

NOTHROLOHMANNIA BALOGHI SP. N. (ACARI: ORIBATIDA),
FROM RAINFOREST IN PAPUA NEW GUINEA, AND
REEVALUATION OF NOTHROLOHMANNIIDAE

R. A. NORTON

*State University of New York, College of Environmental Science and Forestry
Syracuse, New York, USA 13210, E-mail: ranorton@esf.edu*

Nothrolohmannia is a genus of oribatid mites that is endemic to Papua New Guinea (PNG). It has remained monotypic (type species: *N. calcarata*, from eastern PNG) since its proposal and its monobasic family, Nothrolohmanniidae, has been moved to various superfamilies as ideas about relationships changed. A second species, distinguishable by smaller adult size, proportionally smaller setae, and other details, has been collected from rainforest leaf litter in western PNG and is described below as *N. baloghi* sp. n. *Nothrolohmannia* is considered the sister-genus of *Malacoangelia*, which is an unquestioned member of the enarthronote family Hypochthoniidae. Nothrolohmanniidae is therefore reduced to subfamily rank, and expanded in scope to include the latter genus. New diagnoses are presented for Hypochthoniinae, Nothrolohmanninae, *Malacoangelia* and *Nothrolohmannia*.

Key words: oribatid mite, Hypochthoniidae, *Enarthronota*, rainforests

INTRODUCTION

Nothrolohmannia is historically a rather enigmatic genus of macropyline oribatid mites that is unique to rainforest soil in Papua New Guinea. When first proposed by JÁNOS BALOGH (1968), *Nothrolohmannia* was monotypic – the type species being *N. calcarata* BALOGH. No other distributional records have since been published, and no other species of the genus has been named. While the etymology was not explained, the name *Nothrolohmannia* suggests a synthetic appearance, having traits of Nothridae and Lohmanniidae, which are two phylogenetically distant macropyline families. The species epithet *calcarata* probably was in reference to the spurs that are present on the basal leg segments. In the original description, BALOGH proposed the monobasic family Nothrolohmanniidae, but its relationships with other macropyline taxa were not discussed.

Four very different opinions of these relationships exist in the subsequent literature. BALOGH (1972) included the family in Lohmannioidea, along with Lohmanniidae and Xenolohmanniidae. In a cladistic analysis, HAUMANN (1991) considered Nothrolohmanniidae to be the earliest derivative member of the large taxon Holonota, i.e. without close relationship to Lohmanniidae. BALOGH and BALOGH (1992) transferred Nothrolohmanniidae to the Desmonomata, as part of

Crotonioidea (which includes Nothridae). Recently (NORTON 2001), I used a cladistic approach to suggest that *Nothrolohmannia* is the sister-taxon of *Malacoangelia*, the latter being an unquestioned member of the enarthronote family Hypochthoniidae.

The latter study was based largely on a second, unnamed species of *Nothrolohmannia*, the description of which is the main purpose of this paper. It is named in honor of the late JÁNOS BALOGH, a pioneer in the exploration of global oribatid mite diversity. Among his many scientific contributions, perhaps most influential was a series of genus-level taxonomic compilations (1961, 1963, 1965, 1972, 1992) that introduced this fascinating group of animals to two or three generations of acarologists and soil biologists. My own interest in oribatid mites began in earnest when I obtained his 1965 paper, five years after its publication.

Following the description of *Nothrolohmannia baloghi* sp. n., the internal classification of Hypochthoniidae is examined. As briefly suggested earlier (NORTON 2001), Nothrolohmanniidae is lowered to subfamily rank within Hypochthoniidae, and is conceptually expanded to include *Malacoangelia*. New diagnoses for relevant taxa are proposed.

MATERIALS AND METHODS

Specimens of *Nothrolohmannia baloghi* sp. n. were discovered in the unsorted Berlese-funnel collections of the Australian National Insect Collection (CSIRO, Canberra); detailed collection information is below. The holotype of *N. calcarata* was studied, as well as a single topotypic adult taken from the same Berlese-funnel extract as the type series, which was collected at Lae, in eastern Papua New Guinea (6°44'S, 147°0'E). A single protonymph of a *Nothrolohmannia* species was studied, found in a sample collected by BALOGH from roots and soil at 4,800 m elevation on Mt. Wilhelm, and used to address a leg setation question. Since no adult *Nothrolohmannia* was in samples from that region, the species identity of the protonymph is not certain; however, it has the general appearance of *N. calcarata*, including very long lamellar setae and barbed sensillus (see below). Specimens of *Malacoangelia remigera* BERLESE, used for comparisons with *Nothrolohmannia*, are in the author's collection and derive from various sites in Florida (USA), Brazil, the Ivory Coast and Papua New Guinea. Specimens of *Hypochthonius rufulus* C. KOCH, from various collections in New York (USA) and Germany, and of *Eohypochthonius gracilis* (JACOT), from various collections in North Carolina (USA), were studied as representatives of their respective genera. Information on cuticle structure from ALBERTI *et al.* (2001) is incorporated. Other comparative data were found in BECK (1962), FERNANDEZ (1984) and BERNINI *et al.* (1986) for *Eohypochthonius*, and GRANDJEAN (1935) for *Malacoangelia*.

Light microscopy observations were of whole and dissected specimens, using bright-field and differential interference contrast illumination. Scanning electron microscopy was of coated specimens in a Cambridge Stereoscan 120, equipped with Robinson backscatter detector. Morphological terminology is mostly that of F. GRANDJEAN (see TRAVÉ & VACHON 1975 for references). Measurements (often given in parentheses) are in micrometers and, when no other indication is given, represent an average sized specimen.

Nothrolohmannia baloghi sp. n.
(Figs 1–20)

Diagnosis. Distinguishable from the only other known species, *N. calcarata*, by the following character states (those of *N. calcarata* in parentheses). Smaller, total length 328–377 (vs. 520–550). Most dorsal setae proportionally shorter; e.g. *c1* barely reaches insertion of *d1* (vs. twice as long as *c1–d1* distance); exception is *e1*, more than half length of *fl* (vs. less than half). Sensillus distinctly pectinate (vs. inconspicuously barbed). Medial group of notogastral porose areas not strongly convex, with 6–8 areas in anterior row and 3–5 in posterior row (vs. strongly convex and with 8–9 and 4–6, respectively); small porose area between setae *c3* and *cp* absent (vs. present). Epimeral setae heteromorphic, *1a* and *2a* very dissimilar; *1a* large, broadly phylliform, with extended narrow tip, and several weakly formed serial veins, pair nearly adjacent; *2a* long but simple, with inconspicuous coat (vs. pair *1a* not adjacent or modified, similar to *2a*). Fused anal and adanal plates demarcated by groove only posteriorly (vs. sharply defined groove present whole length of plates). Three pairs of adanal setae (vs. two pairs). Subcapitular seta *h* nearly adjacent, with vane-like hyaline coat, unusually large, tapered distally, curved mediad in semicircle (vs. separated by 2 or 3 alveolar diameters, coat thinner, uniform throughout length, only moderately curved).

Size and general appearance. Color orange-yellow. About 1.6–1.9 times longer than broad (depending on extension of sejugal articulation), almost twice as broad as deep; hysterosoma almost twice width of proterosoma (Fig. 1), but general outline nearly elliptical with legs appressed (Fig. 8). Dimensions of contracted specimens (n=8): mean (range) total length 350 (328–377); mean maximum width 209 (196–221). Nearly all exposed cuticle covered with dense pelt of small, sharp spicules (Figs 8–16); larger spicules with well formed edges (Fig. 10) (see Remark 1).

Prodorsum. In dorsal aspect, widest in proximal half, strongly narrowed distally; weakly narrowed at level of bothridium. Structurally complex, mostly due to grooves and concavities associated with coaptation of retracted, appressed legs I. Principal lateral concavity creates slightly recurved, dorsal flange under which middle region of leg I can be appressed (Figs 8, 12), reminiscent of lamella in brachypylina mites; flange directed anteromedial, ending at transverse groove just anterior to seta *le* (Fig. 1). Transverse groove nearly encircles rostrum, setting off truncate or hammerhead-like anterior portion that bears rostral setae. Rostral tectum anteriorly free of spicules, with doubled margin distally (Figs 9, 17); true lateral margin with thin, sharp denticles, additional row of thin submarginal denticles on inner face of tectal limb more conspicuous, divided by ridges in groups of 5 or 6 (Fig. 18). Interlamellar (*in*), anterior exobothridial (*exa*) and lamellar (*le*) setae similar in form: core finely attenuate, but with hyaline coat mostly on outer curvature of seta (therefore visible to variable degrees depending on orientation); coat ciliate proximally, cilia becoming less well defined distally. Setae *in* and *le* curved posteriad, *exa* anteriorly; lengths about 45, 85, and 60, respectively. Posterior exobothridial seta (*exp*) simple, short (18). Rostral seta thicker than others, with inconspicuous, non-ciliate coat; branched near base with posterior ramus short (25), anterior ramus much longer (100) and strongly recurved near rostral margin to form U-shape (Fig. 9). Bothridium with slightly projecting rim; internally with well formed porose sacculae; thin cuticular layer above each saccular

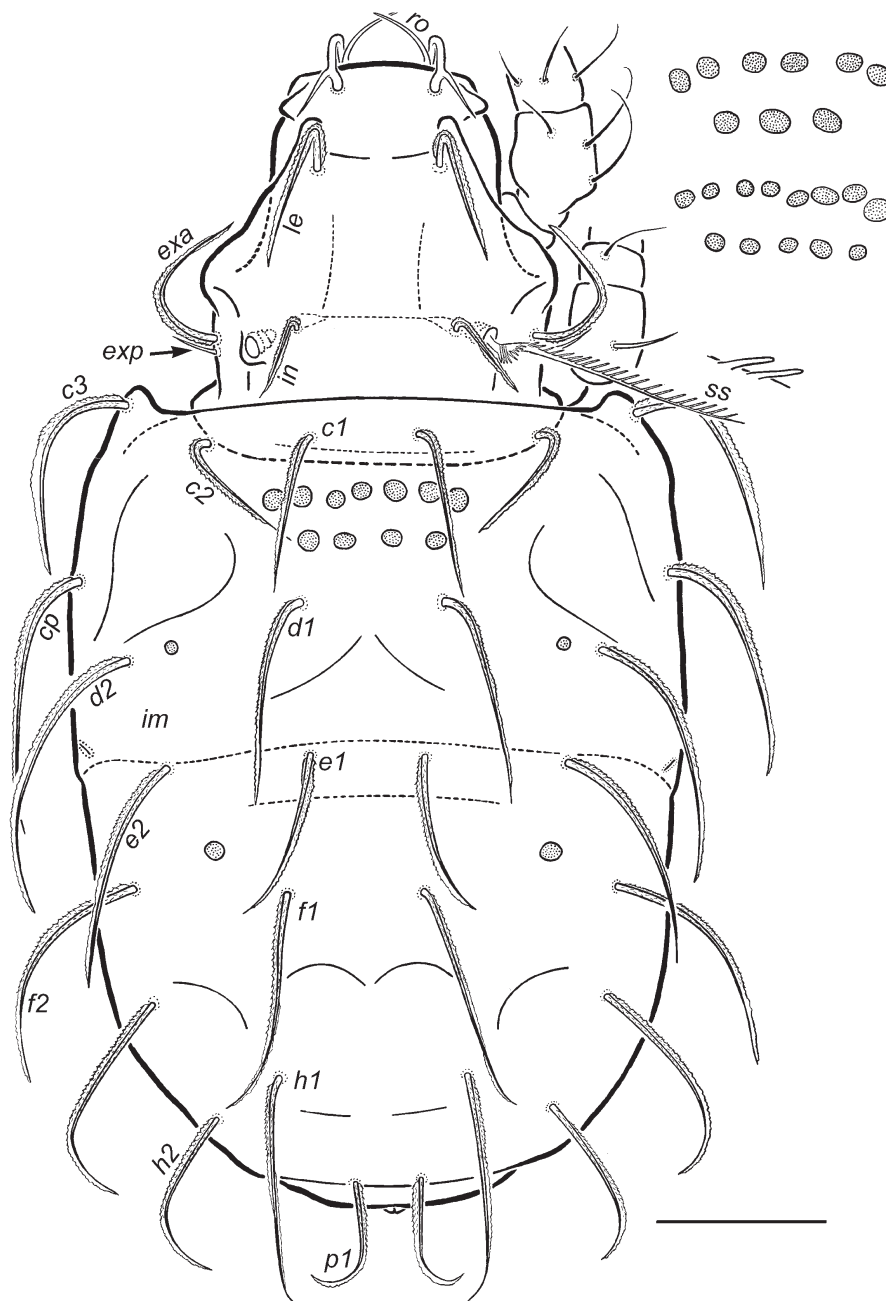


Fig. 1. *Nothrolhmannia baloghi* sp. n., adult female: dorsal aspect, legs only partially drawn (scale bar 50 μ m). Separate details on right include two variations of anterior porose area clusters and detail of tines on sensillus. Small porose area anteromedial to seta *d2* often absent

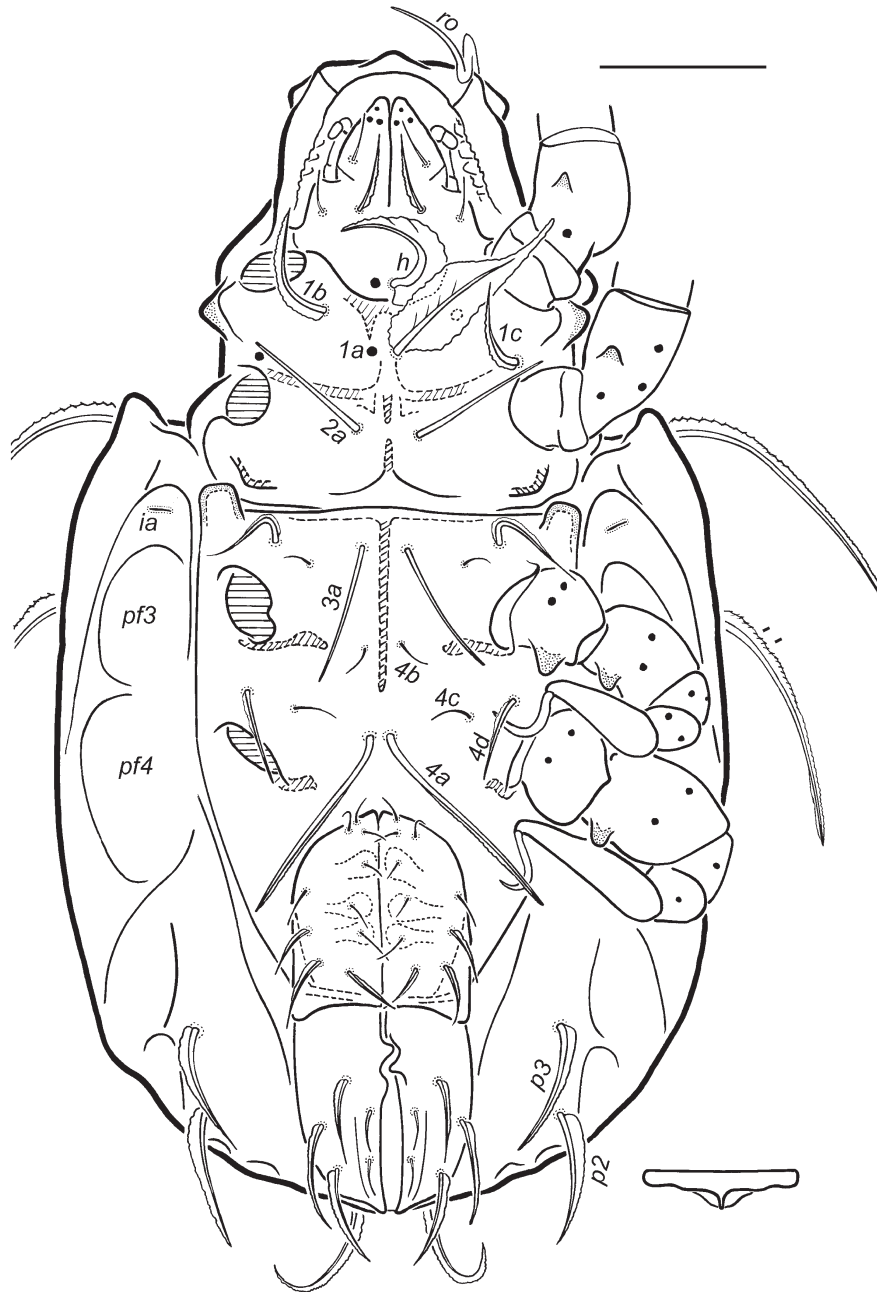
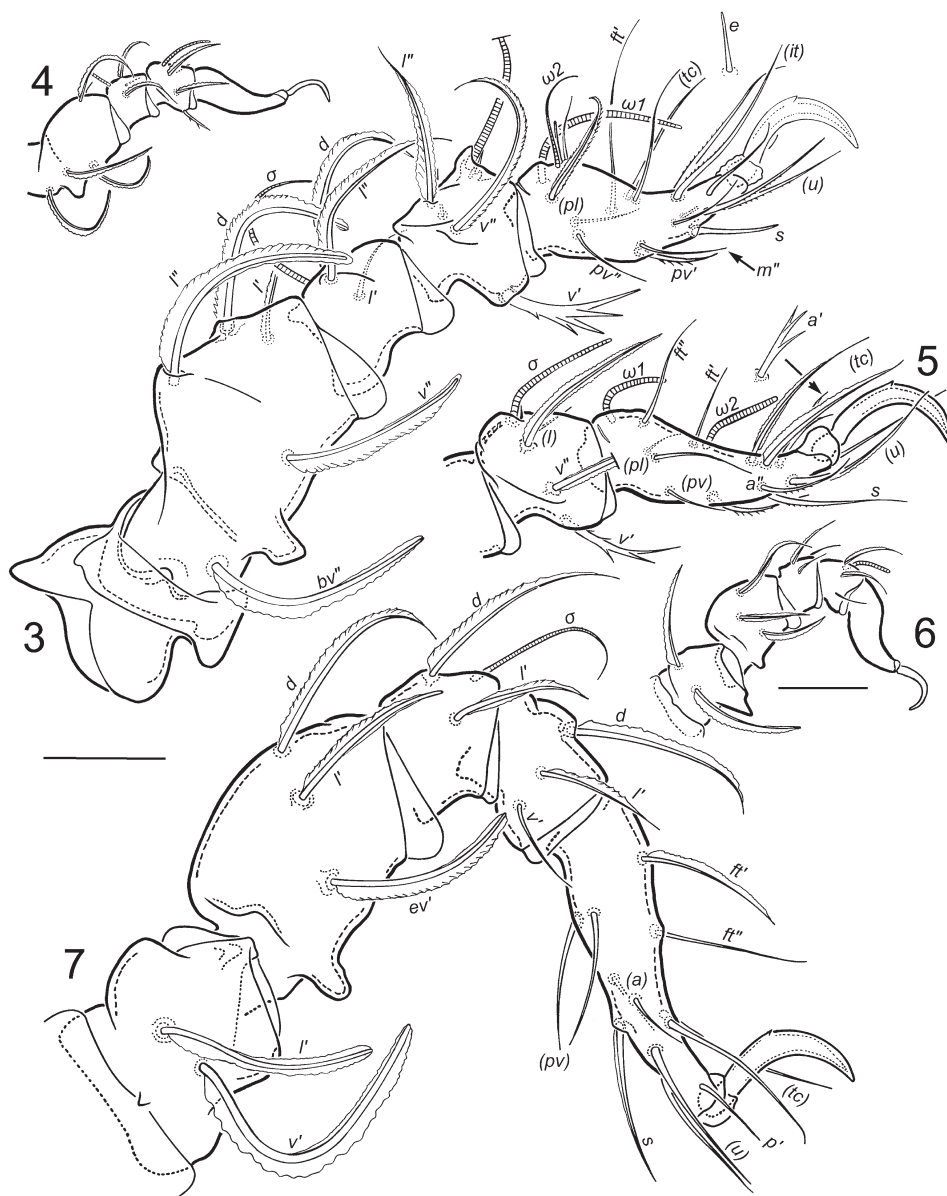
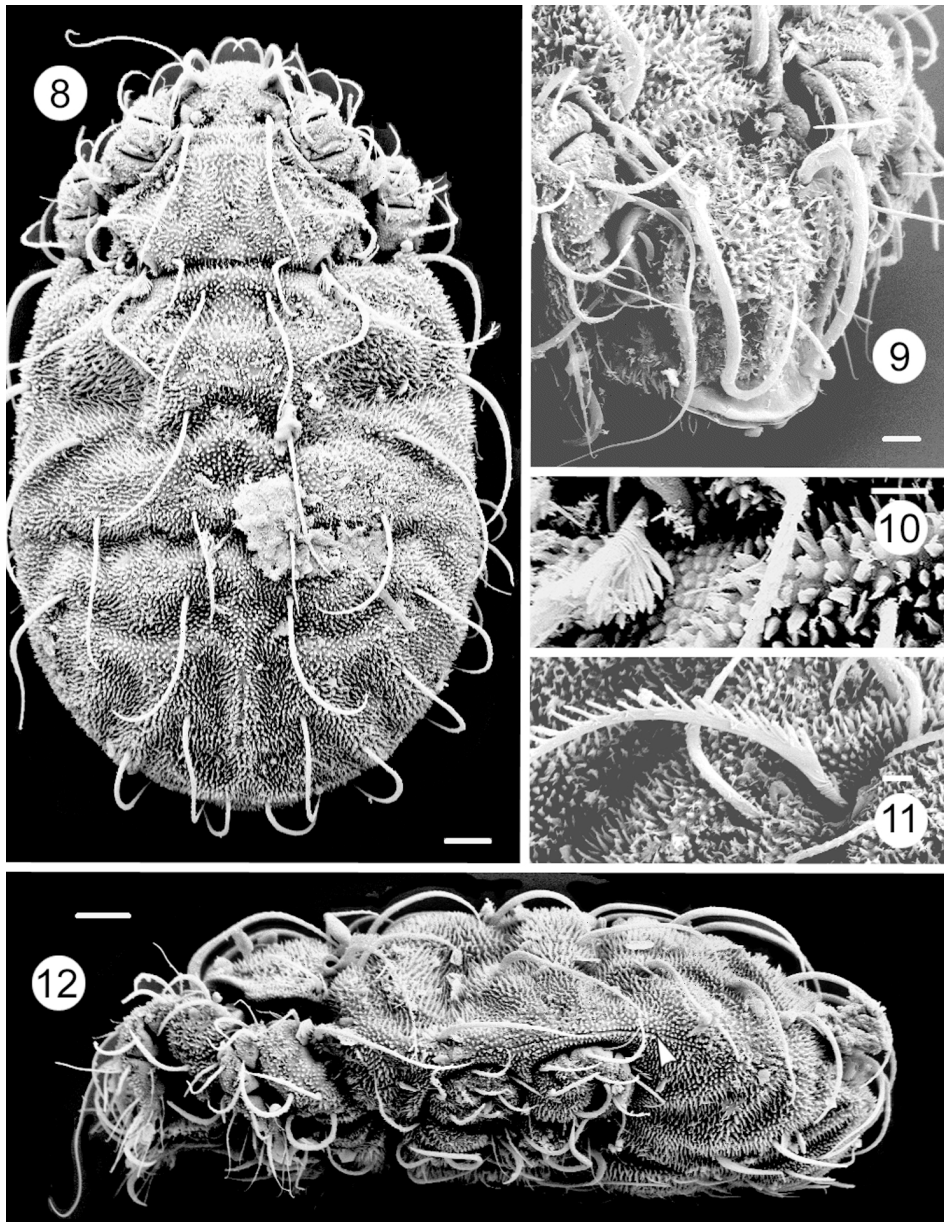


Fig. 2. *Nothrolohmannia baloghi* sp. n., adult female: ventral aspect. Setae of legs, lateral lips of subcapitulum, and some epimere I setae represented only by dots marking their insertions; detail at lower right is preanal plate in posterior aspect (scale bar 50 μ m)



Figs 3–7. *Nothrolahmannia baloghi* sp. n., legs of adult female, abaxial aspect: 3 = right leg I (only basal part of flagelliform solenidion v1 drawn, famulus separately drawn in upper right); 4 = right leg II, trochanter and tarsal setae not drawn; 5 = distal region of right leg II, with seta *a'* drawn separately above tarsus; 6 = left leg III, tarsal seta not drawn; 7 = left leg IV (seta *p'* may be absent from tarsus). Figs 3, 5, 7 to same scale (25 μ m); Figs 4, 6 to same scale (50 μ m)



Figs 8–12. *Nothrolohmannia baloghi* sp. n., adult (scale bar lengths in parentheses): 8 = dorsal aspect, with legs appressed to body in defensive posture (20 μ m); 9 = anterolateral aspect of prodorsum and partial leg I (10 μ m); 10 = detail of left dorsosejugal region in same view as Fig. 8, showing base of sensillus (left) and cuticular spicules (partially seen setae are *in* (center) and *cl*) (5 μ m); 11 = partial frontal view, showing basal half of right sensillus (5 μ m); 12 = left lateral aspect, white arrowhead on suprapleural scissure (20 μ m)

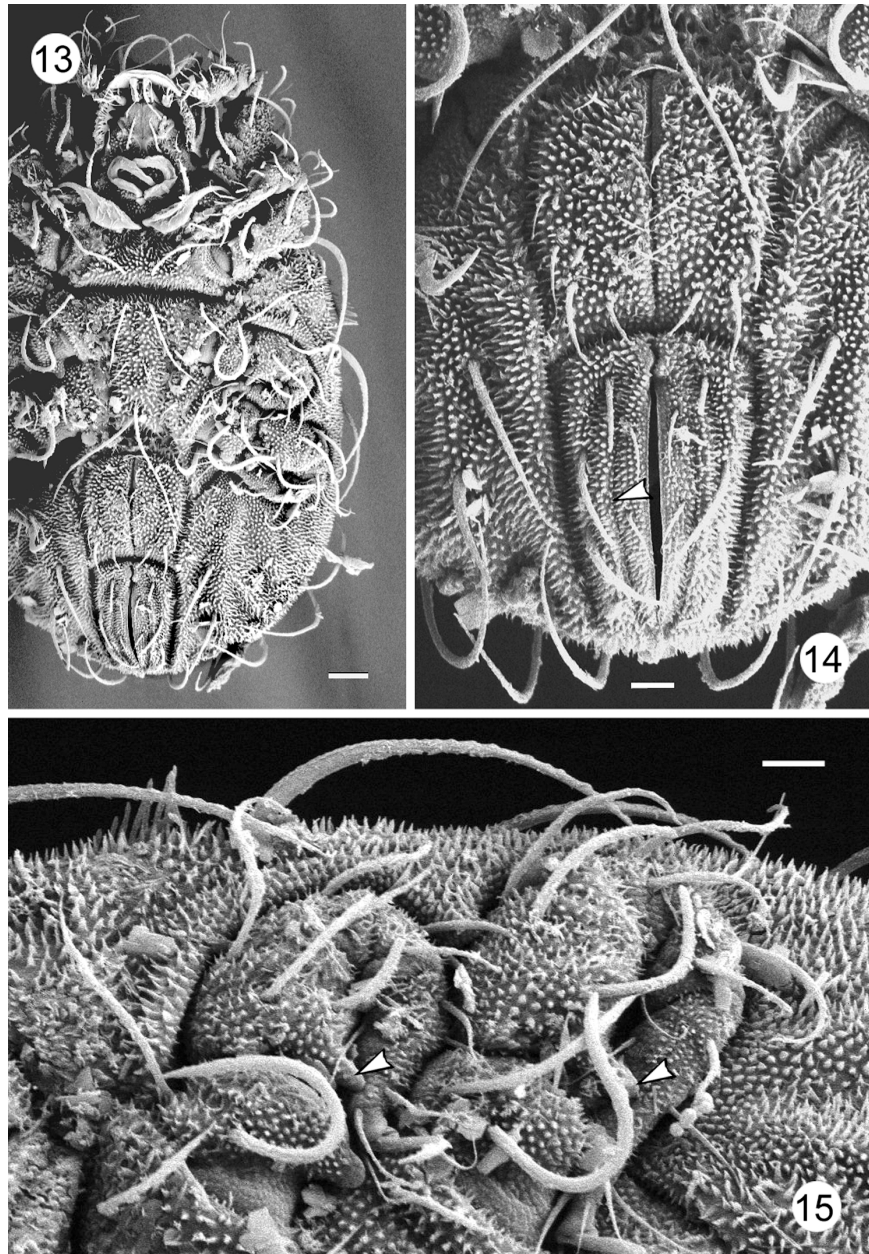
pore canal bulges away from bothridium, creating many thin-walled, minute lobes. Sensillus (*ss*) long (ca. 100), nearly straight or slightly curved, uniformly pectinate for most its length, with other scattered small barbs (Fig. 11); alignment of tines changes abruptly near base, from dorsal to posterior face, edges of basal tines extend across width of sensillus to give effect of closely-spaced annuli (Fig. 10).

Notogaster. Transverse scissures absent, faint lines of weakness seen anterior and posterior to setal row *e* in transmitted light, when notogaster is strongly cleared (Fig. 1) (see Remark 1). Suprapleural scissure (Fig. 12, arrowhead) complete posteriorly, U-shaped, isolating notaspis from paired pleuraspis. Notogastral surface undulating, due to multiple, usually paired, depressions (Figs 1, 8); one transverse depression spans notoaspis, posterior to setal row *e*. Pleuraspis also with depressions, two being more sharply defined and forming pedofossae for receiving retracted legs III and IV, respectively (Figs 2, 15). Humeral region with projecting boss, appearing like tubercle in dorsal aspect and bearing seta *c3*. With two discernable pairs of lyrifissures: *ia* located anterior to pedofossa III (Fig. 2), ventral to suprapleural scissure; *im* near the lateral contour (Fig. 1), dorsal to suprapleural scissure at approximate level of setal row *e*; no evidence of *ip*, *ih*, or *ips*. Without opisthonotal gland. Multiple small (6–8 diameter) porose areas present, mostly in two rows posterior to setae *c1*, anterior row with 6 to 8 areas, posterior row with 3 to 5 areas; one additional pair present anteromedial to seta *f2*, another sometimes present anteromedial to *d2*; no porose area in vicinity of *c2*. Notogastral setae mostly 80–100 long, similar in form to prodorsal seta *le*; *e1*, *p1* shorter (60); *p2*, *p3* shortest (ca 45), with hyaline coat relatively broad basally.

Coxisternum. Overall structure typical of superfamily (Fig. 2): epimeres I and II fully fused, epimeres III and IV fully fused. Anterolateral tubercle of epimere III strongly developed, rectangular, opposed across sejugal articulation by swelling on epimere II. Anterior sternal apodeme weakly developed on epimere II, usually broken at level of seta *2a*; posterior sternal apodeme longer, extending from sejugal articulation posteriorly almost to level of leg IV insertion. Apodeme I moderately developed, projected toward seta *1a*; apodeme II long, nearly reaching sternal apodeme; apodeme III directed medially, reaching halfway to sternal apodeme; apodeme IV similar, but less than half as long. With boss projecting from body outline posterodorsal to leg I insertion. Epimeral setation (I–IV) 3–1–3–4 (see Remark 2); seta *1a* unusually large (70), broadly phylliform, with extended narrow tip and several weakly formed serial veins, pair separated by only alveolar diameter or less; setae *1b*, *1c*, *3c*, *4d* (35–40) with moderate hyaline coat; setae *2a*, *3a* relatively long (50), with only thin hyaline coat; setae *3b*, *4b*, *4c* short (ca 15–20), simple, *4b* inserted far anteriorly, at level of apodeme III; seta *4a* longest of all ventral setae (ca 75), with slight hyaline coat, pair separated by alveolar diameter or less.

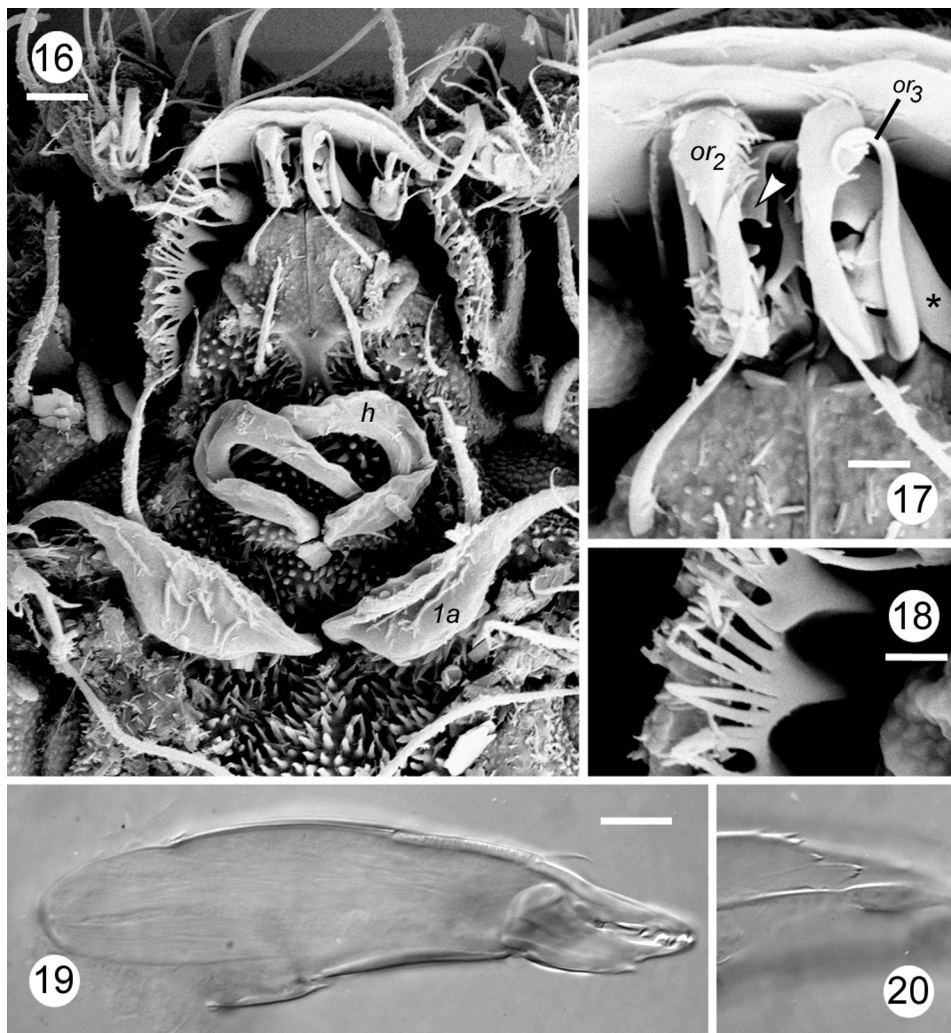
Anogenital region. Aggenital plates fused broadly and imperceptibly with epimere IV; without aggenital seta. Genital and fused anal-adanal plates of similar overall size; each pair almost as wide as long. Preanal plate (Fig. 2, lower right) small, narrow, hidden in vertical cuticle behind genital plate. Genital plate with posterolateral corner expanded as small, subtriangular tectum; setae distributed as shown in Fig. 2, three posterolateral setae (20–25) with small hyaline vanes, others simple and slightly smaller (12–20). Fusion of anal and adanal plates complete, but line of fusion indicated by shallow groove in posterior two-thirds; medial margin of plates interdigitated anteriorly; with two pairs of simple anal setae (ca 15) and three of larger (ca 30), vaned adanal setae.

Gnathosoma. Subcapitulum anarthric, generally similar to that of *Malacoangelia* (GRANDJEAN, 1935), except posterior margin of mentum strongly convex medially, and with subrectangular boss in posterolateral corners. Proximal two-thirds of ventral face with dense spicules, distal third mostly without (Fig. 16). Paired rasp-like patch of fine teeth, with several larger lateral denticles, located on dorsal face of each gena, near base of labrum (see Remark 3). Subcapitular seta (*h*) unusually large (ca 50), hyaline coat strongly developed, especially on external curvature, tapered distally;



Figs 13–15. *Nothrolohmannia baloghi* sp. n., adult (scale bar lengths in parentheses): 13 = ventral aspect (20 μ m); 14 = closeup of posterior venter, with white arrowhead indicating groove between fused anal and adanal plates (10 μ m); 15 = partial ventral aspect (anterior to left) showing left legs III and IV retracted into pedofossae – white arrowheads indicate femoral tubercles, which hold respective tarsi in place (10 μ m)

pair separated only by alveolar width and strongly curved mediad, overlapping, giving outline of heart or circle. Genal seta *a* and lateral of two *m* seta (20) simple or with very slight coat; medial *m* seta (ca 30) with small hyaline coat. Rutellum and adoral setae (Fig. 17) as in *Malacoangelia*, except spatulate *or2* with tines finer and more numerous (about 10). Palp similar in structure and setation to that of *Hypochthonius* (GRANDJEAN, 1946), except genual seta and setae *cmp* and *vt2''* absent. Fused distal eupathid with three branches (*ul'*, *ul''*, *sul*) divergent. Chelicera (Fig. 19) elongated, typical of



Figs 16–20. *Nothrolohmannia baloghi* sp. n., adult (scale bar lengths in parentheses): 16 = ventral aspect, anterior third (10 μ m); 17 = detail of anterior subcapitulum and rostral margin (3 μ m); 18 = detail of submarginal denticles (3 μ m); 19 = chelicera, lateral aspect (10 μ m); 20 = denticles on adaxial face of chelicera (same scale as Fig. 19)

Table 1. Leg setation of adult *Nothrolohmanna baloghi* sp. n. (Parentheses around seta denote a pair; parentheses around seta and solenidion denote coupling)

	trochanter	femur	genu	tibia	tarsus ^a
Leg I	–	d, (l), bv'', v''	d, (l), σ	(d ϕ), (l), (v)	(ft), (pl), (tc), (it), (p), (u), s, (a), (pv), m'', e, ω 1, ω 2
Leg II	–	d, (l), bv'', v''	d, (l), σ	(d ϕ), (l), (v)	(ft), (pl), (tc), (u), s, (a), (pv), ω 1, ω 2
Leg III	l', v'	d, l', ev'	d, l', σ	d, l', v', ϕ	(ft), (tc), (u), s, (a), (pv)
Leg IV	l', v'	d, l', ev'	d, l', σ	d, l' v'	(ft), (tc), p', (u), s, (a), (pv)

^aSeta *p'* absent from tarsus IV on one of four legs studied

family; cheliceral frame attaches at about proximal one-fourth (i.e. basal quarter of chelicera internalized as apodeme; see Remark 4). Chelicera with single seta, inserted mid-dorsally, short, simple, narrow fixed and moveable cheliceral digits each with four opposing teeth (including distal points); with short series of denticles on adaxial face (Fig. 20) and several on dorsal midline.

Legs (Figs 3–6). All legs relatively short (leg IV less than half length of body), with rather complex structure. Trochanters I and II with lamelliform tectum on distal abaxial face, like half-collar in lateral aspect; trochanter III with large ventral spur-like apophysis. Femora all with proximoventral apophysis, under which tarsus lies when legs are retracted (Fig. 15), as well as various keels or ridges. Genua of simple form, but tibiae differently shaped, with various keels or ridges; tibia I with short dorsal spine immediately abaxial to solenidion. Tarsi weakly sigmoid in lateral aspect; lyrifissure present proximally on each tarsus, near dorsal midline, but distinctly on anterior face; claw with single dorsal tooth at midlength. Most setae of basal four leg segments with hyaline coat, commonly with strong serration; core of trochanteral and some femoral setae nearly isodiametric throughout. Other forms include: *l'* of genua and tibiae I and II, and *v'* of tibiae III and IV simple; *v''* of tibiae I and II relatively large, coarsely branched; seta *d* of tibiae I and II minute, inconspicuous, coupled to respective solenidion ϕ , inserted immediately distal to it, in separate alveolus. Setae of tarsi simple, barbed, or with hyaline coat, as indicated in Figs 3–6; seta *s* eupathidial on tarsus I, proral pair probably eupathidial. Setal counts (legs I–IV, famulus included in tarsus I count): trochanters (0–0–2–2), femora (5–5–3–3), genua (3–3–2–2), tibiae (5–5–3–3), tarsi (19–13–11–12); identities given in Table 1, and partially in Figs 3, 5, 7. Iteral setae present only on tarsus I, both proral setae absent from tarsi II and III, and *p''* absent from tarsus IV (*p'* also absent on one of four legs IV studied). Setae of pair *pv* with strong prime disjunction on tarsi I and II but nearly opposite each other on III or IV. Ventral pair with strong abaxial displacement on tibia I; *v'* in ventral midline, *v''* high on abaxial face. Seta *a'* of tarsus II enlarged, strongly branched, inserted high on adaxial face. Solenidial counts: genua (1–1–1–1), tibiae (1–1–1–0), tarsi (2–2–0–0). Genua solenidia piliform; tibial solenidia of various shapes (flagelliform on I, ceratiform on II, baculiform on III); tarsus I solenidia ceratiform (ω 1) and piliform (ω 2), both solenidia of tarsus II baculiform. Only tibial solenidia coupled to respective seta *d*; genu solenidia inserted at level proximal to *d* on I and II, well distal to *d* on III and IV. Famulus (*e*) of tarsus I tapered, but not attenuate, clustered with *ft''* and ω 2.

Type material. Holotype from rainforest litter near Vanimu (2°41'S, 141°18'E), in western Papua New Guinea, collected with Berlese funnel by R. W. TAYLOR, 10-vii-1972 (samples ANIC 413–415); preserved in alcohol and deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra, Australia. Eight paratypes with same data as holotype; four deposited in ANIC (alcohol), one deposited in the Hungarian Natural History Museum, Budapest (alcohol), three in the author's collection (one in alcohol, two dissected on slides).

DISCUSSION AND NEW SUPRASPECIFIC DIAGNOSES

Previously (NORTON 2001), I suggested fourteen synapomorphies that support a sister-relationship between the pantropical genus *Malacoangelia* (with 4 nominal species-group taxa) and the Papua New Guinea endemic genus *Nothrolohmannia* (now with two nominal species). Thirteen other synapomorphies support the inclusion of *Nothrolohmannia* in various higher taxa of Enarthronota, a group that is usually distinguished by the presence of transverse notogastral scissures. The ancestral presence of such scissures in *Nothrolohmannia* is suggested by vestiges that can be seen with transmitted light in strongly cleared specimens.

If this relationship is accepted, several alternative classifications are possible. The one discussed and diagramed earlier (NORTON 2001) is followed here. Nothrolohmanniidae is made subordinate to Hypochthoniidae, as the subfamily Nothrolohmanniinae, and it comprises both *Nothrolohmannia* and *Malacoangelia*. The nominate subfamily, Hypochthoniinae, includes the sister-taxa *Hypochthonius* and *Eohypochthonius*. Below are proposed new diagnoses of each subfamily, and of the genera *Nothrolohmannia* and *Malacoangelia*. Most of the characters used by GRANDJEAN (1935) to distinguish *Hypochthonius* and *Malacoangelia* are, in this context, subfamilial traits. Characters of Hypochthonioidea and Hypochthoniidae were discussed earlier (NORTON 1984, 2001), but the absence of transverse scissures in *Nothrolohmannia* should be incorporated in any formal diagnoses. If Lohmanniidae is shown to belong to Hypochthonioidea, as has been suggested (ALBERTI *et al.* 2001, NORTON 2001), diagnosis of the superfamily will need further modification.

Hypochthoniinae BERLESE, 1910

Hypochthoniidae with the following character states. Mineralized epicuticular chambers either widespread (*Eohypochthonius*) or localized in patches (*Hypochthonius*) on body and legs, but without exterior manifestation as spicules. Hyaline coat on setae of body and legs absent or thin, hardly noticeable. Rostral tectum with simple or serrate margin, but without submarginal row of denticles on its underside. Prodorsum (aspis) fused to coxisternal region (*Hypochthonius*) or not (*Eohypochthonius*); lateral region relatively uniform, without special formation for coaptation of retracted legs. Rostral seta simple. Base of bothridium porose, but without internalized saccule. Notogaster without humeral tubercle. Setae of row *e* usually vestigial (see Remark 5), alveoli on narrow, ribbon-like intercalary sclerite that lies between pronotaspis and pygidium, usually hidden by

them in intact specimens. Notogaster without porose areas, usually without conspicuous depressions. Suprapleural scissures of each side not meeting posteriorly; pleuraspis without depressions for coaptation of legs. Epimere III without anterolateral tubercle. Anal setae present or absent. Genital plates without projecting, posterolateral tectum. Anal plates usually fully articulated with adanal plates by intervening scissure (but plates vestigial and without setae in *Eohypochthonius* subgenus *Neotrichosus*); anal plates without interdigitating zone. Legs not appressed to body in defensive reaction; femora and trochanters without apophyses, trochanters I and II without distal tectum. Proral setae present on all leg tarsi; antelateral seta *a'* of tarsus II in normal position, low on anterior face. Solenidia of genua III/IV and tibia III proximal to respective seta *d*.

Nothrolohmanniinae BALOGH, 1968

Hypochthoniidae with the following character states. Mineral-filled epicuticular chambers extend above general body surface as rounded or pointed spicules, covered with thin cerotegument; spicules widespread, coating most of body and leg surfaces like pelt (see Remark 6). Many setae of body and legs modified with thick hyaline coat or vanes. Rostral tectum with simple or dentate margin, but with dense submarginal row of denticles on its underside. Prodorsum not fused to coxisternal region; with concavities and grooves, one of which nearly encircles rostrum, producing somewhat truncate or hammerhead-like anterior portion that bears rostral setae; legs I and II coapt to these indentations when retracted in defensive posture. Rostral seta biramous, embedded in thick amorphous secretion. Bothridium with porose sacculae. Notogaster with humeral boss that bears seta *c3*. Setae of row *e* large or small, but conspicuous; their narrow sclerite either conspicuous and isolated from pronotaspis and pygidium by scissures, or fused to the latter sclerites. Notogaster with irregular dorsal surface, caused by multiple paired depressions and transverse one posterior to setal row *e*; with one or more porose areas. Suprapleural scissure U-shaped, isolating paired pleuraspis from both pronotaspis and pygidium; pleuraspis with two well defined pedofossae on each side that individually receive retracted legs III and IV. Epimere III with paired quadrate anterolateral tubercle that projects across sejugal articulation. Posterolateral corner of each genital plate extended by small, triangular tectum. Anal plates each with two setae; medial margin of plate with interdigitating zone anteriorly; plate functionally fused with adanal plate, line of fusion fully or partly delineated by groove. Legs relatively short, appressed to body in defensive posture. Legs with conspicuous surface structures: femur of all legs, and trochanter III, with spur-like apo-

physis; trochanters I and II with distal, abaxial tectum. Proral setae (p) absent from tarsi II and III; p'' (and sometimes p') lost from tarsus IV; antelateral seta a' of tarsus II inserted unusually high on anterior face. Solenidia of genua III/IV and tibia III more distal than respective seta d .

Malacoangelia BERLESE, 1913

Nothrolohmanniinae with the following character states. Epicuticular spicules conical or rounded distally. Many setae of body and legs with broad single or double vanes that taper distally. Rostral seta T-shaped or reniform in outline; each branch with large vane. True margin of rostral tectum irregular, but mostly smooth; submarginal denticles narrow, sharp; triangular incision present in rostral margin anterior to denticles, directed toward rostral seta. With large, unpaired notogastral porose area: elongated, strongly convex, located immediately posterior to setal pair $c1$ and at least as long as their mutual distance. Setae of row e small but well formed, vaned; inserted on narrow sclerite clearly separated from pronotaspis and pygidium by scissures. With oblique scissure leading posterolaterad from near seta $e2$ and connecting with suprapleural scissure, thereby isolating subtriangular plate containing seta $f2$. Sternal apodemes of epimeres III and IV separated. Epimeral setae homogeneous and relatively small; pair $4a$ little longer than their mutual distance.

Nothrolohmannia BALOGH, 1968

Nothrolohmanniinae with the following character states. Epicuticular spicules sharply pointed. Most setae of body and legs without broad vanes (some ventral setae of *N. baloghi* are exceptions); generally with narrow, hyaline coat. Branches of rostral seta simple, without noticeable hyaline coat; anteroventral branch long, U-shaped. Rostral tectum anteriorly with double margin; laterally with narrow denticles on both true margin and in conspicuous submarginal row, on underside of tectal limb; with pair of linear sutures running dorsad from margin (just anterior to denticles), approximately toward rostral setae. Notogaster with multiple small, usually paired porose areas; most arranged in double row posterior to setal pair $c1$. Two or three additional pairs present, according to species: one located anteromedial to setae $d2$; another may be present anteromedial to $f2$; another may be present posterolateral to $c2$. Setae of row e as large as, or only slightly smaller than, notogastral setae in adjacent rows. Notogaster with neither transverse nor oblique

scissures present to define separate plates, other than pleuraspis. Posterior sternal apodeme of epimeres III and IV united into single long apodeme. Epimeral setae heterogeneous in size and form; pair *4a* closely adjacent, about as long as genital plates.

MISCELLANEOUS REMARKS

1. The faint transverse line anterior to setal row *e* marks a suture, i.e., a vestige of scissure “ct2” in the nomenclature of GRANDJEAN (1935). The line posterior to row *e* is similarly a vestige of “ct3”; it effaces laterally at a point analogous to where an oblique scissure meets “ct3” in *Malacoangelia*. My interpretation is that setal row *e* in ancestors of *Nothrolohmannia* and *Malacoangelia* was erectile, and that the condition seen in *Nothrolohmannia* is a culmination of a trend toward loss of this defensive mechanism, in favor of augmenting cuticular strength with mineralization.

2. Based on studies of the holotype and topotype of *Nothrolohmannia calcarata*, three corrections or additions should be made to BALOGH’s (1968) original description. First, the large subcapitular seta *h* was incorrectly drawn on epimere I. This certainly created a second problem: the original epimeral setal formula of 3–2–4–3 should instead be 3–1–3–4, the same as in *N. baloghi*. Seta *1c* seems to have been counted among the epimere II setae, and seta *4b*, which inserts on the anterior margin of epimere IV, seems to have been included in the epimere III count. Variations in designating epimere IV setae, which rarely are aligned in a row, are common in the literature. In GRANDJEAN’s (1933) chaetotaxic system, those setae already present in the larva are lettered from medial to lateral on a given epimere, but setae added during ontogeny are given subsequent notations in order of appearance. Because the ontogenetically added seta *4b* is typically far anterior to *4a*, and often placed more medially, the designations for these setae are often incorrectly switched (compare GRANDJEAN 1935 with, e.g. FERNANDEZ 1984 or BERNINI *et al.* 1986).

Also, there seems to be variation in the presence of lateral porose areas. The topotype of *N. calcarata* has a pair not mentioned in the original description; it lies just anterior to notogastral seta *f2* and seems homologous to the similar porose area that is consistently present in *N. baloghi*. However, this pair could not be found on the holotype.

3. A rasp-like patch of denticles on the dorsal face of each subcapitular gena, near the base of the labrum, was first noted in the enarthronote genus *Arborich-*

thonius (NORTON, 1982). Its distribution needs further study, but the patch exists in each of the four genera of Hypochthoniidae.

4. Previously (NORTON 1998) I discussed the proximal internalization of the chelicera, by the movement of the cheliceral frame attachment distally onto the cheliceral body, as a synapomorphy of the higher oribatid mite groups Desmonomata, Brachypylyna and Astigmata. Such internalization also characterizes the chelicera of two families of Enarthronota: Hypochthoniidae and Lohmanniidae. Since the latter families are phylogenetically distant from the former groups, the trait appears to have evolved convergently.

5. Most of the diagnostic characters of Hypochthoniinae are plesiomorphic but one seems to represent a synapomorphy not shared by Nothrolohmanniinae: the reduction of setal row *e* and the intercalary sclerite on which they insert. The setae are represented by only vestiges, and the sclerite is so narrow – and usually hidden by the pronotaspis – as to often be overlooked. However, at least one undescribed species of *Eohypochthonius* in Florida has thin, but well developed setae in row *e*, so the monophyly of Hypochthoniinae remains unproven.

6. GRANDJEAN (1935) noted the unusual cuticle of *Malacoangelia*, and considered the outer layer that gave a matte appearance to be a superficial pellicle of secreted material; he noted no significant difference between this and other common secretions (cerotegument) having a somewhat granular appearance. ALBERTI *et al.* (2001) showed that the ultrastructure of this layer in *Malacoangelia* and *Nothrolohmannia* was actually quite different from that of other known mites. The projections (mostly conical in the former genus, sharp in the latter) are mineral-filled spicules, extensions of epicuticular chambers containing a crystalline calcium-phosphorus compound, probably a form of apatite; outside this deposited material is a thin layer of cerotegument. While apatite-filled epicuticular chambers are also known in other Hypochthoniidae and in Lohmanniidae, only in *Malacoangelia* and *Nothrolohmannia* do the chambers have external projections. These spicules may play a defensive role.

7. The assignment of designations to three of the leg setae of *N. baloghi* – monotropic seta *m*'' on tarsus I and pair (*pl*) on tarsus II – is an inference, rather than a certainty. Each of the inferred setae is fundamental in oribatid mites, i.e. present from the larval instar (GRANDJEAN 1941), but the larva and nymphs of *N. baloghi* are unknown. In particular, to designate the proximal lateral setae of tarsus II as the primilateral pair (*pl*) needs some justification, since primilateral setae are rather rare on tarsus II of oribatid mites, while accessory lateral setae are quite common. For two reasons, it seems likely that these designations are correct. First, all three setae are present in the larva of the confamilial species *Hypochthonius rufulus* (pers. observ.; also GRANDJEAN 1941); the adult leg setation of *N. baloghi*

is identical to that of *H. rufulus* except for the loss of some proral setae, as noted above. Second, the studied protonymph of (probably) *N. calcarata* has these three setae, and an oribatid mite protonymph almost always has the same tarsus II setation as the larva; i.e., if accessory setae develop, they are not added until later instars.

In general, leg setation varies little among members of Hypochthoniidae. Other than abundant differences in shape, the only observed differences among adult mites were mentioned above in the various diagnoses; they include the relative positions of setae *d* and *a'*, and the presence of proral setae.

8. Four paratypes of *Nothrolohmannia baloghi* were cleared well enough to determine gender: each was female. All studied species of Hypochthoniidae appear to be thelytokous (NORTON *et al.* 1993) but such a small sample cannot safely be used to predict the absence of males in *N. baloghi*.

*

Acknowledgements – Dr. BRUCE HALLIDAY (CSIRO, Canberra) was instrumental in my obtaining a Sir Frederick McMaster Fellowship during the time in which this study was initiated; Drs HALLIDAY and MATTHEW COLLOFF both provided research facilities and access to specimens. The late Prof. JÁNOS BALOGH gave me access to his partially sorted material from Papua New Guinea. Dr. SÁNDOR MAHUNKA loaned the holotype of *N. calcarata* from the Hungarian Natural History Museum (Budapest). SUE LINDSAY (The Australian Museum, Sydney) provided the scanning electron micrographs, and I benefitted from discussions with Dr. VALERIE BEHAN-PELLETIER (Agriculture and Agri-food Canada, Ottawa). I am grateful to all.

REFERENCES

- ALBERTI, G., NORTON, R. A. & KASBOHM, J. (2001) Fine structure and mineralization of cuticle in Hypochthonioidea and Lohmannioidea (Acari: Oribatida). Pp. 230–241. In HALLIDAY, R. B., WALTER, D. E., PROCTOR, H. C., NORTON, R. A. & COLLOFF, M. J. (eds): Proceedings of the 10th International Congress of Acarology. CSIRO Publishing, Melbourne.
- BALOGH, J. (1961) Identification keys of world oribatid (Acari) families and genera. *Acta zool. hung.* **7**: 243–344.
- BALOGH, J. (1963) Identification keys of Holarctic oribatid mites (Acari) families and genera. *Acta zool. hung.* **9**: 1–60.
- BALOGH, J. (1965) A synopsis of the world oribatid (Acari) genera. *Acta zool. hung.* **11**: 5–99.
- BALOGH, J. (1968) New oribatids (Acari) from New Guinea. *Acta zool. hung.* **14**: 259–85.
- BALOGH, J. (1972) *The oribatid genera of the world*. Akadémiai Kiadó, Budapest. 188 pp., 71 pl.
- BALOGH, J. & BALOGH, P. (1992) *The oribatid mites genera of the world*. Hungarian Natural History Museum, Budapest, 263 pp.
- GRANDJEAN, F. (1934) Les poils des épimères chez les Oribates (Acariens). *Bull. Mus. nat. Hist. natur.* **6**: 504–512.

- GRANDJEAN, F. (1935) Observations sur les Oribates (8e série). *Bull. Mus. nat. Hist. natur.* **7**: 237–244.
- GRANDJEAN, F. (1941) La chaetotaxie comparée des pattes chez les Oribates (1er série). *Bull. Soc. zool. France* **66**: 33–50.
- GRANDJEAN, F. (1946) Au sujet de l'organe de Claparède, des eupathidies multiples et des taenidies manibulaires chez les Acariens actinochitineux. *Arch. Sci. phys. natur. Genève* **28**: 63–87.
- HAUMANN, G. (1991) *Zur Phylogenie primitiver Oribatiden, Acari: Oribatida*. Verlag für die Technische Universität Graz, Graz. 237 pp.
- NORTON, R. A. (1982) *Arborichthonius* n. gen., an unusual enarthronote soil mite (Acarina: Oribatei) from Ontario. *Proc. Entomol. Soc. Wash.* **84**: 85–96.
- NORTON, R. A. (1984) Monophyletic groups in the Enarthronota (Sarcoptiformes). Pp. 233–240. In GRIFFITHS, D. A. & BOWMAN, C. E. (eds): *Acarology VI*, Vol. I. Ellis Horwood Ltd., Chichester.
- NORTON, R. A. (1998) Morphological evidence for the evolutionary origin of Astigmata (Acari: Acariformes). *Exp. appl. Acarol.* **22**: 559–594.
- NORTON, R. A. (2001) Systematic relationships of Nothrolahmanniidae, and the evolutionary plasticity of body form in Enarthronota (Acari: Oribatida). Pp. 58–74. In HALLIDAY, R. B., WALTER, D. E., PROCTOR, H. C., NORTON, R. A. & COLLOFF, M. J. (eds): *Proceedings of the 10th International Congress of Acarology*. CSIRO Publishing, Melbourne.
- NORTON, R. A., KETHLEY, J. B., JOHNSTON, D. E. & OCONNOR, B. M. (1993) Phylogenetic perspectives 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 & Hall Publ., New York.
- TRAVÉ, J. & VACHON, M. (1975) François Grandjean, 1882–1975 (Notice biographique et bibliographique). *Acarologia* **17**: 1–19.

Received January 6, 2003, accepted February 3, 2003, published March 12, 2003