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Radfordia (Microtimyobia) (Acari, Myobiidae) Associated with Arvicoline Voles (Rodentia, Muridae) in Japan

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ABSTRACT—*Radfordia (Microtimyobia)* mites infesting arvicoline voles in Japan comprise three new subspecies of *Radfordia (M.) lemnina* (Koch, 1841). These new subspecies are defined on the basis of the form of the male genitalia, the shape of the anterior gnathosomal setae, and the chaetotaxy of the female tritonymph. *Radfordia (M.) lemnina hata* ssp. n. is a parasite of *Microtus montebelli* (Milne-Edwards, 1872). *Radfordia (M.) lemnina mikado* ssp. n. infests only *Clethrionomys rutilus mikado* Thomas, 1905 in Hokkaido, and it differs from *Radfordia (M.) lemnina rutila* Fain and Lukoschus, 1977 parasitizing *Clethrionomys rutilus* (Pallas, 1979) in Europe. *Radfordia (M.) lemnina japonica* ssp. n. is found widely on the other *Clethrionomys* and *Eothenomys* voles in Japan. Among these host voles, *Clethrionomys rufocanus bedfordiae* Thomas, 1905 is designated as the type host of this new subspecies. Immature stages of the three new subspecies are described and illustrated. *Radfordia* mites parasitic on *Eothenomys* voles in Taiwan and Japan are much more different from each other than would be expected on the basis of the current systematics of the Arvicolinae proposed by Japanese mammalogists.

INTRODUCTION

Ono (1969) first carried out studies on Myobiidae parasitic on Japanese voles and recorded *Radfordia lemnina* (Koch, 1841) as the only myobiid of Arvicolinae (=Microtinae) (Uchikawa, 1977). Fain and Lukoschus (1977) summarized the 10 subgenera and 19 species and subspecies of the genus *Radfordia* Ewing, 1938 and tabulated the hosts and localities for the thus far known 69 taxa of 10 subgenera including the subgenus *Microtimyobia* Fain and Lukoschus, 1976 associated exclusively with Arvicolinae. The morphology of *R. (M.) lemnina*, which they designated as the type species of the subgenus, was redescribed; then, the nominate and three other subspecies within *R. (M.) lemnina* were characterized (Fain and Lukoschus, 1977). The idiosomal outline and chaetotaxy of the females are almost the same in all four subspecies; Fain and Lukoschus (Fain and Lukoschus, 1977) used these characters to define the species and other features for the subspecies.

Fain and Lukoschus (Fain and Lukoschus, 1977) also examined myobiids found on *Microtus montebelli* (Milne-Edwards, 1872) from Fukuoka, Japan, and *Clethrionomys rufocanus bedfordiae* Thomas, 1905 from Hokkaido, Japan, and identified the forms from both hosts with *Radfordia lemnina lemnina* (Koch, 1841). No detailed study on *Radfordia* asso-

ciated with Japanese Arvicolinae has been made subsequently, although some differences dependent on host-species have been noticed. Meanwhile, material on which to base a discussion of the systematics of Japanese arvicoline-infesting myobiids has been accumulating. In the present study we compare Japanese specimens with European and Taiwanese species, using the type specimens or those taken from respective type hosts. As a result, all the putative subspecies of *R. (M.) lemnina* distributed in Japan are proven to be distinct as described below.

SUBGENUS *Microtimyobia* FAIN AND LUKOSCHUS, 1976

In the family Myobiidae, only the genera *Myobia* von Heyden, 1826 and *Radfordia*, both associated with Rodentia, bear a three-segmented leg I that lacks a claw. The claw formula of legs II–IV is 2-1-1 in *Radfordia*, and 1-1-1 in *Myobia*.

In *Radfordia*, the subgenus *Microtimyobia* is defined as follows (Fain and Lukoschus, 1976, 1977): coxal setae 3-2-0-0; setae *vi* not very long; setae *ve* thick and striated; one long and unstriated dorsal seta each on trochanters III and IV; anterior gnathosomal setae flat or membranous, especially in females; associated mainly with Arvicolinae.

It is significant from a coevolutionary point of view that this combination of remarkable characters is found only in the mites infesting an allied host group, the Arvicolinae.

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Radfordia (Microtimyobia) lemnina (Koch, 1841)

AND ITS SUBSPECIES

Fain and Lukoschus (1977) redefined *R. (M.) lemnina* as follows, using measurements taken from the specimens parasitic on *Microtus agrestis* (Linnaeus, 1761), the type host:

Female: Body (idiosoma + gnathosoma) 1.6–1.92 times as long as wide; setae *vi* 5–9 μ m wide; *sc i* slightly thicker than *sc e*; *l*₁ subequal in width to *d*₁, *d*₂, and *l*₂; *l*₃ about 1.5 times as long as *d*₃; coxal setae *cx l*₁ short and less than 3 μ m in width; *ic*₂ long; *ic*₃ (75–100 μ m long) as long as *ic*₂.

Male: Genital orifice on a level slightly posterior to *vi*, but distinctly anterior to the level of leg III; penis 110 μ m long; *sc i* thin and short (30 μ m long); *d*₄ and *l*₄ not very short (33 and 24 μ m long, respectively); *cx l*₁ short; *ic*₂ long; *ic*₃ and *ic*₄ short.

The nominate subspecies and three others, *R. (M.) lemnina clethrionomys* Fain and Lukoschus, 1977, *R. (M.) lemnina rutila* Fain and Lukoschus, 1977, and *R. (M.) lemnina micromys* Fain and Lukoschus, 1976, have been described.

Although *M. agrestis* from Holland was designated as the type host, *R. (M.) lemnina lemnina* reportedly occurs on *M. agrestis* and the other 8 species of *Microtus* voles from Europe, China, Japan, Russia, and Alaska, as well as on *Clethrionomys rufocanus* (Sundevall, 1846) from Sweden, *Clethrionomys rufocanus bedfordiae* from Hokkaido, and *Clethrionomys gapperi* (Vigors, 1830) from the USA (Fain and Lukoschus, 1977).

Radfordia (M.) lemnina clethrionomys differs from the nominate subspecies in the female having some dorsal setae (*vi*, *sc i*, *sc e*, *l*₁, *d*₂, *l*₂, *d*₃, and *l*₃) shorter than those of the latter and elongate membranous gnathosomal setae, and in the male's genital cone abruptly widening anteriorly (Figs. 14–15, cf. Fig. 9) (Fain and Lukoschus, 1977). We add here the thick male genital setae to the above subspecific characters (Figs. 14 and 15). This subspecies occurs on *Clethrionomys glareolus* (Schreber, 1780) in Belgium (type locality), Italy, and Holland (Fain and Lukoschus, 1977).

Radfordia (M.) lemnina rutila is separable from the above two subspecies principally by the male's genital cone that bears prominent, triangular, lateral projections anteriorly (Fig. 12) and the female's elongate and bifurcate membranous gnathosomal seta (Fain and Lukoschus, 1977). The type host is *Clethrionomys rutilus* (Pallas, 1779) from N. Sweden (Fain and Lukoschus, 1977).

Fain and Lukoschus (Fain and Lukoschus, 1977) relegated *R. (M.) micromys* Fain and Lukoschus, 1976, taken from *Micromys minutus* (Pallas, 1771) from Holland, to a subspecies of *R. (M.) lemnina*. The original description was based only on the female, which bears setae *vi* different in form from those of *R. (M.) lemnina*. Moreover, *Micromys* is exceptional as the host in that it belongs not to the Arvicolinae but to the Murinae. Therefore, it is necessary to reevaluate the systematic position of this subspecies, using specimens of both sexes.

As noted above, *R. (M.) lemnina* has been divided into subspecies based on the shape of the idiosomal and gnathosomal setae of the female and the form of the male genitalia. Uchikawa (1991), on the other hand, proposed a

subspecies of *Myobia kobayashii* Uchikawa and Mizushima, 1975 parasitic on Taiwanese *Apodemus draco* (Barrett-Hamilton, 1900) on the basis of the setation of nymphal stages. Thus, it would be good to compare immature stages as well, to understand subtle differences at the subspecies level, although immature stages have usually been ignored in descriptions of *Radfordia* species and subspecies.

DESCRIPTION

Radfordia (Microtimyobia) lemnina hata ssp. n.

Radfordia (Microtimyobia) lemnina lemnina (Koch, 1841)–Fain and Lukoschus, 1977: 63.

Types: Ex *Microtus montebelli* (Milne-Edwards, 1872). Holotype female, allotype male, 1 female (F) and 2 male (M) paratypes, Okada, Matsumoto City, Nagano Prefecture, 1983. IV. 14; 28 paratypes (9 female tritonymphs, TN(F), 7 male tritonymphs, TN(M), 5 deutonymphs, DN, 5 protonymphs, PN, and 2 larvae, L), Kirigamine, Suwa City, Nagano Pref., 1983. VI. 3.

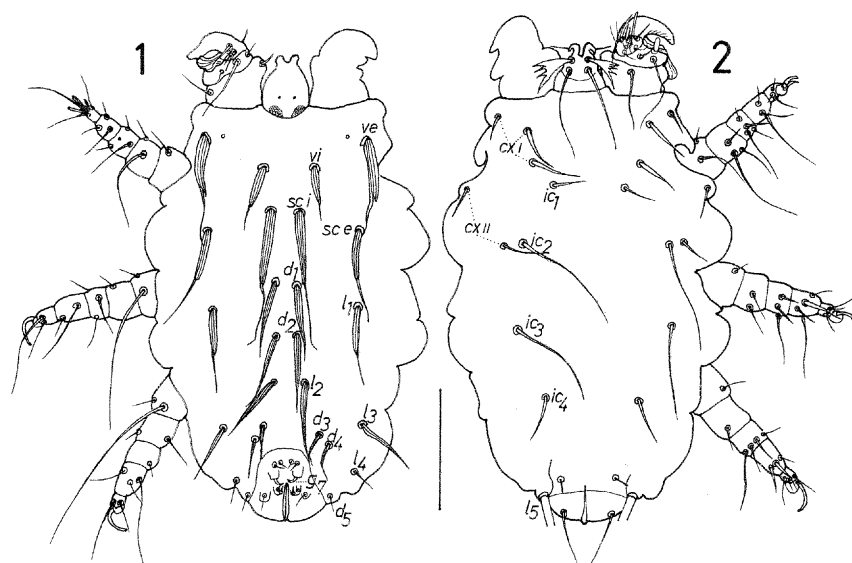
The holotype, allotype, and 5 paratypes (TN(F, M), DN, PN, and L) are deposited in National Science Museum (Tokyo) (registration nos. NSMT-Ac 10701–10707); 7 paratypes (TN(F, M), 2DN, 2PN, and L) in A. Fain's collection, Brussels; and 17 paratypes (M, 12TN(7F, 5M), 2DN, and 2PN) in K. Uchikawa's collection, Matsumoto.

Female (Figs. 1–2, 4): Outline of body (idiosoma + gnathosoma) rather stout, with length/width ratios 1.55–1.93. Idiosomal chaetotaxy as in Figs. 1 (dorsum) and 2 (venter); dorsal setae anterior to *l*₃ long and well striated basally; ventral setae *ic*₂ and *ic*₃ long; *cx l*_{1–2} thickened and longer than *ic*₁. Measurements as in Table 1. Legs and leg chaetotaxy as in Figs. 1 and 2. Anterior membranous gnathosomal seta apically split into 4 points (Fig. 4).

Male (Figs. 7–8, 10): Dorsal setation of idiosoma as in Fig. 7, quite different on hysterosoma from that of female; *d*₁ minute and on genital cone, *d*₂ lacking; *l*₂ and *d*₃ not paired, and each on median line; *l*₃ and *d*₅ lacking. Ventral setation as in female, but only *ic*₂ long and *ic*₃ short (Fig. 8). Legs as in female. Genital opening at level slightly posterior to bases of *vi*; penis slides on genital cone extending anteriorly beyond basal level of *vi*; genital cone wide, with shoulders, and bearing pair of thin genital setae and *d*₁ (Fig. 10). Penis straight. Measurements as in Table 1; setae *ve*, *sc i*, and *l*₁ possibly slightly longer than those of the nominate subspecies. Anterior gnathosomal seta narrow and terminating in 2 points (Fig. 4).

Immature stages (Figs. 17–20, 22): Consisting of larva, protonymph, deutonymph, and tritonymph. Body size variable according to developmental phase within each stage (Table 1), but ontogenetic changes discernible in idiosomal chaetotaxy and development of legs II–IV.

Idiosomal chaetotaxy: Four pairs of propodosomal setae (*vi*, *ve*, *sc i*, and *sc e*) present in all immature stages, and pair of hysterosomal setae added at each stage; accordingly, hysterosomal setae in four stages from larva to tritonymph



Figs. 1–2. Female of *Radfordia* (*Microtimyobia*) *lemnina hata* ssp. n.
(1) Dorsal view. (2) Ventral view. Bar: 100 μ m.

Table 1. Measurements in micrometers of *R. (M.) lemnina hata* ssp. n. and *R. (M.) lemnina lemnina*

Subspecies	<i>R. (M.) lemnina hata</i>							<i>R. (M.) lemnina lemnina</i>		
Stage	Female (F)	Male (M)	TN (F)	TN (M)	DN	PN	L	Female (F)	Male (M)	TN (F)
n	12	6	6	5	5	5	3	3	2	1
Body length (L)	355–435	295–335	305–380	255–400	200–320	178–205	135–213	360–460 (465)	310–330 (336)	410
Body width (W)	205–240	155–195	220–270	195–260	152–215	145–168	108–163	220–230 (270)	180–190 (215)	225
L/W ratio	1.55–1.93	1.61–1.90	1.35–1.52	1.31–1.52	1.24–1.49	1.10–1.41	1.25–1.31	1.64–2.0 (1.72)	1.72–1.74 (1.5)	1.61
vi (L)	50–70	18–20	35–45	30–37	23–28	14–16	8–10	58–65 (60)	?–20 (18)	33
(W)	6–8	2.5–2.5	NM	NM	NM	NM	NM	7–8 (6)	2.5–3 (1.5)	NM
ve (L)	85–107	92–100	50–65	40–53	33–37	19–21	10–12	100–105 (NR)	?–80 (NR)	40
(W)	9–12	8–10	NM	NM	NM	NM	NM	12–15 (NR)	?–8 (NR)	NM
sc i	110–132	37–48	55–70	43–45	31–38	20–25	12–15	110–115 (115)	?–32 (30)	43
sc e	68–88	85–105	90–105	68–75	51–65	25–31	13–15	75–83 (75)	85–88 (100)	80
l ₁	58–88	105–125	112–125	72–85	51–72	27–32	13–14	73–80 (72)	98–100 (NR)	115
d ₁	55–75	minute	43–60	28–34	25–28	15–18	12–15	55–65 (60)	minute	38
d ₂	53–78	–	45–65	28–35	22–26	14–16	10–13	65–70 (60)	–	37
l ₂	65–73	52–70	45–60	25–32	23–27	15–17	12–14	68–75 (66)	58–65 (57)	35
d ₃	24–30	60–65	48–60	23–36	20–29	12–15	13–16	27–30 (30)	60–65 (60)	52
d ₄	25–33	26–33	55–70	30–37	22–43	17–22	lacking	28–33 (NR)	30–34 (33)	60
d ₅	10–18	–	5–8	5–7	5–6	lacking	lacking	10–17 (NR)	–	10
l ₃	45–60	–	65–75	30–40	28–40	15–20	13–16	48–50 (48)	–	65
l ₄	15–18	16–28	13–27	8–15	lacking	lacking	lacking	13–18 (NR)	25–25 (21)	43
ic ₂	88–95	80–90	65–75	57–68	40–60	30–35	lacking	90–102 (95)	?–92 (80)	70
ic ₃	80–90	15–20	21–45	9–11	6–9	5–7	lacking	80–105 (90)	17–18 (20)	75
ic ₄	25–32	28–35	10–11	3–6	4–5	lacking	lacking	32–35 (30)	30–35 (30)	8
g7	8–10	–	–	–	–	–	–	8–10 (8)	–	–
penis	–	125–133	–	–	–	–	–	–	128–130 (115)	–

TN, DN, PN, and L are nymphs and larva, respectively. NM: Not measured.

Figures in parentheses were given by Fain and Lukoschus (1977). NR: Not recorded.

numbering 6 (d_4 , d_5 , and l_4 lacking), 7 (d_5 and l_4 lacking), 8 (l_4 lacking), and 9 pairs (as in adult female), respectively (Figs. 17–20). Nature of all setae of larva different from that of more advanced stages (Fig. 17); each seta gaining in length in accordance with progress of stages (Table 1). Ventral setae also variable in number according to stage; intercoxal setae (ic series) from larva to tritonymph 1-0-0, 1-1-1-0, 1-1-1-1, and 1-1-1-1, respectively, with ic_2 being long in nymphal stages;

coxal setae (cx series) 0-0-0, 1-0-0-0, 1-0-0-0, and 2-1-0-0, respectively, with anterolateral cx I being shell-like in form (Figs. 21–24, right). Sexual dimorphism apparent only in tritonymph; intercoxal setae ic_3 long, often with bilateral asymmetry, in female tritonymph (Fig. 14), but these setae short in male tritonymph (Table 1). Many dorsal setae of idiosoma distinctly longer in female tritonymph than in male tritonymph (Table 1).

Legs II-IV: Fully developed leg of immature stages with four free segments (trochanter, femuro-genu, tibia, and tarsus) and single, strong terminal claw. Larva bearing complete legs II and primodia of legs III; protonymph with complete legs II and small, 3-segmented and sparsely setose legs III lacking terminal claws; deutonymph with complete legs II, 4-segmented legs III with no claws, and primodia of legs IV; and tritonymph having complete legs II and III, and 4-segmented legs IV without claws.

Notes: The immature stages of no *Radfordia* (*Microtimyobia*) species have been studied until now, so their specific characters can not yet be adduced. In the present study, a single female tritonymph of *R. (M.) lemnina lemnina* and all the immature stages of the other three subspecies were available. Among these specimens, the setae *ve*, *sc i*, *sc e*, *d*₁, *d*₂, and *l*₂ seem to be longer, while setae *l*₄ and *ic*₃ are shorter, in the female tritonymph of *R. (M.) lemnina hata* than in that of *R. (M.) lemnina lemnina* (Table 1). The relatively long setae *d*₁, *d*₂, and *l*₂, the relatively short *l*₄, and the very short *ic*₃ are characteristic of this stage of *R. (M.) lemnina hata*. As for other stages, the setae *sc e* of the protonymph of *R. (M.) lemnina hata* are probably shorter than those of the other subspecies (Tables 1–4).

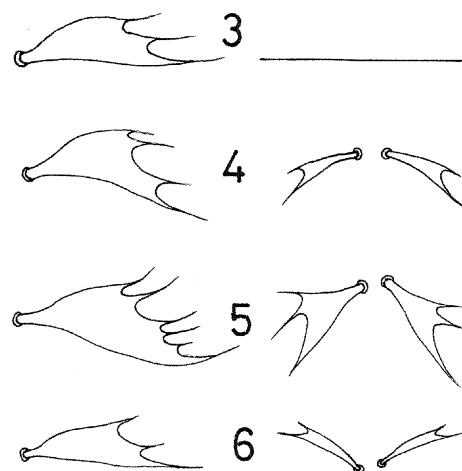
Material examined: In addition to the types, the specimens listed below were taken from *Microtus montebelli* (type host): 2F and 1M, Kirigamine, Suwa City, Nagano Pref., 1983. VI. 6; 3F, 1TN(F), 1PN, and 2L, Tokusawa, Azumi Village, Nagano Pref., 1989. VII. 27; 1F, Kamikochi, Azumi Village, Nagano Pref., 1972. VIII. 4; 2F, Hakuba Village, Nagano Pref., 1971. VII; 1F, 2M, 4TN(F), 2TN(M), and 2DN, Gero Town, Gifu Pref., 1955. II. 26; 2F, 1M, and 1TN (M), Abiko, Chiba Pref., 1995; 1F, Fukuoka Pref., 1981. VII. 14; 1M, Fukuoka Pref., 1972. VII. 1, identified as *R. (M.) lemnina lemnina* by Fain (Fig. 10, left).

Comparative material:

Radfordia (Microtimyobia) lemnina lemnina ex *Microtus agrestis* (type host): 1F, 1M, and 1TN(F), Heer Agimont, Belgium, 1967. IX; 2F, Hatert, Holland, 1968. X. 22 and 1972. IX. 5, respectively; 1F, Hamert, Holland, 1972. VII. 9; 1M, Switzerland, ? date.

R. (M.) lemnina lemnina ex *Clethrionomys glareolus*: 1M, Carreglefn, Anglesey, N. Wales, 1980. VII. 22 (host record to be reconfirmed).

Differential diagnosis: It is very difficult to discriminate the females of *R. (M.) lemnina* spp. from one another (Fain and Lukoschus, 1977). The shape of the anterior membranous gnathosomal setae sometimes differs among subspecies. The setae of *R. (M.) lemnina hata* ssp. n. are apically split into four or more points (Fig. 4), and they differ in shape from those of the female of the nominate subspecies, which bear three points (Fig. 3). However, the membranous setae are variable in form among individuals and, sometimes, even bilaterally on a single specimen. Moreover, the exact shape of these setae is usually difficult to observe. Accordingly, it is difficult to separate subspecies from each other based on



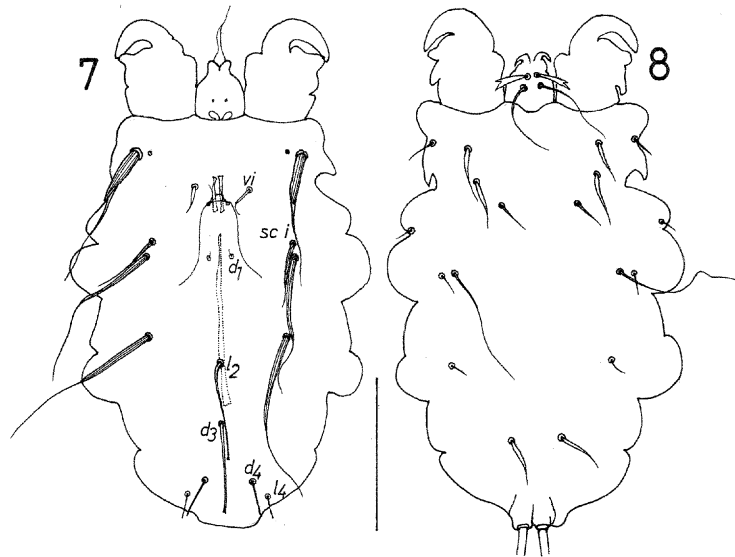
Figs. 3–6. Anterior gnathosomal setae of female (left) and male (right). (3) *Radfordia (Microtimyobia) lemnina lemnina*. (4) *R. (M.) lemnina hata* ssp. n. (5) *R. (M.) lemnina japonica* ssp. n. (6) *R. (M.) lemnina mikado* ssp. n. Bar: 50 μ m.

subtle differences in these setae alone.

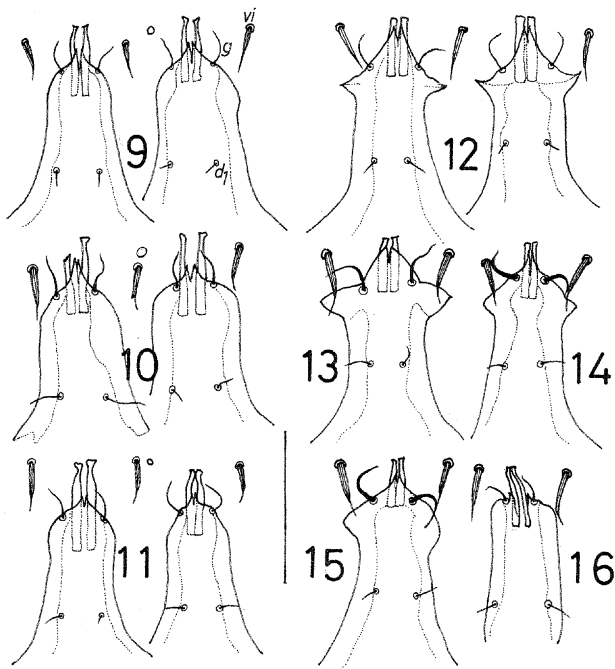
The structure of the male genital region is a more useful character than the gnathosomal setae for differentiating subspecies of *R. (M.) lemnina*. The male genital regions of European specimens parasitic on *M. agrestis* and the Japanese specimen from *M. montebelli* that was identified as *R. (M.) lemnina lemnina* by Fain are shown in Figs. 9 and 10 (left), respectively. It is difficult to find any distinct difference, although the genital setae are slightly longer on the Japanese specimen. Accordingly, Fain and Lukoschus (Fain and Lukoschus, 1977) had good reason to relegate the *Radfordia* mite parasitic on *M. montebelli* to *R. (M.) lemnina lemnina*. However, all the male specimens examined in the present study, exclusive of Fain's specimen, bear a genital cone as drawn in Fig. 10 (right), anteriorly broad and with shoulders and with genital setae longer than those of the nominate subspecies. No other distinctive characters and measurements that warrant subspecies rank have been found in the male.

In the female tritonymph the third intercoxal setae, *ic*₃, are unusually short in all the specimens taken from *M. montebelli* (Fig. 22, Table 1), compared with those of the nominate subspecies (Fig. 21). With this character, *R. (M.) lemnina hata* is clearly defined, which confirms that the above subtle differences in the male genital region are significant for separating subspecies of *R. (M.) lemnina*. Further, some dorsal setae of the idiosoma (*ve*, *sc i*, *sc e*, *d*₁, *d*₂, and *l*₂) are possibly longer in the female tritonymph of *R. (M.) lemnina hata* than in that of the nominate subspecies, and *vice versa* for the setae *l*₄ (Figs. 21 and 22, Table 1).

Remarks: As shown above, some immature stages bear more obvious specific or subspecific characters than the adult stage does. In the subgenus *Microtimyobia*, all the systematic studies so far have been based on the morphology of the adult stage, ignoring immature stages. More attention should be paid to the latter, which are usually more abundant on any



Figs. 7–8. Male of *Radfordia* (*Microtimyobia*) *lemnina hata* ssp. n. (7) Idiosomal dorsum. (8) Idiosomal venter. Bar: 100 μ m.



Figs. 9–16. Male genital regions. (9) *Radfordia* (*Microtimyobia*) *lemnina lemnina*. (10) *R. (M.) lemnina hata* ssp. n. (11) *R. (M.) lemnina japonica* ssp. n. (12) *R. (M.) lemnina rutila*. (13) *R. (M.) lemnina mikado* ssp. n. (14–15) *R. (M.) lemnina clethrionomys*. (16) *R. (M.) eothenomys*. Bar: 50 μ m.

host animal than adults.

Etymology: The subspecies name, *hata*, is a noun in apposition. In Japanese it means cultivated field, one of the preferred habitats for *M. montebelli* (Japanese name, *hata-nezumi*).

***Radfordia* (*Microtimyobia*) *lemnina japonica* ssp. n.**

Radfordia (*Microtimyobia*) *lemnina lemnina* (Koch, 1841)-Fain and Lukoschus, 1977: 63.

Types: Ex *Clethrionomys rufocanus bedfordiae*. Holotype F, allotype M, 48 paratypes (6 each of F, M, TN(F), TN(M with long setae), TN(M with short setae), DN, PN, and L), Tonden, near Sapporo, Hokkaido, 1983. IX. 28–29.

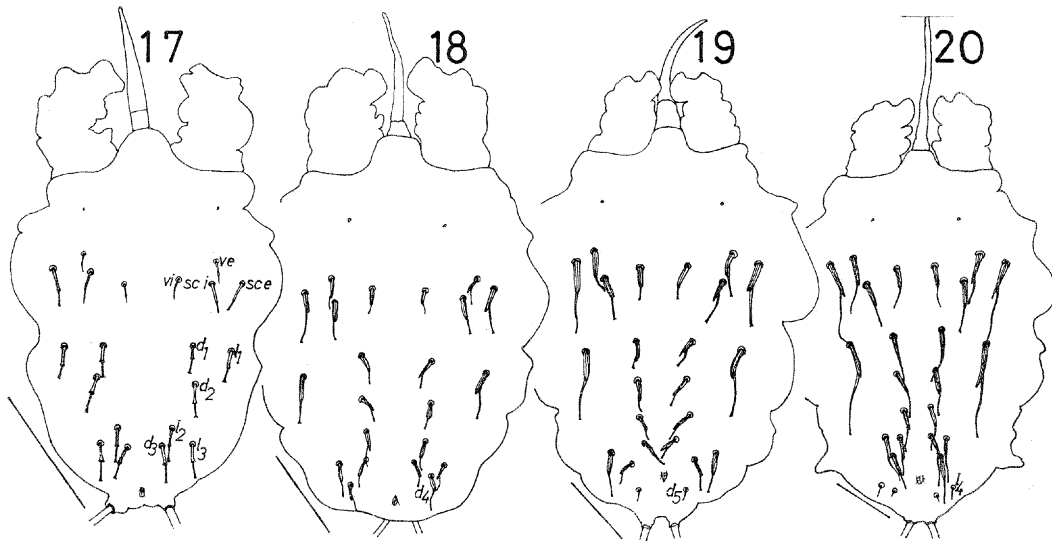
The holotype, allotype, and 8 paratypes (TN(F), 1 of each form of TN(M), DN, 2PN, and 2L) are deposited in National Science Museum (Tokyo) (registration nos. NSMT-Ac 10708–10713); 10 paratypes (F, M, TN(F), 1 of each form of TN(M), DN, 2PN, and 2L) in A. Fain's collection, Brussels; and 30 paratypes (5F, 5M, 4TN(F), 4 of each form of TN(M), 4DN, 2PN, and 2L) in K. Uchikawa's collection, Matsumoto.

Female (Fig. 5): General shape essentially as in preceding and nominate subspecies (cf. Figs. 1 and 2). Measurements as in Table 2. Idiosomal setae *sc i* slightly shorter than those of preceding subspecies, but ranges of setal length of both forms overlapping. Anterior gnathosomal setae relatively large, and split apically into numerous points (Fig. 5).

Male (Figs. 5 and 11): General shape as in preceding subspecies (cf. Figs. 7 and 8). Measurements as in Table 2. Setae *l2* and *ic4* longer than those of preceding subspecies. Genital region as in Fig. 11; genital cone narrow and situated posteriad of basal level of setae *vi*, penis slides not extending anteriorly beyond basal line of these setae. Anterior gnathosomal setae wide and split apically into at least 3 points (Fig. 5).

Immature stages: Formation and setation of idiosoma, gnathosoma, and legs as in *R. (M.) lemnina hata*. Characteristic properties discernible in each developmental stage other than larva when compared with corresponding stage of *R. (M.) lemnina hata*.

Female tritonymph (Fig. 23): Dorsal setae *sc i*, *d1*, *d2*, and



Figs. 17–20. Idiosomal dorsum of immature stages of *Radfordia (Microtimyobia) lemnina hata* ssp. n. (17) Larva. (18) Protonymph. (19) Deutonymph. (20) Male tritonymph. Bar: 50 μ m.

l_2 shorter than those of *R. (M.) lemnina hata*, and *vice versa* for l_4 and ic_3 ; ic_3 distinctly thicker than ic_2 and extraordinary long (100–150 μ m) (Tables 1 and 2).

Male tritonymph: Lengths of idiosomal setae showing vast variation. When examined under the microscope, setae l_1 , d_4 , l_3 , and l_4 apparently shorter on some specimens than others as if different kinds of male tritonymphs were mixed. Of 35 specimens examined, 12 possessing short setae, other 23 bearing long setae. Measurements of the two groups, TN (M, a) and TN (M, b), presented separately in Table 2. Among those with long setae, l_1 , d_4 , l_3 , l_4 , and ic_2 distinctly longer than those of male tritonymph of preceding subspecies.

Deutonymph: Idiosomal setae d_1 , l_2 , and d_4 slightly shorter, but ic_2 longer, than those of *R. (M.) lemnina hata* (Tables 1 and 2).

Protonymph: Idiosomal setae d_4 shorter, but ic_2 longer, than those of *R. (M.) lemnina hata* (Tables 1 and 2).

Larva: As in *R. (M.) lemnina hata* (Tables 1 and 2).

Material examined: In addition to the types, many specimens were taken from arvicoline voles in Japan.

Ex *Clethrionomys rufocanus bedfordiae* (type host): 50F, 15M, 24TN(F), 23TN(M), 61DN, 18PN, and 3L, Tonden, near Sapporo, Hokkaido, 1983. IX. 28–29; 1M (identified as *R. (M.) lemnina lemnina* by Fain), Nopporo, Hokkaido, 1956. V. 30.

Ex *Clethrionomys rex* Imaizumi, 1971: 9F, 2M, 2TN(M), Kitakawaguchi, Teshio Town, Teshio-Gun, Hokkaido, 1989. X. 12–13.

Ex *Eothenomys andersoni* (Thomas, 1905): 1F, 1M, and 3TN(F), Takehara, Yamabe Town, Higashimurayama-Gun, Yamagata Pref., 1982. V–VI; 1F, Donko-Numa, Zaoh, Yamagata Pref., 1965. VII. 24; 1F, Mt. Iwaki, near Hirosaki City, Aomori Pref., 1978. VI. 27; 1F, and 1TN(F), Ohdate, Hakkoda Mts., Akita Pref., 1978. VII. 14; 13F, Tago, Nagano City, Nagano Pref., 1975. I. 14; 7F, 1M, 1TN(F), 1YN(M), 1DN,

and 1PN, Mt. Iizuna, near Nagano City, Nagano Pref., 1975. VIII. 11F, and 7M, Asakawa, Nagano City, Nagano Pref., 1975. I. 11; 1M, Asahi-Yama, Nagano City, Nagano Pref., 1975. I. 13; 3F and 1M, Happa-One, Hakuba Village, Nagano Pref., 1972. X. 29; 4F, 10M, and 2TN(F), Kamikochi, Azumi Village, Nagano Pref., 1988. V. 21.

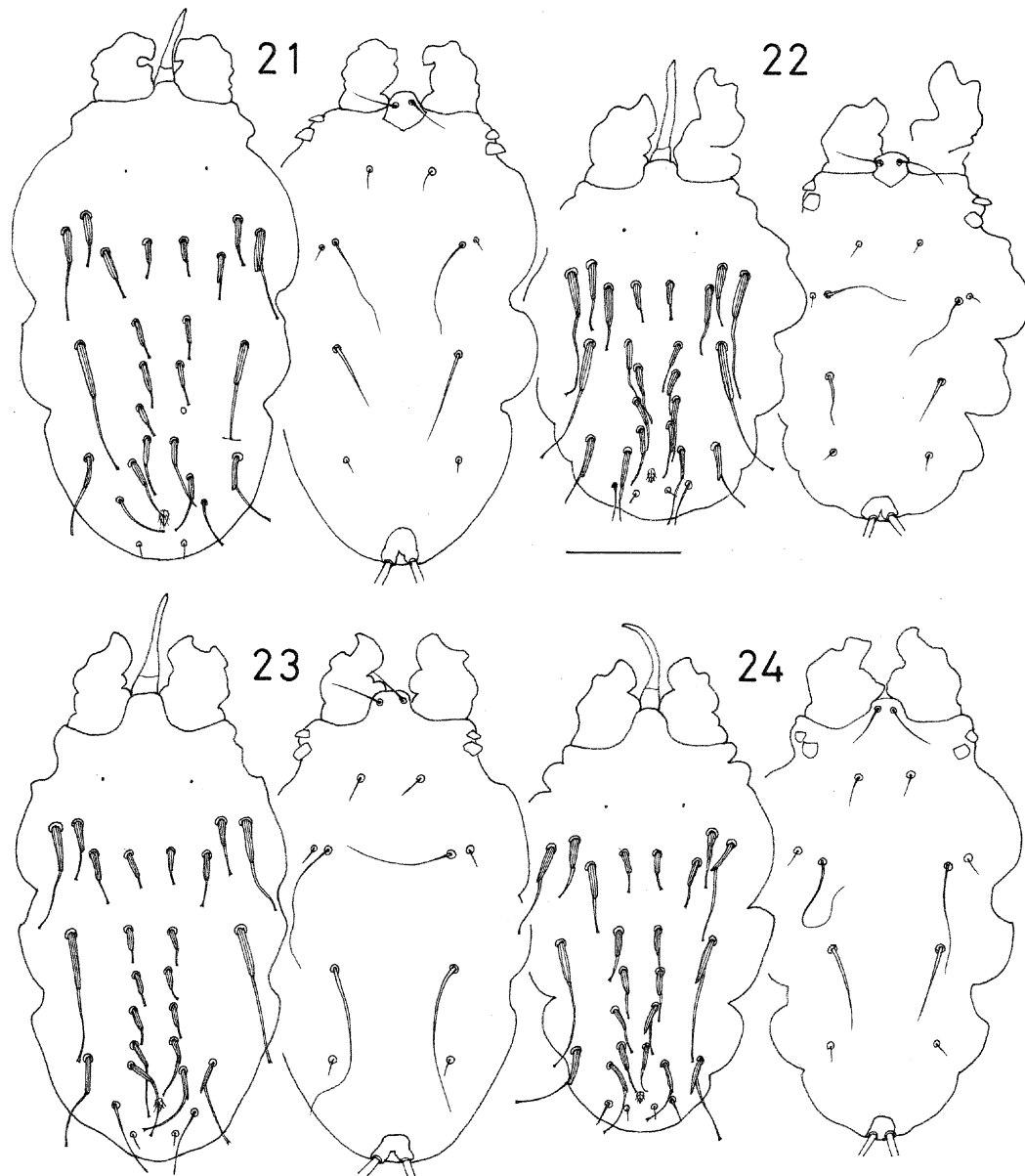
Ex *Eothenomys smithii* (Thomas, 1905): 2F, 2M, 9TN(F), 3TN(M), 7DN, and 1PN, Tashirohara, Kunimi-Cho, Shimabara City, Nagasaki Pref., 1995. IV. 12; 4M, 4TN(F), 1DN, Ohsaka Pass, Hikita Town, Kagawa Pref., 1958. XI. 25; 1M, Sai-ko (Lake), Yamanashi Pref., 1969. VII. 3; 2F, Ohtaga, Asuke Town, Aichi Pref., 1982. XII. 22; 1F, Iwakami, Asuke Town, Aichi Pref., 1983. II. 24; 2F, Goshomitsu, Inabu Town, Aichi Pref., 1983. III. 10.

Comparative material:

Radfordia (Microtimyobia) lemnina clethrionomys ex Clethrionomys glareolus: 1 M, Utrecht, Holland, 1975. VI. 25; 1M, Hamert, Holland, 1972. VII. 4; 1F, Pescasseroli, Holland, 1972. X. 16; 1F, Nijmegen, Holland, 1966. V. 2.

R. (M.) eothenomys Fain and Lukoschus, 1976 ex *Eothenomys* sp.: holotype F and allotype M, Chuei-feng, Taiwan (specimens of the National Museum of Natural History, Washington, deposited in the USDA, Beltsville).

Differential diagnosis: The female of *R. (M.) lemnina japonica* ssp. n. bears anterior gnathosomal setae that are larger and have more apical points than those of the nominate and preceding subspecies. However, this alone is not definitive, since the shape of these setae is variable, as noted above. The male gnathosomal setae are wide and split into 3 points, distinctly different from those of the subspecies *R. (M.) lemnina lemnina* and *R. (M.) lemnina hata*, both of which bear narrow, bifurcate setae (Fig. 5, cf. Fig. 4). The male genital cone is situated relatively more posteriad than those of these



Figs. 21–24. Idiosomal dorsum (left) and venter (right) of the female tritonymphs at the same scale. (21) *Radfordia* (*Microtimyobia*) *lemnina lemnina*. (22) *R. (M.) lemnina hata* ssp. n. (specimen with the longest ic_3). (23) *R. (M.) lemnina japonica* ssp. n. (24) *R. (M.) lemnina mikado* ssp. n. Bar: 100 μ m.

two subspecies, and the cone itself is narrow anteriorly. In some subspecies, as mentioned below, the anterior part of the genital cone is expanded laterally, which is a modification opposed to that of *R. (M.) lemnina japonica*. Accordingly, the position and form of the genital cone, together with the shape of the anterior gnathosomal setae, confirm that the male of *R. (M.) lemnina japonica* is distinct, although Fain and Lukoschus (Fain and Lukoschus, 1977) once identified it with the nominate subspecies.

In comparison to *R. (M.) lemnina hata*, the female tritonymph of *R. (M.) lemnina japonica* bears intercoxal setae ic_3 that are long enough to warrant recognizing the form as distinct. Measurements of some other dorsal setae (sci , d_2 , l_2 ,

and l_4) might also be useful to characterize the female tritonymph of the present new subspecies.

Remarks: *Radfordia* specimens found on *Clethrionomys rex*, *Eothenomys andersoni*, and *Eothenomys smithii* from various localities were all identified with *R. (M.) lemnina japonica* (Table 3). There are disturbing differences in the lengths of some setae on specimens of different origin (Table 3); however, it is reasonable to regard all such differences as intrasubspecific variation. With respect to this subspecies' wide host range, it is interesting to note that European *Clethrionomys rufocanus* is currently recorded as a host of *R. (M.) lemnina lemnina*, and that Taiwanese *Eothenomys* sp. is the host of *R. (M.) eothenomys* Fain and Lukoschus, 1976,

Table 2. Measurements in micrometers of *R. (M.) lemnina japonica* ssp. n. taken from *C. rufocanus bedfordiae*

Stage	Female (F)	Male (M)	TN (F)	TN (M, a)	TN (M, b)	DN	PN	L
n	5	5	10	5	5	10	5	5
Body length (L)	350–425	305–330	320–410	320–375	290–410	245–300	195–235	150–205
Body width (W)	195–230	155–195	215–270	175–250	210–310	175–210	145–170	108–145
L/W ratio	1.63–1.92	1.63–1.97	1.40–1.57	1.03–1.56	1.32–1.50	1.26–1.53	1.22–1.42	1.33–1.42
<i>vi</i> (L)	55–60	13–18	30–37	27–28	31–35	20–24	15–18	8–10
(W)	6–7	2–3	NM	NM	NM	NM	NM	NM
<i>ve</i> (L)	90–103	85–100	45–55	40–44	48–49	28–38	20–23	10–12
(W)	11–12	10–12	NM	NM	NM	NM	NM	NM
<i>sc i</i>	98–110	32–38	42–54	34–42	41–55	26–35	20–23	11–13
<i>sc e</i>	70–80	94–100	73–102	62–70	70–85	40–58	28–32	13–15
<i>l</i> ₁	70–75	98–115	104–130	55–83	100–125	47–63	24–27	13–15
<i>d</i> ₁	48–60	minute	28–35	23–28	29–35	19–22	15–17	13–13
<i>d</i> ₂	58–65	–	26–38	23–28	27–38	18–22	13–15	11–14
<i>l</i> ₂	63–65	70–85	31–41	23–27	33–38	17–20	13–16	11–14
<i>d</i> ₃	28–35	64–73	42–58	22–28	33–55	15–20	13–16	13–14
<i>d</i> ₄	30–35	20–30	60–80	22–30	65–73	18–27	13–14	lacking
<i>d</i> ₅	10–15	–	7–10	5–10	8–9	5–7	lacking	lacking
<i>l</i> ₃	40–48	–	68–82	28–33	68–80	20–35	16–17	13–15
<i>l</i> ₄	16–20	21–25	45–63	13–23	48–60	lacking	lacking	lacking
<i>ic</i> ₂	83–90	85–105	68–90	58–78	75–88	60–70	60–70	lacking
<i>ic</i> ₃	78–93	15–23	105–155	5–7	7–10	4–7	5–7	lacking
<i>ic</i> ₄	28–35	43–48	5–10	6–8	6–9	4–7	lacking	lacking
<i>g7</i>	9–12	–	–	–	–	–	–	–
penis	–	130–150	–	–	–	–	–	–

Abbreviations as in Table 1. TN(M, a and b): Male tritonymphs with short (a) and long (b) dorsal setae.

Table 3. Measurements in micrometers of adults and female tritonymphs of *R. (M.) lemnina japonica* ssp. n. from diverse host voles from various localities

Stage	Female					Male					Female tritonymph		
Host species	<i>C. rex</i>		<i>E. andersoni</i>		<i>E. smithii</i>	<i>C. rex</i>		<i>E. andersoni</i>		<i>E. smithii</i>	<i>E. andersoni</i>	<i>E. smithii</i>	
Locality	Hokkaido	Japan Alps	Nagano City	Nachi	Unzen	Hokkaido	Japan Alps	Nagano City	Nachi	Unzen	Nachi	Unzen	
n	5	7	5	5	2	5	10	5	5	5	8	8	
Body length (L)	360–380	390–510	325–385	365–490	370–385	320–340	330–440	275–330	320–375	315–320	275–475	245–350	
Body width (W)	220–225	235–280	205–225	220–265	220–225	190–195	200–235	175–210	195–215	175–220	220–325	185–265	
L/W ratio	1.64–1.69	1.59–1.83	1.56–1.71	1.66–1.85	1.64–1.75	1.68–1.74	1.62–1.91	1.51–1.69	1.56–1.80	1.50–1.80	1.25–1.49	1.23–1.41	
<i>vi</i> (L)	58–65	57–70	60–70	62–67	57–63	15–18	16–20	15–18	16–19	15–17	33–38	27–35	
(W)	6–7	5–7	6–7	6–6	5–6	2–3	2–2.5	2–3	2–2	2–3	NM	NM	
<i>ve</i> (L)	95–105	93–105	90–95	85–110	90–95	92–105	82–95	85–90	83–90	80–95	47–52	44–55	
(W)	12–13	12–13	11–12	12–13	12–12	10–10	10–11	10–12	10–12	9–10	NM	NM	
<i>sc i</i>	97–105	103–125	105–118	105–120	95–97	32–35	34–45	45–46	30–38	30–38	53–63	42–55	
<i>sc e</i>	70–81	72–82	70–80	70–80	65–80	100–?	92–105	87–105	83–95	100–110	90–100	87–108	
<i>l</i> ₁	68–78	63–78	62–72	70–85	65–65	98–108	90–105	83–108	85–105	105–110	102–125	108–118	
<i>d</i> ₁	51–58	53–58	48–58	50–58	45–53	minute	minute	minute	minute	minute	30–37	25–28	
<i>d</i> ₂	57–63	55–63	55–67	53–58	55–60	–	–	–	–	–	30–37	25–30	
<i>l</i> ₂	62–73	62–68	55–62	58–65	63–65	72–73	60–72	63–70	60–68	58–70	32–40	25–31	
<i>d</i> ₃	28–33	28–35	30–33	25–30	28–32	75–80	58–70	62–68	53–67	62–75	45–65	40–56	
<i>d</i> ₄	28–31	30–33	25–30	25–30	33–42	27–32	25–33	20–30	22–28	24–30	65–80	45–78	
<i>d</i> ₅	13–16	10–15	10–15	7–11	12–14	–	–	–	–	–	5–8	8–13	
<i>l</i> ₃	45–50	42–55	40–53	35–43	42–42	–	–	–	–	–	75–83	60–90	
<i>l</i> ₄	15–18	17–22	13–15	12–15	15–15	22–33	20–28	18–23	20–28	23–28	38–62	30–43	
<i>ic</i> ₂	90–95	95–100	85–93	85–95	83–85	100–?	83–98	90–95	85–95	85–100	70–78	73–88	
<i>ic</i> ₃	90–95	93–95	80–90	85–88	80–85	17–18	17–23	15–18	15–20	15–20	110–140	105–118	
<i>ic</i> ₄	30–34	30–35	28–33	30–33	30–31	30–33	33–43	33–40	35–42	27–45	7–16	10–14	
<i>g7</i>	10–11	8–10	9–10	9–12	9–10	–	–	–	–	–	–	–	
penis	–	–	–	–	–	140–145	133–145	120–134	132–148	135–145	–	–	

which is different from *R. (M.) lemnina* at the species-level (Fig. 16). The problem of host relationships of *R. (M.) lemnina* ssp. and its allies is discussed further below.

Etymology: The subspecies name, *japonica*, is adopted to indicate that the mite is distributed throughout Japan in the range of arvicoline voles.

***Radfordia (Microtomyobia) lemnina mikado* ssp. n.**

Types: Ex *Clethrionomys rutilus mikado* Thomas, 1905. Holotype F, allotype M, 41 paratypes (6 F, 6M, 6TN(F), 6TN(M), 6DN, 6PN, and 5L), Tonden, near Sapporo, Hokkaido, 1983. IX. 28–29.

The holotype, allotype, and 7 paratypes (TN(F), TN(M),

Table 4. Measurements in micrometers of *R. (M.) lemnina mikado* ssp. n. parasitic on *C. rutilus mikado*

Stage	Female(F)	Male(M)	TN(F)	TN(M)	DN	PN	L
n	10 (1)	10 (2)	10	10	10	5	3
Body length (L)	325–405 (410)	305–335 (320–330)	260–400	260–400	240–325	220–270	192–215
Body width (W)	200–220 (230)	180–200 (175–190)	210–245	200–245	175–225	158–200	140–150
L/W ratio	1.55–1.85 (1.78)	1.61–1.81 (1.68–1.89)	1.13–1.66	1.30–1.70	1.30–1.60	1.26–1.52	1.28–1.43
<i>vi</i> (L)	55–65 (55)	20–24 (17–22)	35–40	28–33	24–25	15–18	9–10
(W)	6–7 (7)	2.5–3 (2.5–2.5)	NM	NM	NM	NM	NM
<i>ve</i> (L)	85–105 (98)	73–95 (?–80)	50–63	40–48	30–38	20–23	13–14
(W)	11–13 (12)	10–12 (10–10)	NM	NM	NM	NM	NM
<i>sc i</i>	105–115 (110)	27–35 (30–30)	52–58	40–50	30–42	22–25	13–14
<i>sc e</i>	68–82 (75)	80–105 (90–?)	85–115	68–80	48–63	32–35	15–16
<i>l</i> ₁	65–83 (75)	93–120 (90–93)	100–123	80–105	48–73	31–35	13–14
<i>d</i> ₁	53–65 (55)	minute	35–43	28–35	20–28	15–18	12–13
<i>d</i> ₂	55–68 (63)	–	36–45	28–33	20–25	14–15	12–15
<i>l</i> ₂	60–73 (63)	57–80 (63)	33–46	25–30	20–23	13–16	12–13
<i>d</i> ₃	28–35 (26)	55–73 (?–65)	33–60	23–30	18–23	14–15	12–13
<i>d</i> ₄	26–36 (30)	26–43 (27–35)	55–73	31–42	23–35	16–32	lacking
<i>d</i> ₅	8–15 (10)	–	5–9	4–10	4–8	lacking	lacking
<i>l</i> ₃	43–54 (43)	–	57–85	34–43	23–35	18–18	13–14
<i>l</i> ₄	10–18 (16)	20–36 (23–32)	15–28	8–14	lacking	lacking	lacking
<i>ic</i> ₂	80–90 (90)	80–90 (80–85)	68–85	58–80	55–70	35–50	lacking
<i>ic</i> ₃	85–95 (85)	13–20 (17–18)	63–90	8–12	7–13	4–8	lacking
<i>ic</i> ₄	25–38 (35–40)	35–43 (35–40)	7–23	4–8	4–9	lacking	lacking
<i>g7</i>	8–10 (7)	–	–	–	–	–	–
penis	–	128–143 (133–140)	–	–	–	–	–

Abbreviations as in Table 1. Data in parentheses are those for *R. (M.) lemnina rutila*.

DN, 2PN, and 2L) are deposited in National Science Museum (Tokyo) (registration nos. 10714–10718); 9 paratypes (F, M, TN(F), TN(M), DN, 2PN, and 2L) in A. Fain's collection, Brussels; and 25 paratypes (5F, 5M, 4TN(F), 4TN(M), 4DN, 2PN, and 1L) in K. Uchikawa's collection, Matsumoto.

Female (Fig. 6): General shape essentially as in *R. (M.) lemnina hata* (cf. Figs. 1 and 2). Measurements as in Table 4. Anterior gnathosomal setae rather small and split apically into at least 3 points (Fig. 6).

Male (Figs. 6 and 13): General shape essentially as in *R. (M.) lemnina hata* (cf. Figs. 1 and 2). Measurements as in Table 4. Genital region as in Fig. 13; genital opening at level of bases of *vi*; genital cone with wide lateral projections anteriorly (Fig. 13); genital setae thick and conspicuous. Anterior gnathosomal setae narrow and bifurcate (Fig. 6).

Immature stages: General structure and setation similar to those of corresponding stages of *R. (M.) lemnina hata*. Measurements as in Table 4.

Female tritonymph: Ventral setae *ic*₃ 63–90 µm long, probably as long as those of nominate subspecies; *l*₄ distinctly shorter than those of *R. (M.) lemnina japonica* (Tables 1, 2, and 4).

Male tritonymph: Lengths of setae on idiosomal dorsum not so variable as to separate individuals into groups, and ranging between those of short and long setae of male tritonymphs of *R. (M.) lemnina japonica* (Table 4).

Deuto- and protonymphs and larva: Similar to those of *R. (M.) lemnina hata*.

Material examined: In addition to the types, the following

specimens were taken from *Clethrionomys rutilus mikado* (type host): 25F, 17M, 49TN(F), 39TN(M), 54DN, and 18PN, Tonden, near Sapporo, Hokkaido, 1983. IX. 28–29.

Comparative material:

Radfordia (Microtimyobia) lemnina rutila ex *Clethrionomys rutilus*: 2 paratypes (F and M) and 1M, Bjoerkliden, N Sweden, 1966. VIII. 11 (specimens in A. Fain's collection).

Differential diagnosis: The female of *R. (M.) lemnina rutila* bears anterior gnathosomal setae that are elongate and bifurcate (Fain and Lukoschus, 1977). In *R. (M.) lemnina mikado* ssp. n., the setae are split apically into at least 3 points (Fig. 6). However, as already noted, it is difficult to separate females at the subspecies level based on this character alone.

In the male of the present new subspecies, the anterolateral expansions of the genital cone are broad and triangular and the genital setae are thick (Fig. 13), compared with those of *R. (M.) lemnina rutila* (Fig. 12). In both features *R. (M.) lemnina mikado* is intermediate between *R. (M.) lemnina rutila* and *R. (M.) lemnina clethrionomys* (Figs. 14 and 15). This level of difference in the genital region is thought to be enough to separate subspecies, as was noted for each of the preceding two new subspecies.

Some of the immature stages might be expected to have characters that corroborate the validity of the new subspecies. In the female tritonymph, *R. (M.) lemnina mikado* is easily separable from the other Japanese subspecies, *R. (M.) lemnina hata* and *R. (M.) lemnina japonica*, by the remarkable difference in the length of *ic*₃, but not from *R. (M.) lemnina*

lemnina, which probably bears setae ic_3 of a similar length. However, setae *ve* and *sc e* are longer, and I_4 is distinctly shorter, in *R. (M.) lemnina mikado* than in *R. (M.) lemnina lemnina*. The female tritonymph of *R. (M.) lemnina mikado* is thus separable from those of the nominate and two other Japanese subspecies. However, as suggested above by the shape of the genital cone, *R. (M.) lemnina mikado* might be more allied to *R. (M.) lemnina rutila* and *R. (M.) lemnina clethrionomys* than to the three subspecies just mentioned. The immature stages of the European subspecies have not been described yet, and are not available for comparison.

Etymology: The subspecies name, *mikado*, a noun in apposition, comes directly from the name of the host vole, *C. rutilus mikado*.

DISCUSSION

Immature stages:

Because *Radfordia* and *Myobia* mites share *Mus musculus* as their host, studies of immature stages of these two genera have been made repeatedly (summarized by Paran, 1995). However, the developmental stages of these two genera have often not been properly separated. Although some authors have shown only proto- and deutonymphs as the nymphal stages of *Radfordia* and *Myobia*, three nymphal stages are characteristic of the family Myobiidae.

Some immature stages have features that distinguish subspecies within the genera *Radfordia (Microtomyobia)*, as shown above, and *Myobia* (Uchikawa, 1991). Moreover, each larval or nymphal stage may also exhibit genus-level characters, although the definitions of genera have been made on the adult stage. The ontogenetic changes in legs II–IV described above for three Japanese subspecies of *Radfordia (Microtomyobia) lemnina* are similar to those of *Radfordia (Radfordia) affinis* (Poppe, 1896) (Matuzaki, 1961; Paran, 1995), *R. (R.) ensifera* (Poppe, 1896) (Matuzaki, 1964), and *R. (R.) daltoni* Scheperboer, Fain and Lukoschus (1987), but differ distinctly from those of *Myobia musculi* (Schrank, 1781) (Grant, 1942; Matsuzaki, 1961; Matuzaki, 1970), *M. agraria* Gorissen and Lukoschus (1982), *M. apodemi* Uchikawa (1973), *M. nodae* Matuzaki, 1965 (Matuzaki, 1965; Uchikawa *et al.*, 1988), and *M. kobayashii* spp. Uchikawa, 1991; Uchikawa *et al.*, 1988). Legs IV are incomplete even in the tritonymph of *Radfordia* species, while legs of *Myobia* species become well developed in earlier immature stages. This is probably a genus-level ontogenetic character.

On the other hand, the dorsal chaetotaxy of the idiosoma of immature stages of *Radfordia (Microtomyobia)* represented by the above three Japanese subspecies is different from those of *Radfordia (Radfordia)* (Matuzaki, 1964; Paran, 1995; Scheperboer *et al.*, 1987), and *Myobia* (Matuzaki, 1961, 1964; Paran, 1995; Uchikawa, 1991; Uchikawa *et al.*, 1988). In *Radfordia (Radfordia)*, the setae *sc e* are extraordinarily long, and many nymphal hysterosomal setae have a bulbar expansion (cf. Figs. 18–20) (Matuzaki, 1964; Paran, 1995; Scheperboer *et al.*, 1987). The number of hysterosomal se-

tae seems to be different in *Radfordia (Radfordia)* and *Radfordia (Microtomyobia)* (Matuzaki, 1964; Paran, 1995; Scheperboer *et al.*, 1987). The deuto- and tritonymphs of *Myobia* bear only 7 pairs of hysterosomal setae (Paran, 1995; Uchikawa, 1991; Uchikawa *et al.*, 1988) instead of 8 and 9 pairs, respectively, in these nymphal stages of *Radfordia (Microtomyobia)*. The one (d_6) or respectively two (d_5 and I_4) missing pairs of setae of *Myobia* are only discernible as small circles or dots. Accordingly, the difference in the immature dorsal chaetotaxy may be subgenus-level as well as genus-level, but this requires confirmation based on more material.

The ventral setae of the *cx* series vary in number among the subgenera of *Radfordia* (Fain and Lukoschus, 1977). The ontogenetic development of the *cx* series of *Radfordia (Microtomyobia)*, which advances more rapidly than in *Myobia* species (Paran, 1995; Uchikawa, 1991; Uchikawa *et al.*, 1988), should be compared with those of the 9 other subgenera of *Radfordia* to understand the level at which this character is important.

As documented above, the characters of immature stages are sometimes more reliable for defining species or subspecies of *Radfordia* (and also *Myobia* as in Uchikawa, 1991) than those of adults that closely resemble each other. To adopt immature stages in the classification of any myobiid mite, it is necessary first to distinguish the intra- and intergeneric differences clearly.

Host relations:

Among the 18 known families of symbiotic Prostigmata, only the Myobiidae, Psorergatidae, and Demodicidae have specifically coevolved with the Mammalia (Nutting, 1985), but the known Myobiidae were formerly thought not to be host-species specific with their cosymbiotic mammals (Nutting, 1985). However, it has become evident that there are many monoxenic or host-species specific species as well as a few polyxenic species in the Myobiidae, and that both kinds of species serve as indicators suggesting mammalian phylogeny (Uchikawa, 1988). Since the monoxenic myobiid species are larger, elongate forms and polyxenic ones are smaller and rounded (Uchikawa, 1988), *Radfordia* and *Myobia*, being elongate and rather large, are probably host-species specific. Actually, the 69 species and subspecies of *Radfordia* available for Fain and Lukoschus (1977) comprise 49 monoxenic, 13 dixenic, 4 trixenic, 1 tetraxenic, and 1 hexaxenic species or subspecies and the exceptional *R. (M.) lemnina lemnina*, which has been recorded from 11 species of arvicoline voles (see Addendum) (Bochkov, 1994, 1995; Dusbábek, 1988; Fain and Lukoschus, 1977; Fain *et al.*, 1979). Moreover, of the 17 congeneric taxa described thereafter, 16 are monoxenic and one is dixenic (Bochkov, 1994, 1995; Fain and Lukoschus, 1979a, b; Fain *et al.*, 1979; Gill and Strandtmann, 1977; Lukoschus *et al.*, 1981; Scheperboer *et al.*, 1987; Vesmanis and Lukoschus, 1978). These data indicate that the majority of *Radfordia* species are host-species specific, and that the few oligoxenic species are shared by closely allied rodents. Accordingly, the host relations of the present oligo- and polyxenic

species or subspecies should be thoroughly reevaluated.

When all the myobiids associated with Japanese arvicoline voles were identified as *R. lemnina*, it was reasonable to think that specialization in *Radfordia* has been retarded compared with myobiids of many other genera. Conversely, one could think that voles became fully established in Japan relatively late, thereby not allowing their parasites time to speciate enough to become species-specific. However, Fain and Lukoschus (Fain and Lukoschus, 1977) separated *R. (M.) lemnina* into several subspecies, and they recorded voles of the genera *Microtus* and *Clethrionomys* distributed over a wide geographic range (including *M. montebelli* and *C. rufocanus bedfordiae* from Japan) as the hosts of *R. (M.) lemnina lemnina*, while European *C. glareolus* and *C. rutilus* each yielded a different subspecies of *R. (M.) lemnina*.

Among all the subspecies, only *R. (M.) lemnina lemnina* is purportedly polyxenic as mentioned above, infesting the two host genera *Microtus* and *Clethrionomys* over a wide geographic range. There is thus little cause for surprise, based on the host relations of other myobiids, that *R. (M.) lemnina* spp. parasitic on *M. montebelli* and *C. rufocanus bedfordiae* have proven to be separable from the nominate subspecies. Although we could not examine any specimens taken from European *C. rufocanus*, it is reasonable to suspect that this vole may be associated with an unrecognized subspecies of *R. (M.) lemnina* more similar to *R. (M.) lemnina japonica* than to the nominate subspecies. Accordingly, the present study suggests that specimens supposedly of the nominate subspecies taken from arvicoline voles other than European *M. agrestis* will be separable into several distinct subspecies by more detailed studies.

The presently understood host relations of *R. (M.) lemnina japonica* are arousing the same problem as those of the nominate subspecies. The host voles are *Clethrionomys rufocanus bedfordiae*, *C. rex*, *Eothenomys andersoni*, and *E. smithii*. Since the former two voles are thought to be allied to or, sometimes, synonymous with each other (Musser and Carleton, 1993), it is plausible that these hosts share the same subspecies of mite. On the other hand, it is inexplicable that *Clethrionomys* and *Eothenomys* should be infested with the same subspecies of *R. (M.) lemnina*. Since transfer of myobiid mites to new hosts can only have occurred with difficulty, and since the list of currently known hosts of *R. (M.) lemnina lemnina* including *Microtus* and *Clethrionomys* may be subject to revision as discussed above, there is no reason to expect that the two vole genera should share a subspecies of *R. (M.) lemnina*. Meanwhile, a Taiwanese *Eothenomys* vole is known to be the host of *Radfordia (Microtimyobia) eothenomys* Fain and Lukoschus, 1976 (Fain and Lukoschus, 1977). Accordingly, it is expected on the basis of all the other myobiid data that Japanese *Eothenomys* is probably different at the genus level from Taiwanese *Eothenomys*, although all are currently thought by Japanese mammalogists to be congeneric. Concerning this problem, Musser and Carleton (1993) reinstated *Phaulomys* for Japanese *Eothenomys andersoni* and *E. smithii*, in accordance with earlier and recent works of

Japanese mammalogists, and suggested that *Phaulomys* and *Clethrionomys* are derived from a common ancestor. The present myobiid data give support to Musser and Carleton (1993). However, the genus *Phaulomys* has not gained acceptance in Japan. Renewed studies using all available methods on the myobiids themselves and their hosts are required to interpret the problem of *Phaulomys*.

The fact that European *Clethrionomys rutilus* and Japanese *C. rutilus mikado* harbor similar but distinct subspecies of *R. (M.) lemnina* is also unusual, since all subspecies of a host species are usually associated with the same myobiid species, which is not separable further. We think that Japanese *C. rutilus* on the island of Hokkaido has been isolated geographically apart from the European form for long enough to form a subspecies and for its myobiid to speciate. Based on these considerations, we accepted *C. rutilus mikado* as the host name. The same should be true for the relation between European *C. rufocanus* and Japanese *C. rufocanus bedfordiae*, which is one more reason to expect an unrecognized subspecies of *R. (M.) lemnina* parasitic on European *C. rufocanus*.

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Addendum: After submitting the manuscript, we became aware of a recent paper by Bochkov (1995) dealing with the 9 taxa of *Radfordia* (*Microtimyobia*) associated with the Arvicolinae in Russia and surrounding countries. Bochkov (1995) raised *R. (M.) lemnina clethrionomys* Fain and Lukoschus to full species rank and reduced *R. (M.) lemnina rutila* Fain and Lukoschus to a subspecies of *R. (M.) clethrionomys*, because of the structure of the male genital cone (cf. Figs. 9, 12–15). However, the females of *R. (M.) lemnina* ssp. and *R. (M.) clethrionomys* are not separable from each other in Bochkov's key to species and subspecies. The female characters, which are generally thought to be more conservative in evolution than the male characters, are essential for separating species, as was shown by Fain and Lukoschus (1977). *Radfordia* (*M.*) *rufocani* Bochkov, 1995 was described as a parasite of *Clethrionomys rufocanus* (Sundevall) from Mt. Kykschik, Bashkhiria, Russia. Although this mite is dealt with by Bochkov (1995) as a full species, it corresponds to our unrecognized subspecies of *R. (M.) lemnina* that has been expected above to be closer to *R. (M.) lemnina japonica* than to *R. (M.) lemnina lemnina*. The male of *R. (M.) rufocani* has a narrow, subapically constricted genital cone, genital setae thinner than those of *R. (M.) lemnina lemnina*, and membranous gnathosomal setae with only two apical points (Bochkov, 1995). By these characters, *R. (M.) rufocani* is clearly separable from *R. (M.) lemnina japonica*. The unique shape of the male genital cone of *R. (M.) rufocani* suggests that this form is closer to *R. (M.) lemnina clethrionomys* and *R. (M.) lemnina rutila* than to *R. (M.) lemnina japonica*, contrary to our expectation. However, further comparison of *R. (M.) rufocani* and *R. (M.) lemnina japonica* is necessary, using all the characters described in the present paper, for the clarification of the phylogenetic relationship between the two forms.

Bochkov (1995) tabulated the host species, localities and authors for *R. (M.) lemnina* (not *R. (M.) lemnina lemnina*), adding 7 *Microtus* species and 3 *Chionomys* species to and excluding all the *Clethrionomys* species from the table of Fain and Lukoschus (1977). This indicates that detailed morphological and coevolutional studies of *R. (M.) lemnina* or *R. (M.) lemnina lemnina* can not be done based on adult characters alone.

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