ENIOCHTHONIUS MAHUNKAI SP. N. (ACARI: ORIBATIDA: ENIOCHTHONIIDAE), FROM NORTH AMERICAN PEATLANDS, WITH A REDESCRIPTION OF *ENIOCHTHONIUS* AND A KEY TO NORTH AMERICAN SPECIES

Norton, R. A.[1] and Behan-Pelletier, V. M.[2]

¹State University of New York, College of Environmental Science and Forestry
Syracuse, New York, USA 13210, E-mail: ranorton@esf.edu
²Agriculture and Agri-Food Canada, K. W. Neatby Building, Ottawa, ON, Canada, K1A 0C6
E-mail: behanpv@agr.gc.ca

The oribatid mite genus *Eniochthonius* (Eniochthoniidae) currently comprises five thelytokous species with distributions ranging from cosmopolitan to endemic. Herein we propose *E. mahunkai* sp. n., with the description based on adults and all immature instars. The species is widespread in eastern North America but is restricted to, and often abundant in, *Sphagnum*-rich microhabitats in peatlands. The three species of *Eniochthonius* reported from North America are distinguishable by size, shape, structure of ventral plates and other features that are included in a diagnostic key; new distribution records are given for *E. minutissimus* and *E. crosbyi*. A detailed description of *Eniochthonius* is given for the first time, and the nomenclatural confusion with *Hypochthoniella* is summarized; the latter derives from conflicting belief in a misidentification of the type species.

Key words: oribatid mite, sphagnum moss, bogs, fens, parthenogenesis, thelytoky, Hypochthonioidea, morphology

INTRODUCTION

The oribatid mite genus *Eniochthonius*, in the monogeneric Eniochthoniidae (Enarthronota: Hypochthonioidea), is interesting for several reasons: it is one of the enarthronote genera with cuticle mineralized by whewellite (see Note 1, below); it is the closest outgroup of the ptychoid family Mesoplophoridae (Grand-jean 1965, Norton 1984, 2001); and none of its species is known to be sexual (see Note 2). While it is one of the most widespread and easily recognized genera of oribatid mites, much of its morphology has been described only superficially. For example, two remarkable structures – a porose area within a taenidial system and preanal spines that may represent precocious genital papillae in the larva – are noted herein for the first time.

The genus currently comprises five nominal species. The type species, currently recognized as *E. minutissimus* (Berlese, 1910), is widespread in the Holarctic region but has been reported from all continents except Antarctica (Mar-

SHALL *et al.* 1987, MAHUNKA & MAHUNKA-PAPP 1995). *Eniochthonius sumatranus* (MAHUNKA, 1989) is moderately widespread, known from the Oriental (Brunei, Sumatra) and Ethiopian (Madagascar, Comoro Islands) regions (MAHUNKA 1989, 1993, 1997). Two species – *E. paludicolus* (FUJIKAWA, 1994) **comb. n.** and *E. fukushimaensis* (SHIRAISHI and AOKI, 1994) **comb. n.** – are known only from Japan, while *E. crosbyi* (EWING, 1909) appears restricted to central and eastern North America (see MARSHALL *et al.* 1987 and SUBÍAS 2004 for relevant synonyms).

Our purpose is to propose a sixth species of *Eniochthonius*: *E. mahunkai* sp. n., which seems restricted to sphagnum moss and adjacent microhabitats in peatlands of north-central and north-eastern North America. After a detailed description, based on adults and all immature instars, we include a diagnostic key and distribution records for the three species currently known from eastern North America. We also present a detailed redescription of *Eniochthonius* and discuss technical problems associated with this name and *Hypochthoniella*, which often is used as a synonym.

MATERIALS AND METHODS

Most of the studied specimens of *E. mahunkai* sp. n. were collected from sphagnum and peat hummocks in a lakeside fen in central New York State. Details of all collections of this species, and type repositories, are given below. For comparison, we studied the two cotype specimens of *Eniochthonius crosbyi* in the US National Museum collection – one labeled "*Arthrochthonius crosbyi* (EWING)", the other "*Hypochthonius crosbyi* n. sp." with the genus crossed-out and "*Brachychthonius*" written below. We also studied the cotype slides of its junior synonym *E. borealis* JACOT from the US National Museum – the original balsam slide containing 13 specimens was remounted by R. M. REEVES at an unknown date, with one specimen separated in a second mount. Twenty-nine non-type specimens collected and mounted in balsam and labeled by JACOT were also studied. These are on a balsam slide (containing also *E. minutissimus*) that was donated to R. A. NORTON's collection by the late L. J. METZ; there are no collection data on the slide, but the collection number (37F1-L-11) is similar to that of the cotypes from New Hampshire (37F1-W-4). Studied material of *E. minutissimus* included specimens from England, Poland and Germany (in NORTON's collection), along with many from Canada and the USA. Appendix A gives the locality data for new records of these two species in North America.

Most specimens were cleared and demineralized in Nesbitt's solution, then either: transferred to lactic acid for measurement, study and illustration in cavity slides using the same medium (GRANDJEAN 1949); or transferred to a 50:50 mixture of Nesbitt's and Hoyer's medium in preparation for mounting in the latter, after dissection or rough sectioning (see KRANTZ 1978 for compositions). For rough sectioning, demineralized specimens were placed in a small drop of medium, oriented, and allowed to partially dry prior to hand cutting with a razor blade; sections were then mounted for study. Compound microscopy and photography was with differential interference contrast and bright-field illumination, using demineralized specimens unless otherwise indicated. Several images are composite photographs, layered from different focal planes to increase depth; these

are identified in captions. Specimens used for scanning electron microscopy (SEM) were sputter-coated with 15–20 nm gold/paladium and observed with a JEOL JSM 5800LV microscope.

Terminology is primarily that developed by F. GRANDJEAN (e.g. 1940, 1947; see TRAVÉ & VACHON 1975 for complete reference list). General terminology is reviewed in NORTON and BEHAN-PELLETIER (2008); HAMMEN (1980) and HUNT *et al.* (1998) provided glossaries. NORTON (1977, 2001) reviewed leg setation and notogastral scissure-types. Most measurements of specific structures are given as single numbers; they were taken from average-sized individuals and so may vary slightly around the given value. Mutual distances between setal pairs (or other designated setae) were measured from the center of their alveoli.

Eniochthonius mahunkai sp. n.

Diagnosis. Adult relatively small (length 309–343 µm); notogaster moderately arched in lateral aspect. Bothridial seta slightly broadened and flattened distally, with 2–4 long tines and sparse small barbs. Notogaster obovate in dorsal aspect, with relatively long setae (f_1 reaches insertion of h_1 in dorsal aspect). Aggenital region with three separate plates; seta *ag* inserted on smallest, middle plate. Leg tarsus setation (I–IV, famulus included) 18–15–13–13; each with *it"* present, *it'* absent.

Adult (Figs 1–35, 51A)

Dimensions (n = 20). Mean total length 325 µm (range 309–343 µm); mean maximum width 154 µm (range 147–162 µm). Mean length/width ratio of individual specimens 2.11 (varies with degree of distension); proportions of total length of fully distended specimen contributed by prodorsum 0.35; by soft, pleated sejugal band 0.04; and by hysterosoma 0.61. When fully contracted or distended, alignment of protero- and opisthosoma nearly linear (Figs 2, 51A).

Integument. In reflected light mostly smooth, shiny, pale brownish-yellow; epimeral borders, apodemes, grooves and overlapping edges of sclerites appear darker. Notogaster with two conspicuous dark transverse bands: anterior derives from sulcus (see below), posterior band derives from thickened anterior border of pygidium, showing through tectal limb of scissure by transparency. Cerotegument apparent only as small patches of granular excrescences, inconspicuous except in SEM (Figs 12–13, 20–21), distributed as indicated below. Most regions with irregular shallow grooves or wrinkles, hardly noticeable except in SEM (Fig. 13). Except as noted, epicuticle of cuticular plates with continuous pattern of small, highly refractive chambers, giving irregular, falsely-porose appearance in bright-field illumination, both before and after demineralization (Fig. 18; see Note 1). Chambers on legs 2–3 times as large as those on body (Fig. 17); most chambers on genital plates elongated, directed obliquely (Fig. 16). General cuticle pale brown after demineralization, giving evidence of light sclerotization. Setae evenly birefringent throughout length.

Prodorsum. Roughly triangular in dorsal aspect, with slight constriction at level of lamellar setae (Figs 1, 12). Lateral prodorsal margins undulating; two concavities form niches accommodating legs I and II, respectively, with small flange between them (Fig. 2); more distal concavity delimits rostral lobe, best seen in anterior aspect (Fig. 15). Rostrum with smooth, slightly reflexed margin (Fig. 14). Cuticle thicker in vague groove between bothridia (Fig. 24, arrowhead), giving appearance

of darker band connecting bothridia in transmitted light (Fig. 1), bearing sigilla for cheliceral retractor muscles. Cuticle thinner posterior to groove, where prodorsum narrows slightly, telescoping into hysterosoma, but posterior margin strongly thickened where it attaches to soft sejugal cuticle (Figs 23, 24). Interlamellar (in), lamellar (le) and rostral setae (ro) setae attenuate, with sparse minute barbs on outer curvature; respective lengths ca. 40, 35 and 30 µm; respective mutual distances of pairs 44, 30 and 20 µm. Setae in and le usually erect, slightly curved posteromedially and anteromedially, respectively; seta ro strongly curved at base, directed posterodorsally (all can be deformed during preparation). Two exobothridial setae finely attenuate; xa closely lateral to bothridium, ca. 33 µm, directed anterodorsally; xp posteroventral to xa, ca. 24 µm, directed ventrally (Fig. 2). Bothridium opening on distinct swelling (Fig. 13); with three chambers, outer two with smooth walls, inner one densely spiculate (Fig. 29; see Note 3). Bothridial seta (bo) slightly broadened and flattened distally, with 2–4 long tines (ca. 10 µm) and sparse small barbs (Figs 1, 13); length ca. 65 µm, about equal to mutual distance of bothridial apertures.

   Notogaster (Figs 1, 2, 12). Roughly obovate in dorsal aspect, anteriorly about same width as prodorsum; 1.3–1.5 times longer than maximum width (slightly posterior to mid-length), depending on distension; moderately arched in lateral aspect, confluent with curvature of prodorsum (Fig. 51A). With anterior plate (pronotaspis, NA) bearing setal rows c, d and e; isolated from pygidial region (PY) by single transverse tectiform (type-L) scissure; tectum ca. 20 µm wide (of which solid limb ca. 15 µm) in sagittal plane, decreasing laterally to end at suprapleural plate (sp); difficult to discern in dorsal aspect of whole specimens as posterior border extremely thin (Figs 1, 26, bt). In contracted specimens, anterior margin of pygidium (bp) telescoping underneath tectum to level ca. 20 µm anterior to seta e_1. Transverse sulcus of pronotaspis emphasized in transmitted light by slightly thicker cuticle (Figs 1, 25), weakest medially, between setal pair d_1. Pronotaspis isolated from pleural region (PL) by paired elongated suprapleural plate (ca. 15 times longer than wide), extending anteriorly from about level of setal row f to within about 10 µm of sejugal articulation; plate ca. 125 µm long, 10 µm at widest point, bearing setae h_2, h_3 in posterior quarter (Fig. 2); h_3 reaches posterior end of plate, h_2 extends well beyond it. Pleural region with narrow, laterally projecting carina originating near level of seta c_3 and merging posteriorly with notogastral margin, just posterior to level of legs IV; in anterior half, ventral surface of carina invaginated as taenidium (Figs 30–32). Posterior to leg IV taenidium curves ventrad, away from pleural carina; continuing as short, shallow groove onto aggenital plate (see below). Hidden arched wall of taenidium bearing inconspicuous elongated porose area (ca. 25–30 µm long; see Note 4) in region dorsal to legs III and IV (Figs 2, pa; 33); rarely two widely separated smaller porose areas present instead. Lateral margin of notogaster sharply folded dorsomediad in posterior two-thirds to form plicature plate (Fig. 3, pp), hidden in contracted specimens (see Note 5); plicature plate not mineralized, without epicuticular chambers. Five pairs of lyrifissures present (see Note 6); ia slit-like, inconspicuous, aligned with edge of pleural carina and lying between it and porose area (Fig. 33, arrowhead). Others with cupular form (Figs 2, 3): im posterolateral on pronotaspis, about 10 µm from its lateral edge; ip far anterior in pleural region near posterior end of pleural carina; ih approximately aligned between im and seta p_3, about 30 µm from the latter; ips on plicature plate about at level of seta ad_3. Notogastral setae mostly attenuate, posteriorly directed, slightly curved, with minute serration of barbs dorsally, difficult to see except in profile (Fig. 35). Setae mostly 40–55 µm long; when flattened by coverglass many reaching level of insertions for next most posterior row; e_2 and p_1 longest, latter extending slightly beyond posterior margin in dorsal aspect; seta c_3 much smaller (ca. 15 µm), finely attenuate and flexible, inconspicuously inserted in anterolateral corner of pronotaspis (Figs 1, 13).

   Coxisternum. Epimeres I and II fully fused, ca. 80 µm wide; most of surface with granular cerotegument (Fig. 21) inconspicuous in transmitted light due to epicuticular chambers. Epimere II bending abruptly dorsad just posterior to seta $2a$, then again posteriorly, prior to joining soft articulat-
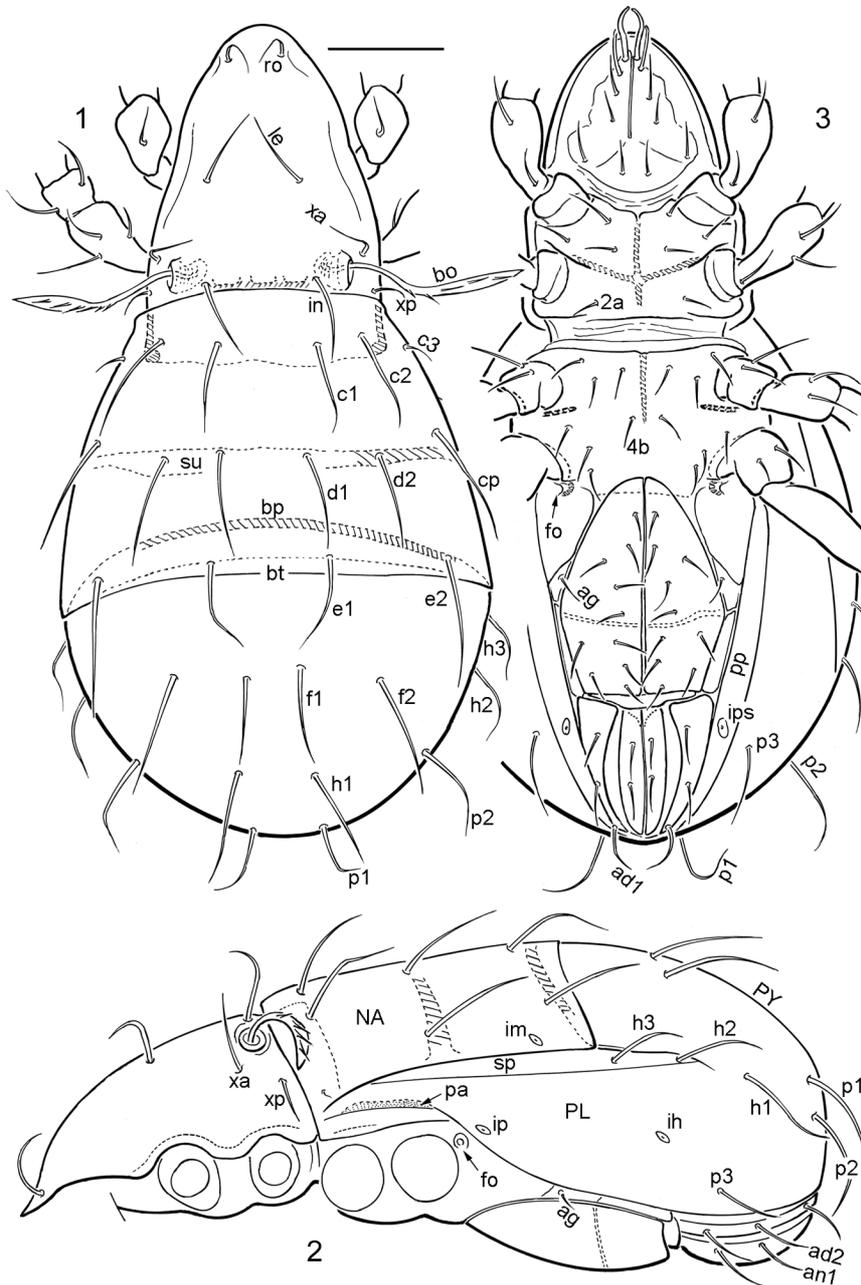
Figs 1–3. *Eniochthonius mahunkai* sp. n., adult (contracted specimen): 1 = dorsal aspect; 2 = lateral aspect; 3 = ventral aspect. Legs and gnathosoma partly shown (1, 3) or omitted (2). All to same scale (50 μm)
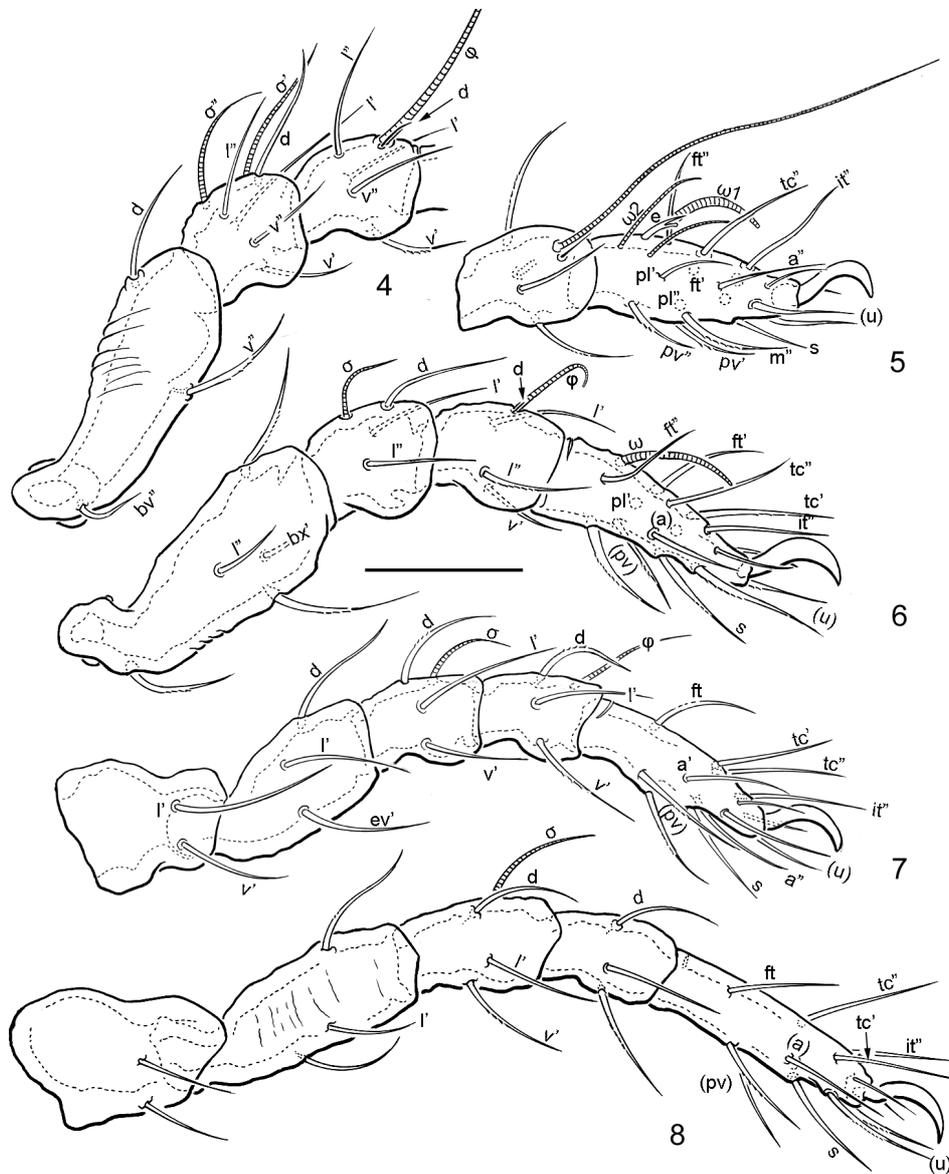
Figs 4–8. *Eniochthonius mahunkai* sp. n., adult: 4 = leg I, femur, genu and tibia; 5 = leg I, tibia and tarsus; 6 = leg II, except trochanter; 7 = leg III; 8 = leg IV. All abaxial view; all to same scale (50 μm). Unlabeled setae include: proral pair (*p*) inserted dorsally at base of claws on all legs; two setae on reverse side of Fig. 5, indicated only by dotted circles: *a'* and *tc'* (respectively below and above seta *a"* in figure); and several others on Figs 6 and 8 that can be interpreted from Figs 4 and 7, respectively.

ing sejugal cuticle, forming "neck" in proterosoma that inserts into hysterosoma during contracted state (Figs 2, 23, 27). Sub-cruciform pattern of narrow grooves on surface (Fig. 21) overlying well formed apodeme 2 and anterior sternal apodeme; latter ending posteriorly at change in contour. Supracoxal gland opening at dorsal margin of epimere I, at level of epimeral seta *1a*; cuticle along canal border projecting internally in row of small teeth for about 15 μm anterior to aperture. Supracoxal seta *eI* ca. 5 μm, spiniform, nearly isodiametric but with minute terminal fork; inserted immediately dorsal to trochanter I, below podocephalic canal. Epimeres III and IV fully fused with each other, ca. 90 μm wide; surface with weak grooves and cerotegument granules marking positions of underlying apodemes (Fig. 21). Epimere IV also fully fused to anterior aggenital plate. Posterior sternal apodeme conspicuous, about 30 μm long, ending posteriorly about at level of seta *4b*. Apodeme 3 short, reaching at most halfway to midline; apodeme 4 absent (Fig. 3). Articulations with leg trochanters sunken, no soft cuticle exposed, approaching ball-socket formation. Epimeral setal formula 3–1–3–4; setae finely attenuate, apparently smooth, mostly 10–15 μm; seta *1a* slightly longer (ca. 20 μm), with inconspicuous barbs.

Anogenital region. With three pairs of mutually articulated aggenital plates that collectively bracket the genital and preanal plates (Fig. 3). Anterior plate largest, roughly triangular, ca. 40 μm long, imperceptibly fused to epimere IV, with two well marked impressions; medial one (close to genital plate) broad, shallow; lateral one (postpedal fossa *fo*) behind leg IV insertion, narrow with well-defined aperture (Figs 2, 21). Vague, shallow groove extending laterally from fossa towards pleural region of notogaster, aligned with pleural taenidium (Fig. 31). Middle aggenital plate small, 4-sided polygon, ca. 22 μm in longest dimension; bearing seta *ag* (simple, ca. 12 μm). Posterior aggenital plate narrowly sub-rectangular, slightly wider posteriorly, ca. 35 μm long. Genital plates roughly pentagonal as pair, each truncated posteriorly; large, ca. 90 μm long, 55 μm at widest point; narrow band of unsclerotized cuticle cutting transversely (slightly obliquely) across plate at widest point and meeting articulation between second and third aggenital plates laterally; band evident by
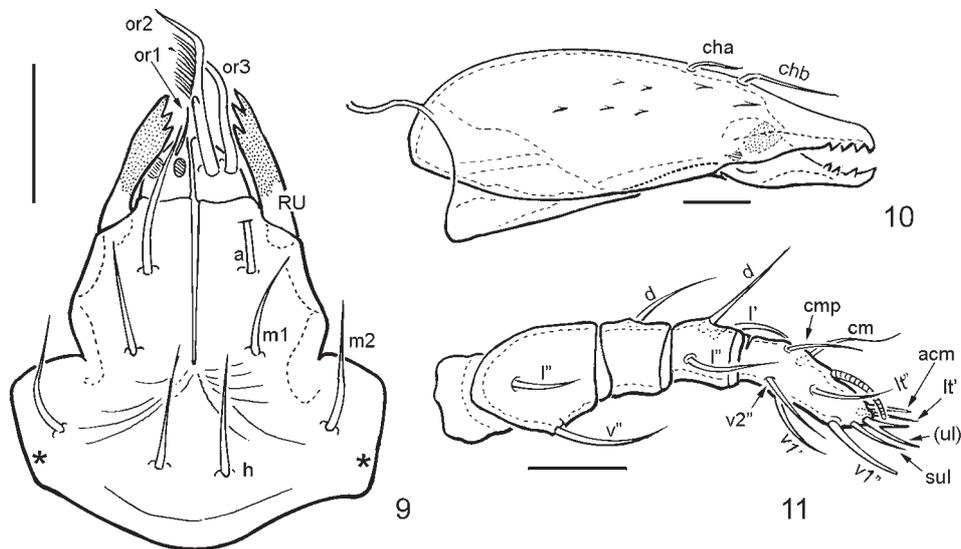
Figs 9–11. *Eniochthonius mahunkai* sp. n., adult: 9 = subcapitulum, ventral aspect (* marks position of postpalpal setae on dorsal face); 10 = chelicera, adaxial aspect; 11 = palp, abaxial aspect. Scale bars: 20 μm (9), 10 μm (10), 25 μm (11).

lightness in transmitted light, chambered epicuticle above it remaining mineralized, but in pattern different from that of surrounding epicuticle (Fig. 16); with sparse cerotegument granules anteriorly (Fig. 21). Ten pairs of genital setae forming two longitudinal rows, seven in medial and three in lateral; four medial and one lateral seta anterior to transverse band; spacing of medial row setae slightly variable; setae attenuate, without noticeable barbs, 12–15 μm. Ovipositor strongly pleated, short, only ca. 30 μm long when folded (just proximal to terminal lobes); directed posteroventrad when in body (Fig. 23, ov), so that paired dorsal lobes in ventral position; with nine pairs of setae: τ_1 and Ψ_1 ca. 35 μm; τ_{2-4}, Ψ_2 and three pairs of coronal setae 13–15 μm; all setae eupathidial. Genital papillae rela-

Table 1. Ontogeny of setae and solenidia in *Eniochthonius mahunkai* sp. n. (Structures are indicated where they are first added and are present through the rest of ontogeny; setae in parentheses represent pairs; dash indicates no additions. See text for variation)

	Trochanter	Femur	Genu	Tibia	Tarsus
Leg I					
Larva	–	d, bv''	d, (l), σ', σ''	d^*, (l), v', φ	(ft), (pl), (pv), (tc), (a), (p), (u), s, m'', e, ω_1
Protonymph	–	–	–	v''	ω_2
Deutonymph	–	v''	–	–	it''
Tritonymph	–	–	(v)	–	ω_3
Adult	–	–	–	–	–
Leg II					
Larva	–	d, bx', bv''	d, (l), σ	d^*, (l), v', φ	(ft), pl', (pv), (tc), (a), (u), (p), s, ω
Protonymph	–	l''	–	–	–
Deutonymph	–	v''	–	–	–
Tritonymph	–	–	–	–	it''
Adult	–	–	–	–	–
Leg III					
Larva	–	d, ev'	d, l', σ	d, l', v', φ	ft, (pv), (tc), (a), (u), (p), s
Protonymph	v', l'	–	–	–	–
Deutonymph	–	l'	–	–	–
Tritonymph	–	–	v'	–	it''
Adult	–	–	–	–	–
Leg IV					
Protonymph	–	–	–	–	ft, (pv), (u), (p)
Deutonymph	v'	d, ev'	d, σ	d, l', v'	tc'', (a), s
Tritonymph	l'	l'	l', v'	–	tc', it''
Adult	–	–	–	–	–

* indicates that seta d is inconspicuous; minute and closely coupled to a solenidion, as described in text
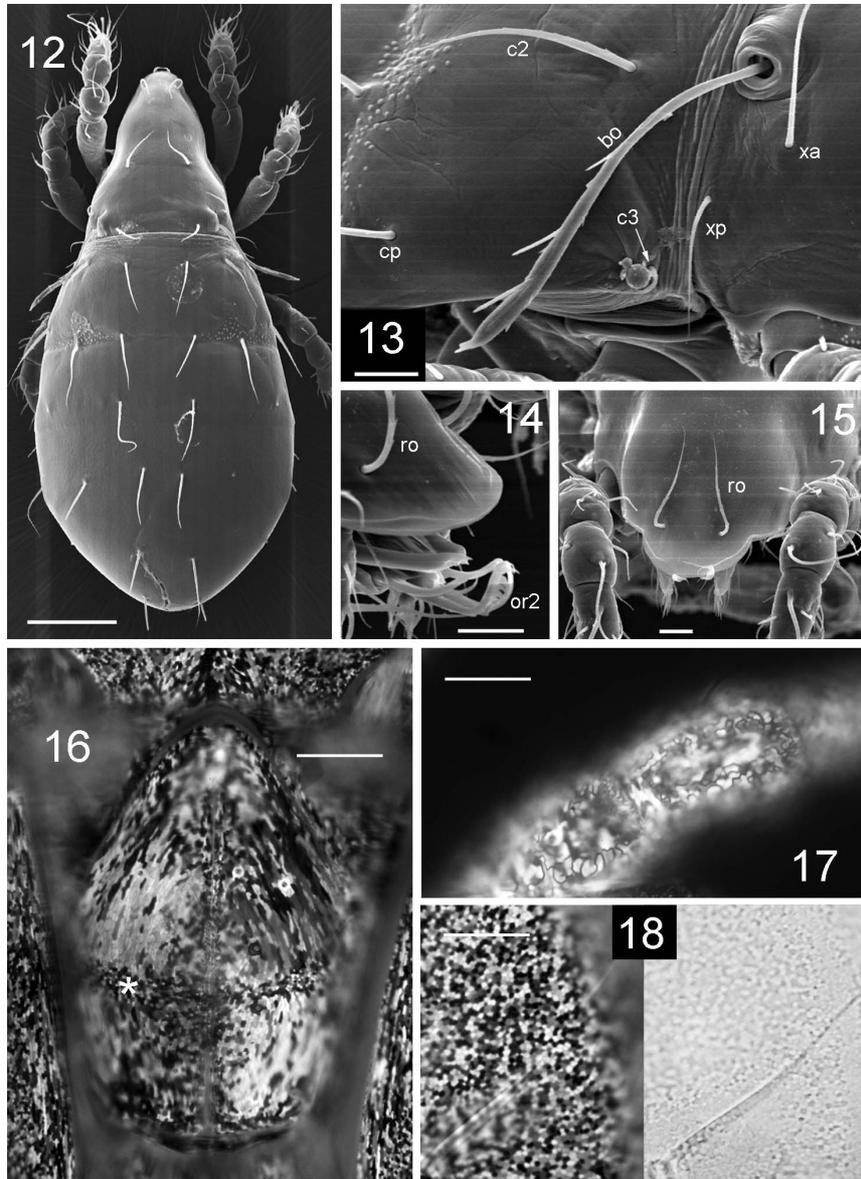
Figs 12–18. *Eniochthonius mahunkai* sp. n., adult: 12 = dorsal habitus; 13 = bothridial seta (*bo*) and sejugal region, dorsolateral aspect; 14 = rostrum and distal region of subcapitulum, lateral aspect; 15 = proterosoma, partial anterior view; 16 = genital region in polarized transmitted light (* marks location of different mineralization pattern covering narrow transverse band of unsclerotized procuticle that divides genital plate); 17 = mineralization pattern on leg III; 18 = mineralization pattern in central notogaster, polarized light on left, unpolarized on right. Figs 12–15 scanning electron micrographs; 16–18 light micrographs. Scale bars: 50 μm (12), 10 μm (13–15), 20 μm (16–18).

tively large (10–12 μm diameter), all three similar. Preanal plate (Figs 22, 28, *pr*) narrow, ca. 45 μm across, may be inconspicuous in contracted specimens. Collectively, anal and adanal plates ca. 60 μm long, 50 μm wide anteriorly, tapering posteriorly to 20–25 μm wide at level of seta ad_1; without noticeable cerotegument. Three pairs of adanal setae 15 μm, two pairs of anal setae 15 μm; all attenuate, smooth. Anteromedial margin of each anal plate projected internally as contiguous pair of solid, horn-like, heavily sclerotized anal apodemes (Fig. 28, *aa*), conspicuous in transmitted light.

Legs (Figs 4–8). Legs all relatively short, similar in size, ca. 0.35 to 0.40 times body length, IV longest; simple in structure, without bosses, tubercles or surface sculpturing other than fine, wrinkle-like grooves running obliquely to transversely across segments. Basally, segments with constriction near articulation; constriction strongest dorsally on femora, ventrally on more distal segments, and only weakly defined on tarsi III–IV. Articulations tight, almost ball-socket type, without clearly defined protecta, but soft articulating cuticle not exposed, even ventrally, regardless of degree of flexing. All trochanters, and femora I and II, with cerotegument granules. All tarsi with normal, proximodorsal lyrifissure. Single claw simple in structure, without barbs or dentition. Leg setae attenuate to sub-flagellate, mostly smooth or with sparse, minute barbs; seta *a'* on tarsi I and II with several strong barbs (not illustrated). Setation (legs I-IV, including famulus but not solenidia) of trochanters (0–0–2–2), femora (3–5–3–3), genua (5–3–3–3), tibiae (5–4–3–3), tarsi (18–15–13–13); no variation noted (but slight variations in ontogeny, described below); setal homologies given in Figs 4–8 and in Table 1 (see also Note 11). Seta *d* of tibiae I and II minute, coupled to respective solenidion φ, in adjacent but separate alveoli; seta *d* of tibia III and of all genua independent of respective solenidia. Solenidial formula (legs I–IV) of genua (2–1–1–1), tibiae (1–1–1–0), tarsi (3–1–0–0). Genual solenidia all piliform; σ"I proximal to seta *d*, σ'I approximately lateral to it; σII placed like σ"I, slightly on posterior face; σ of genua III and IV also slightly on posterior face, but well distal to seta *d*. Tibial solenidion φI tactile (flagellate, ca. 70 μm), directed dorsodistally, about half length of leg I; solenidion φII ceratiform, slightly shorter than segment length, strongly curved toward posterior face; φIII piliform, with form and position similar to σIII, distal to *d*. Tarsal solenidion ω1 large, ceratiform, curved toward segment, and ending directed toward base of claw; ω2 and ω3 piliform, closely aligned together, lateral to famulus on posterior face; ω of tarsus II similar to ω1 of tarsus I, but slightly smaller. Famulus (*e*) aligned between seta *ft'* and solenidion ω2; forked: one branch thick, terminating bluntly or with slight knob-like swelling, other attenuate, bract-like, about one-third longer (Fig. 5).

Gnathosoma. Subcapitulum anarthric but with paired pattern of wrinkles and grooves leading posterolaterally from inferior commissure of mouth (in normal position of labiogenal articulation; see Note 14), delineating region of triangular mentum from paired genae (Figs 9, 20); cerotegument granules small, vague, restricted to periphery. Dorsal surface of genae with extensive, paired, rasp-like region. No dentition observed on labrum. With small, rectangular capitular apodeme, ca. 10 μm wide, projecting 15 μm posteriorly from subcapitular cervix. Rutellum (Fig. 9, RU) narrow, seemingly inserted in genu like large seta, slightly broadened distally with three obliquely aligned terminal teeth (see Note 7). Four setae on subcapitular face, positioned as in Fig. 9; all attenuate, with several minute barbs; hypostomal seta (*h*) 15 μm, median setae (m_1, m_2) 17 μm, anterior seta (*a*) largest (23 μm) and less rapidly tapered than others. Three heterogeneous adoral setae on exposed lateral lips: or_1 and or_3 attenuate, without ornamentation, ca. 8 μm and 20 μm respectively. Seta or_2 complex (Figs 9, 14, 20): main axis (ca. 24 μm) finely attenuate, with small ventral tooth at mid-length, distal half bent strongly dorsad (slightly bowed like parenthesis) then again anteriorly for short distance; vertical portion of or_2 pectinate with more than 10 long, fine, closely adjacent, medially directed cilia, which (as setal pair) interdigitate to form baleen-like sieve. Postpalpal seta 7–8 μm, little tapered, terminating in distal fork; attached without alveolus, and at near right-angle, to vertical post-like tubercle about as long as and little wider than seta (Fig. 34). Palp simple, all five segments fully articulated;
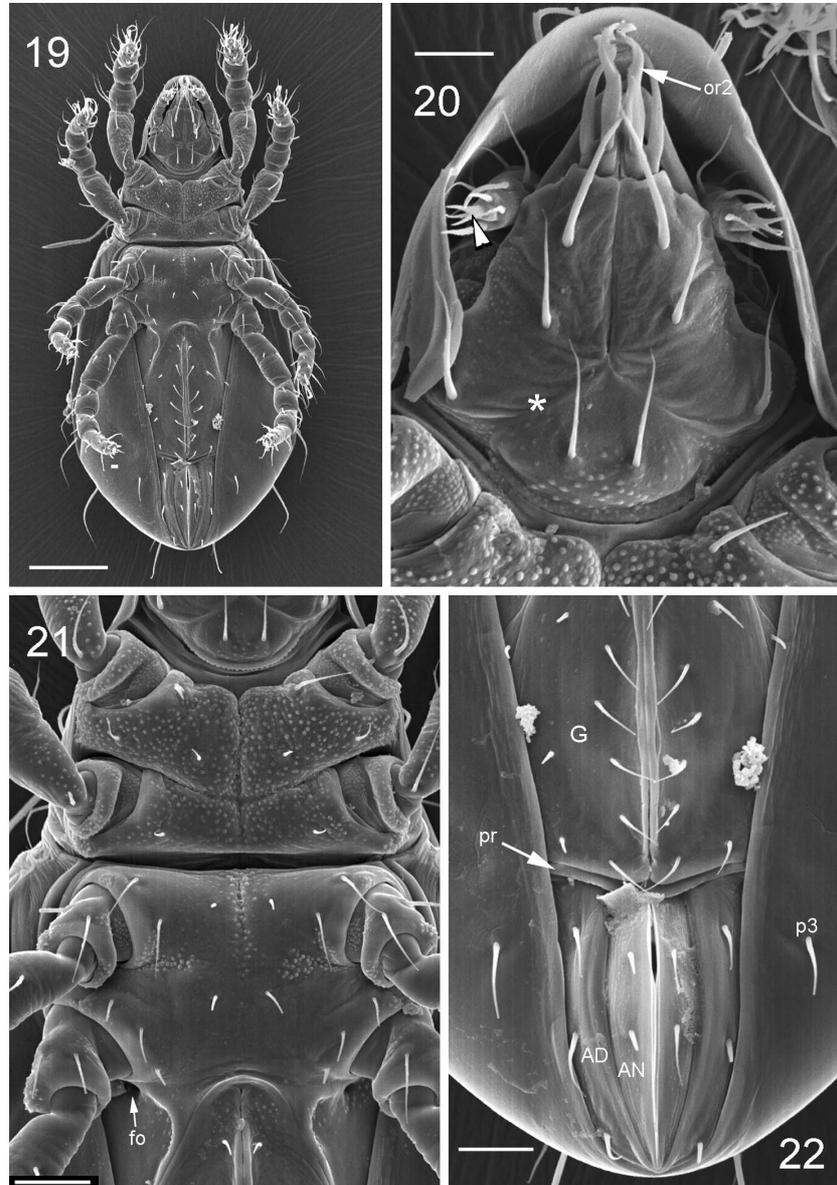
Figs 19–22. *Eniochthonius mahunkai* sp. n., adult: 19 = ventral habitus; 20 = subcapitulum and vicinity, ventral aspect (white arrowhead indicates fused pair of ultimal setae, * marks groove separating gena and mentum); 21 = coxisternum and vicinity, ventral aspect; 22 = anogenital region and adjacent notogaster (AD, AN indicate adanal and anal valves, respectively; G marks position of narrow transverse band of unsclerotized procuticle that divides genital plate). Scale bars: 50 μm (19), 10 μm (20); 20 μm (21, 22).
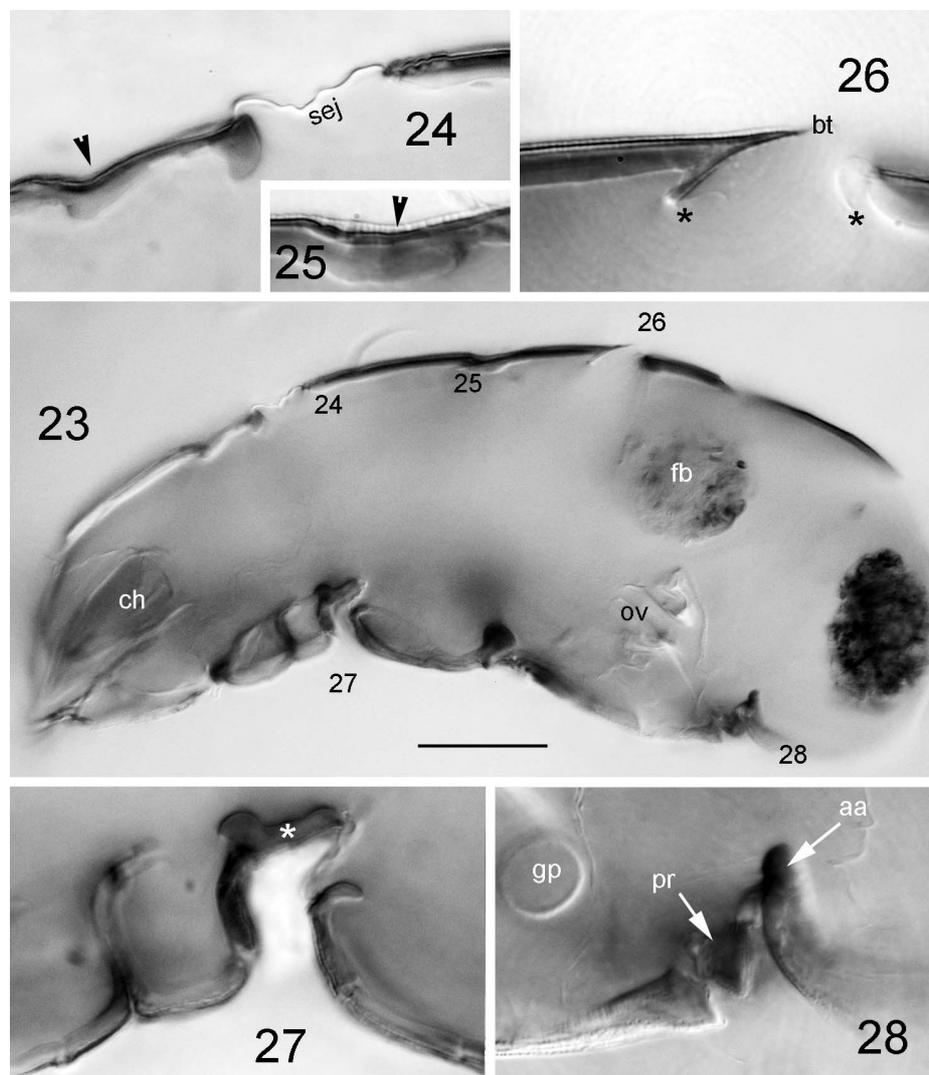
Figs 23–28. *Eniochthonius mahunkai* sp. n., adult, lateral aspect of near-sagittal section, anterior to left: 23 = overview of section, with position of enlarged images marked by respective figure number in similar relative position (ch = chelicera, fb = food bolus, ov = ovipositor); 24 = dorsal sejugal region (sej = soft articulating cuticle, arrowhead indicates thickened cuticle behind which proterosoma narrows slightly to proximal "neck"); 25 = region of transverse sulcus, showing thickened cuticle and overlying chambered epicuticle (demineralized, marked with arrowhead); 26 = telescoping transverse scissure (type-L), showing tectum on pronotaspis (asterisks mark limits of sclerotized cuticle on respective plates; voluminous connecting soft cuticle not shown); 27 = ventral sejugal region (* marks cuticle of proximal "neck", exposed only in distended individuals); 28 = juncture of genital, preanal (pr) and anal plates (aa = anal apodeme; gp = posterior genital papilla). Scale bar: 50 μm (23), others by proportion.
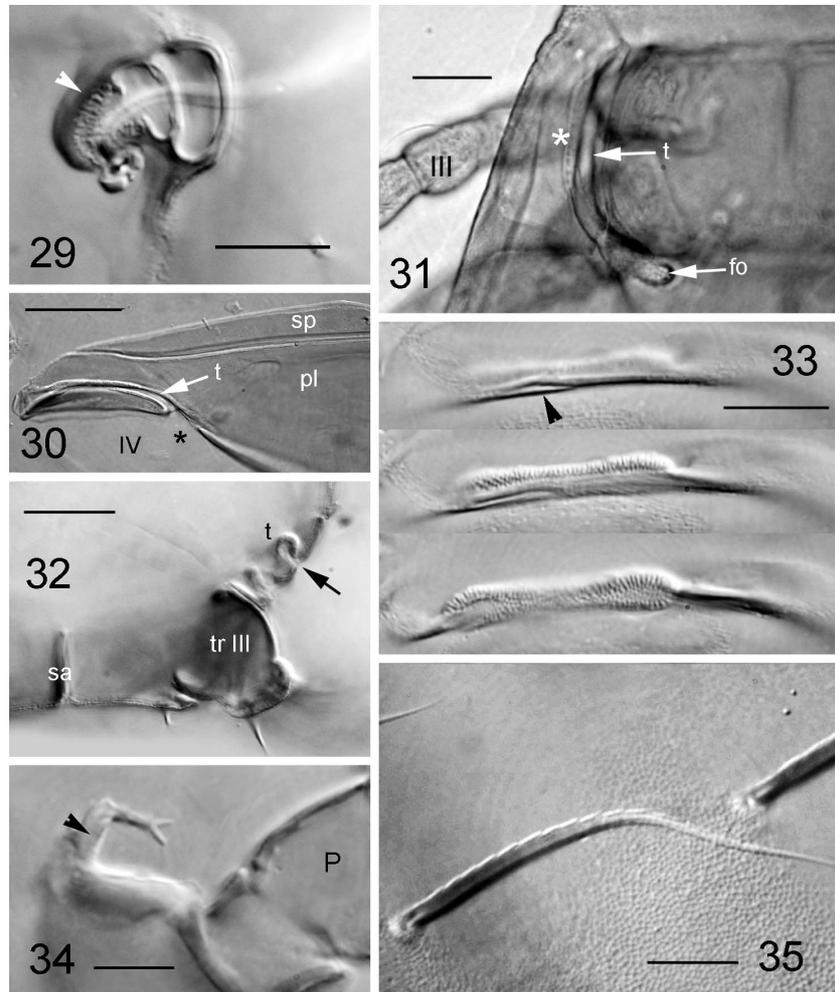
Figs 29–35. *Eniochthonius mahunkai* sp. n., adult: 29 = bothridium, optical section (arrowhead indicates spiculated inner chamber); 30 = anterior region of isolated suprapleural plate (sp) and pleural region of notogaster (pl), lateral aspect (cf. Fig. 2), showing taenidium (t) curving ventrad (* and IV mark approximate positions of postpedal fossa on aggenital plate and leg IV insertion, respectively); 31 = taenidium (t) and fossa (fo) on left side, showing curved alignment seen by transparency on dorsally positioned, slightly flattened specimen (III = leg III, * marks approximate level of section in Fig. 32); 32 = frontal section through notogastral taenidium and porose area (t = taenidium, sa = sternal apodeme of epimere III, tr III = trochanter III, arrow marks open slot of taenidium); 33 = notogastral taenidium and porose area, lateral aspect (cf. Fig. 30), at three progressively deeper focal planes (arrowhead indicates lyrifissure *ia*); 34 = posterodorsal corner of subcapitulum, lateral aspect, showing forked postpalpal seta (P = femur of palp, arrowhead indicates cylindrical stalk on which seta inserts at strong angle); 35 = notogastral seta e_1, showing fine barbs. All but Fig. 31 with differential contrast transmitted illumination; 30 and 34 layered images. Scale bars: 50 μm (30), 20 μm (31, 32), 10 μm (29, 33–35).

femur and tarsus approximately of equal length, about twice that of genu and tibia (Fig. 11). Setation (trochanter to tarsus) 0–2–1–3–11, plus solenidion ω. All setae on femur to tibia and most setae on tarsus attenuate, with sparse minute barbs; unpaired anteroculminal, *acm*, and ultimal pair (*ul*) of tarsus eupathidial, little tapered; ultimal pair fused near base to form strongly diverging fork; v_1" spiniform. Solenidion ω about half length of tarsus, narrowly ceratiform, curved toward tip of segment to end near ultimal fork (Figs 11, 20). Chelicera (Fig. 10) relatively narrow, ca. 65 μm long, 22 μm greatest width, gradually tapered distally; small proximal portion (less than one-tenth of length) internalized through cheliceral frame (body wall). Not mineralized. Ventral trochanter remnant relatively large, extending about half length of chelicera. Main cheliceral body with fine longitudinal striae dorsally (not illustrated), proximal to seta *cha*; adaxial face with several scattered sharp spicules. Digits ca. 21 μm long, tapered to fine tips, each with four teeth; abaxial face of fixed digit with small, seemingly porose region of unknown nature; small, sharp mid-ventral tooth near base of movable digit. Setae inserted as in Fig. 10; *cha*, *chb* ca. 7 μm, 16 μm respectively.

Ontogeny (Figs 36–50)

Dimensions. Mean (range) total length and maximum width measured from 10 specimens of each instar: larva (La): 218 μm (208–230 μm) by 97 μm (93–108 μm); protonymph (Pn) 247 μm (230–260 μm) by 113 μm (105–118 μm); deutonymph (Dn) 279 μm (259–289 μm) by 126 μm (118–132 μm); tritonymph (Tn) 310 μm (294–323 μm) by 146 μm (132–157 μm). As in adult, length varies widely depending on degree of distention; width varies also, being slightly narrower in distended specimens.

Integument. Shiny in reflected light; nearly white in early instars, may have slight yellow tint in nymphs, but always paler than adult. Except at articulations, with strongly chambered, mineralized cuticle in all immature instars, essentially like that of adult; when demineralized, chambers more discernable in nymphs than in larva.

Prodorsum. General structure similar to that of adult, except lateral margin rather simple in La; distinct rostral lobe and concavities for legs appear in Pn. Posterior margin of prodorsum not noticeably thickened in any immature instar. Setation generally similar to that of adult, but setae *in* and *le* acicular and more clearly barbed in La, becoming attenuate in nymphs. Posterior exobothridial seta (*xp*) proportionally smaller than in adult; about one-quarter length of anterior (*xa*). Bothridial seta distally broadened and barbed; number of long tines 0–2 in La (Fig. 43) and 0–4 in nymphs. Bothridium two-chambered in all immature instars, with inner chamber densely spiculate.

Gastronotic region. Larva with notogaster divided into three parts – pronotaspis (NA), mesonotaspis (NM) and pygidium (PY) – by two simple, type-E transverse scissures (Fig. 36). Anterior scissure, between setal rows *d* and *e* (scissure ar_2 of GRANDJEAN 1947) with relatively broader articulating cuticle; posterior scissure, between rows *e* and *f* (*ar3*), very narrow. Scissures reaching laterally to broad, soft, striated pleural band bordering notogaster. Neither suprapleural plate nor plicature plate developed; without distinct pleural carina. Single small, oval porose area (ca. 6 μm long) on vague pleural extension of pronotaspis, posteroventral to seta c_3 (Fig. 44). With 13 pairs of setae representing typical holotrichous setation (Fig. 36). Setae heterotrichous: c_1, c_2, and d_1 acicular and more clearly barbed than in other instars (Fig. 42); *cp* variable (acicular, attenuate or intermediate); f_1 thickest of all notogastral setae, acicular with dorsal row of inconspicuous fine barbs; c_3 attenuate but relatively longer than in nymphs and adult (longer than acicular setae) (Fig. 37). Lyrifissures cupular: *ia* on lateral margin of pronotaspis, about 15 μm anterior to scissure; *im* near lateral margin of mesonotaspis; *ip* far anterior from usual position (see Note 6), ca. 15 μm posteroventral to *im* and 5 μm from notogastral border.
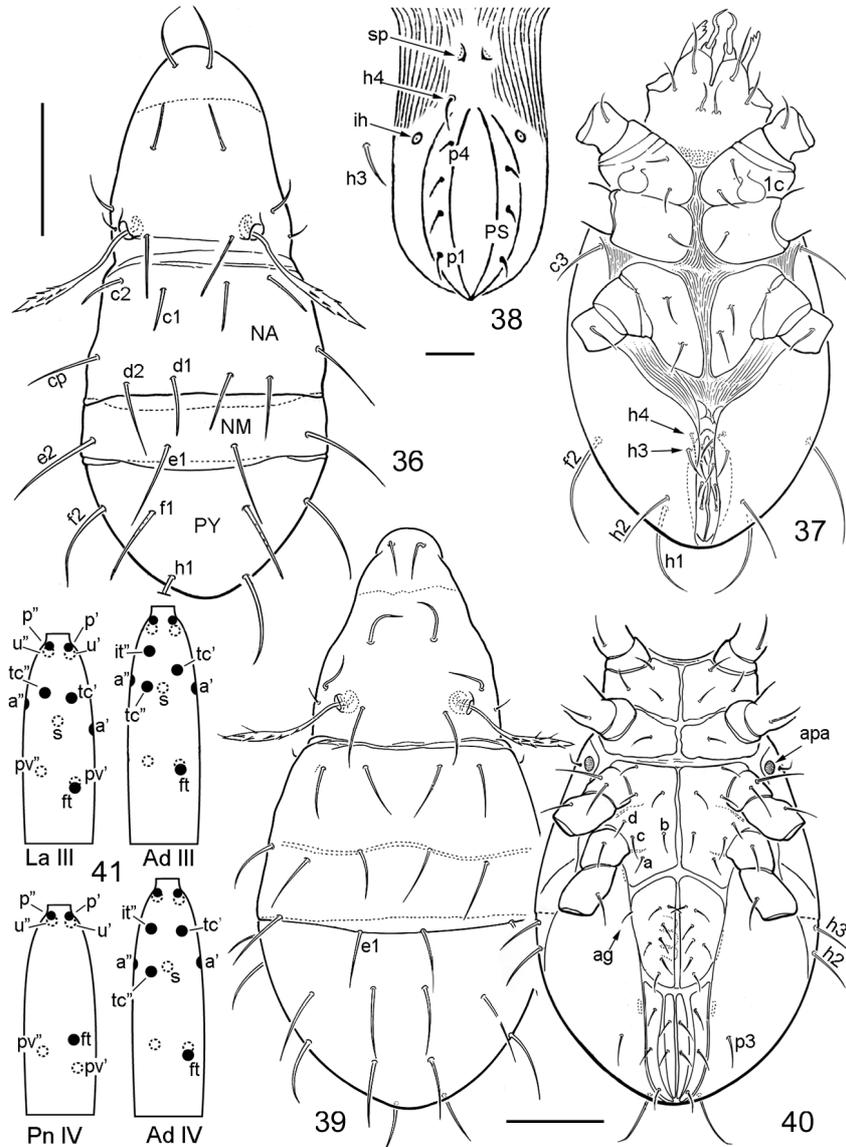
Figs 36–41. *Eniochthonius mahunkai* sp. n., immatures: 36 = larva, dorsal aspect; 37 = same, ventral aspect (specimen contracted, legs incomplete); 38 = opisthosomal venter of distended larva (adapted from GRANDJEAN 1933), contrasting presence of inguinal seta h_4 in *E. mahunkai* (left side) with its absence in *E. minutissmus* (right side); 39 = tritonymph, dorsal aspect; 40 = same, ventral aspect (legs incomplete; apa = anterior porose area); 41 = schematic dorsal view of left tarsi III (top) and IV (bottom) at instars indicated, anterior (') face to right, distal at top (La = larva, Pn = protonymph, Ad = adult); setal insertions indicated by circles: black = dorsal position, visible directly (half-circles are lateral); dotted = ventral position, by transparency). Scale bars: 50 μm (36–37, 39–40), 10 μm (38).

Nymphs with notogastral structure similar to that of adult in having single transverse scissure immediately posterior to setal row e (i.e. pronotaspis carries setal rows c-e; Fig. 39) and suprapleural plate, bearing setae h_2, h_3, but with soft, striated cuticle between notogaster and coxisternum. Suprapleural plate shorter and broader (6–7 times longer than broad) than in adult, reaching anteriorly only to level of leg IV. Transverse scissure without tectal limb, but pronotaspis cuticle bends sharply ventrad at level of row e, forming narrow vertical wall ending at very narrow, hinge-like articulation with pygidial region (Fig. 46, arrowhead); anterior sclerite therefore higher than posterior one in lateral aspect, but without ability to telescope. Indistinct groove present posterior to setal row d (remnant of ar_2), less conspicuous than homologous transverse sulcus of adult. Pleural region with porose area similar to that of La, lying between seta c_3 and anterolateral corner of pronotaspis. Pleural carina present but weakly developed; with second oval porose area (app) on underside (Fig. 45; see Note 4); in dorsoventral aspect, porose area appears between levels of legs III and IV. Cupule ia between porose area and anterior corner of suprapleural plate; im dorsal to latter plate; ip further anterior in pleural region than in La, approximately as in adult; ih anterodorsal to seta p_3, as in adult. Ventrolateral plicature plate develops posteriorly in Pn, fully formed (as in adult) in Dn and Tn; contains cupule ips as in adult. All nymphs with 16 pairs of setae, representing larval complement plus pseudanal setae p_1-p_3 (p_4 absent from nymphs and adult; see Note 8). All notogastral setae with dorsal barbs, usually inconspicuous. Setae of nymphs all attenuate as in adult and with similar relative size.

Coxisternum. Soft cuticle between epimere I and subcapitulum granular. All epimeres with medial band of soft, longitudinally striated cuticle; more apparent in La (Fig. 37) since band folds more deeply in nymphs (Fig. 40). Sejugal articulation with transverse striae, blending into those of epimera II and III, respectively, in dactylographic pattern. In all immatures, each half of epimere I at least weakly fused to respective half of epimere II; separated by conspicuous groove, but without apparent articulation. In nymphs, halves of epimeres III and IV fully fused, with no external or internal delimitation. Postpedal fossa absent from all immatures. Larval Claparède's organ of typical form, without indication of annulations; seta $1c$ scale-like, reverting to normal form in Pn. Otherwise, epimeral setae relatively short, attenuate, smooth or with sparse, minute barbs; generally similar in form and relative size to those of adult. Setal ontogeny as follows: La (3–1–2), Pn (3–1–2–1), Dn (3–1–3 –3), Tn (3–1–3–4); in Fig. 40 setae of epimere IV lettered in order of appearance (a in Pn, b, c in Dn, d in Tn); in two of 11 tritonymphs examined, seta $4d$ absent unilaterally.

Anogenital region. Genital region of larva represented by broad expanse of soft, longitudinally striated cuticle (Fig. 37), except for pair of conspicuous thorn-shaped, sclerotized, laterally flattened preanal spines projecting posteroventrad (Figs 49, 50; see Note 9); nymphs without spines. Genital valves relatively larger in successive nymphs; setation (Pn-Tn) 1–3–7, with Tn having 3 setae in lateral row, 4 in medial row (Fig. 40). Aggenital plates absent. Aggenital seta first forms in Tn (often unilaterally; see Note 10) or adult; if in Tn, it inserts at extreme lateral edge of genital plate (Fig. 40). Preanal plate absent from all immatures. All immatures with apodeme extending internally from anterior walls of paraproctal valves (Figs 49, 50; aa): with dark V-shaped cross section in ventral aspect ("V" pointed anteriorly), subtriangular in lateral aspect. Paraproctal valves of La (segment PS) narrow, well defined, consistently with 4 pairs of setae arranged in uniformly spaced row (Fig. 38, left side). Cupule ips not present on paraprocts; ih in soft cuticle between most anterior pseudanal seta (inguinal seta p_4) and notogastral seta h_3. Inguinal seta h_4 present near anterior end of paraprocts on opposite side of cupule ih from h_3 (transcupular) (Figs 37, 38). Both p_4 and h_4 lost from all later instars (see Note 8). Paraproctal setation 4–3–2–2 (La-Tn); without paraproctal atrichosy. Adanal and anal plates acquire adult form and setation in Dn.

Legs. General form and proportions similar to those of adult, but articulations with soft cuticle exposed, clearly broader ventrally, as typical for oribatid mites. Ontogeny of setae and solenidia given in Table 1; their forms and positions generally as in adult, except as noted below. No variation
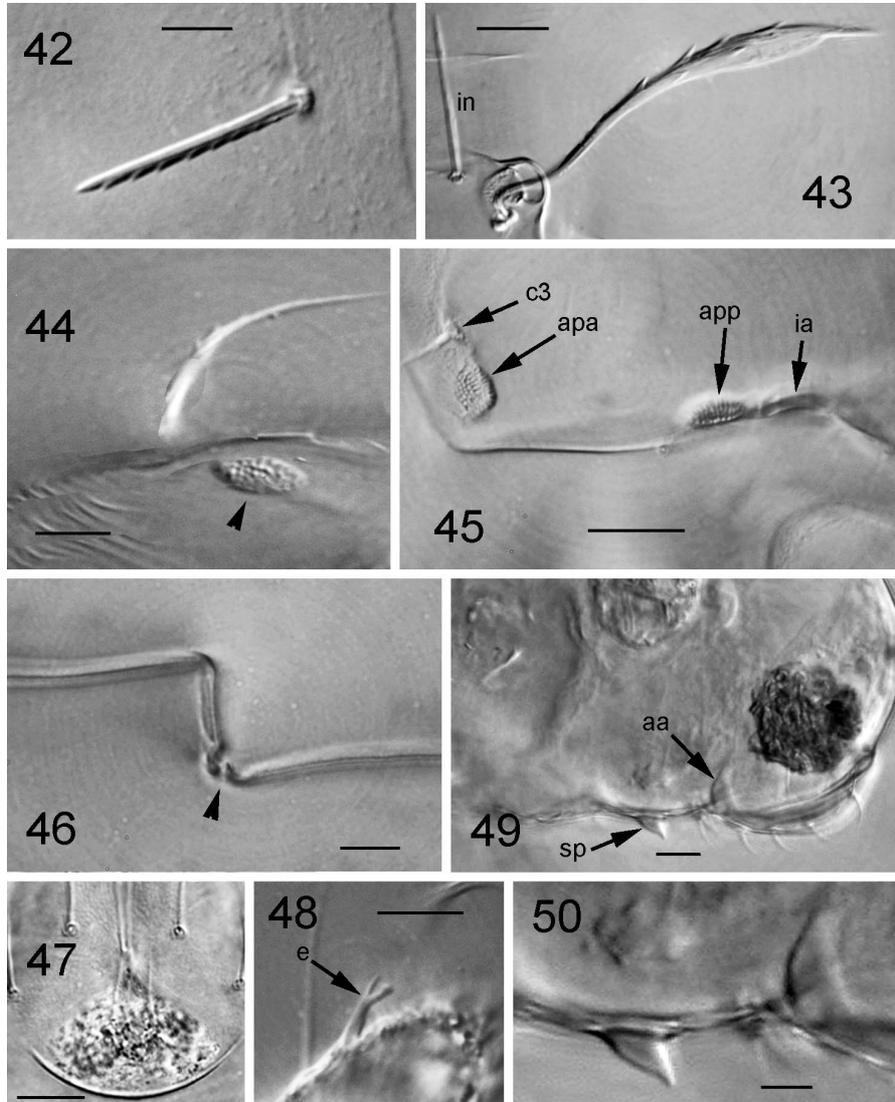
Figs 42–50. *Eniochthonius mahunkai* sp. n., immatures: 42 = notogastral seta c_1 of larva; 43 = bothridial seta and interlamellar seta (*in*) of larva, near-dorsal aspect; 44 = humeral region of larval notogaster, lateral aspect, showing porose area (arrowhead) and seta c_3; 45 = same, but tritonymph with pleural carina bearing posterior porose area (app) and cupule *ia* on underside seen by transparency (apa = anterior porose area); 46 = sagittal section of tritonymph notogaster at transverse scissure (anterior to left; arrowhead indicates extremely narrow articulating cuticle); 47 = subcapitulum of tritonymph, ventral aspect in polarized light, showing lack of demineralization in mentum; 48 = partial tarsus I of tritonymph, lateral aspect, showing famulus (e); 49 = posteroventral region of larval opisthosoma, lateral aspect, showing preanal spine (sp) and anal apodeme (aa); 50 = same, enlarged.
Scale bars: 10 μm (43, 45, 47–49), 5 μm (42, 44, 46, 50). Figs 42 and 44 layered images.

seen in La, Pn or Dn, but slight asymmetrical variations in Tn: of five individuals studied, one lacked seta *l'* from one trochanter IV, another lacked *v'* from one genu I and one genu III, and another lacked *it"* from one tarsus III. Seta *d* of genua II and III minute (2–3 μm), blunt, subspiniform in La, despite not being coupled to respective solenidia; both attaining adult shape and form in Pn. Seta *d* of genu I with similar change in form, but position also changes: one alveolar diameter distal to solenidion σ' in La, but 2–3 diameters distal in nymphs. Leg IV of Pn with typical numerical setation (0–0–0–0–7), but single fastigial seta slightly on anterior, rather than posterior face; position maintained to adult
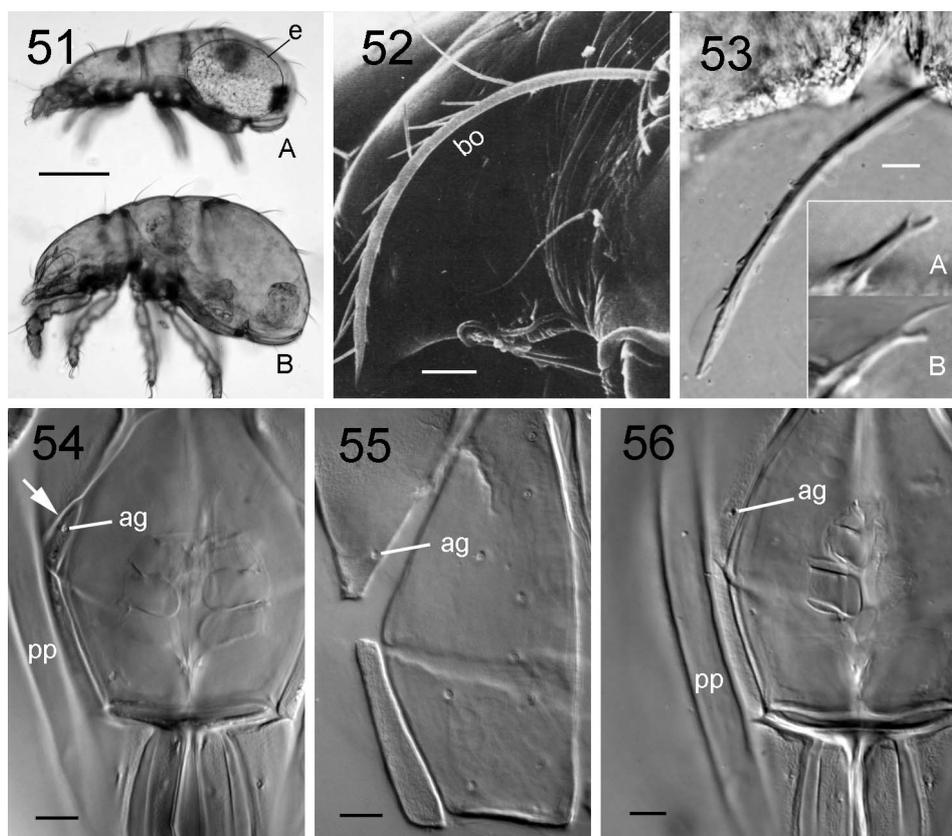
Figs 51–56. *Eniochthonius* spp., adults. 51A = lateral aspect of *E. mahunkai* n. sp. (top, e = egg); 51B = *E. minutissimus* (bottom) from same sample at Cicero, New York; 52 = *E. minutissimus*, anterolateral aspect of bothridial seta (*bo*) and nearby region, specimen from Germany; 53 = *E. crosbyi*, dorsal aspect of bothridial seta, with insert showing dorsolateral aspect of famulus of *E. crosbyi* (A) and *E. minutissimus* (B), each ca. 10 μm; 54 = *E. mahunkai* sp. n., ventral aspect of genital region (cf. Fig. 3; arrow points to oblique articulation between middle and anterior aggenital plates; 55 = *E. crosbyi*, same, but from dissected specimen; 56 = *E. minutissimus*, same (intact specimen from Poland). Scale bars: 100 μm (51), 10 μm (all others); ag = alveolus of aggenital seta; e = egg; pp = plicature plate. Fig. 52 SEM micrograph (from ALBERTI *et al.* 1994); others from light microscope with brightfield (51) or differential interference contrast; Fig. 53 insert layered.

(see Note 11). Solenidia on genua II and III and on tibia III less attenuated (ceratiform) in La, becoming attenuate (piliform) in Pn; other solenidia relatively unchanged through ontogeny. Immatures often have thinner branch of famulus not bract-like as in adult, but blunt and same length as knobbed branch (Fig. 48).

Gnathosoma. General structure as in adult except as noted. Subcapitulum with labiogenal groove slightly less conspicuous (see Note 12, Fig. 47). Adoral seta or_3 formed in Pn; genal seta m_2 formed in Dn. Palp femoral seta v'' *(inf)* formed in Dn, tarsal seta *cmp* formed in Pn.

Etymology. This species is named in honor of Dr. Sándor MAHUNKA (Hungarian Natural History Museum, Budapest), who has studied the systematics of acariform mites for more than four decades. Simply put, his explorations of the global diversity of oribatid mites are unmatched and invaluable.

Material examined. Holotype: USA; New York; Onondaga Co., Baldwinsville; Beaver Lake Nature Center, 43°10.69'N, 76°24.29'W, col. R.A. NORTON, 5-X-2005, ex: sphagnum moss on side of hummocks in lakeside fen. *Paratypes*: 130 adults with same data as holotype. Holotype and 10 paratypes deposited in the collection of the Division of Insects, Field Museum (FM), Chicago, Illinois. Other paratypes deposited as follows: 10 in the Hungarian Natural History Museum, Budapest; 10 in the Acarology Laboratory, The Ohio State University, Columbus, Ohio; 14 in the Canadian National Collection, Ottawa; and 86 in the collection of R. A. NORTON. All paratypes in alcohol except for several on slides in the latter two collections.

Other records. USA. New York. Onondaga Co., Cicero Game Management Area (43°08.87' N, 76°02.87'W), 3-V-2005, R. A. NORTON col., ex: *Sphagnum* and *Polytrichum* moss on sides of hummocks in blueberry bog. *Wisconsin.* Kenosha Co., Salem (W), Van Halter Bog, 15-VIII-1972, W. Suter, col., ex: sphagnum moss. **Canada**. *New Brunswick*. Kent Co., Kouchibouguac National Park, 16-VI–1978, E. Rickey, col., ex: sphagnum and rhododendron litter. *Nova Scotia.* Cape Breton Highlands National Park, North Mt. spruce forest and bog, 8-IX–1983, V. BEHAN-PELLETIER, col., ex: *Sarracenia*, *Sphagnum* and dwarf larch litter.

All known sites inhabited by *E. mahunkai* sp. n. are peatlands (fens or bogs), with sphagnum moss being a consistent component of the microhabitat. It is also consistently collected with *E. minutissimus*, although the microhabitat preferences of these species may differ. Based on unstructured sampling at the type locality and in a blueberry bog (technically a fen) at Cicero, New York, *E. mahunkai* is a dominant mite species in sphagnum moss on hummocks, while *E. minutissimus* is relatively infrequent. By contrast, in adjacent clumps of *Polytrichum* moss at each location *E. mahunkai* is much less abundant, about as frequent as *E. minutissimus*. In forest litter and humus about 100 m from the type locality *E. mahunkai* does not occur, but *E. minutissimus* is common.

COMPARISONS WITH OTHER SPECIES

North American species

The three species of *Eniochthonius* known to occur in eastern North America can be distinguished by the following key.

1.   Smaller species, 309–343 μm total length. Notogastral outline only moderately arched in lateral aspect (Fig. 51A), obovate in dorsal aspect; setae relatively long, f_1 reaching insertions of h_1 in dorsal aspect. Bothridial seta with 2–4 long tines (Figs 1, 13). Aggenital region with three plates; seta *ag* on small middle plate (Fig. 54). Tarsal setation (I–IV) 18–15–13–13; all tarsi with setae *it"* present, *it'* absent.   **E. mahunkai** sp. n.

–   Larger species, 360–400 μm total length. Notogastral outline strongly arched in lateral aspect (Fig. 51B), roughly diamond-shaped in dorsal aspect; setae shorter, f_1 not reaching insertion of h_1. Bothridial seta either with more than nine long tines or with none (Figs 52, 53). Aggenital region with two plates; seta *ag* on larger anterior plate (Figs 55–56). Tarsal setation 18–16–14–13; all tarsi with *it"* present, *it'* present on II and III, absent from I and IV.   2

2.   Bothridial seta pectinate, with nine or more long tines in addition to small barbs (Fig. 52). Body length about 360–380 μm. Thicker branch of forked famulus distally with slight knob, shorter than other (narrower, usually attenuate) branch (Fig. 53, insert B).   *E. minutissimus* (BERLESE)

–   Bothridial seta with small barbs, but without long tines (Fig. 53). Body length about 380–400 μm. Thicker branch of forked famulus distally with slight knob, slightly longer than other (narrower, distally blunt) branch (Fig. 53, insert A).
                                            E. crosbyi (EWING)

   Eniochthonius crosbyi. Including records summarized by MARSHALL *et al.* (1987) and those in Appendix A, this species is known from the states of Missouri, Minnesota, North Carolina, New York and New Hampshire, and from the provinces of Ontario, Québec, New Brunswick, Nova Scotia and Newfoundland. Habitats include both deciduous and coniferous forest litter and decaying wood, moss, bracket fungi and muskeg grass clumps.

   This species was redescribed by WOOLLEY (1956), based on illustrations of the second cotype mentioned above (Materials and Methods) made by E. W. BAKER. There are problems with the illustrations, and thus the redescription, of which the following are most important. Interlamellar and exobothridial setae are present. The bothridial seta (sensillus) was incorrectly described as "flagelliform", but the illustration is reasonably accurate except for the omission of the small barbs. The nature of the dark transverse bands of the notogaster was misinterpreted as two "sutures"; the tectiform scissure was not understood or described. Notogastral setae are not as uniformly arranged in longitudinal rows as illustrated; i.e., setal pair f_1 has a mutual distance less than that of e_1 or h_1; pair p_3 is drawn properly, but is incorrectly said to insert on the "ventral plate." Epimere IV is not separated from

the aggenital plate: the line drawn is an internal contour marking the epimeral border. The genital plate has the typical unsclerotized band separating anterior and posterior sections, as described for *E. mahunkai*. A typical preanal plate is present. The postpedal fossa is present in its typical location and both the taenidium and porose area are present, similar to those of *E. mahunkai* and *E. minutissimus*.

Eniochthonius minutissimus. This species is known from the states of Wisconsin, Michigan, New York, Maine, Vermont, Virginia, North Carolina, and Georgia, and from the provinces of Manitoba Ontario, Québec, New Brunswick, Nova Scotia, Newfoundland and the Northwest Territories (MARSHALL *et al.* 1987, Appendix A). Like *E. crosbyi*, it is eurytopic in forest litter, wood, moss, bracket fungi and muskeg grasses. It can co-occur with the latter species in litter samples, as in the collection by A. P. JACOT (see Materials and Methods), where the species are easily distinguished by size alone. Unlike *E. crosbyi*, it consistently co-occurs with *E. mahunkai* in *Sphagnum* peatlands; where adults can be easily separated by size and shape. Examples of authors who have illustrated *E. minutissimus*, include GRANDJEAN (1933, 1934, 1942, 1957), KUNST (1971), FUJIKAWA (1994) and WEIGMANN (2006).

GRANDJEAN (1957) illustrated and described seta or_2 of *E. minutissimus* as having a series of teeth, analogous to the rutellum. However, all of our specimens from Europe and North America have or_2 like that of *E. mahunkai* and *E. crosbyi*, with a medial row of at least 15 fine cilia. Sometimes several of these cilia cluster together, like a fine brush (cf. Fig. 14), giving the appearance of coarser teeth. The size range given in the key (360–380 µm) is for North American specimens; most European literature gives a similar range, but lengths up to 450 µm have been reported from Japan (FUJIKAWA 1994).

Oriental species

While *E. mahunkai* is the only North American species with an aggenital plate divided into three parts (the aggenital seta being on the small middle section), two eastern hemisphere species – *E. sumatranus* and *E. fukushimaensis* – share this trait. Both of the latter species have shorter notogastral setae (f_1 does not reach insertion of h_1) and more long tines (10 or more) on the bothridial seta (sensillus). The body length of *E. sumatranus* (310–342 µm) is similar to that of *E. mahunkai*, but *E. fukushimaensis* is larger (348–379 µm). The notogaster of *E. fukushimaensis* is obovate, like that of *E. mahunkai*, but that of *E. sumatranus* is diamond-shaped. The only other described species, *E. paludicolus*, differs from *E. mahunkai* in having a unique, two-part aggenital plate with the aggenital seta on the posterior section. The original figures of both Japanese species show a single seta *m* on the gena

of the subcapitulum; this suggests that the deutonymphal seta (m_2) of other species does not appear, but further study is needed. FUJIKAWA (1994) considered the position of lyrifissure *iad* and the famulus shape in *E. paludicolus* to be unique in *Eniochthonius.* However, the fissure she labeled *iad* is actually *ips*, in its normal position on the plicature plate; *iad* does not occur in any species of Enarthronota (the lyrifissure she labeled *ips* is actually *ih*). The famulus in *E. paludicolus* has the asymmetrically forked structure typical of the genus.

ENIOCHTHONIUS – REDESCRIPTION AND NOMENCLATURE

Redescription

The diagnosis of *Eniochthonius* by WEIGMANN (2006) is sufficient for identification, but traits of the genus have never been described in detail. As with his diagnosis, the following description serves for both the genus and family, since Eniochthoniidae includes only the type genus. It is based on our studies of: the three species we discuss above, including all their instars (except we have not seen the larva of *E. crosbyi*); a paratype adult of *E. sumatranus*; and literature descriptions of *E. paludicolus* and *E. fukushimaensis*. Not all relevant characters are yet known for the latter two species.

Adult. With characters of Hypochthonioidea (NORTON 1984, 2001; see Note 3). Thelytokous, males unknown. Integument with light sclerotization and epicuticular chambers mineralized with birefringent whewellite. Prodorsum fully articulated with proterosomal coxisternum; bothridium with three chambers, inner one spiculate, without porose pouch. Supracoxal seta (*eI*) spiniform, with minute distal fork or subterminal barb. Notogaster with transverse sulcus at level of setal row *d* and tectiform (telescoping, type-L) transverse scissure posterior to row *e*; pronotaspis bordered laterally by elongated suprapleural plate, bearing setae h_2 and h_3; pleural region continuous with pygidium, not isolated as pleuraspis. Pleural carina present dorsal to legs III, IV; anterior half of carina bears taenidium, which leaves carina to curve ventrad around leg IV; elongated porose area present within anterior part of taenidium. Normal five pairs of notogastral lyrifissures present; *ia* slit-like, at edge of taenidium, others cupular in form; *ip* far anterior in pleural region. Coxisternum with apodeme 3 short, apodeme 4 not evident. Articulations with leg trochanters sunken, no soft cuticle exposed, approaching ball-socket formation. Genital plate unusually large, pentagonal as pair, subdivided transversely by having narrow band with unsclerotized procuticle but mineralized epicuticle; with 10 pairs of setae in two longitudinal rows (3 lateral, 7 medial). Aggenital plate divided at same level as genital plate: posterior part narrow, elongated; anterior

part large, triangular, with or without secondary oblique scissure isolating small middle plate; anterior plate with postpedal fossa aligned with curving notogastral taenidium; single aggenital seta on anterior, posterior or middle plate (if subdivided). Ovipositor very short, with coronal setae. Anal and adanal plates distinct and fully articulated, with two and three pairs of setae, respectively; anal plates anteriorly with adjacent pair of horn-like apodemes. Paired plicature plate present, bearing lyrifissure *ips*. Legs monodactylous; articulation of segments approaching ball-socket formation, no soft cuticle exposed. Setation (legs I–IV, including famulus but not solenidia) of trochanters (0–0–2–2), femora (3–5–3–3), genua (5–3–3–3), tibiae (5–4–3–3), tarsi (18–15–13–13) or (18–16–14–13); iteral seta *it'* absent from tarsi I and IV, present or absent on II and III. Tarsus I with seta *m"*. Primilateral pair present on tarsus I, absent from III and IV; tarsus II with *pl'* but not *pl"*. Fundamental seta *bx'* present on femur II. Famulus forked, one branch thick, terminating bluntly or with slight knob-like swelling, other narrower, but with various form. Seta *d* of tibiae I and II minute, coupled to respective solenidion σ, in adjacent but separate alveoli; seta *d* of tibia III and of all genua independent of respective solenidia. Solenidial formula (legs I–IV) of genua (2–1–1–1), tibiae (1–1–1–0), tarsi (3–1–0–0). Subcapitulum anarthric but with groove in labiogenal position; gena with two or three setae; medial cilia of adoral seta *or₂* numerous (more than 10), those of pair meeting to form sieve; postpalpal seta distally forked, inserted at nearly right angle to vertical post-like tubercle. Palp setation 0–2–1–3–11, plus solenidion ω.

Immatures. Cuticle less sclerotized than adult, but equally mineralized. Bothridium with two chambers, inner one spiculate. Larva with two simple (type-E) transverse scissures, posterior to setal rows *d* and *e*, respectively; nymphs without anterior scissure, posterior scissure of unique form, with pronotaspis deflected sharply ventrad posterior to row *e* and linear, hinge-like articulation at its base. Suprapleural plate absent from larva; present in nymphs but shorter than that of adult, bears setae h_2 and h_3. Larva with single pair of small porose areas near seta c_3; nymphs with two pairs, second on weak pleural carina. Epimeral setation: La (3–1–2), Pn (3–1–2–1), Dn (3–1–3 –3), Tn (3–1–3–4); *1c* scaliform in larva. Genital setation (La-Tn): 0–1–3–7; aggenital seta formed in Tn or adult. La with adjacent pair of preanal spines, lost in later instars. Inguinal seta h_4 and p_4 present in La or not; if present, lost in later instars. Without paraproctal atrichosy or setal regressions; paraproctal setation 4–3–2–2 or 3–3–2–2 (La-Tn). Seta *d* of leg genua minute, subspiniform in La, normal in later instars. Protonymphal leg setation 0–0–0–0–7; unpaired fastigial seta on anterior face. Subcapitulum with adoral seta or_3 formed in Pn; genal seta m_2 (if present) formed in Dn. Palp femoral seta *v" (inf)* formed in Dn, tarsal seta *cmp* formed in Pn.

Nomenclatural problems

Since the original proposal of *Eniochthonius* by GRANDJEAN (1933), authors have been divided on using that genus name in preference to *Hypochthoniella* BER-LESE, 1910. Confusion stems from possible misidentification of the type species of the latter genus, as well as several subsequent proposals. The most relevant points are briefly described here in chronological order.

1. *Hypochthonius pallidulus* C. KOCH, 1835 was proposed based on material from Regensberg, Germany. There is no type specimen, and both the description and illustration are rudimentary.

2. NICOLET (1855) was first to doubt that KOCH's (1835) specimen was an adult mite. He considered both *H. rufulus* and *H. pallidulus* as "larvae" (used in the sense of immature) of *Leiosoma ovata* C. KOCH (= *Adoristes ovata* (C. KOCH)). For at least *H. rufulus* he was clearly incorrect.

3. MICHAEL (1888) did not follow NICOLET's (1855) assertion and applied the name *Hypochthonius pallidulus* to a mite that, from his clear description and illustrations, is recognizable with certainty as the common and widespread species herein called *Eniochthonius minutissimus* (see below). He did not discuss his interpretation of KOCH's original description, but we suppose that he focused on the rather diamond-shaped notogaster and two dark bands running transversely across it in KOCH's illustration. As described above, *Eniochthonius* species have two such bands in either transmitted or reflected light, one representing the thickened sulcus at setal row *d* on the pronotaspis and the other representing the anterior margin of the pygidium. MICHAEL incorrectly interpreted each of these as a "cut" (scissure), separating the "abdomen" (notogaster) into three parts. No other species of *Eniochthonius* is known to occur in Europe.

4. *Hypochthonius minutissimus* BERLESE, 1904 was proposed based on material from the Boboli Gardens in Florence.

5. In a brief footnote, BERLESE (1910) proposed *Hypocthoniella* (sic; a diminutive of *Hypochthonius*) as a subgenus of *Hypochthonius* C. KOCH. He included only *Hypochthonius pallidulus*, which became the type by monotypy; his species *H. minutissimus* was not mentioned. He wrote that *Hypocthoniella* was distinguishable from the nominate subgenus in having an "abdomen" divided into three parts (only two in *Hypochthonius* sensu stricto). BERLESE neither described nor illustrated his concept of *H. pallidula*, but this trait clearly indicates that he shared the interpretation of MICHAEL (1888). *Hypocthoniella* was subsequently elevated to genus rank and emended to *Hypochthoniella* (SELLNICK 1928; see also HAMMEN 1959).

6. Apparently unaware of BERLESE's (1910) paper, EWING (1917) proposed the genus *Arthrochthonius*, also with *Hypochthonius pallidulus* KOCH as type species.

7. In a footnote, GRANDJEAN (1933) stated unequivocally that KOCH's *Hypochthonius pallidulus* was a nymph of *Hypochthonius rufulus*. He gave no reasons for this interpretation, and we have found no illuminating statements in his subsequent publications. In his opinion such an interpretation had two consequences: 1) *Hypochthoniella* and *Arthrochthonius* were then junior synonyms of *Hypochthonius*; and 2) there was no named genus to accommodate the common mite described by MICHAEL (1888) as *H. pallidulus*. Therefore, he proposed the genus *Eniochthonius*; the etymology was not explained, but the prefix may derive from *aenigma* (L.) or *ainigma* (Gr.) since the situation was certainly enigmatic. Unfortunately, GRANDJEAN chose not to provide a new epithet for the type species, and used an inappropriate attribution: "*Eniochthonius pallidulus* (MICHAEL, 1888)." He did not discuss the various misinterpretations of morphology in the literature, but his excellent paper was the first to disclose the unique body structure of this genus of mites.

8. HAMMEN (1952) recognized the impropriety of GRANDJEAN's (1933) assignment of the species name *pallidulus* to MICHAEL (1888) and proposed the name *Eniochthonius grandjeani* for this common species.

9. In an important work on BERLESE's oribatid mites, HAMMEN (1959) examined type specimens of *Hypochthonius minutissimus* BERLESE. He agreed with BERLESE's handwritten indication that this was conspecific with *Hypochthonius pallidulus*, *sensu* MICHAEL (1888), and therefore with *Eniochthonius grandjeani*. He proposed the combination *Eniochthonius minutissimus* (BERLESE) as a senior synonym of *E. grandjeani*. However, he also maintained that the presence of labeled material in the BERLESE collection made the concept of *Hypochthoniella* unmistakable and that the name was therefore valid. He implied that the choice between generic names was simply a preference.

10. MARSHALL (1968) included the first use of the combination *Hypochthoniella minutissima* (BERLESE) of which we are aware.

11. MARSHALL *et al.* (1987) pointed out that the International Rules of Zoological Nomenclature require cases involving the misidentification of type species to be submitted to the International Commission on Zoological Nomenclature (ICZN) for ruling. They assumed that GRANDJEAN (1933) was correct, and concluded that, pending such a ruling, *Hypochthoniella* was invalid and *Eniochthonius* should be applied to the genus.

Both genus names continue to be used in the literature and the ICZN has not been petitioned for a decision. However, when authors have used *Hypochthoniella* in recent decades (e.g. PÉREZ-IÑIGO 1969, GHILAROV & KRIVOLUTSKY 1975, BALOGH & MAHUNKA 1983, SERGIENKO 1994, SUBÍAS 2004) the type species invariably has been given as *H. minutissimus* (BERLESE). This is clearly inappropri-

ate, since the use of *Hypochthoniella* assumes that MICHAEL's (1888) interpretation of *Hypochthonius pallidulus* was correct, making *H. minutissimus* a junior synonym. The name should be either *Hypochthoniella pallidula* (C. KOCH), or *Eniochthonius minutissimus* (BERLESE), depending on whether the respective opinion of MICHAEL (1888) or GRANDJEAN (1933) is believed.

In the absence of concrete statements, it is difficult to understand GRAND-JEAN's (1933) certainty that KOCH's mite was a nymph of the common species *Hypochthonius rufulus* and not an adult of *Eniochthonius minutissimus*. KOCH's figure seems synthetic. It has a posteriorly tapered notogaster with anterior width equal to that of the prodorsum and two dark transverse bands, all of which suggest *E. minutissimus*; by contrast, *H. rufulus* nymphs have a notogaster that is broad posteriorly, is noticeably wider than the prodorsum anteriorly, and has a single transverse band. However, the long notogastral setae and long interlamellar seta in KOCH's figure are consistent with *H. rufulus*, but not *E. minutissimus*. We see no clear choice and reiterate that this possible misidentification of type can only be formally judged by the ICZN.

NOTES

1. *Mineralization*. The mineralization pattern of both adult and immature *E. mahunkai* – revealed by polarized light in untreated specimens on all exposed parts of the body and appendages – is entirely consistent with that of *E. minutissimus*, described earlier (NORTON & BEHAN-PELLETIER 1991, ALBERTI *et al.* 2001). In the latter species whewellite (monohydrous calcium oxalate) is deposited in small epicuticular chambers. Since the same mineral is found in the related ptychoid species *Archoplophora rostralis* (WILLMANN), and in the more distant *Prototritia major* (JACOT), it probably also fills the chambers of all *Eniochthonius* species.

If untreated, the cuticle is hard and brittle, but when demineralized it becomes more elastic, similar to lightly sclerotized cuticle of non-mineralized Enarthronota. Probably the hardening caused by mineralization is a form of predator defense, one of many defenses known in oribatid mites (NORTON 2007). Epicuticular mineralization can even cover procuticle that is unsclerotized, as in the narrow transverse band dividing the genital plates of *Eniochthonius* species. It seems likely that the band exists to allow the large plates to flex during oviposition, as these mites have large eggs, about 2/5 of the body length (Fig. 51A, *e*); but even that narrow band is protected to some extent by mineralization.

Previously (NORTON & BEHAN-PELLETIER 1991) we suggested that the mineral may be obtained from fungal food, since calcium oxalate often accumulates on

the outside of hyphae as a waste product of incomplete carbohydrate metabolism. The food of *E. mahunkai* seems similar to that of *E. minutissimus* (op. cit.; see also WALLWORK 1964, PANDE & BERTHET 1973, ANDERSON 1975, SCHNEIDER *et al.* 2004). Ventricular and fecal boluses of both adult and immature *E. mahunkai* often contain many small unidentifiable organic fragments, but both clear and pigmented fungal hyphae are also common.

2. *Thelytoky*. Like other studied members of Hypochthonioidea (NORTON *et al.* 1993), all species of *Eniochthonius* are probably thelytokous (i.e. asexual, parthenogenetic). This remains unproven for any species of *Eniochthonius*, but GRANDJEAN (1941) found no males in a large sample of *E. minutissimus* from France, and we found none in any sample of the three species that we studied.

3. *Bothridial spicules: correction.* NORTON (2001) suggested that, among Enarthronota, having a bothridial wall that appeared densely porose was unique to Hypochthonioidea and Heterochthonioidea, though the trait needed further study. While the needed ultrastructural information is still not available, this generalization was incorrect. Among Hypochthonioidea, *Malacoangelia* and *Nothrolohmannia* have a small porose sac, or pouch, which still seems to be a synapomorphy of these two genera. However, in *Hypochthonius*, *Eohypochthonius, Eniochthonius*, and *Heterochthonius* what was interpreted as porosity of the innermost bothridial chamber seems instead to be dense spicules extending from a solid bothridial wall. The spicules could represent a special and highly localized form of cerotegument, as occurs in various more highly derived oribatid mites (e.g. ALBERTI *et al.* 1994), but this is uncertain.

4. *Pleural carina, taenidium and porose area.* GRANDJEAN (1933) illustrated porose areas in the humeral region of all instars of *Eniochthonius minutissimus*, but did not mention them in the text, or in any subsequent paper. His figures were overlooked by NORTON *et al.* (1997) while reviewing the known distribution of porose organs among oribatid mites.

Porose organs may be either respiratory or secretory, depending on the nature of underlying epidermal cells. The taenidium complex of *E. mahunkai*, which ends ventrally in the postpedal fossa and nearby depression, seems consistent with either respiratory or secretory functions. For example, taenidia (or peritremes) may be associated with respiratory surface plastrons (PUGH *et al.* 1987) and the fossa could anchor such a system. Other taenidia, such as the podocephalic canal, serve as open ducts to transport gland products (ALBERTI & COONS 1999). While we have no knowledge of the underlying epidermal cells in *E. mahunkai*, it seems likely that their porose areas are secretory. The areas are much too small to provide meaningful respiratory surface area, and they are not located in a region that would seem to have unusual localized respiratory needs; also, in the larva the porose areas are

immediately adjacent to a large expanse of soft cuticle that should itself be a more efficient respiratory surface. In mites, taenidia associated with gas exchange connect to internalized porose areas with large surface area, such as tracheae, but such is not the case in *E. mahunkai.* The postpedal fossa is certainly not respiratory – it is simply a small blind pouch lined with fully mineralized cuticle. Probably, the porose areas in all instars of *E. mahunkai* emit a surface secretion. In adults, the product is probably drawn posteriorly along the taenidium and across to the depression on the anterior aggenital plate; the fossa may serve to anchor a pool of secretion in this depression.

Notogastral porose areas are also known from other members of Hypochthonioidea, although not in association with a taenidium. Both *Nothrolohmannia* (Hypochthoniidae) and some Lohmanniidae have series of small porose areas, and these are known to be secretory in at least one lohmanniid (NORTON 2001, 2003, ALBERTI *et al.* 1997, 2001). Secretory porose areas are common in the humeral region of poronotic Brachypylina (e.g area Ah: GRANDJEAN 1962, ALBERTI *et al.* 1997), but since these mites are phylogenetically distant from *Eniochthonius* the organs are not likely to be homologues.

5. *Plicature plate.* Plates that lie between the notogaster proper and the adanal plates occur in various groups of macropyline oribatid mites, but their origin, and therefore homology, is not always obvious. In some cases they seem to represent a secondary intercalary plate evolved to stiffen a voluminous articulation, as in the plicature plate, or "sclerotized band of the ventral plicature," of Euphthiracaroidea (see GRANDJEAN 1967, SANDERS & NORTON 2004). In others, such as *Eniochthonius* and *Perlohmannia*, they bear lyrifissure *ips*; since the latter structure belongs to the pseudanal segment (the last segment to be added to the notogaster during ontogeny) these plicature plates may have become detached from an ancestrally complete notogaster by a secondary articulation.

6. *Lyrifissure ip.* This lyrifissure is present on the large majority of oribatid mites, where usually it is the most posterior of the five notogastral pairs. However, it seems to show plasticity in Hypochthonioidea: it has not been reported from any member of Hypochthoniidae and its anterior position on the notogaster of *Eniochthonius mahunkai* (and other species of the genus) is unusual. GRANDJEAN (1933, 1934) first illustrated this for *E. minutissimus*, but his ideas about anamorphosis and lyrifissure homologies were not perfected at that time. The notations used herein are quite certain: in the larva of *Eniochthonius* the cupule between the notogaster and paraprocts is in a position typical for *ih*; the cupule in the vicinity of seta c_3 can only be *ia;* and *im* is in the rather dorsal position typical for that lyrifissure in Hypochthonioidea (NORTON 2001). By default, the mid-pleural cupule

must be *ip*, and in the nymphs and adults it has moved even further forward to the anterior half of the opisthosoma, even slightly anterior to the level of *im*.

7. *Nature of rutellum.* The subcapitular rutellum of *Eniochthonius mahunkai* is similar in all observed details to that of *E. minutissimus* as described by GRAND-JEAN (1957). The distal region, which he interpreted as an ancestral seta, is fully and smoothly fused to a tubercle extending from the gena. This tubercle, or manubrium, is secondarily articulated at its base and is distinguished from the setal portion by the absence of actinopilin – cuticle that is birefringent in polarized light and which characterizes nearly all oribatid mite setae and their derivatives. It seems unlikely that, while studying these structures in polarized light, GRANDJEAN did not notice the striking birefringence of the mineralized epicuticular chambers. These are present on the manubrial portion of the rutellum, just as on the general cuticle of the body; i.e., the whole rutellum is birefringent, but for two different reasons. If he did observe the mineral-derived birefringence, he did not mention it in any publication known to us. GRANDJEAN studied material cleared in lactic acid, but we have found this weak acid to be ineffective at removing the minerals, at least over short periods of time.

8. *Setal ontogeny of segments H and PS.* In many endeostigmatid and early derivative oribatid mites, segments H and PS possess inguinal setae (GRANDJEAN 1942, 1949), a plesiomorphic state. These are setae that form in the larva at the end of the setal row, distal to the respective cupule if it is present (therefore *transcupular* setae), but normally are lost during development. Our study of *E. mahunkai* is the first to find h_4 and the first to find consistently well-developed p_4 in the larva of a species of *Eniochthonius*. GRANDJEAN (1933, 1949) found no trace of an inguinal seta on segment H of *E. minutissimus* and usually none on segment PS (cf. Fig. 38, right side), but did find p_4 vestigial or rarely well-developed in certain French populations. By contrast, in a population we identified as belonging to *E. minutissimus*, located in Warrensburg, New York, all larvae have both h_4 and p_4 well formed. With these discoveries of seta h_4 in larvae, character #23 of NORTON (1984) is shown to be incorrect.

9. *Preanal spines in larva.* STRENZKE (1963) described a pair of thorn-like structures anterior to the paraprocts of larval *Gehypochthonius xarifae* STRENZKE and these structures also exist in *G. urticinus* (BERLESE), a very similar species associated with sphagnum moss in eastern North America that often co-occurs with *E. mahunkai* (new observation). STRENZKE noted that structures with a similar position in larval *Eniochthonius minutissimus* were illustrated – but not discussed – by GRANDJEAN (1933). STRENZKE did not speculate about the nature or homology of these spines, but there are at least two possibilities to consider. In various endeostigmatid mites, Palaeosomata and Enarthronota, the larva has what have

been called vestiges of the "coxae" of suppressed leg pair IV (e.g. GRANDJEAN 1954, TRAVÉ 1967). But such structures are simple swellings, little resembling the preanal spines of *Gehypochthonius* and *Eniochthonius* (Figs 49, 50). Alternatively, the spines may represent precociously-formed genital papillae that normally appear in the secondary genital vestibule of the protonymph; they are surface structures since no vestibule exists in the larva. Like genital papillae the pair is closely adjacent, and they have a tapered shape in lateral aspect that is reminiscent of modified genital papillae in oppioid Brachypylina (BEHAN-PELLETIER 1991). Genital papillae are thought to be osmoregulatory structures (ALBERTI & COONS 1999), so this hypothesis could be tested by examining the spines for similar ultrastructural traits. Since *Gehypochthonius* and *Eniochthonius* are rather distantly related phylogenetically, if the spines prove to be osmoregulatory structures one could examine the idea that environmental moisture or another concomitant physiochemical trait of their shared habitat was a selective force in convergent acceleration of the first pair of papillae.

10. *Ontogeny of aggenital and genital setae*. The ontogeny of the single pair of aggenital setae is variable in *E. mahunkai*. Of the 12 tritonymphs studied, an aggenital seta appears on the lateral edge of both genital plates in five; it is only unilaterally present in six; and it is absent from both plates in one. According to GRANDJEAN (1949) it forms in the adult in *E. minutissimus* (listed as *E. pallidulus*), which was the only oribatid mite known to him to have this aggenital ontogeny; two tritonymphs from Poland that we studied are consistent with this, as they lacked the seta on both sides. We studied two tritonymphs of *E. crosbyi*: one had the seta on both sides, and one had it unilaterally present; when present, it inserts at the very lateral limit of sclerotization on the genital plate, as in *E. mahunkai*. Although the aggenital seta inserts on the genital plate if it forms in the tritonymph, there is no doubt of its identity, since no genital seta has such a position in the adult.

Few oribatid mites have the genital setal ontogeny of *Eniochthonius* (known now in *E. minutissimus*, *E. crosbyi* and *E. mahunkai*), which is 1–3–7–10 (protonymph to adult). In his 1949 summary, GRANDJEAN listed a species of the enarthronote genus *Cosmochthonius* as the only other example with this formula.

11. *Setation of tarsi*. All three studied species of *Eniochthonius* have a peculiar setation on tarsi III and IV: the single fastigial seta is distinctly on the anterior face (') throughout ontogeny (Fig. 41). This is also true of the paratype adult of *E. sumatranus*. Typically, if a single fastigial seta forms it is on the posterior face: *ft*". The oddity of this simple difference is especially clear in the context of the unusual development of tarsus IV in acariform mites, as described by GRANDJEAN (1946 and included references). When it first appears in the protonymph, leg IV has a

setation (trochanter to tarsus) of 0–0–0–0–7 in *Eniochthonius*. This formula is typical of endeostigmatid and oribatid mites, and the seven tarsal setae generally are the proral, unguinal and primiventral pairs, plus fastigial seta *ft"*. Within oribatid mites, GRANDJEAN (1946) claimed there were no exceptions to these setal homologies if seven setae were present in this instar, and we know of no exceptions reported in subsequent literature. Obviously, he knew *Eniochthonius* well, as he included the genus in virtually every survey of ontogenetic traits from 1933 onward. He implied that the seta was *ft"* in a collective statement about tarsus IV in various Enarthronota (GRANDJEAN 1964), but did not question its position on protonymphal tarsus IV.

There are two possible explanations for the *Eniochthonius* pattern. One is that the fastigial is indeed *ft'*, a seta that has been lost from the fundamental setation of tarsus IV in every other oribatid mite species; a corollary must be that *ft"* has been lost, in contrast to the rule. This could happen if regression from an ancestral fastigial pair has taken two different directions, but fastigials are never paired on tarsus IV of oribatid mite protonymphs, so the existence of this pair would have had to predate the suborder. A more parsimonious explanation is that seta *ft"* has shifted to the anterior face in *Eniochthonius*, but we know of no other examples where such a drastic shift has occurred. Therefore, we have labeled the seta simply as *ft* in Figs 8 and 41. A similar seta on tarsus III bears the same label, and poses the same problem: in other mites, when tarsus III has a single fastigial, it is also *ft"*.

The setation of tarsus IV in *E. mahunkai* has two other unusual traits. One is that seta *tc'*, which usually appears with *tc"* in the deutonymph of oribatid mites (GRANDJEAN 1946), is delayed to the tritonymph (Table 1). The other is the addition of a seta we interpret as *it"* in the tritonymph, just as on tarsus III. Previously iteral setae had not been identified on tarsus IV in any species of Hypochthonioidea. These accessory setae have the unusual distribution of being relatively common in derived groups (Desmonomata and Brachypylina), but rare in earlier-derivative groups. In his last review of the subject GRANDJEAN (1964) considered the few possible instances in Enarthronota and Palaeosomata to be questionable. In *E. mahunkai*, there seems to be no doubt that *it"* forms between *p"* and *tc"* and, as on other legs, it is not joined by *it'*. The effect of adding only one iteral is to distort the normal disjunction of the tectal pair (cf. left and right halves of Fig. 41). This seems to be the only known oribatid mite species with *it"* present and *it'* absent on all adult tarsi; in GRANDJEAN's (1964) style, the developmental formula would be unique: [0, n2] – [0, n3] – [0, n3] – [0, n3].

In *E. crosbyi* and *E. minutissimus* both iteral setae appear between the proral and tectal setae in the tritonymph, as a pseudosymmetrical pair, on tarsi II and III; they are either directly opposite each other or have a posterior (") disjunction. The result is that both tectal setae are displaced proximally to about an equal extent, so

that they are also approximately opposite each other in the tritonymph, like they are in the deutonymph. This contrasts clearly with their distribution on tarsi I and IV, where the tectal pair is staggered – has a strong anterior (') disjunction – in the tritonymph because *tc"* (but not *tc'*) is displaced proximally when *it"* appears; it is the same pattern as seen on all tarsi of *E. mahunkai* (e.g. Fig. 41).

GRANDJEAN (1964) had a different interpretation for tarsus IV of *E. minutissimus*: as part of a collective statement about several species of Enarthronota, he indicated that only two setae were added to this region of the tarsus during ontogeny, both in the tritonymph, and considered them the tectal pair; he believed iteral setae are entirely absent from this tarsus. In contrast, we have studied adults and immatures of this species from several European countries and the USA, and consistently three setae are added to this region of tarsus IV, in the manner we describe above.

The studied paratype adult of *E. sumatranus* has the same pattern of iteral setae as *E. crosbyi* and *E. minutissimus*: only *it"* is present on tarsi I and IV, but both *it'* and *it"* are on tarsi II and III. From the figures of FUJIKAWA (1994) *E. paludicolus* also has this pattern; relevant information is not available for *E. fukushimaensis*.

The pattern of primilateral setae in *Eniochthonius* species – both members of the pair present on tarsus I, only *pl'* on tarsus II, and none on tarsi III or IV – is rare in oribatid mites. According to the survey of GRANDJEAN (1959), it is shared only with the apparently unrelated genus *Eulohmannia*.

The distribution of the unusual seta *m"* ("poil monotrope") among early-derivative oribatid mites was reviewed by GRANDJEAN (1962). In *Eniochthonius* it is easily located, since it inserts in the middle of a line drawn between setae *s* and *pv"*.

12. *Seta bx' of femur II.* Early derivative oribatid mites (Palaeosomata, some Enarthronota, Parhyposomata) have three fundamental (larval) setae on femur II, rather than the normal two, which are *d* and *bv"*. The additional seta, which has been lost from more derived taxa (and presumably also lost from femur I of all oribatid mites), is on the anterior face. GRANDJEAN (1965) designated it *bx'*, since it occurs on the basifemur in Palaeosomata (but whether in the *l* or *v* range was equivocal), and speculated that it could be the metameric homologue of *ev'* on legs III and IV. *Eniochthonius minutissimus* is one of the enarthronotes in which he found this seta, and it also occurs in *E. mahunkai*, in all instars (Table 1, Fig. 6). In *E. crosbyi* a seta with a similar position is present in the protonymph, but we have not observed the larva.

GRANDJEAN (1965) noted that *bx'* is present on femur II of *Parhypochthonius*, but he accepted STRENZKE's opinion (1963, his Fig. 26) that the third fundamental seta in *Gehypochthonius xarifae* was *l"*, on the posterior face, and presented this as anomalous. We studied the larva of the very similar species, *G.*

urticinus (see Note 9) and there is no such anomaly; it has three femur II setae, *d*, *bv"* and *bx'*. Clearly, the problem stems from a mislabeling of STRENZKE's Fig. 26: the very proximal seta that he labeled *l"* is actually *bv"* (*bv"* is always the most proximal ventral seta of femora I and II in oribatid mites) and what he labeled *bv* is actually *bx'*. STRENZKE's Figs 16 and 20, which show the leg attached to the body, are more conclusive: these show clearly that the extra seta relative to femur I is at mid-level on the anterior face, i.e. typical of *bx'*, and the figures exactly replicate our larvae of *G. urticinus*.

13. *Ontogeny of leg setae in other species.* The distribution and ontogeny of all setae and solenidia on the legs of *E. minutissimus* and *E. crosbyi* were studied, except the larva of *E. crosbyi* was not available. Other than the addition of iteral setae *it'* on tarsi II and III in the tritonymph, *E. minutissimus* does not differ from *E. mahunkai* (Table 1); it is even variable in the formation of seta *v'* on genu III. Except for the iteral setae, *E. crosbyi* differed only in the following small and perhaps variable ways. Seta *l'* of genu IV was present on both legs IV of our single deutonymph of *E. crosbyi*. This same specimen also had formed *v'* on one genu III, i.e., earlier than in the other two species, and this setae was present on both legs of the two tritonymphs studied.

14. *Anarthric nature of the subcapitulum.* As noted by GRANDJEAN (1957), the subcapitulum of *Eniochthonius minutissimus* (as *E. pallidulus*) is anarthric, i.e. there is no articulation separating paired genae and an unpaired central mentum. This is true of most Enarthronota, and distinguishes them from more derived groups of oribatid mites (e.g. Parhyposomata, Mixonomata and most Desmonomata) that have an inverted V-shaped labiogenal articulation isolating genae and mentum, i.e. the stenarthric construction. However, *Eniochthonius* species have a well defined groove that runs in the exact position of such an articulation (Fig. 20). The groove is fully hardened, but may reflect a suture line between ancestrally separate subcapitular plates. Another indication that these plates had a history of being separate is that when we observed demineralization in nymphs, the genae frequently lost minerals first, leaving a precisely delineated, birefringent, triangular mentum (Fig. 47). According to GRANDJEAN (1957), anarthry in Enarthronota is a primitive state, but the grooves and mineralization pattern of the subcapitulum in *Eniochthonius* might be considered support for WEIGMANN's (1996) contrary idea, that a separate mentum is primitive, and that anarthry is secondarily derived from stenarthry.

<div align="center">*</div>

REFERENCES

ALBERTI, G. (1979) Fine structure and probable function of genital papillae and Claparede organs of Actinotricha. Pp. 501–507. *In* RODRIGUEZ, J. G. (ed.): *Recent Advances in Acarology*, vol. 2. Academic Press, Inc., New York.

ALBERTI, G. (1998) Fine structure of receptor organs in oribatid mites (Acari). Pp. 27–77. *In* EBERMANN, E. (ed.): *Arthropod biology: Contributions to morphology, ecology and systematics. Biosystematics and Ecology Series 14*. Österreichische Akademie der Wissenschaften.

ALBERTI, G. & COONS, B. (1999) *Microscopic anatomy of invertebrates. Volume 8C: Chelicerate Arthropoda*. Wiley-Liss, New York, 768 pp.

ALBERTI, G., MORENO, A. I. & KRATZMANN, M. (1994) The fine structure of trichobothria in moss mites with special emphasis on Acrogalumna longipluma (Berlese, 1904) (Oribatida, Acari, Arachnida). *Acta Zoologica*, *Stockholm* **75**: 57–74.

ALBERTI, G., NORTON, R. A. & KASBOHN, J. (2001) Fine structure and mineralisation of cuticle in Enarthronota and Lohmannioidea. Pp. 230–241. *In* HALLIDAY, R. B., WALTER, D. E., PROCTOR, H. C., NORTON, R. A. & COLLOFF, M. J. (eds): *Acarology: Proceedings of the 10th International Congress*. CSIRO Publishing, Melbourne, Australia.

ALBERTI, G., NORTON, R. A., ADIS, J., FERNANDEZ, N. A., FRANKLIN, E., KRATZMANN, M., MORENO, A. I., WEIGMANN, G. & WOAS, S. (1997) Porose integumental organs of oribatid mites (Acari, Oribatida). 2. Fine structure. *Zoologica*, *Stuttgart* **146**: 33–114.

ANDERSON, J. M. (1975) Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *Journal of Animal Ecology* **44**: 475–495.

BALOGH, J. & MAHUNKA, S. (1983) *Primitive oribatids of the Palaearctic Region. The soil mites of the World*, *Vol. 1*. Akadémiai Kiadó, Budapest, 372 pp.

BEHAN-PELLETIER, V. M. (1991) Observations on genital papillae of pycnonotic Brachypylina (Acari: Oribatida). *Acarologia* **32**: 71–78.

BERLESE, A. (1904) Acari nuovi. Manipulus I. *Redia* **1**: 226–252.

BERLESE, A. (1910) Acari nuovi. Manipulus V–VI. *Redia* **6**: 199–234.

EWING, H. E. (1909) New American Oribatoidea. *Journal of the New York Entomological Society* **17**: 116–136.

EWING, H. E. (1917) A synopsis of the genera of beetle-mites with special reference to the North American fauna. *Annals of the Entomological Society of America* **10**: 117–132.

FUJIKAWA, T. (1994) Oribatid mites from Picea glehni forest at Mo-Ashoro, Hokkaido (10) A new species of the family Eniochthoniidae. *Edaphologia* **52**: 19–27.

GHILAROV, M. S. & KRIVOLUTSKY, D. A. (eds) (1975) *Key to soil-inhabiting mites – Sarcopti-formes*. Nauka Publications, Moscow, 492 pp. [In Russian]

GRANDJEAN, F. (1933) Étude sur le développement des Oribates. *Bulletin de la Société Zoologique de France* **58**: 30–61.

GRANDJEAN, F. (1934) La notation des poils gastronotiques et des poils dorsaux du propodosoma chez les Oribates (Acariens). *Bulletin de la Société Zoologique de France* **59**: 12–44.

GRANDJEAN, F. (1940) Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates. Deuxième partie. *Bulletin de la Société Zoologique de France* **45**: 32–44.

GRANDJEAN, F. (1941) Statistique sexuelle et parthénogénèse chez les Oribates (Acariens). *Comptes Rendus Seances de l'Academie des Sciences* **212**: 463–467.

GRANDJEAN, F. (1942) Quelques genres d'Acariens appartenant au groupe des Endeostigmata (2e série). *Annales des Sciences Naturelles Zoologie 11ᵉ série* **4**: 85–135.

GRANDJEAN, F. (1942) La chaetotaxie comparée des pattes chez les Oribates (2e série). *Bulletin de la Société Zoologique de France* **67**: 40–53.

GRANDJEAN, F. (1946) Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates. Troisième partie. *Bulletin de la Société Zoologique de France* **71**: 10–29.

GRANDJEAN, F. (1947) Les Enarthronota (Acariens). Première série. *Annales des Sciences Naturel-les Zoologie 11ᵉ série* **8**: 213–248.

GRANDJEAN, F. (1949) Observation et conservation des tres petits Arthropodes. *Bulletin du Muséum national d'Historie naturelle, 2ᵉ série* **21**: 363–370.

GRANDJEAN, F. (1949) Formules anales, gastronotiques, génitales et aggénitales du développement numériques des poils chez les Oribates. *Bulletin de la Société Zoologique de France* **74**: 201–225.

GRANDJEAN, F. (1954) Les Enarthronota (Acariens) (4ᵉ série). *Annales des Sciences Naturale Zoo-logie, 11ᵉ série* **16**: 311–335.

GRANDJEAN, F. (1957) L'infracapitulum et la manducation chez les Oribates et d'autres Acariens. *Annales des Sciences Naturel Zoologie, 11ᵉ série* **19**: 233–281.

GRANDJEAN, F. (1959) Observations sur les Oribates (40e série). *Bulletin du Muséum national d'Historie naturelle, 2ᵉ série* **31**: 359–366.

GRANDJEAN, F. (1962) Nouvelles observations sur les Oribates (2ᵉ série). *Acarologia* **4**: 396–422.

GRANDJEAN, F. (1964) Nouvelles observations sur les Oribates (3ᵉ série). *Acarologia* **6**: 170–198.

GRANDJEAN, F. (1965) Nouvelles observations sur les Oribates (4ᵉ série). *Acarologia* **7**: 91–112.

GRANDJEAN, F. (1967) Nouvelles observations sur les Oribates (5ᵉ série). *Acarologia* **9**: 242–272.

HAMMEN, L. VAN DER (1952) The Oribatei (Acari) of the Netherlands. *Zoologische Verhandelingen, Leiden* **17**: 1–139.

HAMMEN, L. VAN DER (1959) Berlese's primitive oribatid mites. *Zoologische Verhandelingen, Leiden* **40**: 1–93.

HAMMEN, L. VAN DER (1980) *Glossary of acarological terminology. Part 1: General terminology*. Junk Publishers, The Hague, 270 pp.

HUNT, G. S., NORTON, R. A., KELLY, J. P. H., COLLOFF, M. J. & LINDSAY, S. M. (1998): *An interactive glossary of oribatid mites*. CD-ROM, CSIRO Publishing, Melbourne.

KOCH, C. L. (1835) *Deutschlands Crustaceen, Myriapoden und Arachniden. Ein Beitrag zur Deutschen Fauna, Heft 1–3*. Herrich-Schäfer, Regensburg.

KRANTZ, G. W. (1978) *A manual of Acarology*. 2nd ed., Oregon State University, Corvallis, Oregon: 509 pp.

KUNST, M. (1971) Nadkohorta Pancirnici – Oribatei. Pp. 531–580. *In*: DANIEL, M. & CERNY, V. (eds): *Klic zvireny CSSR IV*. Academia, Praha.

MAHUNKA, S. (1989) New and interesting mites from the Geneva Museum LXV. Oribatids of Suma-
tra (Indonesia) I. (Acari: Oribatida). *Revue Suisse Zoologie* **96**: 673–696.

MAHUNKA, S. (1993) Oribatids from Madagascar I (Acari: Oribatida). New and interesting mites
from the Geneva Museum LXXVI. *Revue Suisse Zoologie* **100**: 289–315.

MAHUNKA, S. (1997) Oribatids from Brunei II. (Acari, Oribatida) (Acarologia Genavensia LXXXII).
Revue Suisse Zoologie **104**: 661–700.

MAHUNKA, S. & MAHUNKA-PAPP, L. (1995) *The oribatid species described by Berlese (Acari)*.
Hungarian Natural History Museum, Budapest, 325 pp.

MARSHALL, V. G. (1968) Microarthropods from two Quebec woodland humus forms. III. The
Sarcoptiformes (Acarina). *Annales de la Societe Entomologique du Québec* **13**: 65–88.

MARSHALL, V. G., REEVES, R. M. & NORTON, R. A. (1987) Catalogue of the Oribatida of continen-
tal United States and Canada. *Memoirs of the Entomological Society of Canada* **139**: 1–418.

MICHAEL, A. D. (1888) *British Oribatidae. Vol. II*. Ray Society, London, pp. 337–657.

NICOLET, H. (1855) Histoire naturelle des Acariens qui se trouvent aux environs de Paris. *Archives
du Museum d'Histoire naturelle, Paris* **7**: 381–482.

NORTON, R. A. (1977) A review of F. Grandjean's system of leg-chaetotaxy in the Oribatei and its
application to the Damaeidae. Pp. 33–62. *In* DINDAL, D. L. (ed.): *Biology of oribatid mites*.
State University of New York, Syracuse.

NORTON, R. A. (1984) Monophyletic groups in the Enarthronota (Sarcoptiformes). Pp. 233–240. *In*
GRIFFITHS, D. A. & BOWMAN, C. E. (eds): *Acarology VI*, *Vol. 1*. Horwood, Chichester.

NORTON, R. A. (2001) Systematic relationships of Nothrolohmanniidae, and the evolutionary plas-
ticity of body form in Enarthronota (Acari: Oribatida). Pp. 58–75. *In* HALLIDAY, R. B., WAL-
TER, D. E., PROCTOR, H. C., NORTON, R. A., COLLOFF, M. J. (eds): *Acarology: Proceedings of
the 10th International Congress*. CSIRO Publishing, Melbourne, Australia.

NORTON, R. A. (2003) Nothrolohmannia baloghi sp. n. (Acari, Oribatida) from rainforest in Papua
New Guinea, and reevaluation of Nothrolohmanniidae. *Acta Zoologica Academiae Scientia-
rum Hungaricae* **49**: 25–42.

NORTON, R. A. (2007, in press) Holistic acarology and ultimate causes: examples from the oribatid
mites. *In* MORALES-MALACARA, J. B., BEHAN-PELLETIER, V., UECKERMANN, E., PÉREZ, T.
M., ESTRADA-VENEGAS, E. G. & BADII, M. (eds): *Acarology XI: Proceedings of the Interna-
tional Congress*. Universidad Nacional Autónoma de México, México.

NORTON, R. A. & BEHAN-PELLETIER, V. M. (1991) Calcium carbonate and calcium oxalate as cuti-
cular hardening agents in oribatid mites (Acari: Oribatida). *Canadian Journal of Zoology* **69**:
1504–1511.

NORTON, R. A. & BEHAN-PELLETIER, V. M. (2008, in press) Oribatida. *In* KRANTZ, G. W. &
WALTER, D. E. (eds): *A Manual of Acarology, Third edition*. Texas Tech University Press,
Lubbock.

NORTON, R. A., KETHLEY, J. B., JOHNSTON, D. E. & OCONNOR, B. M. (1993) Phylogenetic perspec-
tives on genetic systems and reproductive modes of mites. Pp. 8–99. *In* WRENSCH, D. L. &
EBBERT, M. A. (eds): *Evolution and diversity of sex ratio in insects and mites*. Chapman and
Hall, New York.

NORTON, R. A., ALBERTI, G., WEIGMANN, G. & WOAS, S. (1997) Porose integumental organs of
oribatid mites (Acari, Oribatida). 1. Overview of types and distribution. *Zoologica, Stuttgart*
146: 1–31.

PANDE, Y. D. & BERTHET, P. (1973) Studies on the food and feeding habits of soil Oribatei in a black
pine plantation. *Oecologia* **12**: 413–426.

PÉREZ-IÑIGO, C. (1969) Acaros Oribátidos de suelos de España Peninsular e Islas Baleares (1a parte)
(Acari, Oribatei). *Graellsia* **24**: 143–238.

PUGH, P. J. A., KING, P. E. & FORDY, M. R. (1990) Respiration in Fortuynia maculata Luxton (Fortuyniidae, Cryptostigmata, Acarina) with particular reference to the role of van der Hammens Organ. *Journal of Natural History* **24**: 1529–1547.

SANDERS, F. H. & NORTON, R. A. (2003) Anatomy and function of the ptychoid defensive mechanism in the mite Euphthiracarus cooki (Acari: Oribatida). *Journal of Morphology* **259**: 119–154.

SCHNEIDER, K., MIGGE, S., NORTON, R. A., SCHEU, S., LANGEL, R., REINEKING, A. & MARAUN, M. (2004) Trophic niche differentiation in oribatid mites (Oribatida, Acari): evidence from stable isotope ratios (15N / 14N). *Soil Biology & Biochemistry* **36**: 1769–1774.

SELLNICK, M. (1928) Formenkreis: Hornmilben, Oribatei. Pp. 1–42. *In* BROHMER, P., EHRMANN, P. & ULMER, G. (eds): *Die Tierwelt Mitteleuropas* 3 (4). Quelle & Meyer, Leipzig.

SERGIENKO, G. D. (1994) Lower Oribatids. Pp. 5–204. *In* TOPACEVSKIJ, A. V. (ed.): *Fauna of the Ukraine* 25 (21). Naukova Dumka, Kiev. [In Russian]

SHIRAISHI, H. & AOKI, J. (1994) A new species of the genus Hypochthoniella (Acari: Oribatida) from soils on the suburban roadside in Fukushima City. *Edaphologia* **52**: 29–32.

STRENZKE, K. (1963) Entwicklung und Verwandtschaftsbeziehungen der Oribatidengattung Gehypochthonius (Arach., Acari). *Senckenbergiana Biologica* **44**: 231–255.

SUBÍAS, L. S. (2004) Listado sistemático, sinonímico y biogeográfico de los ácaros oribátidos (Acariformes, Oribatida) de mundo (1758–2002). *Graellsia* **60**: 3–305.

TRAVÉ, J. (1967) Phyllochthonius aoutii nov. gen., nov. spec., un Enarthronota (Acarien, Oribate) nouveau de Cote d'Ivoire, avec la creation d'une superfamilie nouvelle, Phyllochthonoidea. *Zoologische Mededelingen, Leiden* **42**: 83–105.

TRAVÉ, J. & VACHON, M. (1975) François Grandjean, 1882–1975 (Notice biographique et bibliographique). *Acarologia* **17**: 1–19.

WALLWORK, J. A. (1958) Notes on the feeding behaviour of some forest soil Acarina. *Oikos* **9**: 260–271.

WEIGMANN, G. (1996) Hypostome morphology of Malaconothroidea and phylogenetic conclusions on primitive Oribatida. Pp. 273–276. *In* MITCHELL, R., HORN, D. J., NEEDHAM, G. R. & WELBOURN, C. W. (eds): *Acarology IX – Proceedings, Vol. 1.* Ohio Biological Survey, Columbus, Ohio.

WEIGMANN, G. (2006) *Hornmilben (Oribatida). Die Tierwelt Deutschlands, t. 76.* Goecke & Evers, Keltern, 520 pp.

WOOLLEY, T. A. (1956) Redescription of Tumidalvus americana Ewing and Hypochthonius crosbyi Ewing (Acarina: Oribatei, Hypochthoniidae). *Proceedings of the Entomological Society of Washington* **58**: 287–291.

APPENDIX

New distribution records of *Eniochthonius minutissimus* and *E. crosbyi* in North America. Different habitats separated by a ';'. Abbreviations: CNC = Canadian National Collection of Insects and Arachnids, Ottawa, ON; RNC = Collection of R. A. NORTON, Syracuse, New York.

Eniochthonius minutissimus (BERLESE)		
State/Province	Habitat	Coll.
QUÉBEC		
Parc Frontenac	*Larix, Ledum, Vaccinium, Viburnum* litter	CNC
NEW BRUNSWICK		
Kouchibouguac National Park	Coniferous litter & moss; *Sphagnum* and bark; moss & litter; Decaying wood & bark from fallen beech; Den in mixed woods; Moss & litter at base of beech trunk; Mixed decidu-ous, fern, conifer litter	CNC
NOVA SCOTIA		
Liscombe Mills Camp	Mixed conifer litter, larch	CNC
Cape Breton Highlands National Park	Litter at base of old Red oak; Spruce, birch, *Shepherdia* litter; Spruce, fern, cherry litter; *Juniper*, moss *Arctostaphylos* litter; Sugar maple litter; Bracken litter; Beech litter; Decaying veg-etation & moss by stream; Rose, *Shepherdia* litter at edge of lake; Spruce litter, moss & ferns	CNC
NEWFOUNDLAND		
Gros Morne National Park	*Ledum, Myrica, Kalmia* litter; Grass clumps in muskeg; Spruce & fir litter above sea-shore	CNC
Terra Nova National Park	*Ledum, Myrica, Chamaedaphnae* litter with wet moss	CNC
Avalon Peninsula, 5 km S Cochrane Pond	Moss	CNC
2 mi N Eddies Cove	Crowberry, *Vaccinium, Rubus, Juniper* litter	CNC
MAINE		
Old Orchard Beach, Pinehurst Campground,	Mixed conifer litter	CNC
VERMONT		
North Dorset, Emerald Lake Campground	Moss near lake edge	CNC
Mount Equinox	Fern litter	CNC
Mount Mansfield State Forest	Maple & beech litter	
NEW YORK		
Warrensburg, Pack Forest	*Pinus resinosa* litter	RNC
Syracuse, LaFayette Forest Exper. Station	Forest litter	RNC

APPENDIX (continued)

State/Province	Habitat	Coll.
Baldwinsville, Beaver Lake Nature Center	*Sphagnum* and *Polytrichum* moss on hummocks	RNC
Cicero, NY Game Management Area	*Sphagnum* and *Polytrichum* moss on hummocks	RNC
VIRGINIA		
Mountain Lake	Deciduous duff	CNC
Great Smoky Mountains National Park	Oak, hemlock litter	CNC
GEORGIA		
Crooked River State Park	Bract fungus on old snag	CNC
WISCONSIN		
Nicolet National Forest	Hemlock & birch litter	CNC
Salem, Van Halter Bog	*Sphagnum* moss	RNC
Eniochthonius crosbyi (EWING)		
QUÉBEC		
Gaspesie National Park	muskeg	CNC
ONTARIO		
St. Lawrence Islands National Park	Soil beneath moss mat; Mossy litter in seepage area; Mouse nest; Decaying log	CNC
NEW BRUNSWICK		
Kouchibouguac National Park	Coniferous litter & moss; Leaf litter by river; Mossy litter in spring seepage area	CNC
NOVA SCOTIA		
Cape Breton Highlands National Park	*Ledum, Vaccinium, Larix* litter; Bract fungus on dead sugar maple; Thick spruce litter & moss; Beech, spruce, maple litter	CNC
NEWFOUNDLAND		
Gros Morne National Park	*Ledum, Myrica, Kalmia* litter	CNC
Terra Nova National Park	*Ledum, Myrica* litter with wet moss	CNC
2 mi N Eddies Cove	Crowberry, *Vaccinium, Rubus, Juniper* litter	CNC
Pasadena	Bract fungus on fir stump	CNC
40 mi W St. John's	Muskeg grass clumps, moss	CNC
MISSOURI		
Roaring Rocks State Park	Dripping moss on wet rocks	CNC
NEW YORK		
Warrensburg, Pack Forest	*Pinus resinosa* litter	RNC
NORTH CAROLINA		
Durham; Duke Forest	*Pinus taeda* litter	RNC