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Biology of the genus *Hericia* (Algophagidae: Astigmata), with the description of a new species from the eastern United States

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Abstract

New observations concerning the biology of the genus *Hericia* are provided, as well as a discussion of past observations from the literature. A new species, *Hericia janehenleyi*, is described and illustrated from adults, phoretic deutonymphs and non-phoretic deutonymphs collected from fermenting sap flux on oak trees (*Quercus* spp.) in eastern Virginia, U.S.A. Deutonymphs are phoretic on the sap flux inhabiting beetle *Glischrochilus obtusus* (Say) (Coleoptera, Nitidulidae).

Key words: Acari, Algophagidae, *Hericia*, sap flux, *Quercus*, *Glischrochilus obtusus*, United States

Introduction

Canestrini (1888) established the genus *Hericia* based on *Glycyphagus hericius* Robin 1868, an inhabitant of sap flux on elm trees in France. However Canestrini (1888) also changed the specific name from *hericius* to *robinii*, a mistake that has since been corrected and the species is now known as *H. hericia*. To date, four additional species of *Hericia* have been described: *H. georgei* Michael 1903 from the sap of an English black poplar, *H. fermentationis* Vitzthum 1931 from strongly fermenting, sour, milk-white liquid in a cut-off bamboo stump in Sumatra, *H. paradoxa* Türk and Türk 1957 from a deutonymph found in birch rot in Germany, and *H. sanukiensis* Fashing and Okabe 2006 collected from sap flux on oak trees in Japan. Little is known concerning the biology of the genus *Hericia*. The present paper reviews the literature on the biology of the genus and adds new observations. In addition, a sixth species collected from fermenting sap flux on oak trees in the eastern United States is described.

Materials and methods

Bark and wood were collected from areas of sap flux on trees, brought back to the laboratory, and examined for mites under a dissecting microscope. Specimens were cleared in Nesbitt's solution and mounted in Hoyer's medium on microscope slides (Krantz 1978, Evans 1992). Characters were traced onto paper using a drawing tube and measurements made from the tracings. Unless otherwise stated, measurements, in micrometers (μm) and based on a sample size of 10, are given as the mean followed by the range (in parentheses). Mites are not always flattened sufficiently to make structures horizontal and setae are sometimes obscured, bent or broken, thereby making measurements difficult. Setae and other structures are therefore at least as long as indicated. Statistical analyses were performed using SPSS (2006). Nomenclature for idiosomal setae follows Griffiths *et al*. (1990) and for leg setae follows Grandjean (1939). Relative position of setae and other structures are as in

figures.

For observation of characters under the scanning electron microscope (SEM), live specimens were put through several baths of distilled water in an attempt to cleanse them of debris. Mites not involved in mate-guarding were briefly submerged in distilled water near boiling point in order to force protraction of appendages. Those involved in mate-guarding were immersed in liquid nitrogen to fix them in position. Specimens were then dehydrated in ethyl alcohol, dried using the critical point procedure, individually affixed to stubs using double-sided sticky tape, and coated with gold-palladium in a sputter coater. Microscopy was performed on an AMR 1200 and an Hitachi S-4700.

Biology

Sap flux is the external seepage of sap from wounds in the bark or wood on the trunks of trees, and originates from infections of the inner sapwood by bacteria, a condition called wetwood disease (Hartman 2000, Hamilton 1980). The sap contains sugars and other nutrients and is rapidly colonized by airborne yeasts, filamentous fungi, and bacterial species (Hartman 2000). The collective growth of microbes often results it a slimy, frothy texture sometimes called slime flux (Pataky 1999). Fermentation can occur and result in an alcoholic odor.

Oozing sap flux/slime flux provides a stable although seasonal habitat for a number of arthropod species, especially beetles, flies and mites (Kerrigan *et al.* 2004, Jacobi 2005, Robinson 1953). Areas of active flux as well as the surrounding wet areas under the bark constitute the typical habitat for species of *Hericia*. The earliest described species, *H. hericia*, was first collected from elm trees in France (Robin 1868), and subsequently reported from elm and oak trees in England (Michael 1903), from apple, elm, birch, poplar, hornbean, oak, tulip, and service trees in Germany (Ludwig 1906), and from chestnut trees in Germany (Türk and Türk 1957). A second species, *H. georgei*, was described by Michael (1903) based on specimens collected from sap flux under the bark of a black poplar tree, and Samšiňák (1972) reported that *H. georgei* can also be found in Finland, France, Russia and Sweden. Samšiňák did not provide information on host tree species, although he did state that deutonymphs from Finland were collected from moths visiting sap flux on a birch tree. Vitzthum (1931) described *H. fermentationis* based on specimens collected from an unusual habitat in Ranau, South Sumatra; the strongly fermenting, sour, milk-white liquid in a cut-off bamboo stump. *Hericia sanukiensis*, recently described by Fashing and Okabe (2006), has been collected only from sap flux on the oak *Quercus acutissima* Carruth. in Japan, and I have collected *H. janehenleyi*, the species described herein, only from fermenting sap flux on oak trees (*Quercus* spp.) in eastern North America. Although of plant origin, the liquid in the bamboo stump from which *H. fermentionis* was collected is quite deviant from sap flux on trees, the habitat utilized by other species of *Hericia*. It is probable that the normal habitat for *H. fermenationis* is also sap flux on trees, and that the fermenting liquid in the bamboo stump was a fortuitous colonization. Species of *Hericia* are thought to utilize microbes as a food source (see below), and can probably survive and even thrive in other habitats rich in microbial growth. Colonization of new sites, however, must be accomplished by phoretic deutonymphs, and deutonymphs are dependent on the habitat choice of the host on which they are phoretic. As mentioned earlier, sap flux can ferment and thereby give off an alcoholic odor. If the host insect uses that odor as a cue to locate trees with sap flux, it could easily end up at the fermenting liquid of a bamboo stump. It is interesting that *H. janehenleyi*, a species closely related to *H. fermentationis*, is found in fermenting sap flux and that the beetle on which it is phoretic also prefers that habitat.

Sap flux is rich in microbial growth (Pataky 1999), and evidence to date indicates that microbes constitute the primary diet of species of *Hericia*. An examination of food boluses of *H. janehenleyi*

using phase and Nomarski DIC microscopy revealed bacteria, yeast and parts of fungal hyphae. In addition, microbes can be seen on and inside the cheliceral digits using SEM (Figs 1, 2). The mouthparts of species of *Hericia* appear to be well adapted for collecting microbes. The basal sections of the fixed and movable digits are equipped with interlocking, biting teeth that probably function in cutting off sections of fungal hyphae (Figs 2, 5). The distal section of the biting digit forms a basket-like area with small, rigid teeth on the antiaxial margin and longer, more flexible teeth on the tip and paraxial margin (Figs 3–7). The distal section of the fixed digit is narrower and devoid of teeth, however the tip has long flexible projections that interlock with those of the movable digit when the digits are closed (Figs 1, 5, 6). Together the fixed and movable digits form a scoop-like strainer that probably functions in collecting and filtering microbes from the sap flux.

Sap flux is a viscous medium, thereby impeding the movement of small organisms such as mites. Adults and immature instars of *Hericia* other than deutonymphs have adapted by altering their form of movement. Legs I and II articulate dorsally and are more robust than Legs III and IV (Figs 8, 9, 17, 19, 27). Rather than using their legs for walking, they pull themselves through the sap flux using legs I and II; legs III and IV are dragged along behind. This form of locomotion allows them to move through the viscous medium at a surprisingly rapid pace.

Like most free-living astigmatid mites, *Hericia* dispersal is accomplished by a facultative heteromorphic deutonymph that is phoretic on a host that utilizes the same habitat (OConnor 1982). Hosts used in phoretic dispersal have been established for four *Hericia* species. In a study concerning the arthropod inhabitants of sap flux on an elm tree in England, Robinson (1953) found a deutonymph of *H. hericia* attached to the abdomen of a female *Aulacigaster leucopeza* (Meigen) (Diptera:Aulacigasteridae) and another to the leg of a female *Brachyopa insensilis* Collin (Diptera: Syrphidae). Larvae of both species are restricted to the sap flux habitat. Although adults and immature instars of *H. hericia* were found throughout the year, deutonymphs were present only during the months of May and June, a time coinciding with the oviposition period of the flies.

Deutonymphs *of H. georgei* are phoretic on a diverse assemblage of insects that visit sap flux. Although misidentified as *H. fermentationis* (see Samšiňák 1972 for details), Türk and Türk (1957) reportedly found *H. georgei* deutonymphs on the ant *Formica fusca* Wheeler that was nesting at the foot of a birch tree, on the ant *Lasius niger* (L.) that was nesting in a bird house, on a cerambycid beetle (*Aromia moschata* (L.) collected on an old willow tree, on a nitidulid beetle (*Soronia* sp.) collected from sap flux on a birch tree, and on a moth (*Cossus cossus* L.) visiting sap flux of a birch tree. Deutonymphs have also been found on six species of *Catacola* moths native to Finland (Samšiňák 1972). Samšiňák reported that infestation rates were relatively high on *Catacola* moths regardless of collection locality, with 7 to 15% of the moths harboring mites. *Catacola* species collected from the district of Leningrad displayed similar infestation rates, and *H. georgei* deutonymphs were also recovered from *Catocala* species in France and southern Russia, as well as from the following butterflies and moths in Finland: *Nymphalis antiopa* L., *Polygonia c-album* L., *Vanessa atalanta* L., *Apatele psi* L., *Europis occulta* L., and *Scoliopleryz libatrix* L. (Samšiňák 1972).

Deutonymphs of *H. sanukiensis* have been collected only from the sap flux inhabiting beetle *Librodor japonicus* (Motschulsky) (Coleoptera, Nitidulidae) (Fashing and Okabe 2006). An examination of 250 *Cataocla* specimens from Japan revealed no *Hericia* deutonymphs (Samšiňák 1972), and researchers studying the biology of *H. sanukiensis* are certain that deutonymphs have never been collected from *Catacla* moths in Japan (Fashing and Okabe 2006).

To date, I have found deutonymphs of *H. janehenleyi* phoretic only on a nitidulid beetle, *Glischrochilus obtusus* (Say) (Fashing 1991). I have not found deutonymphs on either butterflies or moths, and they have not been observed by curators on lepidopterans in the U.S. National Museum

collection (Robert Robbins, Don Davis, and John Burns, Research Entomologists, Lepidoptera, Smithsonian Institution, per. comm.).

Unlike most astigmatic genera, species of *Hericia* can have a second deutonymphal morph that lacks the morphological attributes associated with phoretic behavior and is never found attached to a dispersal agent (Fashing 1991). Although non-phoretic deutonymphs have been described and associated with adults for only two species (*H. sanukiensis* and *H. janehenleyi*), it is quite probable that future research will reveal deutonymphal dimorphism in all species of *Hericia*. As stated above, Türk and Türk (1957) described *H. paradoxa* based on a single deutonymph that is obviously a non-phoretic morph. To my knowledge, that deutonymphal morph has not been collected again and therefore remains unassociated with adults and phoretic deutonymphs.

Since the morphological attributes of each morph type have been previously described in detail for *H. janehenleyi* (Fashing 1991), only a brief summary will be given. The most striking difference is the well developed, entomophilous-type, sucker plate of the phoretic morph (Fig 10) when compared to the vestigial plate of the non-phoretic morph that lacks suckers and conoidal setae (Fig 11). In addition, the sensory solendia, thought to be associated with locating a host, are significantly reduced both on the gnathosoma and legs of the non-phoretic morph. The legs of the non-phoretic morph are also significantly shorter and their idiosomal articulation more recessed. The pretarsi of legs III and IV are short, whereas those of the phoretic morph are long and, in combination with their claws, reminiscent of "grappling hooks" that presumably function in boarding a host.

Although much remains to be done to fully understand the behavioral ecology of the two deutonymphal forms, the inclusion of both a phoretic and a non-phoretic deutonymph in the life cycle of *Hericia* makes sense when one considers the habitat. Although wetwood is a chronic disease of trees, the development of sap flux is seasonal, being most common in summer and ceasing during the winter (Hartman 2000, Pataky 1999). Sap flux development can be triggered by environmental conditions that are stressful to the tree such as heat and drought (Henn 2004). I have observed the production of sap flux to occur on a single tree three separate times over the course of a summer. Although the sap flux habitat is not continuously present, the chance of it reoccurring on any given tree is relatively high. A non-phoretic deutonymph, presumably adapted to remain more or less dormant for long periods of time, allows the mite to take advantage of subsequent sap fluxes on the host tree. A phoretic deutonymph allows for dispersal and the resultant colonization of sap fluxes on newly diseased trees as well as for out-crossing among populations (trees).

The legs of male *Hericia* differ in many respects when compared to those of females and immature instars. They are much more robust, and when measured as a proportion of idiosomal length, they are significantly longer (Fashing 2001). Especially striking is the fact that coxae IV are located ventral to and mesiad of coxae III, thereby resulting in the articulation of legs IV directly below legs III (Figs 8, 27, 28). Vitzthum (1931) noted the peculiar articulation of legs IV and the fact that they are usually directed forward on preserved specimens, with their tarsi lying next to the gnathosoma. He speculated that legs IV might function in either jumping (e.g., like the furca in Collembola), or in some unknown mode of copulation. He was correct in his latter speculation concerning mating behavior. Males use legs IV to clasp tritonymphal females and carry them about (Fig 12), thereby preventing their acquisition by other males (see Fashing 2001 for details). When the tritonymph molts to an adult, mating takes place. Successful precopulatory mate-guarding prevents other males from gaining access to a virgin female and thereby insures the guarding male's paternity of resultant offspring.

Vitzthum (1931) noted that the idiosoma of a female *H. fermentationis* increased greatly in size as it became distended with eggs, and I have found this to also be true for *H. janehenleyi* (Fig 13 vs Fig 14). Vitzthum (1931) recorded up to 18 eggs in a gravid female, and noted that eggs often hatched and the resultant larvae increased in size while inside the female. He assumed that a female

died as a result. A count of eggs in 40 gravid *H. janehenleyi* females (slides prepared from living individuals) revealed a range of 5–19, a median of 11, and a mean of 11.62. Although embryonic development can be observed within eggs in the reproductive tract of females of *H. janehenleyi*, none of the females contained egg shells nor eclosed larvae.

Systematics

Family Algophagidae Fain, 1981

Subfamily Hericiinae OConnor, 1985

Type-genus *Hericia* Canestrini, 1888

Hericia janehenleyi sp. nov.

Hericia new species. Fashing 1991
Hericia undescribed species. Fashing 2001

Material examined

Holotype: Male collected from fermenting sap flux on Post Oak (*Quercus stellata* Wangenheim) at Mariners' Museum Park, Newport News, VA, USA. Deposited in the U. S. National Museum, Washington, D.C.

Paratypes: Males, females, phoretic deutonymphs and non-phoretic deutonymphs collected by Norman Fashing from fermenting sap flux on *Quercus spp.* at Mariners' Museum Park, Newport News, VA, Waller Mill Park, James City County, VA, and New Quarter Park, York County, VA. Deposited in the U. S. National Museum, Washington, D.C., the Natural Resources Inventory Center, National Institute for Agro-Environmental Sciences, Tsukuba, Japan, the Natural History Museum, London, and the author's collection.

Diagnosis

A small species with idiosomal lengths for males, non-gravid females and gravid females averaging 461, 362 and 522 μm respectively. Cuticle bearing rows of striations interspersed with rows of narrow, pointed, elliptical-shaped mammilations (see Figs 20–22). Male with numerous shallow sclerotized depressions containing irregular cuticle (mean and median 29; range 26–34) between dorsal setae *se* and d_1 (see Figs 27, 29, 30). Female lacking such depressions. Male with dorsal seta f_2 long (~30% of idiosomal length) and thick rather than short and hair-like.

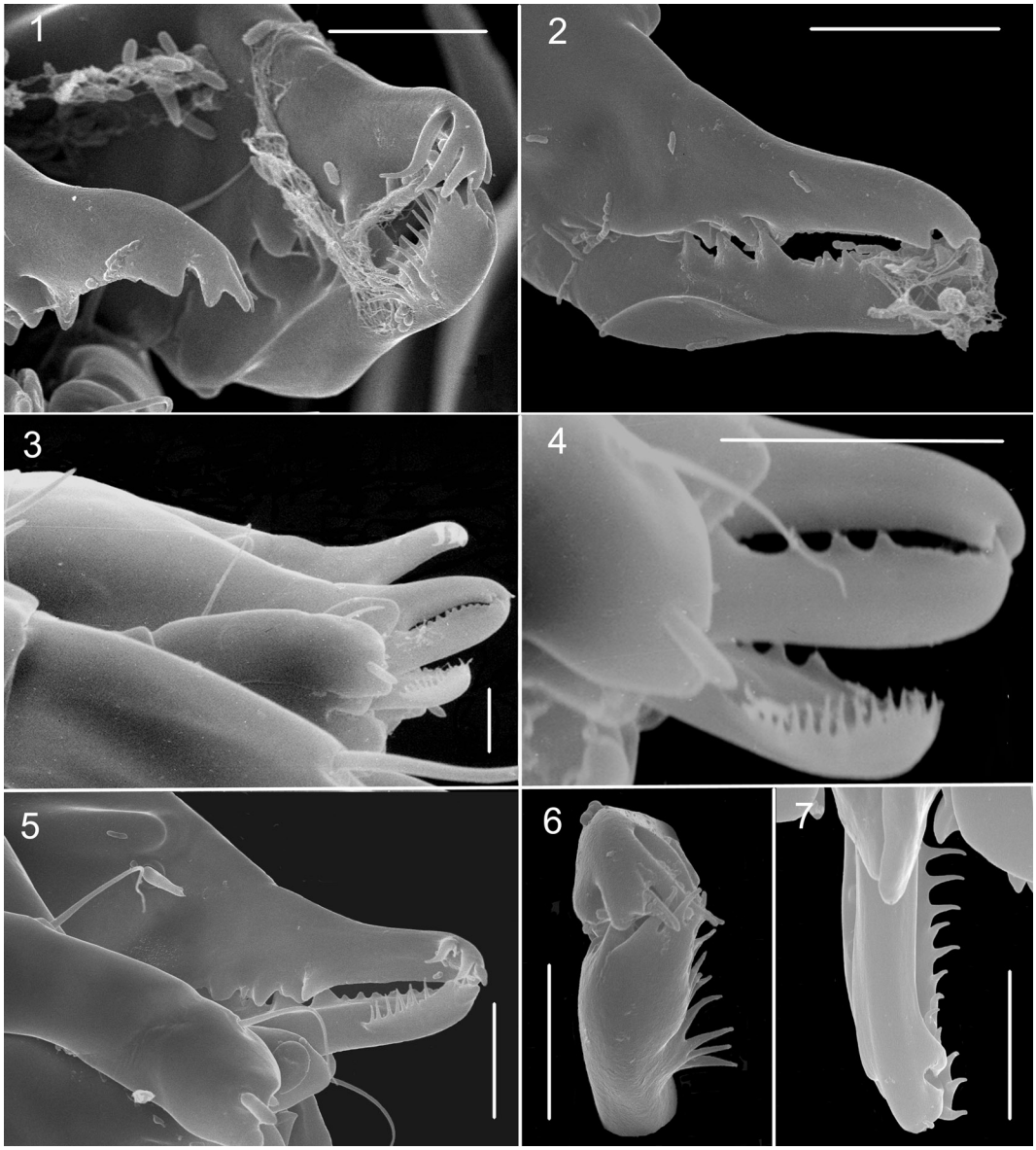
Description

FEMALE (Figs 1–7, 9, 13, 14, 15–26)

Body ovoid. Recently eclosed females (Fig 13): length 362 (330–397); width at level of coxae III 255 (229–282). Gravid females (Fig 14): length 522 (472–561); width at level of coxae III 326 (308–370).

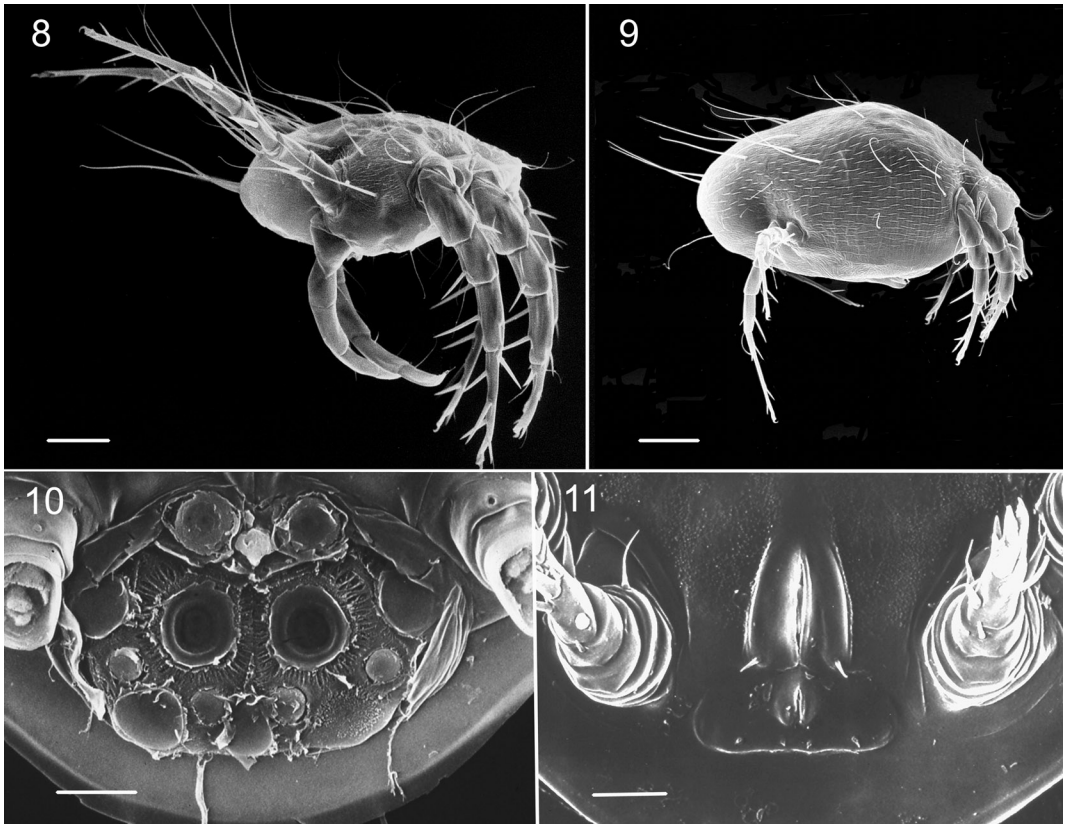
Gnathosoma (Figs 1–7, 15, 16). Chelate chelicerae (Figs 1–5, 15) with cheliceral seta short, spine-like and located near base of a blunt paraxial cheliceral spine (Figs 5, 15). Movable digit and chelate portion of fixed digit with well developed, interlocking teeth in basal section (Figs 2, 5, 15); anterior portion of fixed digit thin, blade-like and curving mesally at distal end (Figs 3, 5–7), and with elongate, downward projections on apical curvature (Figs 1, 5, 6); anterior portion of movable

digit broadly flattened with small apical teeth on the antiaxial margin and elongate upward projections on the apex and paraxial margin (Figs 1, 3–7). Subcapitulum (Fig 16) bearing a pair of short, spine-like, palpal supracoxal setae dorsolaterally and a pair of filiform subcapitular setae ventrally. Each palpal tibia bears a filiform dorsal seta, and each palpal tarsus a filiform dorsal seta, a subapical solenidion, and a basal rounded eupathidium; ventral palpal seta absent.



FIGURES 1–7. *Hericia janehenleyi* **sp. n.** (female). 1, chelicera with microbes, paraxial view; 2, fixed and movable digits of chelicera with microbes, antiaxial view; 3, chelicerae, paraxial view of open digits, antiaxial view of closed digits; 4, chelicerae, antiaxial view of closed digits, paraxial view of moveable digit; 5, chelicera, paraxial view; 6, chelicera, frontal view; 7, chelicera, dorsal view of distal end. Scale bar = 10 μm.

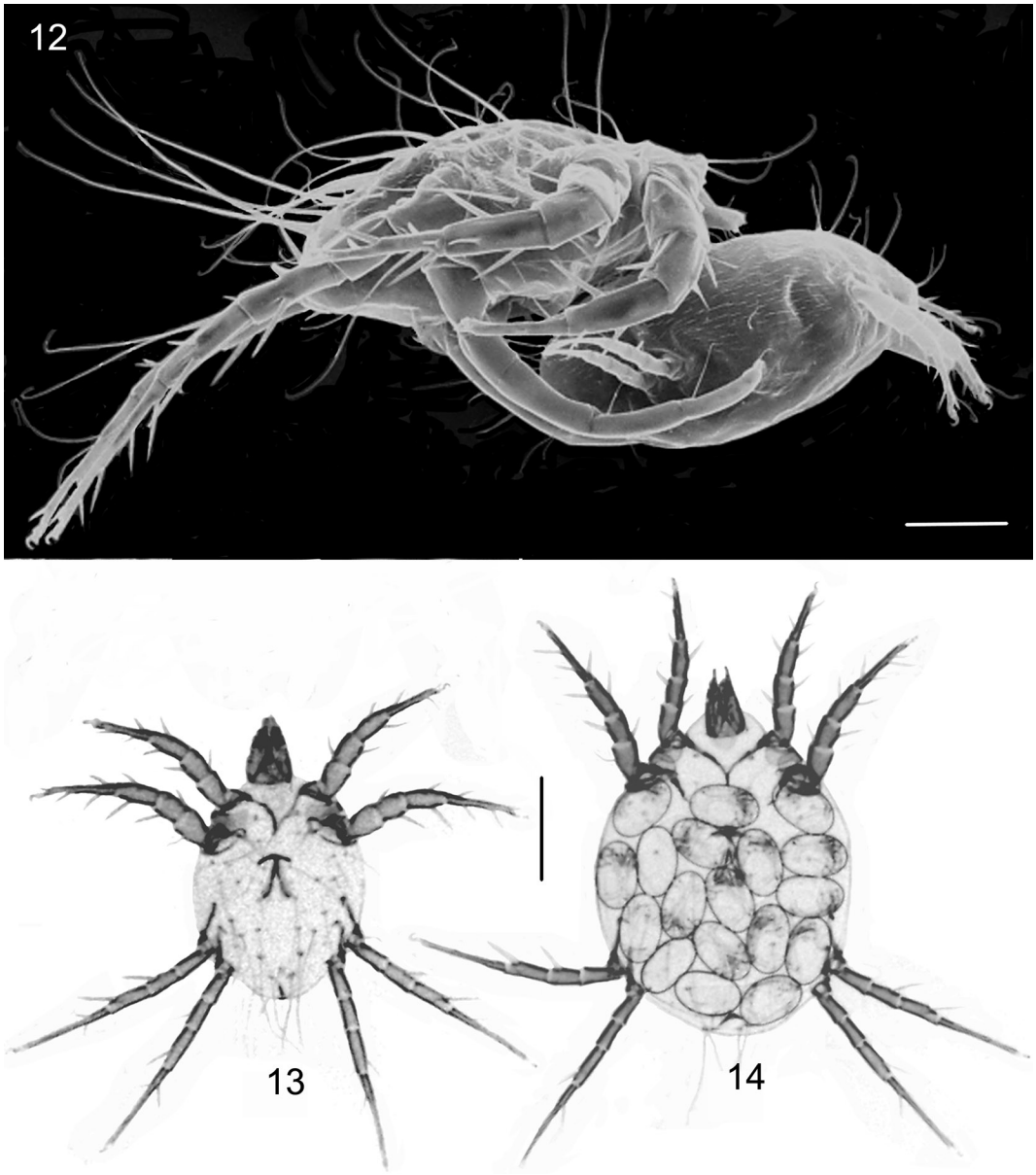
Dorsum (Figs 17, 19). Cuticle lightly sclerotised, bearing rows of striations interspersed with rows of narrow, pointed, elliptical-shaped mammilations (Figs 19–22). Prodorsal sclerite with a reticulate pattern (Figs 17, 19), approximately twice as long as wide, extending to a level slightly below trochanters I. A pair of small unsclerotised areas representing the vestigial alveoli of setae *ve* occur on lateral margins of prodorsal sclerite. Grandjean's organs and supracoxal setae absent. Axillary organs originate dorsally between legs I and II, extend laterally between legs, and ventrally onto coxae I and II. Opisthonotal gland openings (*gla*) located between setae d_1 and d_2. Cupules located as follows: *ia* slightly posterior seta c_2, *im* anterior to and laterad of seta e_2 , and *ip* posterior to setae h_1. Dorsum bearing 16 pairs of filiform setae: *vi* 88 (78–105); *si* 113 (98–133); *se* 90 (75–99); c_1 114 (89–134), c_2 121 (108–142), *cp* 116 (95–131), d_1 149 (127–176), d_2 150 (114–173), e_1 165 (143–179), e_2 170 (140–190), f_2 62 (53–76), h_1 176 (156–196), h_2 202 (168–227), h_3 199 (183–227), ps_1 19 (14–26), and ps_2 19 (11–21). Setae c_3 102 (78–169) filiform, located on lateral margin of idiosoma.



FIGURES 8–11. *Hericia janehenleyi*, **sp. n.** 8, male, lateral view; 9, gravid female, lateral view; 10, phoretic deutonymph, ventral view of sucker plate; 11, nonphoretic deutonymph, ventral view of vestigial sucker plate. Scale bar = 100 μm (Figs 8, 9), 10 μm.(Figs10–11).

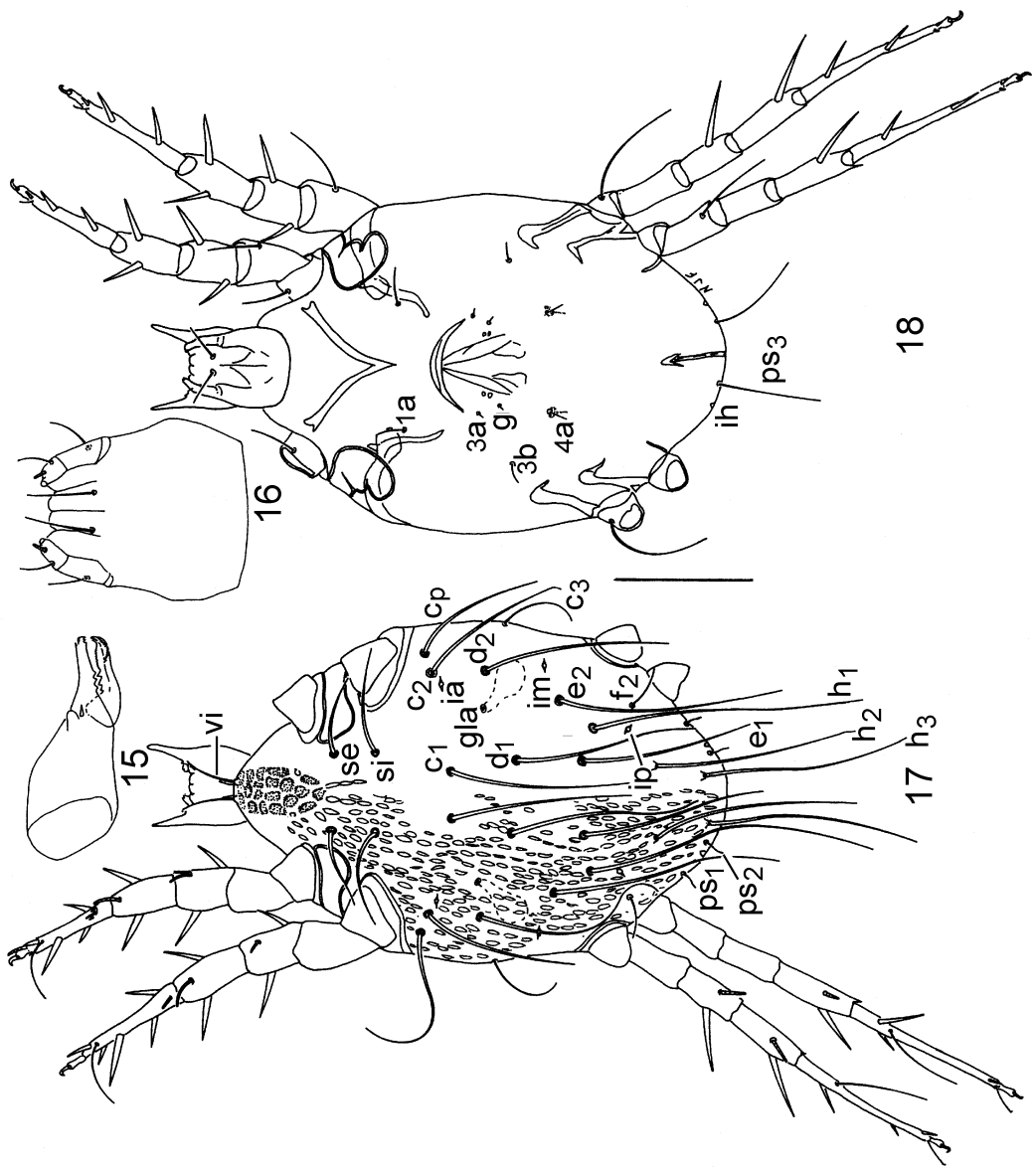
Venter (Fig 18). Cuticle lightly sclerotised. Anterior coxal apodemes I directed posteromedially, joining at midline to form a V-shaped sternum. Anterior coxal apodemes II directed posteromedially; anterior coxal apodemes III and IV directed anteriomedially; posterior apodemes III directed anteriormedially and joining anterior apodemes IV. Epigynial apodeme moderately large, located anterior to oviparous. Genital papillae vestigial. Cupule *ih* on lateral margin between seta ps_1 and

ps_3. Anus ventroterminal. Bursa copulatrix an indentation located slightly dorsal to anus (Fig 20). Venter bearing 6 pairs of hair-like filiform setae: *3a*, and *g* very short; *3b* 15 (12–20), *1a* 30 (21–37) *4a* 14 (10–16); ps_3 101 (75–129).



FIGURES 12–14. *Hericia janehenleyi*, **sp. n.** 12, male clutching quiescent tritonymph; 13, recently eclosed, pre-reproductive female; 14, gravid female. Note lengths of sclerotized structures (e.g. leg and gnathosoma) of recently eclosed females are approximately equal to those of gravid females. Scale bar: 100 μm (Fig 12), 200 μm (Figs 13, 14).

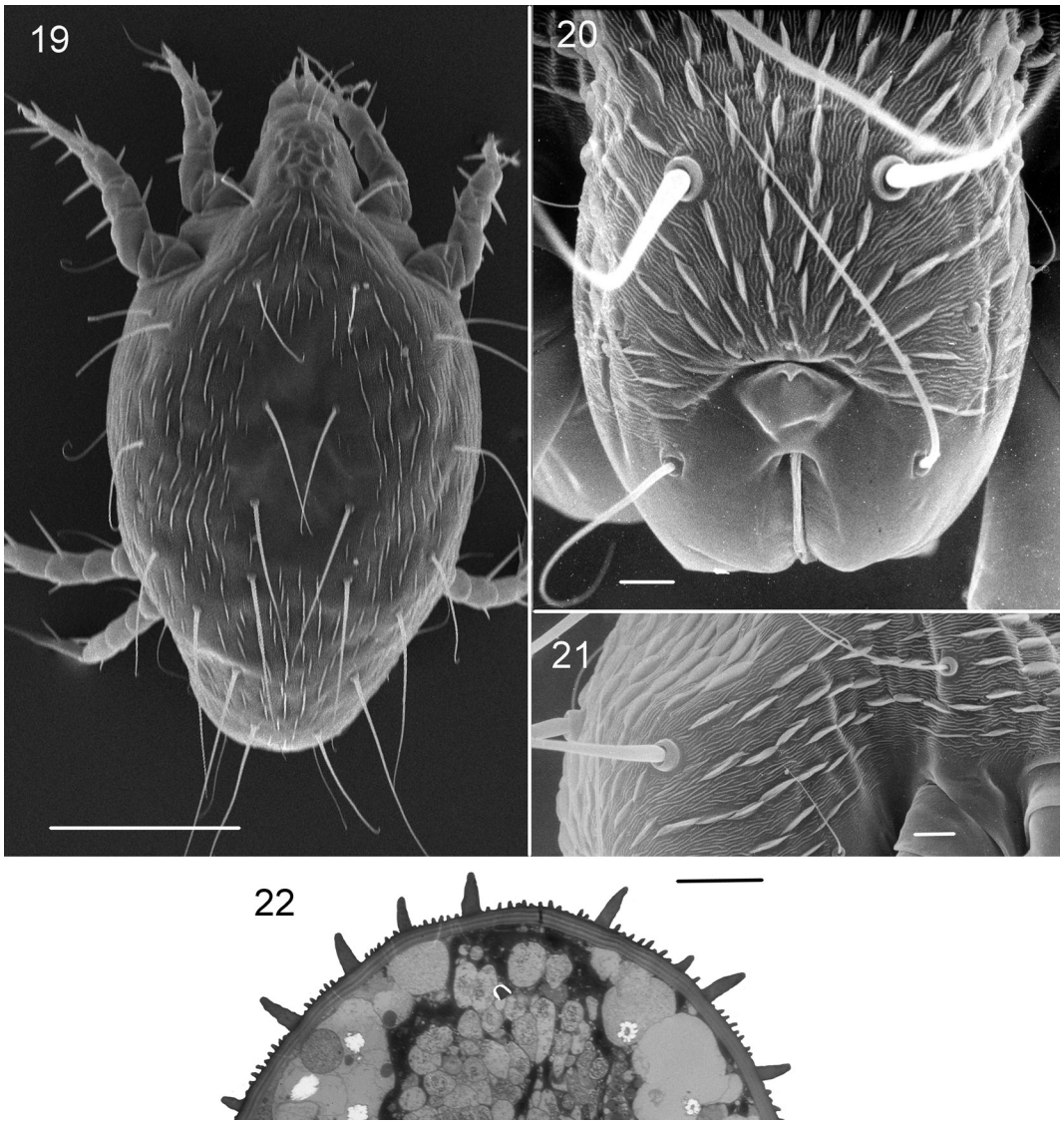
Legs (Figs 23–26). Legs heavily sclerotised; lengths measured from base of femur to tip of tarsus (mean, followed by range and mean percentage of idiosomal length in parentheses): I 242 (223–261, 67%); II 276 (253–296, 77%); III 305 (278–321, 84%); IV 315 (286–336, 87%). Tarsal lengths



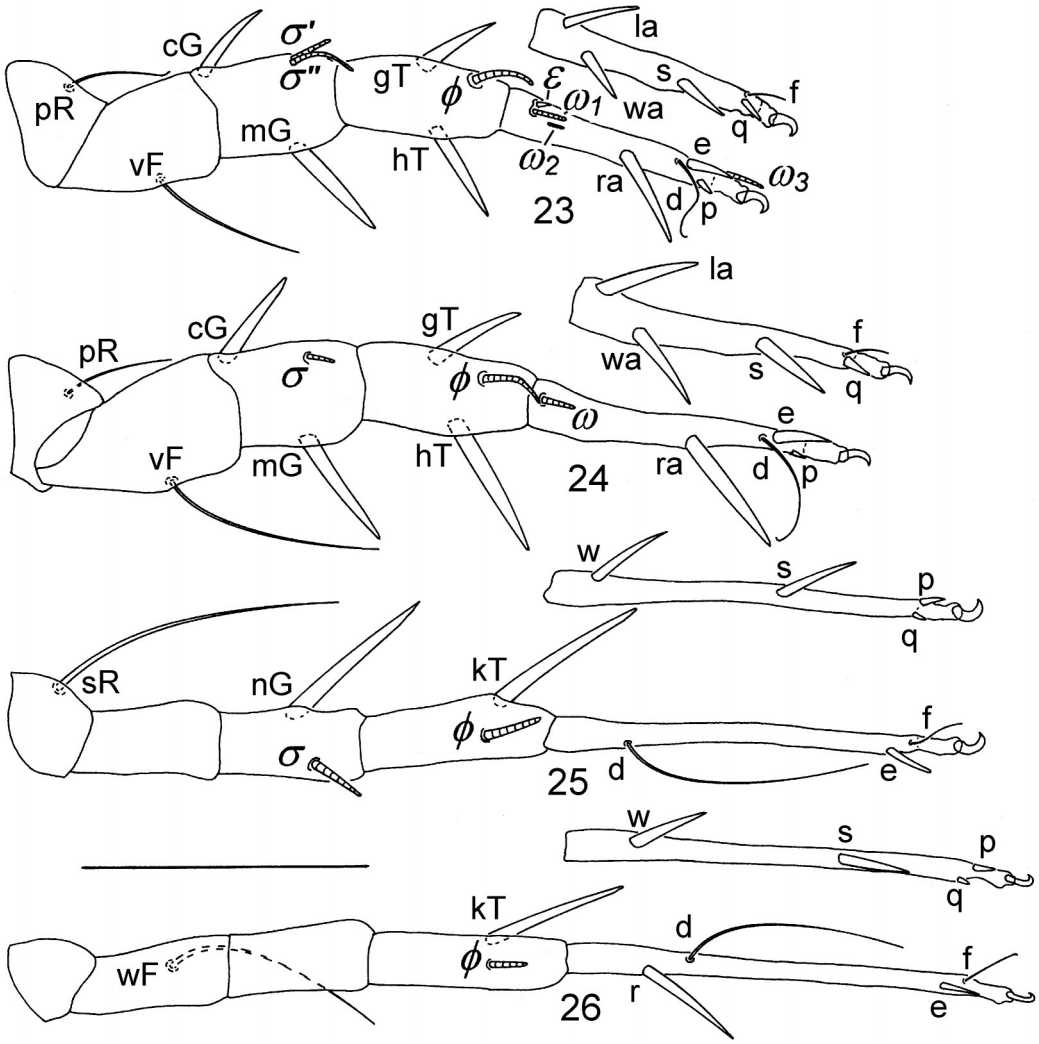
FIGURES 15–18. *Hericia janehenleyi*, **sp. n.** (female). 15, chelicera, paraxial view; 16, gnathosoma, ventral view; 17, dorsum; 18, venter. Scale bar: 50 μm (Figs 15, 16), 100 μm (Figs 17, 18).

(mean, followed by range and mean percentage of idiosomal length in parentheses): I 79 (73–86, 22%); II 101 (95–110, 28%); III 131 (121–139, 36%); IV 143 (134–150, 40%). Trochanteral setation 1-1-1-0; setae *pR* I–II and *sR* III filform. Femoral setation 1-1-0-1; setae *vF* I–II and *wF* IV filiform. Genual setation 2-2-1-0; setae *cG* and *mG* I–II and *nG* III stout spines. Tibial setation 2-2-1-1; setae *hT* and *gT* I–II and *kT* III–IV stout spines. Tarsal setation 9-9-7-8; tarsae I and II with setae *la*, *wa*, *ra*, *s* and *e* stout spines, proral setae (*p* and *q*) short spines, seta *d* long, filiform, and seta *f* short, filiform; tarsus III setae *w*, *s* and *e* stout spines, proral setae (*p* and *q*) short spines, seta *d* long, filiform, and seta *f* short, filiform; tarsus IV similar to tarsus III but with the addition of seta *r*, a stout

spine. Solenidia (I to IV): tarsi 3-1-0-0, tibiae 1-1-1-1, genua 2-1-1-0; solenidia σ of genua I–III originating 1/3 of way from apical end; solenidion σ' 2/3 length of σ''; tibiae I–IV with solenidion ϕ originating approximately 1/3 of way from apical end; tarsus I with solenidion ω_1 basal, slightly anterior to solenidion ω_2, and solenidion ω_3 apical. Tarsus II with solenidion ω originating near segment base. Tarsus I with spinelike famulus ε adjacent to solenidion ω_1. Pretarsi with membranous ambulacra and slender, curved claws; condylophores absent.



FIGURES 19–22. *Hericia janehenleyi*, **sp. n**. (female). 19, dorsal view; 20, oblique view of posterior end showing cuticular sculpturing, bursa copulatrix and anal slit; 21, lateral view of cuticular sculpturing on idiosomal posterior; 22, Cross section of dorsal region of posterior idiosoma demonstrating cuticular striations (small ridges) and mammilations (large ridges). Scale bar = 100 μm (Fig 19), 10 μm (Figs 20–22).



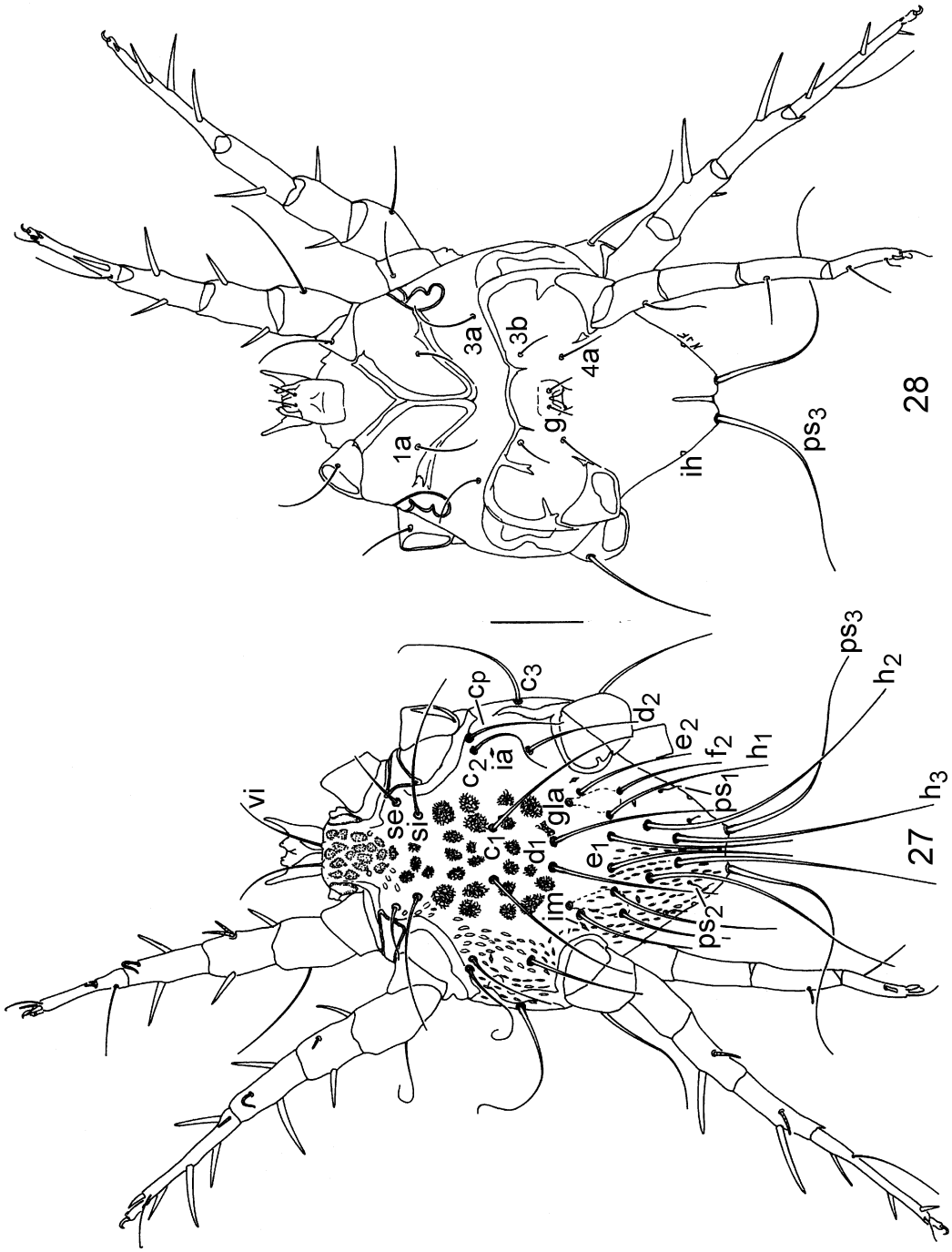
FIGURES 23–26. *Hericia janehenleyi*, **sp. n**. (female). 23, leg I dorsal view, ventral view tarsus; 24, leg II dorsal view, ventral view tarsus; 25, leg III dorsal view, ventral view tarsus; 26, leg IV dorsal view, ventral view tarsus. Scale bar = 50 μm.

MALE (Figs 8, 12, 27–37)

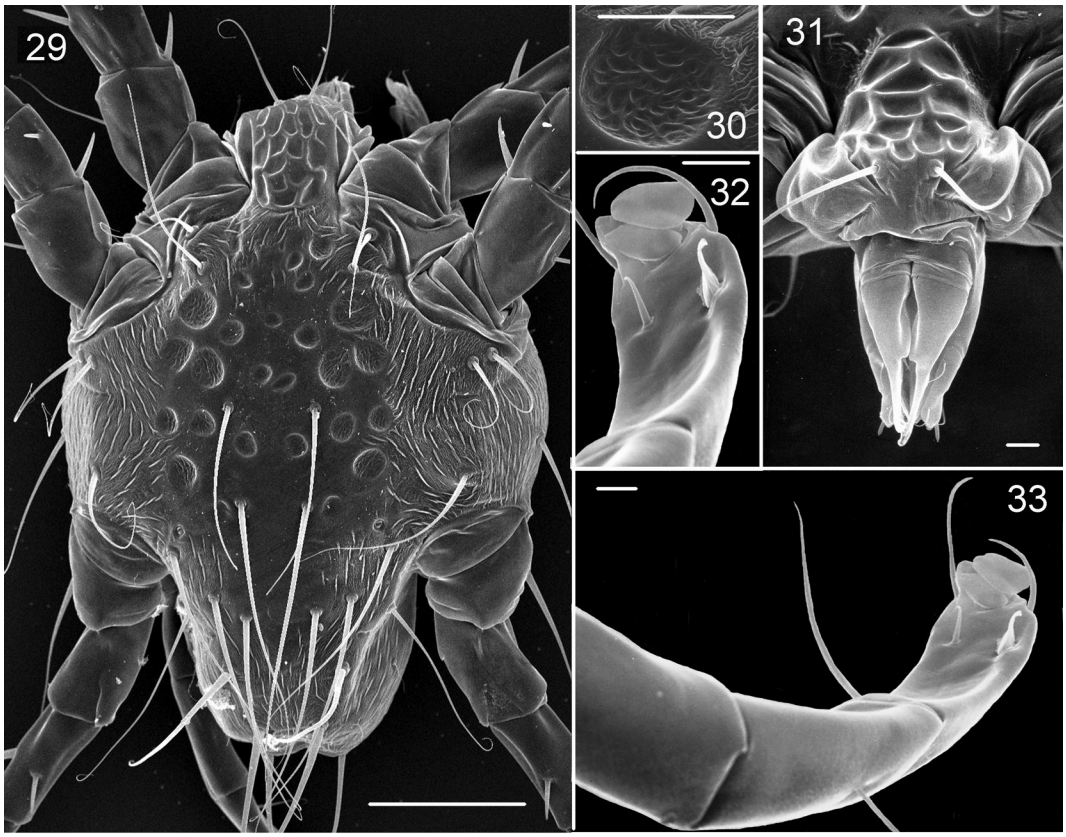
Body broadly oval, but posterior region tapering more than in female; shallow cleft at posterior margin; length 461 (391–560); width just posterior to coxae II 355 (287–424). Axillary organs and gnathosoma similar in appearance to female, but gnathosoma and chelicerae smaller relative to idiosomal size.

Dorsum (Figs 27, 29). Dorsum lightly sclerotized, with cuticular striations and mammilations similar to female on perimeter (Figs 27, 29); numerous shallow sclerotized depressions containing irregular cuticle (Figs 27, 29, 30) between setae *se* and d_1 (mean and median 29; range 26–34). Prodorsal sclerite with a reticulate pattern (Figs 27, 29, 31), extending to level of trochanters I; anterior of prodorsum expanded and flared (Figs 27, 29, 31). Opisthonotal gland openings (*gla*) located anterior to seta e_2. Cupules located as follows: *ia* slightly posterior seta c_2, *im* slightly laterad

setae e_2, and *ip* between setae ps_1 and h_1. Dorsum bearing 18 pairs of filiform setae: *vi* 112 (77–147); *si* 147 (119–176); *se* 96 (75–114); c_1 159 (132–174); c_2 115 (89–128); c_3 190 (156–221); *cp* 130 (101–150); d_1 182 (145–205); d_2 141 (114–166); e_1 187 (137–221); e_2 169 (142–189); f_2 139 (105–166); h_1 186 (153–205); h_2 261 (216–292); h_3 273 (221–296); ps_1 35 (14–61); ps_2 23 (15–30) and ps_3 275 (178–314). Setae ps_1 and ps_2 filiform and hair-like, others robustly filiform.



FIGURES 27–28. *Hericia janehenleyi*, **sp. n**. (male). 27, dorsum; 28, venter. Scale bar = 100 μm.

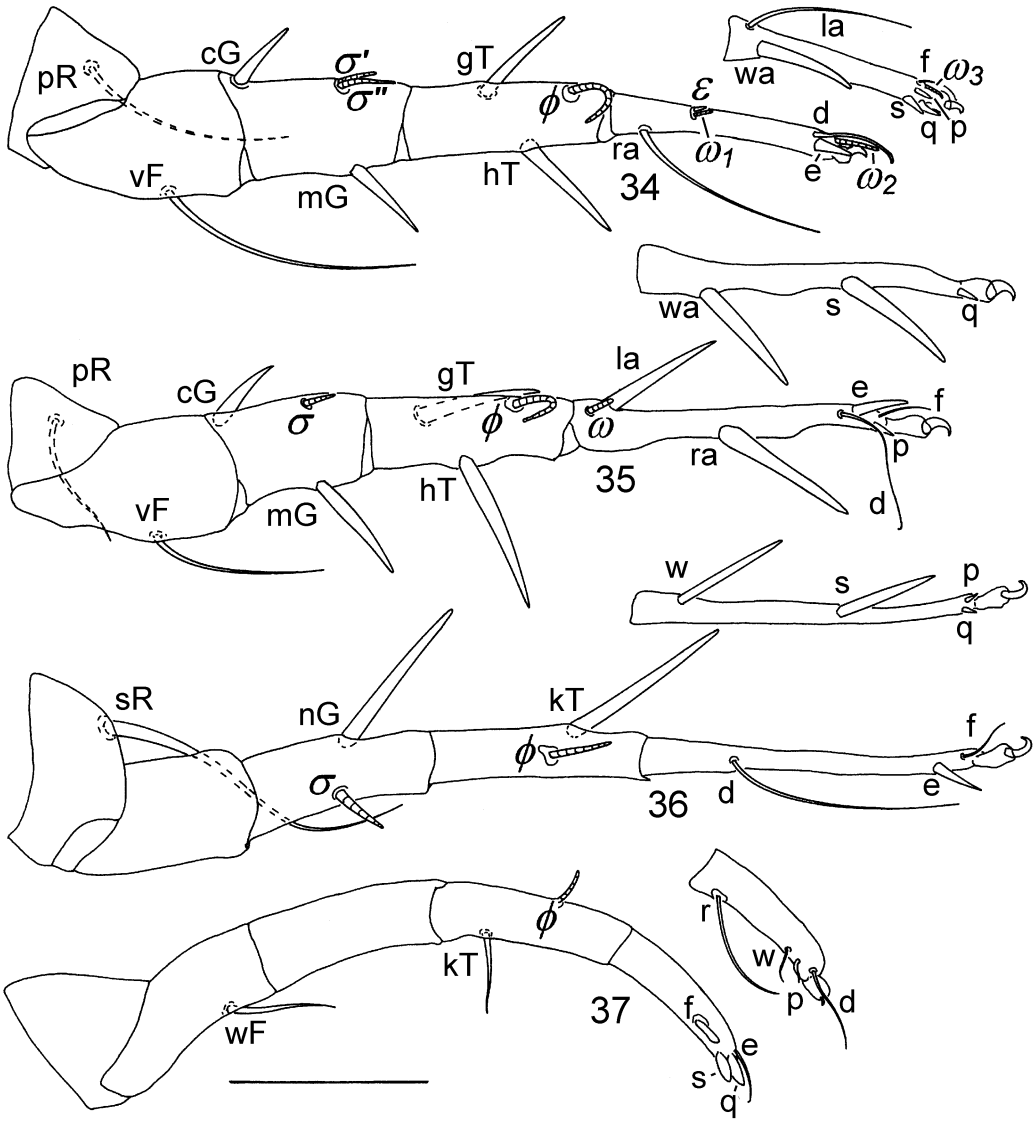


FIGURES 29–33. *Hericia janehenleyi*, **sp. n**. (male). 29, idiosoma, dorsal view; 30, dorsal cuticular depression; 31, gnathosoma and propodosomal shield, frontal view; 32, tarsus IV, ventral view; 33, leg IV, oblique view of lateral margin and venter. Scale bar: 100 μm (Fig 29), 10 μm (Figs 30–33).

Venter (Fig 28). Cuticle lightly sclerotised. Anterior coxal apodemes I and II directed posteromedially; apodemes I joining at midline to form a Y-shaped sternum that extends posteriorly and joins with apodemes II. Coxae IV located ventrad and mesiad coxae III, with the result that legs IV are positioned below legs III (Figs 8, 12, 28). Anterior coxal apodemes III directed anteriomedially and joining medially to form a bridge. Anterior apodemes IV directed anteriomedially and joining anterior apodemes III. Aedeagus located between coxal fields IV. A narrow sclerite containing setae *g* just anterior to adeagus. Anus ventroterminal. Cupule *ih* on idiosomal margin laterad anus. Venter bearing five pairs of filiform setae: *1a* 71 (55–94); *3a* 85 (60–107); *4a* 65 (45–82); *3b* 33 (19–42) and *g* 22 (15–28).

Legs (Figs 32, 33–37). Leg lengths, measured from base of femur to tip of tarsus (mean followed by range and mean percentage of idiosomal length in parentheses): I 386 (299–444, 84%); II 386 (299–444, 93%); III 465 (382–539, 101%) and IV 361 (305–418, 79%). Tarsal lengths (mean followed by range and mean percentage of idiosomal length in parentheses): I 105 (81–122, 23%); II 156 (130–182, 34%) III 173 (137–195, 38%) and IV 82 (73–96, 17%). Legs of male more robust than those of female, and with total lengths as well as tarsal lengths significantly longer. In addition, leg IV with tibia and tarsus broader and flatter, tarsus concave ventrally (Figs 32, 33), ambulacrum reduced to a fleshy pad, and claw absent or vestigial. Although setae and solenidia of legs II and III are similar to those of female, they differ on legs I and IV. Tarsus I with setae *la* and *ra* filiform rather

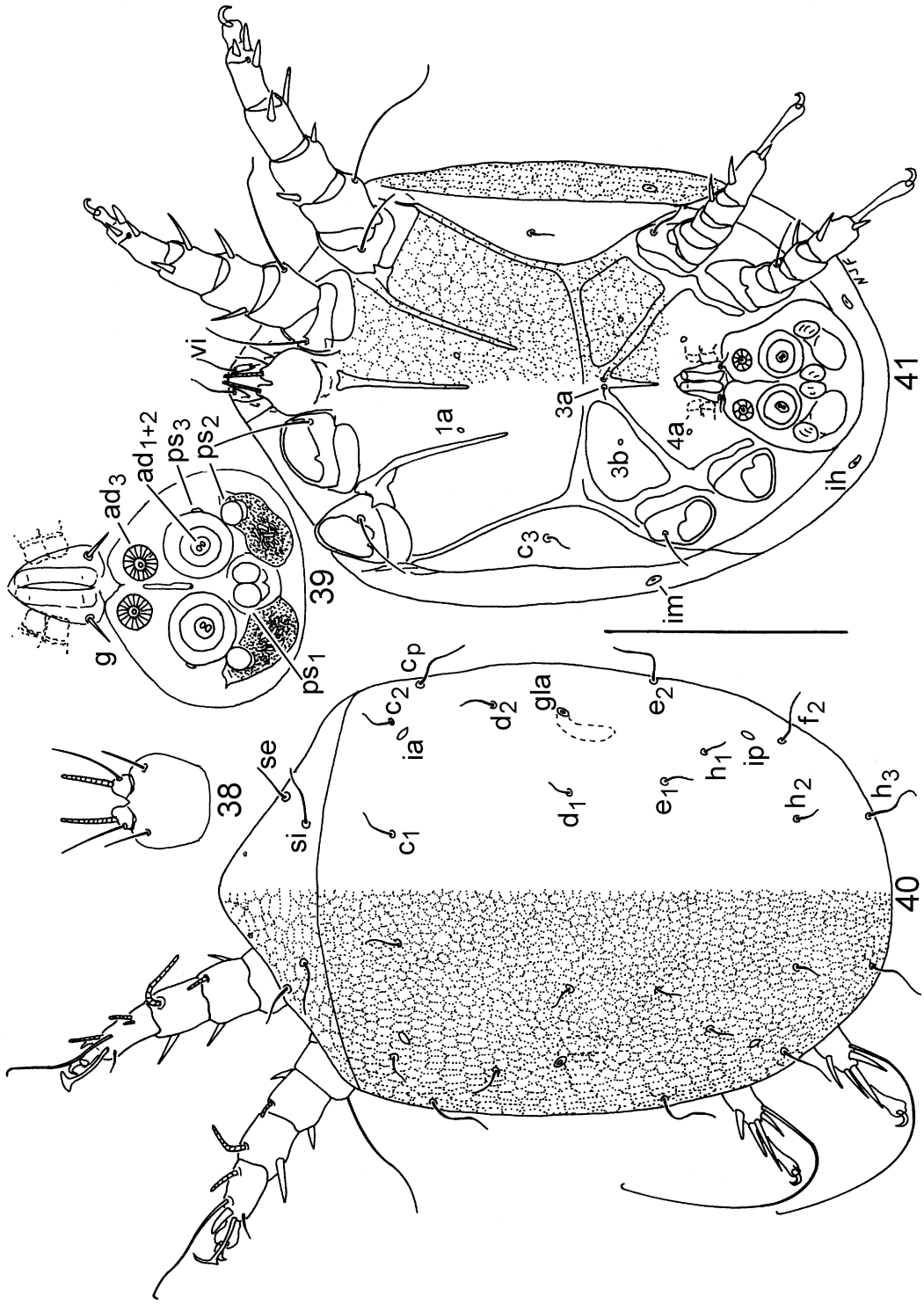
than spines, and solenidion ω_2 located apically near seta *f*. Legs IV (Figs 32, 33, 37) greatly modified for clasping female (Fig 12). Tarsus IV with setae *f*, *q* and *s* broadly expanded to form thin, membrane-like flaps, setae *e* and *w* filiform rather than spines, and seta *d* apical rather than basal.



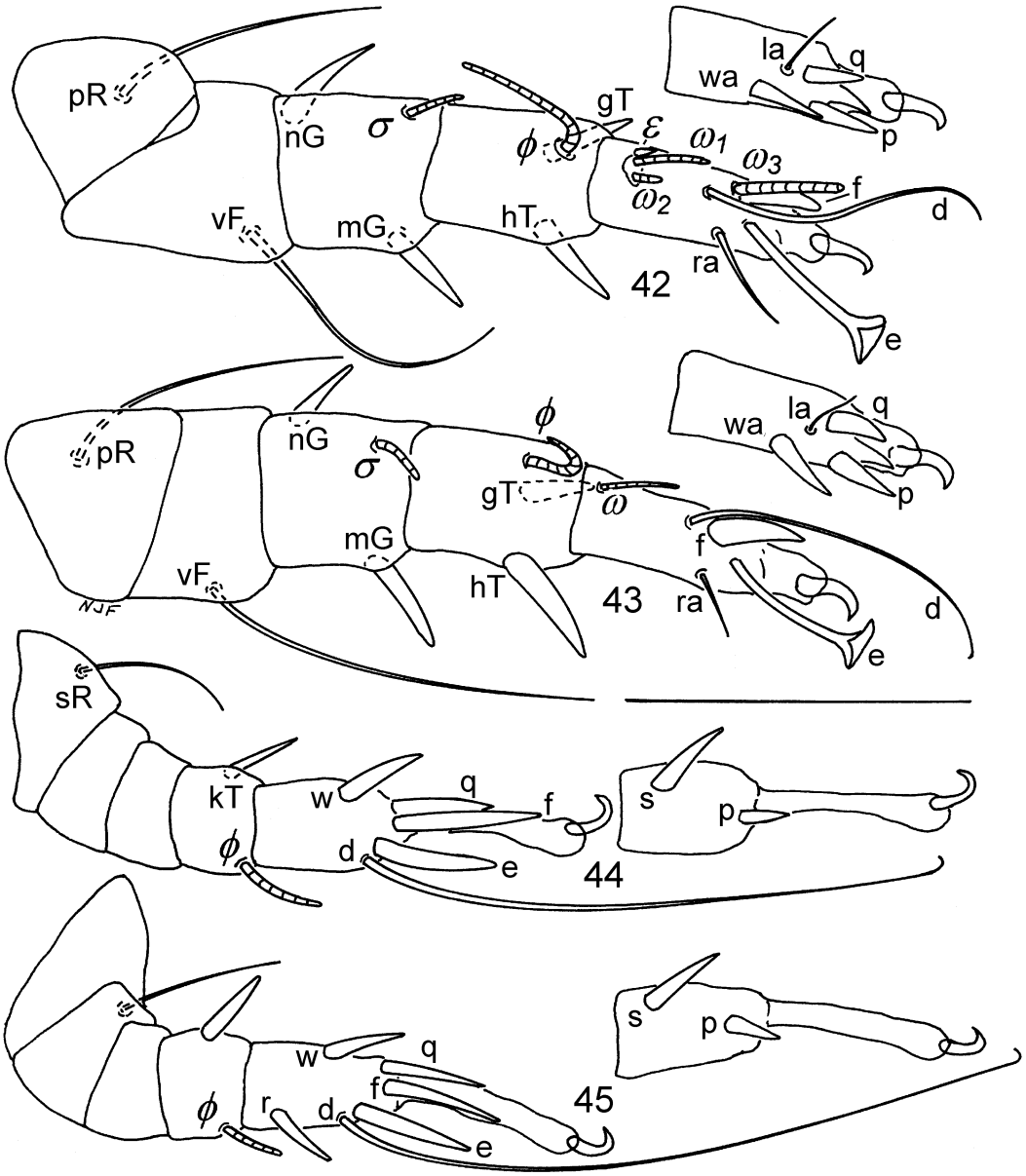
FIGURES 34–37. *Hericia janehenleyi*, **sp. n**. (male). 34, leg I dorsal view, ventral view tarsus; 35, leg II dorsal view, ventral view tarsus; 36, leg III dorsal view, ventral view tarsus; 37, leg IV dorsal view, ventral view tarsus. Scale bar = 50 μm.

PHORETIC DEUTONYMPH (Figs 10, 38–45)

Body shape variable, elliptical to broadly ovoid; length 266 (247–306); width at sejugal furrow 187 (163–222). Gnathosoma with well developed subcapitulum and palps (Fig 38); subcapitulum somewhat rounded in shape, bearing a pair of filiform subcapitular setae. Palpal remnants reduced, each bearing a palpal solenidion apically and a filiform palpal seta laterally.



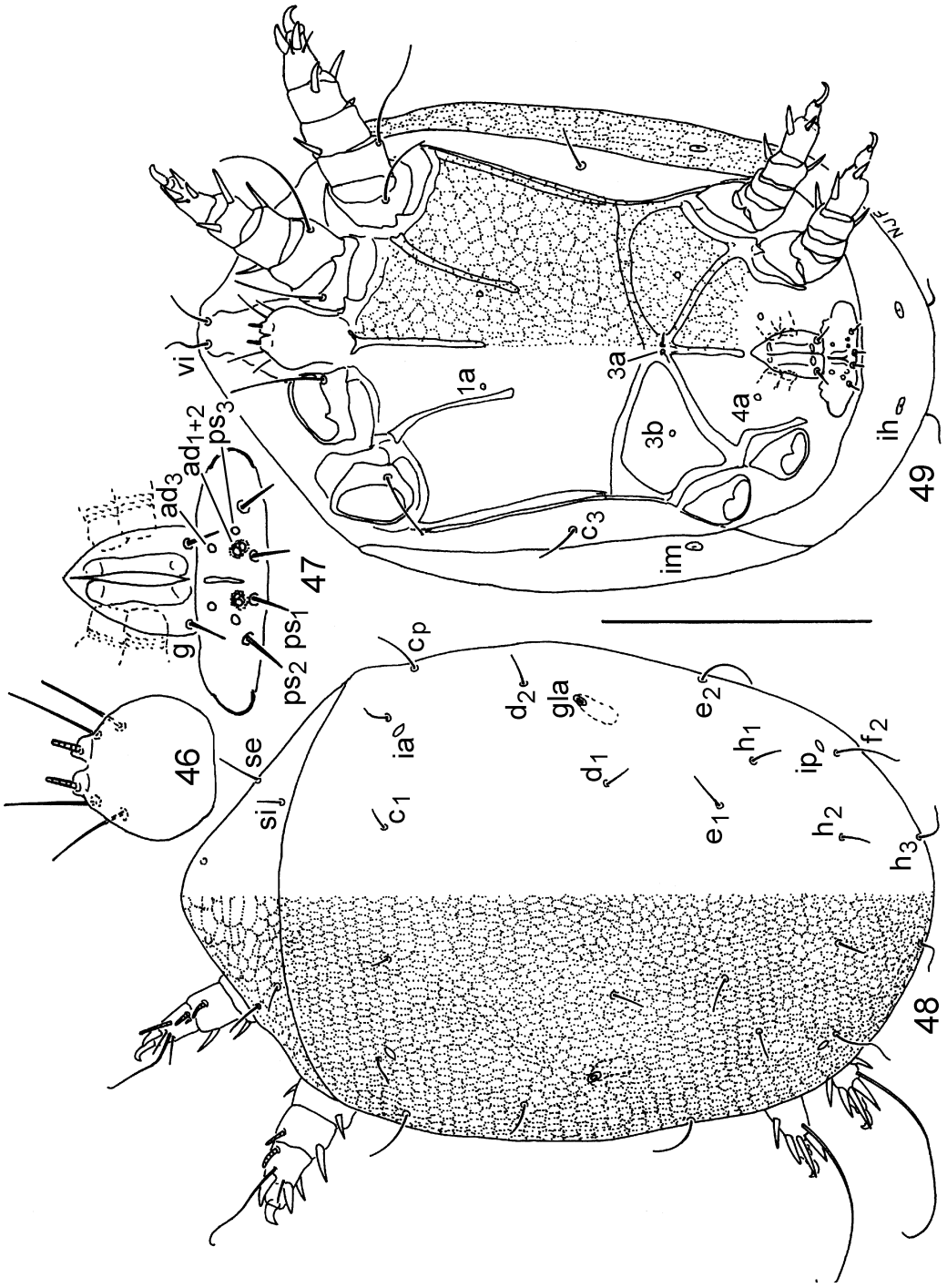
FIGURES 38–41. *Hericia janehenleyi*, **sp. n**. (phoretic deutonymph). 38, gnathosoma, dorsal view; 39, attachment organ; 40, dorsum; 41, venter. Scale bar: 200 μm (Figs 38, 39), 100 μm (Figs 40, 41).



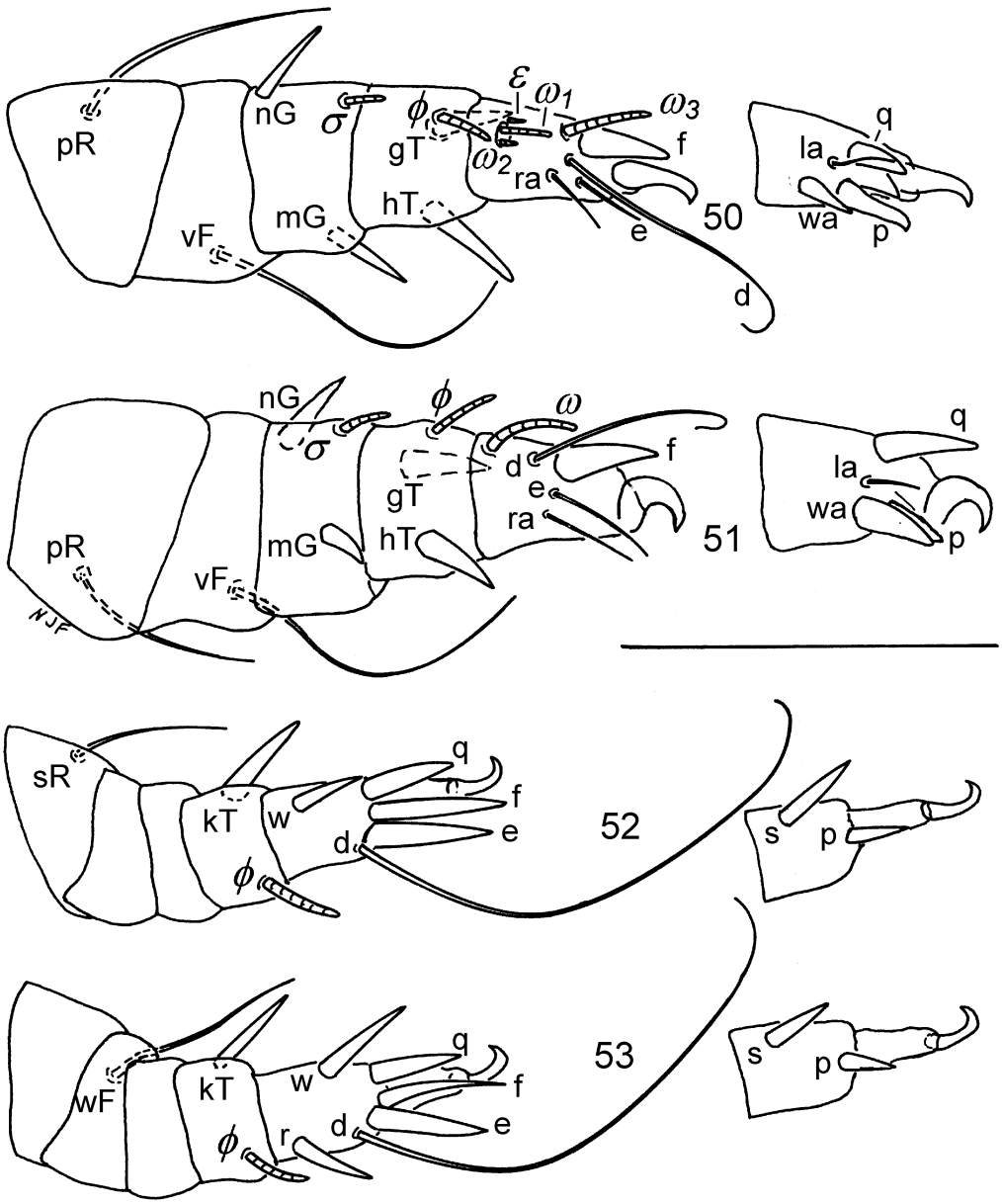
FIGURES 42–45. *Hericia janehenleyi*, **sp. n**. (phoretic deutonymph). 42, leg I dorsal view, ventral view tarsus; 43, leg II dorsal view, ventral view tarsus; 44, leg III dorsal view, ventral view tarsus; 45, leg IV dorsal view, ventral view tarsus. Scale bar = 50 μm.

Dorsum (Fig 40). Dorsum largely covered by reticulate-sculptured propodosomal and hysterosomal sclerites that are separated by a well developed sejugal furrow. Apex of propodosomal sclerite with a pair of unsclerotised areas representing vestigial alveoli of setae *ve*. Propodosoma with three pairs of filiform setae: *vi* 22 (14–31) at apex, *si* 27 (14–37) on lateral margin, and *se* 22 (17–30) posterior to *si*. Hysterosomal sclerite wraps around lateral margin of idiosoma, joining ventral sclerite, and bearing 10 pairs of hairlike setae: c_1 10 (5–13); c_2 11 (8–17); *cp* 25 (13–33); d_1 10 (5–15); d_2 15 (11–20); e_1 10 (6–17); e_2 28 (16–33); f_2 29 (20–38); h_1 9 (7–12), h_2 9 (6–12), and

h_3, 29 (19–33). Opisthosomal gland openings located laterally between setae d_2 and e_2. Cupules *ia* mesiad and slightly anterior setae c_2, and cupules *ip* slightly anterior to setae f_2.



FIGURES 46–49. *Hericia janehenleyi*, **sp. n**. (non-phoretic deutonymph). 46, gnathosoma, ventral view; 47, vestigial attachment organ; 48, dorsum; 49, venter. Scale bar: 200 μm (Figs 46, 47), 100 μm (Figs 48, 49).



FIGURES 50–53. *Hericia janehenleyi*, **sp. n**. (non-phoretic deutonymph). 50, leg I dorsal view, ventral view tarsus; 51, leg II dorsal view, ventral view tarsus; 52, leg III dorsal view, ventral view tarsus; 53, leg IV dorsal view, ventral view tarsus. Scale bar = 50 μm.

Venter (Fig 41). Anterior apodemes of coxal fields I fused to form a sternum; anterior apodemes of coxal fields II curved posteriorly and medially. Posterior apodemes of coxal fields II join anterior apodemes III. Anterior apodemes of coxal fields III fused with each other and with anterior apodemes of coxal fields IV; posterior apodemes III fused with anterior apodemes IV and also with base of anterior apodemes III, coxal fields III completely enclosed. Posterior medial apodeme well developed, extending from anterior apodemes IV to genital opening. Setae c_3 filiform, 17 (13–21),

positioned between legs II and III. Setae of coxal fields I (*1a*), III (*3b*) and IV (*4a*) absent, their positions represented by vestigial alveoli. Setae *3a* often absent, their position represented by vestigial alveoli at junction of apodemes IV and median apodeme (occasionally present as short, filiform setate). Genital opening between coxae IV; setae *g* 10 (9–11) filiform, flanking genital opening. Genital papillae short, two segmented, rounded apically. Cupules *im* on lateral margin of idiosoma mesiad setae e_2, and cupules *ih* on posterior margin. Attachment organ well developed (Figs 10, 39). Anterior suckers (ad_3) with spokes radiating from center. Median suckers larger, consisting of a marginal ring surrounding an inner core containing paired vestigial alveoli (ad_{1+2}). Pair of small refractile spots (vestigial alveoli of ps_3) anteriolateral to median suckers. Setae ps_2 conoidal and situated posteriolateral to median suckers; Setae ps_1 conoidal and situated contiguously, posterior to median suckers. Anus located between anterior and median suckers.

Legs (Figs 42–45). Legs heavily sclerotised, elongate, all segments free. Trochanteral setation 1-1-1-0; setae *pR* I–II and *sR* III thin, filiform. Femoral setation 1-1-0-1; setae *vF* I–II and *wF* IV thin, filiform. Genual setation 2-2-0-0; setae *nG* and *mG* I–II stout spines. Tibial setation 2-2-1-1; setae *hT* and *gT* I–II and *kT* III–IV stout spines. Tarsal setation 8-8-7-8; tarsae I and II with setae *f, wa,q and p* stout spines, setae *la* and *ra* filiform, seta *e* elongate, foliate apically, and seta *d* long, filiform. Tarsus III with setae *w*, *s*, *q*, *f* and *e* elongate spines, seta *p* short spine and seta d filiform and very long. Tarsus IV similar to tarsus III, but with the addition of seta *r*, an elongate spine. Solenidia (I–IV): tarsus 3-1-0-0, tibiae 1-1-1-1 and genua 1-1-0-0. Spinelike famulus ε on tarsus I. Pretarsi of legs I–II consist of short, membranous ambulacra whereas those of legs III–IV consist of elongate membranous ambulacra, all with hooked empodial claws; condylophores not observed.

NON-PHORETIC DEUTONYMPH (Figs 11, 46–53)

Many characters associated with phoresy and dispersal are reduced or vestigial in the non-phoretic deutonymph (see Fashing 1991 for details).

Body broadly ovoid; length 266 (228–303); width at sejugal furrow 194 (158–218). Not significantly different in length ($p = 0.982$, $df = 18$; $t = 0.023$) or width ($p = 0.426$, $df = 18$, $t = 0.814$) to phoretic deutonymph. Gnathosoma (Fig 46) similar to phoretic deutonymph, except palps and palpal solenidia shorter.

Dorsum (Fig 48). Similar in cuticular sculpturing, gland and cupule placement, and setation to phoretic deutonymph. Setal lengths: *vi* 21 (16–26); *si* 24 (17–30); *se* 23 (18–26); c_1 9 (6–12); c_2 10 (7–13); *cp* 26 (21–31); d_1 8 (5–9); d_2 16 (9–24); e_1 9 (8–11); e_2 30 (23–38); f_2 31 (24–38); h_1 6 (5–8); h_2 9 (8–12) and h_3 25 (19–32).

Venter (Fig 49). Idiosoma similar in appearance to phoretic deutonymph. Setal lengths: c_3 18 (14–23); *g* 7 (6–8). Attachment organ greatly modified and devoid of suckers and no longer functional as a sucker plate (Figs 11, 47). Anterior suckers (ad_3) reduced to vestigial alveoli, and median suckers reduced to the paired vestigial alveoli of setae ad_{1+2}. Setae ps_2 6 (4–7) and ps_1 5 (4–6) filiform rather than conoidal.

Legs (Figs 50–53). Chaetotaxy and soleniotaxy similar to that of phoretic deutonymph except tarsal I and II setae *e* filiform rather than foliate. In addition, legs are shorter and pretarsae of legs III–IV short rather than elongate.

Etymology

The species is named in honor of Mrs. Jane Henley of Newport News, Virginia. Mrs. Henley is an avid gardener and nature enthusiast who has generously supported both research and teaching in the William and Mary Biology Department for many years.

Remarks

To date, five species of *Hericia* have been described. While the types of *H. fermentationis* and *H. sanukiensis* are available for examination, types of the other three are either no longer in existence or unavailable for loan. In those cases, species characteristics are taken from the literature.

Türk and Türk (1957) described *H. paradoxa* from a single deutonymph collected from the bark of a birch tree near Erlangen, Germany. They concluded that the habitat and configuration of the apodemes were characteristic of the genus *Hericia*, but were uncertain of its placement due to an extremely reduced sucker plate and short pretarsi. Fashing (1991), investigating *H. janehenleyi*, discovered that species of *Hericia* can have two types of deutonymphs, one phoretic and one non-phoretic. Both deutonymphal morphs have also been found for *H. sanukiensis* (Fashing and Okabe 2006). The deutonymph used to describe *H. paradoxa* is undoubtedly a non-phoretic morph. Non-phoretic deutonymphs of European *Hericia* have not been described, and it is quite possible *H. paradoxa* is a junior synonym for either *H. hericia* or *H. georgei*. Türk and Türk's description is poor and the type unavailable, so little more can be said concerning *H. paradoxa*.

Hericia janehenleyi is smaller than the other described species, with male idiosomal length averaging in the mid-400 μm range and males of the other species averaging in the 500 and 600 μm range. A number of characters separate *H. janehenleyi* from other described *Hericia* species, however the most straightforward ones involve the cuticular ornamentation. Males of *H. georgei* and *H. sanukiensis* have only six shallow sclerotized depressions containing irregular cuticle on their dorsum and these depressions are located between setae *si* and c_1. On the other hand, males of *H. hericia*, *H. fermentationis* and *H. janehenleyi* have greater than 18 patches distributed over a larger portion of the dorsum. *Hericia hericia* can be distinguished from *H. fermentationis* and *H. janehenleyi* in that the cuticle is slightly granular and studded with small spines (Robin 1868, Michael 1903).

Hericia janehenleyi can be more thoroughly compared to *H. fermentationis* since Vitzthum's syntypes deposited in Zoologische Sammlung des Bayrischen Staates Munich were available for examination. The syntypes consist of four males (two on each of slides V3051, V3052), one female (slide V3053) and four phoretic deutonymphs (two on slide V3072, and one each on slides V3070 and V3073). All of the syntypes are in poor condition in deteriorating mounting media, however several characters, especially those involving measurements, can be gleaned from males, deutionymphs, and the single female syntype.

Males: Although Samšiňák (1972) states that the idiosomal length of *H. fermetationis* is 700 μm, Vitzthum's (1931) description lists the range for idiosomal length as 515–610 μm and for idiosomal width as 425–480 μm. My measurements of the four Vitzthum syntypes yielded a mean length of 542. 7 (s.e. = 18.381, range = 467–606) and a mean width of 446.3 (s.e. = 12.829, range = 423–481) . *Hericia janehenleyi* has a mean length of 460.6 (s.e . = 28.715) and width of 355 (s.e. = 14.663) and is significantly smaller in both length (t = 2.938, df =12, p = 0.034) and width (t = 3.682, df = 12, p = 0.003) than *H. fermenationis*. Setal lengths also reveal a difference between the two species. When adjusted to percentage of idiosomal length, 12 of the 16 dorsal setae are longer in *H. janehenleyi* than in *H. fermenationis* (Table 1), and a paired-comparisons *t*-test using mean setal lengths indicates this difference is significant (t = 3.161; df = 15; p = 0.006). In *H. fermenationis*, dorsal seta f_2 is short (17% of idiosomal length) and hair-like (similar in appearance to ps_2 and ps_3), whereas in *H. janehenleyi* it is longer (30% of idiosomal length) and, rather than hair-like, thicker and similar in appearance to other robust dorsal setae (e.g., e_1 and e_2). While males of both species have numerous shallow sclerotized depressions in their dorsal cuticle, in *H. fermenationis* they extend posteriorly to just above setae e_1, and in *H. janehenleyi* they extend to the level of setae d_1. In addition, there are more cuticular depressions in *H. janehenleyi* than *H. fermenationis*. Illustrations by Vitzthum (1931)

depict 19 and those of Samšiňák (1972) 23. An examination of 50 *H. janehenleyi* males revealed the mean number to be 29.2, the median 29 and the range from 26–34.

TABLE 1. Mean dorsal setal lengths ± standard errors calculated as a percentage of idiosomal length of male deutonymphs. Sample size: *H. fermenationis* = 4 and *H. janehenleyi* = 10.

Seta	*H. fermentationis*	*H. janehenleyi*	*H. fermentationis*	*H. janehenleyi*
vi	13.59 ± 0.252	24.61 ± 0.779	6.66 ± 0.285	8.33± 0.742
se	17.36 ± 1.171	20.90 ± 0.618	11.83 ± 0.176	8.41 ± 0.637
si	35.66 ± 1.228	32.36 ± 1.644	14.70± 1.673	10.33± 0.945
c_1	27.51 ± 1.435	35.01 ± 1.883	6.75 ± 1.202	3.88± 0.331
c_2	29.32 ± 2.336	25.10 ± 0.895	6.71± 0.366	4.00± 0.406
c_3	25.73 ± 2.828	41.40 ± 0.955	9.46 ± 0.609	6.48± 0.391
cp	31.82 ± 1.759	28.35 ± 0.740	10.34 ± 1.495	9.43 ± 0.828
d_1	31.39 ± 4.075	40.00 ± 1.659	4.84 ± 0.345	3.95± 0.439
d_2	33.66 ± 2.354	30.88 ± 1.164	11.71 ± 3.293	5.53± 0.476
e_1	33.29 ± 1.542	40.78 ± 1.155	5.67± 0.692	3.98± 0.517
e_2	35.42 ± 3.091	37.07 ± 1.106	11.51± 2.325	10.71 ± 0.794
f_2	16.58 ± 1.906	30.26 ± 1.008	10.77 ± 0.756	11.10± 0.798
h_1	34.16 ± 2.190	40.76 ± 1.316	4.43± 0.534	3.35 ± 0.277
h_2	48.19 ± 8.263	58.99 ± 1.560	6.82± 1.036	3.66 ± 0.604
h_3	57.52 ± 4.300	59.74 ± 1.669	6.54 ± 0.236	10.98± 0.610
ps_3	54.54 ± 3.561	59.85 ± 2.200	-----	-----

Females: Females of *H. fermenationis* are also considerably larger than those of *H. janehenleyi*. Vitzthum's (1931) description gives the idiosomal length of non-gravid females of *H. fermenationis* as 515 μm and the width as 350 μm, and the range for the idiosomal length of gravid females as 610–630 μm and the width as 440–460 μm. Measurements of 10 recently eclosed female *H. janehenleyi* resulted in a mean length of 362 (range 330–397) and width of 255 (range 229–282), and measurements of ten gravid females a mean length of 522 (range 477–561) and width of 326 (range 308–370). Vitzhum (1931) describes the cuticle of female *H. fermenationis* as overall smooth, but with at least five pairs of small, granulated plates on the hystersoma. An examination of the female syntype confirms this. In contrast, the cuticle of *H. janehenleyi* females is striated and interspersed with rows of narrow, pointed, elliptical-shaped mammilations. It is also devoid of granulated plates.

Deutonymphs: Vitzhum (1931) had specimens of only the phoretic morph of *H. fermenationis* and found the range for idiosomal length to be 328–360 μm. My measurements of the four Vitzthum syntypes yielded a mean length of 345.4 (s.e. = 8.064, range = 331–366). With a mean length of 266.1 (s.e . = 6.509), *H. janehenleyi* deutonymphs are significantly smaller (t = 6.850, df =12, p < 0.0005). Setae also reveal a difference between the two species. When adjusted to percentage of idiosomal length, 12 of the 15 dorsal setae are longer in *H. fermenationis* than in *H. janehenleyi* (Table 1), and a paired-comparisons *t*-test using mean setal lengths indicates this difference is significant (t = 2.465; df = 14; p = 0.027). When standardized for size difference by dividing by gnathosomal length, the solonidia on the gnathosomal palpi are significantly longer in *H. janehenleyi* (mean = 65.3%, s.e. = 1.379%, range = 60.0–71.9%) than in *H. fermenationis* (mean = 36.4%, s.e. = 3.553%, range = 30.2–45.0%) (t = 9.387, df = 11, p < 0.0005). Measured as a percentage of the

sternal length, the sternal apodeme is also significantly shorter in *H. janehenleyi* (mean = 53.7%, s.e. = 0.792, range = 50.8–58.9%) than in *H. fermentationis* (mean = 85.4%, s.e. = 2.732, range = 80.9–92.8%) (t = 15.092, df = 11, $p < 0.0005$). In all cases, tarsal lengths, when standardized by dividing by idiosomal length, are significantly longer ($p < 0.0005$) in *H. fermenationis* (Tarsus I 9.0 $\pm$ 0.130% vs 6.5 $\pm$ 0.144%; Tarsus II 9.6 $\pm$ 0.290% vs 6.8 $\pm$ 0.163%; Tarsus III 8.4 $\pm$ 0.245% vs 5.5 $\pm$ 0.149%; Tarsus IV 8.9 $\pm$ 0.156% vs 5.6 $\pm$ 0.266%).

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