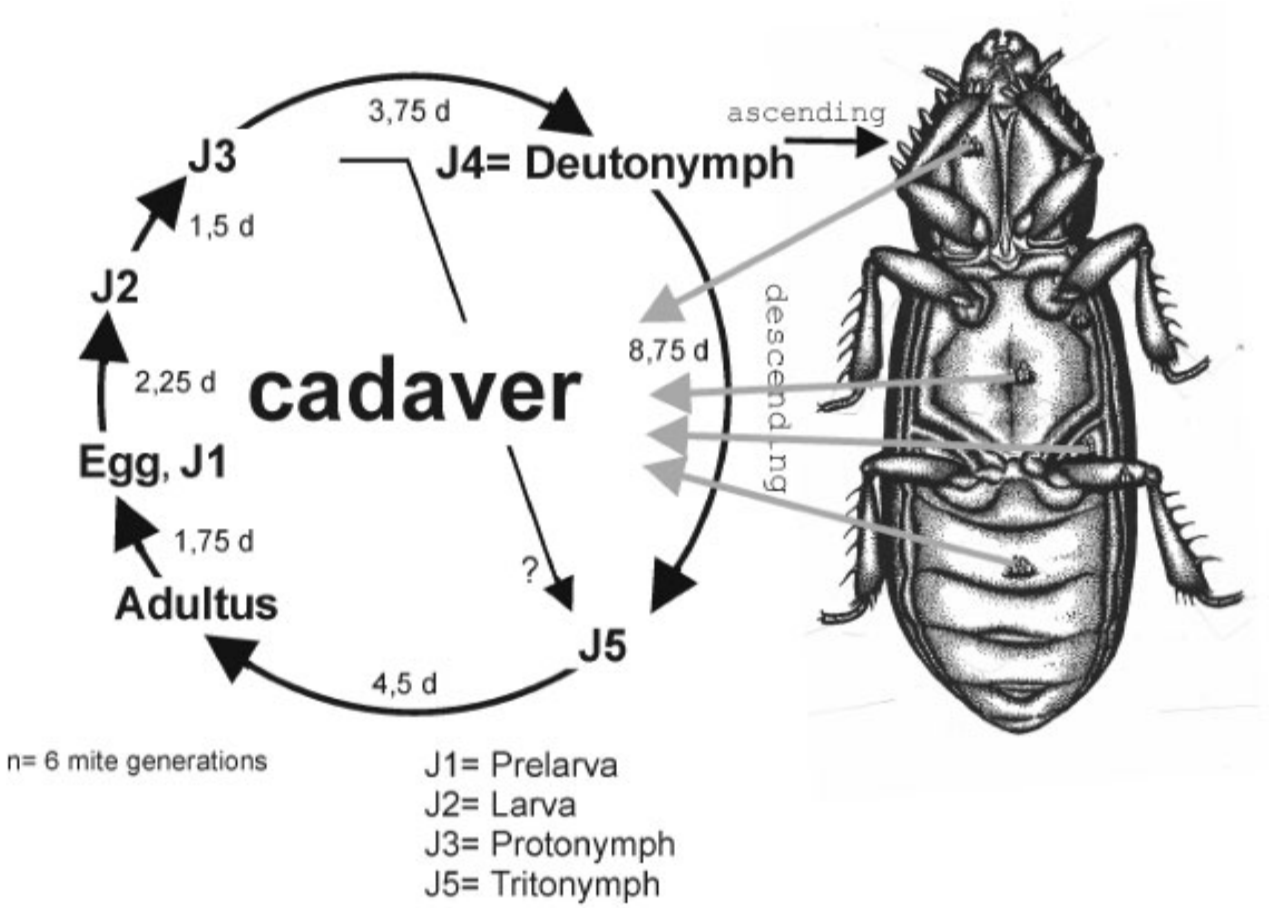


Fig32:
Life-cycle of *Histiostoma maritimum*. The deutonymphs ascend the living beetle and develop on its cadaver. Development-period of stages in days (=d).

TABLE 2:
Choice test between two different earwig species. In each culture were one individual of *Forficula auricularia* and one of another earwig species. The numbers of ascended deutonymphs were compared. s.= significant different, n.s.= not significant different

Test number	*Forficula auricularia*	*Apterygida media*	Chi²
1	152	55	s.
2	161	45	s.
3	208	89	s.
4	153	88	s.
5	77	28	s.
6	23	3	s.
7	83	29	s.
	Forficula auricularia	*Chelidurella acanthopygia*	
1	476	38	s.
2	37	4	s.
	Forficula auricularia	*Forficula decipiens*	
1	100	80	n.s.
2	62	52	n.s.
3	61	76	n.s.

TABLE 3:
Deutonymph numbers of *Histiostoma polypori* on individuals of different stages of *Forficula auricularia* captured in the field. Earwig individuals with the highest and those with the lowest mite-deutonymph number are shown (for example 1-7).

Medians of deutonymph numbers between earwigs from different locations and between earwig stages do not differ significantly (u-test).

Origin of earwigs	N3	n	Median	N4	n	Median	N5	n	Median	Adulti	n	Median
Brandenburg							1-13	8	1.5	1-3	2	2
Berlin	2	1	-	1-7	5	1	1-12	8	4	1-13	7	4
Saarland				2-7	9	5	1-22	23	6.5	1-21	19	8
Sardinia										1-19	18	7

TABLE 4:
Numbers of *Histiostoma maritimum*-deutonymphs sitting on *Heterocerus* individuals from the field. Beetle-individuals with the highest and those with the lowest mite-deutonymph number are shown (for example 1-3).
Numbers of May and June are compared with those of August.

month	deutonymph numbers on *Heterocerus fenestratus*	deutonymph numbers on *Heterocerus fusculus*
May, June	n beetle= 5 **1-3** $\overline{X}$= 1.8	n beetle= 5 no occupied individuals
August	n beetle= 7 **8-23** $\overline{X}$= 13.4	n beetle= 8 **2-9** $\overline{X}$= 4.38
$\overline{X}$= 13.4 is significantly different to $\overline{X}$= 1.8 and $\overline{X}$= 4.38		

TABLE 5:
Mite individuals of *Histiostoma maritimum* found on beetles of the genera *Heterocerus*, *Bembidion* and *Elaphrus* were crossed with each other to prove that they all belong to the species *H. maritimum*. Always one female and 2-3 males were put together. += offspring existent, was grown to adult and able to reproduce, -= no offspring.

	Mites on beetles:		
Experiment Number	***Elaphrus***	***Elaphrus*** (control)	Success
1 2-6	male male	female female	+ -
	Heterocerus	***Bembidion***	
1-4	female	male	-
	Heterocerus	***Elaphrus***	
1 2	female female	male male	+ +