Phylleremus n. gen., from leaves of deciduous trees in eastern Australia (Oribatida: Licneremaeoidea)

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Abstract

We propose a new genus of licneremaeoid oribatid mite, Phylleremus, based on two new species collected from leaves of woody dicots in Queensland, New South Wales, Victoria and Tasmania, Australia. Description of the type species, Phylleremus leei n. sp., is based on adults and all active immature stages; that of Phylleremus hunti n. sp. is based on adults and tritonymphs. Phylleremus adults have the notogastral octotaxic system of dermal glands developed either as 1 or 4 pairs of saccules, and nymphs are bideficient and plicate. We discuss the characteristics and relationships of this genus to others in Licneremaeoidea and argue for an affiliation with Adhaesozetidae.

Key words: Oribatida, Phylleremus, Licneremaeoidea, new genus, new species, Australia, leaves

Introduction

Licneremaeoidea is a diverse assemblage of oribatid mite families, none of which is rich in described species. All members of included families, Adhaesozetidae, Dendroeremaeidae, Lamellareidae, Licneremaeidae, Micreremidae, Passalozetidae, Scutoverticidae, have aperedermous immatures with plicate hysterosomal integument, and adults with the octotaxic system of dermal glands (Grandjean 1954a; Behan-Pelletier et al. 2005). These character states are shared by the Achipteriidae, Tegoribatidae and Epactozetidae (Achipterioidea) and Phenopelopidae (Phenopelopoidea), and thus, these early derivative poronotic mites are sometimes referred to as the `higher plicates’ (Norton & Alberti 1997). Among this group, Licneremaeoidea seem the earliest derivative superfamily, as members lack pteromorphs in the adult and the octotaxic system is variably developed (Norton & Alberti 1997).

We describe a new genus of Licneremaeoidea for which material representing two new species is available for study. These species are found infrequently on leaves of woody dicots in arboreal habitats in eastern Australia. Thus, they share the same general habitat as Adhaesozetes polyphyllos Walter & Behan-Pelletier 1993, but are usually found on plants with densely tomentous leaves, and only rarely on plants with the smooth leaves favoured by A. polyphyllos (Walter & Behan-Pelletier 1993). As family placement is problematic, it is treated in a concluding discussion.

Materials and methods

Sampling and specimen preparation

Specimens were obtained during a study by the junior author of arboreal mites in eastern Australia. Mites
were collected from leaves of trees, shrubs, and vines at 75 sites representing dry to wet sclerophyll forest and cool-temperate to tropical rainforest from Tasmania to northern Queensland between 18 November 1990 and 11 June 1992.

Shoots were the basic unit of sampling. Within each shoot, either a single fully expanded leaf or all of the most recent flush of growth was collected. Leaves were placed in plastic bags in an ice chest, transported to a laboratory, and scanned under a dissecting microscope (up to 80X) using fibre optic illumination. Any detritus (e.g. exuviae, webbing) or structures (e.g. erinea or domatia) that could obscure mites were dissected with a scalpel. Mites were removed with a brush or probe and transferred to 70% ethanol for storage, or directly into Nesbitt's solution for clearing prior to mounting on glass slides using Hoyer's medium (Krantz and Walter 2007). Stored specimens were subsequently studied in lactic acid using cavity slides, or prepared for scanning electron microscopy (SEM).

**SEM**

Specimens were cleaned by soaking in Terg-a-zyme® solution for 6–12 h, followed by brief (1–2 s) submersion in an ultrasonic bath. They were then critical point dried, mounted on Al-stubs with double sided sticky tape, and gold-coated in a Hummer sputter apparatus.

**Terminology**

Measurements and descriptions are based on specimens mounted in temporary cavity slides and on permanent slides. Terminology used in this paper follows F. Grandjean (see Travé & Vachon (1975) for references), and Mahunka & Zombori (1985). The following conventions of measurement and description are used: *Total length*: measured from tip of rostrum to posterior edge of notogaster. *Length of notogaster*: measured from anterior margin to posterior edge. *Width of notogaster*: refers to maximum notogastral width. *Mutual distance between setae of prodorsum and notogaster*: measured between central points of insertion of setal pairs. *Abbreviations for setae of prodorsum*: ro: rostral seta; le: lamellar seta; in: interlamellar seta; ex: exobothridial seta; bo: bothridial seta. *Leg and palp setal formulae*: famulus is included in tarsal setal count on leg I and solenidial counts are in parentheses. The unideficient nomenclature for notogastral setae is used herein as outlined by Norton in Balogh and Balogh (1988).

**Abbreviations**

ANIC Australian National Insect Collection, CSIRO, Canberra, Australia
CNC Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa, Canada

**Phylleremus n. gen.**

Type-species: *Phylleremus leei n. sp.*

**Diagnosis.** Species in this genus have the following unique combination of character states: adult with tuberculate, non-birefringent cerotegument; taenidium laterally on prodorsum; notogaster with one or four pairs of minute saccules, saccule Sa positioned on anterior margin of notogaster, far anterior of seta c; nine pairs of notogastral setae; posterior notogastral tectum present, with posteromedial incision covered by pair of overlapping lobes; palpal eupathidium *acm* attached to solenidion along length; two pairs of adanal setae; immatures apheredermous, plicate; seta *p* absent from both immatures and adults; seta *d* absent from genua and tibiae in immatures and adults; femora, tibiae and tarsi with ridges running dorsoventrally in nymphs and adults; tarsi I to IV of immatures and adults with large, subunguinal pulvillus.
**Description. Adult:** Body and legs with weakly developed, tuberculate, non-birefringent cerotegument. Integument with microtubercules. Dorsophragmata and pleurophragmata present, dorsophragmata positioned medially (Fig. 1). Lamellae and genal notch absent. Bothridial seta capitate (Figs 1, 6). Bothridium small, with internal ring-like ridges (Fig. 3). Porose area Ad posterolateral to seta in (Fig. 3). Pedotecta I and II cov-
ering base of acetabula I and II, respectively (Fig. 3). Taenidium extending from seta ex to edge of rostrum (Figs 3, 6). Pedotectum I extending dorsally to base of seta ex (Fig. 3). Coxisternal setation: 3-1-2-2 (Fig. 2). Apodemes 2 and sejugal apodeme almost transverse. Custodium absent, discidium developed as tubercle between acetabula III and IV (Fig. 2). Tracheal system normal. Genital setae 5 or 6 pairs. Aggenital setae 1 pair. Anal setae 2 pairs. Adanal setae 2 pairs. Lyrifissure _ian_ absent. Preanal organ as caecum. Postanal porose area absent. Humerosejugal porose areas Am and Ah, absent. Sublamellar porose area Al absent (Fig. 3). Notogaster fused with prodorsum medially, slightly flattened anteriorly, ahumerate (Fig. 1). Octotaxic system present as one or four pairs of sacculae, Sa positioned near anterior edge of notogaster, anterior to seta _c_, and dorsal to dorsosejugal porose area Ad (Figs 1, 19) Nine pairs of notogastral setae present, _c_., _l_ and _h_ series positioned laterally; setae _p_1 and _p_2 positioned marginally (Fig. 2); _c_, _c_, _da_, _dm_, _dp_, and _p_1, absent. Notogastral tectum present, indented and overlapping posteromedially (Fig. 7). Lyrifissures _ia_ positioned slightly posterolaterally of setae _c_., _im_ positioned between setae _lm_ and _lp_; _ih_ positioned lateral of setae _h_ and _p_., _ip_ and _ips_ positioned laterally on notogaster anterior to seta _p_2. Pteromorphs absent. Subcapitulum diarthric, axillary sacculae absent from base of palp. Rutellum pantelobasic. Chelicera chelate-dentate with 2 slender, barbed setae. Trägårdh’s organ present. Palp with normal 5 segments and tarsal lyrifissure; setal formula: 0-2-1-3-9(1). Eupathidium _acm_ fused with solenidion along length (Fig. 17). Legs monodactyl, tarsi with subunguinal pulvillus (Figs 15, 16). Femora I to IV and trochanters III and IV with porose areas (Figs 8–11). Famulus (e) rod-like, rounded distally. Seta _d_ absent from tibiae I to IV and genua I to III. Solenidia on tibiae and genua short, other than _φ_1 on tibia I. Tibia I without tubercle projecting over base of tarsus I.

**Immatures:** Apherdermous, plicate, without hysterosomal macrosclerites or excentrosclerites. Line of dehiscence extends anterior to seta _c_ (Fig. 12). Cerotegument tuberculate (Fig. 18). Integument smooth. Prodorsal porose regions present (Fig. 12). Gastronotal setation bideficient; larva with 12, nymphs with 14 pairs of setae (_f_, _p_ absent). Gastronotal setae of _c_, _d_, and _l_ series monomorphic in nymphs (Figs 12, 20). Opisthonal gland present in all instars. Coxisternal porose regions present in all nymphs (Fig. 13). Porose regions present lateral of genital region, in adanal region, and surrounding opening of opisthonotal gland in all nymphs (Fig. 13; porose regions lateral of genital region not illustrated). Apodemato-acetabular tracheal system or porose homologues absent. Paraprocts atrichous in larva, protonymph and deutonymph. Genital and aggenital setal formula (larva to adult): 0-1-3-5-6 or 0-1-?-4-5, and 0-0-1-1-1, respectively. Cupule development normal. Bothridium, bothridial seta and seta _in_ fully formed in all immatures. Bothridium cup-shaped. Seta _d_ absent from tibiae I to IV and genua I to III. Setation of protonymphal leg IV normal: 0-0-0-0-7.

**Etymology.** The generic prefix “Phyll” is from the Greek “phyllon” meaning leaf, and refers to the leaf habitat of members of this genus; “eremus” is a common suffix for oribatid genera and is from the Greek “ere-mos’ meaning solitary.

**Phylleremus leei** n. sp.


**FIGURES 4–7.** *Phylleremus leei* n. sp., scanning electron micrographs of adult females: 4, lateral aspect; 5, frontal aspect; 6, detail of lateral view of prodorsum with taenidium indicated by arrow; 7, posterior aspect showing overlapping notogastral tectum.
FIGURES 8–11. *Phylleremus leei* n. sp., legs of adult female, all abaxial aspect: 8, leg I (trochanter removed); 9, leg II (trochanter removed); 10, leg III (solenidion φ broken from tibia); 11, leg IV.

**Diagnosis.** Total length of adults 280–332 μm; mutual distance of tubercles on notogaster about 3–8 μm; setae *le* about 14–16 μm long; setae *ex* about 8–10 μm long; saccule Sα present, S1, S2, S3 absent; six pairs of genital setae.
Description. Adult. Measurements: Mean total length: female (n = 9) 322 μm (range 308–332); male (n = 2) 291 μm (280, 296). Mean notogastral width: female (n = 8) 184 μm (range 172–192); male (n = 2) 152 μm (152, 152).

Color: Mature adults brown.

Integument: Underlying microtubercles on all sclerotized integument. Notogaster with large flattened tubercles extending almost to margin of notogaster laterally, shape circular to oval, circular tubercles about 5 μm in diameter, oval tubercles about 5–8 μm long; tubercles irregularly spaced, mutual distance about 3–8 μm. Tubercles extending almost to margin of notogaster laterally.

Prodorsum: Rostrum rounded. Weak transverse ridges present between setae ro and le and laterally on prodorsum (Figs 4, 5). Longitudinal ridges extending between setae le and in transverse or U-shaped ridge anterior to setae in (Fig. 1). Development of transverse or U-shaped ridge varies from poorly to well-developed within populations. Setae ro 28–38 μm long, barbed along length, except smooth basally, acuminate, mutual distance at base about 22 μm. Setae le about 14–16 μm long, thin, barbed, tapered, mutual distance of pair about 30–36 μm. Setae in 30–36 μm long, thick, plumose, flattened to abruptly tapered distally; mutual distance of pair 40–54 μm. Bothridial setae 24–28 μm long, with finely barbed globular head, subequal in length to narrow stalk. Bothridium with internal ring-like ridges. Exobothridial setae about 8–10 μm long, thin, smooth, tapered (Figs 3, 6).

Lateral Region: Pedotectum I covering posterior half of acetabulum I, narrowing along length, curving dorsally to level of seta ex and merging with taenidium (Fig. 3).

Notogaster: Longer than wide, ratio about 1.3:1.0. All nine pairs of notogastral setae about 16 μm long, curved posteriorly to posterolaterally, barbed along length, except smooth basally, acuminate (Fig. 1). Saccule Sa very small, positioned anteriorly on notogaster, far anterior to seta c, dorsal to porose area Ad, about 11 μm long (Fig. 1). Saccules S1, S2 and S3 absent.

Ventral Region: With short ridges in coxisternal region, on genital plates, and surrounding genital and anal plates (Fig. 2). Six pairs of genital setae. Epimeral and genital setae smooth, acuminate, about 16 μm long. Aggenital, anal and adanal setae about 11 μm long, smooth, acuminate.

Gnathosoma: Mentum with fingerprint pattern laterally (Fig. 2). Subcapitular setae a, m and h smooth, tapered, relative lengths: h > m > a.

Legs: Leg segments, other than genua, with 10–20 ridges running dorso-ventrally (Figs 8–11). Claws of legs I and II proportionally larger than those on legs III and IV; all claws with small spines proximodorsally (Figs 15, 16). Pulvilli of tarsi I and II smaller than those of tarsi III, IV (Figs 8–11, 15, 16). Leg setal formulae (trochanter to tarsus): leg I, 1-5-3(1)-4(2)-18(2); leg II, 1-5-3(1)-3(1)-15(2); leg III, 2-2-1(1)-3(1)-13; leg IV, 1-2-1-3(1)-12. Setae (v) not developed on tarsus I, and (ii) not developed on tarsus III. Seta tc” absent unilaterally from tarsus IV on one specimen (illustrated in Fig. 11).

Description. Immatures. Measurements: Mean length: larva (n = 1) 195 μm; protonymph (n = 1) 200 μm; deutonymph (n = 2) 247 μm (240, 254); tritonymph (n = 6) 288 μm (range 270–296).

Tritonymph. Prodorsum: Aspis with transverse porose area posterior to setae in and bothridia. Lateral porose areas present anterior of bothridia, broadest posteriorly, narrowing anteriorly (Fig. 12). Seta ro finely barbed along length, about 20 μm long. Seta le thin, smooth, about 8 μm long. Seta in about 25 μm long, thick, barbed, tapered. Setal pairs ro, le and in about 13, 16 and 36 μm apart, respectively. Seta ex about 5 μm long, smooth. Bothridial seta about 20 μm long, globular, head subequal in length to stalk, identical in shape to that of adult.

Gastronotic Region: Integument of plicae alternatively slightly sclerotized and unsclerotized, slight sclerotization indicated by stippling on Fig. 12. Gastronotal setae c, l, and h series about 15 μm long, with minute barbs. Gastronotal setae of d series and p1 and p2 short, thin, tapered, about 5–8 μm long (Fig. 12).

Ventral Region: Medial margins of epimeral plates weakly defined (Fig. 13). Epimere I with narrow mentotectum, greatest width about 5 μm, overlying base of subcapitulum (Fig. 13). Epimeral, genital, aggenital,
anal and adanal setae smooth, acuminate, about 5–13 μm long, with seta 1b longest. Integument of genital region weakly sclerotized. Development of epimeral setae (protonymph–adult): 3-1-2-1, 3-1-2-2, 3-1-2-2, 3-1-2-2. Development of genital, aggenital, anal and adanal setae (protonymph–adult): 1-3-5-6, 0-1-1-1, 0-0-2-2, 0-2-2-2, respectively.

FIGURES 12–14. Phylleremus leei n. sp., immatures; 12, tritonymph, dorsal aspect, 13, tritonymph, ventral aspect (gnathosoma incomplete; legs I and II represented only by trochanters and femora, legs III and IV removed); 14, larva, dorsal aspect.
Legs: Development of setae and solenidia given in Table 1. Proral setae of tarsus I appear eupathidial in all nymphal instars. Subunguinal seta of tarsus I of normal form and inserted proximal to antelateral pair in all nymphs; becoming eupathidial in adult, and moving distal to antelateral pair. Porose areas on femora I to IV clearly present. Tarsal pulvilli present in all instars.

*Protonymph and deutonymph.* As for tritonymph except overall size and length of setae proportionally shorter.

*Larva.* As for tritonymph, except overall size and length of setae proportionally shorter. Seta c2 barbed, about 13 μm, other gastronotal setae, smooth, about 8 μm long (Fig. 14).

**Etymology.** The specific epithet is in honour of our deceased colleague and friend, Dr. David Lee, who contributed so much to our knowledge of Australian acarology.

*Phylleremus hunti* n. sp.

**Material examined.** **Holotype:** adult female. Australia: Victoria: Wilson’s Promontory National Park, 38°55’S,146°23’E, Chinamen’s Creek, 100 m elevation, 18.xi.1990, from leaf of *Pomaderris aspera*; deposited in the ANIC.

**Paratypes:** 2 females 1 adult male with same data as holotype; Australia: Victoria: Wilson’s Promontory, Chinamen’s Creek, 17.x.1991, Roaring Meg Gulley, 4 females from leaf of *Zieria arborescens*; 1 female from leaf of *Bedfordia arborescens*; Victoria: Otway Ranges, Mait’s Rest Rainforest Walk, 38°45’S,143°34’E, 23.iii.1992, 1 female, 1 male from leaf of *Bedfordia arborescens*; Tasmania: Mt. Field National Park, Mawson Plateau, 1.i.1992, 4 females, 2 males, 1 tritonymph from leaves of *Olearia pinifolia*; deposited in the ANIC and CNC.

**Diagnosis.** Total length of adults 292–328 μm; mutual distance of tubercles on notogaster about 5–9 μm; setae le about 5–8 μm long; setae ex about 5–8 μm long; saccule Sa, S1, S2, S3 present; five pairs of genital setae.

**Description.** **Adult.** Measurements: Mean total length: female (*n* = 3) 323 μm (range 320–328); male (*n* = 9) 301 μm (range 292–312). Mean notogastral width: female (*n* = 2) 192 μm (192, 192); male (*n* = 9) 170 μm (range 160–180).

Color: Notogaster of newly emerged adults distinctly grey-brown medial to notogastral setae and area medially to anteriorly on rostrum; rest of integument pale brown. Color of mature adults brown.

Integument: Underlying microtubercles on all sclerotized integument. Notogaster with large flattened tubercles circular to oval, circular tubercles about 5 μm in diameter, oval tubercles about 5–8 μm long; tubercles irregularly spaced, but mutual distance about 5–9 μm. Tubercles positioned medially of notogastral setae in specimens from Victoria, extending laterally of notogastral setae almost to margin of notogaster in specimens from Tasmania.

Prodorsum: Rostrum rounded. Weak transverse ridges present between setae ro and le, and laterally on prodorsum (Fig. 19). Longitudinal ridges extending between setae le and transverse or U-shaped ridge anterior to setae in (Fig. 19). Transverse or U-shaped ridge poorly developed. Setae ro about 27–30 μm long, barbed distally, smooth basally, acuminate, mutual distance at base about 20 μm. Setae le about 5–8 μm long, thin, barbed, tapered, mutual distance at base about 27–32 μm. Setae in about 26–34 μm long, thick, plumose setae, flattened to abruptly tapered distally; mutual distance at base about 48–50 μm. Bothridial setae 24–28 μm long, with finely barbed globular head, subequal in length to narrow stalk; head wider than long. Bothridium with internal ring-like ridges. Exobothridial setae about 5–8 μm long, thin, smooth, tapered.

Lateral Region: Pedotectum I covering posterior half of acetabulum I, narrowing along length, and curving dorsally to level of seta ex, and merging with taenidium. Pedotectum II covering base of acetabulum II.

Notogaster: Longer than wide, ratio about 1.3:1.0. All nine pairs of notogastral setae about 16 μm long, curved to geniculate in posterior to posterolateral direction, barbed along distal half, smooth basally, acumi-
nate (Fig. 19). Saccules Sa very small, positioned anteriorly on notogaster, anterior to seta c, dorsal to porose area Ad, about 8 µm long (Fig. 19). Saccules S1, positioned posterior to seta lp, about 3 µm long, or reduced to pore; S2 positioned between setae h, and h,., about 3 µm long, or reduced such that only pore discernable; and S3 positioned between setae h, and h,., dorsal to lyrifissure ip, about 3 µm long (Fig. 19).

**FIGURES 15–18.** Phylleremus leei n. sp., scanning electron micrographs; 15, adult: distal half of tarsus I (pulvillus indicated by arrow); 16, adult: distal half of tarsus IV (pulvillus indicated by arrow); 17, adult: lateral aspect of palp; 18, tritonymph, anterior half, dorsolateral aspect.
Ventral Region: Ventral region with short ridges in coxisternal region, on genital plates, and surrounding genital and anal plates. Five pairs of genital setae. Epimeral and genital setae smooth, acuminate, about 11–16 µm long. Aggenital, anal and adanal setae about 10–14 µm long, smooth acuminate.

Gnathosoma: Mentum with fingerprint pattern laterally. Subcapitular setae $a$, $m$ and $h$ smooth, tapered, relative lengths: $h > m > a$. 

**FIGURES 19, 20.** *Phylleremus hunti* n. sp.: 19, dorsal aspect of adult female; 20, tritonymph, dorsal aspect.
TABLE 1. Development of setiform organs in *Phylleremus leei* n. sp. Setae (Roman) and solenidia (Greek) are listed opposite the instar in which they first appear; parentheses indicate pairs of setae.

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Legs: Leg segments, other than genua, with 10–20 ridges running dorso-ventrally. Claws of legs I and II proportionally larger than those on legs III and IV; all claws with small spines proximodorsally. Pulvilli of tarsi I and II smaller than those of tarsi III, IV. Tibiae of legs I and II longer than respective tarsi. Leg setal formulae (trochanter to tarsus): leg I, 1-5-3(1)-4(2)-18(2); leg II, 1-5-4(1)-3(1)-15(2); leg III, 2-2-1(1)-3(1)-13; leg IV, 1-2-1-3(1)-12. Setae (v) not developed on tarsus I, and (ii) not developed on tarsus III.

*Tritonymph.* Measurements: Length: (n = 2) 286 μm (280, 293).

Prodorsum: Aspis with transverse porose area posterior to setae in and bothridia. Lateral porose areas present anterior of bothridia, broadest posteriorly, narrowing anteriorly. Seta *ro* finely barbed along length, about 16 μm long. Seta *le* thin, smooth, about 3 μm long. Seta *in* about 25 μm long, thick, barbed, tapered (Fig. 20). Setal pairs *ro*, *le* and *in* about 8, 20 and 50 μm apart, respectively. Seta *ex* about 4 μm long, smooth. Bothridial seta about 20 μm long, globular, head subequal in length to stalk, identical in shape to that of adult.

Gastronotic Region: Integument of plicae alternatively slightly sclerotized and unsclerotized, area medial to setae *c₁*, *l* and *h* series more heavily sclerotized than lateral areas; sclerotization indicated by stippling on Fig. 20. Gastronotal setae *c₁*, *l* and *h* series about 15 μm long, with minute barbs. Gastronotal setae of *d* and *p* series short, thin, tapered, about 5–8 μm long (Fig. 20).

Ventral Region: Medial margins of epimeral plates weakly to well-defined; coxisternal porose areas present. Epimere I with narrow mentotectum, greatest width about 5 μm, overlying base of subcapitulum.
Sclerotization in genital region with pattern of about 10 irregular plates, absent in single tritonymph from Tasmania. Epimeral, genital, aggenital, anal and adanal setae smooth, acuminate, about 5–13 μm long, with seta $1b$ longest. Epimeral setae 3–1-2-2; genital setae 4 pairs.

**Legs:** Setation as for tritonymph of *P. leei* (Table 1).

**Etymology.** The specific epithet is in honour of our deceased colleague and friend, Dr. Glenn Hunt, who contributed so much to our knowledge of Australian acarology.

**Discussion**

A number of families have been included in Licneremaeoidea since Grandjean (1954a, p. 445) considered the Ameronothroidae, Cymbaeremaeoidea and Licneremaeoidea to form a natural group straddling pycnonotic and poronotic apherdermous Brachypylina (Behan-Pelletier *et al.* 2005). These families, Licneremaeidae, Passalozetidae, Scutoverticidae, Micreremidae, Adhaesozetidae, Lamellareidae, Fenichelidae, Dendroeremaeidae and Charassobatidae, display a diversity of expression of the octotaxic system of dermal glands, leading Norton & Alberti (1997) to suggest that the superfamily is paraphyletic. In the character analysis below we consider Ameronothroidae and Cymbaeremaeoidea as outgroups, and use these taxa and licneremaeoid families to help determine character state polarities in *Phylleremus*, and to propose a family placement.

**Character analysis: immatures**

*Phylleremus* nymphs are plicate and apherdermous, as are immatures of all licneremaeoid families for which immatures are known, i.e., Adhaesozetidae (*Adhaesozetes polyphylos* (Walter & Behan-Pelletier 1993)), Charassobatidae (*Charassobates cavernosus* (Grandjean 1958)), Dendroeremaeidae (*Dendroeremaes krantzi* (Behan-Pelletier *et al.* 2005)), Lamellareidae (*Tenuelamellarea argentinensis* (Martinez *et al.* 1995)), Licneremaeidae (*Licneremaes lichenophora* (Grandjean 1958)), Micreremidae (*Micreremus spp.* (Grandjean 1954c)), Passalozetidae (*Passalozetes africanus* (Grandjean 1932)), and Scutoverticidae. (*Argentinovertex coineaudi* (Fernandez & Cleva 2002) and Shtanchaeva & Netuzhilin (2003)) and *Provertex delamairei* (Travé 1963).

Setation: Immatures of *Phylleremus* lack setal pairs $f_1$ and $p_3$, as do immatures of Adhaesozetidae, Lamellareidae and Licneremaeidae. Absence of seta $p_1$ from immatures and adults is unique to these taxa among Brachypylina with plicate immatures, and we consider it a synapomorphy.

Gastronotal setae of nymphal *Phylleremus* are monomorphic, with centrodorsal setae subequal in size and shape to the $c$, $l$ and $h$ series setae; this state is shared by immatures of Passalozetidae, Adhaesozetidae, Charassobatidae and Licneremaeidae, and we consider this condition plesiomorphic. Dimorphism of centrodorsal setae is found in Micreremidae, Scutoverticidae, Lamellareidae, and Dendroeremaeidae. However, in *Phylleremus leei* larva setae $c_2$ are barbed and longer than other setae.

*Phylleremus* species do not add a third adanal seta in the deutonymph, and it remains absent in subsequent instars. This loss of $ad_3$ is a synapomorphy also found in Licneremaeidae and Lamellareidae.

Porose Regions: Distinct prodorsal, aggenital and adanal porose regions and porose regions surrounding the opening of the opisthonotal gland and in the coxisternal region are found in some immatures of both ameronothroid and cymbaeremaeoid species. Among Licneremaeoidea they occur in *Phylleremus* and in Adhaesozetidae, Dendroeremaeidae and Micreremidae.

**Legs:** Seta $d$ on the genua and tibiae is retained to the tritonymph in all licneremaeoid families, except Micreremidae, Adhaesozetidae, Dendroeremaeidae, and *Phylleremus* where it is absent from all instars. The loss is a possible synapomorphy of these families (Behan-Pelletier *et al.* 2005). The leg setation of adult *Phylleremus* is reduced, with iterais absent from tarsus III, and ventrals not developed on tarsus I. Iteral setae
are absent from tarsi I to IV of Adhaesozetidae, and we consider this loss a synapomorphy of Phylleremus and Adhaesozetidae. Iteral setae are also absent from certain species in the families Zetorchestidae, Hermannielidae and Plasmobatidae (Grandjean 1961, 1964), brachypyline families only distantly related to Licneremaeoidea.

Immatures and adults of Phylleremus have large, broad subunguinal tarsal pulvilli on tarsi I to IV. These are slightly dorso-ventrally flattened, and smaller on tarsi I and II than on tarsi III and IV. Tarsal pulvilli are comparatively rare among Oribatida (Grandjean 1970, Walter & Behan-Pelletier 1993). They are also found in adults and immatures of Adhaesozetes (Adhaesozetidae) and in immatures of Ametroproctus and Cymbaeremaeus (Cymbaeremaeidae) among apheridemous plicate taxa, and in immatures and adults of all genera of Zetorchestidae (Grandjean 1954b), and adults of some genera of Oripodoidea, (Nasozetes (Scheloribatidae) (Grandjean 1959, 1970)), Ingella (Scheloribatidae) (Hammer 1967), and Symbioribates (Symbioribatidae) (Walter & Behan-Pelletier 1993). The distribution of this structure among these disparate taxa suggests that it has independently evolved many times, and it appears correlated with their arboreal or epilithic ecology.

Character analysis: adults

Notogaster: Among the Licneremaeoidea the complete system of 4 pairs of octotaxic organs occurs in relatively few taxa. In Passalozetidae (porose areas), Dendroeremaeidae (saccules); in the micreremid Porofenicchelia porosa (Mahunka) (porose areas) (Mahunka 1985), and in Glanderemaeus, where it is expressed as 4 pairs of porose areas in females and 3 pairs of porose areas and 1 pair of saccules in males (Norton & Alberti 1997), and in Phylleremus hunti n. sp. where it is expressed as 4 pairs of saccules. Other taxa have fewer porose organs and the numbers can vary according to species. Adults of Scutoverticidae have 0 to 3 pairs of saccules and other species of Micreremidae have 0 to 3 pairs of porose areas (Micreremus subglaaber Ito (Ito 1982)) or saccules (Fenicchelia spp.), adults of Licneremaeidae and Lamellareidae have 2 pairs of porose areas, and adults of Adhaesozetidae have 1 (occasionally 2) pair of porose areas (Norton & Alberti 1997). Clearly, the variable number of saccules in species of Phylleremus is not unusual among Licneremaeoidea, and we are no closer to interpreting the polarity of the octotaxic system in the superfamily than were Norton & Alberti (1997). This difference in expression of the octotaxic system in Phylleremus reinforces the need for identification of genes responsible for this system to help elucidate polarity.

However, the position of saccule Sa, on the anterior notogastral margin is unique among plicate apheridemous taxa, and we consider it an autapomorphy for the genus.

Phylleremus has 9 pairs of notogastral setae, with setae c1, c3, the d series, and p3 absent; among Licneremaeoidea this is shared only with Lamellareidae. In Phylleremus all dorsolateral setae remain in a lateral position and the central region of the notogaster is glabrous. Usually in apheridemous taxa that lack dorsocentral setae in adults, one or more dorsolateral setae (lm and lp) shift medially to occupy the central space, as is found in some Lamellareidae and Passalozetidae. The plesiomorphic lateral positioning of lm and lp is also found in Dendroeremaeidae (Behan-Pelletier et al. 2005).

Lateral and ventral region: The lateral prodorsal taenidium of Phylleremus is unique in known Licneremaeoidea. This structure is easily overlooked under light microscopy and we have confirmed its absence in Micreremidae (Micreremus brevipes Berlese), Licneremaeidae (Licneremaeus sp. from North America), Adhaesozetidae (Adhaesozetes polyphylllos), Passalozetidae (Passalozetes sp. from North America), and Scutoverticidae (Scutovertex sp. from North America).

The typical adult brachypylina coxisternal setation of 3-1-3-3 is reduced to 3-1-2-2 in licneremaeoid families, other than Lamellareidae, Passalozetidae and some members of Scutoverticidae. However, this character state — the loss of setae 3c and 4c — is present in Ameronothroidea and Cymbaeremaeoidea and it is possibly homoplastic in plicate apheridemous taxa.

Phylleremus lacks the humerosejugal porose area Ah. As Norton et al. (1997) noted, this porose area is rarely absent in poronotic Brachypylina; the state is known only in Licneremaeidae and Scutoverticidae.
The preanal apodeme in *Phylleremus* is a small, narrow, caecum-shaped apodeme, as it is in Micreremidae, Scutoverticidae, Lamellareidae and Licneremaeidae. In contrast, in the licneremaeoid families Dendroeremaeidae, Passalozetidae and Adhaesozetidae, and in Phenopelpoidea and Achipteroidea, the preanal apodeme is a goblet-shaped structure, with a narrow to broad neck like that of members of the Oripodoidea.

Gnathosoma: *Phylleremus* lacks an axillary saccule at the base of the palp, as do members of the Licneremaeidae, Micreremidae, Passalozetidae and Charassobatidae. This structure is common in poronotic taxa, including the licneremaeoid families Scutoverticidae, Adhaesozetidae and Dendroeremaeidae, the Phenopelpoidea and the aclipherioid family Tegoribatidae. It is absent from another achiphrioid family, Achipteriidae, and most non-poronotic Brachypylina (Chen *et al.* 2004). In *Phylleremus*, as in all Licneremaeoidea, with the exception of Licneremaeidae and Scutoverticidae, eupathidium acm is fused with the palp tarsal solenidion.

Systematic relationships

Similarities in character states supporting a relationship between *Phylleremus* and various licneremaeoid families are as follows. (1) The octotaxic system is expressed as 4 pairs, shared with Dendroeremaeidae, Passalozetidae and some species of Micreremidae. (2) The posterior notogastral tectum is divided medially with overlapping lobes, shared with Adhaesozetidae, Licneremaeidae and Micreremidae. (3) The coxisternal setation is 3-1-2-2, shared with Adhaesozetidae, Dendroeremaeidae, Lamellareidae, Licneremaeidae, Micreremidae, and some Scutoverticidae. (4) Seta d is absent from tibiae and genua of both immatures and adults, shared with Adhaesozetidae, Dendroeremaeidae, and Micreremidae. (5) Eupathidium acm is fused to the palptarsal solenidion, shared with Adhaesozetidae, Dendroeremaeidae, Lamellareidae, Passalozetidae. (6) The preanal sclerite is a small, narrow, caecum-shaped apodeme, shared with Charassobatidae, Lamellareidae and Licneremaeidae. (7) Seta ad3 is lost, shared with some Lamellareidae and Licneremaeidae. (8) Adults and late nymphal stages lack seta p, shared with Adhaesozetidae, Lamellareidae and Licneremaeidae. (9) Adults have all notogastral setae positioned laterally, shared with Dendroeremaeidae. (10) The iteral setal pair is lost from tarsus III, shared with Adhaesozetidae. (11) Adults and immatures have a subunguinal tarsal pulvillus on tarsi I to IV, shared with Adhaesozetidae. (12) Immatures have prodorsal and adanal porose regions, shared with Adhaesozetidae, Dendroeremaeidae, Micreremidae. Of these, we consider only character states 2, 4, 5, 7, 8, 9 and 10 as apomorphic within Licneremaeoidea. *Phylleremus* shares five apomorphies with Adhaesozetidae (2,4,5,8,10), three apomorphies with each of Lamellareidae (5,7,8), Licneremaeidae (2,7,8), and Dendroeremaeidae (2,5,9) and two apomorphies with Micreremidae (2,4).

Based on this distribution of synapomorphies we include *Phylleremus* as the second genus in Adhaesozetidae. These two taxa are also unique among Licneremaeoidea in having character state 11. Although we tentatively consider it a sympleiomorphy based on outgroup comparison with Cymbaeremaeidae, as indicated above tarsal pulvilli have independently evolved in various non-soil taxa, so this character may in fact be a sixth synapomorphy. Because of a rather mosaic distribution of proposed apomorphies among families, and the significant number of homoplasies this classification requires, we consider inclusion of *Phylleremus* in Adhaesozetidae to be provisional. A larger-scale cladistic analysis of Licneremaeoidea and related families, aided by molecular data, will be necessary to clarify this relationship.

Ecology

Collections: Species of *Phylleremus* were collected at 11 sites from southern Tasmania to southeastern Queensland. *Phylleremus leei* has been collected from 12 plant species representing 9 families, whereas *P. huntii* has been collected from only 4 species representing 3 families (Table 2). The mite species are restricted to different plant species, except that both are found on *Pomaderris aspera*, where they are especially common and abundant (Walter & Behan-Pelletier 1993). In contrast *Adhaesozetes polyphyllos* was collected from the leaves of 51 species representing 23 families (Walter & Behan-Pelletier 1993), including 12 of the 15 plant species from which *Phylleremus* has been collected (Table 2).
**TABLE 2.** *Phylleremus* spp. have been collected from the leaves of 15 species of trees, shrubs and vines in cool-temperate, warm-temperate, montane subtropical, and in moist gullies in wet sclerophyll forests in eastern Australia. (* indicates: *Adhaesozetes polyphyllos* was also collected from these plant species).

<table>
<thead>
<tr>
<th>Plant species</th>
<th><em>Phylleremus leei</em> n. sp.</th>
<th><em>Phylleremus hunti</em> n. sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asteraceae</td>
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</tr>
<tr>
<td><em>Bedfordia arborescens</em> Hochr.</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td><em>Olearia argophylla</em> (Labill.) Benth.</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td><em>Olearia pinifolia</em> (Hook. f.) Benth</td>
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<td>-</td>
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<tr>
<td>Cunoniaceae</td>
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<td></td>
</tr>
<tr>
<td><em>Caldeclusia paniculosa</em> (F. Muell.) Hoogland</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td><em>Callicoma serratifolia</em> Andr.</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td><em>Vesselowskya rubifolia</em> (F. Muell) Pampan.</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Elaeocarpaceae</td>
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</tr>
<tr>
<td><em>Elaeocarpus reticulatus</em> Smith</td>
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<td>-</td>
</tr>
<tr>
<td><em>Sloanea woolssi</em> F. Muell.</td>
<td>+</td>
<td>-</td>
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<tr>
<td>Goodeniaceae</td>
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<tr>
<td><em>Goodenia ovata</em> Sm.</td>
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<td>Proteaceae</td>
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<tr>
<td><em>Banksia collina</em></td>
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<td>Rhamnaceae</td>
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<td><em>Pomaderris aspera</em> Sieb. ex DC.</td>
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<td>+</td>
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<tr>
<td>Rubiaceae</td>
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<tr>
<td><em>Randia benthamiana</em> F. Muell.</td>
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<td>-</td>
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<tr>
<td>Rutaceae</td>
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<tr>
<td><em>Zieria arborescens</em> Sims</td>
<td>-</td>
<td>+</td>
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<td>Sapindaceae</td>
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<tr>
<td><em>Sarcopteryx stipata</em> F. Muell.</td>
<td>+</td>
<td>-</td>
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<tr>
<td>Gesneriaceae</td>
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<td></td>
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<tr>
<td><em>Fieldia australis</em> A. Cunn.</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>

Habitat Use: Compared to *Adhaesozetes polyphyllos* species of *Phylleremus* are not as restricted to plants in protected sites, and are found on plants in dry forests and rainforest margins. While *A. polyphyllos* is only found on leaf surfaces, species of *Phylleremus* are also found on the twigs of plants. In contrast with *A. polyphyllos*, which is a generalist living on a variety of plant species with very different leaf morphologies, species of *Phylleremus* are abundant only on hairy leaves. Both *Phylleremus* species are most abundant on *Pomaderris aspera*, whose leaves have stellate hairs that form a miniature canopy over the leaf surface. *Phylleremus hunti* is rare on *Bedfordia arborescens*, whose leaves have a dense coating of long tomenta, and is sometimes moderately abundant on leaves of *Olearia argophylla* which have a dense coating of short appressed hairs. *Phylleremus* spp. were rarely found on species with glabrous leaves, such as *Elaeocarpus reticulatus*.

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References


