

# Mutualism between armoured scale insects and ants: new species and observations on a unique trophobiosis (Hemiptera: Diaspididae; Hymenoptera: Formicidae: *Melissotarsus* Emery)

SCOTT A. SCHNEIDER<sup>1,2,3</sup>, JAN H. GILIOME<sup>4</sup>, JOHN W. DOOLEY<sup>5</sup> and BENJAMIN B. NORMARK<sup>1,2,3</sup>

<sup>1</sup>Graduate Program in Organismic & Evolutionary Biology, University of Massachusetts, Amherst, MA, U.S.A., <sup>2</sup>Graduate Program in Entomology, University of Massachusetts, Amherst, MA, U.S.A., <sup>3</sup>Biology Department, University of Massachusetts, Amherst, MA, U.S.A., <sup>4</sup>Centre for Invasive Biology, Department of Botany & Zoology, Stellenbosch University, Stellenbosch, South Africa and <sup>5</sup>United States Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine (USDA, APHIS, PPQ), San Francisco, CA, U.S.A.

**Abstract.** The association between African armoured scale insects (Hemiptera: Coccoidea: Diaspididae) and ants belonging to *Melissotarsus* Emery (Hymenoptera: Formicidae: Myrmicinae) is the only trophobiosis known in which ants do not receive honeydew or nectar in exchange for protection and other services. Food reward for the ants in this mutualism remains unknown, despite repeated suggestions that diaspidids are consumed by the associated ants, thus serving as ‘domestic cattle’. We describe new observations on interactions between *Melissotarsus emeryi* Santschi and the diaspidid *Morganella conspicua* (Brain) from South Africa. Worker ants exhibited previously undescribed tending behaviours, most notably a ‘squeezing and licking’ performed on an adult female diaspidid and ‘culling’, in which a worker removed an adult female armoured scale from the host plant. These could represent the gathering of secretory products and the cultivation of an individual for consumption, respectively. An ant exclusion study over 12 days of isolation showed that adult female diaspidids and second-instar nymphs secreted no wax or exudates that attending ants would ordinarily collect. Workers of *M. emeryi* did not defend their nest against invading colonies of *Crematogaster* and other unidentified ants: we hypothesize that the primary mode of defence is maintenance of isolation within galleries. We describe three new ant-associated diaspidid species: *Affirmaspis cederbergensis* Schneider **sp.n.** from South Africa, *Diaspis doumtsopi* Schneider **sp.n.** from Cameroon, and *Melissoaspis incola* Schneider **sp.n.** from Madagascar. *Melissoaspis formicaria* (Ben-Dov) **comb.n.** is transferred from *Morganella* (Brain). Diagnostic characteristics for *Melissoaspis* Ben-Dov are revised, and additional taxonomic information defining this genus allows ease of identification. An updated identification key to the species of ant-associated diaspidids is provided.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:632C1122-954A-4DE6-B946-8E6AB6A4D27F>.

## Introduction

The association of ants with honeydew-producing Hemiptera (aphids, scale insects, membracids, etc.), or with nectar-producing larvae of lycaenid butterflies, is a well-studied phenomenon termed trophobiosis. Trophobioses are complex,

Correspondence: Scott Schneider, Biology Department, University of Massachusetts, 181 Presidents Dr., Amherst, MA 01003, U.S.A.  
E-mail: scott@psis.umass.edu

typically mutualistic, relationships in which ants provide protection and other benefits to a partner species and procure a reliable food reward from this partner in exchange for their attendance (reviewed by Way, 1963; Hölldobler & Wilson, 1990; Gullan, 1997; Gullan & Kosztarab, 1997; Delabie, 2001; Pierce *et al.*, 2002). The only ant–hemipteran trophobiotic relationship in which honeydew appears not to be a ‘currency’ of exchange involves ants of the genus *Melissotarsus* Emery (Hymenoptera: Formicidae: Myrmicinae: Melissotarsini) and certain armoured scale insects (Hemiptera: Diaspididae). The Diaspididae are one of a few families of scale insects that do not produce honeydew (Beardsley & Gonzalez, 1975; Foldi, 1990a, 1990b). Armoured scale insects feed on the parenchyma tissues of host plants rather than on phloem or xylem fluids, which obviates the need to expel excess water and sugars as honeydew. It is uncertain what food source *Melissotarsus* ants procure from diaspidids and how stable mutualisms are maintained between such unlikely partners. However, *Melissotarsus* workers actively tend diaspidid populations within their nests to the benefit of both parties and the association is obligate for the ants and potentially for the diaspidids as well (Mony *et al.*, 2007; Ben-Dov & Fisher, 2010).

A detailed review on the trophobiosis between *Melissotarsus* ants and diaspidids by Ben-Dov & Fisher (2010) is summarized briefly later on. Here, we describe new observations on associations between the ant *Melissotarsus emeryi* Santschi and the diaspidid *Morganella conspicua* (Brain) in South Africa. We describe three new species of ant-associated diaspidids and expand our understanding of the taxonomy and distribution of the trophobiosis.

### ***Melissotarsus* ants and Diaspididae: natural history and associations**

The relationship between *Melissotarsus* ants and armoured scale insects was first discovered in the 1970s in Côte d’Ivoire (Delage-Darchen, 1972; Delage-Darchen *et al.*, 1972) and shortly thereafter in South Africa (Prins *et al.*, 1975; Ben-Dov, 1978). The association occurs throughout continental Africa as well as Madagascar and Saudi Arabia (Ben-Dov & Matile-Ferrero, 1984; Collingwood, 1985; Dejean & Mony, 1991; Mony *et al.*, 2002). Little is known about *Melissotarsus* ants, due to their cryptic habits. These are gallery-forming ants with large polygynous colonies ranging from several thousand to over 1.5 million individuals (Mony *et al.*, 2002). Worker ants birthed from multiple queens operate as a single unified colony within one host tree; there is little intercolony aggression (Mony *et al.*, 2007). Workers excavate a network of tunnels in the bark of live trees and diaspidid populations are housed within the nest chambers along with ant brood. *Melissotarsus* workers enclose their galleries against the surrounding environment by forming a mortar from silk, sawdust and frass used to seal the entrances (Prins *et al.*, 1975; Fisher & Robertson, 1999). They are the only adult ants that produce silk. When a segment of the gallery roof is removed, workers immediately divert their attention to repairing and enclosing the nest chambers. It is difficult to

observe normal behaviours and interactions between ants and diaspidids directly, due to this cloistered habit, but workers have been observed frequently to tend diaspidids (Delage-Darchen *et al.*, 1972; Prins *et al.*, 1975; Ben-Dov, 1990; Mony *et al.*, 2007). *Melissotarsus* workers do not forage outside of their galleries due to an unusual configuration of their middle pair of legs, which are tilted at an angle of nearly 180° to the front legs. This configuration allows workers to anchor themselves on the sides or roof of the tunnel, but renders them incapable of walking effectively on flat surfaces (Delage-Darchen, 1972; Mony *et al.*, 2007). Workers will stagger and flail about when placed on a flat surface.

Within the galleries of *Melissotarsus*, various insect inhabitants have been found, including putative predators and parasitoids (Encyrtidae, Reduviidae, and Bethyridae) and social parasites (Thysanura, Anthochoridae, and Aradidae) (Prins *et al.*, 1975), but these are rare. Diaspidids are the only other abundant and consistent nest inhabitants, and it is likely that the nutritive demands of these massive ant colonies are derived in some form from diaspidids.

All life stages of diaspidids are found within *Melissotarsus* galleries, including first- and second-instar nymphs, adult females and adult males in biparental species (Ben-Dov & Matile-Ferrero, 1984). Diaspidids are abundant within ant nests. One census found the diaspidid *Morganella pseudospinigera* Balachowsky to outnumber ants (*Melissotarsus beccarii* Emery) approximately three to one from randomly selected twigs (Ben-Dov & Matile-Ferrero, 1984). Mony *et al.* (2002) estimated colonies of *Melissotarsus weissii* Santschi and *M. beccarii* in mango (*Mangifera indica* L.) and safou (*Dacryodes edulis* Lam), respectively, to contain from 330 000 to 556 000 diaspidids. These staggering numbers suggest that diaspidids benefit from the association, and Ben-Dov & Matile-Ferrero (1984) proposed that the primary benefit received by diaspidids is protection within the enclosed galleries of ant nests. Aided dispersal is another potential benefit that may be received by diaspidid partners, but it remains unknown as to how ant colonies acquire diaspidids and if they are transported actively or recruited during colony foundation. Possibly ants participate actively in the introduction of diaspidids as crawlers (mobile first-instar nymphs) to the galleries (Ben-Dov & Fisher, 2010).

All populations of ant-associated diaspidids are scale-less; they lack the characteristic scale covering for which the ‘armoured’ scales have been named. The majority of ant-associated diaspidid species are known only from scale-less populations living with ants; however, *M. conspicua*, *M. pseudospinigera* and *Melanaspis madagascariensis* Mamet were originally described from free-living populations with normal scale covers (Brain, 1919; Mamet, 1951; Balachowsky, 1956; reviewed in Ben-Dov & Fisher, 2010). In free-living populations the scale cover provides mechanical protection throughout most of the life stages (reviewed in Foldi, 1990a) and provides effective protection even against predatory *Pseudomyrmex* ants associated with *Acacia* (Janzen, 1966; Kosztarab, 1987). For ant-associated populations, sequestration

within galleries is apparently an effective substitute for this mode of protection.

It is unclear why ant-associated diaspidids lack scale covers. If diaspidids attempt to produce wax in galleries then ants either collect that wax or prevent its production, perhaps through chemical manipulation (Ben-Dov, 1978). An exception apparently occurs for male diaspidids; the prepupal and pupal instars of *M. conspicua* possess scale covers from which adult males emerge (Prins *et al.*, 1975; S. A. Schneider, personal observation). If ants are responsible for the absence of scale covers, this suggests that *Melissotarsus* workers differentiate between the sexes and only interfere with females producing wax. Female diaspidids possibly cease wax production in the presence of *Melissotarsus* ants: wax production may be costly and it may be advantageous for diaspidids to invest in growth or reproduction instead. One symbiotic species of *Aspidiotus* completely lacks dorsal macroducts, the major secretory glands that are responsible for producing the scale cover (Delage-Darchen *et al.*, 1972). Several other ant-associated diaspidids have few dorsal macroducts as well (Ben-Dov, 2010). Currently we cannot know if the macroducts are functional in these species, because all known populations are ant-associated.

Authors have speculated about the potential food rewards that *Melissotarsus* could receive from diaspidids. Waxy glandular secretions from the macroducts have been suggested to serve as the primary food source for *Melissotarsus* (Ben-Dov & Matile-Ferrero, 1984). Worker ants frequently probe the dorsum and pygidium of diaspidids with their mandibles; it is possible that they are collecting secretions in this way. This hypothesis is not supported by the observation that several ant-associated diaspidids either lack macroducts or possess only a few on the dorsal pygidium. However, both scale-covered and scale-less populations of *M. conspicua* have been found on the same tree in free-living and ant-associated populations, respectively (Prins *et al.*, 1975), and so this possibility has not been ruled out. It has also been suggested that ants are maintaining armoured scale insects as 'domesticated cattle' that are consumed as a source of 'meat' (Ben-Dov, 1978). Trophobiotic ants occasionally consume mutualist partners in addition to harvesting honeydew, but the degree to which this occurs is largely unknown (Stadler & Dixon, 2008). This would be the first trophobiosis in which meat is the primary (and perhaps only) food reward for ant attendance. Meat farming would make for more than just an interesting case of natural history, as it would suggest that the relationships between *Melissotarsus* ants and diaspidids are simultaneously mutualistic and predatory. Further dietary studies of *Melissotarsus* ants are required to fully understand the nature and dynamics of this unusual form of mutualism.

### Interactions between *M. emeryi* and *M. conspicua* from South Africa

#### Methods

We made several new observations on live populations of the ant species *M. emeryi* and the diaspidid *M. conspicua*

in the Western Cape province of South Africa. In January 2012, S.A.S. and J.H.G. revisited Nardouwsberg, the locality from which Prins *et al.* (1975) first discovered this association within host trees of the species *Leucospermum praemorsum* (Meisn.) Phillips (Fabaceae). Ant colonies were discovered in 10 trees of *L. praemorsum* from several farms located between Nardouwsberg and Vanrhynsdorp in the Clanwilliam district (localities are listed under the heading for *M. conspicua* in 'Material examined' below). Infested trees were identified easily by vein-like markings on the smooth bark, indicating the presence of galleries under the surface. We haphazardly selected branches from infested trees, sawed them off and brought them back to Stellenbosch University for observation in the laboratory. We removed the bark to expose galleries and then observed the interactions between ants and diaspidids through a Leica Wild M8 dissecting microscope. Any evidence of ant-feeding behaviours was of particular interest.

We exposed ant galleries on two segments of branch, each approximately 17 cm in length, cut from a tree at Duikerfontein farm in Nardouwsberg (locality: 32° 1' 55.56'' S, 18° 51' 54.30'' E). All worker ants were removed from these branch segments, such that the resident diaspidids (both adult females and second-instar nymphs) remained isolated from ant attendance for a total of 12 days. The goal of this ant exclusion was to determine whether or not armoured scale insects would produce filaments of wax from their dorsal macroducts or droplets of exudate from the anus that ants would ordinarily collect. Armoured scale insects were observed daily for any such evidence. One branch segment was left uncovered and exposed (Fig. 1); the other was wrapped in a piece of black plastic in an attempt to simulate an intact gallery roof. This latter attempt proved unsuccessful, due to accumulating condensation resulting in the growth of mould in the galleries. The mould grew over rapidly and killed most of the armoured scale insects on this branch. We report observations for the uncovered branch only.

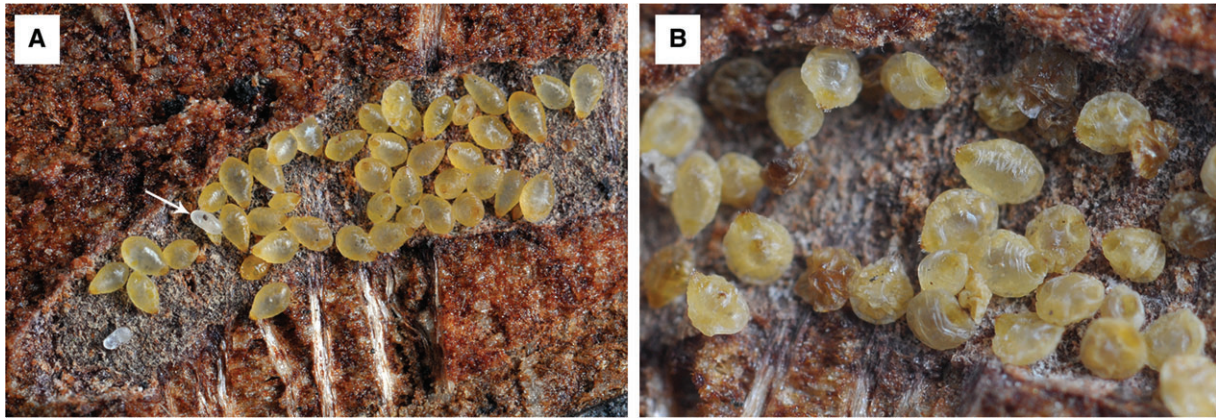
#### Ant behaviours observed

##### Tending

Consistent with previous reports, worker ants generally divert their attention to repairing exposed galleries with a combination of silk, sawdust and frass (Fisher & Robertson, 1999). A few workers did focus attention on tending to brood and to armoured scale insects. These workers were often busy using silk to coat the gallery walls and also sometimes placing strands of silk on larvae, pupae and diaspidids. The silk may be effective at reducing the build-up of moisture within galleries, as the tunnels appear to be considerably drier than the surrounding wood. Workers also used silk to bundle larvae together for transport to new locations.

We observed two curious tending behaviours that have not been reported previously in the literature. On one occasion we saw a worker ant tending an adult female armoured scale that had a first-instar nymph partially breaching from the vulva. The worker ant repeatedly grabbed the adult female





**Fig. 1.** A segment of exposed galleries from the ant-exclusion study with adult females and second-instar nymphs of *Morganella conspicua*. (A) This photograph was taken at the beginning of the ant exclusion study on 7 January 2012. The white arrow indicates an ant larva that is also visible at the far left of the second pane. (B) This photograph was taken 20 days later on January 27, 2012. Daily observations were made for the period of January 7th through January 18th. During this time no armoured scale insects were observed secreting wax from the macroducts or exudate from the anus. Individual diaspidids that died during this interval appear darkened and shrivelled. (Photograph: Anton Jordaan, Stellenbosch Centre for Photographic Services.)

diaspidid around the thoracic/anterior abdominal margin with its mandibles and gently squeezed the body. The worker then grazed its mouthparts along the mid-dorsum of the diaspidid in what appeared to be a 'licking' behaviour. This sequence of behaviours, 'squeezing and licking', was repeated multiple times for the duration of only a few minutes. The worker then ceased this behaviour and walked away. The first-instar nymph took several hours to fully emerge from the female. It is possible that the 'squeezing and licking' was a form of foraging behaviour, but without further information this remains purely speculative. If fluid or wax was secreted during this process, the amounts were too minute to see under the microscope at full magnification. On a separate occasion, a worker ant antennated an adult female diaspidid and then seized the scale insect with its mandibles and pulled it away from the gallery wall. The worker drew the armoured scale out until its mouthparts were mostly removed from the wood and then placed it down and walked away. The armoured scale was marked to see if workers would come back to claim it later; however, all workers within this branch were killed soon after by an invading colony of unidentified ants that were present in the laboratory. The adult female diaspidid died within 24 h after being removed from the tree. It remains unclear whether this diaspidid was being harvested for consumption or if there is an alternative explanation for this behaviour. There were no direct observations of ants consuming armoured scales.

### Defence

The invasion of *Crematogaster* workers and another unidentified ant species into the galleries of one branch presented an unexpected opportunity to observe the defensive behaviours of *M. emeryi* workers. *Melissotarsus* workers did not aggressively defend their galleries; when faced with an intruder, workers would pause or tuck themselves into small crevices.

Invading workers of the unidentified ant species stung and killed *Melissotarsus* workers with little to no resistance. Invading *Crematogaster* workers were also observed pinching workers of *M. emeryi* with their mandibles, eliciting the same retreat response from *Melissotarsus*. This suggests that *Melissotarsus* colonies primarily defend themselves by maintaining enclosed galleries and avoiding interaction with competitors and/or predators. Invading workers took *Melissotarsus* larvae and pupae but did not pay any attention to the diaspidids.

### Diaspidid products

#### Free-living *M. conspicua*

One sampled tree (at coordinates 31°59'33.30''S, 18°49'14.97''E) had a free-living population of *M. conspicua* with white scale covers on the exterior bark next to what appeared to be a tunnel leading into the branch. All diaspidids within the ant galleries lacked scale covers with the exception of males. This corresponds to a similar observation of free-living individuals of *M. conspicua* on trees containing ants and diaspidids made by Prins *et al.* (1975). All individuals from this population were dead upon discovery. The bodies of adult females from the free-living population were generally larger than those from within the galleries, but otherwise were similar in appearance.

### Ant-exclusion study

For the duration of the ant exclusion, no diaspidids produced wax filaments from their macroducts or exuded any waste products from the anal opening. A more rigorous ant-exclusion experiment would certainly be necessary in order to draw any significant conclusions, but this observation at least indicates that, under the given conditions, adult female diaspidids and

second-instar nymphs were not regularly producing secretory or excretory products (Fig. 1).

### Taxonomy and distribution of species

Delimitation of new species was based upon discrete gaps in morphological character sets of adult females, primarily involving features of the pygidium. Such gaps are inferred to indicate long-standing reproductive isolation and divergence among lineages under the biological species concept. Diaspidid specimens were slide-mounted following the techniques of the Systematic Entomology Laboratory (ARS, USDA, Beltsville, MD; <http://www.ars.usda.gov/Main/docs.htm?docid=9832>). Morphological terminology follows that of Miller & Davidson (2005).

The abbreviations for type depositories are as follows: BMNH, The Natural History Museum, London, U.K.; CASC, The California Academy of Sciences Collection, San Francisco, CA, U.S.A.; UMEC, University of Massachusetts, Amherst Entomology Collection, Amherst, MA, U.S.A.; USNM, United States National Entomological Collection, U.S. National Museum of Natural History, Washington, D.C., U.S.A., housed at the U.S. Department of Agriculture, Beltsville, MD, U.S.A.

#### *Affirmaspis cederbergensis* Schneider sp.n.

(Fig. 2)

<http://zoobank.org/urn:lsid:zoobank.org:act:785258DB-7A20-445B-8F12-5B17B63741E3>

*Description of adult female.* Features of scale covering unknown, all specimens of type series scale-less. Mounted on a microscope slide, body turbinate, 0.62–0.71 mm long, widest at metathorax, 0.5–0.54 mm wide. Pygidium with pair of well-developed median lobes; second and third lobes represented by membranous points; third lobes sometimes absent. Median lobes each with one medial and one lateral notch, large paraphysis-like sclerotizations along medial margins of lobes, smaller sclerotizations at the base of lateral margins; second and third lobes triangular, poorly developed and about one-third the length of median lobes. Segmental setae of pygidium stout flagellate, those delineating abdominal segment VIII shortest, 13–14 µm; all others similar in length, 18–21 µm long. Plates present between median lobes and in first and second spaces, highly variable in type and shape; those between median lobes in pairs, either simple or trifurcating; two fringed plates present in first space, variable in shape; second space with two to three plates in various combinations of type and shape; simple, bifurcating, and fringed plates all represented in second space. Pair of large clavate paraphyses on VIII, lateral to median lobes. Dorsal pygidial macroducts of one-barred type, positioned along margin and with two submarginal rows running anteroposteriorly, length greater than five times the width of the opening, longest 36 µm. Shorter macroducts, 14–21 µm, present in groups of four to

five on submargin of abdominal segment IV, three to four on submargin of abdominal segment III, and in pairs or triplets at margins of mesothorax through abdominal segment III. Long, thin ventral microducts in group of six on submargin of abdominal segment IV, 16 µm long; singular or in pairs along submargin of metathorax through abdominal segment III, 14 µm long; a few microducts also distributed medially on the head and thorax, 12 µm long. Intersegmental line between abdominal segments IV and III with sclerotized bands, one medial and two lateral. Anal opening 8 µm wide at longest axis, located about two times the width of anal opening from pygidial apex. Vulva located about four times further from the pygidial apex than the anal opening. Cicatrices present on dorsal submargin of prothorax and abdominal segment I, diameter 5 µm. Eye represented by small spur or dome near margin of mesothorax and level with middle of clypeolabral shield. Without perivulvar pores. Antennal tubercles each with one stout seta.

*Material examined. Holotype:* Adult ♀, SOUTH AFRICA, Cederberg Mts, 8 km NE Clanwilliam, Western Cape, 32°7'59.8794''S, 18°58'0.1194''E, found in nest galleries of *M. emeryi* from a branch of *Maytenus oleoides* Loes., ID# D1876D, 19.v.2002 (*D.O. Burge*) (CASC). *Paratypes:* SOUTH AFRICA, same data as holotype, one adult ♀ (D1876F) (USNM), one adult ♀ and one second-instar nymph (D1876A, D1876E) (UMEC), one adult ♀ (D1876C) (BMNH).

*Etymology.* The epithet is a Latin adjective, formed from Cederberg (referring to the Cederberg Mountains of the Western Cape, South Africa) + *-ensis*, meaning 'of or from a place'. The Cederberg Mountains are currently the only locality from which this species has been collected.

*Comments.* Using Balachowsky's (1958) key to the genera of African Aspidiotina, this species keys out as *Diclavaspis*, which Balachowsky (1956) erected for three species: *Diclavaspis ehretiae* (Brain), *Diclavaspis socotrana* (Lindinger), and *Diclavaspis mashonae* (Hall). Two of these species, *D. ehretiae* and *D. socotrana*, had previously constituted the genus *Affirmaspis* MacGillivray (MacGillivray, 1921). *D. socotrana* is the type species of *Affirmaspis* and *D. ehretiae* is the type species of *Diclavaspis*. Thus, under either MacGillivray's or Balachowsky's generic concepts, *Affirmaspis* and *Diclavaspis* are synonyms and *Affirmaspis* is the senior synonym and thus the valid name (Ben-Dov, 2013).

Adult females of *A. cederbergensis* are most similar to *Affirmaspis ehretiae* but may be distinguished by the following suite of characteristics. The second lobes are triangular and are not notched as in *A. ehretiae*. There are no plates anterior to the third lobes. Pairs of cicatrices are present on the dorsal submargins of the prothorax and abdominal segment I. The dorsal pygidial macroducts have wider openings and the ducts are not as long and thin as those in *A. ehretiae*. The dorsal macroducts are also more numerous on the pygidium and have a distinctive patterning, with clusters of four to five on the



Fig. 2. *Affirmaspis cederbergensis* sp.n. adult female. Variable plates are illustrated below.

dorsal submargin of abdominal segment IV and three to four on the submargin of III.

This is the first species of *Affirmaspis* found associated with *Melissotarsus* ants. *Affirmaspis cederbergensis* was discovered within the galleries of *M. emeryi* from a host tree of *M. oleoides*. Whether free-living populations of *A. cederbergensis* exist, and whether these populations would produce a scale cover in the absence of ant attendance remain unknown.

***Andaspis formicarum* Ben-Dov, 1978: 316 – 319**

This species was discovered originally in 1976 from East London in Eastern Cape Province, South Africa. It has now been discovered for the second time in association with *M. emeryi* from East London. Adult females lacked scale covers.

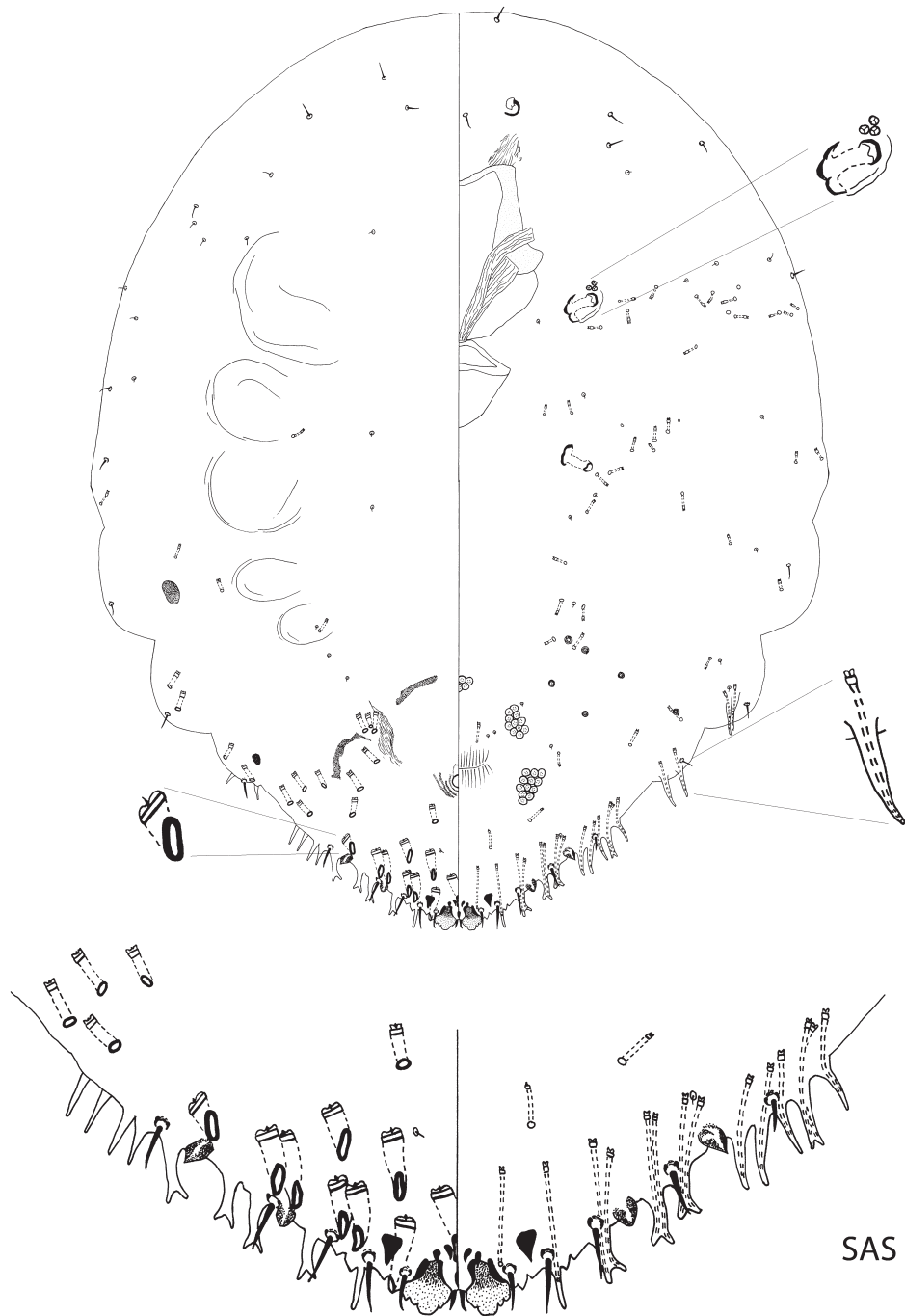
*Material examined.* SOUTH AFRICA, Eastern Cape, East London (*Ficus* sp.) 26.iii.2012 (*K. Cole*), one adult ♀ (D3660A) (UMEC).

***Diaspis doumtsopi* Schneider sp. n.**

(Fig. 3)

<http://zoobank.org/urn:lsid:zoobank.org:act:0A98FE3D-0E53-4CC1-9FC4-BEE05EB1E80B>

*Description of adult female.* Features of scale covering unknown; all specimens of type series lacking scale. Mounted on a microscope slide, body oval, 0.63–0.7 mm long, widest at metathorax, 0.53–0.56 mm wide. Median lobes appear serrate with one medial notch and two lateral notches, well developed



**Fig. 3.** *Diaspis doumtsopi* sp.n. adult female.

and sclerotized with large paraphysis-like sclerotizations along the medial edge and smaller sclerotizations at the lateral base, medial edges parallel or only slightly divergent, with one short pair of simple setae between median lobes; second and third lobes poorly developed and membranous, each with one notch near the centre; position of fourth lobes occupied by a sclerotized spur on margin of abdominal segment V, triangular with blunted apex, more conspicuous

than second and third lobes; with a sclerotized spur on margin of abdominal segment IV, resembling a fifth pair of lobes. One pair of large turbinate paraphyses close to the notch of second lobes and intersegmental setae of segment VII, one pair of elongated comma-shaped paraphyses near medial base of fourth lobes. Segmental setae stout, flagellate, those of abdominal segment VIII projecting about as far as median lobes, 12–13 µm long; remaining pygidial segmental setae



15–20 µm long. Gland spines following formula (0, 1, 1, 3, 5–8, 2); gland spines of third and fourth spaces bifurcate, each apex subtended by a long, thin microduct, 40–45 µm long; remaining gland spines usually simple, with only one microduct. Dorsal pygidial macroducts of two-barred type present in two forms: large barrel-shaped macroducts with oval slit-like openings 9–10 µm wide at opening, 13–17 µm long, one present between proximal base of median lobes, two pairs present on submargin of abdominal segments VI and V, one pair at margin of VII, two pairs on margin of VI, two pairs on margin of V, one pair at margin of IV; thin, elongate macroducts with circular openings 4–5 µm wide at opening, 12–16 µm long, one pair present on submedian of abdominal segment VI with one pair of short setae always located posterior to them, 10–12 present on submedian/submargin of abdominal segments IV and III, in pairs on margins of III. Few ventral microducts present on submedian and submargin of pygidial segments, 9–14 µm long; present in bands running anteroposteriorly along the submargin of abdominal segment IV–mesothorax, 6–13 µm long. Perivulvar pores present in five clusters surrounding vulva, anterior-most group with six to eight pores, middle groups with 10–14 pores, posterior-most group with 12–15 pores, distribution of pores often asymmetrical but posterior-most clusters always containing more pores than others. Two sets of intersegmental sclerotizations present at median and lateral positions between abdominal segments IV and III. Anal opening round, 7–10 µm wide, separated from pygidial apex about nine times the width of anal opening. Vulva approximately 50 µm wide, level with position of anal opening. Cicatrices sometimes present on dorsal submargins of abdominal segment III and prothorax, 6–12 µm in diameter, often absent or inconspicuous. Two to four pores present next to anterior spiracles. Dorsum of each segment from prothorax through abdominal segment III with large submarginal and submedial dorsal protuberances on each side, largest at prothorax and growing progressively smaller posteriorly, giving dorsum a coarsely hedgehog-like appearance. Eyes present and indicated by small dome-like projections at submargin of head. Antennal tubercles each with one stout seta.

**Material examined. Holotype:** Adult ♀, CAMEROON, Nkolbisson, 1°42'9.83"N, 11°42'9.83"E, elevation 602 m, found in nest galleries of *M. weissi* from *Mangifera* sp., ID# D3670A, 22.iv.2012 (*A. Doumtsop*) (UMEC). **Paratypes:** Same data as holotype, one adult ♀ (D3670E) (USNM); CAMEROON, Evoudoula, found in nest galleries of *M. weissi* from *Dacryodes* sp., 28.iv.2012 (*A. Doumtsop*), one adult ♀ (D3669A) (UMEC), one adult ♀ (D3669C) (USNM), one adult ♀ (D3669E) (BMNH); CAMEROON, Nkolbisson, 1°44'57"N, 11°42'9.83"E, elevation 602 m, found in nest galleries of *M. emeryi* from *Dacryodes* sp., 7.v.2012 (*A. Doumtsop*), one adult ♀ (D3674A) (USNM).

**Etymology.** This species is named in honour of our colleague Armand Rodrigue Pascal Doumtsop Fotio, of the University of

Maroua, Cameroon, who collected all known specimens, and who graciously provided S.A.S. and B.B.N. with samples of ants and armoured scale insects from several infested mango and safou trees.

**Comments.** In Hall's (1946) key to African Diaspidini (Diaspidinae sensu Takagi, 2002), adult females of *D. doumtsopi* key to genus *Epidiaspis*. They resemble adult females of the only African species of *Epidiaspis*, *Epidiaspis ficifoliae* Hall, of Zimbabwe, but differ from *E. ficifoliae* in having perivulvar pores and furcate gland spines with multiple microducts.

Characters that distinguish *Diaspis* from *Epidiaspis* relate to the pygidial lobes. *Epidiaspis* has prominent median lobes, whereas those of *Diaspis* are sunken into the apex of the pygidium. The second and third lobes are well developed in *Diaspis* and reduced or obsolete in *Epidiaspis*. These are the same characters that distinguish the bark versus leaf phenotypes in polyphenic species of *Chionaspis* and *Diaspidiotus*, in which bark phenotypes have prominent median lobes and reduced second and third lobes, while the leaf phenotypes have recessed median lobes and more prominent second and third lobes (Liu *et al.*, 1989; Miller & Davidson, 2005). They are thus somewhat suspect as genus-defining characters. We place the species in *Diaspis* on the basis of DNA evidence indicating that *D. doumtsopi* is more closely related to the type species of *Diaspis* than to the type species of *Epidiaspis* (B.B. Normark *et al.*, unpublished data).

Dejean & Mony (1991) collected an unidentified *Diaspis* sp. in Cameroon inside galleries of *M. beccarii* from *D. edulis*. It is possible (yet remains to be confirmed) that these were also collections of *D. doumtsopi*. It is unknown whether free-living populations of *D. doumtsopi* exist and if these populations would produce a scale cover in the absence of ants.

***Melissoaspis* Ben-Dov 2010: 50 (type species: *Melissoaspis reticulata* Ben-Dov)**

*Melissoaspis fisheri* Ben-Dov, 2010: 51

*Melissoaspis formicaria* (Ben-Dov, 2010: 54) **comb.n.**

*Melissoaspis incola* **sp.n.**

*Melissoaspis reticulata* Ben-Dov, 2010: 52

**Diagnosis.** Body of adult female circular to oval in shape with pygidium heavily constricted near abdominal segment V; pygidial segments often compressed and forming roughly triangular projection at posterior end. Pygidium comprising segments V, VI, VII, and VIII, with two to four pairs of lobes. Median lobes simple and poorly developed, appearing continuous with abdominal segment VIII, without paraphysis-like sclerotizations or other features defining basal boundaries. Setae of abdominal segment VIII short, lanceolate. Dorsal macroducts and ventral microducts long and thin, present in small numbers on pygidium and other body segments. Paraphyses present or absent; when present, only occurring in pairs between abdominal segments VIII and VII, VI and V. Two pairs of cicatrices present on dorsum of prothorax and abdominal segment I or II. Antennal tubercle submarginal



with one seta. Spiracles without perispiracular pores. Plates absent, sometimes possessing pygidial marginal microducts with protruding orifices that resemble simple plates. Without perivulvar pores.

*Comments.* We gathered new information regarding *Melissoaspis* through inspection of additional specimens. Two diagnostic characteristics are modified herein from the original generic description, regarding the absence of paraphyses and the presence of distinctive patterning on the pygidium. S.A.S. has noted that paraphyses are sometimes present on adult female specimens of *M. fisheri* and are always present on *M. formicaria* and *M. incola*. The presence of distinctive light and dark patterning on the dorsal pygidium of *M. fisheri* and *M. reticulata* may be a synapomorphy linking these two as sister species; however, it is not characteristic of the genus as a whole. We describe multiple traits that help to link species and further characterize *Melissoaspis*, especially regarding the constriction and shape of the pygidium, the development of the median lobes, the presence and distribution of cicatrices, and the description of the posterior-most pair of segmental setae. Characterizing these traits has allowed us to reassign *M. formicaria* and to place the new species, *M. incola*. Phylogenetic analyses of DNA sequence data recover *Melissoaspis* as a monophyletic clade (S.A. Schneider *et al.*, unpublished data).

***Melissoaspis fisheri* Ben-Dov, 2010: 51–52**

Additional collections of this species have been made from the nests of *Melissotarsus insularis* Santschi in Madagascar (nine specimens, eight from two new localities). Adult females lack scale covers. Identity of specimens confirmed by Y. Ben-Dov.

*Material examined.* MADAGASCAR, Toliara, Berenty, Forêt de Bealoka, 14.6 km 329° NNW Amboasary, 24°57'24.84''S, 46°16'17.4''E, elevation 35 m, 3–8.ii.2002 (*B.L. Fisher*), six adult ♀ (D1885B,C,D,E,F, D2733C) (UMEC); MADAGASCAR, Toliara, Forêt de Mîte, 20.7 km 29° WNW Tongobory, 23°31'27.12''S, 44°07'16.6794''E, elevation 75 m, 27.ii.2002–2003.iii.2002 (*B.L. Fisher*), one adult ♀ (D1895A) (CASC); MADAGASCAR, Toliara, Andohahela National Park, Manantalinho Forest, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, 24°49'0.84''S, 46°36'35.9994''E, elevation 150 m, 12.i.2002 (*B.L. Fisher*), two adult ♀ (D1897A,C) (CASC).

***Melissoaspis formicaria* (Ben-Dov) comb. n.**

*Morganella formicaria* Ben-Dov, 2010: 54–56

Prior to Takagi's (2007) revision of *Morganella*, five African species were placed in the genus: *M. acaciae* Munting, *M. conspicua* (Brain), *M. pseudospinigera* Balachowsky, *M. spinigera* (Lindinger), and *M. villeti* (Marchal). Takagi excluded all five of these species from *Morganella*, and remarked that they were not particularly closely related to

*Morganella*, but did not indicate to what genus they ought to belong. When Ben-Dov (2010) described *M. formicaria* and placed it in *Morganella*, he did not cite Takagi (2007) or propose an alternative to Takagi's restricted definition of *Morganella*.

The transfer of this species to *Melissoaspis* was based upon the poor development of median lobes that appear continuous with abdominal segment VIII, distinctive lanceolate setae on abdominal segment VIII, and a pygidium that is compressed and triangular in shape. These combined characteristics are unique to *Melissoaspis*.

Additional collections of this species have been made from the nests of *M. insularis* in Madagascar (six specimens, two from a new locality). Adult females lack scale covers.

*Material examined.* MADAGASCAR, Toliara, Forêt de Beroboka, 5.9 km 131° SE Ankidranoka, 22°13'59.16''S, 43°21'58.68''E, elevation 80 m, 12–16.iii.2002 (*B.L. Fisher*), three adult ♀ (D1880A, D1883B,C) (UMEC); MADAGASCAR, Toliara, Berenty, Forêt de Bealoka, 14.6 km 329° NNW Amboasary, 24°57'24.84''S, 46°16'17.4''E, elevation 35 m, 3–8.ii.2002 (*B.L. Fisher*), one adult ♀ (D1882A) (CASC); MADAGASCAR, Toliara, Forêt de Mîte, 20.7 km 29° WNW Tongobory, 23°31'27.12''S, 44°07'16.6794''E, elevation 75 m, 27.ii.2002 (*B.L. Fisher*), two adult ♀ (D1890A,B) (CASC).

***Melissoaspis incola* Schneider sp. n.**

(Fig. 4)

<http://zoobank.org/urn:lsid:zoobank.org:act:7866FBCD-E4A9-47AC-AB6C-A5C3FD709BD1>

*Description of adult female.* Scale cover unknown; all specimens of type series lack scales. Mounted on microscope slide, body circular to ovoid, 0.44–0.6 mm long, widest at metathorax, 0.37–0.46 mm wide. Median and second lobes present, simple and poorly developed. Median lobes with lateral notch, apex of each lobe rounded, medial edges either parallel or slightly converging. Second lobes about one-half length of median lobes and narrowly triangular coming to sharp pointed apex without notch, pressed closely to lateral edge of median lobes. Pygidium strongly constricted between abdominal segments V and VI, segments VI, VII, and VIII forming roughly triangular projection at posterior apex. Intersegmental space between segments IV and III with sclerotized bands, one medial and two lateral. Comma-shaped paraphyses in pairs between median and second lobes and at pygidial constriction between abdominal segments V and VI, medial paraphysis larger than lateral. Pair of segmental setae delineating abdominal segment VIII distinctively stout, lanceolate, extending slightly beyond apex of median lobes, 6–8 µm long; remaining pygidial segmental setae stout, flagellate, 20–28 µm long. Plates absent. Few long, thin dorsal macroducts of one-barred type present primarily at pygidial margin, one or two sometimes present at submargin, one situated between median lobes; shortest at anterior 16–28 µm, longest at posterior apex 32–44 µm, diameter

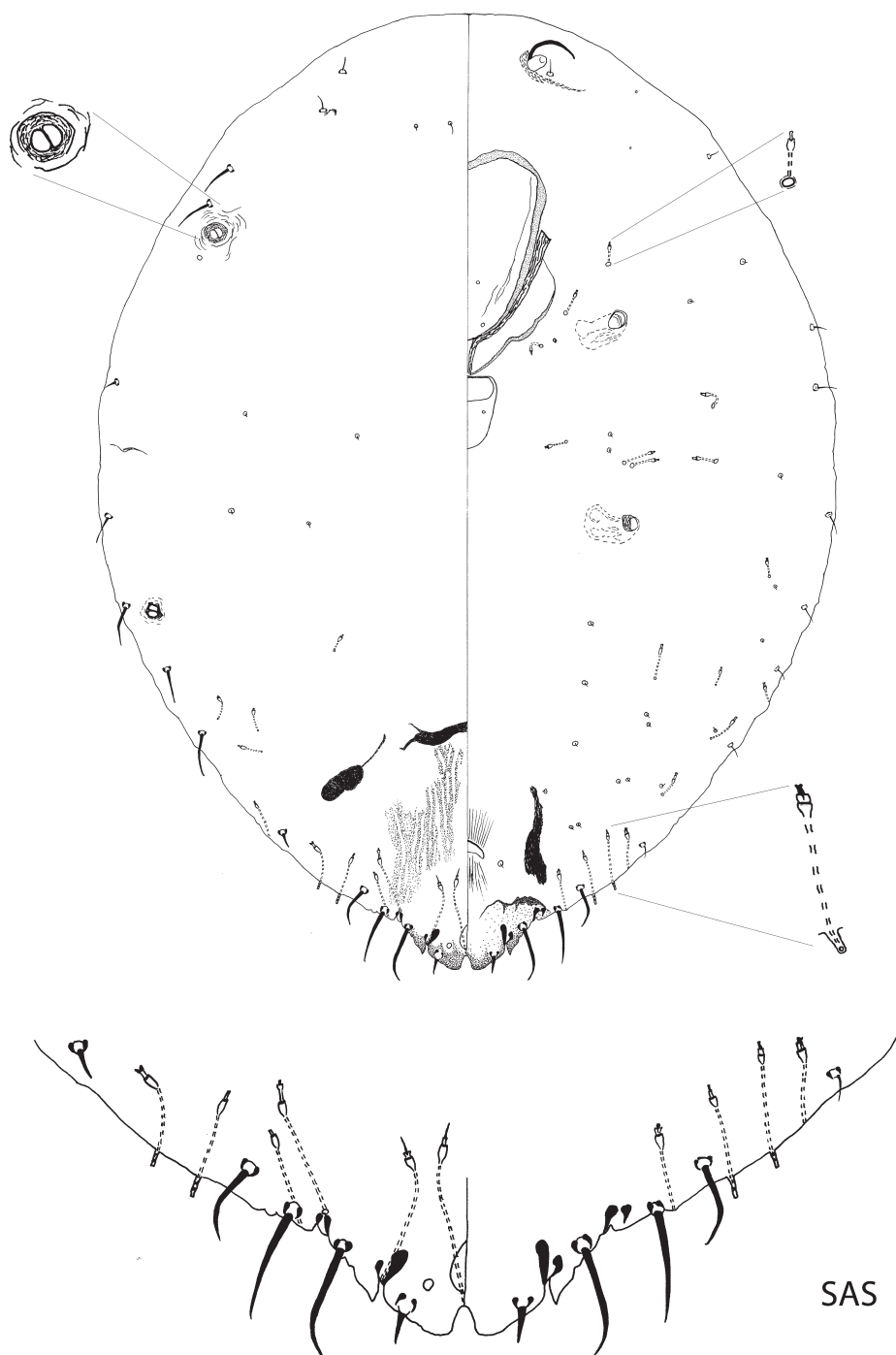


Fig. 4. *Melissoaspis incola* sp.n. adult female.

of each macroduct opening approximately  $1\mu\text{m}$ . Pygidium with pair of microducts with protruding orifices that extend beyond body margin, resembling simple plates; position variable but falling between abdominal segments IV–VI. Few submarginal and submedial ventral microducts present on head, thorax, and abdominal segments I–III,  $9\text{--}18\mu\text{m}$  long. Anal opening  $10\text{--}14\mu\text{m}$  wide at longest axis, located 0.5–1.5 times

the width of anal opening from the pygidial apex. Opening of vulva approximately  $16\text{--}22\mu\text{m}$  wide, situated 2.5–5 times further from the pygidial apex than the anal opening. Pairs of cicatrices present on prothorax and abdominal segment I, diameter  $8\text{--}10\mu\text{m}$ . Eyes present and indicated by small dome-like projections at submargin of head. Without perivulvar pores. Antennal tubercles each with one stout seta.

**Material examined. Holotype:** Adult ♀, MADAGASCAR, Toliara 6 km 146° SSE Belo sur Mer, 20°46'18.1194''S, 44°02'48.12''E, elevation 15 m, found in nest galleries of *M. insularis* from *Euphorbia* sp., ID# D1875D, 10.xii.2001 (*B.L. Fisher*) (CASC). **Paratypes:** Same data as holotype, one adult ♀ (D1875A) (UMEC); MADAGASCAR, Toliara, 6 km 131° SE Lavanono, Soamanitra, elevation 150 m, 25°26'44.1594''S, 44°59'44.88''E, found in nest galleries of *Melissotarsus insularis* from *Euphorbiaceae* sp. undet., 17.ii.2002 (*B.L. Fisher*), one adult ♀ (D1877A) (USNM); MADAGASCAR, Toliara airport, 23°22'59.8794''S, 43°43'0.12''E, elevation 40 m, found in nest galleries of *M. insularis* from *Euphorbiaceae* sp. undet., 7.i.2001 (*B.L. Fisher*), one adult ♀ (D1896A) (BMNH), one adult ♀ (D1896B) (UMEC), one adult ♀ (D1896C) (USNM).

**Etymology.** The Latin noun 'incola' means 'resident' and is used here in reference to the symbiotic relationship that exists between this species and *Melissotarsus* ants. Like its congeners, *M. incola* is unknown outside the nest galleries of *M. insularis*.

**Comments.** Adult females of *M. incola* are most similar in appearance to *M. formicaria*, particularly in that both species lack the distinctive reticulated light and dark patterning that is found on the dorsal pygidium of *M. fisheri* and *M. reticulata*. The following suite of characteristics distinguishes *M. incola* from its congeners. The median lobes in adult females of this species possess a lateral notch and the second lobes are without notches. By contrast, none of the lobes are notched in *M. fisheri* and *M. reticulata*, and in *M. formicaria* this trait is reversed, i.e., the second lobes possess a notch rather than the median lobes. The adult female of *M. incola* is further distinguished from *M. formicaria* by the absence of ventral microducts on the pygidial submargin and the presence along the pygidial margin of protruding microduct orifices resembling simple plates or gland spines.

### *Morganella conspicua* (Brain)

*Diaspis* (*Epidiaspis*) *conspicua* Brain, 1919: 228.

*Morganella conspicua* (Brain); Balachowsky, 1956: 124.

Additional collections of this species were made from Madagascar in association with *M. insularis*, from South Africa in association with *M. emeryi*, and from Cameroon in association with *M. weissii* (35 new specimens, 32 from 12 new localities). Male prepupal and pupal instars from ant-associated populations form normal scale covers, but adult females and second-instar nymphs lack scale coverings. Collections from South Africa also represented free-living diaspidids with scale covers found on the exterior bark of *Leucospermum praemorsum* containing ant and armoured scale insect populations lacking scale covers (identified as D3610B,C,D, D3611B). *M. conspicua* is apparently the most geographically widespread of the ant-associated diaspidids.

Following Takagi (2007), this species clearly does not belong in *Morganella*, but lacking allocation to another genus, for the present it remains in *Morganella*.

**Material examined.** MADAGASCAR, Toliara, Libanona, Tolganaro, 25°2'13.9194''S, 46°59'53.88''E, elevation 35 m, 10.i.2001 (*D.O. Burge*), one adult ♀ (D1881A) (CASC); MADAGASCAR, Toliara, Réserve Privé Berenty, Forest Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, 24°57'24.84''S, 46°16'17.4''E, elevation 35 m, 3–8.ii.2002 (*B.L. Fisher*), one adult ♀ (D1892B) (CASC); MADAGASCAR, Toliara, Andohahela National Park, Mantalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, 24°49'0.84''S, 46°36'35.9994''E, elevation 150 m, 12–16.i.2002 (*B.L. Fisher*), two adult ♀ (D1898A,B) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Nardouw farm, 32°0'4.26''S, 18°50'20.40''E, elevation 358 m, 5.i.2012 (*S.A. Schneider*), four adult ♀ (D3559A,C, D3579A, D3582A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Duikerfontein farm, 32°1'55.56''S, 18°51'54.30''E, elevation 439 m, 4.i.2012 (*S.A. Schneider*), one adult ♀ (D3567A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Duikerfontein farm, 32°2'3.78''S, 18°52'2.82''E, elevation 443 m, 5.i.2012 (*S.A. Schneider*), two adult ♀ (D3570A, D3572A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Duikerfontein farm, 32°1'55.80''S, 18°51'52.86''E, elevation 437 m, 5.i.2012 (*S.A. Schneider*), four adult ♀ (D3573A, D3575A, D3576A, D3577A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Brakfontein farm, 31°54'58.14''S, 18°46'15.66''E, 5.i.2012 (*S.A. Schneider*), two adult ♀ (D3588A, D3589A) (UMEC); SOUTH AFRICA, Western Cape, Gifberg near Vanrhynsdorp, 31°48'36.48''S, 18°46'24.78''E, elevation 400 m, 5.i.2012 (*S.A. Schneider*), two adult ♀ (D3599A, D3600A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Brakfontein farm, 31°54'32.34''S, 18°45'49.14''E, elevation 349 m, 5.i.2012 (*S.A. Schneider*), three adult ♀ (D3606A, D3607A, D3608A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Nardouw farm, 31°59'33.30''S, 18°49'14.76''E, elevation 386 m, 6.i.2012 (*S.A. Schneider*), eight adult ♀ (D3610B,C,D, D3611B, D3613A, D3614A, D3615A, D3616A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Nardouw farm, 31°59'33.00''S, 18°49'16.86''E, elevation 389 m, 6.i.2012 (*S.A. Schneider*), two adult ♀ (D3620A, D3621A) (UMEC); SOUTH AFRICA, Western Cape, Clanwilliam, Nardouw farm, 31°59'32.04''S, 18°49'15.60''E, elevation 389 m, 6.i.2012 (*S.A. Schneider*), one adult ♀ (D3631A) (UMEC); CAMEROON, Nkolbisson, 1°9'44.57''N, 11°42'9.83''E, elevation 602 m, 22.iv.2012 (*A. Doumtsop*), two adult ♀ (D3668A, D3672A) (UMEC).

### Key to the species of ant-associated armoured scale insects (adapted from Ben-Dov, 2010)

1. Pores present near anterior and/or posterior spiracles; macroducts and microducts of two-barred type ..... 2
  - Pores absent from areas adjacent to spiracles; macroducts and microducts of one-barred type ..... 3
2. Antennal tubercle with six setae; pygidium with two pairs of lobes ..... *Andaspis formicarum* Ben-Dov

- Antennal tubercle with single seta; pygidium with five pairs of lobes ..... *Diaspis doumtsopi* Schneider **sp.n.**
3. Fringed plates present in first and second spaces; macroducts with large round openings occurring in pairs or triplets along margin of thorax through abdominal segment III .....  
..... *Affirmaspis cederbergensis* Schneider **sp.n.**
- Plates present or absent; if present, never fringed; macroducts of this type absent from margin of metathorax through abdominal segment III ..... 4
4. Body strongly constricted near proximal base of pygidium at abdominal segment V; pygidium compressed and roughly triangular; stout spine-like setae on abdominal segment VIII; plates absent; median lobes simple and poorly developed ... (*Melissoaspis*) ..... 5
- Body gently tapering toward posterior end without a strong constriction near proximal base of pygidium; pygidium may be flat, rounded, or triangular in shape; stout flagellate setae on abdominal segment VIII; plates present or absent; median lobes well developed and sclerotized ..... 8
5. Pygidial dorsum with a reticulated pattern of bright and dark lines disposed perpendicular to margin; paraphyses typically absent ..... 6
- Pygidial dorsum without such a reticulated pattern; paraphyses always present in pairs ..... 7
6. Median lobes distinctly projecting from margin .....  
..... *Melissoaspis fisheri* Ben-Dov
- Median lobes not projecting from margin .....  
..... *Melissoaspis reticulata* Ben-Dov
7. Pygidium with submarginal microducts present on venter; median lobes without notch, second lobes with one lateral notch ..... *Melissoaspis formicaria* (Ben-Dov) **comb.n.**
- Pygidium lacking submarginal microducts on venter, only present along margin; median lobes with one lateral notch, second lobes without notch .....  
..... *Melissoaspis incola* Schneider **sp.n.**
8. With ten pairs of paraphyses on pygidium .....  
..... *Melanaspis madagascariensis* Mamet
- With two pairs of paraphyses on pygidium ..... 9
9. All pygidial plates simple with pointed apices .....  
..... *Morganella conspicua* (Brain)
- Some pygidial plates with bi- or trifurcating apices .....  
..... *Morganella pseudospinigera* Balachowsky

### Concluding remarks

The unique trophobiosis between *Melissotarsus* ants and Diaspididae remains poorly understood: any observations of foraging behaviours and interactions between species provide useful information regarding the nature of the association and merit attention. Future studies should focus on determining the diet of *Melissotarsus* ants and the nature of interactions between these unlikely partners. There are now ten described species of ant-associated armoured scale insects (Ben-Dov & Fisher, 2010; and the new species described herein) and it is likely that more new species await discovery within the galleries of *Melissotarsus* ants.

### Acknowledgements

Funding was provided by the National Institute of Food and Agriculture (2009-02310) and by the UMass Natural History Collections. We appreciate the helpful reviews provided by Penny J. Gullan, Brian L. Fisher, and Yair Ben-Dov on an earlier version of this manuscript. We wish to thank the following researchers and institutions for providing specimens: D.O. Burge, Brian L. Fisher and Norman Penny (California Academy of Sciences), Kevin Cole (East London Museum), and Armand Doumtsop (University of Maroua, Cameroon). We thank Yair Ben-Dov for examining specimens and providing identifications. Thanks to Dug Miller for discovering that *Affirmaspis* is a senior synonym of *Di clavaspis*, and to Douglas Williams for his concurring opinion. S.A.S. thanks Stellenbosch University for providing access to laboratory space during his visit to South Africa. Special thanks go to Bennie and Carina Bezuidenhout for their gracious hospitality on Nardouw Farm and for their enthusiasm regarding this project. Thanks to John Martins (Mount Holyoke College) for providing assistance with figure editing.

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Accepted 26 June 2013

First published online 22 August 2013