

A new genus and species of Macrochelidae (Acari: Mesostigmata) associated with the Texas leafcutting ant, *Atta texana* (Buckley) in Louisiana, USA

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Adults and nymphs of a new genus and species of the family Macrochelidae are described from detritus cavities of the leaf-cutting ant, *Atta texana*. This new species is notable in having peritremes with no posterior loop, a series of small subterminal teeth on the fixed cheliceral digit rather than the single large tooth typical of other macrochelids and well-developed paranal cribral extensions in both the protonymph and the deutonymph, but not in adults.

Keywords: Mesostigmata; Macrochelidae; *Atta*; myrmecophile; cheliceral and peritrematic morphology; cribrum

Introduction

The mite fauna associated with the social Hymenoptera is vast and includes obligate and facultative representatives of all major acarine orders except for the ticks (Ixodida). A number of mite species have been described from vespid wasps (Vespidae) and the primitively social sweat bees (Halictidae) or their nests, but most of the known species are associated with members of the eusocial apoid families Anthophoridae, Bombidae, Apidae (Meliponinae and Apinae) and Formicidae (O'Connor 1982; Hunter and Rosario 1988; Eickwort 1990; Krantz and Walter 2009). Formicids and their nests are home to many of these mites.

Myrmecophilous mites often display morphological and/or behavioural adaptations that may have evolved to better protect them in a hostile nest habitat. These adaptations include a variety of structural modifications and devices such as holdfast mechanisms to prevent displacement from their worker ant hosts and physical and/or behavioural mimicry of the ant larva to allow them access to brood chambers and to assure safe transport by worker ants during periods of migration (Cross 1965; Elzinga and Rettenmeyer 1975; Elzinga 1978, 1981, 1982a, 1982b, 1989, 1993, 1998; Hunter and Rosario 1988; Eickwort 1990; Krantz 2009). It is likely that morphological or behavioural mimicry in these situations is also reinforced by chemical mimicry. The development of total body armour could be considered as an adaptation to nest habitats in some nidicolous lineages, although many soil- and litter-inhabiting mites also display this character.

Some ant-associated members of the gamasine family Macrochelidae exhibit singular morphological modifications for myrmecophily. For example, *Macrocheles rettenmeyeri* Krantz has greatly elongated legs IV that serve as surrogate tarsal claws III for its ecitonine ant host (Krantz 1962; Rettenmeyer 1962), and *Aethosoma burchellestes*

Krantz is an unusually well-armoured nest associate of *Eciton burchelli* (Krantz 1962, 1998a). However, most of the known myrmecophilous Macrochelidae are unremarkable in terms of their morphology. It was for this reason that we took particular notice of one of three undescribed macrochelid species collected from fungus garden detritus in a laboratory colony of the Texas leafcutting ant, *Atta texana* (Buckley), in Louisiana, USA. Among other notable characters, the idiosoma of the new species has strong overall sclerotization, the cheliceral fixed digit has a series of small distal teeth rather than the large subterminal tooth typical of most macrochelids (Krantz 1998b), the internal cheliceral arthrodial brush is inordinately long and well developed and the peritreme is not looped proximally. Although this suite of characters may suggest a new generic status, only the strong idiosomatic sclerotization can immediately be identified as a possible adaptation to a potentially hazardous ant nest habitat.

Materials and methods

Collections of the new species were made from detritus cavities located below the ground surface in nests of *A. texana* in Natchitoches, Rapides and Winn Parishes, Louisiana, USA, over a period of nearly 50 years (1960–2009) by JCM and his cooperators at the USDA Southern Research Station (Forest Service), Pineville, LA, USA. Specimens were cleared in lactophenol and mounted in Berlese's solution either as whole mounts or as dissections and later sent to GWK at Oregon State University, Corvallis, OR, USA, for identification. A Zeiss GFL phase contrast microscope equipped with drawing tube (Carl Zeiss AG, Jena) was used for examination, preparation of illustrations and descriptions. Measurements cited in the text are in micrometres.

Systematics

Odontocheles gen. nov.

Diagnosis

With general characteristics of the family as defined by Mařán (2003), but displaying the following unusual set of character states: female, male and deutonymph without posterior peritrematic loop; fixed digit of female and nymphal chelicerae with a series of small teeth subterminally rather than the single large subterminal tooth typical for the family; internal cheliceral arthrodial brush thickened proximally and tapering distally, strongly produced and considerably longer than adjacent cheliceral digits, external arthrodial brush greatly reduced in male and nymphal stages; proximal tine of palptarsal apotele greatly reduced; lateral elements of gnathotectum insensibly fused to median forked element; nymphal stages with strongly developed cribrum that includes paranal cribral extensions.

Type species

Odontocheles attaphilus sp. nov., by original designation.

Odontocheles attaphilus Krantz and Moser, sp. nov.

(Figures 1–15)

Female (Figures 1–7) of moderate size (overall length averages 649, width averages 512 ($n = 15$)). Dorsal shield (Figure 1) broadest at level just behind coxae IV, rounded posteriorly, strongly reticulate throughout, with a distinctive pattern of elongate reticulations between setae j_5 and J_2 , shield in mature specimens bordered laterally and posteriorly by a broad, heavily tanned band of striated integument; shield proper with 28 pairs of setae, all but three pairs of which are long enough to reach or surpass the insertions of the setae behind them, j_1 and J_5 pectinate, other dorsal setae ciliate and often appearing narrowly rounded distally (Figure 6), setae j_1 and J_5 short, z_1 weakly ciliate and subequal in length to j_1 , insertions of setae j_5 well posterior to those of adjacent setae z_5 ; with 22 pairs of dorsal pores and crobylophores, individual crobylophores occasionally unpaired (e.g. crobylophore pJ_2 absent on the right side in illustrated specimen); with eight (occasionally seven) pairs of distally pectinate marginal (r ; R) setae inserted in the marginal sclerotized band, all of which are shorter than the adjacent S setae on the shield proper. Peritremes each arising in a peritrematic shield that is fused anteriorly to dorsal shield at level of coxae III–IV and is free of exopodal elements, without posterior loop.

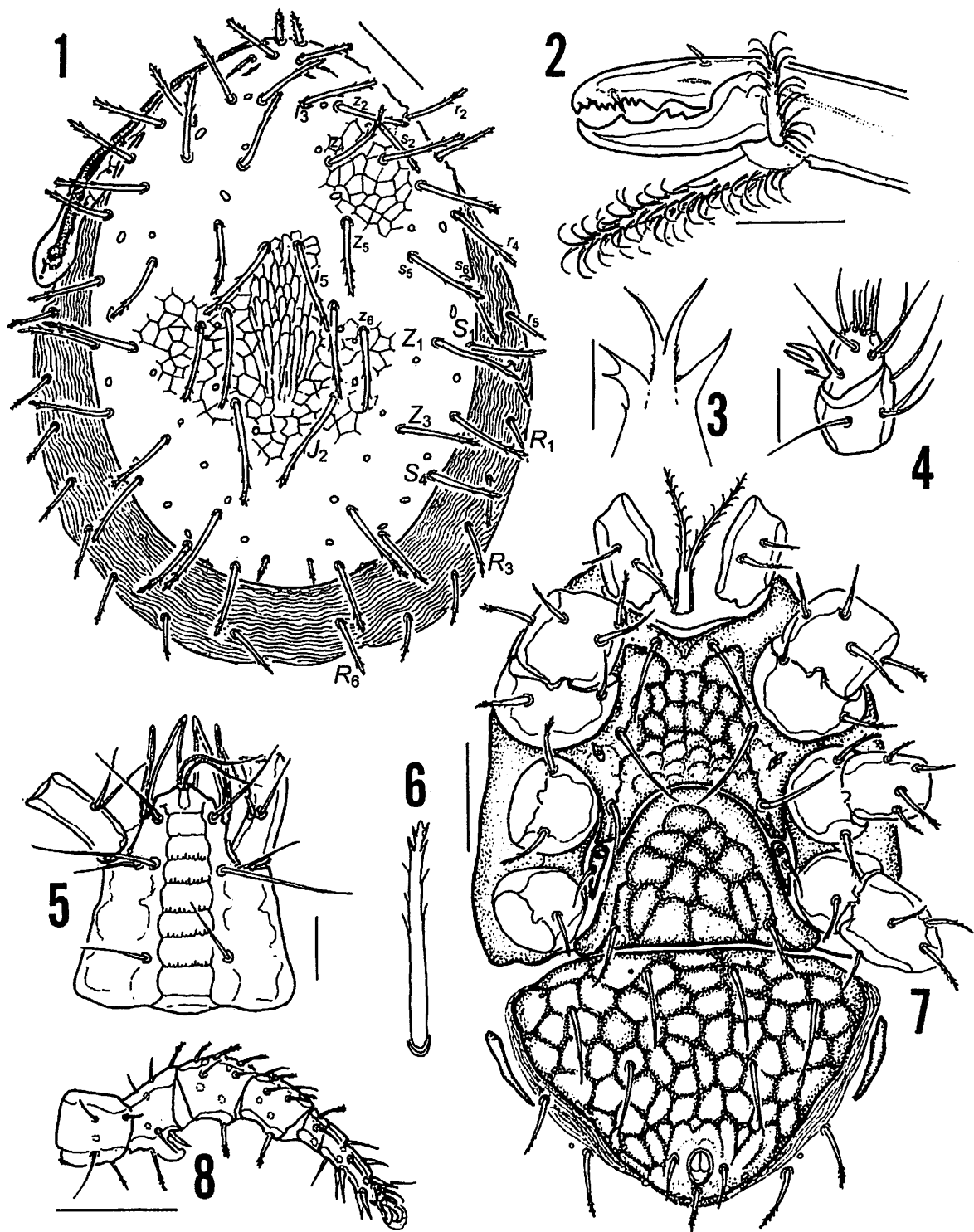
Ventral shielding (Figure 7) extensive, with little intervening integument; sternal shield large and strongly reticulate, extending posterolaterally to the posterior angles of coxae III, free of endopodal elements between coxae III and IV, with three pairs of long setae (st_{1-3}) that reach the insertions of the setae behind them, st_1 weakly ciliate distally. St_{2-3} smooth, with associated slit sense organs behind st_1 and st_3 ; epigynal shield with reticulations similar to but larger than

those on sternal shield, broadly rounded anteromarginally and truncated posteriorly, with a pair of posterolateral, distally ciliate setae that are little more than half the length of the sternals, postepigynal platelets absent; metasternal shields nearly contiguous with posterolateral sternal angles, each with a pore and a short, smooth seta (st_4); ventrianal shield reticulate, considerably broader than long, broadest anteriorly and narrowing and rounded posteriorly, reticulations often appearing smaller than on epigynal shield and more angular, with three pairs of ventrianal setae (Jv_1 , Zv_2 , Jv_3) that are somewhat longer than epigynals but shorter than sternals, weakly ciliate distally, paranal setae short and smooth, postanal seta subequal to paranals but ciliate distally, cribrum obscure, represented by a narrow band of spicules lying behind postanal seta and between paired cribral gland openings; shield in mature specimens with a narrow lateral band of tanned, striated integument similar to that bordering dorsal shield; with a pair of elongate metapodal platelets lying anterad from integumental setae Jv_4 and adjacent to the striated band of ventrianal shield integument, narrower posteriorly than anteriorly; endopodal and exopodal elements contiguous and closely bordering coxae II–IV. Tritosternum typical for family, with strongly plumose paired laciniae and a base that is longer than broad. Sacculus foemineus obscure in available whole-mount specimens.

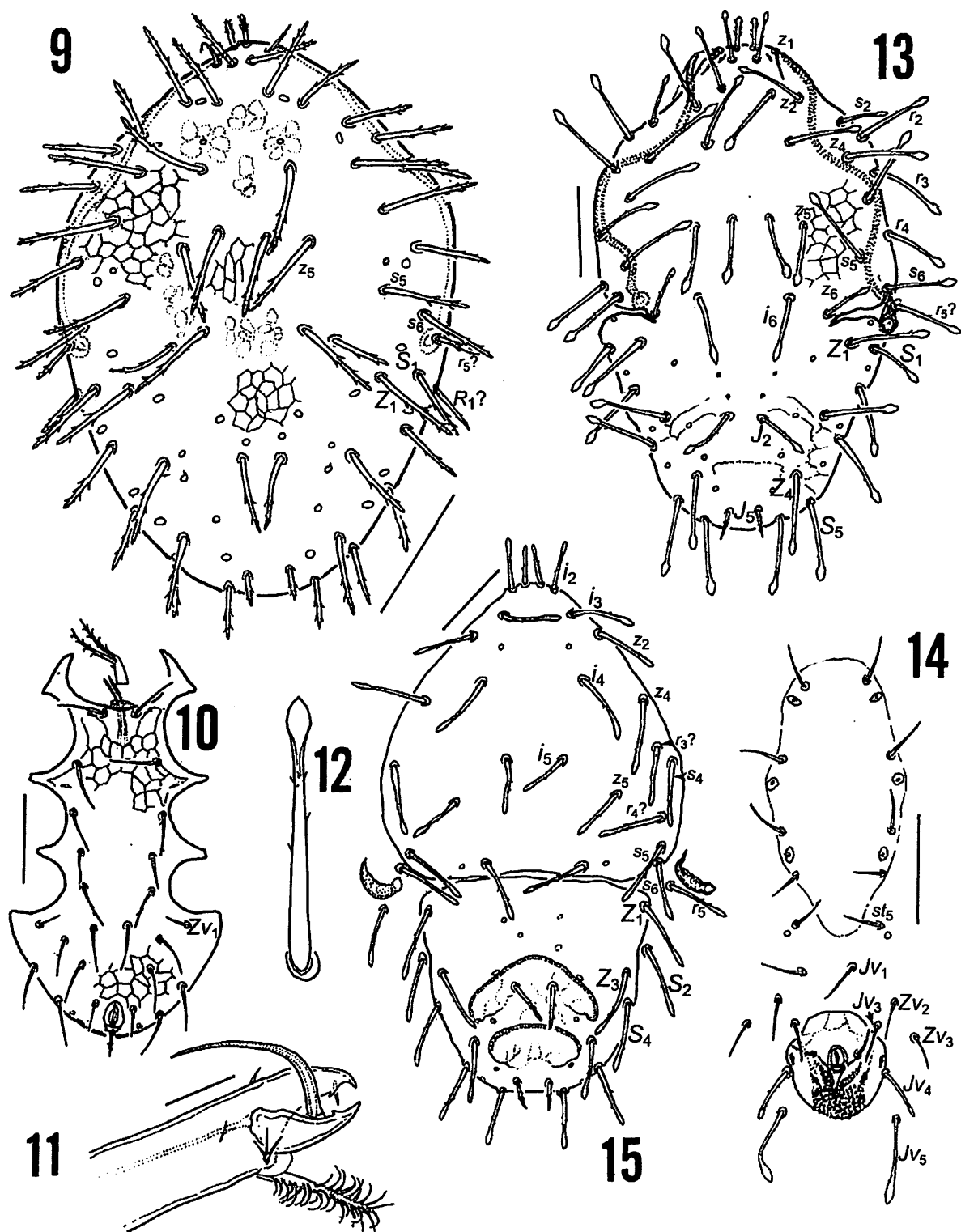
Venter of gnathosoma (Figure 5) with broad capitular groove and five rows of deutosternal denticles (~10 denticles/row) in the portion of groove bordered posteriorly by palpcoxal setae and anteriorly by hypostomatics 2, remaining rows (one proximal, two distal) without distinctive denticles; palptrochanteral setae (v_1 , v_2) may have separate, approximate or contiguous (as illustrated) insertions, proximal tine of palptarsal apotele (Figure 4) weakly developed, often obscure; hornlike corniculi flanked by conspicuous salivary styli; movable digit of chelicera (Figure 2) with two proximal teeth forming a weakly defined bidentate tooth, with a more distal single tooth; fixed digit with a large median tooth flanked distally by a row of six small teeth and a smaller subterminal tooth, pilus dentilis inserted above distal row, dorsal seta narrow, uneven terminally; arthrodial brushes strongly plumose, stalk of internal brush considerably longer than cheliceral digits, greatly thickened basally and tapering distally, external brush smaller but strongly developed; lateral elements of gnathotectum (Figure 3) either acuminate or divided distally, insensibly fused to a forked median element extending well beyond lateral elements.

Legs typical for family, legs I narrow, antenniform, without ambulacra; legs II considerably broader than other legs and subequal in length to legs I and IV; legs III about two-thirds length of other legs; leg setae distally ciliate or smooth, genu IV with six setae.

Male (Figures 8–11) smaller than female (overall length averages 442, width averages 318 ($n = 4$)). Dorsal shield (Figure 9) narrower than that of female and not covering dorsum laterally and posteriorly, broadest at level of



Figures 1–8. *Odontocheles attaphilus* gen. nov., sp. nov., female: 1. dorsum; 2. chelicera, adaxial aspect; 3. gnathotectum; 4. palptibia and tarsus; 5. gnathosoma, venter; 6. dorsal seta; 7. venter. 8. *Odontocheles attaphilus* gen. nov., sp. nov., male – leg II (coxa omitted). Scale bars: (1, 7, 8) 100 μm; (5) 50 μm; (2–4) 25 μm.



Figures 9–15. *Odontocheles attaphilus* gen. nov., sp. nov., male – 9. dorsum; 10. venter; 11. chelicera, adaxial aspect. 12–14. *Odontocheles attaphilus* gen. nov., sp. nov., deutonymph – 12. dorsal seta; 13. dorsum; 14. venter. 15. *Odontocheles attaphilus* gen. nov., sp. nov., protonymph – 15. dorsum. Scale bars: (9, 10, 14) 100 μ m; (13, 15) 50 μ m; (11) 25 μ m.

coxae II, reticulate throughout but without distinct median elongate reticulate pattern as in female, striated marginal integumental band absent; with 30 pairs of setae rather than 28 as in female (with two additional pairs of marginal setae (r_5 , R_1 ?)), j_1 short and pectinate, z_1 appearing smooth or nearly so, other dorsal setae distally ciliate and generally with a rounded tip (as in Figure 6), insertions of j_5 and z_5 more or less on same level; anterior lyrifissures (pz_1) obscure in all observed specimens.

Venter (Figure 10) with a reticulated holovernal shield, sternal and metasternal setae smooth, long enough to reach insertions of setae behind them, epigynal setae (st_5) weakly ornamented; with six pairs of smooth ventral setae, of which setae Zv_1 are the shortest, paranal setae smooth, subequal to Zv_1 , postanal seta ciliate distally, cribrum weakly developed. Peritremes, tritosternum and most gnathosomatic structures similar to those of female; fixed digit of chelicerae (Figure 11) with a simple retrorse tooth subterminally, without row of small subterminal teeth found in female and nymphal stages, pilus dentilis prominent, dorsal seta acuminate; movable cheliceral digit with a single small retrorse tooth subterminally, with a long, recurved spermatodactyl arising medially on the interior face of the digit, internal arthrodial brush prominent, similar in form to that of female and clearly longer than cheliceral digits, external brush weakly developed, consisting of a short base and a brush of three or four radiating spines; insertions of palptrochanteral setae separate in all observed specimens. Legs similar in most respects to those of female, femur of leg II (Figure 8) armed with a terminally rounded ventral spur (v_1).

Deutonymph (Figures 12–14) similar in length (444) and width (317) to female ($n = 2$). Dorsal shield (Figure 13) lightly reticulate and weakly tanned throughout, incised laterally, with a shallow, crescentic depression between insertions of setae Z_4 , with 29 pairs of setae (28, if r_5 (?) is inserted adjacent to shield rather than on it (Figure 13, right side)), most of which are strongly clavate distally, often with a few fine cilia on setal shaft (Figure 12), setae z_1 smooth and J_5 ciliate, both subequal in length to j_1 ; lyrifissures pz_1 distinct. Stigmata near level of dorsal shield incisions, opening anteriorly to sinuous peritremes that terminate near the insertions of z_1 .

Venter (Figure 14) with smooth, spinose sternal setae (st_{1-4}) and associated pores inserted in a weakly defined unornamented sternal shield, epigynal setae and pores (st_5 , iv_4), along with opisthogastric setae, inserted behind shield in weakly striated integument; opisthogastric setae Jv_{4-5} longer than other opisthogastrics, distally expanded, Jv_4 weakly ciliate, shorter than Jv_5 , inserted adjacent to or on the margin of anal shield; anal shield well defined, peltate and weakly reticulate, with centrally located anal opening flanked by short, smooth paranal setae and a slightly expanded postanal seta; cribrum well developed and covering region behind postanal seta, with additional narrow

rows of cribal spicules extending anterolaterally nearly to paranal setal insertions, with two pairs of pore or gland openings that may represent ivp and gv_3 of Gerdeman and Klompen (2003). Movable digit of chelicera with two unidentate teeth, fixed digit with a median tooth and a more distal region of three or four small teeth (rather than six as in female), internal arthrodial brush strong, subequal in length to adjacent movable digit; external brush consisting of a short base and three or four radiating spines.

Protonymph (Figure 15) measures 378 in length and 222 in width ($n = 1$). Dorsal shield divided medially, podonotal shield without clear ornamentation, with 11 distally expanded and mostly weakly ciliate setae inserted on the left side of shield (j_{1-6} , $z_{2,4-5}$, s_{4-5}) and 14 on the right side (with an accessory seta between z_4 and s_4 (r_3 ?), and one between z_5 and s_5 (r_4 ?); seta s_6 also inserted on the right side of shield), distal expansion of idiosomatic setae generally less pronounced than in deutonymph (Figure 13); pygidial shield with eight setal pairs, J_5 short and ciliate, other pygidial setae longer, expanded distally and occasionally weakly ciliate, with two distinctive arched depressions between insertions of Z_3 – Z_4 , shield otherwise unornamented. Peritremes small, crescentic, confined to region between coxae III and IV. Chelicerae similar to those of deutonymph, with three small teeth subterminally on the movable digit; palptarsal apotele appears two-tined (proximal element not visible in the available specimen). Venter similar to that of protonymph, sternal shield evanescent or absent, anal shield similar to that of deutonymph in shape, cribal and pore/gland development and surrounding setal pattern (Figure 14), except that insertions of setae Jv_3 and Jv_4 are well removed from the shield border.

Larva not seen in collected samples.

The genus *Odontocheles* may be differentiated from other genera of the family Macrochelidae on the basis of its singular cheliceral, peritrematic and setal morphologies (see above). The strong ventral sclerotization, the fused form of the gnathotectum and the ornamentation of the dorsal shield of adult *O. attaphilus* most closely resemble species of the genus *Glyptholaspis* (Filipponi and Pegazzano 1960). However, the dorsal shield of *Glyptholaspis* adults has a denticulate rather than a smooth margin as in *O. attaphilus*, and it lacks the strongly tanned marginal band of integument common to mature females of the new species. The absence of a posterior peritrematic loop in *O. attaphilus* is unique to the family except for certain species of the Old World genus *Neopodocinum* Oudemans (Mařán 2003). However, the latter species have an anal rather than a ventrianal shield, a unipartite gnathotectum and seven setae on genu IV. It should be noted here that the tanned integument band bordering the dorsal and ventrianal shields of mature *O. attaphilus* females (absent in teneral specimens) also occurs in certain other macrochelid assemblages (Krantz 1967, 1998a) and appears to be age related.

Type material

Holotype female and five paratype females with the following data: ex fresh detritus from fungus garden cavity 2.5 metres below the nest cavity of *A. texana*, Kisatchie National Forest, Natchitoches Parish, Louisiana, 4 August 2004 (S. Dash et al., colls.); two females ex detritus 2.6 metres deep in *A. texana* nest, Winn Parish, Louisiana, 4 June 2009 (L. Bui and J. Moser, colls.); 10 females ex detritus cavity, 2 metres deep in *A. texana* nest, 18 January 1960 (J. Moser, coll.); one female attached to leg of *A. texana* major worker at nest surface, Bentley, Louisiana, 1 July 1966 (J. Moser, coll.). Allotype male ex fresh detritus from fungus garden cavity 2.5 metres below the nest cavity of *A. texana*, Kisatchie National Forest, Natchitoches Parish, Louisiana, 4 August 2004; two males ex detritus 2.6 metres deep in *A. texana* nest, 4 June 2009 (L. Bui and J. Moser, colls.); one male ex detritus cavity 2 metres deep in *A. texana* nest, 18 January 1960. One deutonymph ex fungus garden detritus in a laboratory colony of *A. texana*, 1 December 2004, taken from 2.5 metres below the nest surface, Kisatchie National Forest, Natchitoches Parish, Louisiana, 4 August 2004 (S. Dash et al., colls.); one deutonymph ex detritus 2.6 metres deep in *A. texana* nest, 4 June 2009 (L. Bui and J. Moser, colls.). One protonymph ex nest detritus 2 metres deep in *A. texana* nest, 18 January 1960 (J. Moser, coll.). Additional material in the collection of USDA Forest Service, Research Project SRS 4552, Pineville, LA.

Type repositories

Holotype female and allotype male in National Museum of Natural History, Washington, DC. Paratypes in Oregon State Arthropod Collection, Corvallis; Southern Research Station, USDA Forest Service, Pineville, LA; Acarology Laboratory, Ohio State University, Columbus, OH, USA; Canadian National Collection, Ottawa, ON, Canada; Australian National Insect Collection, Canberra, ACT, Australia; and Natural History Museum, London, UK.

Discussion

Morphological considerations

The genus *Odontocheles* is erected to accommodate a new species of ant-associated Macrochelidae that displays a singular set of morphological characters. Among its more unusual attributes are the lack of a posterior peritrematic loop (also seen in some species of the genus *Neopodocinum* Oudemans) and the presence of a subterminal row of small teeth on the fixed cheliceral digit (Figure 2). The gnathotectum (Figure 3) has fused lateral and medial elements, a trait common to a number of unspecialized soil- and litter-inhabiting macrochelids (Mašán 2003; Emberson 2010). An interesting dichotomy is seen in dorsal shield setal morphology, with those of adults being terminally obtuse or rounded (Figure 6) and those of nymphal stages being clavate (Figure 12). In addition, the observed number of

dorsal setae varies between stages and sexes (28 pairs in the female, 30 in the male and 28 or 29 in the deutonymph). Incongruities also have been observed in cribral development and in arthrodial brush morphology, as described below.

The cribrum of adult *O. attaphilus* is marginal and often obscure, but it is strongly developed in both the protonymph and the deutonymph and has anterolateral extensions of cribral spicules that nearly reach the paranal setal insertions (Figure 14). Extensions of this type are typical in adults of some early derivative free-living macrochelid lineages (Mašán 2003; Emberson 2010), and have been presumed to provide a broader platform for dispersion of cribral gland-generated sex pheromones among free-living species that, unlike many phoretic forms, do not aggregate on insular substrates (Krantz and Redmond 1988). The discovery of paranal extensions in *O. attaphilus* nymphs and their absence in adults clearly points to a need for further research on cribral function. Regarding arthrodial brush morphology, while the chelicera of *O. attaphilus* females has strongly developed internal and external arthrodial brushes, the external brush in males and nymphs comprises an abbreviated base and three or four radiating spines (Figure 11). A similar but less dramatic difference in brush development is seen in males and females of *Glyptolaspis americana* (Berlese), a species in which the male external arthrodial brush (setate excrescences of Krantz and Wernz 1979) may play a role in sperm transfer.

The series of tiny teeth on the fixed cheliceral digit of *O. attaphilus* is a unique character of the family. Their appearance suggests a scraping function, which in turn raises the possibility that the mite feeds on fungal spores in the detritus cavities. In fact, a number of spores and mycelial strands have been recovered from the body cavities of several female mites taken from detritus cavities (JCM, personal observation). However, the well-developed capitular groove of *O. attaphilus* (Figure 5) tends to support a liquid diet rather than a solid diet. The presence of a weakly defined bidentate tooth on the female movable cheliceral digit suggests that phoresy could play a role in mite colonization of new nests in that a bidentate tooth is often correlated with a phoretic lifestyle in macrochelid mites (Krantz 1998b). Support for this assumption, however, is limited to two observations, namely a single female of *O. attaphilus* recovered from a winged *A. texana* queen at a light in 2011 (slide 11125) and another found attached to the leg of a worker on a nest surface in 1966 (slide 52866).

Habitat considerations

Odontocheles attaphilus is one of 17 mite species and 8 non-acarine inquilines found in nests of *A. texana* in Louisiana (JCM, personal observation). Recorded nest habitats for these species include galleries, fungus gardens and detritus cavities (Moser 2006). Fungus gardens in *A. texana* nests flourish for only a month, after which they senesce and are removed to detritus cavities by ant workers.

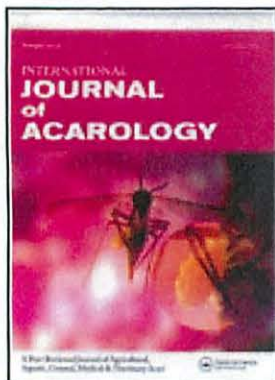
Some arthropod species are routinely found in fungus gardens or galleries, but *O. attaphilus* has been collected only from detritus cavities, a niche that is difficult to pinpoint in nest excavations where a bulldozer or a backhoe is often the principal excavating tool, and where nests may exceed a depth of 12 feet (Moser 2006). Only three of the nests excavated in Louisiana since 1960 have contained *O. attaphilus*, and all of the specimens have occurred in detritus cavities. *Odontocheles attaphilus* has been successfully maintained in laboratory colonies at the USDA Research Station in Pineville for short periods of time on nest detritus taken from the field, and limited reproduction has been observed.

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