Systematics, Ecology and Host Associations of *Naiadacarus* (Acari: Acaridae) in the Great Lakes Region

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SYSTEMATICS, ECOLOGY AND HOST ASSOCIATIONS OF *NAIADACARUS* (ACARI: ACARIDAE) IN THE GREAT LAKES REGION

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ABSTRACT

Naiadacarus arboricola Fashing, is reported from adults collected from water-filled treeholes and deutonymphs phoretic on *Mallota* species, *Eristalis bardus* and *Somula decora* (Diptera: Syrphidae) from Michigan, Illinois, and New York. *Naiadacarus fashingi*, new species, is described from deutonymphs phoretic on *Brachypalpus oarus* and seven other species of Syrphidae from Michigan, New York and New Jersey. *Naiadacarus mydophilus,* new species, is described from deutonymphs phoretic on *Brachypalpus oarus* from Michigan. Based upon known biologies of host insects and other mite species which utilize these hosts, it is hypothesized that *N. fashingi* and *N. mydophilus* may inhabit wet decaying wood and/or moist treeholes rather than water-filled treeholes. *Naiadacarus* is hypothesized to be closely related to the genera *Schwiebea, Histiogaster* and *Thyreophagus*. The subfamily name Naiadacarinae is placed in synonymy with Rhizoglyphinae.

The genus *Naiadacarus* was proposed by Fashing (1974) for two new species of acarid mites, *N. arboricola* and *N. oregonensis,* collected from water-filled treeholes in North America. Fashing (1975) reported that *N. arboricola* feeds by skeletonizing decaying leaves in the treeholes, and deutonymphs disperse via phoresy on syrphid flies of the genus *Mallota.* During studies of the astigmatid mite fauna of the Huron Mountains in northern Michigan, specimens representing two species of *Naiadacarus* were collected, *N. arboricola* Fashing, and a new species which is described below. Additional specimens of these and a second new species, removed from syrphid flies in the collections of the University of Michigan Museum of Zoology (UMMZ), are reported which extend the known geographic and host ranges of the genus. This additional information allows new hypotheses to be developed concerning the phylogenetic relationships of *Naiadacarus* and its historical ecology.

METHODS AND MATERIALS

Mites were collected from microhabitats and insects on the property of the Huron Mountain Club as described in OConnor and Houck (1989). Specimens of *Naiadacarus* were recovered from water-filled treeholes and from two species of field-collected Syrphidae, *Brachypalpus oarus* (Walker) and *Chalcosyrphus (Xylotomima) vecors* (Osten Sacken). In order to determine if other fly taxa could serve as phoretic hosts, 5100 specimens, representing 64 genera and 231 species of Syrphidae in the collections of the

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UMMZ were examined for mites. Selected examples of other wood-breeding Diptera were also examined. These flies were primarily from Michigan localities, with a few from other North American sites. In addition, specimens of *N. arboricola,* previously removed from dipteran hosts in the Cornell University Insect Collection, Ithaca, New York, were also examined.

In the following descriptions and table, all measurements are given in micrometers (μm) and are given as holotype, mean (range) of 10 individuals from the type-locality for new taxa and mean (range) of 10 individuals from Ann Arbor, Michigan, for *N. arboricola.*

Institutions serving as depositories for mite and/or host specimens are abbreviated as follows: University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ); U.S. National Museum of Natural History, Washington (USNM); Field Museum of Natural History, Chicago (FMNH); The Acarology Laboratory, The Ohio State University, Columbus (OSU); Cornell University Insect Collection, Ithaca (CUIC); Canadian National Collection, Ottawa (CNC); British Museum (Natural History), London (BMNH); L'Institut Royal des Sciences Naturelles, Brussels (IRSNB); Hungarian Natural History Museum, Budapest (HNHM).

SPECIES ACCOUNTS

Naiadacarus arboricola Fashing

Fashing (1974) reported this species from water-filled treeholes in Kansas, Michigan, Minnesota, Pennsylvania, Virginia and Arkansas. Deutonymphs were originally reported from the syrphid flies, *Mallota posticata* (F.) and *M. bautias* (Walker) from Kansas, New York and Illinois. No additional distributional or host information on this species has been subsequently published. Specimens from the following hosts and localities are housed in the UMMZ collection (slides and fluid specimens bear the collection numbers indicated).

Feeding stages (adults and non-deutonymphal immature instars) from water-filled treeholes as follows: MICHIGAN: Marquette Co., Huron Mountain Club (T51N, R28W, sect 4, SE 1/4), 15 August 1987, B.M. OConnor (BMOC #87–0815–14), unidentified tree; Marquette Co., Huron Mountain Club (T52N, R28W, sect 30, SE 1/4), 17 August 1987, B.M. OConnor (BMOC #87–0817–7), *Acer saccharum;* Washtenaw Co., Pinckney State Recreation Area, 10 June 1981, B.M. OConnor (BMOC #81–0610–3), *Quercus* sp.; ILLINOIS: Franklin Co., Wayne Fitzgerrell State Park, 24 October 1982, B.M. OConnor (BMOC #82–1024–14), unidentified tree; NEW YORK: Chautauqua Co., Westfield, 8 October 1981, B.M. OConnor (BMOC #81–1008–20), unidentified tree; Broome Co., Greenwood County Park, 19 August 1980, B.M. OConnor (BMOC #80–0821–4), *Fagus grandifolia;* Tompkins Co., Brooktondale, 25 April 1979, B.M. OConnor (BMOC #79–0425–4), unidentified tree; Tompkins Co., Buttermilk Falls State Park, 4 May 1980, B.M. OConnor (BMOC #80–0504–2), unidentified tree; Tompkins Co., Ringwood Preserve, 3 July 1979, B.M. OConnor (BMOC #79–0703–1), *Fagus grandifolia;* Tompkins Co., Ringwood Preserve, 13 August 1979, B.M. OConnor (BMOC #79–0813–2), unidentified tree; Tompkins Co., Michigan Hollow, 4 July 1979, B.M. OConnor (BMOC #79–0704–1), *Fagus grandifolia.*

Deutonymphs have been recovered from the following hosts (all Diptera: Syrphidae, housed in UMMZ unless otherwise indicated and bearing voucher labels stating, ''Mites removed, B.M. OConnor'' and the collection number):

From *Mallota posticata* (Fabricius); MICHIGAN: Washtenaw Co., Ann Arbor, 21 June 1927, N.K. Bigelow (BMOC #89–0113–37) (24 deutonymphs); Washtenaw Co., Ann Arbor, 19 June 1927, N.K. Bigelow (BMOC #89–0113–38) (9 deutonymphs); Gratiot Co., 7 June 1941, R.R. Dreisbach (BMOC #89–0113–40) (26 deutonymphs); Oakland Co., 30 May 1929, A.W. Andrews (BMOC #89–0113–41) (1 deutonymph); NEW JERSEY: Mercer Co., Trenton, 13 June 1908 (BMOC #89–0113–39) (111 deuto-

nymphs); NEW YORK: Tompkins Co., Ithaca, Six-mile creek, 16 July 1937, P.P. Babiy (BMOC #79–0131–2) (host in Cornell University Insect Collection (CUIC)) (42 deutonymphs). Of a total of 27 individuals of this host species in UMMZ, *N. arboricola* was found on 0 of 14 males and 5 of 13 females, giving an infestation rate of 0% on males and 38% on females.

From *Mallota bautias* (Walker); MICHIGAN: Washtenaw Co., Ann Arbor, 27 May 1927, N.K. Bigelow (BMOC #89–0113–33) (2 deutonymphs); Schoolcraft Co., Floodwoods, 14 July 1915, J.S. Rogers (BMOC #89–0113–34) (2 deutonymphs); NEW YORK: Tompkins Co., Ithaca, 31 May 1957, J.G. Franclemont (BMOC #79–0131–1) (host in CUIC) (14 deutonymphs); MISSOURI: Knox Co., near Knox City, 19 May 1987, M. Arduser (BMOC #89–0113–36) (3 deutonymphs). Of a total of 53 individuals of this host species in UMMZ, *N. arboricola* was found on 0 of 39 males and 3 of 14 females, giving an infestation rate of 0% on males and 21% on females.

From *Eristalis bardus* (Say); MICHIGAN: Washtenaw Co., Ann Arbor, 3 June 1974, H.D. Cameron (BMOC #89–0113–31) (3 deutonymphs). Of a total of 60 individuals of this host species in UMMZ, *N. arboricola* was found on 0 of 39 males and 1 of 21 females, giving an infestation rate of 0% on males and 5% on females.

From *Somula decora* Macquart; NEW YORK: Tompkins Co., Town of Dryden, Ringwood Road, 26 June 1972, G.R. Mullen (BMOC #89–0113–43) (4 deutonymphs). This specimen also harbored *N. fashingi* n. sp. as did other specimens of *S. decora* (see page 88). Of a total of 31 individuals of this host species in UMMZ, *N. arboricola* was found on 0 of 16 males and 1 of 15 females, giving an infestation rate of 0% on males and 7% on females.

Diagnosis: *Naiadacarus arboricola* deutonymphs differ from the two species described below in the larger body size, generally greater lengths of legs, pretarsi and sensory structures (see Table 1), much greater length of the distal palpal seta which is always greater than the combined length of subcapitular and palpal remnants (Fig. 7), the form of the dorsal ornamentation, and the invariant presence of solenidion σ on genu III. Fashing (1974) noted variation in the form of setae *cx IV* in this species. In the specimens examined here, these setae were distally filiform with a strongly expanded basal region (Fig. 10). In a single specimen, a unilateral variant was observed which was more conoidal in form, having the expanded base more elongate and lacking the flagellar distal portion. Other variation noted in the present specimens included the presence of a very tiny second solenidion σ'' on genu I in approximately one-quarter of the specimens examined. Variation in the form and length of propodosomal setae *vi* was also observed. Most specimens have these setae short and spine-like, as in the other species noted below. In several specimens, however, they were much longer and filiform (one also had an extra *vi* seta). Alveoli of the absent setae *ve* were visible in a number of specimens of *N. arboricola* but not in the other species.

Specimen Deposition: Voucher specimens of *N. arboricola* from the above collections are deposited in the UMMZ and CUIC.

Naiadacarus fashingi OConnor, **new species**

This species is known only from the deutonymph.

Deutonymph. Body broadly ovoid, widest in sejugal region; idiosomal length 209, 215 (178–238), width 156, 156 (130–176). Gnathosoma (Fig. 8) consisting of relatively elongate subcapitular remnant and very short, rounded palps bearing palpal solenidia (ω) apically and filiform dorsal palpal setae (*dm*) dorsolaterally. Supracoxal setae of palps (*elc p*) absent from subcapitular remnant, their positions marked by refractile spots. Positions of other gnathosomal setae present in non-deutonymphal stages of other astigmatid mites (ventral subcapitulars, ventral palpal tibials and dorsal palpal tarsals) also marked by refractile spots.

Dorsum (Fig. 1). Propodosoma and hysterosoma each covered by heavily punctate sclerite. Internal vertical setae (*vi*) short, positioned slightly anterior to apex of

Table 1. Comparative measurements of deutonymphs of *Naiadacarus* species. Measurements given as holotype, mean (range) for new species and mean (range) for *N. arboricola* (N = 10). (− = structure absent; b = structure broken; * = mean value significantly different from others (ANOVA, followed by Tukey HSD test, p < .05))

	N. fashingi	*N. mydophilus*	*N. arboricola*
gnathosoma	19 22(19–30)	18 19(16–23)*	23(19–26)
gnathosomal solenidion	43 44(37–51)	35 38(35–42)*	47(42–50)
palp supra-coxal seta	—	3 3(2–4)	3(3–4)
palp tibial seta (*dm*)	9 9(7–10)	7 8(6–10)	24(19–30)*
cxI	15 19(13–26)	15 15(12–20)	32(22–41)*
cxIII	16 17(12–25)	15 15(13–17)	28(21–31)*
cxIV	3 4(3–5)*	12 10(8–12)*	15(12–18)*
ga	16 15(10–19)	15 14(10–17)	24(21–28)*
gp	12 14(12–17)	15 13(11–15)	15(11–18)
vi	5 5(4–6)	5 5(4–6)	10(5–24)*
sci	4 4(3–6)	5 5(4–6)	5(4–6)
sce	10 10(9–15)	9 9(7–11)	17(13–20)*
scx	10 11(10–13)	9 8(7–10)*	11(9–13)
d₁	4 5(4–5)	5 5(3–6)	5(4–6)
l₁	4 5(4–5)	5 5(3–5)	6(4–6)*
h	10 11(8–16)	10 11(10–12)	17(12–21)*
sh	8 7(6–9)	6 6(6–7)*	8(6–10)
d₂	6 5(4–7)	b 5(3–5)*	6(5–7)
l₂	8 9(6–11)	8 8(5–10)	13(10–14)*
d₃	9 10(7–14)	10 10(8–11)	11(8–14)
l₃	10 9(7–12)	10 10(9–11)	14(11–17)*
d₄	9 9(7–11)*	7 7(5–8)*	12(10–15)*
l₄	9 8(6–10)	8 8(7–9)	9(5–11)
d₅	10 10(7–11)	10 10(9–12)	16(13–19)*
l₅	44 46(34–58)*	30 31(24–36)*	54(43–65)*
leg I[1]	123 132(103–147)	100 104(88–118)*	136(124–145)
tarsus I	52 55(45–60)	40 44(37–49)*	51(47–54)
empodium I	15 17(12–20)	14 16(15–19)	23(21–26)*
ω_1	21 21(19–25)	18 18(16–21)*	23(22–26)
ω_2	9 10(9–12)*	9 8(7–9)*	7(6–8)*
ω_3	12 13(11–14)	13 12(10–13)	12(11–14)
ϵ	5 6(5–7)	5 5(4–6)	5(4–6)
d I	110 105(70–136)	73 74(66–84)*	92(71–103)
e I	27 30(23–37)	24 25(23–27)*	33(29–37)
f I	33 36(31–39)	35 33(27–38)	48(39–55)*
wa I	12 14(9–15)	14 13(11–15)	13(10–18)
ra I	35 41(35–48)*	33 33(28–39)*	48(43–53)*
la I	41 42(37–47)	31 33(27–40)*	45(39–50)
p I	24 23(21–26)	22 21(15–24)	27(23–31)*
q I	23 24(22–26)*	20 21(14–26)*	30(26–34)*
ϕ I	65 71(62–81)	62 66(65–74)	92(66–103)*
gT I	8 10(8–12)	9 10(8–13)	13(11–16)*
hT	12 15(12–16)	14 14(13–17)	18(14–21)*
σ I	16 20(16–23)	20 19(16–21)	24(17–30)*
cG I	7 8(7–8)	8 8(8–9)	11(9–11)*
mG I	9 11(9–14)*	9 9(7–10)*	13(10–15)*
vF I	48 45(30–57)	33 33(27–43)*	46(37–54)
pR I	42 43(30–50)*	34 32(28–34)*	61(54–69)*
leg II[1]	107 11(91–127)*	89 93(79–102)*	125(113–134)*

Table 1 continued

	N. fashingi	N. mydophilus	N. arboricola
tarsus II	41 45(40–48)	39 38(31–42)*	45(42–48)
empodium II	16 16(13–19)	15 16(13–18)	22(19–24)*
ω II	21 21(19–24)	21 22(20–24)	21(19–23)
ba II	29 27(23–32)	22 24(22–27)*	28(24–32)
d II	70 76(61–87)	67 71(65–90)	85(76–91)*
e II	23 26(18–34)*	21 22(19–24)*	33(26–36)*
f II	30 34(29–42)	28 30(27–35)	43(36–50)*
wa II	9 13(9–15)	14 14(12–18)	12(9–13)
ra II	37 39(30–43)*	32 31(25–34)*	43(38–49)*
la II	36 39(29–45)	30 31(26–33)*	41(31–46)
p II	20 21(18–24)	17 20(17–22)	25(20–28)*
q II	22 24(20–27)*	21 20(17–24)*	27(21–31)*
φ II	43 45(36–54)	46 46(38–50)	67(59–73)*
gT II	7 9(7–10)	8 9(8–10)	11(9–13)*
hT II	19 19(15–22)	15 16(13–19)*	20(18–23)
σII	10 11(6–13)	11 9(5–11)	14(10–18)*
cG II	5 7(5–8)	7 7(6–8)	9(8–11)*
mG II	9 9(8–11)	7 8(7–11)	12(10–13)*
vF II	55 55(44–64)*	47 49(45–55)*	74(65–86)*
pR II	51 53(44–58)*	45 44(38–48)*	73(62–79)*
leg III[1]	76 81(69–93)*	68 72(65–78)*	99(86–104)*
tarsus III	32 35(30–39)*	31 31(30–33)*	40(36–43)*
empodium II	114 16(13–19)	14 15(14–17)	23(21–24)*
d III	87 92(76–106)	69 85(69–109)	123(106–137)*
e III	26 28(23–34)	23 23(19–28)*	29(24–34)
f III	33 41(33–52)	31 31(26–37)*	44(36–55)
w III	38 39(35–43)	35 34(26–41)*	39(34–43)
r III	27 28(23–33)	22 26(18–40)	29(23–31)
s III	19 17(13–19)	19 18(15–21)	22(19–25)*
p III	16 15(10–17)*	15 12(11–15)*	19(15–23)*
q III	26 25(23–38)*	22 22(18–25)*	29(26–32)*
φ III	47 45(33–53)	37 37(32–40)*	48(40–52)
kT III	17 18(15–21)	16 17(16–20)	18(16–20)
σ III	— 4(3–4)[2]	—	6(3–7)
sR III	38 40(27–45)*	28 30(26–33)*	61(51–68)*
leg IV[1]	76 81(76–92)	70 79(70–87)	100(87–106)*
tarsus IV	35 39(34–46)	35 37(36–39)	44(38–46)*
empodium IV	16 17(12–20)	15 15(13–17)	22(20–23)*
d IV	b 95 (79–109)*	101 110(91–122)*	131(101–142)*
e IV	26 28(19–34)	24 23(17–28)*	28(23–32)
f IV	70 70(55–80)	68 68(64–81)	80(60–89)*
w IV	37 37(34–45)	35 37(29–45)	38(30–45)
r IV	20 24(20–26)	25 23(18–27)	26(23–28)*
s IV	19 19(16–24)	18 19(16–23)	23(20–27)*
p IV	14 12(9–15)	11 9(6–13)	17(14–20)*
q IV	25 26(18–37)	25 21(16–26)*	28(22–33)
φ IV	7 7(5–9)	6 6(5–8)	8(7–11)*
kT IV	18 16(15–21)	16 17(15–20)	17(16–21)
wF IV	26 29(22–36)*	25 23(19–25)*	48(43–57)*

[1]Legs measured from base of femur to tip of tarsus.
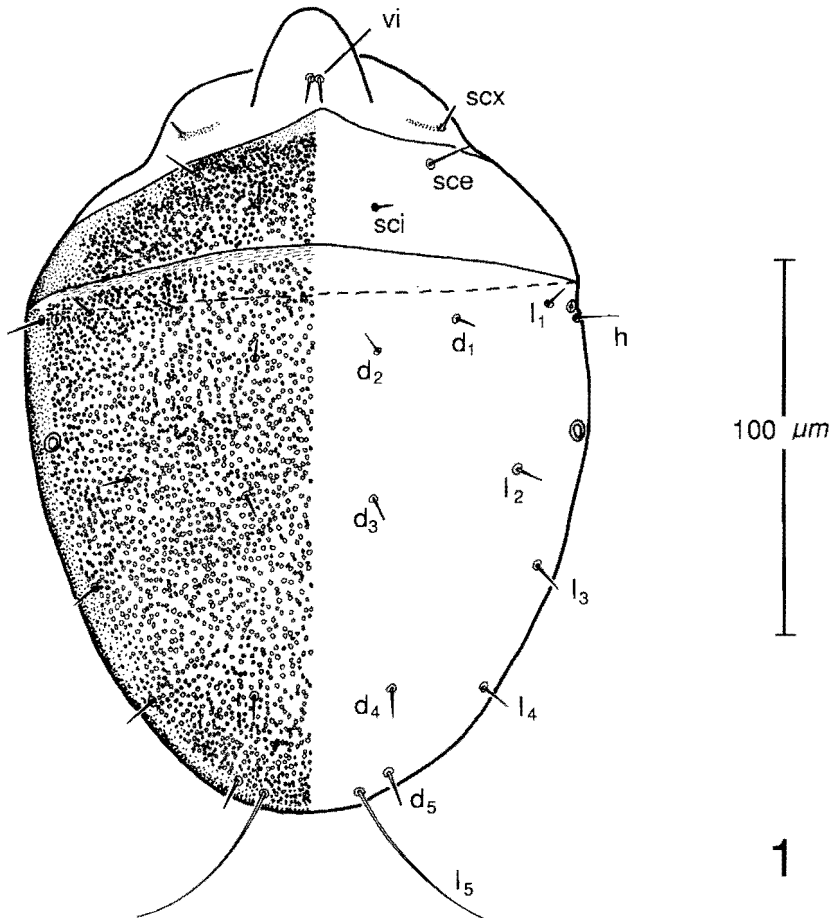[2]Solenidion variably present; mean and range given for specimens with solenidion present.

Figure 1. *Naiadacarus fashingi* n. sp., deutonymph, dorsum.

propodosomal sclerite; external vertical setae (*ve*) absent; internal scapular setae (*sci*) distinctly posterior and medial to external scapulars (*sce*); supracoxal setae of legs I (*scx*) relatively short and filiform, positioned on thin sclerites above legs I. Sejugal furrow well developed. Hysterosoma with 11 pairs of simple, filiform setae on sclerite (d_{1-5}, l_{1-5}, h), setae l_5 much longer than others. Opisthosomal gland openings (gla) between setae l_1 and l_2. Three pairs of cupules observed: *ia* between setae l_1 and *h*, *im* not observed, *ip* ventral, lateral to posterior edge of trochanters IV, *ih* ventral, lateral to posterior portion of attachment organ.

Venter (Fig. 2). Coxal fields sclerotized, coxal fields IV more heavily sclerotized in anterior half. Anterior apodemes of coxal fields I fused forming sternum. Anterior apodemes of coxal fields II curved medially. Posterior apodemes of coxal fields II broad, curved medially and ending near apices of anterior apodemes II. Anterior apodemes of coxal fields III fused with each other and anterior apodemes of coxal fields IV. Posterior
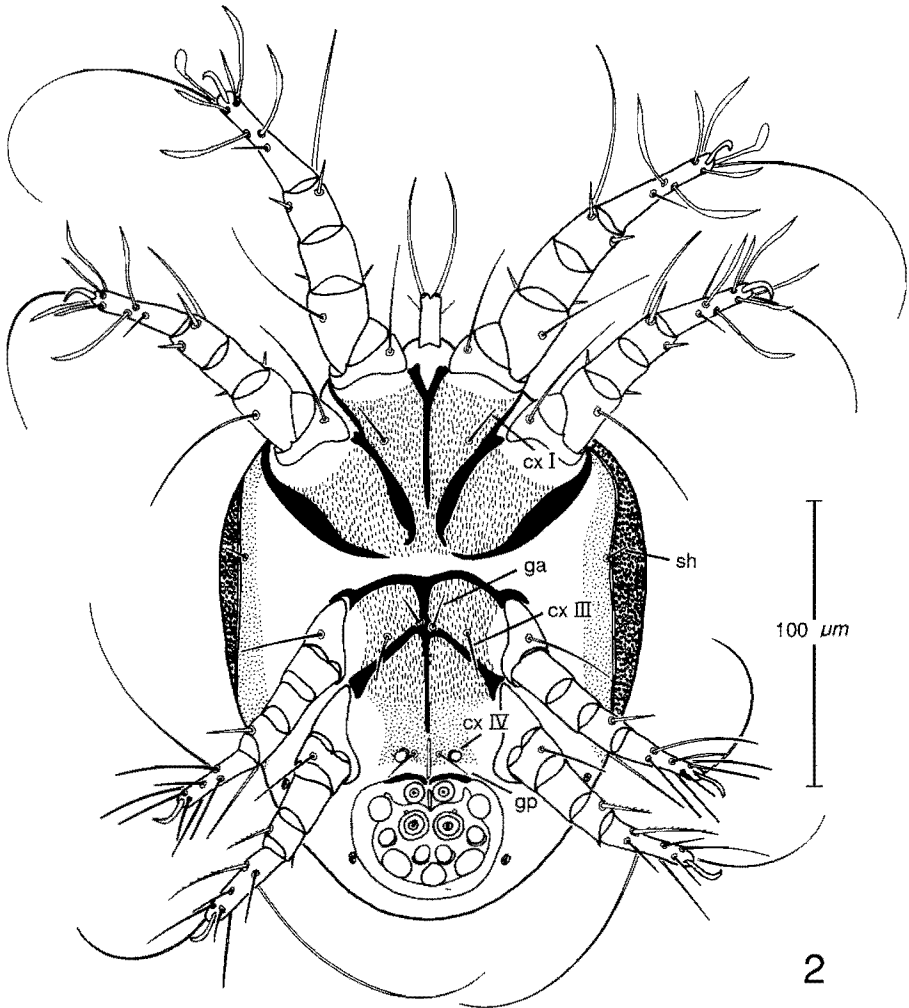
Figure 2. *Naiadacarus fashingi* n. sp., deutonymph, venter.

medial apodeme well developed, extending from anterior apodemes IV almost to genital opening. Posterior apodemes IV short, transverse, positioned directly anterior to attachment organ. Dorsal hysterosomal sclerite separated from ventral surface by a distinct suture on each side; lateral margins of ventral surface sclerotized. Subhumeral setae (*sh*) short, filiform, positioned on ventral surface between legs II–III, adjacent to sutures separating dorsal sclerite from venter. Setae of coxal fields I and III filiform. Setae of coxal fields IV in the form of small conoids. Genital region in posterior portion of coxal fields IV (Fig. 11); opening elongate, ovoid, with two pairs of genital papillae within genital atrium; papillae relatively large, two segmented, with rounded apices. Anterior

genital setae (*ga*) filiform, positioned at junctions of anterior coxal apodemes IV and posterior median apodeme; posterior genital setae (*gp*) laterad of genital opening. Attachment organ posterior to coxal fields. Anterior suckers round, median suckers slightly larger, consisting of large sclerotized margins surrounding paired vestigial alveoli. Pair of small refractile spots anterolateral to median suckers. Lateral conoidal setae of attachment organ situated slightly posterior to a line joining centers of median suckers; posterior conoidal setae posterior to median suckers and slightly more medial. Anterior and posterior lateral and posterior median cuticular suckers well developed. Anus positioned between anterior suckers.

Legs (Figs. 3–6). Legs elongate, all segments free. Trochanters I–III each with filiform seta (*pR, sR*). Femoral setation 1-1-0-1; setae *vF* I–II and *wF* IV filiform, smooth. Genual setation 2-2-0-0; setae *mG* and *cG* I–II somewhat spine-like, seta *nG* III absent. Tibial setation 2-2-1-1; setae *hT* and *gT* I–II and *kT* III–IV spine-like. Tarsal setation 8-9-8-8; tarsus I with 5 thinly foliate setae (*ra, la, p, q,* and *f*), seta *d* elongate and filiform, seta *e* spoon-shaped, seta *wa* filiform to somewhat spine-like, setae *aa* and *ba* absent; tarsus II similar to tarsus I except seta *ba* present and filiform and seta *e* with much smaller spoon-shaped apex. Tarsus III with all 8 setae (*w,r,s,p,q,e,f,d*) smooth, setae except *d,r* and *s* slightly flattened apically. Tarsus IV similar to tarsus III except only setae *p* and *q* slightly flattened, seta *w* larger, thicker and distinctly barbed, and setae *d* and *f* longer. Solenidia consisting of following: ω_1 on tarsi I–II cylindrical, with rounded apices; ω_3 on tarsus I shorter than ω_1, with bulbous apex, positioned directly adjacent to ω_1; ω_2 of tarsus I thin, expanding slightly apically, positioned somewhat more basal and posterior to other solenidia; ϕ of tibiae I–II–III elongate, tapering, ϕ IV short and stout; σ of genu I elongate, tapering slightly, σ of genu II shorter, cylindrical, σ of genu III variably present, when absent, position marked by refractile spot. Famulus ϵ of tarsus I short, pointed, between solenidia ω_1 and ω_3. Setal and solenidial anomalies were noted on several specimens: several specimens bore a second very short solenidion σ'' on each genu I; one of these specimens also bore a filiform dorsal seta (*d*) on one genu I. All pretarsi consisting of hooked empodial claws arising from tarsal apices, short paired condylophores visible within tarsal apices.

Etymology: This species is named for Dr. Norman Fashing, whose excellent studies on the morphology and ecology of *Naiadacarus* have made this genus one of the best known taxa in the Acaridae.

Material Examined: Holotype and 14 paratype deutonymphs from *Brachypalpus oarus* (Walker) (Diptera: Syrphidae): USA, Michigan, Marquette Co., Huron Mountain Club; 26 June 1986; B.M. OConnor (BMOC #86–0626–33). Host fly deposited in UMMZ, labelled "Mites removed, B.M. OConnor #86–0626–33." This host also harbored 1 deutonymph of *Histiogaster cyclopis* Woodring, 2 deutonymphs of an undescribed species of *Schwiebea* (family Acaridae), and 4 deutonymphs of an undescribed species of *Bonomoia* (family Histiostomatidae).

An additional 268 paratype deutonymphs from the following Michigan hosts (all hosts belong to the family Syrphidae and are deposited in UMMZ with voucher numbers and labels as above): from *B. oarus:* Kalkaska Co., 26 May 1957, R. & K. Dreisbach (BMOC #89–0113–3) (9 deutonymphs) (this host also harbored 1 deutonymph of an undescribed *Schwiebea* species and 1 deutonymph of an undescribed *Divilia* species, family Hemisarcoptidae); Emmet Co., 27 May 1960, R. & K. Dreisbach (BMOC #89–0113–4) (18 deutonymphs) (this host also harbored 1 deutonymph of an undescribed *Schwiebea* species). All three infested flies were females. An additional 11 specimens of *B. oarus* examined did not carry *N. fashingi* although 3 carried *Naiadacarus mydophilus* n. sp. (see below). Of a total of 14 individuals of this host species in UMMZ, *N. fashingi* was found on 0 of 5 males and 3 of 9 females, giving an infestation rate of 0% on males and 33% on females.

From *Chalcosyrphus (Xylotomima) vecors* (Osten Sacken): Marquette Co., Huron Mountain Club, 27 June 1986, B.M. OConnor (BMOC #86–0627–24) (3 deutonymphs) (this host also harbored 1 deutonymph of an undescribed *Bonomoia* species and 20 deutonymphs representing 4 undescribed species of *Schwiebea*); Chippewa Co., 25 June
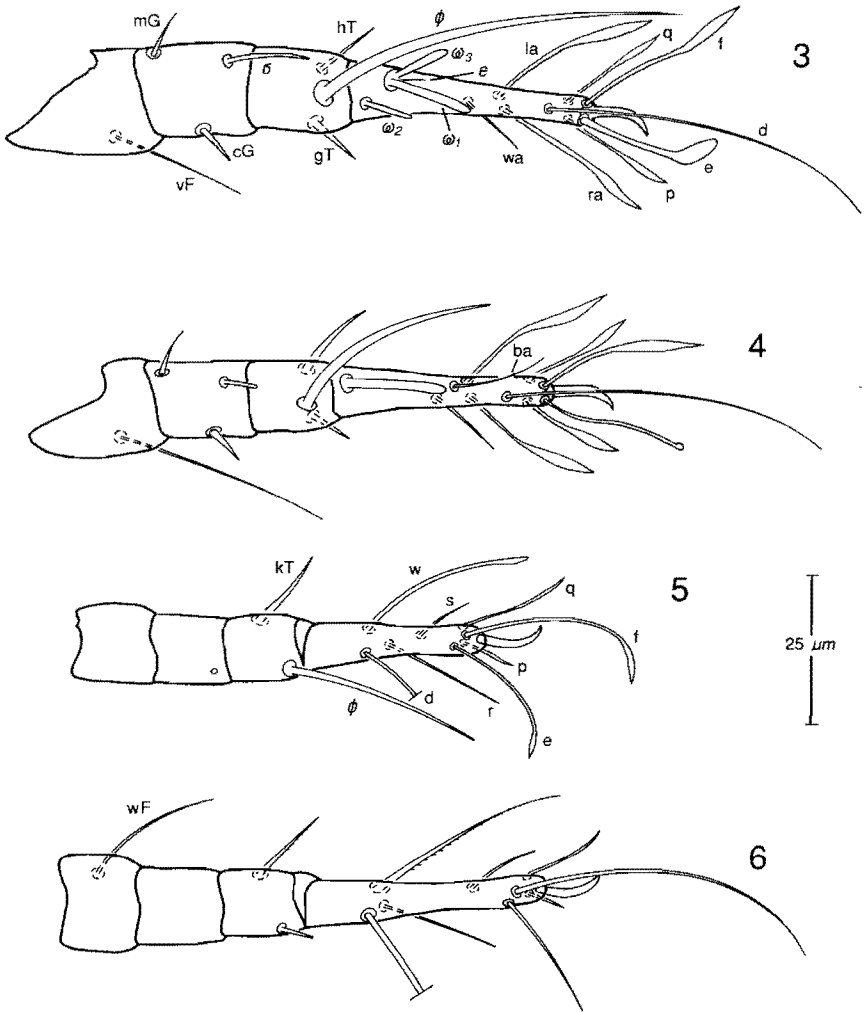
Figures 3–6. *Naiadacarus fashingi* n. sp., deutonymph, legs in dorsal view. 3. Leg I. 4. Leg II. 5. Leg III. 6. Leg IV.

1960, R. & K. Dreisbach (BMOC #89–0113–12) (3 deutonymphs) (this host also harbored 3 deutonymphs representing 2 undescribed species of *Schwiebea*, 1 deutonymph of an undescribed *Bonomoia* species, and 3 deutonymphs of *Dendrolaelaps* sp., family Digamasellidae); Ontonogan Co., 18 June 1960, R. & K. Dreisbach (BMOC #89–0113–13) (19 deutonymphs) (this host also harbored 1 deutonymph of *Dendrolaelaps* sp.); Kalkaska Co., 19 June 1949, R.R. Dreisbach (BMOC #89–0113–14) (1 deutonymph) (this host also harbored 1 deutonymph of an undescribed species of *Schwiebea* and 1 deutonymph of an unidentified rhizoglyphine genus); Schoolcraft Co., 5 July 1947,

R. R. Dreisbach (BMOC #89–0113–15) (1 deutonymph) (this host also harbored 1 deutonymph of an undescribed *Schwiebea* species and 1 deutonymph of *Hormosianoetus mallotae* [Fashing], family Histiostomatidae). Of a total of 15 individuals of this host species in UMMZ, *N. fashingi* was found on 0 of 8 males and 5 of 7 females, giving an infestation rate of 0% on males and 71% on females.

From *Somula decora* Macquart: Saginaw Co., 13 June 1943, R.R. Dreisbach (BMOC #89–0113–44) (2 deutonymphs) (this host also harbored 20 deutonymphs of *Histiogaster arborsignis* Woodring); Cheboygan Co., University of Michigan Biological Station, Indian Trail, 19 June 1985, J.T. Rotenberry (BMOC #89–0113–52) (9 deutonymphs) (this host also harbored 1 deutonymph of *Dendrolaelaps* sp.). Of a total of 31 individuals of this host species in UMMZ, *N. fashingi* was found on 0 of 16 males and 3 of 15 females (including the New York record noted below), giving an infestation rate of 0% on males and 20% on females.

From *Blera analis* (Macquart): Livingston Co., E.S. George Reserve, 31 May 1982, M. & A. O'Brien (BMOC #89–0113–21) (7 deutonymphs). Of a total of 12 individuals of this host species in UMMZ, *N. fashingi* was found on 0 of 7 males and 1 of 5 females, giving an infestation rate of 0% on males and 20% on females.

From *Blera armillata hunteri* (Curran): Keweenaw Co., Isle Royale, 15 July 1938, G. Steyskal (BMOC #89–0113–22) (12 deutonymphs) (this host also harbored 2 deutonymphs of an undescribed *Schwiebea* species and 1 deutonymph of an undescribed species of Histiostomatidae). The infested host was a female. No other specimens of this host species were examined.

From *Blera badia* (Walker): Delta Co., 11 June 1960, R. & K. Dreisbach (BMOC #89–0113–23) (15 deutonymphs) (this host also harbored 1 deutonymph of an undescribed *Bonomoia* species). Of a total of 5 individuals of this host species in UMMZ, *N. fashingi* was found on 0 of 1 males and 1 of 4 females, giving an infestation rate of 0% on males and 25% on females.

From *Blera confusa* Johnson: Keweenaw Co., Isle Royale, 14 July 1938, G. Steyskal (BMOC #89–0113–24) (119 deutonymphs) (this host also harbored 1 deutonymph of an undescribed *Bonomoia* species); Gogebic Co., 15 June 1960, R. & K. Dreisbach (BMOC #89–0113–25) (27 deutonymphs); Chippewa Co., 25 June 1960, R. & K. Dreisbach (BMOC #89–0113–26) (23 deutonymphs) (this host also harbored 5 deutonymphs of an undescribed *Schwiebea* species, 2 deutonymphs of *Histiogaster cyclopis,* 1 deutonymph of an undescribed *Bonomoia* species, and 1 deutonymph of *Dendrolaelaps* sp.). Of a total of 9 individuals of this host species in UMMZ, *N. fashingi* was found on 0 of 4 males and 3 of 5 females, giving an infestation rate of 0% on males and 60% on females.

Two collections comprising 10 paratypes of *N. fashingi* were recovered from non-Michigan hosts as follows: from a female *Blera umbratilis* (Williston); New Jersey, Camden Co., Clementon, 2 May 1902 (BMOC #89–0113–27) (6 deutonymphs). No other specimens of this host species were examined. From a female *Somula decora;* New York, Tompkins Co., Town of Dryden, Ringwood Road, 26 June 1972, G.R. Mullen (BMOC #89–0113–43) (4 deutonymphs) (this host also harbored 4 deutonymphs of *Naiadacarus arboricola*).

Specimen Deposition: Holotype and paratypes in UMMZ; additional paratypes in USNM, CNC, FMNH, OSU, CUIC, BMNH, IRSNB, HNHM, and in the collection of Dr. Norman Fashing, College of William and Mary, Williamsburg.

Diagnosis: Deutonymphs of *Naiadacarus fashingi* differ from those of *N. arboricola* and *N. mydophilus,* new species, in lacking the palpal supracoxal setae on the gnathosomal remnant and having setae *cxIV* in the form of rounded conoids. In the other species, the palpal supracoxal setae are present and setae *cxIV* are generally filiform with expanded bases. Solenidion σ on genu III is variably present in *N. fashingi,* while always present in *N. arboricola* and always absent in *N. mydophilus.* Additionally, *N. fashingi* differs from *N. arboricola* in the form of the dorsal ornamentation (dense punctations in *N. fashingi,* irregular protuberances separated by sinuous grooves in *N. arboricola*), and the distinctly barbed form of setae *kT* of tibia IV and *w* of tarsus IV (unbarbed in *N. arboricola*).

Two characters exhibited marked intraspecific variation in *N. fashingi*. The size and density of punctations on the dorsal sclerites varied considerably. This variation was most noticeable in northern populations, while southern populations were generally invariant, all individuals having small and dense punctations. The presence of solenidion σ of genu III varied within 11 of 16 populations where more than one individual was examined. In the four southernmost populations (Saginaw and Livingston Counties, Michigan, Tompkins County, New York, and Camden County, New Jersey), the solenidion was invariably present. In one population (Delta Co., Michigan), it was invariably absent. Variation in the other populations ranged from 26–84% present. In the variable populations, presence of the solenidion was generally correlated with body size, with larger individuals always having the structure present.

Naiadacarus mydophilus OConnor, **new species**

This species is known only from the deutonymph.

Diagnosis: Deutonymph very similar to *N. fashingi* in body and leg form, sclerotization pattern, dorsal ornamentation and leg setation. Overall measurements averaging generally smaller than *N. fashingi* (see Table 1), body length 177, 187 (170–208), width 134, 140 (128–155). Compared with *N. fashingi, N. mydophilus* retains the palpal supracoxal setae on the gnathosomal subcapitular remnant, these setae having the form of small spines and almost contiguous bases (Fig. 9), the setae of coxal fields IV are filiform rather than rounded conoids (Fig. 12), and solenidion σ of genu III is invariably absent.

Etymology: The name *mydophilus* comes from the Greek *mydos* (= dampness) and *philios* (= lover of).

Material Examined: Holotype and 207 paratype deutonymphs from *Brachypalpus oarus* (Walker), Michigan, Washtenaw Co., Ann Arbor, 3rd Woods, 16 May 1922, T.H. Hubbell (BMOC #89–0113–1).

An additional 171 paratypes from the same host species from the following Michigan localities: Wayne Co., Detroit, 12 May 1907 (BMOC #89–0103–2) (2 deutonymphs) (this host also harbored 25 deutonymphs of an undescribed *Schwiebea* species); Roscommon Co., 22 May 1954, R.R. Dreisbach (BMOC #89–0113–5) (169 deutonymphs). Of a total of 14 individuals of *B. oarus* in UMMZ, *N. mydophilus* was found on 2 of 5 males and 1 of 9 females, giving an infestation rate of 40% on males and 11% on females.

Specimen Deposition: Holotype and paratypes in UMMZ. Other paratypes deposited in institutions listed above for *N. fashingi*.

ECOLOGICAL ASSOCIATIONS OF *NAIADACARUS FASHINGI* AND *N. MYODPHILUS*

Although the non-deutonymphal instars of *N. fashingi* and *N. mydophilus* have not yet been collected, habitat associations of the syrphid flies upon which these species are phoretic may suggest the natural habitat of the mites. Unlike the phoretic hosts of *N. arboricola,* most hosts of *N. fashingi* and *N. mydophilus* are not associated with water-filled treeholes. Larvae of *Brachypalpus oarus,* host to both new species, and those of *Chalcosyrphus* species, the hosts having the highest rates of infestation with *N. fashingi,* live in subcortical spaces and decaying wood (Tesky 1976, Maier 1982). Mite deutonymphs presumably attach to female flies during oviposition, as evidenced by the presence of mites on only females of most host species. The association of *N. mydophilus* deutonymphs with male as well as female *Brachypalpus oarus* correlates with the behavior of this fly species. Males of *B. oarus* defend mating territories around oviposition sites (Maier 1982), where mites presumably attach to flies of either sex landing on the substrate.

Additional evidence for the association of the new species with decaying wood comes
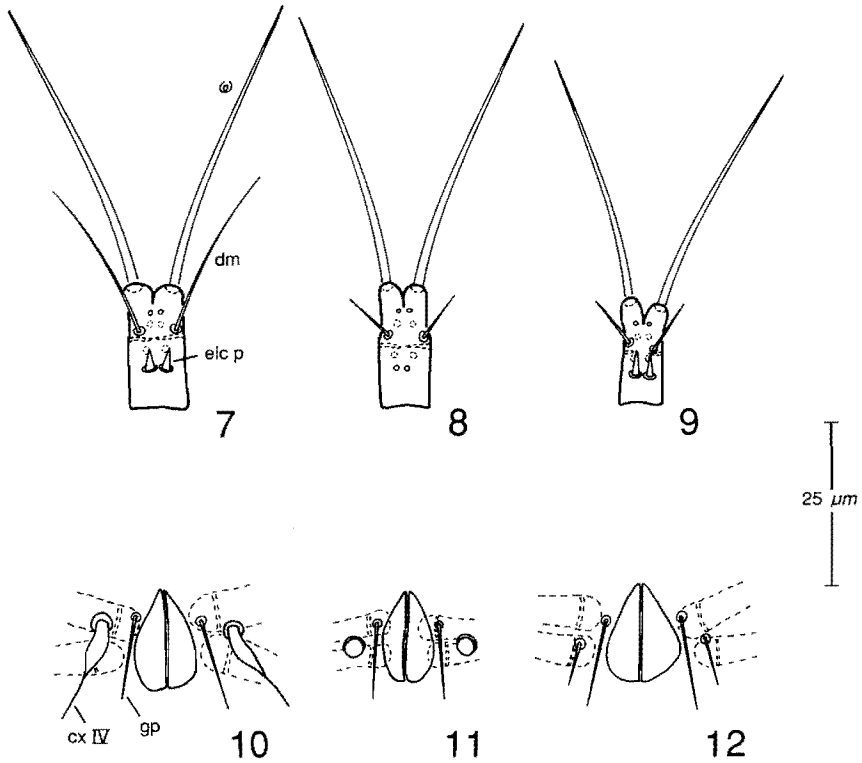
Figures 7–9. Gnathosomas of *Naiadacarus* deutonymphs in dorsal view. 7. *N. arboricola*. 8. *N. fashingi*. 9. *N. mydophilus*.
Figs. 10–12. Genital regions of *Naiadacarus* deutonymphs. 10. *N. arboricola*. 11. *N. fashingi*. 12. *N. mydophilus*.

from the other mite species co-occurring with them on the syrphid hosts. Although most of the co-occurring species remain undescribed, known species in the genera *Schwiebea*, *Histiogaster*, *Bonomoia*, and *Dendrolaelaps* are common inhabitants of decaying woody substrates. In contrast, except for the one collection of both *N. arboricola* and *N. fashingi* from a single individual *Somula decora* (BMOC #89–0113–43), no specimens of species known to inhabit water-filled treeholes (e.g., *Hormosianoetus mallotae*, *Histiostoma* spp.) co-occurred with *N. fashingi* or *N. mydophilus*, although they commonly co-occurred with *N. arboricola*. A number of collections made in subcortical habitats in the Huron Mountains in 1986 and 1987 failed to yield specimens of *Naiadacarus*. However, these collections consisted of relatively dry materials from the upper surfaces of fallen trees and did not contain larval Syrphidae. I suspect that additional collecting in moister substrates such as the lower surfaces of fallen logs or tree falls in bogs or pond margins may yield the actual habitat of the new species.

A second potential habitat for *N. fashingi* suggested by the biological associations of its phoretic hosts is moist treeholes which do not continuously hold water. Species of *Blera* and *Somula* are known to use this habitat type for larval development (Tesky 1976, Ferrar 1987). The collection of both *Naiadacarus fashingi* and *N. arboricola* deutonymphs from

a single female of *Somula decora* is evidence that that individual fly had visited the habitats of both mite species. Maier (1982) reported the co-occurrence of larvae of *Mallota posticata* and *Somula decora* in a single treehole, which suggests that *S. decora* females will visit wet treeholes. On the other hand, while observers have noted the habitat of larval *Somula decora* as "moist detritus in treeholes" (Maier 1982) and "decaying pocket in tulip tree" (Tesky 1976, citing Greene 1917), the larval habitat of *Mallota* species is cited by the same authors as "wet." This suggests that the normal breeding habitat of *S. decora,* and thus potentially *N. fashingi,* is not completely aquatic.

SYSTEMATIC POSITION OF THE GENUS *NAIADACARUS*

In describing the genus *Naiadacarus,* Fashing (1974) proposed the subfamily Naiada-carinae to accomodate only the new genus. Following prior revisions of the Acaridae (Zakhvatkin 1941, Nesbitt 1945, Krantz 1960), Fashing recognized two other subfamilial groupings in the family, Acarinae and Rhizoglyphinae. He indicated that *Naiadacarus* was more closely related to the Rhizoglyphinae than to the Acarinae. The paraphyly of the subfamily Acarinae in the sense of the above mentioned authors is apparent from the plesiomorphic character states used to diagnose the group (graphically demonstrated in the dendrogram of generic relationships in Nesbitt [1945]). The monophyly of the Rhizo-glyphinae, apparent from Nesbitt's (1945) dendrogram, was reiterated by Lombert et al. (1982) in their study of the early derivative genus *Cosmoglyphus.* It is clear from the character states mentioned by Fashing (1974) and others as well, that *Naiadacarus* shares a common ancestry with the Rhizoglyphinae. However, in order to retain the subfamilial name Naiadacarinae in a completely phylogenetic classification, it would be necessary to demonstrate that *Naiadacarus* is the sister-group of the remaining Rhizoglyphinae. A number of character states suggest that this is not the case and that *Naiadacarus* shares a more recent common ancestry with certain genera within the Rhizoglyphinae than with the group as a whole.

Fashing (1974) mentioned 4 character systems of the adult mites (not all unit characters) shared among *Naiadacarus* and the Rhizoglyphinae: "well-defined sexual dimorphism, reduction in the number of idiosomal setae, smooth dorsal setae which are swollen at the base, and similar tarsal setation." I will duscuss these character systems in order.

Sexual dimorphism takes many forms in acarid genera and is "well-defined" in many taxa, not all belonging to the Rhizoglyphinae. Two modifications of male *Naiadacarus* are apparent. The presence of a large sclerite on the posterior opisthosoma of males is shared among *Naiadacarus* and several genera of Rhizoglyphinae: *Schwiebea, Histio-gaster* and *Thyreophagus* (including *Michaelopus*). This sclerotization is not present in more basal rhizoglyphines such as *Cosmoglyphus, Sancassania* (including *Caloglyphus*) and *Rhizoglyphus.* It is interesting to note that this sclerotization is present also in females of *N. oregonensis,* but not *N. arboricola.* I regard the presence of the male sclerotization as potentially synapomorphic for *Naiadacarus, Schwiebea, Histiogaster* and *Thyreoph-agus.*

Relative enlargement of leg III in males is a common phenomenon in the Rhizoglyph-inae although the homology of the condition in *Naiadacarus* with that in rhizoglyphines is uncertain. If *Cosmoglyphus* is considered as the basal clade in the Rhizoglyphinae (Nesbitt 1945, Lombert et al. 1982), then the male polymorphism involving leg III (Woodring 1969) may ancestrally characterize the subfamily. However, such polymor-phism, documented in *Cosmoglyphus, Sancassania, Rhizoglyphus, Schwiebea, Histio-gaster,* and *Thyreophagus,* has not been reported in other rhizoglyphine genera such as *Acotyledon, Neoacotyledon, Neotropacarus,* and *Bromeliaglyphus,* where only homeo-morph males are known. The situation in *Naiadacarus* is unique in that while leg III is slightly enlarged in males of both known species, the empodial claw of pretarsus III is slightly enlarged and apparently fused to the end of the tarsus only in *N. oregonensis.* This condition recalls but is certainly not the same as the "heteromorphic" condition found in

Cosmoglyphus and the other genera noted above. In the "heteromorphic" condition in rhizoglyphine males, leg III is extremely thickened, the tarsus is very much foreshortened, has a reduced setation and a very large empodial claw. These legs are used to kill rival males by impaling them from above (Woodring 1969, personal observations). *Naiadacarus* legs III do not show these other modifications, and there is no evidence that they are used for fighting. It seems possible that such a system of male combat might not be functional in the aquatic environment in which these *Naiadacarus* species live. The density of the medium might inhibit the force of the thrust of the modified legs, rendering them useless as weapons. In such an environment, a reversal to a more ancestral condition (i.e. loss of the "heteromorphic" male morph) might be selectively favored.

Naiadacarus exhibits a strong reduction in dorsal setation in the non-deutonymphal instars, having only 2 pairs of propodosomal setae (*vi* and *sce*) and 7 pairs of dorsal hysterosomal setae (h,l_2,d_3,l_3,d_4,d_5 and l_5). A similar pattern is found in *Schwiebea, Histiogaster,* and *Thyreophagus.* Other rhizoglyphine genera generally retain the complete ancestral complement of 4 propodosomal pairs and 12 hysterosomal pairs. Fashing (1974) noted the smooth form of the setae in *Naiadacarus* as similar to that in the Rhizoglyphinae. This condition is a potential apomorphy for the entire Rhizoglyphinae as most non-rhizoglyphine acarid taxa have barbed or pectinate dorsal setae.

The final character system mentioned by Fashing (1974) involves the leg setation. The leg setation of *Cosmoglyphus* is similar to the presumed ancestral acarid condition, suggesting that the modifications seen in *Naiadacarus* and other rhizoglyphine genera evolved within the subfamily. Specifically, *Naiadacarus* shares the loss of seta *aa* on tarsus I with *Rhizoglyphus, Schwiebea, Histiogaster,* and *Thyreophagus* among others, while *Cosmoglyphus, Sancassania, Acotyledon* and others retain the seta. In the same group of genera which has lost *aa,* tarsal setae *ba* I–II are modified in form and position, being spine-like and positioned more basally, adjacent to solenidion ω_1, or absent. *Cosmoglyphus, Sancassania,* and *Acotyledon* retain the ancestral thin form and more apical position of these setae.

Two characters of the deutonymphs of *Naiadacarus,* not mentioned by Fashing (1974), show a similar pattern of distribution among taxa. Deutonymphs of *Naiadacarus, Schwiebea, Histiogaster, Thyreophagus,* and some additional genera whose adults are unknown, share the loss of the external vertical setae (*ve*). These setae are retained in deutonymphs of *Rhizoglyphus, Sancassania* and *Cosmoglyphus* among others. *Naiadacarus* deutonymphs and adults lack seta *nG* on genu III. This seta is lacking in all deutonymphs of *Schwiebea* and *Thyreophagus* which I have examined, although it is present in some described *Schwiebea* adults and all stages in most species in the other rhizoglyphine genera.

The simplest conclusion from these data is that *Naiadacarus* shares a common ancestor with the genera *Schwiebea, Thyreophagus* and *Histiogaster.* This clade is characterized by the presence of a posterior opisthosomal sclerite in the male, the loss of 7 homologous pairs of dorsal setae in the adults and the loss of the external vertical setae in the deutonymph. This clade in turn is related to *Rhizoglyphus,* sharing the loss of tarsal seta *aa* I and the modification of setae *ba* I–II in the non-deutonymphal instars. *Sancassania* and *Cosmoglyphus* represent even more basal rhizoglyphine lineages. The exact position of *Naiadacarus* with respect to *Schwiebea, Thyreophagus* and *Histiogaster* must await further revisionary work with these and other genera.

HISTORICAL ECOLOGY OF *NAIADACARUS*

The genus *Naiadacarus* is unusual among the more derived rhizoglyphine genera in that phoretic associations are restricted to a single lineage of host insects, the subfamily Melesiinae of the family Syrphidae. Phoretic deutonymphs of *Naiadacarus fashingi* have been collected from 8 species of syrphid flies: *Brachypalpus oarus, Chalcosyrphus vecors, Somula decora* and five species of *Blera.* These fly species belong to the closely related tribes Xylotini (*Brachypalpus, Chalcosyrphus*) and Melesiini (*Somula,Blera*)

(*sensu* Hippa 1978). *Naiadacarus arboricola* is associated with 3 species of the tribe Eristalini (*Mallota bautias, M. posticata* and *Eristalis bardus*) and one species of Melesiini (*Somula decora*), although the low incidence on the latter two species may indicate only accidental associations. *Naiadacarus mydophilus* is known only from associations with *Brachypalpus oarus*, and phoretic associations of *N. oregonensis* remain unknown. This pattern of association might suggest a historical (cospeciational) association between *Naiadacarus* and a lineage of Syrphidae within the subfamily Milesiinae. However, two observations suggest otherwise. First, *Naiadacarus* is known only from the Nearctic region, while the host groups are widely distributed. Second, while the associations between *Naiadacarus* species and most of the host species reported above certainly represent more than accidental occurrences (i.e., infestation rates up to 60%), species closely related to known hosts have not been verified as hosts. Xylotini occurring in the Great Lakes region which I examined without finding *Naiadacarus* included 62 specimens representing 5 species of *Chalcosyrphus* other than *C. vecors,* 178 individuals of 8 species of *Xylota* and 2 individuals of *Brachypalpoides.* No species of Melesiini outside the genera *Blera* and *Somula* yielded *Naiadacarus.* It should be noted that based upon collection data from UMMZ specimens, the flight period for most of these species in Michigan corresponds to the known dispersal period of *Naiadacarus* species, eliminating different phenology as a potential reason why these species do not carry the mites. Thus, a cospeciational hypothesis involving long term historical association between *Naiadacarus* species and their syrphid hosts would require a great deal of extinction to explain the present distribution of hosts. Similarly, the utilization of the same host species by two species of *Naiadacarus* (i.e., *Brachypalpus oarus* by *N. fashingi* and *N. mydophilus,* and *Somula decora* by *N. fashingi* and *N. arboricola*) is not compatible with a purely cospeciational historical hypothesis.

A more likely explanation for the association between *Naiadacarus* species and their dispersers lies in the nature of the ecological association between the mites and flies and their microhabitat preferences. *Naiadacarus arboricola* is active only in water-filled treeholes (Fashing 1975, 1976, 1979), the larval habitat of *Mallota* species (Fashing 1975, Tesky 1976, Maier 1982). Fashing (1976) pointed out that the dispersal period of *N. arboricola* corresponds exactly with the breeding season of *Mallota* species (May–June, although some specimens in UMMZ were collected through mid-July), perhaps suggesting some adaptation by the mites to the phenology of their phoretic hosts. Collection dates for available *S. decora* suggest a flight period similar to that of *Mallota* species, May through June, although one specimen was collected as late as 4 August. The larval habitat of *Eristalis bardus* has not been described although some species of *Eristalis* are known to use tree holes as larval habitats (Tesky 1976). (The collection of treehole associated mites besides *N. arboricola* (i.e. *Hormoisianoetus mallotae, Histiostoma* spp.) from this host species strengthens the hypothesis that it breeds in wet treeholes.) Similarly, although the exact microhabitat preferences of *N. fashingi* and *N. mydophilus* are not known with certainty, the known phoretic hosts are associated with decaying wood and moist tree holes. The timing of dispersal in these species is similar to that for *N. arboricola.*

It is interesting to note that most of the phoretic hosts of *Naiadacarus* species are mimics of Hymenoptera. Species of *Blera* and *Brachypalpus* mimic dark colored colletid and anthophorid bees; *Mallota* species and *Eristalis bardus* are *Bombus* mimics; *Chalcosyrphus vecors* resembles certain black and red patterned Ichneumonidae, Sphecidae and Pompilidae, while *Somula decora* is a vespid mimic. Like many mimetic Syrphidae, these species have flight seasons generally restricted to spring and early summer, a period before the appearance of naive bird predators (Waldbauer and Sheldon 1971, Waldbauer and LaBerge 1985). Thus, the correlation between the dispersal period of *N. arboricola* and the flight period of *Mallota* species noted by Fashing (1975) may be a more general phenomenon involving all *Naiadacarus* species and their phoretic hosts and may, in fact, be an ancestral characteristic for the genus.

The phylogenetic position of *Naiadacarus* proposed above is well correlated with this historico-ecological scenario. Species in the related genera *Schwiebea, Histiogaster* and

Thyreophagus live in decaying wood and peripheral habitats such as fungal fruiting bodies (some *Schwiebea* also live in the soil). Species in these genera show little preference for phoretic hosts, using many groups of Coleoptera, Diptera, Hymenoptera and Myriapoda. If the ancestor of *Naiadacarus* adapted to relatively wet decaying wood, the potential diversity of phoretic hosts would have been substantially reduced. At this point, the association with Syrphidae may have become fixed.

ACKNOWLEDGMENTS

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